

Remember the Magic? How Curiosity Elicitation and the Availability of Extrinsic Incentives Shape Memory Formation and its Neural Mechanisms During Encoding and Early Consolidation

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Abstract

While curiosity – the intrinsic desire to know – is a concept central to the human mind and knowledge acquisition, scientific research targeting the understanding of curiosity is still in its infancy and has only recently begun to unravel it. Studies on information-seeking, a popular way to manipulate and measure curiosity in the lab, found that information shows similar rewarding properties as other, extrinsic rewards/incentives like food or money. Indeed, both can motivate behaviour and elicit a response in the dopaminergic structures of the neural reward circuits. The dopaminergic response further enhances encoding of information that is presented around its release by influencing dopamine-dependent cellular mechanisms of learning in the hippocampus. As such, extrinsic rewards/incentives and curiosity motivate and facilitate learning, illustrating their importance in educational contexts and knowledge acquisition. Taken together, their large overlap in neural response and behavioural effects suggests that both may be supported by common neural processes. However, this implies that their combined use would be associated with sub-additive effects. On the other hand, if both were supported by differential neural effects, they could be used in an additive manner. Importantly, the question of how extrinsic rewards/incentives and curiosity interact in their effects on behaviour and cognition overall and memory in particular can only be answered if both effects are studied in conjunction rather than individually as often done in previous research. Another limitation stems from the way how studies thus far have investigated the effects of curiosity on memory, and in some cases, its interaction with extrinsic rewards/incentives, not only because they nearly exclusively all use the same paradigm, but more so because the paradigm itself has some inherent limitations that might affect how curiosity is conceptualised.

The present work tries to address these gaps in the literature. In doing so, a new paradigm – the *magic trick paradigm* – was developed, in which curiosity and the availability of extrinsic incentives were manipulated to measure their effects on encoding. In the magic trick paradigm, curiosity was elicited using short videos of magic tricks. Participants engaged in an orientation task combined with ratings of the “subjective feelings of curiosity” and performance therein was incentivised using a between-subject design. Unbeknown to the participants, their memory for the magic tricks was tested a week later. Crucially, after behavioural pilots, the paradigm was adopted for usage with functional magnetic resonance imaging (fMRI) to be able to investigate the neural underpinnings of incentive- and/or curiosity-motivated incidental learning during encoding as well as early consolidation.

To the best of our knowledge, the associated fMRI dataset – the *Magic, Memory, and Curiosity (MMC) Dataset* – is the first of its kind, making it highly valuable to the nascent field investigating the effects of curiosity on memory because (1) fMRI data was acquired during the magic trick paradigm, but

also before and after, allowing to study neural mechanisms underlying encoding as well as early consolidation, and (2) videos of magic tricks as dynamic stimuli allow for a plethora of analysis approaches to answer myriads of research questions. Chapter 2 describes the methods and procedures used to generate the MMC Dataset ($N = 50$), presented in a way that allows independent researchers to re-use it according to their needs. Additionally, high data quality comparable to other openly available datasets in the field has been demonstrated by performing data quality assessments and basic validation analysis. This further lays the groundwork for Chapters 3 and 4 where the fMRI data acquired during encoding and consolidation, respectively, will be used.

In Chapter 3, a meta-analytical approach was used to analyse the behavioural data from three studies (two behavioural studies and one fMRI study) using the magic trick paradigm to investigate the effects of curiosity, the availability of extrinsic incentives, and their interaction on memory. The main memory outcome was high-confidence recognition, a recollection-based memory measurement, but other indices were also examined to derive a more detailed picture. This revealed positive effects of curiosity and monetary incentives on encoding, in the absence of interaction effects. Exploratory analyses further showed that curiosity and monetary incentives might impact encoding differently, overall suggesting that the effects might be at least partially non-overlapping. Analysing the fMRI data acquired during the presentation of magic tricks using the intersubject synchronisation framework to account for the dynamic nature of the stimuli, we found that while the effects of curiosity on memory were located in the hippocampus and dopaminergic brain areas, neither the effects of curiosity nor incentives themselves were found in the often-implicated reward network, but instead were associated with regions involved in processing uncertainty and attention. Likewise, the effects of curiosity on memory spread further across broad cortical and subcortical networks. Overall, this suggests that the subjective feeling of curiosity and its effects on memory recruits broad brain networks when investigated with dynamic stimuli, caveating a too narrow focus on a small list of regions-of-interest while there is yet so much more to be learned about the effects of curiosity on memory.

In Chapter 4, resting-state data acquired before and after learning was used to investigate changes in brain activity at rest following learning. The pre-learning rest data can be used as a baseline, allowing any changes from pre- to post-learning to be attributed to the learning experience itself. Because previous research has repeatedly pointed to similarities between extrinsic rewards/incentives and curiosity, our analysis focused on the change in resting-state functional connectivity between the dopaminergic midbrain and the anterior hippocampus, a dopaminergic consolidation mechanism previously reported in the context of extrinsically motivated learning. Contrary to our hypothesis, we did not find an overall change nor that individual differences therein predicted behavioural measures of learning. However, brain-behaviour correlations differed significantly depending on the availability of extrinsic incentives. In

sum, this suggests that curiosity-motivated learning might be supported by different consolidation mechanisms compared to extrinsically motivated learning and that extrinsic motivation could re-configure resting-state networks supporting early consolidation.

Overall, this work adds to the literature by replicating the effects of curiosity on encoding. More importantly, however, this work suggests that the systems supporting extrinsically and curiosity-motivated learning might differ more than previously assumed, especially when investigating activity across the whole brain rather than focusing on *a priori* candidate regions implicated in dopaminergic effects. Indeed, our results allow for the possibility that other neurotransmitter play a role as well in extrinsically and curiosity-motivated learning, further highlighting the need for more research in the area.

Declaration of original authorship

Declaration: I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

Stefanie Meliss

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COVID-19 Impact Statement

Due to COVID-19 and associated university closings (including fMRI facilities), the focus of my PhD has been mitigated towards data that had already been collected. Still, the forced switch to remote work impacted my work, mainly due to issues related to the access to the fMRI data on the cluster environment as well as to necessary computational resources. More specifically, I was unable to gain access to my data for multiple months and faced ongoing fMRI software issues due to a lack of admin rights. Those lead me to move my fMRI analysis to a local Apple machine to be able to install and execute software according to my individualised needs. However, due to differences in Linux and Apple operating systems (most likely associated with different random number generators), substantial differences in the output of pre-processing were observed, making it necessary to run the pre-processing on a Linux machine. Setting up the required environment was time-consuming so that pre-processed data was not available before July 2021, hence limiting the amount and depth of analysis that could still be carried out in the time window left.

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Chapter 1: General Introduction

“Sapiens did not forage only for food and materials. They foraged for knowledge as well.”

(Harari, 2014, p. 54)

In the best-selling book “Sapiens: A brief History of Humankind” Yuval Noah Harari (2014) describes how *Homo sapiens* made its way to the top of the food chain, for better or for worse. More specifically, he pinpoints this development to what he terms the cognitive revolution, taking place roughly between 70,000 and 30,000 years ago. The cognitive revolution enabled *Homo sapiens* to adapt their behaviour quickly to meet the requirements of their ever-changing environment, encountered due to their nomadic lifestyle, rather than having to wait for much slower genetic, evolutionary changes. In essence, Harari identifies three abilities acquired during the cognitive revolution that had far-reaching consequences for the species: the ability to transmit larger quantities of information about (1) the surrounding world, (2) social relationships, and (3) non-material concepts like tribal spirits. Such a focus on the transmission of information, and therefore language abilities in general, is able to explain how *Homo sapiens* was able to (1) plan and carry out complex actions, (2) live in large groups with up to 150 individuals, and (3) cooperate with strangers and rapidly innovate social behaviours. However, language does not exist in isolation. The ability to transmit information requires that information is, firstly, encountered (thereby relying on information-seeking behaviours) and, secondly, encoded (thereby relying on the ability to store information for later retrieval).

Indeed, the human brain can store vast amounts of information, however, due to limited capacities, certain types of information need to be prioritised. This, however, is not a flaw as case reports of people with highly superior autobiographical memory, initially termed “hyperthymestic syndrome”, show (Parker et al., 2006): highly superior autobiographical memory is characterised by the ability to remember every detail of every event in one’s personal life, but thereby memory becomes “nonstop, uncontrollable, and automatic”. As such, selectivity of memory seems like an advantage. Since Darwin’s theories about evolution, the idea holds that the organism that fits its environment best survives and gets to pass on its genes to the next generation. But what is the role of memory in that process? Memory allows past experiences to guide present and future behaviour and decision-making in the service of survival and reproduction. Our ancestors had higher chances of survival if they remembered where to find food, which food is edible and which is poisonous, but also if they learned from threatening situations like encounters with dangerous animals.

Whilst the importance of food and liquid as well as potentially other materials for the survival of any organism or species is undeniable, the quote above suggests that humankind was additionally driven

by a hunger for knowledge. This can still be observed today, as we spend considerable amounts of time seeking and/or consuming information, especially since the age of computers, internet, and smartphones when the amount of information services (including social media) has risen to unprecedented heights. This might seem counterintuitive at first glance – why would humans now and then spend so much time gathering information if such activities do not have an apparent benefit for survival? The answer is simple: information-seeking in and of itself is beneficial for survival. Imagine *Homo sapiens* – as hunters and gatherers – going to the same forest to gather edible mushrooms, berries, and nuts, thereby pursuing what has proven to be a good option. However, given the effects of seasons, but also general time frames required for food to grow to a point that it is ripe enough to be eaten, only having one location to go to find food will likely lead to shortages and potentially starvation in the future. Hence, searching for and knowing of alternatives, even before they are needed, ensures survival by preventing shortages that might lead to starvation.

This constitutes a fundamental trade-off between the exploitation of best options amongst known resources and exploration of new options that any organism, not only humans, has to balance in order to survive and reproduce (Kidd & Hayden, 2015). Information-seeking or active sampling might serve a specific instrumental purpose, like the quest for food, but at other times, for instance when we read Harari's book, there is no obvious benefit for it other than doing it for the mere sake of it, in a non-instrumental fashion. The former case can be described as extrinsically motivated information-seeking, as a means to an end whereas the latter is intrinsically motivated, as a goal in and of itself (Gottlieb et al., 2013). From an evolutionary point of view, the instrumental, extrinsically motivated information-seeking seems more intuitive, e.g., when *Homo sapiens* did not only exploit the one forest but also kept roaming around for more diverse sources of food, in line with homeostatic drive concepts securing survival (for a review, see Berridge, 2004). However, also intrinsic, non-instrumental information-seeking shows important benefits as it resolves uncertainty regarding the surroundings, thereby building and modifying internal presentations of the world that may or may not be needed in the future (Gottlieb et al., 2013; Kidd & Hayden, 2015). Information-seeking can further be distinguished into information sampling, i.e., gathering information for a familiar task, and information search, i.e., exploration without prior knowledge of the task or goal (Gottlieb & Oudeyer, 2018). Likely, both serve the expansion of knowledge, but information sampling might be more closely linked to the reduction of uncertainty with rather immediate effects whereas information search requires a considerable amount of effort and time to eventually reduce uncertainty and potentially obtain positive outcomes. Crucially, information search, in some way the ability to be motivated for learning for its own sake, is what enabled *Homo sapiens* to transition from hunters and gatherers to settlers, cultivating and domesticating plants and animals to citizens of societies that walked on the moon.

Chapter 1: General Introduction

The intrinsic “drive state for information”, expressed through information-seeking, is often described as curiosity (Kidd & Hayden, 2015, p. 450). Despite curiosity being a common term in everyday language, it has proven difficult to find a generally agreed-upon definition (Murayama, FitzGibbon, et al., 2019) and different kinds of curiosity have been discussed (Berlyne, 1966), e.g., perceptual curiosity (directed towards specific stimuli) and epistemic curiosity (directed towards acquiring knowledge). Whatever curiosity may or may not be, curiosity results in autonomously generated motivation driven towards satisfying the intrinsic desire to know (Gottlieb & Oudeyer, 2018). However, this motivation can only be explained and understood by assuming that our brains (as well as those of other species) assign value to the learning of information *per se* in a similar manner as it is the case for e.g., securing food supply (Gottlieb et al., 2013). Indeed, similar behavioural effects on decision-making have been found for information and food, supported by overlapping brain areas (Lau et al., 2020). As such, curiosity can be understood as a “motivational state that stimulates exploration” (Gruber & Ranganath, 2019, p. 1014) and, consequently, learning. Above, it was proposed that, in addition to language, information-seeking and memory abilities fuelled the cognitive revolution and the ascent of *Homo sapiens* to the top of the food chain. Importantly, these abilities are far more intertwined. Not only does curiosity motivate information-seeking, allowing humans to encounter information that can be encoded so that past experiences can be used to guide future behaviour, but curiosity enhances the likelihood of encoding (Fastrich et al., 2018; Gruber et al., 2019; Gruber & Ranganath, 2019; Kang et al., 2009). Hence, curiosity as an intrinsic motivational state is one of the factors that affect the selectivity of memory encoding. Since memory allows the past to inform the present and future, information encountered in high states of curiosity is – because it is more likely to be encoded – also more likely to be used in the future as it constitutes part of one’s individual knowledge, potentially contributing towards more information-seeking and knowledge acquisition in the same or related area in the future. Importantly, because neurocomputational mechanisms assign value to information in and of itself, knowledge acquisition has positive, reinforcing qualities, overall forming a positive feedback loop (Murayama, FitzGibbon, et al., 2019).

Although this interplay between curiosity and memory appears vital to the progress our species has made, surprisingly little has been investigated in their conjunction in scientific research within psychology and neuroscience (Gruber & Ranganath, 2019). However, understanding the effects of curiosity on memory will not only help us understand how our ancestors were able to not only harvest food as well as knowledge, driving the progress of the species, but it also has important implications for today. The most obvious is that a better understanding of the effects of curiosity on memory would be valuable for educational settings. More specifically, it would be important to determine whether teachers and policymakers should focus on fostering intrinsic or extrinsic motivation in students or potentially a

combination of both. Effects of curiosity on encoding have been observed across the lifespan (Fandakova & Gruber, 2021; Galli et al., 2018; McGillivray et al., 2015; Swirsky et al., 2021) and curiosity has been discussed regarding its relevance for healthy, adaptive ageing (Sakaki et al., 2018), further stressing the importance of the topic. Moving beyond humans, an understanding of the mechanisms of autonomous learning would immensely enhance the field of artificial intelligence and robotics (Dubey & Griffiths, 2020). Even from a theoretical point of view, this topic is important. As indicated earlier, intrinsically and extrinsically motivation might share neural mechanisms, but especially research in psychology sees them as distinct and potentially sub-additive (Murayama, 2019). As such, a better understanding of curiosity-motivated learning and if and how it interacts with extrinsic motivation promises fruitful insights for the young line of research regarding underlying mechanisms.

The aim of this thesis is to investigate the effects of curiosity on memory. More specifically, this research focuses on the question whether curiosity increases the likelihood of encoding and which neural processes during encoding and consolidation support these effects. Crucially, previous research on curiosity on memory has relied on very simple, static stimuli to induce curiosity, predominantly within the same paradigm. Hence, a main goal of this work was to determine whether the effects of curiosity on memory are generalisable to more complex, dynamic stimuli. This constitutes an important step on the road towards connecting research and the classroom. Additionally, this work seeks to determine whether the effects of curiosity on encoding interact with extrinsic motivation in an additive or sub-additive manner. Throughout the remainder of this chapter, core concepts and findings related to memory and motivated learning and their neural underpinnings will be reviewed, with special emphasis on curiosity-motivated learning and a reflection of strengths and weaknesses of the gold-standard paradigm used in the field. Taken together, this will illustrate gaps in the literature this work tries to address.

Learning and Memory

Imagine a scenario where everything you experience, everything you see with your eyes and hear with your ears at any given moment in time is recorded and stored on a little device, in first-person perspective, for you to go back to any moment, situation, or event of your past, and re-watch it. All you would need is a little device called “grain”, not larger than a grain of rice, implanted just behind the ear, in the skin/tissue covering the temporal bone, recording everything the user sees and hears from the moment that the grain is inserted. The grain is controlled using a little remote console that can be used to select any moment since its insertion to watch it again internally or even on a screen. This is the premise of “The Entire History of You” (Amstrong & Welsh, 2011), an episode of the British science fiction anthology television series “Black Mirror”, roughly set in 2050. How the grain “benefits” its user is shown in many ways, for instance, in order to make a good impression at a dinner party with his wife’s

friends, the protagonist goes back to a specific date in the past where he previously met one of the other guests at a garden party to re-watch the information about this person on the device.

As such, the grain has the ability to acquire information about facts and events, or put differently, its function resembles memory, that is “the capacity of an organism to acquire, store, and recover information based on experience” (Josselyn et al., 2015, p. 521), more specifically, declarative (or explicit) memory (Squire & Zola-Morgan, 1991) by making previous experiences and information accessible to conscious recollection. Endel Tulving (1972) described declarative memory as an information processing system that receives sensory and other information, retains this information, and is able to transmit the retained information to other systems including those responsible for conscious awareness and behaviour. He further proposed two different declarative memory systems that store different information, namely episodic memory storing “information about temporally dated episodes and events, and temporal-spatial relations among these events” (Tulving, 1972, p. 385) and semantic memory as “organised knowledge a person possesses about words and other verbal symbols, their meaning and referents, about relations among them, and about rules, formulas, and algorithms for the manipulation of these symbols, concepts, and relations” (Tulving, 1972, p. 386). As such, an episodic memory contains information specific to the place (the “where”) and time (the “when”) of its acquisition and is thereby more detailed whereas semantic memory is not tied to the context of its acquisition and merely concerns the facts (the “what”) (Moscovitch et al., 2016). Importantly, these two systems are not distinct and rather intertwined and episodic and semantic representations of the same event will likely show time- or demand-dependent variations (Renoult et al., 2019): As such, the semantic memory not only contains facts, but also schematic representations of previous (remote) episodic memories that are retrieved. For instance, while remembering the episodic memory “I read an article about mRNA vaccinations as a means to acquire immunisation against the coronavirus at home this morning” contains temporal and spatial context, the knowledge “mRNA vaccines can be used to produce an immune response against the coronavirus” extracted from this – if retained over time – would be considered a semantic memory. This also highlights different claims that can be made to express the memory verbally, in the former case, the statement refers to “remembering” whereas the latter expresses “knowing” (Tulving, 1972).

The Study of Memory

In the scientific study of human learning and memory, for instance within psychology or cognitive (neuro)science, participants are typically presented with materials/memoranda (e.g., word lists or pictures) that is encoded either intentionally (i.e., participants know that their memory will be tested after studying) or incidentally (i.e., participants perform a separate task during encoding, e.g., judgements about the nature of stimulus presented, to ensure that they are paying attention to the stimulus, but are not informed that their memory will be tested afterwards). This is followed by a memory assessment, either

immediately or with various delays between study and test during which participants retrieve the information during which recall (i.e., ability to remember previously presented stimuli in their absence; Squire et al., 2007) and/or recognition (i.e., ability to distinguish previously presented stimuli from those that were not; Squire et al., 2007) are tested, often in combination with cues, hence measuring episodic memory where the study period is regarded as an episode. For instance, if participants learned a list of words, during recall, they would be asked to retrieve as many words as possible from the learned list whereas during recognition, studied words (“old” items) would be presented together with unstudied words (“new”) and participants are asked to decide based on whether the item has been presented before. The item recognition can then be analysed based on Signal Detection Theory (Green & Swets, 1966).

To determine which brain areas are involved in learning or memory, encoding or retrieval phase (or both) can also take place while participants lie inside an magnetic resonance imaging (MRI) scanner exposed to a functional sequence (fMRI) that measures changes in haemoglobin oxygenation using a blood-oxygen-level-dependent (BOLD) contrast, an indicator of blood flow. This assumes that as brain areas are active, oxygenated blood is supplied to them. In subsequent memory (SM) paradigms (Brewer et al., 1998; A. D. Wagner et al., 1998) – also called difference due to memory paradigms – participants are scanned during encoding and the behavioural performance from the memory test is used to compare neural activity during subsequently remembered with subsequently forgotten trials. If participants are scanned during retrieval, brain activity between hits and misses or hits and correct rejection is compared (Spaniol et al., 2009).

Recognition judgements indicate distinct types or processes of memory, often referred to as recollection and familiarity (Yonelinas, 2002) where recollection reflects the retrieval of qualitative information about the past episode (such as where and when an item was studied) and familiarity the absence thereof (Diana et al., 2007; Renoult et al., 2019). To distinguish between both processes, different approaches can be used (reviewed by Yonelinas, 2002). For instance, when comparing recall to recollection performance, recall can be seen as a measurement of recollection. Studies also often use item/associative recognition methods where participants are required to make judgements about the co-occurrence of items (item-item associations; e.g., where these two stimuli presented together), or other aspects of study like how the item was presented (item-feature association; e.g., word spoken by male or female voice) or where the item was presented (item-context associations; e.g., where on the screen the item was presented). In these instances, item memory would be treated as a measure of familiarity whereas associative memory is regarded as an index of recollection. These paradigms are also referred to as source memory paradigms and represent an objective measure of the underlying memory process by differentiating between item (e.g., a picture of a banana was presented) and relational memory (e.g., the banana was presented together with a beach scene) (Davachi, 2006). A more subjective approach of

distinguishing both processes is to obtain recognition confidence ratings. If the retrieval during recognition reflects recollection, specific details of the study would be retrieved thereby leading to increased confidence in the response whereas familiarity contributes to a wider range of confidence ratings (Diana et al., 2007). The confidence ratings can either be used to determine recollection-based recognition based on high confidence ratings or by examining the Receiver Operating Characteristic (ROC; Yonelinas, 1994). An ROC is a plot of the cumulative proportion of hits versus false alarms for each decision criteria (i.e., confidence level) and the degree of its asymmetry or curvilinearity reflects the degree of recollection and familiarity within the recognition responses. Subjective measurements of recollection and familiarity also include “remember/know” judgements where after each “old” judgements in the recognition test, the participants are asked to indicate whether they “remember” the item from the study phase or whether they “know” the item is old, the former reflecting recollection and the latter familiarity. A discussion of the advantages and disadvantages of each of these measures are beyond the scope and can be found elsewhere (Migo et al., 2012; Yonelinas, 2002), but it is important to point out that the “remember/know” procedure was initially suggested by Tulving (1985) to separate episodic and semantic memory judgements rather than recollection and familiarity in episodic memory retrieval and conceptual/semantic processes might play a role in familiarity-based judgements (Renoult et al., 2019).

The Neuroanatomy of Learning and Memory

The seminal studies of H.M. (Scoville & Milner, 1957; Squire, 2009) – a patient who developed amnesia after the large parts of the bilateral medial temporal lobe (MTL) and amygdala were surgically removed – established the fundamental role of the MTL in learning and memory. Following the surgery, H.M. was unable to encode new declarative (or explicit) information, regardless of whether it was episodic (i.e., events occurring in one’s life) and semantic (i.e., learning of facts and meaning) in nature. Importantly, however, H.M. still had normal working memory and was able to learn new procedural tasks, a form of nondeclarative (or implicit) memory, and could retrieve remote declarative memory from before the surgery. Any autobiographical memory retrieval. On the other hand, it lacked episodic features of time and place and appeared rather semantic (see Corkin, 2002 for an overview of published results obtained with H.M. over several decades). This suggests that there are at least two forms of long-term memory (declarative and procedural; N. J. Cohen & Squire, 1980). While the MTL seems to be involved in the former, but not the latter, the dissociation between intact remote memories and inability to form new ones suggests that the brain does not have a single region where all explicit memories are stored that would resemble the grain device from the Black Mirror episode described above. Instead, memory relies on distinct operations, namely encoding, storage, consolidation, and retrieval, depending on different interactions between MTL and association cortices (Schacter & Wagner, 2013), overall suggesting that

while the MTL might be vital for initial encoding and consolidation, it is not the permanent repository but rather memories are being retrieved directly from cortical regions (Squire et al., 2004).

The MTL refers to the combination of the parahippocampal region and hippocampus (HPC) where the parahippocampal regions consists of cortical areas surrounding the HPC, including the perirhinal cortex, parahippocampal cortex, and entorhinal cortex (Eichenbaum et al., 2007) and has been described as memory system (Squire & Zola-Morgan, 1991). The HPC – a C-shaped structure at the end of the cortical processing hierarchy – can be divided into the cornu ammonia (CA) fields (CA1-CA4) referred to as hippocampus proper, the dentate gyrus, and the subicular complex (Squire et al., 2004).

The HPC receives sensory input from the entorhinal cortex which in turn receives the majority of its input from perirhinal and parahippocampal cortices, which in turn receive input from unimodal and polymodal cortices in the frontal, temporal, and parietal lobes and retrosplenial cortex (Squire et al., 2004; Squire & Zola-Morgan, 1991). More specifically, information from association areas processing unimodal sensory information about qualities of objects (i.e., “what” information, ventral stream) is projected to the perirhinal cortex that relays the information to the lateral entorhinal cortex, whereas spatial information processed in polymodal association areas (i.e., “where” information, dorsal stream) enters the medial entorhinal cortex via the parahippocampal cortex (Eichenbaum et al., 2007). As such, the hippocampus is a point of convergence where information from high-level perceptual areas are integrated (Diana et al., 2007) to bind individual elements together or combine elements with the context of the episode (Davachi, 2006).

As information enters the HPC from the entorhinal cortex, the information flow within the HPC is unidirectional and an indirect and a direct pathway have been described whereby information is projected to the CA1 as major output area (Vago et al., 2014): The indirect pathway is also referred to as trisynaptic pathway because as it consists of in total three excitatory synapses projecting from layer II of the entorhinal cortex to the granule cells in the dentate gyrus (via the perforant pathway) to pyramidal cells in CA3 (via the mossy fibre pathway) to pyramidal cells in CA1 (Schaffer collateral pathway). Additionally, there is a direct pathway (termed temporoammonic pathway) where neurons from layer III in the entorhinal cortex directly project onto distal dendrites of CA1 pyramidal cells. The CA1 then projects to the subiculum or directly to the entorhinal cortex. Deep layers in the entorhinal cortex then use feedback connections to relay the HPC output back to the perirhinal and parahippocampal cortex and from there to the areas in the neocortex from which the initial inputs originated (Eichenbaum et al., 2007).

Importantly, while the studies of patient H.M. briefly described above suggested that the MTL is involved in the formation of declarative memories in general and also in the retrieval of episodic, but not semantic memory, they do not allow conclusions about whether the MTL in total or only subregions therein are involved in or necessary for declarative memory as the whole MTL as well as the amygdala

were removed. However, later imaging studies using the SM paradigms described above showed that MTL structures are involved in encoding: Two studies published in the same volume of the journal *Science* showed that the parahippocampal region is more activated during the encoding of later remembered compared to later forgotten pictures (Brewer et al., 1998) and words (A. D. Wagner et al., 1998). Many more studies were conducted thereafter and meta-analytic evidence suggests that SM effects (i.e., larger brain activity during remembered compared to forgotten items; in this case by comparing hits and misses in recognition memory) are located predominantly in the left hemisphere in the HPC and parahippocampal gyrus as well as in dorsolateral and ventrolateral prefrontal cortex (PFC), in the fusiform gyrus and other occipitotemporal areas, as well as in the intraparietal sulcus/superior parietal lobe (Spaniol et al., 2009). The left-hemispheric dominance could be explained by the heavy reliance on verbal stimuli (20 out of 26 studies included used words as stimuli). Indeed, a later meta-analysis (Kim, 2011) confirmed stronger bilateral SM effects in the MTL (centred on the anterior hippocampal formation and extending into the amygdala), as well as inferior frontal, fusiform, premotor, and posterior parietal cortex when including all 74 studies into the contrast. Importantly, the studies used different materials (verbal and pictorial) as well as item and associative memory assessments.

As described above, item-memory would be regarded as a measure of familiarity whereas associative memory is a measure of recollection. Of note, because Spaniol and colleagues (2009) used contrasts comparing hits and misses, this most likely constitutes item memory. When only looking at studies that used verbal material, the SM effects for items were still located in the same brain regions, but this time only found in the left hemisphere, whereas clusters were symmetrical and only included the hippocampal formation (rather than the whole MTL) when only including studies using pictorial material in the item SM contrast. SM effects in the left hippocampal formation (amongst other regions) were found in the verbal-associative memory subgroup whereas in the pictorial-associative subgroup, SM effects were located in the bilateral hippocampal formation. In a direct comparison between verbal and pictorial material (carried out separately for item and associative memory), the left inferior frontal cortex extending into the middle frontal gyrus showed greater SM effects for verbal compared to pictorial encoding (i.e., both item and associative memory) whereas the bilateral hippocampal formation as well as the fusiform/occipital and posterior parietal cortex showed greater SM effects during the encoding of pictorial compared to verbal material. Lastly, when comparing item and associative memory (separately for each material), stronger item compared to associative SM effects were found in the left premotor and bilateral posterior parietal cortex regardless of material, whereas larger effects for associative compared to item memory were located in the left hippocampal region for pictorial material and in the left posterior inferior frontal cortex/anterior insula for verbal material.

Overall, both meta-analyses (Kim, 2011; Spaniol et al., 2009) suggest that the MTL (as well as other cortical areas including the PFC, see below) does show an increased BOLD response during the presentation of material that is later remembered, suggesting that they are involved in encoding. However, structures within the MTL might contribute differently to the encoding of different materials where verbal encoding is more left-lateralised, whereas pictorial encoding is more symmetrical and also more hippocampus-dependent. Likewise, in a direct comparison of item and associative verbal memory (i.e., familiarity- and recollection-based measurements), the SM effects are more pronounced for associative memory compared to item memory, potentially suggesting that different regions in the MTL contribute to distinct encoding mechanisms.

Reviewing imaging literature, Davachi (2006) suggested a distinct contribution of different structures within the MTL serving encoding and proposed (a) a domain-general role of the HPC in relational binding mechanisms (measured using e.g., item-source paradigms) where object and contextual representations are integrated into a coherent episodic memory trace, (b) domain-specific roles of perirhinal and parahippocampal cortex that contribute differently to encoding. More specifically, the perirhinal cortex could be involved in item memory and in the binding of perceptual and conceptual item-level features into a coherent object (e.g., shape and colour of a cucumber together with the semantic information that it is edible) to signal the object information to the hippocampus. The parahippocampal cortex, on the other hand, does not show a clear distinction between item and source memory and might provide information about the spatial layout to the HPC. Of note, due to problems in the signal-to-noise ratio in the entorhinal cortex, it has not been included in that review.

Expanding on this proposal for item and relational memory, the “binding of item and context” model (Diana et al., 2007) more specifically refers to familiarity and recollection according to which the former is correlated with activity in the perirhinal cortex (signalling item information) and the latter with activity in HPC (involved in binding) and parahippocampal gyrus (signalling context information in general not limited to the spatial domain). Importantly, others argued that the search for neural correlations of recollection and familiarity is not fruitful because research leads to contradictory results and because the paradigms used to distinguish between both processes are more likely to distinguish between strong and weak memory (Squire et al., 2007).

Despite such conceptual disagreements, researchers generally agree that the HPC is necessary for episodic memory because the HPC binds together elements of multimodal representations originating from cortical representations into a memory trace or engram (Davachi, 2006; Diana et al., 2007; Eichenbaum et al., 2007; Moscovitch et al., 2016). Importantly, though, hippocampal activation and its interaction with surrounding cortical areas and the neocortex more broadly varies depending on moment-to-moment demands of a task (forming “process-specific alliances”; Moscovitch et al., 2016). As

described above, the hippocampus consists of subfields (i.e., dentate gyrus, CA1, and CA3). Importantly, the subfields are not uniformly distributed along the hippocampal longitudinal axis and instead, show different ratios where dentate gyrus and CA3 dominate the posterior HPC (pHPC) and CA1 is concentrated in the anterior HPC (aHPC) (Ding & Van Hoesen, 2015; Malykhin et al., 2010). pHPC and aHPC also show different connectivity patterns during resting state where the pHPC is more associated with posterior perceptual areas (local, spatio-perceptual aspects of experience) whereas the aHPC shows stronger connectivity with anterior higher-order cognitive areas including the amygdala (emotion), PFC (working memory and schemas), and anterior temporal cortex (semantics) (Moscovitch et al., 2016; Ranganath & Ritchey, 2012). Likewise, within the MTL, the aHPC shows stronger connectivity with the perirhinal cortex and the pHPC with the parahippocampal cortex (Libby et al., 2012). Based on these and other findings, Poppenk and colleagues (2013) have proposed a functional segregation along the longitudinal axis of the HPC according to which the aHPC is predominantly involved in motivational processing, global spatial features, memory for the “gist” of an event, and encoding more general while the pHPC is relevant for spatial processing, local spatial features, memory for details of an event, and retrieval. This further strengthens the proposal by Moscovitch and colleagues (2016) that different regions within the temporal lobe might be involved in memory formation depending on specific demand characteristics of the task that could vary throughout.

Besides the MTL, the PFC and more specifically different regions therein (i.e., ventrolateral (vlPFC), dorsolateral (dlPFC), and ventromedial (vmPFC)) play a vital role in memory encoding processes. Through interactions and anatomical connections between aHPC and PFC, conceptual aspects of the experience are determined (Moscovitch et al., 2016): as sensory information is integrated into complex events with phenomenological characteristics, top-down modulation from the PFC supports the persistence of representations (e.g., of the event, context, or objects) within working memory. Part of these transient working memory representations are then transformed into long-lasting traces within the cortex and HPC supported by PFC-driven schematic relational and semantic processes. As representations of information encountered in the environment become increasingly complex, the lateral PFC provides critical top-down control of encoding processes based on current goals and task demands to provide discrete and elaborate representations for long-term storage (Simons & Spiers, 2003). Here, it has been proposed that the dlPFC (i.e., BA 9, 46, 9/46) is involved in the organisation of the to be remembered material within working memory and building relationships among items whereas the vlPFC (i.e., BA 44, 45, 47, 12/47) contributes to elaborative semantic and phonological processing and categorisation to ensure that traces are distinct and direct attention in alignment with relevant task goals (Blumenfeld et al., 2011; Blumenfeld & Ranganath, 2007; Simons & Spiers, 2003). Schemas, i.e., associative knowledge networks created based on multiple past experiences, further support encoding because they provide

structures to organise incoming information (Dudai, 2012; Moscovitch et al., 2016). Neuroimaging studies (e.g., van Kesteren et al., 2010) indicate that vmPFC is a hub to bind event representations and general knowledge together, thereby allowing to make predictions and guide the interpretation of the environment. More specifically, the vmPFC-HPC interactions support the encoding and retrieval of schematic information (Moscovitch et al., 2016; Preston & Eichenbaum, 2013).

Cellular Mechanisms of Learning

Overall, the literature reviewed thus far strongly indicates a central role of the HPC in memory. The question then arises how learning is achieved. Over a century ago, Santiago Ramon y Cajal suggested that learning is a result of changes in the strength of synapses, later termed synaptic plasticity. Indeed, such synaptic plasticity processes were found in the synapses in the perforant pathway¹ where high-frequency electric stimulation over brief periods resulted in an increase of the strength of the stimulated synapse over multiple days (Bliss & Lomo, 1973) – a process termed long-term potentiation (LTP). This discovery has fuelled important research (reviewed by Nicoll, 2017) resulting in the overall agreement that LTP is a suitable cellular model for learning and memory. In the context of declarative learning, LTP refers to a “family of processes that strengthen synaptic transmission at different hippocampal synapses through distinct cellular and molecular mechanisms” (Siegelbaum & Kandel, 2013, p. 1490) by increasing the amplitude of excitatory postsynaptic potentials.

This results in increased associations between pre- and postsynaptic neurons in response to the same stimuli (Vago et al., 2014). While first described in the perforant pathway, later studies found forms of LTP at each synapse within the trisynaptic pathway as well as in the direct pathway. Across all, bursts of electrical stimulations enhance transmission, however, the contribution of N-methyl-D-aspartate (NMDA) receptors differ. More specifically, in the Schaffer collateral pathway, LTP additionally requires NMDA receptor activation in the postsynaptic CA1 cell. The detailed mechanisms are beyond the scope of this chapter (for an extensive review of the cellular and molecular mechanisms, see Kandel et al., 2014), but in brief, the NMDA receptor acts as a “coincidence detector” with Hebbian associative properties because two events need to coincide for the NMDA receptor to open. Firstly, presynaptic glutamate release (caused by action potentials in the presynaptic CA3 neuron) is needed and secondly, a strong depolarisation of the postsynaptic neuron (associated with an action potential in the CA1 neuron).

¹ The standard model of the HPC posits that the perforant pathway also projects from the entorhinal cortex directly to CA3 (Norman & O’Reilly, 2003; R. C. O’Reilly & Rudy, 2001) while others use the term to refer to projections from the entorhinal cortex to the dentate gyrus (Witter, 2007a).

Chapter 1: General Introduction

As such, Hebbian learning is a cellular mechanism whereby connections between pre- and postsynaptic cells are strengthened if the postsynaptic cell is successfully activated by the presynaptic cell (Fell & Axmacher, 2011). Put in simpler terms, cells that fire together, wire together.

The opening of the postsynaptic NMDA receptor induces LTP and leads to calcium ion influx in the postsynapse, inducing LTP by triggering molecular cascades that activate protein kinases. Protein kinases are enzymes catalysing the transfer of phosphate groups onto target proteins, thereby activating the protein (for a review of protein kinase supporting learning and memory, see Giese & Mizuno, 2013). Importantly, protein kinases are reversible (by a group of enzymes referred to as phosphatases), allowing for flexible signalling. The expression of LTP has an early phase (lasting 1-3h) that can be induced by a single train of high frequency stimulation and is independent of protein synthesis and a late phase (lasting at least 24h) induced by multiple trains of high frequency stimulation that is dependent on protein synthesis (for a review, see Baltaci et al., 2019). Early and late LTP have been hypothesised to reflect differences between short- and long-term memory (S.-H. Wang & Morris, 2010). During early phases of LTP (predominantly depending on calcium/calmodulin-dependent protein kinase II (CAMKII)), ion channel density and/or conductivity is regulated. Additionally, retrograde messengers might be released increasing the probability of transmitter release in the presynapse. During late phases of LTP (depending on, e.g., cyclic adenosine monophosphate (cAMP) dependent protein kinase A (PKA) activating the cAMP responsive element binding protein (CREB) or mitogen-activated protein kinase (MAPK)), new proteins are synthesised, and gene expression is regulated, leading to a sustained increase of ion channel in the postsynaptic membrane and the growth of new synaptic connections. While an increase of receptors/ion channels is observed during early and late LTP, the number of receptors decays back to baseline after early LTP whereas the synthesis of plasticity-related proteins during late LTP anchors new receptors over time (Redondo & Morris, 2011).

The physical substrate of memory has been termed “engram” and involves the strengthening of synaptic connections between neurons that are active during encoding, forming neuronal ensembles (Josselyn et al., 2015). Such increases in synaptic strength during encoding enhances the likelihood that the same neural ensemble will be activated at a later stage, e.g., during retrieval. Therefore, the HPC must be capable to bind the features of similar stimuli (evoking similar patterns of activity in the neocortex due to shared perceptual features) into a single representation that is distinct/unique to minimise inference, while at the same time, the HPC has to be able to use cues (i.e., partial representations) to retrieve the encoded representation (R. C. O’Reilly & McClelland, 1994). According to a standard model of the HPC (Norman & O’Reilly, 2003; R. C. O’Reilly & McClelland, 1994; R. C. O’Reilly & Rudy, 2001), the HPC performs pattern separation at the time of encoding and pattern completion at the time of recall.

saImportantly, in the entorhinal cortex, similar stimuli create largely overlapping activity that is projected to the HPC via perforant pathways. Therefore, to achieve pattern separation, computational models suggest that the dentate gyrus creates sparse, orthogonalised representations of the input that is projected to CA3 (using the mossy fibre pathways) to create a non-overlapping pattern of neural activity within the CA3 (Treves & Rolls, 1994). Due to the circuit structure in the dense collaterals (branches) found in the CA3 pyramidal neurons (CA3 recurrent pathway), the CA3 functions as an autoassociative network able to combine inputs from distributed cortical origins into an association or engram represented by increased synaptic connections between CA3 neurons that are increased after Hebbian learning mechanisms (Witter, 2007b). Importantly, because the CA1 also receives direct projections from the entorhinal cortex, this creates an invertible representation in the CA1. This means that both representations of the cortical input (pattern-separated representation in CA3 and invertible representation in CA1) are bound together using synaptic processes in the Schaffer collateral pathway described above. Later, during retrieval, the cue elicits cortical activity that enters the HPC via the entorhinal cortex and is projected to the dentate gyrus and CA3 where the partial input will activate the full CA3 representation (engram) because the synapses have undergone LTP resulting in increased postsynaptic excitability. This process is referred to as pattern completion whereby the partial activation of the CA3 engram leads to a reconstruction of the original CA3 engram. The reactivated CA3 representation then activates the corresponding invertible CA1 representation that in turn reactivates the representation in the entorhinal cortex to reinstate neocortical activity supporting retrieval. Evidence from high-resolution fMRI suggests that the dentate gyrus and CA3 show activity consistent with the role of pattern separation whereas activity in the CA1 implies a role in pattern completion (Bakker et al., 2008; Lacy et al., 2011).

Learning and Dopamine

Overall, the evidence reviewed so far suggests that information that is transmitted from association cortices to the HPC via the entorhinal cortex is encoded based on the synaptic plasticity processes within the hippocampal transmission pathways. More specifically, according to Hebb's rule (Hebb, 1949), synaptic transmission is strengthened if activity in the presynaptic cell activates the postsynaptic cell. However, it has been pointed out that mere association might not be the complete story (Lisman et al., 2011): if activity in CA3 neuron A was representing stimulus A (e.g., an object) and activity in CA3 neuron B was representing stimulus B (e.g., a face), the co-occurrence of both stimuli would strengthen the synapse between the CA3 neurons A and B (forming an engram). This cellular mechanism should hence manifest in associative memory where cueing one of the stimuli should activate the internal presentation of the other by mechanisms of pattern completion. However, everyday experiences as well as laboratory experiments show that simultaneous presentation of two items or stimuli does not guarantee their paired encoding (Davachi, 2006; Diana et al., 2007; Lisman et al., 2011). In an

attempt to solve this shortcoming in Hebb's rule, Lisman and colleagues (2011) have proposed a neo-Hebbian framework whereby encoding relies on importance being attached to the items. More specifically, the authors propose that while the Hebbian principle applies to the hippocampal default encoding mode, its effect is probably limited to early LTP (not lasting longer than 3h), indicating that late LTP might be governed by additional principles and biochemical processes signalling importance. They suggest that such importance for encoding might be signalled by the neurotransmitter dopamine.

In fact, converging evidence indicates a role of dopamine in late LTP in CA1 (Lisman et al., 2011; Lisman & Grace, 2005). Dopamine is a neurotransmitter that is predominantly released by dopaminergic neurons in the ventral tegmental area (VTA) and substantia nigra (SN) in the midbrain (Haber & Knutson, 2010). Dopamine binds on several receptor types (D1-D5) that can be grouped into D1-like (D1, D5) and D2-like (D2, D3, D4). Dopamine binding at D1-like receptors stimulates adenylyl cyclase and cAMP production also referred to as cAMP/PKA pathway (Gurevich et al., 2016) and dopamine stimulates protein synthesis needed for late LTP (Y. Y. Huang & Kandel, 1995; W. B. Smith et al., 2005). Administration of a D1/D5 antagonist results in blockage of late LTP in CA1 (Swanson-Park et al., 1999), and memory impairments, evident only after long, but not short delays, in line with the idea that dopamine supports late phases of LTP (O'Carroll et al., 2006). However, some evidence suggests that dopamine also impacts early LTP through D1/D5 receptors and cAMP (Otmakhova & Lisman, 1996). Most intriguingly, tracing studies revealed dopamine mesencephalic projections to the HPC (Gasbarri et al., 1994), providing the neuroanatomical basis for the interaction between dopamine and LTP in the HPC in the context of learning. These results from studies in rodents are complemented by findings from fMRI studies suggesting an intrinsic functional connectivity (FC) between VTA/SN and HPC in humans during rest (Kahn & Shohamy, 2013; Murty et al., 2014) as well as during learning where interactions between both brain areas might support learning of new information (Ripollés et al., 2016) and the generalisation of knowledge by integrating discrete episodes (Shohamy & Wagner, 2008). Importantly, FC between HPC and VTA/SN predicts memory encoding in delayed, but not immediate tests (Duncan et al., 2014). Overall, this indicates a strong association between dopaminergic activity, originating in the VTA/SN, and hippocampal learning processes, on cellular and neuroanatomical level, further reflected in behavioural measures of learning.

Studies in rodents have shown that dopaminergic neurons in the VTA/SN are constantly inhibited by the ventral pallidum (Grace et al., 2007), but when activity in the nucleus accumbens (NAcc) inhibits the ventral pallidum, the neurons in the VTA/SN become disinhibited and fire spontaneously and irregularly (Düzel et al., 2010; Grace et al., 2007). This tonic firing provides baseline dopamine levels necessary for cognitive functioning. Importantly, the HPC projects onto the NAcc, hence enabling hippocampal influences on dopaminergic activity (Floresco et al., 2001). In addition to input from the

striatum, the midbrain receives projections from the brainstem providing glutaminergic and serotonergic inputs as well as direct sensory input from the superior colliculus (Haber & Knutson, 2010). As such, in the context of certain behaviourally relevant stimuli or events, additional excitatory input can cause brief bursts in firing, called phasic response (Grace et al., 2007).

For instance, novel stimuli have consistently shown novelty-dependent dopaminergic firing in the VTA/SN as evidenced by single cell recordings (Ljungberg et al., 1992) and human fMRI (Bunzeck & Düzzel, 2006). Such dopamine release is in line with the idea that exploring novel environments might be associated with beneficial outcomes or model updates. In the same fMRI study, in addition to increased activity in the VTA/SN, stimulus novelty was also associated with an increased response in the HPC (Bunzeck & Düzzel, 2006) and converging evidence suggests the role of the (a)HPC as novelty-detector (Kafkas & Montaldi, 2018). The mechanisms are not fully understood yet, but it has been proposed that the HPC and more specifically the CA1 operates a comparator generating mismatch/associative novelty signals when prior predictions (arriving via the trisynaptic pathway) are violated by sensory inputs (signalled via the direct pathway) thereby generating prediction errors (Duncan et al., 2012; Kumaran & Maguire, 2007; Lisman & Grace, 2005). Of note, different forms of novelty might be computed by different areas within the MTL and then projected to the HPC (Lisman et al., 2011), likely in a dynamic manner (Murty et al., 2013). It is further assumed that the computed novelty signals are projected from the CA1 to the subiculum and from there to the NAcc to be relayed to the VTA/SN via the ventral pallidum as described above. As such, this downward arc from the HPC to the VTA/SN signals novelty and causes the release of dopamine in the VTA/SN. Additionally, an upward arc exists in which dopamine innervates the CA1, thereby providing dopamine necessary for synaptic LTP at the cellular level. This HPC-VTA/SN loop (Lisman & Grace, 2005) forms the neural basis explaining behavioural novelty-dependent memory benefits (Schomaker, 2019) and human fMRI studies show an involvement of HPC and VTA/SN support these behavioural effects (Bunzeck et al., 2012; Wittmann et al., 2007). Importantly, because the NAcc also receives input from the prefrontal cortex (Haber & Knutson, 2010), novelty signals and goal-directed information can be combined to only relay goal-relevant novel information to the VTA/SN. Likewise, because the VTA/SN receives excitatory input from the pedunculopontine tegmentum driven by limbic afferents, affect- and salience-related information is conveyed (Haber & Knutson, 2010). Overall, the HPC-VTA/SN loop provides a framework explaining how events that elicit a dopaminergic response are preferably encoded into hippocampus-dependent declarative memory.

Crucially, it has been found that the effects of novelty on encoding are not limited to the stimuli that were novel but also extend to stimuli that were presented in the context of novelty. Fenker and colleagues (2008) presented novel photographs of landscapes and scenes to participants for 5 min before

being presented with familiar words that they were instructed to encode. In comparison with participants that viewed familiar photographs, those in the contextual novelty condition showed better recollection memory for the following words, with more enhanced effects at the delayed (24h) compared to the immediate memory test. This novelty-related effect was replicated and extended in elementary school children by showing that novelty exposure one hour, but not four hours, before and after learning enhances memory across different materials (Ballarini et al., 2013). Overall, this suggests that the release of dopamine (as associated with the experience of novelty) creates a “penumbra” surrounding the events triggering the release of dopamine (Lisman et al., 2011). More specifically, according to the Synaptic Tag and Capture Hypothesis (Frey & Morris, 1997; see Redondo & Morris, 2011 for a revised version), early LTP, i.e., LTP independent of protein synthesis, creates a short-lasting “synaptic tag” (decaying after 1-3h) at the potentiated synapse indicating where newly synthesised plasticity-related proteins (necessary for the expression of late LTP) should be delivered to be “captured” by the tagged synapse to result in its potentiation. Synaptic tags can be defined as “molecular changes at synapses that mark plasticity as having occurred” (Redondo & Morris, 2011, p. 18). Importantly, early LTP can be induced by weak stimulation that would normally not establish late LTP and protein-dependent synaptic changes. However, if the same group of neurons undergoes strong/frequent stimulation inducing late LTP, the presence of a synaptic tag will result in late LTP at every tagged synapse. For instance, imagine three neurons A, B, and C where C is the postsynaptic neuron for A and B. Let’s further assume that A and C were weakly stimulated (creating a synaptic tag, inducing early LTP, but not protein-dependent late LTP), whereas B and C were frequently stimulated (creating a synaptic tag, inducing early LTP and protein-dependent late LTP). Because late LTP is expressed by protein synthesis within the postsynaptic neuron C and those proteins are delivered to any “tagged” synapse, both synapses A-C and B-C will be strengthened by the expression of late LTP. Notably, synaptic tag and plasticity-related proteins have considerable lifetimes, so that events that fall within the timeframe of events triggering late LTP also undergo late LTP based on their temporal proximity.

Note that in a more recent conceptualisation (Redondo & Morris, 2011) of the Synaptic Tag and Capture Hypothesis posits that the induction of early LTP and the setting of synaptic tags can be independent. For instance, slow-onset synaptic potentiation has been observed where the synapse is strengthened over time in the absence of excitatory postsynaptic potentials following the application of a D1/D5 agonist (Navakkode et al., 2007). Importantly, while the synaptic tag has previously been considered to a very limited number of proteins, Redondo and Morris (2011) propose that a large number of proteins are involved making the tag a temporal “state” of the synapse involving structural and functional changes at the excitatory synapse that are part of the expression of early LTP (e.g., temporary incorporation of new receptors). This provides a way of extending the time course during which the

memory system can determine whether late LTP processes are expressed, and also explains the phenomena of “behavioural tagging” (Moncada et al., 2015; Morris, 2006) whereby an experience that would only create a short-term memory representation is encoded into long-term memory if a triggering event occurs around the time of encoding that can upregulate the synthesis and distribution of plasticity-related proteins. For instance, novelty, assumed to trigger the release of dopamine thereby catalysing the synthesis of plasticity-related proteins, can enhance memory for events experienced after the novelty exposition in both rodents (Moncada & Viola, 2007; S.-H. Wang et al., 2010) and humans (Ballarini et al., 2013; Fenker et al., 2008).

Tagging processes can explain the penumbra effect of dopamine observed in the behavioural experiments described above: the information presented around the exposure to novelty is preferably encoded because it was presented within the penumbra of dopamine (Lisman et al., 2011). More specifically, information that would have only given rise to a short-lasting memory received a behavioural tag that led to its encoding as a longer-lasting memory due to the dopamine-related catalysation of protein synthesis during late LTP (Moncada et al., 2015). As such, this implies that dopamine supports the encoding of events before, during, and after its release (for a review, see Shohamy & Adcock, 2010). Importantly, dopamine acts on the synapses during late rather than early phases of LTP, suggesting that the effects of dopamine on learning are not limited to the time of encoding, but extend to the consolidation of stimuli.

Consolidation Processes

Consolidation (for reviews, see Dudai, 2004, 2012) can be defined as a process during which new memory traces become increasingly stabilised in (at least) two distinguishable timescales (Dudai, 2012; Wamsley, 2019): an immediate stage (seconds to hours after encoding) targeting the stabilisation of local circuits (cellular-level consolidation) and a delayed stage (hours to weeks following encoding) involving a reorganisation of memory traces across brain circuits within the hippocampus and across hippocampal-cortical networks (systems-level consolidation) (for a review, see Frankland & Bontempi, 2005). Studies of H.M. provided first indications that memory encoding and memory storage might be associated with different areas in the brain because while H.M. was unable to encode new information, he was still able to retrieve remote memory from before the surgery (Corkin, 2002). Indeed, the hippocampal-neocortical interactions theory of memory formation (Morris, 2006; S.-H. Wang & Morris, 2010) proposes that (1) activity-dependent hippocampal synaptic potentiation reflects automatic recording of attended events, forming a memory trace that might be representative of the location of neurons in the neocortex encoding sensory features of the stimulus, (2) hippocampal traces decay rapidly to avoid oversaturation unless encoding takes place around the time of synthesis, distribution, or capture of plasticity-related proteins at tagged synapses, (3) hippocampal traces enables processes by which connections in the relevant module

of the cortex are built (enhanced in the context of prior schema), and (4) retrieval of the encoded event reactivates hippocampal traces reactivating memory traces in the neocortex and allowing for cellular mechanisms for reconsolidation or memory update. Cellular-level consolidation mechanisms typically include the synthesis and synaptic capture of plasticity-dependent proteins described in the introductory chapter to stabilise encoding at the level of an individual synapse whereas systems-level consolidation of connected neurons within the HPC (i.e., the engram) and neocortex (S.-H. Wang & Morris, 2010). This further implies that cellular-level consolidation strengthens the memory within the HPC for long enough to be consolidated at slower systems-level, but also filters what should be retained and what can be erased. Systems-level consolidation then changes the distribution of memory representations across brain regions, stabilising memories over time (Cowan et al., 2021).

Importantly, immediate post-encoding activity can be further divided into processes that occur seconds after encoding compared to those minutes after encoding where each time window might be associated with unique processes (N. Cohen et al., 2015). To study the effects of these offline periods (i.e., periods following the “online” stimulus presentation) on memory formation, different post-learning states can be investigated/manipulated (Wamsley, 2019) ranging from an active wake state where participants are engaged in a sensorimotor task (e.g., a distractor task or listening to music), to a quiet wake state (i.e., typically an awake rest where attention to sensory stimuli is reduced), or sleep (i.e., a nap or overnight sleep). While the effects of sleep on learning have been well documented (Diekelmann & Born, 2010; Stickgold, 2005; Stickgold & Walker, 2007), recent evidence suggests that periods of quiet rest after learning also boosts later memory (Brokaw et al., 2016; Dewar et al., 2012).

A main mechanism thought to support consolidation mechanisms is linked to repeated reactivation of the memory trace/engram (recently reviewed by Tambini & Davachi, 2019) whereby neurons within the HPC as well as within cortical areas that were activated during encoding are reactivated during rest to strengthen the representations of events. More specifically, research in rodents showed that neural ensembles in the HPC of neurons that were recently active are reactivated during sleep and quiet wake states (Foster & Wilson, 2006; M. A. Wilson & McNaughton, 1994). The reactivation occurs in short events characterised by transient hippocampal network events called sharp wave ripples comprised of negative potentials (sharp waves) and fast frequency oscillations (ripples) (Atherton et al., 2015; Buzsáki et al., 1992). If reactivation patterns extend into sequences in either the same or opposite temporal order as observed during behaviour, this is referred to as forward (A. K. Lee & Wilson, 2002) or reverse (Foster & Wilson, 2006) replay. As reactivation has previously been linked to learning (Dupret et al., 2010), sharp wave ripples and the reactivation they induce, have been discussed as a neural substrate of consolidation during sleep and quiet rest periods (Carr et al., 2011; O’Neill et al., 2010; Rasch & Born, 2007). While there is still some uncertainty as to how replay occurs, it might be related to lingering

excitability of the neurons and synaptic plasticity processes (for a detailed explanation, see Atherton et al., 2015).

Intriguingly, sharp-wave ripples have also been observed using electrophysiological recordings in the HPC and rhinal cortex of epilepsy patients during a nap, predicting memory performance thereafter (Axmacher et al., 2008). Additionally, simultaneous electrophysiological recordings and fMRI scanning revealed that the sharp wave ripples in the HPC are captured well by the hemodynamic response function (HRF) and that activity in the HPC was accompanied by activation in across most of the cortex (except from the primary visual cortex) and a deactivation in the thalamus, basal ganglia, and midbrain where the thalamic activity suppression precedes the hippocampal and cortical activation (Logothetis et al., 2012). Importantly, it has been shown in rodents that hippocampal-neocortical and cortico-cortical correlation observed during encoding re-emerge during rest (Hoffman & McNaughton, 2002; Qin et al., 1997).

Taken together, this provides the rationale to measure reactivation in humans as it should manifest in changes in the BOLD signal as well as in functional connectivity (FC) patterns over minute-long timescales (Tambini & Davachi, 2019). To study reactivation effects and how they relate to memory formation, studies typically collect a baseline or pre-learning resting state scan, then participants perform a memory task inside the fMRI scanner followed by a post-learning scan (Deuker et al., 2013; Gruber et al., 2016; Kukolja et al., 2016; Murty et al., 2017, 2019; Tambini et al., 2010; Tambini & Davachi, 2013). This design ensures that any effects are related to encoding and not intrinsic properties of resting state per se by comparing pre- and post-learning scans where any changes from pre- to post-learning can be attributed to the encoding task. To analyse the data, two main approaches of subsequent analysis can be found (as reviewed by Tambini & Davachi, 2019). The first targets activity within a specific brain region, often by applying multivoxel pattern analysis (cf. Staresina et al., 2013 for an example using Representational Similarity Analysis) that either targets the local activation or the multi-voxel correlation structure. The second approach focuses on interregional correlations of BOLD time courses, i.e., their FC. In both cases, changes from pre- to post-learning (either increased pattern similarity between activity at encoding and rest, or increased FC) are interpreted as related to the ongoing strengthening of memory traces, especially when related to encoding.

For instance, Tambini and Davachi (2013) observed that hippocampal encoding patterns persisted into rest, with different encoding tasks associated with distinct patterns, and that the patterns observed during post-learning rest predict learning. Intriguingly, especially hippocampal presentations of items appear to be selective. For instance, items that have not been learned well previously seem to be preferably reactivated and this reactivation predicts memory improvement after repeated studying, however, only if participants have slept in between encoding sessions (Schapiro et al., 2018). According to the authors, this might suggest that awake reactivations could form the basis for later consolidation

processes during sleep, potentially reflecting synaptic tagging as discussed as a mechanism underlying replay (Atherton et al., 2015). However, reactivation activity supporting learning does not appear to be limited to the HPC or even the MTL. Reactivations predicting encoding in the bilateral entorhinal cortex (but not the bilateral HPC) and the left retrosplenial cortex have further been found during an active delay while participants performed a numerical judgement task (Staresina et al., 2013). Deuker and colleagues (2013) found reactivations in the occipital lobe stretching into the inferior temporal lobe during wakeful rest and sleep predicted subsequent memory. More strikingly, after the learning of associations (A-B), reactivations in the fusiform face area predicted subsequent learning of overlapping associations (B-C) as well as of inferences regarding unstudied associations (A-C), even after controlling for the encoding performance of unrelated items (X-Y) (Schlichting & Preston, 2014). Going further, Schlichting and Preston (2014) showed that resting-state functional connectivity (RSFC) between HPC and fusiform face area in a post-encoding awake rest following the initial learning of associations (A-B) predicted the encoding of overlapping pairs and (B-C) and inferences (A-C). These effects were observed after controlling for RSFC observed following the associative encoding of unrelated items (X-Y) as baseline as well as the associative encoding performance.

Overall, this suggests that reactivation/replay activity in the HPC and neocortex as well as the interaction between them strengthen memory encoding. During sleep, electrophysiological recordings in rodents showed overlapping, correlated replay activity in the HPC and cortex (Ji & Wilson, 2007). Changes in reactivation influence neural FC patterns in human fMRI, thereby possibly reflecting neural oscillations (Josselyn et al., 2015), i.e., period and continuous variation of neural signals across brain networks with certain frequencies (for a review, see Fell & Axmacher, 2011). More specifically, oscillations if correlated across brain regions (a process called phase synchronisation) – likely support cognitive functions by facilitating the communication among neuronal groups (e.g., coincidence detection coordinates timing of input into target region) and plasticity (e.g., precise timing of action potentials promoting LTP). Evidence suggests that oscillatory processes are related to declarative memory during encoding and consolidation (Hanslmayr et al., 2016, 2020).

Both, cellular-level consolidation (i.e., selective potentiation of synapses due to late-LTP mechanisms within the HPC) as well as subsequent systems-level consolidation (i.e., stabilisation of memory traces through cross-regional, HPC-cortico interactions) are supported by replay and/or reactivation processes where sharp wave ripples originating in the HPC facilitate the coordinated reactivation of cortical traces through oscillations (Cowan et al., 2021). Given that reactivation of the HPC might be linked to oscillation supporting memory during encoding and consolidation, it is not surprising that a second line of research has focused on changes in RSFC between the HPC and other brain areas from pre- to post-learning rest and how they relate to behaviour. For instance, Tambini and

colleagues (2010) found that RSFC between HPC and the lateral occipital complex significantly increased following a task with high, but not low, subsequent encoding. More importantly, the individual differences in the change in RSFC between both regions are predictive of individual encoding performances. These results and those by others (Murty et al., 2017; Schlichting & Preston, 2014; Tomparry et al., 2015) highlight a key mechanisms of systems-memory consolidation: memory for visual material is stabilised over time by post-encoding interactions between the HPC and sensory cortices associated with the initial encoding, more specifically the ventral visual stream. Likewise, changes in the multivoxel correlation structure of hippocampal voxels from pre- to post-learning rest predict encoding performance (Tambini & Davachi, 2013). Within the MTL, changes in RSFC between HPC and perirhinal cortex predict memory encoding (Murty et al., 2019). Likewise, changes in cortico-cortical RSFC from pre- to post-learning have been observed (Kukolja et al., 2016; Tambini et al., 2010) that predict subsequent memory (Kukolja et al., 2016).

Taken together, changes in RSFC are likely to reflect systems-level consolidation processes associated with reactivations in the HPC, promoting consolidation by providing an index of experience-dependent plasticity (Tambini & Davachi, 2019). Importantly, these effects of early consolidation cannot solely be explained by rehearsal as (1) different declarative memory mechanisms are affected (Groen et al., 2011), (2) effects of post-encoding rest have also been found in non-declarative learning like motor (Albert et al., 2009; Debas et al., 2014) and procedural (Peigneux et al., 2006) as well as visual perceptual learning (Lewis et al., 2009), and (3) effects are also found in active rest states (A. O. Cohen et al., 2021; Peigneux et al., 2006; Tomparry et al., 2015).

In addition to supporting subsequent memory by strengthening HPC-cortico coupling, systems-level consolidation further supports a transformation of memory traces by integrating experiences into existing knowledge and schemas (Cowan et al., 2021; Moscovitch et al., 2016). As mentioned earlier, a key structure associated with schemas during encoding is the vmPFC, so it is perhaps not surprising that the vmPFC has further been implicated in the development of integrated experiences over time (Tomparry & Davachi, 2017; van Kesteren et al., 2012). Using the same associative learning paradigm described above, Schlichting and Preston (2016) further found a significant increase in RSFC between HPC and medial PFC following the encoding of overlapping associations (B-C), potentially reflecting memory updating. Such a mechanism could support the integration of new information into existing knowledge where the availability and extent of prior knowledge/schema further determines the degree of RSFC between HPC and medial PFC following encoding (van Kesteren et al., 2010). As memories mature (i.e., as time passes and memories become less detailed/episodic and more schematic/semantic), they become less reliant on the HPC and more dependent on the vmPFC, further integrating multiple events into more generalised and abstract knowledge (Moscovitch et al., 2016).

Motivated Learning

As discussed earlier, while the Hebbian rule postulates that cells that wire together, fire together, a more recent neo-Hebbian framework on synaptic plasticity suggests that while the Hebbian rule might be suitable to explain early LTP, late LTP requires additional signals, for instance those of dopamine, signalling importance (Lisman et al., 2011). In addition to responding to novelty, evidence suggests that dopamine neurons more generally code value and salience (Bromberg-Martin et al., 2010). At the most rudimentary level, resources that maintain welfare, survival, and reproduction have value to any organism. For evolution to produce any form of life on earth that was meant to inhabit the planet, any organism would need mechanisms to approach objects in the environment that would support its survival and avoid those that threaten it. The driving force underlying behaviour is often referred to as motivation, derived from the Latin word “movere” meaning “to move”: In the broadest sense, motivation can be defined as process(es) that energise, direct, and sustain behaviour; elicited by extrinsic and intrinsic factors/sources that are appetitive or aversive (Pennartz et al., 2011; Reeve & Lee, 2019).

Extrinsic sources of motivation include food, juice, or money, but also social signals like a smile of a person or praise. Intrinsic sources are often found if tasks have an inherent value, for instance, if they spark curiosity, enjoyment, interest, or surprise, or arise from feelings of autonomy or competence (W. Lee, 2016). When these sources (or stimuli) are used to actively motivate behaviour based on predefined contingencies, they may be referred to as incentives (Greene, 2010), somewhat communicating a “do well” message. Rewards, on the other hand, can be conceptualised as positive stimuli that reinforce behaviour on which outcome they are dependent upon (Matyjek et al., 2020; Schultz, 2015), hence conveying a “well done” message. Rewards that are given after successful performance are often referred to as reinforcers (Berridge, 2000). While conceptually distinct, the same stimuli could be an incentive in one scenario, and a reward in another scenario, or even first function as an incentive used before the motivated behaviour occurs and then as a reward after the occurrence of motivated behaviour. If the incentive is known in advance, both incentive and its hedonic value form cognitive action-outcome presentations establishing causal links between both to an extent where “when one engages specifically in that incentive-related action, one does so with the expectation of earning the reward” (Berridge, 2000, p. 259). This is perhaps why research often uses these terms interchangeably to refer to positive, appetitive, and desired stimuli motivating behaviour (e.g., Adcock et al., 2006 investigated “reward-motivated learning” using a “monetary incentive delay” task). In the following, the terms are used based on these preliminary definitions and/or based on the terms used by the authors of previous work; however, a clear-cut distinction is often non-trivial (Murayama, 2019).

While early theories strongly linked the rewarding properties of positive stimuli (i.e., rewards/incentives, although this line of literature often uses the term reward) to their ability to reduce

drive (e.g., food satisfies hunger) and thereby reinforce behaviour, such views have been abandoned in favour of incentive motivation concepts according to which the motivational properties of rewards are incentive properties that are motivating because they lead to hedonic experiences (see Berridge, 2000 for a historical review of reward and incentives concepts). Of note, current drive states can modulate the incentive value, e.g., food is associated with different subjective value depending on the metabolic state (hunger vs. satiety) (Jiang et al., 2014). Such observations were summarised in the Incentive Salience Model (Berridge, 1996) postulating that incentive processing of rewards is associated with different psychological components, i.e., a motivational (“wanting”, i.e., incentive salience), an affective (“liking”, i.e., pleasurable, hedonic experience), and a learning component (Berridge & Kringelbach, 2015; Berridge & Robinson, 2003). “Wanting” dominates the appetitive phase during which future rewards (i.e., incentives) are anticipated/expected and action is taken to attain rewards, whereas “liking” is linked to the consummatory phase characterising the hedonic impact of receiving a reward (Webber et al., 2021).

Besides this temporal dissociation, these processes can also be dissociated on a neurobiological level (Berridge & Kringelbach, 2015; Kringelbach & Berridge, 2016): “Wanting” is strongly associated with dopamine and is supported by largely distributed brain areas including dorsal and ventral striatum, amygdala, VTA, as well as insula, orbitofrontal, anterior cingulate, and medial prefrontal cortices. “Liking”, on the other hand, has been linked to opioids and small hedonic hotspot within e.g., the NAcc, ventral pallidum, and orbitofrontal cortex. For instance, using the monetary incentive delay task to disentangle neural activity during anticipation and outcome feedback, Knutson and colleagues (2001) showed that anticipation recruited the ventral striatum, particularly the NAcc, while outcome feedback was linked to activity in the vmPFC. This further adds to other findings by the researchers (Knutson, Adams, et al., 2001; Knutson et al., 2000) that have linked mesolimbic structures and within that the NAcc to the anticipation of rewards and their expected positive incentive value. Various meta-analyses (Knutson & Greer, 2008; Oldham et al., 2018; R. P. Wilson et al., 2018) of fMRI studies using the monetary incentive delay paradigm showed that the anticipation of rewards recruits the striatum (caudate nucleus, putamen, and NAcc), midbrain, amygdala, and thalamus, as well as in superior and middle frontal gyri extending into insular and anterior cingulate cortex, the latter known to be part of the salience network (Seeley et al., 2007). Importantly, activity in overlapping areas was found when anticipating losses, suggesting that motivational processes during anticipation are independent of valence (Oldham et al., 2018). Further contrasting reward anticipation and feedback, it was shown that ventral striatum and amygdala were conjointly activated during both phases whereas anticipation more strongly recruited caudate nucleus, dorsal striatum, motor areas, thalamus, and anterior insula; and outcome was associated with responses in orbitofrontal cortex (OFC)/vmPFC. Other meta-analyses contrasting reward

anticipation and feedback more broadly by integrating activation maps from various paradigms (Diekhof et al., 2012; Liu et al., 2011) overall replicated these effects showing that anticipation of rewards recruits the ventral striatum, VTA, insular as well as anterior cingulate cortices whereas the processing of outcome feedback is associated with the OFC and vmPFC with a regional overlap between both processes in the ventral striatum, suggesting a phase-independent role. Again, the OFC and vmPFC, but also the posterior cingulate cortex were more strongly linked to feedback than to anticipation. With respect to ventral striatum and especially the NAcc, however, results are less consistent with one meta-analysis suggesting that is stronger activated during anticipation than feedback (Diekhof et al., 2012) and the other meta-analysis reporting the opposite finding (Liu et al., 2011).

Taken together, especially the ventral striatum (prominently the NAcc) and medial parts of the PFC (i.e., OFC and vmPFC) are strongly implicated in value-based representations of rewards processing and have both been found to also track reward magnitude (Diekhof et al., 2012; Knutson & Greer, 2008; Oldham et al., 2018). The medial PFC, part of the mesocortical dopaminergic pathway, processes reward feedback, potentially representing outcome value. The ventral striatum, part of the mesolimbic dopaminergic pathway, seems to be less selective and involved in reward anticipation and feedback. Its role in reward anticipation can be linked to reward prediction as well as to representations of expected reward magnitude; and responses in the ventral striatum shifts from the rewarding event to its predictor once reward contingencies are successfully learned (Diekhof et al., 2012; Knutson, Adams, et al., 2001; Knutson, Fong, et al., 2001; O’Doherty et al., 2003). However, because experimental paradigms (as well as real-life scenarios) also show a degree of uncertainty with respect to reward deliveries where rewards outcomes or variants in magnitude thereof are presented (omitted) unexpectedly, the ventral striatum response during reward feedback can be interpreted as a prediction error (PE), i.e., a difference between the received and predicted reward (Schultz, 1998). A reward larger (smaller) than predicted results in positive (negative) reward PEs and an increased (decreased) dopaminergic response that will be used to update future predictions. As such, the response in the ventral striatum during reward feedback likely reflects an uncertainty-driven consummatory response (Diekhof et al., 2012). Any associated dopaminergic response during reward anticipation or feedback signals the importance of associated stimuli and events to not only motivate behaviour but as discussed earlier, also to modulate memory by influencing late LTP. As such, dopamine release during motivated states enables the encoding of the context to allow past experience to modify future behaviour, forming the basis for “adaptive memory” (Shohamy & Adcock, 2010).

Extrinsically Motivated Learning

Cell recordings of the dopaminergic midbrain in monkeys revealed that dopamine neurons respond to extrinsic rewards like food or liquids, but not only during their unexpected delivery, but also

when they are expected by a preceding conditioned stimuli (Schultz, 1998). In the latter case, the dopamine response is transferred to the earliest predictive stimuli and dopaminergic activity is depressed if an expected reward is omitted or enhanced if larger than expected or at any time other than the predicted one (Tobler et al., 2005). As such, dopamine neurons in the midbrain have often been associated with reward prediction with their response signalling PEs. In addition to the VTA/SN, many brain regions are involved in reward processing, forming a reward network or circuit between the frontal cortex and the basal ganglia, with the striatum as well as ventromedial prefrontal and orbitofrontal cortex as key players responding to and monitoring rewards (Haber & Knutson, 2010). Pharmacological studies in healthy humans have also highlighted the strong relationship between dopamine and reward functioning (Webber et al., 2021).

In line with the proposal that the release of dopamine is associated with enhanced encoding of the stimuli associated with reward, consistent memory-enhancement effects of rewards have been observed (for a review, see Miendlarzewska et al., 2016). For instance, the effects of extrinsic rewards on intentional encoding have been studied using monetary incentive encoding paradigms (Adcock et al., 2006). In doing so, reward cues are incorporated into the encoding paradigm where the reward cue preceding the target indicates the reward for correctly remembering the target in a subsequent memory assessment. Results from this and others studies indicated better memory for high- compared to low-reward targets (Adcock et al., 2006; Gruber et al., 2013; Gruber & Otten, 2010; Murty et al., 2017; Wolosin et al., 2012). Likewise, in the context of incidental encoding, items studied in the context of high- compared to low- (or the absence of) reward are preferably encoded (Bunzeck et al., 2010, 2012; Gruber et al., 2016; Murayama & Kitagami, 2014; Murty & Adcock, 2014; Patil et al., 2017; Stanek et al., 2019; Wittmann et al., 2008, 2011). For instance, pictures whose category (living vs. man-made objects) predicted that an upcoming trial of a numerical reaction time task would be rewarded or not, were better remembered (using item- and source memory measurements) than pictures predicting a neutral trial (Wittmann et al., 2005).

In the absence of novelty, dopamine release is not triggered by the HPC and the downward arc of the HPC-VTA/SN loop, but rather by direct sensory input from the superior colliculus as a response to the rewarding stimuli (May et al., 2009; Redgrave et al., 2010; Takakuwa et al., 2017). It is hence even more intriguing that, when investigating the neural underpinnings of the effects, it has been found that reward-motivated learning is supported by activity in the VTA/SN and HPC as well as FC between both (Adcock et al., 2006; Wittmann et al., 2005; Wolosin et al., 2012) – the same areas as implicated during learning in the context of novelty (Wittmann et al., 2007). A further similarity to novelty is that the release of dopamine in the context of extrinsic rewards is also associated with a penumbra. In a clever study, Murayama and Kitagami (2014) examined whether monetary rewards would also cause a retrograde

memory enhancement by presenting images followed by cues that would indicate whether an upcoming, unrelated task would be rewarded. They found a post-encoding reward effect on memory where images were better encoded if the cue for the unrelated task indicated increased memory performances for images followed by irrelevant reward cues. However, this retroactive effect might be limited and selectively only enhance encoding of related items (Patil et al., 2017). In both paradigms, memory for unrelated information presented before the reward cue was enhanced, thereby showing that also the release of dopamine in the context of reward is associated with a penumbra enhancing the encoding of information around the time point of reward.

In addition to such automated processes that lead to an increased encoding of valuable information supported by the HPC-VTA/SN loop, more strategic processes to engage in deeper semantic processing of the information can be identified (M. S. Cohen et al., 2017; Knowlton & Castel, 2022). Especially in intentional encoding paradigms where higher value (e.g., in the form of points or monetary bonus payments) is assigned to the successful encoding of some items, participants might focus on the encoding of high-value items while avoiding the encoding of low-value items (M. S. Cohen et al., 2014; Murty et al., 2017; Patil et al., 2017). To support the effective encoding of high-value information, different strategies might be used, for instance, by investing more time, building associations, or using mental imagery that are likely to be monitored meta-cognitively (Knowlton & Castel, 2022). Neuronally, strategic learning of valuable information (i.e., word lists) were linked to increased activity in the left inferior frontal gyrus (IFG) and posterior middle temporal gyrus, areas associated with semantic processing (M. S. Cohen et al., 2017). When using images, higher activation in frontoparietal and lateral occipitotemporal cortices was associated with the successful encoding of high-value images and strategic memory control affected activity in the posterior parietal cortex (M. S. Cohen et al., 2019).

Curiosity-Motivated Learning

Single-cell recordings revealed that the same dopaminergic neurons fire not only in the context of upcoming extrinsic rewards but in situations involving information (Bromberg-Martin & Hikosaka, 2009). Likewise, humans actively engage in non-instrumental information-seeking (Kobayashi et al., 2019; van Lieshout et al., 2021) and are willing to invest small costs to receive information (Bennett et al., 2016; Brydevall et al., 2018; Kang et al., 2009; Kobayashi & Hsu, 2019; Marvin & Shohamy, 2016; van Lieshout et al., 2018). Humans still seek information despite the risk of receiving an electric shock (Lau et al., 2020), or experiencing negative emotions like regret (FitzGibbon et al., 2021). These observations have led researchers to propose that information is a reward (Marvin & Shohamy, 2016) and can function as a motivationally salient incentive (FitzGibbon et al., 2020) triggering a strong motivational urge (Lau et al., 2020) also known as the subjective feeling of “wanting” (Berridge, 2004). Indeed, research suggests that the subjective value of information and basic extrinsic rewards share a

common neural code expressed in the striatum and ventromedial prefrontal cortex (Kobayashi & Hsu, 2019) and participants are willing to take the same risks for information primary and information rewards and both are signalled by similar patterns of brain activation within the reward network (Lau et al., 2020). Taken together, these results suggest that non-instrumental information in and of its own can have rewarding properties and influence behaviour.

This intrinsic desire for information observed in studies on information-seeking is often referred to as curiosity (Blanchard et al., 2015; Gottlieb et al., 2013; Kidd & Hayden, 2015), but some might also refer to it as interest or interestingness (e.g., Fastrich et al., 2018; Murayama & Kuhbandner, 2011). In fact, researchers often use both terms interchangeably or strategically only use one of them, most likely because no agreed-upon definitions for these concepts have been found yet (Murayama, FitzGibbon, et al., 2019), despite their similarities and differences being discussed (e.g., Grossnickle, 2016). However, curiosity and interest are also naïve labels that are used in everyday life to describe distinct subjective feelings associated with the components of the same process of autonomous knowledge acquisition within a reward-learning framework rather than distinct processes with *a priori* defining characteristics (Aslan et al., 2021; Donnellan et al., 2022; Murayama, FitzGibbon, et al., 2019). The framework suggests that knowledge acquisition constitutes a process where information-seeking is initiated to reduce a state of uncertainty associated with a perceived gap in one's knowledge (see also Loewenstein, 1994) and the acquisition of knowledge to close said gap is associated with a subjective, rewarding feeling. Both motivational components (i.e., the state of uncertainty related to the awareness of knowledge gaps and the rewarding experience associated with knowledge acquisition) are likely accompanied by specific neural and psychological processes. Importantly though, both components are assumed to contribute to knowledge acquisition and hence, learning.

In fact, the component associated with a state of uncertainty due to the awareness of knowledge gaps – which we will refer to as subjective feeling of curiosity hereafter to increase readability in alignment with previous work (Fandakova & Gruber, 2021; Gruber & Ranganath, 2019; McGillivray et al., 2015) – has been shown to facilitate memory encoding (for recent reviews, see Gruber et al., 2019; Gruber & Ranganath, 2019). More specifically, the subjective feeling of curiosity elicited by a cue (i.e., a trivia question; cf. Jepma et al., 2012) facilitates the intentional encoding (Duan et al., 2020; Halamish et al., 2019) of the target item (i.e., the answer to trivia question; cf. Jepma et al., 2012), but the same curiosity effects have also been found in incidental encoding paradigms after short (Brod & Breitwieser, 2019; Galli et al., 2018; Gruber et al., 2014; Jepma et al., 2012; Ligneul et al., 2018; Mullaney et al., 2014; Murphy, Dehmelt, et al., 2021; Poh et al., 2021; Stare et al., 2018) and long (Fastrich et al., 2018; Gruber et al., 2014; Kang et al., 2009; Marvin & Shohamy, 2016; Murayama & Kuhbandner, 2011; Stare et al., 2018; Swirsky et al., 2021) delays between encoding and retrieval. Similar as observed for learning

in the context of novelty and rewards, the information presented around the elicitation of curiosity is better encoded. More specifically, unrelated, irrelevant information presented between curiosity-eliciting cue and target information is more likely to be encoded if presented in a state of high compared to low curiosity and close temporal proximity to the cue (Galli et al., 2018; Gruber et al., 2014; Murphy, Dehmelt, et al., 2021; Stare et al., 2018). This penumbra effect suggests that the effects of curiosity on encoding could also be dopaminergic in nature: incidental information presented after a cue eliciting a strong feeling of curiosity (hence, a dopaminergic response; Bromberg-Martin & Hikosaka, 2009; Gruber et al., 2014) is preferably encoded because it was presented within the penumbra of dopamine (Miendlarzewska et al., 2016). Therefore, the incidental information (that would have only given rise to a short-lasting memory) received a behavioural tag that led to its encoding as a longer-lasting memory due to the dopamine-related catalysation of protein synthesis during late LTP (Moncada et al., 2015).

Indeed, fMRI studies in humans support such a dopaminergic account of curiosity. Examining the neural underpinnings of states of curiosity, Kang and colleagues (2009) found increased activation during the elicitation of high- compared to low-curiosity states (i.e., brain activity with the cue/trivia question) in the left caudate nucleus, as well as in the bilateral PFC including the inferior frontal gyrus (IFG) and parahippocampal gyri. More specifically, the activity in the left caudate nucleus and bilateral IFG also increased linearly with increasing curiosity ratings. Extending these findings, Gruber and colleagues (2014) found that activity in the NAcc and the VTA/SN, but also more general in the dorsal and ventral striatum, as well as the left IFG, left superior medial gyrus and the cerebellum during curiosity elicitation (i.e., cue/trivia question presentation) linearly increased with increasing curiosity ratings. The activity in the striatum and the dopaminergic midbrain (VTA/SN) – both central parts of the reward network in the brain (Haber & Knutson, 2010) – was interpreted as curiosity being linked to the anticipation of information whose delivery is rewarding, consistent with the information gap hypothesis of curiosity (Loewenstein, 1994), and analogue to the anticipation of extrinsic rewards (Knutson, Adams, et al., 2001; Knutson et al., 2000; Murty & Adcock, 2014; Schott et al., 2008).

Further shedding a light onto the brain mechanisms behavioural memory-enhancing effect of curiosity, Gruber and colleagues (2014) also investigated whether brain activity during curiosity elicitation at cue presentation (i.e., the trivia question) predicts later memory for the upcoming target information (i.e., the answer to the trivia question). They found that while the dopaminergic midbrain was more activated during the anticipation of later remembered compared to later forgotten targets irrespective of the degree of curiosity elicitation, the right HPC and the bilateral NAcc showed increased activation for remembered compared to forgotten targets only for high-, but not low-curiosity cues. Activity in the left HPC during curiosity elicitation (i.e., cue/trivia question presentation) was larger during successful compared to the unsuccessful encoding of incidental information that was presented

within the temporal proximity of the curiosity-eliciting cue but was semantically unrelated in nature. However, this was not further influenced by the current curiosity state. Yet, a strong correlation was found between the curiosity-driven memory benefit for incidental information and the curiosity-related subsequent memory effects in the VTA/SN and the HPC as well as the FC between both during high, but not during low curiosity trials.

A recent re-analysis of the same dataset (Murphy, Ranganath, et al., 2021) showed that high compared to low states of curiosity are further accompanied by increased activity in the frontoparietal and default mode network that also support the effects of curiosity on memory. It was further shown that during the elicitation of curiosity (i.e., when the curiosity-eliciting cue question was presented), the memory-facilitating effects of curiosity are supported by subcortical FC between HPC and VTA/SN, but also by cortical FC between frontoparietal and default mode networks. When curiosity is relieved (i.e., when the curiosity-satisfying target information was presented), the effects of curiosity on encoding are supported by cortical FC between frontoparietal and default mode networks as well as by cortico-subcortical FC between HPC and the default mode network. As such, the re-analysis shows that states of curiosity in the HPC-VTA/SN loop communicate with higher-order cortices to support the effects of curiosity on memory.

Poh and colleagues (2021) provide a mechanism for the memory benefits of curiosity during the anticipation phase, i.e., in the delay interval between cue and target presentation, testing the premise that hippocampal anticipatory states are linked to activity in the VTA. Using univariate analysis, they found that higher states of curiosity are associated with increased activity in the VTA, but not the HPC, during the anticipation period following cue presentation. Greater activity in the VTA was associated with a greater likelihood of recall regardless of curiosity states. However, the main interest of the authors was the hippocampal “convergence state” during the anticipation of the target information. The convergence state represents an optimal subspace of the HPC for subsequent learning during which multiple cognitive and physiological factors converge. The authors reasoned that if the hippocampal state in the anticipatory phase at any given trial is more similar to the average HPC state, it shows higher convergence and less variability, assuming that any variability from the average state represents a deviation from the optimal subspace for learning. Indeed, they found that high states of curiosity are associated with greater HPC convergence compared to low states of curiosity and higher convergence was associated with a higher likelihood of later recall, even after controlling for univariate HPC activity. Crucially, univariate activity in the VTA predicted convergence in the HPC: greater VTA activity was associated with greater convergence, i.e., more closeness to the optimal subspace, even after accounting for univariate HPC activity. Mediation analysis further revealed that the effects of VTA activity on encoding are mediated by hippocampal convergence. As such, curiosity supports encoding by increased activity in the dopaminergic

midbrain that switches the HPC into an optimal encoding state. Taken together, fMRI studies on the effects of curiosity on encoding suggest that anticipatory activity in the mesolimbic dopaminergic circuit supports the learning benefits associated with high compared to low states of curiosity, potentially by neuromodulatory influences on the hippocampal convergence state as well as by recruiting higher-order cortices.

Overall, the influence of curiosity on learning has been summarised within the recently proposed Prediction-Appraisal-Curiosity-Encoding (PACE) framework (Gruber & Ranganath, 2019). According to this framework, the effects can be understood as a cycle at the start of which curiosity is elicited by PEs that are either context-based due to novelty/surprise (signalled by HPC) or information-based after the detection of a knowledge gap (signalled by anterior cingulate cortex). PEs trigger an appraisal process (supported by the lateral PFC) on the basis of which further actions and underlying mechanisms are determined: uncertainty associated with the PE might induce anxiety and anxiety-related amygdalar processes leading to inhibition, or alternatively elicit curiosity and related dopaminergic processes manifesting in exploration. In the latter case, curiosity facilitates learning by enhanced attentional processes during information-seeking and retention via enhanced memory consolidation. If uncertainty is resolved and the information gap is closed, the cycle is completed. However, similar to the reward-learning framework of knowledge acquisition (Murayama, FitzGibbon, et al., 2019), the PACE framework also states that initial satisfaction of curiosity might elicit further PE starting a new PACE cycle. As such, the PACE framework can be seen as an extension providing a more neuroscientific account of knowledge acquisition.

Similarities and Differences Between Extrinsically and Curiosity-Motivated Learning

In human fMRI, VTA/SN activation was found in the context of extrinsic rewards (Aberg et al., 2020; Wolosin et al., 2012) and epistemic curiosity (Gruber et al., 2014; Poh et al., 2021). In line with the prediction that stimuli eliciting a dopaminergic response in the VTA/SN are preferably encoded due to dopaminergic effects on late LTP in HPC synapses, memory-enhancing effects of both extrinsic rewards/incentives and curiosity have been found (for reviews, see Gruber & Ranganath, 2019; Miendlarzewska et al., 2016). When investigating the neural underpinnings of these effects, it has been found that both reward- and curiosity-motivated learning are supported by activity in the VTA/SN and HPC as well as FC between both (Adcock et al., 2006; Gruber et al., 2014; Murphy, Ranganath, et al., 2021; Poh et al., 2021; Wittmann et al., 2005; Wolosin et al., 2012). Importantly, the effects of motivation on encoding are predominantly located in the aHPC in alignment with the specialisation of the HPC along the longitudinal axis discussed above (Poppenk et al., 2013) and with findings in rodents (Fanselow & Dong, 2010).

Collectively, the literature suggests that information as an intrinsic reward with incentive salience associated with wanting the information and a post-reward hedonistic component of liking impacts information seeking in a way that is similar to extrinsic rewards. Moreover, the anticipation of information is signalled by the same areas in the reward network as observed for extrinsic rewards. This anticipatory activity during cue presentation has been further shown to promote memory formation of information presented in high-curiosity and high-reward states alike via dopaminergic projections within the mesolimbic pathway often referred to as the HPC-VTA/SN loop (Lisman & Grace, 2005). This puts forward the interpretation that both extrinsic and intrinsic rewards are processed within the reward network, indicating a shared mechanism to produce motivated behaviour in general and influence cognition including the promotion of learning (“commonality view”; Murayama, 2019).

While this summary suggests that extrinsically and curiosity-motivated learning are characterised by overlapping behavioural and neural effects, the effects of monetary rewards and, more recently, curiosity have been studied in isolation and only a very small number of studies have actually looked at their conjunction. However, examining both effects in the same study is necessary to conclude that they indeed share similarities and neural mechanisms in how they benefit learning. This would not only inform research in psychology and neuroscience but is also of utter relevance for applied disciplines including, but not limited to, educational (and clinical) fields. More specifically, an understanding of how extrinsic rewards and curiosity interact could inform general teaching practices. Recommendations would be very different if the effects of intrinsic rewards were larger in the presence of extrinsic incentives, compared to a situation where extrinsic incentives would actually decrease the impact of intrinsic rewards. The former case would imply that the effects are additive and hence likely to be supported by independent neural systems, whereas the latter conforms with the proposal that curiosity and monetary rewards/incentives influence encoding using a common neural mechanism and are hence sub-additive (Halamish et al., 2019). In fact, it has repeatedly been shown that extrinsic rewards can undermine intrinsic motivation (Deci et al., 1999; cf., Goswami & Urminsky, 2017) manifesting in less voluntary task engagement and a decrease in activity in the anterior striatum (Murayama et al., 2010). This further aligns with the idea that intrinsic and extrinsic rewards are integrated and rely on the same system.

Despite the importance of the topic, it has received surprisingly little attention and to the best of our knowledge, only four studies have looked at the effects of both curiosity and monetary rewards/incentives on encoding. When participants were presented with curiosity-inducing cues (i.e., trivia questions) and corresponding targets (i.e., answers to trivia questions) some of which are “bonus cues” allowing them to earn money upon retrieval of the associated target a week later, both curiosity and monetary reward facilitate delayed recall, however, no interaction between them was found indicating that both rewards increase memory independently in an additive manner, and therefore, potentially

relying on different neural systems (Duan et al., 2020; Halamish et al., 2019). Indeed, brain activity during this paradigm showed that curiosity-driven intentional learning relies on fronto-parietal networks during elicitation (i.e., cue/trivia question presentation) and the reward network during relief (i.e., target/answer presentation) whereas monetary reward effects were located in the reward network during cue presentation, but during target presentation, a down-regulation of irrelevant areas (precuneus and postcentral gyrus) was found to support reward-driven intentional learning (Duan et al., 2020).

These results are somewhat contrasting compared to the literature reviewed above studying both effects in isolation implying both facilitate encoding using a shared mechanism. However, it is possible that no interaction between curiosity and reward was observed because they operate at different stages of memory formation (i.e., curiosity during encoding; reward during successful retrieval). In fact, in an incidental memory paradigm where participants were rewarded for correctly guessing the target (i.e., answer to the trivia question) upon cue presentation (i.e., trivia questions) during encoding, Murayama and Kuhbandner (2011) found that both monetary reward and the interestingness of the cue (as rated by a separate sample) had an enhancing effect on encoding, but the main effects were further qualified by an interaction where monetary rewards only enhanced encoding of cues rated as not interesting. The authors interpreted these findings in light of the undermining effect: for interesting items, monetary rewards undermine the effect of intrinsic value leading to a decreased memory performance; however, this effect was potentially counteracted by facilitating effects of memory on encoding (irrespective of their intrinsic value) producing an overall null effect for items with high intrinsic value.

While obtaining ratings of the intrinsic value of the cue from a separate sample is not ideal given the high within-person variances in experiencing curiosity (Fastrich et al., 2018; Ozono et al., 2021), the main and interaction effects of monetary reward and curiosity have recently been replicated when measuring curiosity and its effect on curiosity in the same sample (Swirsky et al., 2021). Taken together, the results suggest that in incidental learning – where effects of curiosity and reward both operate during encoding – the effects are sub-additive and hence, potentially share the same neural mechanisms; nonetheless, this has not empirically been tested yet. On the other hand, temporal contingencies of the behavioural effects of extrinsically and curiosity-motivated learning suggest differential underlying mechanisms, pointing towards additive effects. More specifically, in the context of extrinsically motivated learning, effects of reward on encoding are often only found after long, but not short delays between encoding and memory test (Murayama & Kitagami, 2014; Murayama & Kuhbandner, 2011; Patil et al., 2017; Wittmann et al., 2005). In the context of curiosity, on the other hand, memory-facilitation effects have been found to be independent of delay (Stare et al., 2018). As such, more research is needed to understand the interaction between curiosity and extrinsic rewards/incentives in the context of memory encoding.

Limitations in Paradigms Investigating the Effects of Curiosity on Memory

As indicated above, memory effects are examined using pairings between a cue and a target item, where the cue is used to elicit curiosity and the encoding of the target is later tested. Blurred pictures have been used to elicit perceptual curiosity (i.e., curiosity related to sensory stimuli like ambiguous images; Berlyne, 1954) while the encoding of the later presented clear picture was tested (Jepma et al., 2012). To look at epistemic curiosity (i.e., curiosity related to conceptual stimuli like knowledge questions; Berlyne, 1954), trivia questions are used to elicit curiosity and to test the effect on the encoding of the later presented answer (Gruber & Ranganath, 2019). In fact, previous literature has referred to trivia questions and their answers as a “learning list” (Stare et al., 2018, p. 103) or “cue-target pairs” (Fastrich et al., 2018, p. 229) and converging effects have been found using trivia question-answer pairs and word pairs as stimuli in memory tests (Kornell et al., 2009).

Use of reductionist stimuli. An important constraint in the nascent research on curiosity and its effect on memory encoding lies in the nature of the stimuli used to investigate the effects. While there are benefits in investigating the effects of curiosity on memory in a similar manner to classical memory research in cognitive science as this makes effects comparable and relatable, this method also shares the general limitation: the overall reductionist approach. When investigating encoding, research often relies on discrete, static elements lacking the complex, contextual and narrative nature of everyday events (Shamay-Tsoory & Mendelsohn, 2019). As such, images or word lists are often used (Kim, 2011), but they bear little resemblance to the continuous stream of perception and events that real-life cognition entails contributing to the dilemma between the real world or laboratory, often (falsely) referred to as ecological validity (Holleman et al., 2020; Kihlstrom, 2021; cf., Shamay-Tsoory & Mendelsohn, 2019). However, to use the research on curiosity and memory to guide policy-making and make recommendations for teachers, it is vital to translate laboratory-based findings to applied settings (Gruber et al., 2019; Gruber & Ranganath, 2019). Although cognitive neuroscience relies traditionally upon simple and highly controlled tasks with abstract stimuli to isolate cognitive processes in subtraction-based approaches (Sonkusare et al., 2019), it is possible to increase the degree to which neuroimaging findings translate into real-life by linking neuroimaging measures to real-life variables and follow-up studies, including teachers and other stakeholders at all stages of research, and using portable neuroimaging devices, as well as more naturalistic tasks and stimuli (van Atteveldt et al., 2018). Naturalistic paradigms are “tasks employing any stimulus that demanded continuous, real-time integration of dynamic streams of information” (Bottenhorn et al., 2019, p. 29), whereas naturalistic stimuli are “a class of stimuli to evoke more naturalistic patterns of neural response than traditional controlled artificial stimuli” (Vanderwal et al., 2019, p. 2).

To take the first steps in translating research to real-life settings, neuroscientists are indeed utilising more naturalistic paradigms with more complex, naturalistic stimuli (Sonkusare et al., 2019). For instance, rather than using single images (Brewer et al., 1998) or words (A. D. Wagner et al., 1998), memory research has started to also use dynamic stimuli like episodes of a series and movies (J. Chen et al., 2017; Hasson, Furman, et al., 2008; Kauttonen et al., 2018; Song et al., 2021; van Kesteren et al., 2010) or short video clips (Ben-Yakov & Dudai, 2011; Ren et al., 2018). Research on the effects of curiosity on memory, however, has thus far been relying on fairly simplistic stimuli (i.e., trivia question and answer or blurred and clear images) leaving the open question of whether the effects found can be generalised to other, more complex and dynamic stimuli; although it should be noted that a recent study replicated the effect of (perceptual) curiosity on incidental encoding in a virtual reality environment (Cen et al., 2021).

Research heavily relies on the same material and methods to induce curiosity. In the domain of epistemic curiosity, on the other hand, the majority of studies examining its effect on memory encoding have utilised what is often referred to as the trivia question paradigm (summarised in Table 1.1). In the trivia question paradigm, participants are presented with trivia questions and asked to rate their curiosity about the answer (cf., Murayama & Kuhbandner, 2011 where ratings were obtained by a separate sample) and often also their confidence in knowing the answer before being presented with the answer (Duan et al., 2020; Fandakova & Gruber, 2021; Fastrich et al., 2018; Gruber et al., 2014; Kang et al., 2009; Murphy, Dehmelt, et al., 2021; Poh et al., 2021; Stare et al., 2018; Swirsky et al., 2021). Depending on the study, the curiosity ratings are obtained in a screening session (Duan et al., 2020; Fandakova & Gruber, 2021; Gruber et al., 2014; Murphy, Dehmelt, et al., 2021; Poh et al., 2021; Stare et al., 2018; Swirsky et al., 2021) or during (Brod & Breitwieser, 2019; Fastrich et al., 2018; Galli et al., 2018; Halamish et al., 2019; Kang et al., 2009; Ligneul et al., 2018; McGillivray et al., 2015; Mullaney et al., 2014; Wade & Kidd, 2019) and after (Marvin & Shohamy, 2016) the encoding phase. In part of the experiments, participants are asked to actively make guesses about the correct answers during the encoding phase (Brod & Breitwieser, 2019; Kang et al., 2009; McGillivray et al., 2015; Mullaney et al., 2014; Murayama & Kuhbandner, 2011; Swirsky et al., 2021; Wade & Kidd, 2019). In some designs, incidental information is additionally displayed between the elicitation (i.e., cue) and relief (i.e., target) of curiosity (i.e., faces paired with a judgement task; Fandakova & Gruber, 2021; Galli et al., 2018; Gruber et al., 2014; Murphy, Dehmelt, et al., 2021; Stare et al., 2018; Swirsky et al., 2021). Additional measurements can also be obtained after the answer to the trivia question was presented (prospective curiosity, Duan et al., 2020; interestingness of answer, Fandakova & Gruber, 2021; level of interest when presented with answer, Fastrich et al., 2018; interestingness of answer, Halamish et al., 2019; surprise

level, Ligneul et al., 2018; satisfaction with answer; Marvin & Shohamy, 2016; judgement of learning and interest in piece of information, McGillivray et al., 2015; surprise about answer, Wade & Kidd, 2019).

While the trivia question paradigm has reliably shown that epistemic curiosity during the presentation of the trivia question not only enhances memory for the answer to the trivia question, but also for incidental information presented in between (Gruber & Ranganath, 2019), voices have been raised repeatedly that the generalisability of findings needs to be established using a broader range of materials and manipulation methods to elicit curiosity (Fastrich et al., 2018; Murphy, Dehmelt, et al., 2021). Given the direct implication of research on curiosity on memory encoding for education, it could be beneficial to induce curiosity in the laboratory using more complex, dynamic stimuli to enhance the translation of findings from neuroscience and psychology into real-life settings. Additionally, to be able to study the effect of curiosity across languages and cultures as well as across the developmental trajectory and within clinical populations or people with neurocognitive deficits or learning disabilities, elicitation of curiosity with non-verbal material is needed that can be understood intuitively and has hence greater universal appeal.

Likewise, with respect to different approaches to manipulate curiosity, it should be noted that curiosity is elicited by the detection of a knowledge gap (i.e., information-based PEs; Gruber & Ranganath, 2019) which is perhaps why uncertainty is seen as a major triggering factor (Ozono et al., 2021). However, curiosity can also be elicited in novel environments or when events violate expectations and create a sense of surprise (i.e., context-based PEs; Gruber & Ranganath, 2019). In line with this prediction, surprising events and outcomes violating expectations enhance encoding (Antony et al., 2021; Brod et al., 2018; Stahl & Feigenson, 2015). Likewise, research has shown that novel environments elicit higher curiosity and are associated with higher incidental encoding rates (Cen et al., 2021); that generating predictions stimulates surprise (Brod et al., 2018) and curiosity (Brod & Breitwieser, 2019); and that the effect of cognitive incongruity on exploratory behaviour is mediated by surprise and curiosity where surprise predicts curiosity (Vogl et al., 2019). However, the role of violation of expectations and surprise in relation to curiosity and its effect on memory encoding has been relatively under-examined (Ozono et al., 2021).

Elicitation of curiosity is confounded with the anticipation of rewarding information. A further constraint in how curiosity within the trivia question paradigm is elicited to measure its effect on encoding is in most cases, the elicitation of curiosity (i.e., presentation of the trivia question as cue) is inherently confounded with the anticipation of rewarding information (i.e., presentation of the answer to the trivia question as target). More specifically, in the trivia question paradigm, the answer is usually presented in all trials (100% certain outcome, see Figure 1.1 (A); cf., Ligneul et al., 2018) to be tested in subsequent memory assessments. However, this limits the scope of how teachers could use the insights on

the effects of curiosity on memory to the recommendations for using question-answer methods to impart knowledge. Moreover, we think this does not really portray everyday curiosity and knowledge acquisition as (a) information-seeking is not limited to explicit, visible behaviour but can include more internal processes (e.g., mental sense-making; Murayama, FitzGibbon, et al., 2019) and (b) information-seeking does not relieve curiosity with certainty. Most academics can probably relate to a situation where they have become aware of a lack of knowledge regarding a specific question (i.e., elicitation of curiosity) and even engaged in a literature search (i.e., information-seeking), yet were unable to find the answer (i.e., no knowledge acquired and curiosity not relieved). We would argue even in the absence of relief, curiosity was experienced (as defined by the awareness of a knowledge gap and an associated state of uncertainty) which could have impacted learning. However, insights from the trivia question paradigm are applicable here only to a limited extent because curiosity is predictably relieved.

In fact, very little is known about the effects of curiosity on memory if detached from the anticipation of information. The arguments presented above comparing the trivia question paradigm with cue-target pairings in the context of memory research also apply in the context of reward research. In fact, when investigating the effects of monetary reward on encoding, paradigms often rely on the presentation of a certain cue (directly or indirectly indicating the amount of reward) followed by a target that is later used in a subsequent memory test (Adcock et al., 2006; Gruber et al., 2016; Gruber & Otten, 2010; Murty & Adcock, 2014; Stanek et al., 2019). As such, these studies are looking at pre-encoding processes, i.e., processes that occur prior to encoding (N. Cohen et al., 2015). This bears striking similarities to the trivia question paradigm where the trivia question cues an anticipated value (curiosity ratings could be a proxy to estimate this intrinsic value) whereas the trivia answer as a target is the certain delivery thereof. It is hence possible that the similarities between curiosity- and reward-motivated learning are partly caused by the overlap between the paradigms related to the anticipation of the certain delivery of targets.

More specifically, results by Kang et al (2009) and Gruber et al (2014) have both implied that dopaminergic structures in the striatum and midbrain linearly increase their activation as curiosity increases; Gruber and colleagues (2014) have further linked activity in the striatum and midbrain during elicitation to the curiosity-driven benefit of the encoding of the answer in the absence of such effects during the answer presentation. The authors concluded that curiosity-driven memory benefits are supported by neural mechanisms during the anticipation rather than the relief of curiosity, i.e., the reception of rewarding information. However, when rewards are expected and delivered at 100% contingency, there is no discrepancy between expected and actual reward outcomes leading to a reward PE of zero. In that case, as described earlier, dopamine neurons coding reward PE transfer from signalling the delivery of rewards to signalling reward-predicting stimuli (Knutson, Adams, et al., 2001; Schultz, 1998; Tobler et al., 2005). Among other regions, these indifferent PE signals have been found in the

ventral striatum (O'Doherty et al., 2003). Due to the full predictability of outcomes (i.e., answer to trivia question always delivered with no jitter between trivia question and answer presentation) in the trivia question paradigm in general and specifically, in the designs used by Kang et al (2009) and Gruber et al (2014), the PE signal is likely to be zero and neural effects that could have been associated with the receipt of the target were migrated towards to predictive cue (see Figure 1.1A). Critically, when a jitter is used to separate neural activation in response to the elicitation of curiosity and the anticipation of the answer (delivered at 100% of trials), the elicitation of curiosity (i.e., question presentation) was not associated with dopaminergic activity, but subsequent memory effect modulated by curiosity was supported by striatal activity during the relief of curiosity (i.e., presentation of the answer to the trivia question; Duan et al., 2020). Likewise, in a version of the trivia question paradigm where the answer to the trivia question was only presented in half of the trials (i.e., 50% relief/delivery), the activity in the ventral striatum was not modulated by curiosity during the question presentation, but only during the answer presentation and only if the delivery is stochastic (Ligneul et al., 2018). The involvement of the ventral striatum in a stochastic manner was further supported by Jepma and colleagues (2012) when perceptual curiosity was relieved in only half of the trials as well as by Lau and colleagues (2020) using different curiosity arousing stimuli in a gamble where accepting and winning the gamble increased the likelihood of the curiosity relief at the end of the experiment. Taken together, these considerations suggest that the trivia question paradigm might lead to a premature conclusion about the neural underpinnings and behavioural effects on memory of the elicitation of curiosity as it is confounded with the anticipation of rewarding information.

Additional factors and processes enhancing memory formation for target information.

Within the trivia question paradigm, the primary dependent variable of interest is recall performance, a measurement of recollection. In paradigms that present incidental information in between elicitation and relief of curiosity, the encoding of the incidental information is predominantly tested using recognition memory tests with old/new combined with confidence judgements (Fandakova & Gruber, 2021; Gruber et al., 2014; Stare et al., 2018), remember/know judgements (Galli et al., 2018) or a combination thereof (Murphy, Dehmelt, et al., 2021; Swirsky et al., 2021). While it is assumed that recollection underlies correct responses in the free recall of answers to trivia questions, the recognition of incidental faces could be supported by both recollection and familiarity (Yonelinas, 2002). While more research is needed to determine the influence of curiosity on familiarity and recollection-based encoding processes, the trivia question paradigm might only offer limited answers. This is partly due to the fact that answers and incidental faces are most likely associated with different processes as one of them represented cued target information and the other incidental information. So could it be that curiosity effects only emerged in recollection-based recognition in the context of incidental information, but that curiosity affects

recollection and familiarity in the encoding of target information. However, with the current version of the trivia question paradigm, only recollection-based memory encoding of target information can be quantified, highlighting its limitation to investigate the dissociation of memory.

A closely related limitation with respect to recall of trivia answers is that what is tested in the memory tests is what satisfied/relieved the curiosity (i.e., answers to trivia questions or targets) rather than what elicited curiosity (i.e., trivia questions or cues). However, the answer presentation in and of itself could evoke memory-enhancing processes on its own merit that might be partly or fully independent from the curiosity manipulation itself (see Figure 1.1B). So could it be that especially in paradigms where participants are encouraged or asked to guess the correct answer, the retrieval attempt itself could enhance subsequent learning, even if unsuccessful (Kornell et al., 2009). Furthermore, research has demonstrated that generating a prediction (as done when guessing) enhances encoding and that surprise-related pupillary responses differentiating between outcomes consistent with or violating expectations only occur after predictions, but not in the context of postdictions (Brod et al., 2018). While speculative, one could assume that this could be confounded with curiosity where higher curiosity leads to more effortful retrieval attempts and guessing as a form of information-seeking. After guessing, the anticipation of feedback about the guess, especially if delayed, increases encoding (Carpenter & Vul, 2011) and this delay-of-feedback benefit interacts with curiosity such that it is more likely to occur in the context of high compared to low states of curiosity (Mullaney et al., 2014).

The presentation of the answer itself might further have an impact on its later encoding and guessing might be an important factor here as well. While Kang and colleagues (2009) reported that correct guesses are better remembered, later research often excluded questions after the screening phase if the confidence in knowing the answer exceeded a certain threshold (Gruber et al., 2014; Murphy, Dehmelt, et al., 2021; Poh et al., 2021; Stare et al., 2018) or if participants indicate that they know the answer (Marvin & Shohamy, 2016), or removed trials from the analysis if the participant guessed correctly in the learning phase (Brod & Breiwieser, 2019; Fastrich et al., 2018; McGillivray et al., 2015; Mullaney et al., 2014; Murayama & Kuhbandner, 2011; Swirsky et al., 2021; Wade & Kidd, 2019). Yet, it has been demonstrated that confidence in knowing the answer positively predicts the encoding of the actual answer (Duan et al., 2020; Fastrich et al., 2018; McGillivray et al., 2015) and that answers with high compared to low confidence in knowing are better encoded (Stare et al., 2018). This is in line with previous research showing that high-confidence errors (here, incorrect guesses made despite high confidence in knowing the answer) promote learning, potentially the correct answer is perceived as unexpected and surprising and is hence assigned attentional priority (Butterfield & Metcalfe, 2001, 2006). This “hyper-correction effect” (Butler et al., 2011) could be supported by increased activity in the putamen and left IFG during the presentation of answers following incorrect compared to correct guesses.

Moreover, activity during incorrect guesses in the left parahippocampal gyrus and left IFG as well as HPC and midbrain linearly increased with curiosity (Kang et al., 2009), areas well known for their role in encoding (Brewer et al., 1998; A. D. Wagner et al., 1998).

Taken together with behavioural results showing that confidence in knowing the answers and curiosity are interrelated (Fastrich et al., 2018; Kang et al., 2009; McGillivray et al., 2015; Stare et al., 2018; Wade & Kidd, 2019), this implies that curiosity and confidence in knowing the answer – often seen as a proxy for prior knowledge – not only independently facilitate learning (Brod et al., 2013; Gruber & Ranganath, 2019; van Kesteren et al., 2010), but are intertwined in their effect on memory. In fact, a recent study showed preliminary evidence for such bi-directional effects: In a modified version of the trivia question, curiosity was predicted by the learner’s metacognitive estimate of their prior knowledge and learning, on the other hand, was predicted by curiosity together with an objective measure of the learner’s prior knowledge (but not by the learner’s metacognitive estimate), rendering the effect of curiosity small once objective prior knowledge is accounted for (Wade & Kidd, 2019). These bi-directional relationships also support predictions from the reward-learning framework of autonomous knowledge acquisition (Murayama, FitzGibbon, et al., 2019) of a positive feedback loop where an extended knowledge base facilitates the awareness of further knowledge gaps sparking curiosity. It is worth noting that previous studies mainly used a meta-cognitive judgement (related to the confidence in the own guess or in knowing the answer) as a proxy of prior knowledge and found that the effects of curiosity on memory remain, while only a small percentage of variance in the curiosity effect on memory can be accounted for by the effect of prior knowledge (Stare et al., 2018). Wade and Kidd (2019) also included such a measurement, but additionally recorded the initial guess and had its similarity to the correct answer rated by independent raters to create an objective measurement of prior knowledge. While the meta-cognitive judgement of prior knowledge only showed marginal effects of learning, objective prior knowledge substantially predicted learning. However, objective knowledge is often not assessed within the trivia question paradigm, so analysis cannot control for its effect. In fact, it seems that within the trivia question paradigm prior knowledge (even if only partial), curiosity, and memory are inherently confounded (Fastrich et al., 2018). This feeling of knowing in the context of partial prior knowledge, often referred to as the “tip of the tongue phenomenon”, evokes curiosity (Metcalf et al., 2017), facilitates encoding (Bloom et al., 2018), and activates the ventral striatum (Ligneul et al., 2018). The confoundedness of the effects of prior knowledge, curiosity, and learning on a neural level is further supported by the proposal that the lateral PFC is not only implicated in the appraisal of the information within a PACE cycle, but also contributes to the effects of prior knowledge on memory (Brod et al., 2013), and its response to incorrect guesses is modulated by curiosity (Kang et al., 2009).

Lastly, as stated in the reward-learning framework of knowledge acquisition (Murayama, FitzGibbon, et al., 2019), the acquisition of knowledge itself is associated with a feeling of reward where the magnitude is depending on the magnitude of uncertainty reduction and the value signal related to the newly acquired knowledge (Murayama, FitzGibbon, et al., 2019). In fact, during the presentation and processing of the answer to the trivia question, activity in the reward network has been observed (Duan et al., 2020; Ligneul et al., 2018) that can account for unique proportions of variance in addition to activity during the trivia question presentation (Poh et al., 2021). This can be linked to the information-as-reward hypothesis: Marvin and Shohamy (2016) had participants rate their curiosity about the question and satisfaction with the answer. These values were used to calculate an information PE as the difference between the actual value of information received (satisfaction) and the anticipated value of information (curiosity). Using information PE and curiosity to predict encoding, they found that both increased the likelihood of correctly recalling an item where participants were more likely to remember information for which satisfaction was greater than curiosity. Taken together, this suggests that the relief of curiosity during target presentation (i.e., the answer to the trivia question) has rewarding properties whose magnitude depends on the target information and can influence its encoding.

Later research (Fandakova & Gruber, 2021; Fastrich et al., 2018; Halamish et al., 2019; McGillivray et al., 2015) tried to further disentangle the processes related to curiosity (i.e., the state of uncertainty in relation to the awareness of a knowledge gap) from the rewarding component associated with the acquisition of new knowledge within the trivia question paradigm. In these studies, this component is referred to as “interest”; we will use this term hereafter to support consistency and readability. Firstly, it was found that the interest ratings are higher for high curiosity compared to low curiosity questions (Halamish et al., 2019) and that curiosity and interest are highly correlated (Fandakova & Gruber, 2021; Fastrich et al., 2018; Halamish et al., 2019; McGillivray et al., 2015). Secondly, the effects of curiosity and information PE on encoding were replicated when information PE was calculated as the difference between interest and curiosity (Fandakova & Gruber, 2021; Fastrich et al., 2018). Thirdly, results regarding the effects of interest and curiosity on encoding when included in the same model are mixed. While some found a significant interaction between them where the effect of interest was especially strong in the context of low curiosity (Fandakova & Gruber, 2021), others found that only interest, but not curiosity predicted encoding (McGillivray et al., 2015). Results from structural equation models indicate that while curiosity had an indirect mediated positive effect on recall via interest and interest had a positive effect on recall, there is less evidence supporting a direct, unmediated effect of curiosity on recall as results differ across experiments (Fastrich et al., 2018; Halamish et al., 2019). Lastly, Fastrich and colleagues (2018) also found that the positive effect of confidence in knowing the answer on encoding discussed above can partly be explained by increased interest in the answer.

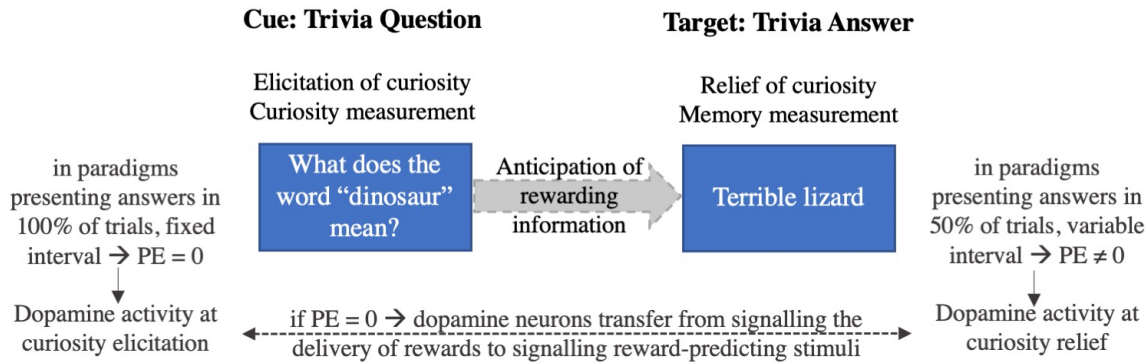
In addition to sparking interest, the acquisition of knowledge likely also leads to the experience of other epistemic emotions. Epistemic emotions (e.g., surprise, boredom, confusion) are a group of various emotions closely related to knowledge and the generation thereof and can be aroused by discrepant information and cognitive incongruity (Pekrun et al., 2017). Such cognitive incongruity could also stem from high-confidence errors discussed above (Vogl et al., 2019). Similar to interest, it seems reasonable that any epistemic emotion could have an impact on encoding. For instance, Ligneul and colleagues (2018) investigated the role of surprise triggered by the answers in the trivia question paradigm, highlighting that while both are positively associated with recall, surprise and curiosity are not only correlated with one another but also mediate each other's influence on memory encoding. However, while the influence of curiosity is partly captured by surprise, the effect of curiosity was only significant in the context of low surprise. Also, similar to the context of interest, prior knowledge seems to influence surprise in a way that prior knowledge is associated with higher ratings of surprise.

While more research is needed to understand the exact processes, the literature reviewed here clearly indicates an interplay between curiosity, interest, and other epistemic emotions in their effects on encoding, where distal processes associated with the feeling of curiosity predict more proximal processes associated with interest and other epistemic emotion that predict encoding in their own merit. In fact, a recent re-analysis of the fMRI data from Gruber et al (2014) showed that cortical regions in the default mode and fronto-parietal networks support curiosity-motivated learning, but are indifferent to the time point (i.e., curiosity elicitation compared to its relief; Murphy, Ranganath, et al., 2021). This evidence supports the claim that curiosity not only has a direct influence on encoding but that the influence of curiosity on encoding is mediated by processes upon acquisition of knowledge potentially causing neural effects of curiosity on learning observable at elicitation and satisfaction. However, according to the reward-learning framework of knowledge acquisition (Murayama, FitzGibbon, et al., 2019), these are distinct components. Within the trivia question paradigm – at least in the way most commonly used – these components are inherently intertwined because a cue is used to quantify and elicit curiosity whereas the target is used to measure the effect on encoding. Collectively, this shows that within the trivia paradigm a plethora of processes could impact the memory performance for the target item (answer to the trivia question) before (e.g., generating a prediction, retrieval attempts, anticipation of feedback) or after its presentation (e.g., hyper-correction effect, prior knowledge, triggering of a rewarding feeling or epistemic emotions). Thus, future research on the effects of curiosity on memory could benefit from a paradigm that can investigate the effects of curiosity in the absence of any effects related to processes triggered upon knowledge acquisition.

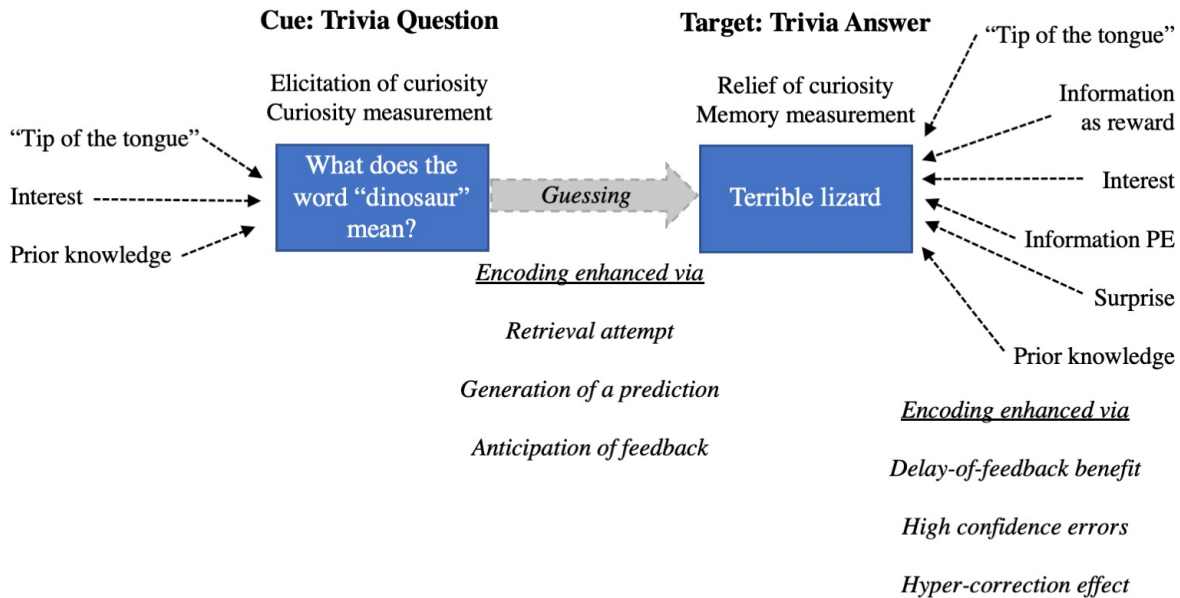
Figure 1.1

Limitations of the Trivia Question Paradigm

A Elicitation of curiosity is confounded with the anticipation of rewarding information



B Additional factors and processes enhancing memory formation for target information



Note. This figure illustrates possible pitfalls within the trivia question paradigm. (A) Because in most studies, the answer to the question is revealed in 100% of stimuli at a fixed time interval, the elicitation of curiosity is confounded with the anticipation of rewarding information. Thereby, it is possible that dopaminergic activity that would be observed during the answer presentation is transferred to the cue presentation, leading to the misleading interpretation that the elicitation, but not the relief of curiosity, is associated with a dopaminergic response. (B) In the trivia question paradigm, the trivia question is used as a curiosity-eliciting cue, but the memory test uses the information presented at the answer stage as target. However, the elicitation itself might be confounded with other factors than curiosity that might facilitate encoding. Likewise, various processes influencing encoding might be triggered when the answer to the

question is presented. The number of other processes might be even larger in versions of the paradigms that encourage guessing (shown in italics). PE = Prediction error.

Table 1.1

Overview of Methodological Aspects in Studies Using the Trivia Question Paradigm

Authors (Year)	Type	Encoding strategy	Delay	R/I?	II?	Design	Curiosity assessment	PK?	G?	Post-answer ratings
Kang et al (2009)	fMRI, behav, & eye tracking	incidental	long	no	no	within-subject (curiosity)	during	confidence in knowing the answer assessed	yes	no
Gruber et al (2014)	behav & fMRI	incidental	short (fMRI) & long (follow-up)	no	yes	within-subject (curiosity)	screening	likelihood in knowing the answer assessed	no	no
Ligneul et al (2018)	behav & fMRI	incidental	short	no	no	within-subject (curiosity)	during	button press if answer already known	no	surprisingness of answer
Marvin & Shohamy (2016)	behav	incidental	long	no	no	within-subject (curiosity * valence)	after	no	no	satisfaction with answer
McGillivray et al (2015)	behav	incidental	50% of items short, 50% of items long	no	no	mixed-design (curiosity * between variable: age)	during	confidence in knowing the answer assessed	yes	interest in answer, judgement of learning
Galli et al (2018)	behav	incidental	short	no	yes	mixed-design (curiosity * between variable: age)	during	assessed whether answer was already known	no	no

How Curiosity and Incentives Shape Memory Formation

Mullaney et al (2014)	behav	incidental	short	no	no	within-subject (curiosity * feedback delay)	during	no	yes	no
Fastrich et al (2017)	behav	incidental	long	no	no	within-subject (curiosity)	during	confidence in knowing the answer assessed	yes	interest in answer
Stare et al (2018)	behav & eye tracking	incidental	short and long manipulated between subjects	no	yes	mixed-design (curiosity * between variables: sleep & delay)	screening	confidence in knowing the answer assessed	no	no
Wade & Kidd (2019)	behav	incidental	short	no	no	within-subject (curiosity)	during	subjective and objective assessment of how close provided guess is to answer	yes	surprisingness of answer
Brod & Breitweiser (2019)	behav & eye tracking	incidental	short	no	no	within-subject (curiosity * generation of predictions)	during	no	yes	no
Murphy et al (2021)	behav	incidental	short	no	yes	within-subject (curiosity *)	screening	confidence in knowing the answer assessed	no	no

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Poh et al (2021)	behav & fMRI	incidental	short	no	no	anticipation delay) within-subject (curiosity)	screening	likelihood in knowing the answer assessed	no	no
Fandakova & Gruber (2020)	behav	incidental	short	no	yes	mixed-design (curiosity * between variable: age)	screening	confidence in knowing the answer assessed	no	interest in answer
Murayama & Kuhbander (2011)	behav	incidental	50% of items short, 50% of items long	yes	no	mixed-design (curiosity * between variable: reward)	interestingness of questions rated by separate sample	no	yes	no
Halamish et al (2019)	behav	intentional	long	yes	no	mixed-design (curiosity * between variable: reward)	during	no	no	interest in answer
Swirsky, Shulman & Spaniol (2021)	behav	incidental	long	yes	yes	mixed-design (curiosity * between variables: reward & age)	during	confidence in knowing the answer assessed	yes	no

Duan et al (2020)	behav & fMRI	intentional	long	yes	no	mixed- design (curiosity * between variable: reward)	screening	confidence in knowing the answer assessed	no	ratings of prospective curiosity
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Note. “Type” refers to the type of data collected where “behav” indicates behavioural data. “Encoding strategy” reflects whether an incidental or intentional encoding paradigm was used. “Delay” specifies the delay between encoding and subsequent memory tests. “R/I?” indicates whether a reward/incentive manipulation was implemented whereas “II?” indicates whether incidental information (i.e., faces) was presented between cue and target stimuli. A brief description of the design is included as well as of the curiosity assessment where “during” and “after” means that the curiosity ratings were obtained during or after encoding, respectively, whereas “screening” indicates that the study protocol included a screening phase to create a set of high and low curiosity questions. “PK?” describes whether prior knowledge was assessed and “G?” shows whether guessing was actively encouraged in the paradigm. Lastly, any ratings collected after the answer presentation are described.

Summary and Scope of this Work

Every day, we are embedded in a continuous stream of events and face countless information. Remembering all of them, 24 hours per day, 365 days per year, for approximately 80 years that an average life lasts, would not make us superhumans, it would more so hamper us in functioning adaptively in our environments. As such, it is not a weakness but a strength that our memory is selective and prioritises certain events over others. As reviewed in this chapter, one of the prime candidates to link experiences with importance is the neurotransmitter dopamine. Dopamine makes memories last by enhancing synaptic plasticity, i.e., the cellular mechanism of learning, by influencing late LTP associated with the synthesis of plasticity-related proteins used to strengthen existing synapses and build new ones to enhance signal transmissions between neurons. Memory processes are not limited to the time point when information is presented (i.e., encoding), but also critically rely on stabilisation processes (i.e., consolidation). Importantly, while dopamine is released during encoding, enhancing memory for information presented within its penumbra, the effects depend on consolidation processes during which lasting changes at the synapses occur.

While dopamine release is often discussed in the context of extrinsic rewards, more recently it has been shown that intrinsic rewards can also cause a dopaminergic response. As such, it is not surprising that both types of rewards are associated with enhanced memory for information presented around their occurrence. In humans, extrinsic rewards are often operationalised using money whereas the effects of intrinsic rewards are investigated through the lens of curiosity. Indeed, results of studies investigating the effects of monetary rewards and curiosity on memory encoding have yielded largely overlapping results, with respect to behavioural effects as well as their neural underpinnings within the HPC-VTA/SN loop. However, some differences have also emerged. Crucially, the effects are often studied in isolation and less is known about their interaction, especially on a neural level. To better understand if and how they interact in their effects on encoding, they need to be studied simultaneously. This is why the current research aims to address this by manipulating both, the availability of extrinsic incentives as well as levels of curiosity to measure the effects on incidental encoding. In doing so, we hope to gain a better understanding of whether motivated learning is supported by a common system or whether different sources of motivation affect encoding via different mechanisms.

Likewise, it is unclear whether part of the overlap observed thus far could be due to the paradigms used, especially in the research on the effects of curiosity on memory that is dominated by the trivia question paradigm and static stimuli. In trying to address these limitations in previous research on the effects of curiosity on memory, we have developed a new paradigm. More specifically, while previous research often induced curiosity using trivia questions as cues and then testing the memory for the target

information presented in form of the trivia answer, we here use short video clips of magic tricks to elicit curiosity and assess memory for the magic tricks themselves. Unlike previous studies, we, therefore, test the effects of curiosity on encoding focusing on the events that elicited curiosity rather than those that satisfied it. As such, this work critically focuses on one component of the reward-learning framework of autonomous knowledge acquisition, i.e., the awareness of a lack of knowledge and an associated state of uncertainty (i.e., the subjective feeling of curiosity when watching a magic trick) independent of the actual process of knowledge acquisition and its rewarding properties (e.g., knowledge about the method used in the magic trick to achieve the “magical” effect) to investigate whether curiosity in and of itself has an effect on encoding. Magic trick videos were taken from a stimulus database and validly induce curiosity (Ozono et al., 2021). After the presentation of each magic trick, curiosity was assessed using subjective ratings. Importantly, to further understand the interaction between curiosity and extrinsic motivation, the availability of extrinsic incentives was manipulated. When watching the magic tricks, participants performed a task to orient their attention toward the magic tricks. The performance in the orientation task was incentivised using a between-subject design. In the incentivised group, participants were instructed that correct judgements would be associated with monetary bonus payments whereas such instructions were omitted in the control group. Crucially, neither of the groups received performance feedback and the bonus payment was received after a delayed memory test. As such, our paradigm used an incentive, rather than a reward manipulation where contingencies were known to the participants (i.e., how each correct answer would translate into bonus payments) but not received as an outcome of motivated behaviour (i.e., reward) until much later. Although this manipulation of monetary incentives is different from prior studies in the field of motivated learning, it bears resemblance with the conceptualisation of curiosity based on distinct components within the reward-learning framework of knowledge acquisition: the subjective feeling when facing a lack of knowledge and associated uncertainty (referred to as *curiosity*) triggers information-seeking (where gaining information/resolving uncertainty is an *incentive* for information-seeking behaviour) whereas the actual knowledge acquisition process and the associated resolution of uncertainty is the outcome of information-seeking (thereby similar to the concept of *rewards*).

This magic trick paradigm was used across two behavioural and one fMRI study to study the effects of curiosity on encoding behaviourally as well as in terms of its neural underpinnings. Since memory is not only dependent on brain activity during encoding, but also on consolidation processes, the fMRI study implemented a post-encoding design where brain activity was not only measured during encoding but also at rest before and after encoding. To allow researchers to re-use this rich dataset, Chapter 2 contains a detailed description of the experiment and dataset including its technical validation, illustrating its high quality. fMRI data described in Chapter 2 is then analysed in Chapters 3 and 4.

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Chapter 3 examines the behavioural data from all three studies using a meta-analytical approach to investigate the effects of curiosity and monetary incentives as well as their interaction on memory encoding. Additionally, the fMRI time series data from the encoding phase is used to identify the neural underpinnings of curiosity, memory, and the curiosity-motivated learning enhancement as well as the effects of the availability of extrinsic incentives therein. As such, Chapter 3 examines the behavioural effects as well as the underlying neural mechanisms during encoding. Chapter 4, on the other hand, focuses on post-encoding rest data, thereby capturing brain activity associated with early consolidation.

In sum, this thesis aims to enhance our understanding of curiosity-motivated learning using a new paradigm by looking at behavioural effects as well as neural underpinnings during encoding and consolidation, respectively. By including an extrinsic incentive manipulation, we hope to further contribute insights to the question of whether intrinsic and extrinsic motivation are based on shared (sub-additive) or distinct (additive) neural processes to be able to not only enhance the theoretical understanding of both processes but to potentially also inform educational practices.

Chapter 2: Magic, Memory, and Curiosity – an fMRI Dataset of People Incidentally Encoding and Consolidating Magic Tricks

Curiosity is the intrinsic desire to know even in the absence of any instrumental value of the information (Gottlieb et al., 2013). It belongs to a group of emotions that are referred to as epistemic emotions, those that are crucial for learning and generating knowledge (Muis et al., 2018; Pekrun et al., 2017). In fact, curiosity is so crucial that it is formalised in algorithms and implemented in robotics (Gordon, 2020; Gottlieb & Oudeyer, 2018; Hester & Stone, 2017; Oudeyer et al., 2007) and studies in humans have found that curiosity leads to exploration (Berlyne, 1966) and information seeking (FitzGibbon et al., 2020; Gottlieb et al., 2013; Kobayashi et al., 2019; van Lieshout et al., 2018) even if costs are involved (Bennett et al., 2016; FitzGibbon et al., 2021; Lau et al., 2020; Rodriguez Cabrero et al., 2019), guides attention (Jepma et al., 2012; Wojtowicz & Loewenstein, 2020) and influences gaze (Baranes et al., 2015) as well as pupil dilation (Brod & Breitwieser, 2019). Despite such immanent importance of curiosity, research has only recently started to investigate it with a (neuro-)scientific focus. The purpose of this chapter is to describe the dataset collected throughout the current work in detail and to perform thorough quality checks of the data, (1) laying the groundwork for the following empirical chapters and (2) providing sufficient information for independent researchers to re-use this dataset to answer their independent research questions.

Evidence from functional magnetic resonance imaging (fMRI) studies suggests that higher feelings of curiosity are associated with increased activity in key structures known as the reward network (Haber & Knutson, 2010), including the nucleus accumbens, caudate nucleus, and midbrain (Gruber et al., 2014; Kang et al., 2009; Lau et al., 2020; Ligneul et al., 2018; Poh et al., 2021). These results suggest that the feeling of curiosity itself can be conceptualised as a cognitive and motivational state (Gruber & Ranganath, 2019) driven by an intrinsic rewarding value of information (FitzGibbon et al., 2020; Loewenstein, 1994; Marvin & Shohamy, 2016; Murayama, FitzGibbon, et al., 2019; van Lieshout et al., 2020). Put differently, curiosity may work in a similar manner as seen with other, extrinsic rewards/incentives like money or food. In fact, a recent study found similar patterns of striatal activations for curiosity and extrinsic food rewards (Lau et al., 2020), supporting the idea that subjective value of information and their expected utility are represented by the same area in the ventral striatum using a common code (Kobayashi & Hsu, 2019).

Curiosity also enhances memory encoding across the lifespan (Fandakova & Gruber, 2021; Galli et al., 2018; McGillivray et al., 2015; Swirsky et al., 2021). Previous studies show robust memory enhancement effects of curiosity using incidental (Fandakova & Gruber, 2021; Fastrich et al., 2018; Galli et al., 2018; Gruber et al., 2014; Kang et al., 2009; Ligneul et al., 2018; Marvin & Shohamy, 2016;

McGillivray et al., 2015; Murayama & Kuhbandner, 2011; Stare et al., 2018; Wade & Kidd, 2019) and intentional (Duan et al., 2020; Halamish et al., 2019; Mullaney et al., 2014) encoding paradigms. Gruber and colleagues (Gruber et al., 2014) showed that curiosity-dependent memory enhancements are supported by anticipatory activity in the hippocampus and dopaminergic midbrain as well as their functional connectivity. These findings show a parallel with the studies investigating the effects of monetary rewards or incentives on memory encoding --- such studies not only find that the availability of rewards enhances encoding (Bunzeck et al., 2010; Gruber et al., 2016; Mason et al., 2017; Murayama & Kitagami, 2014; Murayama & Kuhbandner, 2011; Murty et al., 2017; Patil et al., 2017; Wittmann et al., 2011), but that the enhancement effects are supported by dopaminergic modulation of hippocampal activity originating from the midbrain (Adcock et al., 2006; Miendlarzewska et al., 2016; Wittmann et al., 2005). These results further confirm the idea that curiosity and extrinsic incentives/rewards are processed in the brain in a similar manner.

One problem with the previous fMRI research on curiosity is that studies have predominantly relied on trivia questions (Duan et al., 2020; Gruber et al., 2014; Kang et al., 2009) or arbitrary gambling tasks (Kobayashi et al., 2019; van Lieshout et al., 2018) to induce curiosity inside the fMRI scanner. However, their sparse, static, and discrete nature misses the fundamental aspect of how curiosity manifests in our daily life --- curiosity is normally triggered by complex and dynamic stimuli in the environment. For instance, in the classroom, information is not presented one by one on a screen for a fixed amount of time in written form, but is rather embedded in a continuous perceptual stream potentially stemming from multiple sources and modalities. While insights gained using the trivia question and gambling paradigms are highly valuable, their lack of ecological validity makes it challenging to reach a full understanding of curiosity that is operative in our real life. In fact, the observed overlap between curiosity and extrinsic rewards in previous fMRI work may have been a consequence of such simplified stimuli to induce curiosity --- using real-life materials, previous behavioural studies showed that curiosity and extrinsic rewards have many different properties (Murayama, 2022). Increasing the stimulus complexity by using naturalistic compared to simplistic stimuli is a necessary step on that “promising translational research avenue” (Gruber et al., 2019, p. 413).

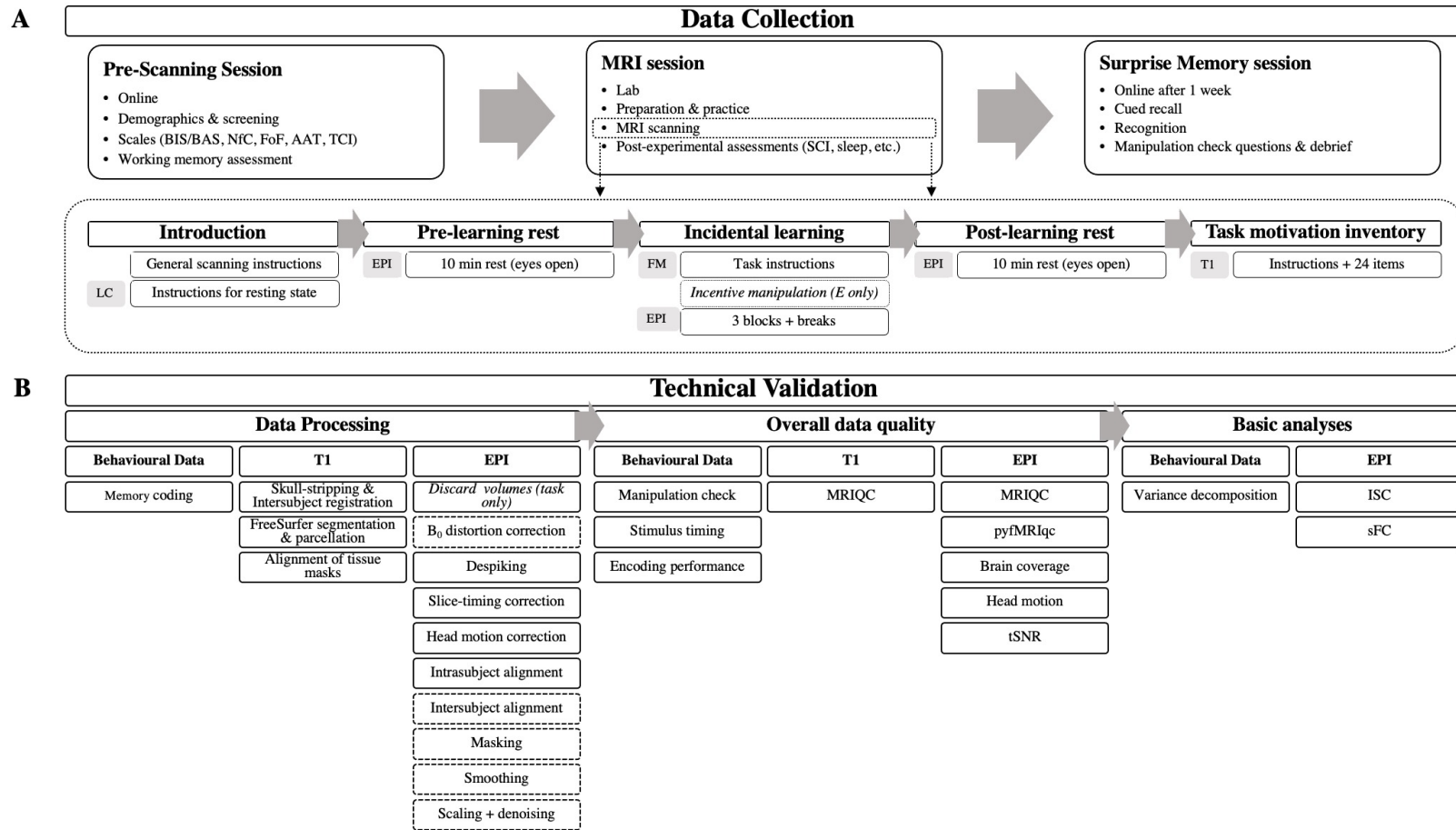
To allow researchers to address limitations from previous studies, we here describe, validate, and share the Magic, Memory, and Curiosity (MMC) Dataset (summarised in Figure 2.1). It consists of behavioural, anatomical, and functional data of 50 participants performing an incentives- and/or curiosity-motivated incidental learning paradigm. Incentives were manipulated as a between-subject factor whereas curiosity was operationalised as a within-subject factor using magic tricks videos taken from a validated stimulus database (Ozono et al., 2021). Magic tricks violate causal relationships and thereby expectations by producing an apparently implausible effect (like an object vanishing) using methods based on, e.g.,

misdirection or illusion without the spectator knowing the method and how the trick works (Danek et al., 2015; Kuhn et al., 2008; Parris et al., 2009; Rensink & Kuhn, 2014). In doing so, they create surprise and trigger curiosity (Lau et al., 2020; Moss et al., 2017; Ozono et al., 2021; Subbotsky, 2010). Additionally, they have universal appeal due to their non-verbal nature (Ozono et al., 2021). Individual brain activity was measured before, during, and after learning using fMRI and memory was quantified with a surprise cued recall and recognition memory test one week later.

With the MMC Dataset, researchers can investigate different processes associated with memory encoding to help understand curiosity-based learning and gain insights important for educational settings. The use of magic tricks enables us to test whether effects observed using static trivia questions generalise to naturalistic stimuli like magic tricks. Naturalistic stimuli are rich, contextualised, and dynamic triggering real-time integration of information and have increasingly been used in neuroscientific studies in recent years because they show high ecological validity (Aliko et al., 2020; Bottenhorn et al., 2019; Sonkusare et al., 2019). Their complexity allows to study different features of interests (e.g., surprise, prediction errors, or misdirection by the magician) by using annotations combined with a plethora of possible analysis approaches making sharing of naturalistic datasets like the current one extremely valuable for the neuroscientific community (DuPre et al., 2020; Sonkusare et al., 2019).

Figure 2.1

Overview of Data Collection and Technical Validation Procedures



Note. Illustration summarising the procedures used during Data collection (top) and Technical Validation (bottom). (A) The data collection involved three sessions: a pre-scanning session, an MRI session, and a surprise memory test. The upper part of the figure highlights which assessments were carried out during each session, whereas the lower part (dotted line) gives more details on the MRI scanning. The white

rectangles summarise what was presented on the screen and the grey rectangles indicate which sequences were run simultaneously. (B) For the technical validation, data from different sources (behavioural data, functional data (EPI) and anatomical data (T1)) was pre-processed as indicated. Regarding the pre-processing of EPI data, solid lines indicate steps that were carried out in the minimal and full pre-processing pipeline, while dashed lines indicate that the steps were part of the full pre-processing pipeline but not of the minimal pre-processing pipeline. To determine overall quality of imaging data, raw (MRIQC, pyfMRIqc) or minimally pre-processed (brain coverage, head motion, tSNR) data was used, whereas fully pre-processed functional data was used for basic validation analysis (ISC, sFC).

BIS/BAS = Behavioural Inhibition/Activation Scale, NfC = Need for Cognition, FoF = Fear of Failure, AAT = Approach & Avoidance Temperament, TCI = Trait Curiosity Inventory, SCI = State Curiosity Inventory, E = experimental group, LC = Localizer, EPI = echo-planar imaging, FM = field map, T1 = anatomical scan, MRIQC / pyfMRIqc = softwares used to determine overall data quality, tSNR = temporal signal-to-noise ratio, ISC = intersubject correlation, sFC = seed-based functional connectivity. *Italic font indicates that certain procedures were used for a subset of participants/datasets.*

Methods

Participants and Design

Due to a lack of previous MRI studies investigating differential effects of rewards/incentives and curiosity on incidental encoding, sample size considerations were based on previous behavioural studies (Murayama & Kuhbandner, 2011), sample size recommendations to test for reliable between-group similarities and differences in neural responses to naturalistic stimuli (Pajula & Tohka, 2016; Yeshurun, Nguyen, et al., 2017) as well as the results of behavioural pilot experiments with the same paradigm (Meliss & Murayama, 2019). The *a priori* defined, intended sample size was in total 50 participants (i.e., $N = 25$ in each, control and experimental group). Sensitivity analysis carried out with G*Power 3.1 (Faul et al., 2007, 2009) showed that this sample size is sufficient to detect a moderate-to-large between-group effect (J. Cohen, 1992) of Cohen's $d = .7$ with a power of $\beta = .8$ and an error probability of $\alpha = .05$.

To reach this number, leaflets were distributed on the university campus as well as cafés and leisure centres. In total, we were approached by 110 interested participants via email who were then screened for MRI safety (e.g., no pacemaker or other active implants) and inclusion criteria. The latter required that participants be right-handed, fluent in English, aged between 18 and 45, healthy and not suffering from any chronic illness, psychiatric disorders or cognitive impairments and not taking any psychoactive drugs. Moreover, participants needed to have normal hearing and normal or corrected vision using contact lenses. For females, it was additionally necessary that they were not nursing, pregnant, or intending to become pregnant.

In total, 64 participants met inclusion criteria and consented to take part in the study. They were assigned ascending participant identification numbers (IDs, i.e., 1, 2, 3, etc.) that were assigned to the groups in interleaved manner: odd IDs were assigned to the control group (C), whereas even IDs were assigned to the experimental group (E). However, during the pilot phase of data collection (i.e., the first six participants), the first three participants were assigned to the control group whereas the remaining three participants were assigned to the experimental group. They were scheduled for all three sessions of data collection: (1) a pre-scanning online session, (2) MRI session in the lab and (3) an online surprise memory test a week after scanning. Four participants (2 in C, 2 in E) dropped out after consenting, but before completing the pre-scanning online assessment and another three participants (2 in C, 1 in E) completed the first session, but did not show up for the MRI scanning session in the lab. Another two participants (1 in C and 1 in E) withdrew their consent during the MRI session (one due to feeling claustrophobic and one due to a blocked nose). Additionally, five participants (2 C and 3 E) were excluded after acquisition but before data analysis due to technical issues during the scan. Any assigned IDs of dropped out participants were reassigned until the intended sample size was met.

The final sample consisted of 50 participants (36 females, range of age 18-37 years, $M = 25.32$, $SD = 5.19$), most of them being research-naïve as no recruitment platform was used. Table 2.1 provides a summary of participant demographics for each group. The groups did not differ in demographics (all $p \geq 0.103$).

Table 2.1

Description of participants means (standard deviation) in each group

	Control Group	Experimental Group	Statistics group comparison
Age	26.52 (5.46)	24.12 (4.7)	$t(46.96) = 1.665, p = 0.103$
Sex assigned at birth (% female)	68	76	$\chi^2(1) = 0.099, p = 0.753$
Ethnicity (% BAME)	32	24	$\chi^2(1) = 0.099, p = 0.753$
Years of Education	16.12 (2.62)	15.92 (2.04)	$t(45.282) = 0.301, p = 0.765$
Corsi span	5.56 (2.36)	5.8 (1.19)	$t(35.43) = -0.453, p = 0.653$
n-back (% accuracy)	73.83 (20.01)	65.84 (23.17)	$t(47.007) = 1.306, p = 0.198$

Note. All participants were right-handed and fluent in English. Sex is expressed as percentage female.

Ethnic background is expressed as percentage Black, Asian, and Minority Ethnic (BAME). Statistics of group comparison report χ^2 test and Two-Sample Welch t-test for categorical (sex and percentage BAME) and continuous data (age, years of education, Corsi span, and n-back accuracy), respectively. $t = t$ value. $p = p$ value.

This study used a between-subject design manipulating whether performance in an orientation task was incentivised: Participants in the experimental group were instructed that they could earn a performance-dependent additional bonus of £0.80 for each correct answer in the 36 trials of the magic trick watching task (see below). Participants in the control group did not receive such an instruction.

Participants were compensated with £30 for their participation in the study and all participants – regardless of the group they were assigned to – received an additional bonus payment of £7.20. This reflects chance level performance in the incentive-manipulated, four-alternative forced choice orientation task. The incentive orientation task was designed as part of the cover story to keep participants engaged and ensure they were paying attention; however, there were no correct or wrong answers. Hence, out of courtesy, all participants received the same bonus payment after the debrief at the end of the study.

The study design was approved by the University Research Ethics Committee (UREC) of the University of Reading (UREC 18/18). Participants provided informed written consent to participate in the study and to share their data in anonymised form.

Material

Magic trick stimuli were obtained from the Magic Curiosity Arousing Tricks (MagicCATs) stimulus set (Ozono et al., 2021) containing 166 short magic trick video clips. We selected 36 to use as stimuli in the experiment; ensuring that they (a) had a duration between 20 und 60s, (b) included a range of different materials and features so that they were distinguishable when used in a cued recall paradigm, and (c) elicited curiosity to varying degrees based on the ratings reported in the database (Ozono et al., 2021). All videos in the database are muted on purpose to reduce verbal interference. However, due to the non-verbal nature, the magic tricks are still understandable. Magic tricks relying on subtitles were excluded. The number of stimuli was equal to previous fMRI studies using magic tricks from the same database (Lau et al., 2020). The final selection of stimuli was edited using Adobe®Premiere Pro CC® (2015) software to achieve a similar dark background and viewing focus. Where necessary, additional editing was performed, e.g., removing subtitles. The faces of the magicians were hidden as much as possible.

Furthermore, we created a mock video for each magic trick separately to capture transient, non-specific activity at stimulus onset (Nastase et al., 2019). For this, the first frame of the magic trick was used as a still image and presented for the duration of six seconds during which it was overlaid with a black video (opacity 99.7%) including a viewing focus that gradually expanded and smoothed to match the viewing focus used in each magic trick file. Mock video and magic tricks were combined into one video (range of duration in seconds 26.6 - 58.64, $M = 38.53$, $SD = 8.63$) and saved at a size of 1280x720 pixels in mp4. Additionally, we selected two more magic tricks to be used during the practice trials according to the same criteria and edited them as described above. A description of each magic trick used can be found in Table A2.1 in the appendix.

We rated each magic trick with respect to its moment(s) of surprise, i.e., the moment(s) of violation of expectations and then selected a frame for each magic trick from before the (first) moment of surprise that was distinctive enough to cue the respective magic trick without revealing the trick entirely. This frame was then used as a cue image (size 1920x1080 pixels) in the memory task. The timestamps of the moment(s) of surprise and cue image can be found in Table A2.2 in the appendix.

Tasks and Measurements

Magic trick watching task. During each trial (range of length 49.94 - 87.99s, $M = 63.29$ s, $SD = 8.71$ s; see Figure 2.2) in the incidental learning phase, participants were presented with a magic trick video and afterwards had to give an estimate as to (a) how many people (out of 100) would be able to correctly figure out the solution to this magic trick with answer options of “0-10”, “11-20”, “21-30”, and “31 and more” (“estimate rating” containing the incentives manipulation, highlighted in yellow, see

below) and (b) how curious they were while watching the trick using a 7-point scale (1 = “not at all”, 7 = “very”; “curiosity rating”).

Responses were recorded using a four-button MRI compatible response device (<https://www.curdes.com/mainforp/responsedevices/buttonboxes/hhsc-1x4-cr.html>) where the index finger would be on the first (i.e., blue) button, the middle finger on the second (i.e., yellow) button, the ring finger on the third (i.e., green) button and the small finger on the fourth (i.e., red) button. This was practised on a colour-coded keyboard outside the MRI scanner. The beginning of each magic trick presentation was in alignment with the beginning of the acquisition of a volume by synchronisation with the scanner TTL (transistor-transistor logic) pulse. Likewise, the fixation (white dot on black screen) presented for 4 - 10s (jittered; $M = 4.83s$, $SD = 1.81s$) presented after the magic trick was aligned to sync with the TTL pulse and a blank screen was presented between the end of the magic trick and the fixation ($M = 0.87s$, $SD = 0.62s$, $min = 0.01s$, $max = 2.00s$). For the estimate rating, each of the four answer options were presented in the colour corresponding to the finger on the button box that needed to be pressed to select a given option (i.e., “0-10” in blue, “11-20” in yellow, “21-30” in green and “31 and more” in red). The participants were given a fixed response window of 6s to select an option. If they had made their choice before the end of the response window, the answer options changed from coloured to white and the screen was presented until the end of the response window followed by a fixation presented for 0.05s. Afterwards, the curiosity rating was presented with one number randomly highlighted in red. Participants were then asked to move the number to the left (pressing the blue button with the index finger) and/or to the right (pressing the yellow button with the middle finger) until the highlighted number corresponded to their curiosity which was confirmed by pressing the red button with the little finger. The response window was 5.95s long and if an answer had been given before the end of the response window, all writing would be presented in white until the end of the response window. This was again followed by a fixation presented for 4 - 10s (jittered; $M = 5.00s$, $SD = 2.00s$) before the next trial started.

During each trial, we collected the estimate and curiosity responses as measurements as well as their respective reaction times (in seconds). Additionally, we recorded the number that was randomly highlighted at the start of the curiosity rating as well as the number of clicks.

In total, 36 magic tricks were presented over three experimental blocks (i.e., 12 trials per block). The first trial in each block started with a fixation (2s). To control for any effects of trial order and to ensure that any similarity in brain responses between subjects can be attributed to similarity in curiosity ratings rather than to similarity in trial orders, the trial orders were pseudo-randomised. To achieve this, curiosity ratings from Ozono and colleagues (2021) were used to categorise each selected magic trick based on the median split as a high or low curiosity magic trick. In total, 25 trial orders (due to N per group = 25) were simulated in R (R Core Team, 2020) so that high and low curiosity magic tricks were

equally distributed across blocks (i.e., six each per block) while restricting the maximum number of consecutive tricks of either category to four. Additionally, the simulations were restricted so that the maximum range of Spearman-rank correlations of all pairwise trial orders did not exceed a threshold of 0.7. Each of the simulated trial orders was used once in the control and experimental group.

When presenting magic tricks inside the MRI scanner, Lau and colleagues (2020) analysed their data using a standard General Linear Models (GLM) approach defining onset and duration of each magic trick. Likewise, specific features in each magic trick could be annotated and used as regressors in a GLM (Sonkusare et al., 2019). When trying to optimise the design for GLM-based analysis, it was not possible to do so for possible contrasts future researchers might be interested in based on what was presented in the magic trick (e.g., the occurrence of a third person supporting the magic trick by picking a card) or based on the curiosity rating and/or encoding performance. However, to support GLM-based analysis as much as possible, the design efficiency was maximised using AFNI's (Cox, 1996) '@stim_analyze' program for the contrast between the video (i.e., mock video and magic trick combined) and ratings (solution and curiosity rating combined including fixation between both) by estimating the optimal jitter for the fixation following the magic trick video and curiosity rating, respectively. Firstly, 1000 random stimulus timings were produced ('make_random_timing.py'). For that, we defined two ordered stimulus categories (video and rating) and their length (average magic trick file length = 38s, length rating = 12s) as well as number of trials and blocks (i.e., twelve and three, respectively), block length (720s) and minimum and maximum rest (4 and 10s, respectively). In a second step, the program evaluates the produced timings ('3dDeconvolve -nodata') to determine the iteration best suited to deconvolve overlapping hemodynamic responses with the smallest amount of unexplained variance (https://afni.nimh.nih.gov/pub/dist/HOWTO/howto/ht03_stim/html/AFNI_howto.html). The corresponding stimulus timings were used to calculate both jitter durations (i.e., fixation after watching the magic trick and fixation after the ratings) and the same values were used for all participants.

Memory task. Memory for all 36 magic tricks was tested using (1) a cued recall and (2) a four-alternative forced choice recognition paradigm (see Figure 2.3 upper half). During each cued recall trial, participants were presented with the cue image of a magic trick and asked to describe what has happened in this magic trick according to their memory using a free answer format text input. Participants were informed that their answer would be used to categorise whether they recalled a given magic trick. They were hence asked to be as specific and descriptive as possible. Additionally, they were instructed to write "no recall" if they could not recall it.

During the recognition task, each trial started with the presentation of the same cue image paired with the question "What happens in this magic trick" and four verbal answer options (see Table A2.1 Table A2.1 in the appendix) presented in random order. Participants were asked to select one of the

options and to afterwards rate their confidence on a scale from 1 (“not confident at all”) to 6 (“very confident”). For both answers, their response times were collected.

Participants’ recall for all magic tricks was tested before testing their recognition. Both assessments were self-paced and the cue images for each magic trick were displayed in independent, random order.

Working memory tasks. To measure working memory, we used the Corsi block tapping task (Corsi, 1972; Kessels et al., 2000) and a modified version of the 2-back task (Kirchner, 1958), both available in the PsyToolkit (Stoet, 2010, 2017) library (<https://www.psychtoolkit.org/experiment-library/>). The Corsi Block Tapping task is a measurement of immediate spatial memory (Corsi, 1972). The participants saw nine cubes (impartially arranged) that were highlighted in sequence starting with two cubes. Immediately afterwards, the participants had to click on the cubes in exactly the same order. When successful, the next trial had the next higher number of cubes, otherwise, there was one more attempt for another sequence with the same number of cubes. The Corsi span was determined as the maximum number of cubes the participant was able to click on in the correct order.

The 2-back task was also used to measure working memory (Conway et al., 2005; Jaeggi et al., 2010; cf. Kane et al., 2007). Participants were shown a sequence of letters on the screen (each for max 2000ms; 15 different letters used) and were asked to decide whether they saw the same letter two trials ago (i.e., $n = 2$ back). If the participants thought they saw the same letter, they had to press M (M for memory), otherwise they were asked to press N (N for no). The task started with a practice block in which feedback was provided followed by four task blocks without feedback. Each block consisted of 20 trials each.

Questionnaires. Throughout the data collection, different questionnaires were given to the participants. The whole questionnaire battery can be found in the appendix.

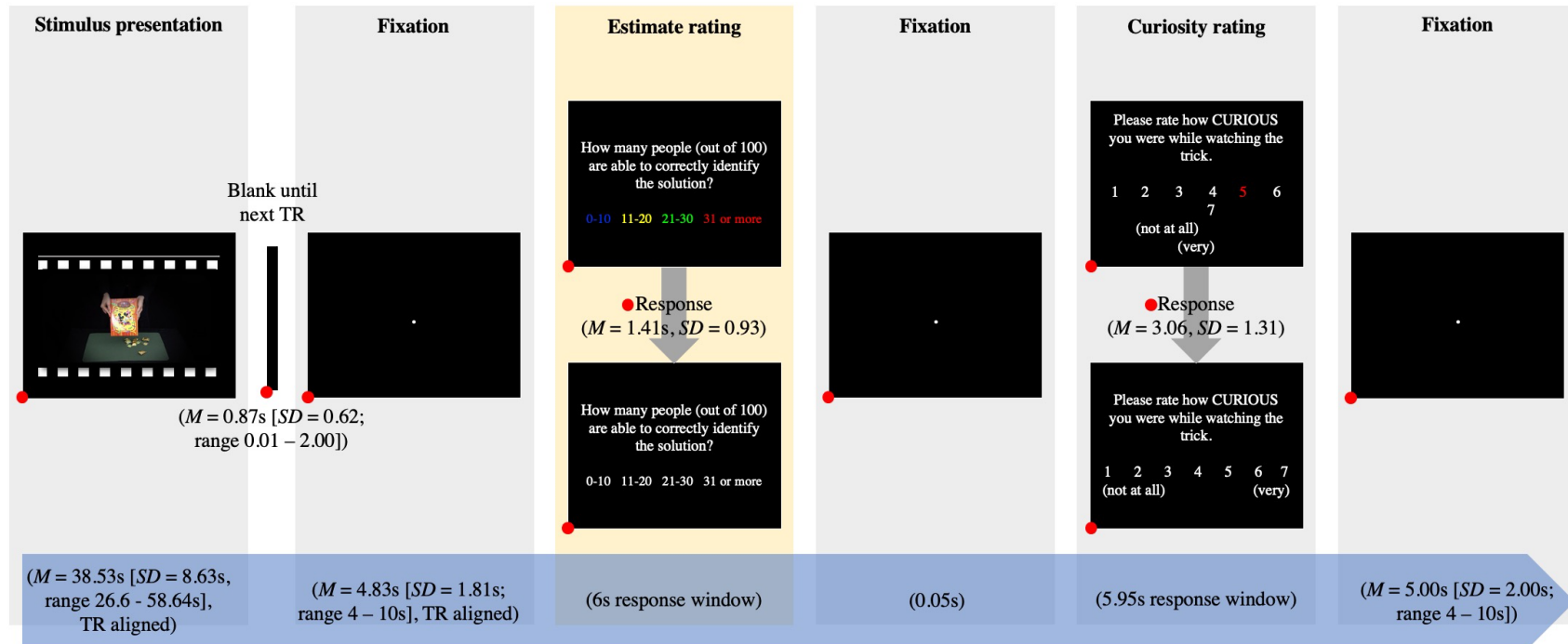
Constructs relevant in the context of curiosity, reward and incentive/reward-motivated learning were assessed in the pre-scanning session. Questionnaires included the Behavioural Inhibition and Behavioural Activation Scales (BIS/BAS; Carver & White, 1994) [20 items on a 4-point Likert scale ranging from 1 = “very false for me” to 4 = “very true for me”], Need for Cognition (Cacioppo et al., 1984) [18 items on a 9-point Likert scale ranging from -4 = “very strong disagreement” to +4 = “very strong agreement”], Fear of Failure (Spence & Helmreich, 1983) [9 items on a 5-point Likert scale ranging from 1 = “strongly disagree” to 5 = “strongly agree”], Approach and Avoidance Temperament (Elliot & Thrash, 2010) [12 items on a 7-point Likert scale ranging from 1 = “strongly disagree” to 7 = “strongly agree”], and trait curiosity (Naylor, 1981) [18 items on a 4-point Likert scale ranging from 1 = “almost never” to 4 = “almost always”].

Additionally, at the end of the scanning session, a task motivation inventory (intrinsic motivation (Elliot & Harackiewicz, 1996), task engagement (Elliot & Harackiewicz, 1996), interest (Wigfield & Eccles, 2000), boredom (Pekrun et al., 2002), effort (Ryan, 1982), and pressure (Ryan, 1982)) as well as task compliance and whether they were able to see the magic tricks properly were assessed inside the MRI scanner while we acquired the anatomical scan. The item order was randomised and participants could answer on a 7-point Likert scale from 1 (“definitely disagree”) to 7 (“definitely agree”). Similar to the curiosity ratings, a random number was highlighted in red and participants were asked to move the number to the left (i.e., by pressing the blue button with the index finger) or right (by pressing the yellow button with the middle finger) until the highlighted number corresponded to their rating (confirmed by pressing the red button with the little finger). Outside the scanner, state curiosity (Naylor, 1981) [20 items on a 4-point Likert scale ranging from 1 = “not at all” to 4 = “very much so”] was measured together with sleep and alcohol consumption in the last 24 hours. Moreover, we asked the experimental group about their expectations about the bonus payments and whether they invested effort to increase their bonus payments (7-point Likert scale from 1 = “strongly disagree” to 7 = “strongly agree”) and how much reward they expected to have earned (free text answer). As a manipulation check, we asked all participants to describe the hypothesis of the experiment.

At the end of the memory tests, a final questionnaire was administered to determine whether participants were aware of their memory being tested and whether they intended to encode the magic trick while watching them on a 6-point Likert scale (6 = “Definitely agree”, 1 = “Definitely disagree”). Additionally, participants in the experimental group were asked whether they believed the incentives manipulation. Lastly, we asked about any internet connection problems as well as experience regarding producing magic tricks.

Figure 2.2

Overview of Trial Structure During the Magic Trick Watching Task



Note. In each trial, participants viewed a magic trick and were asked to estimate how many people (out of 100) are able to find the solution (“estimate rating”) and to rate their curiosity while watching the magic trick (“curiosity rating”). The movie framing surrounding the stimuli is for illustration purposes only and was not used in the experiment. The start of the magic trick presentation and the beginning of the fixation afterwards were aligned with the beginning of the acquisition of a volume (“TR aligned”) by synchronisation with the scanner TTL pulse. A blank screen was presented between the end of the magic trick and the beginning of the next TR (i.e., start of fixation). Fixations were jittered using the same jitter intervals for all participants. All response windows were fixed. If a response was given before the end of the response window, the coloured font turned white, but the trial would not progress until the end of the response window. All time stamps collected are marked with red dots. While the

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trial structure looked identical for participants in both groups, participants in the experimental group were instructed that each correct response in the estimate rating (highlighted in yellow) would lead to an additional monetary bonus of £0.80. M = mean, SD = standard deviation.

Experimental Procedure

To be able to investigate incidental encoding (similar to previous research; Murayama & Kuhbandner, 2011), participants were presented with a cover story that the study investigates problem solving, social cognition and the associated brain processes. They were briefed that they would be performing a viewing and judgement task involving magic tricks inside the MRI scanner and that there would be an online follow-up assessment related to their responses a week later. They were scheduled for all sessions of data collection: (1) a pre-scanning online session, (2) MRI session in the lab, and (3) an online surprise memory test a week after scanning (see Figure 2.1A).

Pre-Scanning Session. Participants were instructed to follow a weblink (<https://www.psychtoolkit.org/cgi-bin/psy2.5.3/survey?s=Y9a>) in order to take part in the session. The link directed them to an online assessment implemented using PsyToolkit (Stoet, 2010, 2017) version 2.5.3 assessing demographics, current and lifetime disease diagnoses, MRI safety criteria, questionnaires and working memory measurements. Participants took 89.3 min on average ($SD = 274.74$, median = 25.5) to complete the session.

MRI session. The MRI experiment was divided into the following critical stages: (a) participant preparation and practice, (b) a pre-learning rest phase, (c) an incentive- and/or curiosity-motivated incidental learning phase, (d) a post-learning rest phase, and (e) a post-experimental assessment of intrinsic motivation and state curiosity (see Figure 2.1A, lower half outlined in dotted line). The experiment was presented using PsychophysicsToolbox 3 (Brainard, 1997) with GStreamer media framework run on Matlab (R2018b) on a 13inch Apple MacBook Pro (2018) that was connected to the 32inch bold back projection screen (BOLDScreen, Cambridge Research Systems LTD., UK) mounted at the head end of the scanner bore in the MRI suite. Participants looked at the screen through an eye-tracking sensitive mirror attached to the head coil. The MRI session lasted approximately two hours. An exact record of the instructions that were presented to the participants can be found in the appendix.

Participant preparation and practice. Upon arrival in the MRI area, the participants were demetalled and underwent two practice trials of the magic trick watching task. The practice trials were presented using PsychophysicsToolbox 3 (Brainard, 1997) with GStreamer media framework run on Matlab (R2016a) on a 13inch MacBook Air (2013). The responses were collected using the laptop keyboard that had the letters H, J, K, and L marked in blue, yellow, red, and green, respectively. Participants were given the opportunity to ask questions before they were accompanied to the MRI suite by MRI trained experimenters. There, they were introduced to the button box before inserting noise cancelling earplugs. Next, participants were placed on the scanner bed and pillows were placed under their knees and on either side of their heads for comfort and to minimise movements during the scan. Participants held the button box in their right hand and were given a bulb into their left hand that they

could squeeze in case of an emergency. They were instructed to not cross their arms or legs at any time and to try to keep as still as possible through the duration of the scan, but that they could “wiggle their arms and legs” in between scans when the experimenters communicated with them through the intercom. After being moved to the isocenter, the localizer and field map were acquired whilst the participant read through the instructions for the resting phase.

Pre- and post-learning rest phases. Similar to previous studies, we implemented pre- and post-learning rest phases to measure post-encoding and consolidation processes (Gruber et al., 2016; Murty et al., 2017; Tambini & Davachi, 2013). During the rest phases (10min each), participants were laying in the scanner and were instructed to keep as still as possible with eyes open while presented with a white screen (without fixation). They were further asked to blink as usual and to try to not think about anything. These instructions were presented in written form on the screen and also repeated by the experimenter through the intercom.

Incentives and/or curiosity motivated incidental learning phase. After the pre-learning rest phase, participants were asked to read again through the instructions of the magic trick watching task whilst a field map was acquired. For the experimental group only, the instructions included a statement that participants could earn an additional bonus payment of up to 50% of their compensation: each correct answer to the question of how many people would be able to find the solution (estimation rating in Figure 2.2, highlighted in yellow) translated into a reward of £0.80². This information was highlighted in green and had to be confirmed by pressing the third (i.e., green) button on the button box. The control group, however, did not receive such information. In each of the three task blocks, 12 magic trick videos were presented. Due to variation in the length of the video clips and their randomisation, each block lasted on average 12.66min ($SD = 0.41$ min, range in minutes = 11.67 - 13.77). In between the task blocks, participants were offered a break at the end of which participants in the experimental group were reminded of the possibility of additional monetary bonus payments. Before the start of each block, the experimenters talked with the participants through the intercom to ensure that the participants knew what to expect and what to do. The incentives- and/or curiosity-motivated incidental learning phase lasted on average 37.98min ($SD = 0.02$ min; range 37.97 - 38min) plus breaks.

Post-experimental assessments. After the post-learning rest phase, the anatomical scan was acquired. During the sequence, participants completed the task motivation inventory described above. The questionnaire was self-paced. If participants finished the questionnaire before the end of the anatomical

² 50% additional bonus payment should have translated to £0.40 per correct answer. However, no participant reported to have noticed this error.

sequence, they were asked to stay still until the end of the scan after which they were removed from the MRI scanner. Outside the MRI scanner, participants filled in another questionnaire, again implemented using PsyToolkit (Stoet, 2010, 2017) version 2.5.3 (<https://www.psychtoolkit.org/cgi-bin/psy2.5.3/survey?s=JDPGx>).

Surprise Memory session. Approximately one week after scanning (range = [6d 19h 55min; 9d 11h 18min], $M = 7d 10h 19min$, $SD = 13h 41min$), participants took part in a surprise memory test online (consisting of cued recall and recognition) implemented using a developmental version of Collector (Haffey et al., 2020). They were asked to do this experiment roughly around the same time as they participated in the lab experiment and were reminded two days in advance via email. Upon completion of the memory task, participants filled in a short questionnaire (see appendix), e.g., about whether they were aware that their memory would be tested. Afterwards, they were debriefed about the scope of the study and the between-group incentives manipulation. All participants received a bonus payment of £7.20. Participants took on average 47.98min ($SD = 42.81min$) to complete the assessment. Due to software development, the original link cannot be assessed anymore. However, we re-created the experiment as close to the original version as possible here https://magic-memory-curiosity.github.io/fmri/App/Run.html?platform=github&location=magicmemory_fmri_redo&name=condition_1 and a record of instructions presented to the participants can be found in the appendix.

Coding of Memory Measurements. Data collected in the cued recall block of the memory test was coded using dummy coding (1 = recalled, 0 = not recalled) in two steps: firstly, R (R Core Team, 2020) was used to automatically assign a zero to all answers containing “no recall” or variants thereof. In a second step, a trained rater coded all answers manually. The coding was performed for each trick separately to apply the same standard across participants and reviewed for consistency at the participant level. Any cases requiring further attention or correction were flagged up and resolved after discussion. For a trick to be coded as recalled, it was essential that the change that occurred was remembered, however, minor details could be wrong. Strict and lenient criteria were applied. The strict criteria captures whether the participants referred correctly to the change that occurred. If they recalled something related to the change that occurred without correctly specifying the change that occurred, a one would be assigned to the lenient, but not the strict criteria, hence reflecting a more gist-based memory. For instance, let us assume the magician changed the colour of the back of the card from blue to red (as done in the trick with stimulus id K21_long). If the participants wrote that the magician changed the colour of the cards, but used wrong colours, they would still fulfil the strict criteria (and hence, lenient as well). However, if the participants remembered that the appearance of the cards was changed without recalling that it was the colour that changed, they would fulfil the lenient criteria as this is related to the actual change, but would not pass on the strict criteria as the actual change was not recalled. In comparison, the

trick would be classified as not recalled on both criteria if the participant had written that the cards disappeared. Overall, the coding of recall performance on the lenient compared to strict criteria only differed in 81 out of 1800 trials (or 4.5%).

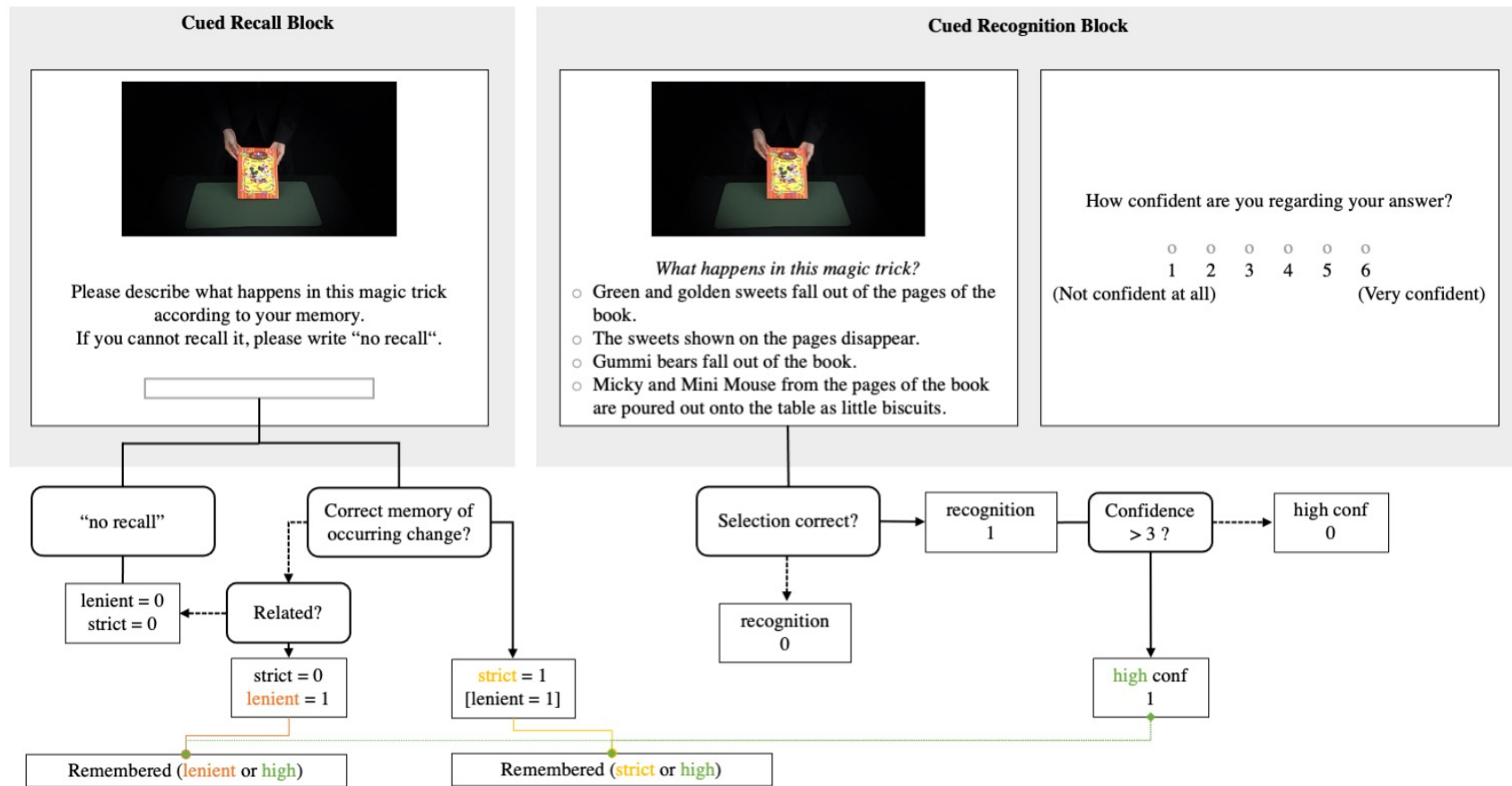
To code the recognition performance, the response was compared to the correct answer and coded with one if they were the same and with zero if they differed. Additionally, we combined recognition and confidence to measure recollection-based recognition (Yonelinas, 2001b, 2002) using “high confidence recognition” (i.e., recognised with a raw confidence rating larger than 3).

Similar to previous studies investigating memory encoding using naturalistic stimuli (Hasson, Furman, et al., 2008), we also combined recall and recollection-based recognition in which a trick is classified as “remembered” if participants succeeded in either of the cued recall (lenient or strict) or recollection-based recognition criteria, hence creating another two memory thresholds (remembered (lenient or high) and remembered (strict or high)). All coding procedures are illustrated in the lower half of Figure 2.3.

For the 2-back task, responses given in the four task blocks were used to determine the number of observations in each cell of the stimulus-response matrix according to Signal Detection Theory (Green & Swets, 1966). Additionally, hit rate ($n_{\text{hits}} / n_{\text{n-back trials}}$) and false alarm rate ($n_{\text{false alarms}} / n_{\text{non n-back trials}}$) were computed to derive accuracy (or discrimination index; hit rate – false alarm rate) (Jaeggi et al., 2010; Snodgrass & Corwin, 1988).

Figure 2.3

Surprise Delayed Memory Test



Note. Memory for the magic tricks was tested using a firstly, cued recall (left side) and secondly, a four-alternative forced choice recognition (right side) paradigm, in a blocked manner (highlighted in grey). In the recall block, participants were presented with cue images and asked to describe what happened in the magic trick according to their memory. The recognition block used the same cue images and participants were asked to select one out of four options before rating their confidence.

The lower part of the figure shows how both memory tasks were coded. Rectangles with rounded corners illustrate decision points and the inclusion of question marks highlights yes/no choices. The consequence of a “no answer” is linked with dashed black arrows whereas consequences of “yes answers” are connected by solid black arrows. Final decision outcomes are illustrated as rectangles with straight corners. In short, free answers from the cued recall paradigm were coded by the experimenters if participants did not write “no recall”. A magic trick was coded as “recalled” if the change that occurred was remembered. The selected answer from the recognition memory test was processed in a scripted manner by comparing the selected item against the corrected item. If an item was recognised, additional coding was performed based on the confidence threshold (larger than three). In the last step, the remembered criteria were coded based on whether the magic trick was either recalled (orange and yellow font/lines) or (indicated as a vertical slash) recognised using recollection-based memory (dotted green lines and font).

fMRI Acquisition

We used a Siemens Magnetom Prisma_ft 3.0 T scanner (software syngo MR E11) with a 32-channel head matrix coil to acquire anatomical and functional images at the Centre for integrative Neuroscience and Neurodynamics (CINN), University of Reading, during a single 90-min scanning session.

Functional whole-brain images were acquired using a T2*-weighted gradient-echo echo planar imaging (EPI) pulse sequence with 37 axial slices (in-plane resolution of 3 x 3 x 3 mm, interslice gap of 0.75 mm), interleaved ascending from bottom to top (echo time (TE): 30 ms; repetition time (TR): 2000 ms; flip angle (FA): 90°; field of view (FOV): 1,344 x 1,344 mm²; in-plane matrix: 64 x 64; phase encoding direction: P>>A). The rest phases were acquired in one run each containing 300 volumes (i.e., 10min) after which the scanner stopped automatically. During the task, 1140 volumes were acquired over three runs (run 1: $M = 379.88$, $SD = 14.73$; run 2: $M = 377.84$, $SD = 10.57$; run 3: $M = 381.64$, $SD = 10.88$) and the scanner was stopped manually at the end of each run. Slices were positioned to cover the whole brain based on the localiser scan and slice positioning from the first resting-state scan was used as reference and copied to all following acquisitions. For individuals with large heads, superior parts of the brain were prioritised so that the most inferior slices of the cerebellum are missing for some participants (see “Brain coverage” below).

B₀ data were acquired on the same image matrix and the same geometric prescription as the functional data, using a dual-TE 2D gradient-echo sequence with the following parameters: TR = 488 ms, TE1/TE2 = 5.19/7.65 ms, FA = 60°.

A high-resolution T1-weighted three-dimensional anatomical image was collected using an MPRAGE-gradient sequence with 192 x 1-mm slices (in-plane resolution of 1 x 1 x 1 mm; TE: 2.29 ms; TR: 2300 ms; inversion time (TI): 900 ms; FOV: 240 x 240; FA : 8°).

During the scanning, participants were monitored using a camera and an eye tracker to ensure that participants attended all stimuli and kept their eyes open during rest phases. Further, scanning output was monitored throughout acquisition to ensure high quality of the data. The structural scans were manually reviewed for incidental findings.

fMRI Pre-processing

MRI data were converted from dicom to NIfTI format using pyBIDSconv v1.1.9 (<https://github.com/DrMichaelLindner/pyBIDSconv>) and pre-processed using the AFNI (version 21.2.03) software suite (Cox, 1996), unless indicated differently, with specific AFNI programs indicated using parentheses. The outputs of all pre-processing steps were inspected manually.

Anatomical. The anatomical scans were segmented, parcellated and inflated with FreeSurfer (Fischl, 2012; Fischl et al., 2002) version 6.0.0 using ‘*recon-all*’ and default parameters. For three participants (ID 7, 35, and 37), the white matter or pial surfaces were edited manually. FreeSurfer output was converted to NIFTI using AFNI’s (version 21.0.02) `@SUMA_Make_Spec_FS` to create tissue masks for the lateral ventricle (VENT) and white matter (WM; ‘*adjunct_suma_fs_mask_and_qc*’). The grey matter (GM) segmentations based on the Desikan-Kiliany cortical atlas (Desikan et al., 2006) were used to create the GM mask (‘*3dcalc*’). Cardinalised FreeSurfer output was obliquified to match the affine matrix of the raw anatomical images.

In a separate step, the raw anatomical images were uniformized, anisotropically smoothed, ceiling-clipped, skull-stripped in two iterations and non-linearly registered to ICBM 2009c Nonlinear Asymmetric Template (Fonov et al., 2011) using `@SSWarper`. The affine matrix applied to transform the original anatomical dataset to the template was saved for use during functional pre-processing (see below).

Functional. Pre-processing of the functional data included multiple steps and separate pipelines.

Post-acquisition processing. Due to variation in the task block length caused by pseudo-randomised stimulus presentation, the scanner was stopped manually at the end of each task block. During resting state acquisition, however, the scanner was stopped automatically after 10min (300 volumes). To discard any volumes that were acquired after the task had stopped, but before the scanner was stopped, we cut (using ‘*3dTcat*’) each functional task run to the total block length (i.e., the end of the fixation after the curiosity rating for the twelfth magic trick presented in this block). This was important because the volumes acquired after the task block had ended could have been subject to increased head motion and hence biased data quality assessments. Additionally, this ensures that no lag is induced when all volumes from all three task runs are combined into one time series at the end of the pre-processing as that could hamper later concatenation steps necessary for the data validation analysis (see below). The cut time series are regarded as raw data hereafter.

Minimal pre-processing pipeline. For part of the data quality assessment, minimal pre-processing was applied to each EPI time series separately to avoid additional interpolation associated with cross-run alignments using `afni_proc.py`. The pipeline consisted of despiking, slice-timing and head-motion correction and intrasubject alignment between skull-stripped anatomical and functional scans (see Figure 2.1B). The latter two steps both used a low-motion volume (i.e., the volume with the lowest outlier fraction determined based on respective EPI time series data) and transformations were combined into one interpolation. This pipeline was used to determine brain coverage, head motion, and temporal signal-to-noise ratio (tSNR, option ‘*-volreg_compute_tsnr*’).

Full pre-processing pipeline. In addition to the minimal pre-processing, full pre-processing was applied to the data in a separate pipeline. As a first step, the EPI time series were distortion-corrected (*'epi_b0_correct.py'*) along the encoding axis (P>>A) using the phase difference map (Roopchansingh et al., 2020). The resulting distortion-corrected EPIs were then processed separately for each task, but scans from the same task were processed together. The same blocks were applied to both, task and resting-state distortion-corrected EPI data using *afni_proc.py*: despiking, slice-timing and head-motion correction, intrasubject alignment between anatomy and EPI, intersubject registration to MNI, masking, smoothing, scaling, and denoising (see Figure 2.1B).

Head-motion correction to a low-motion volume was carried out within each run, adding a cross-run registration step to align each within-run base to the volume used for intra-subject alignment (*'-volreg_post_vr_allin yes -volreg_pvra_base_index MIN_OUTLIER'*). Intrasubject alignment was based on the skull-stripped anatomical image created using *@SSWarper* and the low-motion volume from the first run. Intersubject registration to the ICBM 2009c Nonlinear Asymmetric Template was achieved using non-linear transformation to apply the affine matrix computed using *@SSWarper*. Due to variation in slice coverage (see “Brain coverage” below), the extent mask (a mask of voxels that have valid data for every TR) was not applied (*'-volreg_no_extent_mask'*). Transformations for motion correction and intra- and intersubject alignment were concatenated and applied in a single step to avoid repeated resampling and interpolation. To eliminate additional spatial effects induced by non-linear transformations potentially resulting in diversity of spatial correlations across voxels (Wu et al., 2011), data was spatially smoothed to achieve a fixed, global smoothness with full-width half maximum kernel (FWHM) of 8mm (using *'-blur_to_fwhm -blur_size 8'*). The chosen kernel mirrors recommendations for the smoothness of data in intersubject correlation (ISC) to be slightly more than twice the voxel size (Pajula & Tohka, 2014) and was also applied to the resting state data in the interest of consistency. Finally, time series were scaled to a mean of 100.

The tissue maps created using FreeSurfer were resampled to EPI resolution and eroded before applying them to create local WM regressors using fast ANATICOR (Jo et al., 2010) and to derive the first three principal components (PC) of the VENT. Those together with two Legendre polynomials, six demeaned (per run) motion parameters and the derivatives of the motion parameters were included as regressors with VENT PC and motion regressors for each run used as separate regressors, hence allowing the magnitude of the regressors to vary over time. Bandpass filtering was performed during regression (*'-regress_bandpass 0.01 1'*). Time points were censored if motion (Euclidean norm of motion derivatives) exceeded 0.3 or if $\geq 10\%$ of the brain were outliers. Censored timepoints were not removed but set to zero to preserve the temporal structure of the data. This pipeline implements the latest guidance for pre-processing of resting state data (https://afni.nimh.nih.gov/pub/dist/doc/program_help/afni_proc.py.htm)

and is oriented on previous work (G. Chen et al., 2017; Finn et al., 2018) applying similar analysis methods as used in this publication.

Pre-processing was validated by manual inspection of the single subject html quality report that was created by *afni_proc.py* visualising volumes, intra- and intersubject registration as well as seed-based correlation maps. To identify any outliers after pre-processing, *gen_ss_review_table.py* was used to generate a table with the basic summary quantities from pre-processing. Additionally, we implemented checks for left-right orientation errors (Glen et al., 2020) (using `'-align_opts_aea -check_flip'`). The final outputs of the pre-processing were denoised time series with 1140 and 600 volumes, respectively, which were used for the basic fMRI validation analysis (ISC and seed-based functional connectivity analysis).

Basic Data Validation Analyses

All behavioural analyses were carried out using R (R Core Team, 2020) version 3.6.3.

Timing. Due to the naturalistic nature of the stimuli used in this study, standard GLM analysis approaches based on modelling the BOLD response with respect to onset and duration of the stimuli may not be fully suited and model-free approaches like ISC often used in the context of naturalistic fMRI could be preferable. To allow for the rationale of correlating voxel-wise time series across participants, the visual input must be held constant across participants and time-locked with the TR. This is why the beginnings of crucial events (i.e., stimulus presentation and fixation afterwards) were time-locked with the TR and why jitter durations and response windows were equal to (or multiples of) the TR. To be able to validate stimulus timing, observed durations (computed using timestamps collected during experiment presentation) were compared to their intended (i.e., programmed) duration.

Variance decomposition. To address the question whether the MMC Dataset is suitable to investigate within-person variability in curiosity, confidence, and memory encoding, mixed-effects models were applied to decompose the data into three different variance components (Fastrich et al., 2018; Ozono et al., 2021): *participant variance* captures overall individual differences between participants (i.e., a participant might have a high overall memory performance or generally gives high curiosity ratings for all magic tricks), whereas *stimulus variance* reflects differences between the magic tricks (i.e., a trick was very easily encoded by all participants or generally rated low on curiosity). Additionally, *participant x stimulus variance* represents individual differences in participants' responses to different stimuli hence indicating that a participant encoded/was curious about a magic trick due to one's specific conditions and preferences. While participant x stimulus variance serves as a proxy for within-person variability, it also includes variance from measurement errors that cannot be separated statistically.

In the context of binomial data like memory encoding, a simple variance decomposition is not available. However, if the underlying probabilities are not extreme, the binomial data can be treated as if

it was normally distributed to get an approximate indication for the variance decomposition (Goldstein et al., 2002). Given the non-extreme nature of the encoding probabilities in the MMC Dataset, the same mixed effects model (dependent variable $\sim (1|\text{participant id}) + (1|\text{stimulus id})$) was applied to all dependent variables using the *lme4* package (Bates et al., 2015) version 1.1.26.

fMRI Data Quality Assessments. In addition to the preliminary quality control (QC) during the scanning, several other assessments were carried out to assess quality of the data. Raw data of all participants was inspected manually. However, because manual QC is prone to subjectivity and human error, we additionally used two softwares (MRIQC (Esteban et al., 2017, 2021) and pyfMRIqc (Williams & Lindner, 2020)) to derive a variety of image quality metrics (IQMs) based on the raw Nifti scan in a standardised manner. In the MMC Dataset, there are in total five functional scans, two stemming from the resting-state and three from the magic trick watching task. Both tools generated html reports including data visualisation for each scan that were reviewed manually.

Additionally, IQMs for functional scan were extracted for further examination for task- and group related patterns using custom-made R markdown scripts to create different plots and summary statistics of IQMs averaged within participants after standardising each IQM. Additionally, linear-mixed effects (LME) models ($\text{IQM} \sim \text{group} + \text{task} + (1|\text{ID}) + (1|\text{acquisition})$ with $\text{acquisition} = \text{three magic trick watching plus two resting-state scans}$) were applied to the IQMs to test for group and task (i.e., difference in IQM in the magic trick watching task compared to resting-state). Bonferroni correction ($\alpha = 0.05/n(\text{IQMs})$) was applied. If data quality is not affected by task or group, we would expect to not find significant main effects here.

MRIQC. MRIQC (Esteban et al., 2017, 2021) version 0.16.1 was deployed using Docker (version 20.10.2). MRIQC implements a nipype workflow to apply minimal pre-processing to individual anatomical and functional scans before extracting IQMs (one value per IQM per scan). IQMs for anatomical data can be grouped into four broad categories (Esteban et al., 2017, 2019): measures based on noise measures, measures based on information theory, measures targeting specific artefacts, and other measures. IQMs for functional data (Esteban et al., 2019) include some of the same spatial measures used for the anatomical scans as well as measures of temporal information (e.g., tSNR), and measures targeting specific artefacts like head motion (e.g., framewise displacement; Power et al., 2012) as well as IQMs implemented from AFNI. In total, there were 37 IQMs derived from the functional scans, leading to a Bonferroni-corrected p -value of $\alpha = 0.05/37 = 0.0014$ for the LME analyses.

In addition to a summary JSON file (per participant for anatomical data or per scan for functional data) containing the IQMs, a comprehensive html file is created including reports for visual assessments. Additionally, group reports are created separately for the anatomical and functional modality. These

include a table with all IQMs for each scan as well as an interactive group html report that was reviewed for outliers.

Due to the fact that many IQMs are no-reference metrics (Woodard & Carley-Spencer, 2006), context is provided for both, anatomical and functional data by plotting IQMs observed in our data set against those of crowdsourced MRIQC IQMs from the MRIQC Web-API (Esteban et al., 2019).

pyfMRIqc. pyfMRIqc (Williams & Lindner, 2020) was used to further examine data quality of the functional scans. pyfMRIqc extends the functionality of MRIQC by including slice-wise difference measurements for consecutive functional volumes as well as whole-brain NIfTI files of computed QC metrics. The generated html reports do not only allow to identify artefacts and local/global signal loss, but also highlight the effects of motion and can be used to identify problems related to head motion, slice dropouts and local signal loss and artefacts related to e.g., slice leakage as described here (McNabb et al., 2020). To determine head motion, AFNI's '3dvolreg' was run on the raw nifti files and the parameters were passed onto pyfMRIqc. In total, pyfMRIqc generates 23 IQMs derived from the functional scans, resulting in a Bonferroni-corrected p -value of $\alpha = 0.05/23 = 0.0022$ for the LME analyses.

Brain coverage. To quantify the brain coverage in each functional scan, a brain mask was created based on FreeSurfer parcellation excluding the brain stem and slightly dilated to fill holes ('3dcalc' and '3dmask_tool'). This mask was intersected with the EPI mask created by afni_proc.py ('3dAutomask'). A box was fitted for each of the resulting two masks to determine its extent in slices ('3dAutobox') and their difference in slices in inferior-superior direction was calculated (see Aliko et al., 2020 for a similar approach to determine cerebellar coverage).

Head motion. Head motion is a common artefact in fMRI data (Power et al., 2012). While MRIQC quantifies head motion as framewise displacement (FD), the information extractable is limited to the mean value for each scan as well as number and percentage of volumes above a given threshold (specified as 0.5mm). To be able to further investigate and plot FD distributions, motion estimates for each scan created during minimal pre-processing were used to calculate FD following the definition by Power et al. (2012): After transforming degree measurements for roll, pitch, and yaw into mm assuming a 50mm head radius, motion derivatives were calculated and the six parameters were summarised into one scalar per volume. As a next step, mean FD was calculated for each scan and then averaged for each participant to create a per-participant summary metric to quantify the amount of head motion in the sample.

Temporal signal-to-noise ratio (tSNR). To assess image quality, tSNR is often used as it captures the ratio of mean signal to the standard deviation of noise in a time series (Welvaert & Rosseel, 2013). In a similar manner to FD, tSNR is calculated automatically by MRIQC, but only the median value for each scan is included as output. To inspect tSNR values in a similar way as done for FD, data from the

minimal pre-processing pipeline has been used. More specifically, by specifying ‘*-volreg_compute_tsnr*’ tSNR maps were created automatically using the despiked, slice timing and head motion corrected EPI time series that were aligned to the anatomical scan to compute the mean and dividing it by the standard deviation (the latter after detrending). To create a grey matter mask to extract the tSNR values for each voxel, the FreeSurfer whole brain parcellation was resampled to EPI resolution, binarised, and dilated to fill any holes (‘*3dmask_tool*’), then ventricle and white matter were removed (‘*3dcalc*’). The extracted values were averaged within each participant separately for each scan before computing the mean within each participant.

To further quantify tSNR across the whole brain, the tSNR maps automatically created during the full pre-processing pipeline were used. The time series from all runs for each task were combined to calculate the mean of the total time series before the nuisance regression step. The mean was divided by the standard deviation of the time series after nuisance regression. These maps were then used as input for a One-Sample T-test (carried out separately for task and rest with ‘*3dttest++ -Clustsim*’) and the resulting map was Bonferroni-corrected for multiple comparisons (see section on “Thresholding” for details). Comparing the resulting maps (‘*3ddot*’) showed high similarity ($r_{\text{mean tSNR}} = .997$; $r_{z\text{-values}} = .999$), so that maps were averaged within each participant before re-computing the One Sample t-test. To determine whether there were any group effects, the within-participant averaged tSNR maps were also included in a Two-Sample t-test separately applying the same thresholding as described above.

Intersubject correlation. In ISC analysis, a data-driven and model-free approach, the time course of each voxel is correlated for each pair of participants to create pairwise ISC maps where the voxel value reflects the correlation (Hasson et al., 2004). By computing correlations across pairs of participants, the stimulus-driven driven (and hence time-locked) extrinsic component of the BOLD response determines the level of synchronicity in the voxel-wise time courses across participants while the internally-fluctuating intrinsic component is usually cancelled out as noise (Nummenmaa et al., 2018). During the magic trick watching task, participants were asked to view and rate the presented magic trick stimuli. Because neural responses during ratings are more likely to be driven by higher cognitive functions involved in the decision-making process rather than by what was presented on the screen, ISC analysis focused on volumes acquired during magic trick presentation.

The fully pre-processed and denoised BOLD task time series (1140 volumes) were concatenated (again using ‘*3dTcat*’). This step was necessary to remove all volumes acquired during the fixations, mock video presentation, and estimate and curiosity rating as well as to re-order the volumes acquired during pseudo-randomised stimulus presentation so that all volumes acquired during magic trick presentation are in the same order. Such steps have previously been performed by others (Thomas et al., 2018) presenting short video clips in pseudo-randomised order before calculating ISC maps. Onset and

duration were converted from seconds into volumes using the formula $volumes = ceil(round(time\ in\ secs)/TR)$ to select volumes acquired during the magic trick presentation. Due to non-systematic variation in the duration of the magic trick presentation (stimulus-wise computed deviation in seconds ranging from 0.00-0.14 with $M = 0.06$ and $SD = 0.05$; see “Timing” below), the average display duration of each magic trick was used to determine the duration to ensure that the concatenated time series will have the same number of volumes for all participants. The actual length of magic trick presentation differed slightly from the average length (range of absolute difference in seconds: 0-0.6, $M = 0.02$, $SD = 0.07$); however, after converting, the average duration in volume differed from the actual duration in volume in only 49 out of 1800 (or 2.72%) total trials.

The final concatenated task time series (594 volumes) was used to compute pairwise Pearson correlations between each pair of participants for each voxel (using ‘*3dTcorrelate*’). This resulted in $(0.5 * n * (n-1)) = 1225$ pairwise correlations maps that were Fisher’s z -transformed. To determine brain areas that exhibited a significant ISC, a voxel-wise LME model with crossed random effects accounting for the interrelatedness of the pairwise ISC maps (G. Chen et al., 2017) was applied (‘*3dISC*’).

Seed-based resting-state functional connectivity. In seed-based functional connectivity (sFC) analysis, the time course of a seed region – an *a priori* region-of-interest – is extracted and correlated with the time course of all other voxels within the brain to show the regions or networks that are most strongly functionally correlated with the seed (Biswal et al., 1995; D. M. Cole et al., 2010; Margulies et al., 2010). This model-based approach sheds light on the question to which network a specific seed or region belongs to. Based on resting-state data from 1000 participants, Yeo and colleagues (2011) proposed a coarse parcellation of the human cortex into seven networks (e.g., visual and default mode network). The knowledge of these networks allows us to use sFC as a validation analysis: if a seed region within a given network is used to perform sFC, the resulting map of regions exhibiting a high correlation should show overlap with the network the seed region is part of. In fact, AFNI uses this approach as part of their automated quality control within *afni_proc.py*: in the absence of any stimuli files, sFC is automatically calculated for each participant using three seeds and a 6mm sphere around them in the left precuneus (MNI coordinates 5L, 49P, 40S), the right primary visual cortex (MNI coordinates 4R, 91P, 3I), and the left auditory association cortex (MNI coordinates 64L, 12P, 2S) and plotted for each participant separately thresholded at $r \leq -0.3$ and $r \geq 0.3$.

To replicate these analyses for the whole sample, the fully pre-processed and denoised resting-state time series concatenated across both runs were prepared for sFC analysis using ‘*3dSetupGroupInCorr*’ whilst restricting the volumes with an average slightly dilated GM masks averaged across the sample. The resulting data file containing all time series within the mask from all datasets was passed to ‘*3dGroupInCorr*’ together with the three seeds (spheres of 6mm around the seeds

voxels specified above created using `'3dUndump'`) to create maps of the mean Fisher's z -transformed correlation for each seed voxel separately. The maps were then thresholded at $r \leq -0.3$ and $r \geq 0.3$ **after inverting Fisher's z -transformation** (`'3dcalc -expr 'tanh()'`) to create binary masks of first nearest neighbours (`'3dClusterize'`) showing strong functional correlation with each seed region.

To compare these masks with established networks, parcellations from Yeo and colleagues (2011) were downloaded from https://surfer.nmr.mgh.harvard.edu/fswiki/CorticalParcellation_Yeo2011 and the `Yeo2011_7Networks_MNI152_FreeSurferConformed1mm_LiberalMask.nii.gz` file was resampled to the grid of our EPI data in MNI space (`'3dresample'`) to then extract masks for visual, somatomotor, and default network (`'3dcalc'`). To specify similarity between the network and thresholded sFC masks, Dice coefficients were calculated (`'3ddot -dodice'`). Additionally, the overlap between these networks and visual, auditory, and precuneus seed was quantified (`'3dABoverlap'`).

Thresholding. All fMRI analyses are performed on whole-brain level applying a grey matter mask: during pre-processing (full pipeline), the GM mask based on FreeSurfer parcellation was transformed to MNI space and EPI resolution for each participant. These masks were averaged across the sample and thresholded at 0.5 so that a voxel is included in the group GM mask if it is included in the GM mask in at least 50% of the sample (`'3dMean'` and `'3dcalc'`). In total, the mask included 53,204 voxels as determined by `'3dBrickStat'`.

To account for the multiple testing problem due to mass-univariate testing, stringent Bonferroni correction was applied using an initial p -value threshold of $p = 0.05$ and dividing it by the number of voxels inside the mask multiplied by the number of tests carried out. In total, we here report eight tests on whole-brain level (three One Sample t -tests, one Two Sample t -test, one ISC, and three sFC), leading to a Bonferroni corrected p -value threshold of $p = 0.05 / (8 * 53,204) = 0.000001174724$. Additionally, cluster extent thresholding was carried out based on the output of cluster size threshold simulations performed using `'3dClustSim'` for first nearest neighbours clustering (faces of voxels touch) and a cluster threshold of $\alpha = 0.05$ resulting in a threshold of two or three voxels for t -tests and ISC/sFc, respectively.

Data Records

The raw data was converted from dicom to NIfTI format and standardised according to Brain Imaging Data Structure (BIDS; Gorgolewski et al., 2016) using `pyBIDSconv v.1.1.9` (<https://github.com/DrMichaelLindner/pyBIDSconv>) to facilitate sharing and the usage of BIDS apps (Gorgolewski et al., 2017). Anatomical data and other data that could be used to identify participants has been removed from all records. Functional volumes acquired during the task after the scanner was stopped were discarded. The resulting files will be made available on the OpenNeuro platform for sharing

neuroimaging data³. In addition to the raw data, pre-processed data for each participant will be shared in the derivatives directory together with files necessary for nuisance regression. The overall data structure is detailed below.

Participant responses

Location MMC_demographics.csv, MMC_scores.csv, MMC_raw_quest_data.csv,
MMC_other_information.csv, MMC_scan_subj_sum.csv, MMC_experimental_data.csv

File format comma-separated value

Participants' responses to demographic questions, questionnaires, and performance in the working memory assessment as well as both tasks are available in comma-separated value (CSV) files.

Demographic and questionnaire data as well as scores and other information are structured as one line per participant with questions and/or scores as columns. Explicit wordings and naming of variables can be found in the appendix. Participant scan summaries contain descriptives of brain coverage, tSNR, and framewise displacement (one row per participant) averaged first within acquisitions and then within participants. Participants' responses and reaction times in the magic trick watching and memory task are stored as one row per trial per participant and a description of variables can be found in Table A2.3 in the appendix.

Anatomical Data

Location sub-`<group><ID>/anat/sub-<group><ID>_rec-NORM_T1w.nii.gz`

Space [space] orig, MNI152NLin2009cAsym

Description [desc] anatUAC, skullstripped, surfvol

Atlas name [atlas] DesikanKilliany, Destrieux

Label [label] GM, WM, VENT, brain, surfvol

File format NIfTI, gzip-compressed; plain text

Sequence protocol sub-`<group><ID>/anat/sub-<group><ID>_rec-NORM_T1w.json`

The raw, defaced anatomical images (pre-normalise filter applied by scanner) are available as a compressed 3D image file, stored as sub-`<group><ID>/anat/sub-<group><ID>_rec-NORM_T1w.nii.gz`. The skull-stripped image created using `@SSwarper` is available in original and ICBM 2009c Nonlinear Asymmetric Template space as derivatives/sub-`<group><ID>/anat/sub-<group><ID>_space-`

³ Following peer-review and upon publication, the dataset will be made available in the form described here, accompanied by the code used for pre-processing and analysis. Additionally, the R environment to reproduce all figures and tables will be made available.

[space]_desc-skullstripped_T1w.nii.gz together with the corresponding affine matrix (derivatives/sub<group><ID>/anat/sub-<group><ID>_aff12.1D) and incremental warp (derivatives/sub<group><ID>/anat/sub-<group><ID>_warp.nii.gz).

Output generated using @SUMA_Make_Spec_FS (anatomical image, whole brain and tissue masks, as well as FreeSurfer discrete segmentations based on the Desikan-Killiany cortical atlas (Desikan et al., 2006) and the Destrieux cortical atlas (Destrieux et al., 2010; Fischl et al., 2004)) are also available as derivatives/sub<group><ID>/anat/sub-<group><ID>_space-orig_desc-surfvol_T1w.nii.gz, derivatives/sub<group><ID>/anat/sub-<group><ID>_space-orig_label-[label]_mask.nii.gz, and derivatives/sub<group><ID>/anat/sub-<group><ID>_space-orig_desc-[atlas]_dseg.nii.gz, respectively.

Functional Data

Location sub-<group><ID>/func/sub-<group><ID>_task-[task]_run-[1-3]_bold.nii.gz

Task name [task] magictrickwatching, rest

File format NIfTI, gzip-compressed; tab-separated value

Sequence protocol sub-<group><ID>/func/sub-<group><ID>_task-[task]_run-[1-3]_bold.json

Event file

sub-<group><ID>/func/sub-<group><ID>_task-magictrickwatching_run-[1-3]_events.tsv

The raw fMRI data (volumes for task data already discarded) are available as individual time series files, stored as sub-<group><ID>/func/sub-<group><ID>_task-[task]_run-[1-3]_bold.nii.gz.

To enhance re-usability (see Usage Notes for details), the fully pre-processed and denoised files are shared as derivatives/sub-<group><ID>/func/sub-<group><ID>_task-[task]_desc-fullpreproc_bold.nii.gz. Additionally, partially pre-processed files (distortion corrected, despiked, slice-timing/head-motion corrected, aligned to anatomy and template space) are uploaded as derivatives/sub-<group><ID>/func/sub-<group><ID>_task-[task]_run-[1-3]_desc-MNIaligned_bold.nii.gz together with slightly dilated brain mask in EPI resolution and template space where white matter and lateral ventricle were removed (derivatives/sub-<group><ID>/func/sub-<group><ID>_task-[task]_space-MNI152NLIin2009cAsym_label-dilatedGM_mask.nii.gz).

Field Maps

Location sub-<group><ID>/fmap/sub-<group><ID>_[map].nii.gz

Field map name [map] magnitude1, magnitude2, phasediff

File format NIfTI, gzip-compressed

Sequence protocol sub-<group><ID>/fmap/sub-<group><ID>_[map].json

The field maps are available as sub-<group><ID>/fmap/sub-<group><ID>_[map].nii.gz.

Nuisance Regressors

Location derivatives/sub-`<group><ID>/regressors/sub-<group><ID>_task-[task][_run[1-3]]_label-[estimate]_regressor.1D;nii.gz`

Task name [task] magictrickwatching, rest

Estimates [estimate] mot, motdeman, motderiv, ventriclePC, outlierfrac, censorTRs, localWM

File format plain text; NIfTI, gzip-compressed

All nuisance regressors stem from the outputs of `afni_proc.py` (full pre-processing pipeline, see description above). They are provided as space-delimited text values where each row represents one volume concatenated across all runs for each task separately. Those estimates that are provided per run contain the data for the volumes of one run and zeros for the volumes of other runs. This allows them to be regressed out separately for each run.

The motion estimates show rotation (degree counterclockwise) in roll, pitch, and yaw and displacement (mm) in superior, left, and posterior direction. In addition to the motion parameters with respect to the base volume (derivatives/sub-`<group><ID>/regressors/sub-<group><ID>_task-[task]_label-mot_regressor.1D`), motion derivatives (derivatives/sub-`<group><ID>/regressors/sub-<group><ID>_task-[task]_run[1-3]_label-motderiv_regressor.1D`) and demeaned motion parameters (derivatives/sub-`<group><ID>/regressors/sub-<group><ID>_task-[task]_run[1-3]_label-motdemean_regressor.1D`) are also available. The derivatives/sub-`<group><ID>/regressors/sub-<group><ID>/regressors/sub-<group><ID>_task-[task]_run[1-3]_label-ventriclePC_regressor.1D` files contain time course of the first three PCs of the lateral ventricle. Additionally, outlier fractions for each volume are provided (derivatives/sub-`<group><ID>/regressors/sub-<group><ID>_task-[task]_label-outlierfrac_regressor.1D`) and derivatives/sub-`<group><ID>/regressors/sub-<group><ID>_task-[task]_label-censorTRs_regressor.1D` shows which volumes were censored because motion or outlier fraction exceeded the limits specified. The voxelwise time course of local WM regressors is shared as derivatives/sub-`<group><ID>/regressors/sub-<group><ID>_task-[task]_label-localWM_regressor.nii.gz`.

Quality Control Reports

Location derivatives/[tool]/sub-`<group><ID>`

Quality assessment tools [tool] mriqc, pyfMRIqc

File format plain text/html/json

These directories contain a large collection of IQMs. A complete description of the metrics used by MRIQC and pyfMRIqc can be found at <https://mriqc.readthedocs.io/en/stable/measures.html> and <https://drmichaellindner.github.io/pyfMRIqc/>, respectively.

Technical Validation

Stimuli and Behavioural Data

Manipulation check. To verify the effectiveness of the incentives manipulation, participants in the experimental group were asked at the end of the MRI session to indicate whether they invested effort to increase their monetary bonus payments and how much bonus they expected to have earned. Moreover, participants were asked whether they believed that they would receive monetary rewards depending on their performance in the magic trick watching task at the end of the memory test. Indeed, participants in the experimental group reported that they invested efforts ($M = 5.16$, $SD = 1.03$, $\text{min} = 3$, $\text{max} = 7$; 1 = “strongly disagree”, 7 = “strongly agree”), expected bonus payments ($M = \text{£}4.23$, $SD = \text{£}4.13$, $\text{min} = \text{£}0.00$, $\text{max} = \text{£}18.00$), and believed in the incentives manipulation ($M = 3.36$, $SD = 1.73$, $\text{min} = 1$, $\text{max} = 6$; 1 = “Definitely agree”, 6 = “Definitely disagree”).

To check whether we successfully measured incidental memory encoding, participants were asked at the end of the memory test to indicate whether they were aware that their memory would be tested later and whether they tried to encode the magic tricks while watching them (6 = “Definitely agree”, 1 = “Definitely disagree”). Answers revealed that participants were largely unaware that their memory would be tested ($M = 3.76$, $SD = 1.27$, $\text{min} = 1$, $\text{max} = 6$), but still had some intention to encode them ($M = 3.12$, $SD = 1.99$, $\text{min} = 1$, $\text{max} = 6$). Reviewing the answers, the participants gave when asked about their hypothesis regarding the aim of the study at the end of the MRI session, however, showed that, while some participants suspected the study to be related to curiosity, motivation, and incentives or rewards, no participant named encoding, memory, and learning as a main objective.

Timing. To use stimulus annotations as well as intersubject correlation approaches, synchronous timing is important. To demonstrate timing accuracy, intended and actual stimulus timings were compared. The resulting differences (in ms) are summarised in Table 2.2 separately for each group. Overall, timing is largely accurate (range of mean difference per trial component: [-0.144ms; 62.32ms]; range of absolute mean difference per trial component: [1.301ms; 62.32ms]). Welch Two Sample t-tests did not indicate any group-specific timing issues (all $p > .664$).

Variations seen in the stimulus display duration are most likely caused by system-induced latencies in displaying the video clips frame by frame. Additionally, the timestamp of video onset was collected when the video was loaded rather than when the first frame was displayed. The observed minimum delay $\geq 35.42\text{ms}$ supports the assumption that loading in the video caused some processing time, hence adding to the differences between intended and observed presentation times. However, they are relatively minor given the low temporal resolution of fMRI and a TR of 2s and can be accounted for in analysis by either including the actual duration or by using the average display duration for each stimulus as described above.

Table 2.2

Descriptive summary of deviation (in ms) between programmed and observed duration of different trial components separately for each group

Trial component	Mean control group (SD) [min; max]	Mean experimental group (SD) [min; max]	Result Welch Two Sample t-Test
Stimulus display duration	62.32 (78.831) [36.063; 678.637]	61.966 (77.63) [35.42; 636.866]	$t(1797.576) = 0.096$, $p = 0.924$
Fixation after stimulus display	0.407 (2.467) [-5.917; 10.271]	0.444 (2.212) [-6.435; 7.894]	$t(1777) = -0.339$, $p = 0.735$
Fixation between ratings	-0.114 (3.974) [-6.17; 33.398]	-0.103 (3.766) [-5.599; 39.348]	$t(1792.803) = -0.062$, $p = 0.951$
Fixation after ratings	0.356 (2.2) [-6.848; 8.099]	0.311 (2.255) [-8.92; 8.091]	$t(1796.918) = 0.435$, $p = 0.664$

Note. Differences were averaged across all 1800 trials. Group differences were tested for significance using Welch Two Sample t-Tests. $t = t$ value. $p = p$ value.

Encoding performance. To ensure that the MMC Dataset can be used to study memory, encoding performance for each subject was calculated for each memory level and summarised in Table 2.3. Recall performance was comparable to recollection-based recognition and roughly around 36-42%. As expected, recall performance was higher on the lenient compared to the strict criteria and higher encoding performance was found in recognition regardless of confidence and the remembered criteria (53-62%). These results generally overlap with what was observed in the behavioural pilots (Meliss & Murayama, 2019) and encoding is significantly above zero (in the context of recall and remembered criteria) or chance (i.e., 25% given a four-alternative forced choice recognition paradigm), respectively (all $t(49) \geq 18.871$, all $p < 0.001$).

Variance decomposition. Similar to other studies (Fastrich et al., 2018; Ozono et al., 2021), we examined whether this dataset is suited to investigate within-person variability in curiosity, confidence, and memory encoding using mixed-effects models to decompose the data into participant variance, stimulus variance, and participant x stimulus variance. Table 2.3 reports SD (computed over all 1800 trials) of each dependent variable as well as the percentage of variance explained by participant, stimulus, and participant x stimulus variance, respectively. The effect of participant variance ranges from 3.33 to 22.77%. Participant variance explains larger proportions of variance in ratings of curiosity (22.77%) and confidence (12.19%) compared to variance in memory encoding (3.33 - 6.89%) suggesting that individual differences may be larger in ratings compared to encoding or that the former is more prone to response

biases (Podsakoff et al., 2003) than the latter. While stimulus variance explains a low proportion of variance in curiosity (6.71%), the effects are more pronounced in confidence (19.95%) and memory encoding (16.49 - 30.09%). Across all dependent variables, participant x stimulus variance effects between 63.57 and 80.18% indicate that the dataset has sufficient within-person variability. The findings are consistent with what has been reported in the magic trick stimulus database (Ozono et al., 2021) and with another study investigating the impact of epistemic emotions on encoding (Fastrich et al., 2018).

Table 2.3

Average ratings (summarised within participants) for all dependent variables, their standard deviation (SD) over all trials, and results of their variance decomposition

	subject-wise mean (SD) [min; max]	SD (all trials)	Participant variance	Stimulus variance	Participant x stimulus variance
Curiosity	4.407 (0.838) [2.611; 6.972]	1.68	0.2277	0.0671	0.7053
Confidence	3.747 (0.639) [1.694; 4.944]	1.696	0.1219	0.1995	0.6785
Cued recall (strict)	0.368 (0.138) [0.056; 0.667]	0.482	0.0634	0.3009	0.6357
Cued recall (lenient)	0.413 (0.143) [0.111; 0.722]	0.493	0.0652	0.2614	0.6735
Recognition (all confidence level)	0.626 (0.114) [0.417; 0.889]	0.484	0.0333	0.1649	0.8018
Recognition (high confidence)	0.421 (0.149) [0.083; 0.75]	0.494	0.0689	0.1708	0.7603
Remembered (strict or high)	0.531 (0.147) [0.194; 0.833]	0.499	0.0663	0.2245	0.7093
Remembered (lenient or high)	0.553 (0.148) [0.222; 0.861]	0.497	0.0678	0.2033	0.729

Note. Curiosity (scale 1 to 7) and confidence (scale 1 to 6) were directly rated by the participants during the magic trick watching task and recognition memory test, respectively. Memory measurements were coded as zero or one and the numbers represent the fraction remembered (out of 36 trials) on different thresholds. Cued recall captures the coded performance in the cued recall block applying strict and lenient criteria. Recognition captures whether the correct alternative was selected in the four-alternative forced choice recognition paradigm (regardless of the confidence rating). High confidence recognition reflects that the correct alternative was selected with a confidence rating above three. A magic trick was coded as remembered if it was recalled or recognised with high confidence (Hasson, Furman, et al., 2008). Overall, the MMC Dataset has good encoding performances while avoiding floor and ceiling effects. Likewise,

high participant x stimulus variance suggests that the data is suitable to investigate within-person variability. SD = standard deviation.

Imaging Data

Data quality assessments. In addition to the preliminary quality control (QC) during the scanning, several other assessments were carried out to assess quality of the data. Raw data of all participants was inspected manually. However, because manual QC is prone to subjectivity and human error, we additionally used two softwares to derive a variety of IQMs in a standardised manner and the results are described below.

Due to a lack of “gold standard” of MRI data quality, however, we did not exclude any participants based on the image quality assessment reported here. Instead, all outputs and reports are shared together with the data to allow other researchers to use the data as they find it appropriate.

MRIQC. Assessing data quality using MRIQC showed that the MMC Dataset is of good quality. The comparison to the crowd-sourced data from the web API (Esteban et al., 2019) indicated that the IQMs from functional and anatomical data are comparable with other data sets. Reviewing the group html report, outliers were observed in some IQMs. These are highlighted in an R Markdown file (<https://osf.io/hdbne/>) summarising the explorative analyses of the functional data IQMs together with the web API comparison for anatomical and functional data. This file is shared together with all other outputs generated by MRIQC.

Overall, the IQMs were stable over the course of the experiment (mean participant-wise SD summarised across all standardised IQMs 0.35, $SD = 0.25$, min = 0.08, max = 1.08). The LME analysis showed that there were no group effects in any of the 37 functional IQMs (all $p > 0.150$). However, main effects of task were found for the number of volumes (“size_t”: estimate -77.41, $p < 0.001$ surviving Bonferroni-corrected threshold of $\alpha = 0.05/37 = 0.0014$), and two descriptive background statistics (“summary_bg_mad”: estimate -0.09, $p < 0.001$; “summary_bg_median”: estimate -0.07, $p < 0.001$; all other $p > 0.02$), all indicating smaller values in resting state vs task data.

pyfMRIqc. Reviewing the reports, no indication was found that artefacts or signal loss had occurred. The additional analyses revealed that metrics were stable within each participant over the course of the experiment (mean participant-wise standard deviation summarised across all standardised IQMs 0.34, $SD = 0.24$, min = 0.09, max = 1.08). In the LME analyses, no main effects of group (all $p > 0.318$) were found and only the effect of task on number of volumes (estimate -77.46 indicating lower values during resting state, $p < 0.001$; all other $p > 0.03$) survived Bonferroni correction ($\alpha = 0.05/23 = 0.0022$). Any outliers were reviewed more thoroughly by inspecting the associated NIfTI files of computed QC metrics, but no issues were identified. While there was high variance in motion estimates between participants, there was no slice-wise displacement larger than voxel size observed in the sample.

The results of the additional analyses are summarised in a R Markdown file (<https://osf.io/wfqvd/>) and uploaded to the pyfMRIqc root directory together with the individual html reports.

Brain coverage. Overall, most of the brain was scanned for the majority of scans as indicated by on average 98.17% ($SD = 2.75\%$) of the number of slices in z direction (i.e., inferior-superior) included in the brain mask covered by the EPI mask. More specifically, 85.48% of scans had either zero (50.0%) or one (35.5%) slices missing. The mean number of missing slices was 0.82 slices ($SD = 1.24$ slices) when averaged across scans or 0.82 slices ($SD = 1.01$ slices) when averaging within participants first.

The mean number of missing slices increased throughout the course of the experiment, however, both groups were equally affected by this (see Table 2.4). This can most likely be attributed to the fact that participants have moved in the breaks in between scans as slice positioning was copied from the first resting-state scan without repeating localiser and slice positioning ahead of each scan. There are, however, no variations in brain coverage between the groups (all $p > 0.269$).

Table 2.4

Missing slices for each scan separately for each group

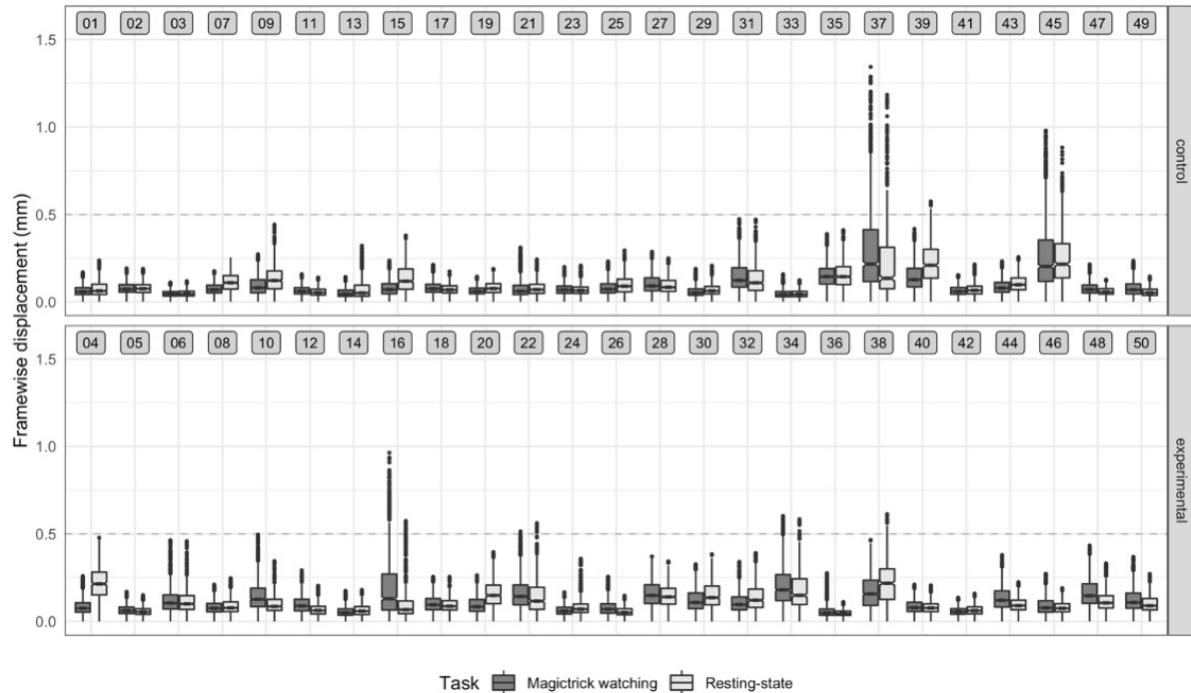
Scan	M control group (SD) [max]	M experimental group (SD) [max]	Result Welch Two Sample t- Test
1 Pre-learning rest	0.64 (0.7) [2]	0.52 (1.05) [5]	$t(41.914) = 0.477, p = 0.636$
2 Magic trick task block 1	0.6 (0.65) [2]	0.6 (1.15) [5]	$t(37.665) = 0, p = 1$
3 Magic trick task block 2	0.68 (0.69) [2]	0.92 (1.41) [5]	$t(36.619) = -0.786, p = 0.437$
4 Magic trick task block 3	0.72 (0.74) [2]	1.12 (1.48) [5]	$t(35.203) = -1.209, p = 0.235$
5 Post-learning rest	1.08 (1.78) [8]	1.2 (1.76) [7]	$t(47.993) = -0.24, p = 0.811$

Note. The extents of the EPI mask in inferior-superior direction were compared with those of the FreeSurfer parcellation mask. The table shows the mean (M) difference (standard deviation; SD) [maximum] in slices for each group and scan separately together with the results of the Welch Two Sample t-Test. $t = t$ value. $p = p$ value.

Head motion. For the MMC Dataset, mean FD across all scans as calculated by MRIQC was 0.13mm. This is comparable to the mean FD of 0.16mm computed based on the data from the MRIQC Web API (Esteban et al., 2019). Re-computing head motion based on the motion estimates from the minimal pre-processing pipeline led to similar results. Overall, head motion was low in the data set as indicated by mean FD below 0.5mm for all participants (mean of participant mean = 0.13mm, $SD = 0.06$ mm, min = 0.06mm, max = 0.33mm) and is illustrated in Figure 2.4 separately for each task.

Figure 2.4

Frame-wise displacement (FD, in mm) for each participant



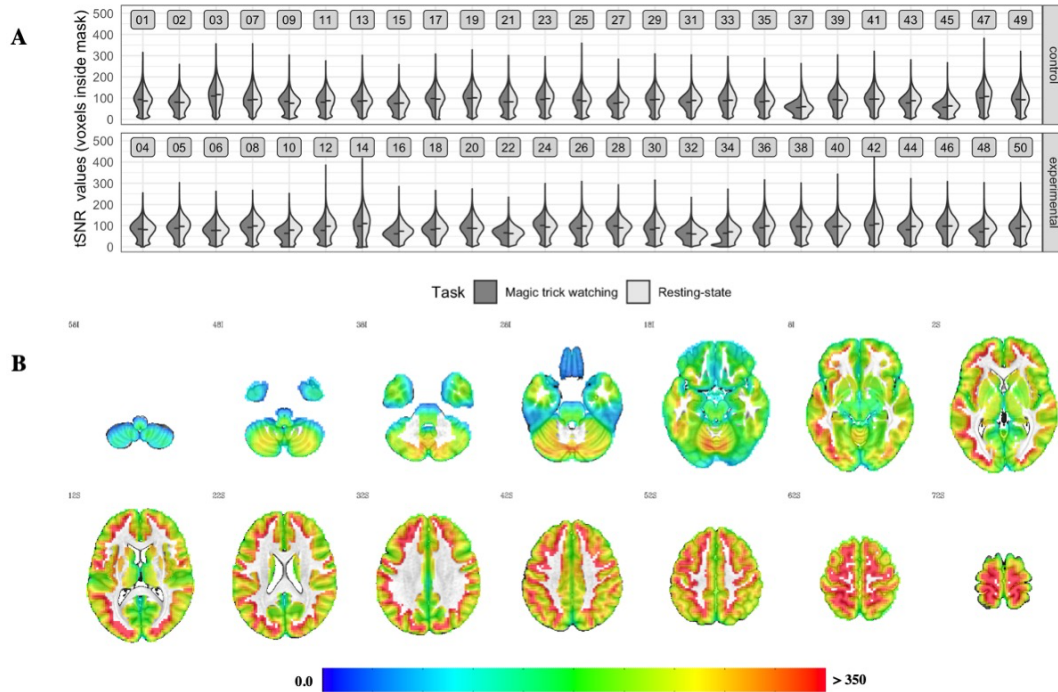
Note. FD was calculated based on motion estimates from the minimal pre-processing pipeline. For each scanner run, FD was determined using the formula provided by Power and colleagues (2012) and concatenated within each task. Data for each task is shown as a notched boxplot where the left one (dark grey) shows FD from the magic trick watching task (across all three blocks) and the right one (light grey) the data from the resting-state scans (across both runs), respectively. To prevent scaling issues, outliers (values smaller $1.5 \times$ lower quantile or larger $1.5 \times$ upper quantile) were removed from the data before plotting. Two panels show data from the control group on the top and data from the reward group on the bottom. Participant ID labels were added above the boxplots. FD was low in the MMC Dataset within each participant as indicated median values below the threshold of 0.5mm (grey dashed line). Further, values were comparable during task and rest as well as for both groups.

Temporal signal-to-noise ratio (tSNR). tSNR values per scan as computed by MRIQC are comparable between MMC Dataset and Web API (Esteban et al., 2019) (mean median tSNR = 49.64 or 46.51, respectively). The minimally pre-processed data set has a satisfactory tSNR (mean of participant mean = 85.53, SD = 11.64, min = 59.72, max = 111.59) which is comparable with previous dataset presenting naturalistic stimuli (Aliko et al., 2020; di Oleggio Castello et al., 2020; Nastase et al., 2018; Sengupta et al., 2016). Additionally, Figure 2.5A shows the distribution of tSNR values separately for task and rest whereas Figure 2.5B shows the mean whole brain tSNR values surviving thresholding. As

expected, all voxels show tSNR values significantly above zero, but there are variations in tSNR across different brain areas: while the values are especially high in lateral and superior cortical areas (shown in red), lower tSNR is found in e.g., ventral and inferior parts of the brain (shown in turquoise). The Two-Sample t-test revealed no significant differences in tSNR between the groups.

Figure 2.5

Temporal signal-to-noise ratio (tSNR)



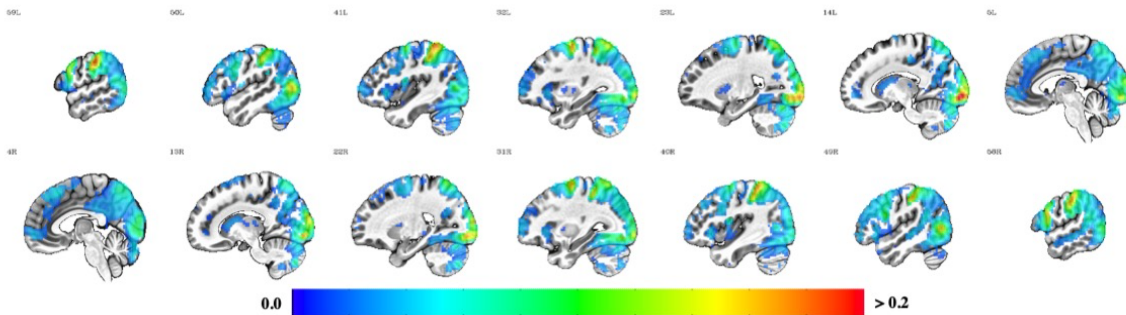
Note. (A) Values were extracted from the tSNR maps created as part of the minimal pre-processing pipeline using a dilated grey matter mask and concatenated within each task. Data is shown as a split violin plot where the left side (dark grey) of the plot shows estimates from the magic trick watching task (across all three blocks) and the right side (light grey) the data from the resting-state scans (across both runs), respectively. Horizontal cross bars indicate the median values. The panel structure is as in Figure 4. Overall, minimally pre-processed time series show satisfactory tSNR values. Their distribution is comparable for task and rest and between groups. (B) To plot the distribution of voxel-wise tSNR values, the tSNR maps generated in the full pre-processing pipeline were averaged within each participant before computing the mean tSNR map shown. Overall, tSNR varies across the brain: cortical values are high while areas close to air-tissue boundaries show lower tSNR values.

Intersubject correlation. To show that watching short magic tricks leads to similar intersubject synchronisation as reported when e.g., watching movies, ISC analysis was carried out. After Bonferroni-

correction and cluster-extent thresholding, significant ISC was observed in large portions of the brain (see Figure 2.6): spanning from the cerebellum to visual cortices (BA17, BA18, BA19) to the superior (BA7) and inferior (BA39, BA40) lateral parietal cortex including temporo-parietal junction to the superior temporal sulcus and middle temporal gyrus (posterior parts of BA20, BA21, BA22), the fusiform gyrus (BA37) as well as primary somatosensory (BA1, BA2, BA3, BA43) and (pre-)motor cortices (BA4, BA6) and stretching into prefrontal areas including frontal eye fields (BA8), lateral (BA9, BA44, BA45, BA46) and anterior (BA10) prefrontal cortex. Medially, significant ISC was observed in the cuneus (BA17, BA19), precuneus (BA7), and cingulate cortex (BA23, BA24, BA30, BA31, BA32) and subcortically in striatum and thalamus. While the maximum ISC ($r = .25$) is comparable to previous work (Aliko et al., 2020; Pajula & Tohka, 2016), most voxels had fairly low correlation values which is why additional thresholding at $r > 0.1$ was performed for plotting purposes (Figure 2.7A). As expected, when presenting dynamic visual stimuli of moving body parts and objects, primary visual and association cortices as well as somatosensory and motor areas show high ISC values. In comparison, no ISC was observed in the primary auditory cortex which is in alignment with the absence of sound in the video clips.

Figure 2.6

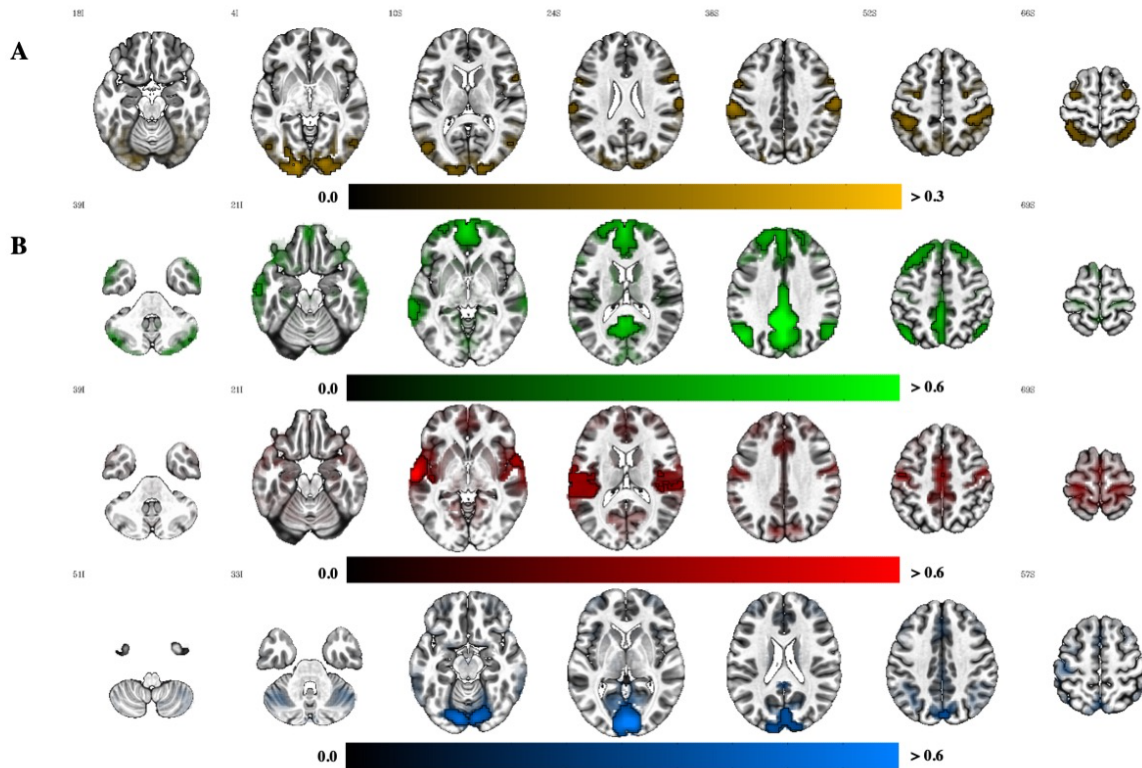
Intersubject correlation analysis



Note. The map shows clusters surviving Bonferroni and cluster size extent thresholding. To avoid scaling issues, the top of the colour bar was matched with $r \geq .2$. Overall, the results validate the magic trick data by demonstrating synchronicity of areas across the brain with highest ISC values found in visual areas. ISC observed in other areas such as precuneus and temporo-parietal junction, regions putatively involved in various cognitive processes, as well as prefrontal cortices potentially highlight a plethora of cognitive processes and associated research questions that can be addressed with the MMC Dataset.

Figure 2.7

Summary of basic whole-brain data validation analyses



Note. After correcting for multiple comparisons (using Bonferroni corrected and cluster-extent thresholding), the resulting maps were thresholded to only show voxels exceeding small (ISC) or moderate (sFC) correlation coefficients. The effect of thresholding was further softened by applying opacity information so that values closer to the threshold would be shown with higher opacity and a box was added around supra-threshold voxels only. (A) A threshold of $r > 0.1$ was applied to the ISC map (shown in amber) highlighting high ISC in visual and sensory-motor areas. (B) To threshold the sFC maps in a similar manner as *afni_proc.py*'s automatic QC scripts, $r > 0.3$ was used as the cut-off value. As expected, the precuneus seed (MNI 5L, 49P, 40S; map shown in green) is correlated with other areas in the default mode network whereas the auditory seed (MNI 64L, 12P, 2S) is predominantly functionally connected with other auditory and somatosensory areas (map shown in red). Likewise, the time series of the visual seed (MNI 4R, 91P, 3I) co-varies with activity in other parts of the visual cortex (map shown in blue).

Seed-based resting-state functional connectivity. The thresholded sFC maps show distinct, non-overlapping cortical networks (all Dice coefficients of maps created using different seeds ≤ 0.015) that are shown in Figure 2.7B: The precuneus seed (Figure 2.7B, green) showed strong correlations with

other voxels in the precuneus (BA7), posterior (BA23, BA29, BA30, BA31) and anterior (BA24, BA32) cingulate cortex, as well as dorso- (BA9) and ventromedial (BA10, BA12) prefrontal cortex including frontal eye fields (BA8), angular gyrus (BA39) and middle temporal lobe (BA21). Overall, it shows high similarity with the default network mask (Dice coefficient = 0.504) of which 90.625% of voxels are part of.

The sFC map created using the seed from the auditory cortex (Figure 2.7B, red) shows predominantly functional connectivity within the superior (BA41, BA42, BA43, BA21, BA22) temporal gyrus, the frontoparietal operculum (BA43). Additionally, clusters in somatosensory (BA1, BA2, BA3) and primary motor (BA4) cortex and supplementary motor area (BA6) are found. The sphere shares 84.849% of voxels with the somatomotor network with which its similarity is moderate (Dice coefficient = 0.219).

The seed located in the visual cortex (Figure 2.7B, blue) exhibits strong correlations within the lateral and medial occipital lobe, cuneus, Calcarine and lingual gyrus (BA17, BA18, BA19, BA37). In total, 96.97% of voxels within the sphere are part of the visual network and the Dice coefficient of 0.294 shows satisfactory similarity.

Discussion

Overall, the validation analyses show that the MMC Dataset is of high quality. To facilitate reusability, we share the raw data as well as the output of the full pre-processing pipeline. For researchers that wish to modify the pre-processing pipeline (e.g., by applying a different FWHM kernel or algorithm for smoothing), partially pre-processed data that is already in MNI space is shared together with all nuisance regressors used.

While naturalistic stimuli are often too rich to be captured in GLMs with predefined events modelled as regressors, specific features can be annotated and used as regressors to localise sensitive brain areas (Bartels & Zeki, 2004; Sonkusare et al., 2019) or time courses can be extracted in reverse correlation analyses to characterise contents in the movie leading to peaks and troughs in the time series of a voxel or ROI (Hasson et al., 2004; D. D. Wagner et al., 2016). To assist such analysis approaches, we provide markers based on manual coding performed by the experimenters. However, these annotations can be extended in numerous directions. For instance, independent samples could rate the moment(s) of surprise for each magic trick or a more objective approach could be developed. Antony and colleagues (Antony et al., 2021) developed a model to characterise surprise in basketball games that were correlated with subjective ratings. Likewise, this dataset is also valuable in an emerging field referred to as “science of magic” where it can be used to study e.g., perception and other cognitive processes (Kuhn et al., 2008;

Rensink & Kuhn, 2014). Stimuli will be uploaded to the OpenNeuro directory in a password-protected folder together with the request procedure.

All in all, this dataset has the potential to foster our understanding of the neural underpinnings of curiosity- and incentive-motivated incidental learning as well as cognitive mechanisms related to processing violations of predictions, however, some limitations that should be considered are discussed below.

First, with respect to the MRI data acquisition, the study was conducted without multiband acceleration. While EPI multiband acquisition leads to a higher overall temporal resolution, this is not necessarily the case in regards to the detection of mesolimbic reward responses (Srirangarajan et al., 2021). Further, artefacts are commonly observed (Todd et al., 2016) and it has recently been demonstrated that the artefact severity is related to eye movements (McNabb et al., 2020). During naturalistic viewing, information is presented across the whole screen and the lack of fixations encourages free eye movements. Hence, to avoid the occurrence of inter-slice leakage and intra-slice aliasing, we opted for an acquisition protocol without multiband. In fact, the same protocol was deployed as used during the data acquisition of Lau and colleagues (2020) who also presented magic tricks inside the fMRI scanner taken from the same database.

Secondly, it should be acknowledged that presenting naturalistic stimuli inside the MRI scanner is only an approximation to everyday life. While critical discussions of this issue are presented elsewhere (Shamay-Tsoory & Mendelsohn, 2019; Sonkusare et al., 2019), some important arguments are summarised here. Although naturalistic stimuli share features with real-life situations where items are not perceived in isolation and detached from context but embedded in a dynamic, multisensory stream of fore- and background, passive naturalistic viewing paradigms cannot fully capture real-life, complex brain processes. This is amplified by restrictions of e.g., head movements and difficulties to understand the sound due to scanner noise. Additionally, despite the broad range of what constitutes naturalistic stimuli (e.g., movies/TV shows, audio books, commercials/advertisements, musical/theatrical productions), they all are often rather constructed and/or edited. For instance, movies – often used as stimuli in naturalistic paradigms (see e.g., Aliko et al., 2020; di Oleggio Castello et al., 2020; Hanke et al., 2014) – are directed to guide the viewer’s attention, evoke certain emotions and present the underlying narrative of the movie, often relying on verbal information making them (a) often lengthy in duration and (b) inherently dependent on language and culture. Because movies are usually not produced for the use in research but for other purposes including entertainment, this leaves little experimental control to the researcher and the reliability, validity, and generalisability of findings from a given movie are often not established.

To find a balance between rich, naturalistic stimuli on the one hand and experimental control, we decided to present stimuli from a validated database that not only induce curiosity reliably, but also are as

standardised as possible: for example, all magic tricks have the same dark background and viewing focus, the magicians were similar clothing, and all videos are muted. While muted clips certainly circumvent the problems of scanner noise interfering with the auditory experience and language (and culture) dependency, the lack of multimodal stimulation also reduces the resemblance to real-world stimuli. On a broader level, one could argue that magic tricks themselves are not necessarily the most accurate presentation of real-world experiences and stimuli. However, on the continuum between highly controlled, laboratory stimuli and real-life, they are more naturalistic, dynamic, and complex than static trivia questions presented on a screen. We hope that researchers will find the added ecological validity of the MMC Dataset helpful when satisfying their intrinsic desire to know more about curiosity- and incentive-motivated learning.

Chapter 3: Broad Brain Networks Support Curiosity-Motivated Incidental Learning of Naturalistic Dynamic Stimuli With and Without Monetary Incentives

“We find ourselves in a bewildering world. We want to make sense of what we see around us and to ask: what is the nature of the universe? What is our place in it and where did it and we come from?

Why is it the way it is?”

(Hawking, 2016, p. 205)

With the words above, Stephen Hawking introduced the concluding chapter of his famous book “A Brief History Of Time” where he aimed to explain our universe to a non-scientific audience. The wonder the words capture, the intrinsic desire to know, has not only motivated scientists to dedicate their careers to trying to find answers to the big questions of the universe, but also the readers of the more than 10 million copies sold to spend their time and money to acquire knowledge about the Big Bang. This is intriguing because, arguably for most of them, being able to understand how to combine weak and strong nuclear forces with those of gravity and electromagnetism into a single unified theory will have no instrumental value to maximise their rewards in their everyday lives.

In line with this anecdotal evidence, research has found that humans actively engage in non-instrumental information-seeking (Kobayashi et al., 2019; van Lieshout et al., 2021), even if it requires a small cost (Bennett et al., 2016; Brydevall et al., 2018; Kang et al., 2009; Kobayashi & Hsu, 2019; Marvin & Shohamy, 2016; van Lieshout et al., 2018), involves taking the risk of receiving an electric shock (Lau et al., 2020), or leads to experiencing negative emotions like regret (FitzGibbon et al., 2021). These observations have led researchers to propose that information is a reward (FitzGibbon et al., 2020; Marvin & Shohamy, 2016), functioning like extrinsic rewards to govern our behaviour. In fact, in monkeys the same dopaminergic neurons in the midbrain that signal the expected amount of primary extrinsic rewards also signal the expectation of information (Bromberg-Martin & Hikosaka, 2009). Likewise, in humans the subjective value of information and basic extrinsic rewards share a common neural code expressed in the striatum and other reward-related areas such as the ventromedial prefrontal cortex (Kang et al., 2009; Kobayashi & Hsu, 2019; Lau et al., 2020).

Curiosity-Motivated Learning

Importantly, previous studies showed that the subjective feelings underlying our desire to know – which we will refer to as “subjective feeling of curiosity” – has been shown to facilitate memory encoding (for recent reviews, see Gruber et al., 2019; Gruber & Ranganath, 2019). More specifically, the subjective feeling of curiosity elicited by a curiosity-triggering cue (i.e., a trivia question; cf. Jepma et al., 2012) facilitates the intentional encoding (Duan et al., 2020; Halamish et al., 2019) of the target item (i.e.,

the answer to trivia question; cf. Jepma et al., 2012). Indeed, enhancing effects of curiosity on memory for the target information have repeatedly been identified (Brod & Breitwieser, 2019; Fastrich et al., 2018; Galli et al., 2018; Gruber et al., 2014; Jepma et al., 2012; Kang et al., 2009; Ligneul et al., 2018; Marvin & Shohamy, 2016; Mullaney et al., 2014; Murayama & Kuhbandner, 2011; Murphy, Dehmelt, et al., 2021; Poh et al., 2021; Stare et al., 2018). Even more interestingly, incidental information that is semantically unrelated to the cue eliciting the feeling of curiosity but presented in close temporal proximity (i.e., during a state of high compared to low curiosity) is also preferably encoded (Galli et al., 2018; Gruber et al., 2014; Murphy, Dehmelt, et al., 2021; Stare et al., 2018).

Neuroimaging research has suggested that such curiosity-motivated learning is related to the activity and interaction between three brain areas: the nucleus accumbens (NAcc), the dopaminergic midbrain (VTA/SN), and the hippocampus (HPC). Specifically, Gruber and colleagues (2014) investigated whether the brain activity during curiosity elicitation at cue presentation (i.e., the trivia question) predicts later memory for the upcoming target information (i.e., the answer to the trivia question) and found that while the dopaminergic midbrain was more activated during the anticipation of later remembered compared to later forgotten targets irrespective of the degree of curiosity elicitation, the right HPC and the bilateral NAcc showed increased activation for remembered compared to forgotten targets only for high-, but not low-curiosity cues. They also found a strong correlation between the curiosity-driven memory benefit for incidental information and the curiosity-related subsequent memory effects in the VTA/SN and the HPC as well as the functional connectivity between them for high, but not low curiosity trials. Taken together, the results suggest that anticipatory activity in the mesolimbic dopaminergic circuit and the hippocampus supports the learning benefits associated with high compared to low states of curiosity (Gruber & Ranganath, 2019).

However, despite the increasing number of studies on curiosity-motivated learning, the vast majority of studies have relied only on a single type of material (for exceptions, see e.g., Cen et al., 2021; Jepma et al., 2012) — trivia questions (e.g., Fastrich et al., 2018; Gruber et al., 2014; Kang et al., 2009; Marvin & Shohamy, 2016; Murayama & Kuhbandner, 2011; Wade & Kidd, 2019). Although the trivia question paradigm has obvious benefits, as the paradigm allows researchers to examine memory in a similar manner with traditional memory experiments (e.g., questions are “cues” and answers are “targets”), we identify two issues. First, the paradigm examines memory encoding by relying on discrete, static elements, which lacks the complex, contextual and narrative nature of everyday events (Shamay-Tsoory & Mendelsohn, 2019). In fact, the actual process of curiosity elicitation is more dynamic. In classrooms, for example, students’ curiosity ebbs and flows over time while watching the lecture, and various factors contribute to the temporal dynamics (Hidi & Renninger, 2006). In other words, the state of curiosity should not be seen as a snapshot phenomenon, but as embedded within the sequence of events

and psychological processes (Murayama, 2022). Thus, it is important to induce curiosity using more complex, dynamic stimuli to ensure ecological validity.

Second, while trivia questions trigger curiosity by promoting the detection of a gap in people's knowledge (i.e., information-based prediction errors (PEs); Gruber & Ranganath, 2019), there has been increasing consensus that curiosity is elicited by multiple different factors, which may be governed by different psychological and neural mechanisms (Gruber & Ranganath, 2019; Jach et al., 2021; Kobayashi et al., 2019; Sharot & Sunstein, 2020). The heavy reliance on trivia questions may have researchers overlook some important neural mechanisms underlying our information-seeking behaviour. For example, the subjective feeling of curiosity can also be elicited in novel environments or when events violate expectations and create a sense of surprise (i.e., context-based PEs; Gruber & Ranganath, 2019). In fact, research has shown that novel environments elicit higher curiosity and are associated with higher incidental encoding rates (Cen et al., 2021); that violation of the expectation stimulates surprise, curiosity, and learning (Brod et al., 2018; Brod & Breitwieser, 2019); and that surprise induced by cognitive incongruity is a reliable predictor of curiosity (Vogl et al., 2019). However, the role of this surprise-based curiosity on memory encoding has been under-examined, and little research has addressed the neural correlates underlying it (cf. Ligneul et al., 2018 for an account of the effects of surprise within the trivia question paradigm).

Role of Extrinsic Incentives

Another critical issue is the role of extrinsic incentives and rewards⁴ in curiosity-motivated learning. Overall, the facilitating effects of curiosity on memory encoding – as operationalised using cue-target pairings where curiosity can be understood as the anticipation of rewarding information (Gruber et al., 2019) – bear a striking resemblance to the effects of extrinsic rewards on memory in the literature (for a review, see Miendlarzewska et al., 2016): it has been shown that providing monetary incentives and rewards not only increases intentional encoding of incentivized items (Adcock et al., 2006; Gruber et al., 2013; Gruber & Otten, 2010; Wolosin et al., 2012), but also the incidental encoding of information

⁴ In previous literature on motivated learning, the terms “rewards” and “incentives” have been used rather interchangeably (e.g., Adcock et al., 2006), but are yet distinct concepts. Incentives are “plans that have predetermined criteria and standards, as well as understood policies for determining and allocating rewards” (Greene, 2010, p. 219). As such, incentives can be seen as a promise of later rewards whereas rewards are the outcome of motivated behaviour that are received/perceived/consumed (Matyjek et al., 2020; Schultz, 2015).

presented in the context of rewarded task (Bunzeck et al., 2010, 2012; Gruber et al., 2016; Murayama & Kitagami, 2014; Murty & Adcock, 2014; Patil et al., 2017; Stanek et al., 2019; Wittmann et al., 2005, 2008, 2011). Neuroimaging studies have linked these behavioural effects on intentional encoding to activity in NAcc, HPC, and VTA showing an enhanced activity during cue presentation for later remembered compared to forgotten targets only in the context of high, but not low rewards (Adcock et al., 2006) and further showed that functional connectivity between HPC and VTA/SN supports the behavioural effects (Adcock et al., 2006; Wolosin et al., 2012). This involvement of VTA/SN and HPC is consistent with the hypothesis that incentives and rewards promote memory formation via dopamine release modulating hippocampal synaptic encoding processes during long-term potentiation (Lisman et al., 2011; Lisman & Grace, 2005; Shohamy & Adcock, 2010).

While the effects of monetary incentives/rewards and, more recently, curiosity have been studied in isolation leading to very valuable insights, only a small portion of studies have actually looked at their conjunction. However, studying both effects in the same study is necessary to closely understand the similarities and differences of neural mechanisms in how they benefit learning. In addition, studying the simultaneous effects of curiosity and extrinsic incentives and rewards is of theoretical and practical importance because there is a reason to believe that they have an interactive effect to influence learning — specifically the effects of curiosity may be suppressed in the presence of extrinsic rewards (called undermining effect; Deci et al., 1999; Murayama et al., 2010). In fact, Murayama and Kuhbandner (2011) found that both monetary reward and the interestingness of trivia questions (as rated by a separate sample) had an enhancing effect on encoding, but the main effects were further qualified by an interaction, where monetary rewards only enhanced encoding of trivia questions rated as not interesting. The findings were replicated in younger and older adults (Swirsky et al., 2021) although some other studies failed to find the interaction effects (Duan et al., 2020; Halamish et al., 2019). Thus, the literature suggests the possibility that there may be unique non-additive neural patterns when both curiosity and monetary incentives are present (Murayama & Kuhbandner, 2011).

Current Research

The current chapter aims to expand our understanding of curiosity-motivated learning in two substantive manners. First, to capture the dynamic nature of curiosity, we used novel naturalistic stimuli that strongly trigger curiosity — videos of magic tricks. Magic tricks induce curiosity independent of language and prior knowledge by showing implausible, if not impossible events (Kuhn et al., 2008; Rensink & Kuhn, 2014). Because the viewer generates predictions as the magic trick unfolds, any violation of causal relationships would also violate the viewer's expectations, triggering a relatively strong surprise-based curiosity (i.e., context-based or perceptual PE; Zacks et al., 2007). Indeed, previous research has shown that magic tricks are rated as surprising, violate cause and effect relations, and lead to

unexpected outcomes (Danek et al., 2015; Parris et al., 2009), trigger epistemic emotions (surprise in response to the trick, interest in the trick, and curiosity in the solution; Ozono et al., 2021), and elicit curiosity to motivate risky decision making in a similar way as trivia questions do, supported by the ventral striatum (Lau et al., 2020).

Second, we manipulated the availability of extrinsic incentives such that we can examine the potential interactive effects of curiosity and extrinsic incentives on learning. As indicated earlier, despite the strong suggestion that information-seeking is driven by reward learning mechanisms, neuroimaging studies on motivated learning examined curiosity and extrinsic incentives rather separately, making it difficult to understand how these two types of motivating factors enhance (or do not enhance) memory altogether. The current work provides a first attempt to examine the interactive effect.

We conducted three studies (two behavioural, one fMRI) which have a similar structure. In all experiments, participants viewed a series of magic trick videos and performed an incentive orientation task including curiosity ratings. To examine the effects of extrinsic incentives, half of the participants were promised additional monetary incentives for the orientation task whereas the other half of participants did not receive such instructions. A week later, the memory for the magic tricks was assessed using surprise recognition and recall tests. Based on the previous literature, we hypothesised that both curiosity and monetary incentives would facilitate memory encoding, both of which may be supported by similar neural processes located in the HPC-VTA loop (Lisman & Grace, 2005), hence we also examined the potential interaction between curiosity and monetary incentives. We found both curiosity and incentive effects on incidental memory (albeit weaker effects of incentives), but they seem to be supported by the different memory processes (i.e., recollection and familiarity). Interestingly and contrary to our expectation, neither the effects of curiosity nor of incentives themselves were located in the reward network of the brain or the hippocampus. However, the effects of curiosity, but not of incentives, on encoding were located within the reward network and the hippocampus. Additionally, all effects were also distributed across higher order cortices. These results suggest that curiosity-motivated learning may recruit a broader range of neural processes than previously thought, not solely based on mesolimbic structures often identified using simple stimuli (i.e., trivia questions).

Methods

Study 1: Behavioural Study

Participants & Design. The *a priori* defined intended sample size was in total 80 participants. Participants were recruited using Prolific (<https://prolific.co>) for an online study consisting of two parts spaced one week apart. Both parts took approximately 45min each and participants were reimbursed

£7.50 for their time. For inclusion, the following criteria were defined: aged between 18 and 37, fluent in English, minimum approval rate of 95% and at least ten previous submissions.

Unbeknownst to the participants, the study operationalised a between-group incentive manipulation where the experimental group was instructed that they could earn additional monetary bonus for their performance in an incentive orientation task whereas the control group did not receive such instructions. The amount of the bonus was defined as £0.10 per correct answer in the orientation task. By incentivising performance in the orientation task rather than in the memory assessment, our task examined the effects of monetary incentives on incidental encoding.

Considering potential attrition, we oversampled participants against the predefined sample size. In total, we received data from 47 and 44 participants in the control and incentives condition, respectively, out of which five and three participants were excluded due to incomplete data. All 83 participants who had submitted complete datasets were invited to participate in the second part of the study and 42 and 39 participants in the control and incentives group responded. In total, four datasets were excluded from the second part (3 due to incomplete data and 1 due to a self-reported age below 18, all from the control condition). The final sample size included in the analysis included $N = 77$ participants ($n_c = 38$, $n_i = 39$). The participant characteristics are described in Table 3.1. The study was reviewed and approved by the University of Reading's School Research Ethics Committee (SREC; 2016-109-KM).

Material. We displayed short magic trick videos to participants. The same magic tricks as described in the previous chapter were used. The magic trick videos were selected from the Magic Curiosity Arousing Tricks (MagicCATs) stimulus collection (Ozono et al., 2021) containing 166 magic tricks that are edited to achieve a similar background and viewing focus and muted purposefully to minimise the effects of verbal interference. To select magic tricks used here, the following criteria were applied: (1) duration between 20 and 60s, (2) broad range of different materials and features so that magic tricks are distinguishable in a cued recall paradigm, (3) varying degrees of curiosity ratings as reported in the database, and (4) understandable without the use of subtitles. Additional editing was performed using Adobe® Premiere Pro CC® (2015) software where needed, for instance to remove subtitles. Magic tricks were exported in a slightly larger size than available in the database (1280x720 pixels). In total, 36 magic tricks were displayed in the experiment and additional two were used for practice trials. This number is equivalent to what has been used previously when studying cognition using magic tricks (Lau et al., 2020).

A frame of each magic trick video was extracted as a cue image (1920x1080 pixels) for the memory test. For this, a frame was selected from before the moment(s) of surprise (i.e., moments violating one's expectations) that was distinctive enough to cue the magic trick without revealing it entirely.

Tasks and Measurements. Different tasks were used and are described below.

Magic trick watching task. During each trial of the magic trick watching task (see Figure 3.1A), participants watched a magic trick video and were then asked to estimate how many people (out of 100) are able to correctly figure out the solution. For this, participants could choose out of the following answer options: “0 - 10%”, “11 - 20%”, “21 - 30 %”, and “31 % and more”. Afterwards, participants were asked to rate how curious they were while watching the magic trick on a 7-point Likert scale (1 = “not curious at all”, 7 = “very curious”). Importantly, the estimate rating was combined with the between-subject incentives manipulation. The incentives manipulation was part of the task instructions. Hence the task trial looked the same in both conditions.

In total, the magic trick watching task consisted of 36 trials randomised across three blocks (12 trials each). There were no fixed response windows. Participants were able to take breaks in between blocks (self-paced).

Surprise recall and recognition task. Approximately one week later, participants’ memory of the magic tricks was tested using a cued recall and a four-alternative forced choice recognition block (see Figure 3.1B). During each trial in the cued recall block, the cue image was presented, and participants were asked to describe what has happened in the cued magic trick according to their memory using a free answer format text input. They were instructed to be as descriptive and detailed as possible because their answers would be used to categorise whether they remembered a magic trick. Additionally, they were asked to write “no recall” if they were unable to recall what happened.

During the cued recognition task trials, the same cue image was presented, but this time paired with four choices to answer the question of what happened in this magic trick. The answer options were presented in random order. Behavioural piloting was conducted to achieve wordings of distractor items that do not lead to floor or ceiling effects. After participants selected an answer (self-paced), they were asked to rate their confidence on a scale from 1 (“not confident at all”) to 6 (“very confident”). All 36 magic tricks were cued in the recall and recognition task in independent, random order. A break was offered in between both blocks.

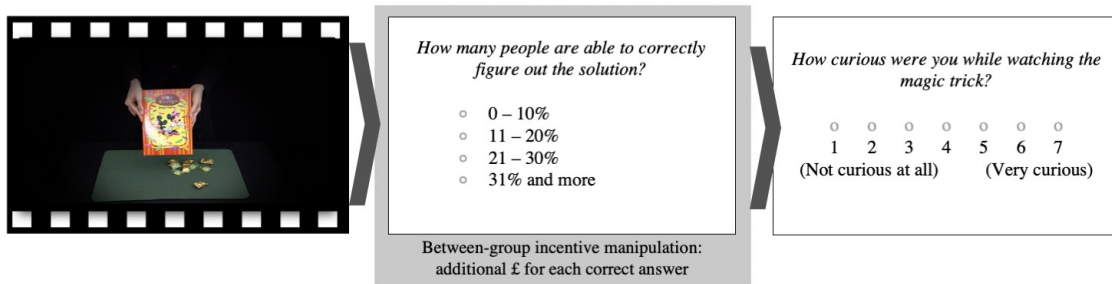
Task motivation inventory. To measure task dependent motivational constructs after the magic trick watching task, the Task Motivation Inventory (TMI) was used. More specifically, the subscales intrinsic motivation (3 items; Elliot & Harackiewicz, 1996), task engagement (3 items; Elliot & Harackiewicz, 1996), interest (3 items; Wigfield & Eccles, 2000), boredom (3 items; Pekrun et al., 2002),

effort (5 items; Ryan, 1982), and pressure (5 items; Ryan, 1982)⁵ were used. Participants answered on a 7-point Likert scale from 1 (“definitely disagree”) to 7 (“definitely agree”). The item order was randomised, but the same order was used across all participants.

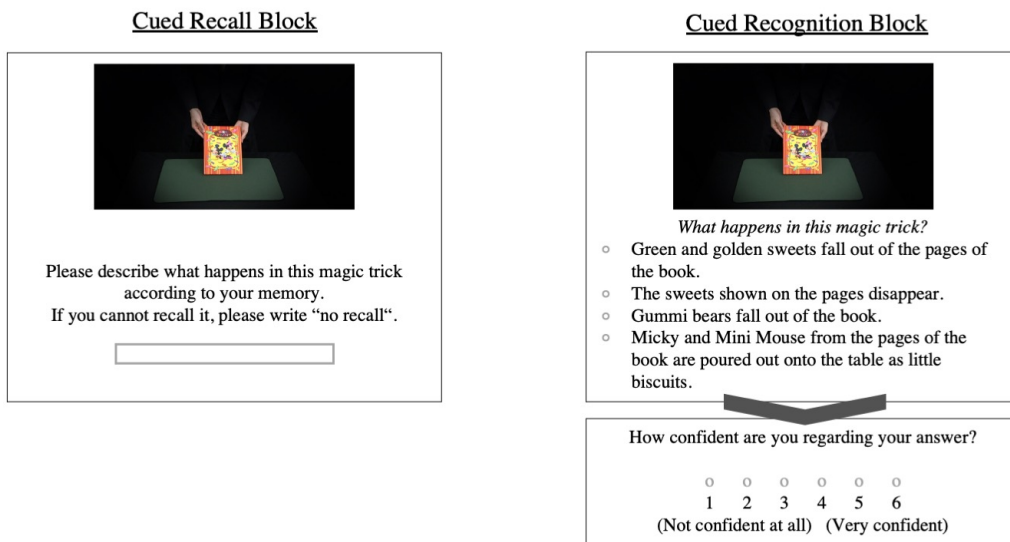
Figure 3.1

Overview of the task trials

A Magic Trick Watching Task



B Surprise Recall and Recognition Task



Note. The figure illustrates the incidental incentives-motivated learning task (A) as well as the surprise memory test (B). Task flow is indicated using dark grey arrows. (A) shows the magic trick watching task trial as used in the online studies. After a magic trick was displayed, participants were asked to give an

⁵ Due to an error, one item was not included into the inventory. The pressure scale was computed based on 4 instead of 5 items.

estimate of how many people (out of 100) could find the solution to the magic trick. In a between-subject design, participants were instructed that they could earn additional monetary rewards for each correct estimate or did not receive such an instruction. Participants were further asked to rate their curiosity regarding the magic trick. The same task was used in the fMRI experiment, but stimuli were edited and jittered fixations in between the magic trick video and ratings were introduced. For details on the trial structure for the fMRI task, please refer to the previous chapter. (B) shows the memory task consisting of a cued recall and cued recognition block. Cue images were taken from the magic tricks and the same images were used during both blocks.

Experimental Procedure. Participants were informed prior to starting the first part that they will be invited to a second part. They were asked to only proceed with the first part if they could participate in the second part one week later. After providing informed consent, participants filled in a quick demographics questionnaire. Afterwards, participants read through the task instructions containing the between-subject incentives manipulation. Half of the participants (incentives condition) were instructed that they could earn additional £0.10 for each time they estimated correctly how many people would be able to figure out the solution to the magic trick (pseudo task). The other half of participants, however, did not receive such an instruction (control condition). Participants were additionally informed that another study was run simultaneously on Prolific, indicating that there was a correct estimate, but that the data collection was still running so that there was no feedback. Afterwards, participants completed two practice trials followed by 36 trials of the magic trick watching task distributed across three blocks. At the end, participants completed the TMI. A week later, participants were invited to participate in the second part of the study consisting of the surprise recall and recognition task. Both experiments were executed using a developmental version of Collector (Haffey et al., 2020).

Study 2: Replication Behavioural Study

Participants & Design. To ensure the robustness of effects, we ran a replication of the initial behavioural study with small adjustments. The study was again conducted using Prolific, aiming for 40 participants per group applying the same inclusion criteria. As the initial behavioural study, the replication study was set up as a two-part study spaced one week apart. The incentives manipulation was operationalised using a between-subject design setting up two different studies on Prolific. The wording of the incentives manipulation was adopted, so that it could be translated to other study settings. More specifically, participants in the incentives condition were instructed that it is possible to earn an additional 50% bonus payment on top of the payment for both tasks if they estimated correctly how many people would be able to figure out the solution on all 36 trials and that this translates into additional £0.10 per

correct estimate. Participants were reimbursed £7.50 for their time and received a bonus payment of £0.90 upon completing both parts, mirroring chance level performance in the incentive orientation task.

Complete data from the first session was received from 40 participants in each group. Because 2 participants in the incentives group did not complete the second session, the final sample size included in the analysis was $N = 78$ participants ($n_e = 40$, $n_i = 38$). The sample description can be found in Table 3.1. The study was conducted as part of the same ethics approval mentioned above (2016-109-KM).

Material. The same magic trick movie stimuli and cue images were used as described above.

Tasks and Measurements. The same tasks as described above were used. Small adjustments were made in the wordings in the recognition task items to enhance readability (e.g., by adding articles). In total, five (or 3.47%) of 144 answer options were affected. Additionally, the TMI included all five items for the pressure scale.

Experimental Procedure. Procedures were not modified in between data collections other than the above-mentioned change in the wording of the incentives manipulation. Data was collected using a later developmental version of Collector.

Study 3: fMRI Study

In addition to behavioural effects, we were also interested in the neural mechanisms underlying curiosity-motivated learning of dynamic stimuli, so we adapted the magic trick watching task for use in the fMRI scanner and also added a 10 min rest pre and post learning (the results from the pre- and post-learning rest will be described in the next chapter). The Magic, Memory, and Curiosity (MMC) Dataset was described in the previous chapter⁶, and only the fMRI acquired during the magic trick watching task will be analysed here.

Participants & Design. Participants (see Table 3.1 for demographic information) were recruited using leaflets that were distributed around the campus to achieve a final sample size of $N = 50$ (i.e., 25 participants per group). Participants were required to be right-handed. The *a priori* sample size considerations were based on sample sizes used in previous behavioural studies (Murayama & Kuhbandner, 2011) as well as on sample size recommendations for between-subject effects in naturalistic imaging (Pajula & Tohka, 2016; Yeshurun, Swanson, et al., 2017). Similar to the behavioural studies, the fMRI study consisted of multiple sessions: a pre-scanning online assessment, the fMRI lab experiment where the magic trick task was performed inside the fMRI scanner, and the surprise memory session

⁶ Methods will be briefly repeated and summarised here, so that the chapters can be read independently.

performed online a week later. In total, participants were reimbursed with £30 for their time plus £7.20 additional bonus payment (i.e., chance level performance in the incentive orientation task, see below).

The fMRI also included a between-subject incentives manipulation and participants were assigned to the experimental conditions in an interleaved manner. Using the same wording framework as in the behavioural replication study, participants in the incentives group were instructed that they could receive an additional 50% on top of their payment for the whole data collection if they estimated all 36 trials correctly and that this translates into additional £0.80 per correct estimate⁷. The study protocol was approved by the University of Reading Research Ethics Committee (UREC; 18/18).

Material. In the fMRI study, the same magic tricks were presented as before, but the video files themselves underwent further editing to optimise them for usage within the MRI scanner. More specifically, luminance, for instance, was adapted where necessary. Furthermore, a mock video was created individually for the beginning of each magic trick. Over a period of 6s, the first frame of each magic trick was displayed overlaid with a black video including a viewing focus that gradually opened up to match the viewing focus of the magic trick file. The resulting magic trick files were on average 38.5s long ($SD = 8.63$, $min = 26.6s$, $max = 58.64$). The same frames as described above were used to create cue images.

Tasks and Measurements. Overall, the tasks were not substantially changed and only adapted for the fMRI environment. The study protocol included more tasks, however, here only the tasks used for the analyses are described.

Magic trick watching task. Participants were asked to perform the magic trick watching task inside the fMRI scanner. The experiment was displayed on a black background and all text was presented in white unless indicated differently. The beginning of the display of each magic trick video was synced with the scanner TTL (transistor-transistor logic) pulse at the beginning of each repetition time (TR). A jittered fixation (4-10s, TTL aligned, only even integers) was displayed in between the end of the magic trick and the estimate rating. Different from the behavioural studies, the percentage sign was omitted in the answer options and the answer options were displayed in colours matching the button colours on the four-button MRI compatible response device

(<https://www.curdes.com/mainforp/responsedevices/buttonboxes/hhsc-1x4-cr.html>). Estimate ratings were recorded by pressing the button in the colour of the corresponding estimate. There was a fixed response window of 6 s. If participants chose an estimate sooner, the answer options would turn white.

⁷ 50% additional bonus payment should have translated to £0.40 per correct answer. However, no participant reported to have noticed this error.

After a brief fixation (0.05s), the curiosity rating was displayed and a random number was highlighted in red. Participants were instructed to move the highlighted number to the left or right (using index and middle finger, respectively) before confirming their selection using the red button. The fixed response window was 5.95s.

Participants completed two practice trials outside the fMRI scanner. Inside the fMRI scanner, participants completed 36 trials of the magic trick watching task distributed over three blocks. The order in which magic tricks were displayed was pseudo-randomised to control for trial order effects. Trial orders were simulated so that high and low curiosity magic tricks were equally distributed across blocks (low and high curiosity magic tricks were defined based on data by Ozono and colleagues (2021)) while no more than four magic tricks of each category could follow consecutively. Furthermore, trial orders were restricted so that the maximum range of Spearman-rank correlations between any two trial orders did not exceed a threshold of 0.7. In total, 25 trial orders were simulated and used once in each group.

Self-paced breaks were offered in between blocks. Participants in the incentives group were exposed to the incentives manipulation in written form before the start of the first task block and had to confirm it by pressing a button on the button box. The incentives manipulation was also repeated verbally by the experimenters. Before the start of the second and third block, the incentives manipulation was repeated.

Surprise recall and recognition task. No changes were made with respect to the memory task.

Task motivation inventory. The TMI was completed inside the fMRI at the end of the experiment. Items were displayed in random order and participants' responses were collected akin to the curiosity ratings.

Experimental Procedure. After screening procedures and pre-scanning assessments (described in the previous chapter), participants were invited to a fMRI scanning session at the Centre for Integrative Neuroscience and Neurodynamics (CINN) at the University of Reading for a two-hour session. Practice and experiment were presented using PsychophysicsToolbox 3 (Brainard, 1997) with GStreamer media framework run on Matlab on a 13inch Apple MacBook. Practice trials were completed outside the MRI scanner looking directly at the screen, whereas back projection was used during the experiment. Before and after the magic trick watching task, resting-state data (10min, eyes open) was acquired. At the end of the experiment, the TMI was presented during which the anatomical sequence was run. Follow-up memory test was conducted online: One week later, participants received the link to the surprise memory assessment executed using Collector.

Table 3.1

Participant Characteristics

	Behavioural study		Replication		fMRI study	
	Control group	Incentive group	Control group	Incentive group	Control group	Incentive group
Subjects per group	n = 38	n = 39	n = 40	n = 38	n = 25	n = 25
	27.87 (4.58)	26.46 (5.14)	25.62 (4.89)	26.24 (4.70)	26.52 (5.46)	24.12 (4.70)
Age	[18; 35]	[18; 35]	[18; 35]	[18; 35]	[18; 37]	[19; 37]
Gender (% female)	36.84	38.46	30.00	39.47	68.00	76.00
Ethnicity (% BAME)	60.53	66.67	60.00	39.47	32.00	24.00
	14.46 (1.77)	14.72 (2.99)	13.43 (2.72)	15.08 (1.89)	16.12 (2.62)	15.92 (2.04)
Years of Education	[10; 18]	[8; 24]	[5; 17]	[12; 21]	[13; 22]	[11; 19]
	7.21 (0.66)	7.22 (0.50)	7.29 (1.02)	7.23 (0.82)	7.50 (0.67)	7.36 (0.45)
Days between sessions	[6.90; 10.80]	[6.90; 8.99]	[6.29; 10.82]	[6.57; 11.02]	[6.83; 9.49]	[6.87; 8.20]
Experience with magic tricks	1.66 (0.99)	1.36 (0.71)	1.68 (0.89)	1.76 (0.75)	1.56 (0.87)	1.44 (0.77)
	[1.00; 4.00]	[1.00; 4.00]	[1.00; 4.00]	[1.00; 3.00]	[1.00; 4.00]	[1.00; 4.00]

Note. For interval-scaled variables, the table shows mean (standard deviation) [minimum; maximum] separately for each group and data collection. Experience with magic tricks relates to the participant's rating of their experience in producing magic tricks on a scale from 1 = "never" to 6 = "very frequently".

Data Pre-processing and Analysis

Behavioural data. Behavioural data from each data collection was processed and analysed in the same way. All behavioural pre-processing and analysis were carried out in R 3.6.3 (R Core Team, 2020).

To test for between-group differences in motivation (TMI scores as well as ratings of curiosity obtained in the magic trick watching task), data from the TMI was analysed using Welch's Two-Sample t-tests. Curiosity ratings for the magic trick movies were analysed using Linear Mixed Effects (LME) models with the *lme4* package (Bates et al., 2015) specifying a fixed effect (FE) for incentives (effect coded; -1 = control group, 1 = incentives group) and random effects (RE) for intercepts of participants and stimuli.

Data from the recognition block was dummy-coded by comparing the chosen response to the correct answer. Additionally, recognition performance was combined with confidence ratings. Specifically, the correct answer chosen with a confidence larger than three was coded as correct for "high confidence recognition", a recollection-based recognition memory measurement (Yonelinas, 2001b, 2002). Coding the answers given in the cued recall paradigm, a script was used to assign zero to all answers matching "no recall" (or variants thereof). All remaining answers were coded by the same rater across all three data collections. A trick was rated as recalled if the change that occurred was remembered.

Our main analyses focused on the effects of curiosity, monetary incentives, and their interaction on memory encoding. Encoding data was analysed using a meta-analytic approach. For each data collection, Generalised LME (gLME) models were applied specifying FE for curiosity, incentives, and their interaction as well as RE for the participant and stimulus intercept and random slopes for the curiosity effect. Curiosity ratings were mean-centred within each participant and incentives manipulation was again effect coded. Although high confidence recognition (i.e., correct recognition with a confidence rating above three) is the main dependent variable of the current study, we also examined the results with correct recognition and cue recall results to have a better grasp of the findings. The same model was run on three different memory thresholds: correct recognition (regardless of confidence), high confidence recognition, and cued recall. To further investigate whether incentives and curiosity influence the quality of memory in an exploratory analysis, a gradual confidence cut-off was applied, creating additional dependent variables (recognition with confidence > 0 through to recognition with confidence > 5) and the same gLME model as described above was used to model encoding. The unstandardised parameter estimates from the gLME models (i.e., beta estimates and standard errors) from each data collection were extracted and submitted to a FE meta-analysis (weighted least squares) using the *metafor* package (Viechtbauer, 2010) to integrate individual coefficients from the three data collections.

fMRI data. After pre-processing, fMRI time series were analysed within the intersubject synchronisation framework.

fMRI acquisition and pre-processing. fMRI data was obtained in a 3.0T Siemens Magnetom Prisma scanner with a 32-channel head coil. Whole brain images were acquired (37 axial slices, 3 x 3 x 3 mm, interslice gap of 0.75mm) using an echo-planar T2*-weighted sequence (repetition time = 2000ms, echo time = 30ms, field of view: 1,344 x 1,344 mm², flip angle: 90°).

Pre-processing steps included B₀ distortion correction, despiking, slice-timing and head motion correction and normalisation to MNI space using the ICBM 2009c Nonlinear Asymmetric Template. Additionally, data was smoothed to achieve an approximate smoothness of full width half maximum kernel of 8mm, and time series were scaled to a mean of 100. Local white matter time series, the first three principal components of the lateral ventricles as well as motion estimates were included regressors of no interest to denoise the data. During linear regression, time courses were also band-pass filtered for frequencies between 0.01 and 0.1 Hz. Time points were censored (i.e., set to zero) if the Euclidean norm of per-slice motion exceeded 0.3mm or if more than 10% of brain voxels were outliers.

Intersubject correlation analysis.⁸ Due to increased stimulus complexity in naturalistic paradigms, the applicability of traditional analysis methods developed for task-based fMRI relying on specifying onset and duration of stimuli (e.g., general linear models; GLMs) is limited and model-free approaches are used frequently (Sonkusare et al., 2019). One of these data-driven methods is intersubject correlation (ISC; Hasson et al., 2004). Here, the assumption is that the brain response, when perceiving and processing naturalistic stimuli, is composed of a stimulus-driven signal as well as spontaneous activity unrelated to the stimulus (Nummenmaa et al., 2018). The stimulus-driven signal is time-locked to the stimuli and shared across subjects whereas the intrinsic fluctuations are cancelled out as noise. To determine brain areas that encode information about the presented stimuli consistently across subjects, the time course of a given voxel in subject A is correlated with the time course of the same voxel in subject B. This is repeated for each voxel in the brain for each pair of participants in the sample creating pairwise ISC maps (see Figure 3.2B).

During the magic trick watching task, the beginning of each magic trick video was aligned with the beginning of a TR. Likewise, the jittered fixation after the magic trick presentation was aligned with

⁸ Please note that this analysis is highly overlapping with what has been presented in the previous chapter. In contrast to the previous chapter, we here apply a correction for the HRF lag, thereby shifting the time course. This additional step increased the maximum ISC ($r = .32$) observed, further validating this step.

the beginning of a TR and presentation times and response windows were multiple of the TR. These steps were undertaken to allow that the time series could be concatenated (see Figure 3.2A) to (a) remove volumes of no interest, (b) reorder the volumes so that the concatenated order would remain invariant across subjects irrespective of the pseudo-randomised order in which the magic tricks were presented (see Thomas et al., 2018), and (c) account for the delay in the hemodynamic response function (HRF) by shifting the time course. Volumes acquired during mock video presentation, fixation and estimate/curiosity ratings were considered as volumes of no interest because ISC critically relies on subjects receiving the same time-locked stimuli and transient, non-specific activity can be found at stimulus onset (Nastase et al., 2019). As assumptions regarding the duration of the HRF lag to account for in ISC analyses vary (Hasson et al., 2004; Nummenmaa et al., 2012; Zadbood et al., 2017), intersubject pattern correlation (ISPC; J. Chen et al., 2017) – a spatial form of ISC – was computed to determine the optimal HRF lag. This preliminary analysis indicated the optimal HRF lag to be 4 TRs (see supplementary analysis in the appendix and Figure A3.1 therein). The concatenated time series consisting of 594 volumes were correlated for each pair of participants (using AFNI's *'3dTcorrelate'*, Figure 3.2B) resulting in 1225 pairwise ISC maps that were Fisher's *z*-transformed.

To determine brain areas showing significant synchronicity between subjects, LME models with crossed random effects (LME-CRE models; G. Chen et al., 2017) were specified to predict the pairwise Fisher's *z*-transformed ISC maps. The LME-CRE framework does not only account for the interrelatedness in the pairwise ISC map data by specifying crossed random intercepts for both subjects in each pair, but also offers analytical flexibility to specify grouping variables to investigate the effects of incentives on ISC during magic trick watching as well as of other covariates (see below). To specify the fixed effect of incentives, deviation coding was adopted where 0.5 was assigned to subjects in the control group and -0.5 was assigned to subjects in the incentives group. By adding up these values for each pair, group was defined as 1 (both subjects in control group), 0 (both subjects in different groups), or -1 (both subjects in the incentives group).

Intersubject representational similarity analysis. Nastase and colleagues (2019) proposed a formal definition of ISC where they divided the stimulus-driven component further into processes that are consistent across subjects and idiosyncratic responses that are nonetheless induced by the stimulus, but characterised by timings and intensities specific to each subject. The consistent response can be estimated by averaging the ISC given that subject-specific and spontaneous responses will average out. To quantify the subject-specific responses in the time courses, other known information about the subjects can be used to “anchor” the response – an approach known as intersubject representational similarity analysis (IS-RSA; Finn et al., 2020; Nummenmaa et al., 2012). More specifically, the similarity in participant's behavioural data (e.g., trait scores, Finn et al., 2018; age, Moraczewski et al., 2018; recall performance,

Nguyen et al., 2019; behavioural ratings, Nummenmaa et al., 2012) can be used to predict the similarity in the brain response (Figure 3.2C) by firstly, calculating subject-by-subject similarity matrices separately for behavioural and brain data. In a second step, the geometry of both matrices can be compared or matched correlationally based on the second-order isomorphism within representational similarity analysis (RSA; Kriegeskorte et al., 2008). The second order similarity can be evaluated using LME-CRE models. Importantly, the pseudo-randomisation of trials allows that similarities in brain responses between participants can be attributed to the behavioural anchor rather than to similarities in the trial order.

Here, we were interested in how similarity in (1) curiosity, (2) memory encoding, and (c) curiosity-motivated learning enhancement (CMLE) predicts similarity in the neural responses across subjects (Figure 3.2D). To calculate the subject-by-subject similarity matrices in the first two instances, the trial-by-trial values (subject-wise mean-centred curiosity ratings and dummy-coded encoding performance on the high confidence criteria, respectively) were correlated for each pair of participants (after re-ordering the values for each subject to account for the pseudo-randomisation). To control for potentially shared variance between the similarity matrix of curiosity and the similarity matrix of memory, Fisher's z -transformed pairwise curiosity correlations were residualised by removing the proportion that can be linearly predicted by Fisher's z -transformed pairwise memory correlations. Likewise, Fisher's z -transformed pairwise memory correlations were residualised by removing the proportion that can be linearly predicted by Fisher's z -transformed pairwise curiosity correlations.

CMLE was quantified by extracting the individual curiosity beta values (estimated by the specification of random slopes predicting memory with curiosity) from the gLME model⁹ for high confidence recognition and mean-centering them. The beta value quantifies the magnitude of the association between curiosity and memory for each individual (Figure 3.2D). Because there was only one value per subject (rather than a time course), the similarity matrix was calculated using the Anna Karenina (AnnaK) model providing a metric reflecting the absolute position on the scale, i.e., the mean of

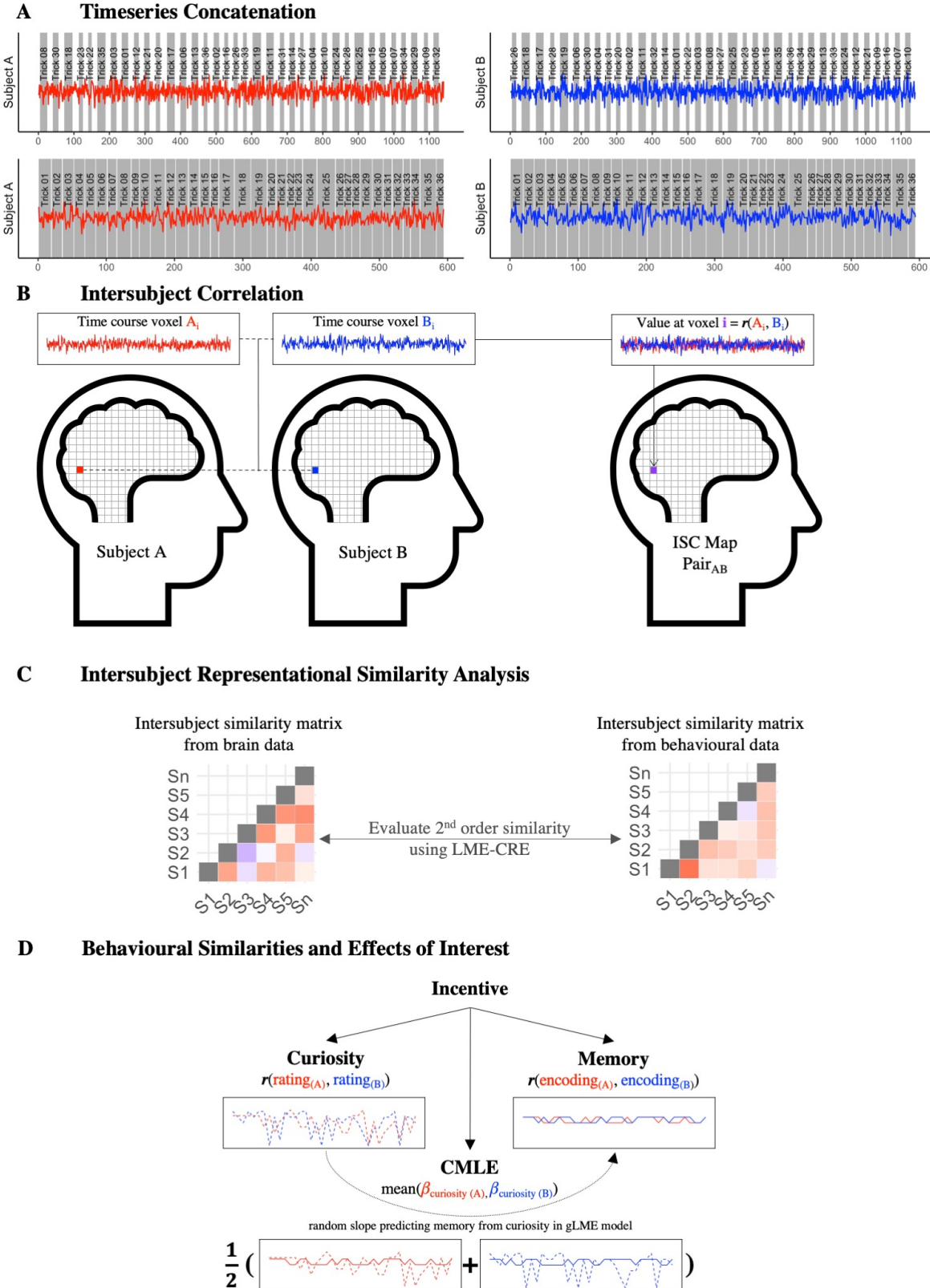
⁹ Due to singular fit warnings for the dependent variable high confidence recognition in the fMRI data, the model was also executed using a simplified RE structure where the random intercepts for subject and random slopes for the curiosity effect were specified, but random intercepts for stimuli were removed allowing the model to converge without warnings. The individual curiosity beta values from both models were highly correlated ($r = 0.992$) and the gLME model specification did not affect the IS-RSA whole-brain results (correlation unthresholded effect size map = .988, correlation unthresholded statistics map = .989, dice coefficient of masked cluster-extend thresholded results = 0.904) nor reported ROI results.

both subjects (Finn et al., 2020). This is preferable compared to using a relative distance metric like the Euclidean distance as it allows for a scenario where low scoring subjects are more similar to other low scoring ones, but high scoring subjects are less similar to each other. Previous studies using working memory in IS-RSA found that the AnnaK model fitted the data better than the Euclidean distance and yielded to higher replicability between samples (Finn et al., 2020). Another benefit of using the mean is that effects in both directions can be captured: if the correlation between brain and behaviour is positive, then high scorers are alike and low scorers different whereas a negative sign indicates that low scorers are alike and high scorers different.

To link idiosyncratic responses in the stimulus-driven brain response to the behavioural effects of interest, LME-CRE models were used to predict the pairwise Fisher's z -transformed ISC maps. Separate models were estimated for unique curiosity, unique memory, and CMLE, again specifying crossed random intercepts for both subjects in each pair. Fixed effects were specified for group, the respective behavioural similarity as covariate, as well as their interaction. Group was defined as described above. The covariate was grand-mean centred before computing the interaction term by multiplying the group variable with the covariate.

Figure 3.2

Illustration of processing and analysis methodology within the intersubject framework



Note. To account for the dynamic nature of the stimuli, ISC analysis was applied. (A) In the first step, data was concatenated to remove volumes of no interest, reorder volumes and account for the lag in the HRF. (B) The concatenated time series of each voxel were correlated for each pair of participants creating pairwise ISC maps representing similarity in the brain response between participants (adopted from Nastase et al., 2019). (C) To anchor idiosyncratic response patterns to behavioural measurements, IS-RSA was used relating similarities in the brain response to similarities in behavioural measurements (adopted from Finn et al., 2020). (D) Behavioural measures of interest were curiosity, encoding and CMLE. To determine behavioural similarities in curiosity and encoding, the time courses of rating and encoding were correlated for each pair of participants. For CMLE, each subject's random slope predicting memory encoding with curiosity estimated by the behavioural gLME was extracted and the mean as a non-parametric difference measure was calculated for each pair.

Intersubject functional connectivity. ISC uses shared variance in the brain response between subjects to capture synchronicity of a given brain region inter-individually. Functional connectivity (FC; Biswal et al., 1995), on the other hand, computes the correlation of the seed regions (voxels or ROIs) within a subject to quantify synchronicity of different brain regions intra-individually. Intersubject functional connectivity (ISFC; Simony et al., 2016) combines ISC and FC by using the time course of a seed region in one subject to correlate it with the time courses of all other regions or voxels in another subject's brain hence isolating shared, stimulus-evoked FC patterns (Vanderwal et al., 2019). While FC is prone to artefacts (e.g., head movement; Power et al., 2012) as well as stimulus-unrelated, spontaneous activity, ISFC isolates the stimulus-dependent inter-regional correlation between subjects because intrinsic neural dynamics and artefacts within a subject are not correlated across brains and hence provides an estimate for the temporal consistency of responses between regions (Nastase et al., 2019; Simony et al., 2016; Simony & Chang, 2020). Like FC, ISFC can be used to correlate the activity of a seed region with the activity in pre-defined ROIs (ROI-to-ROI ISFC, Figure A3.2A in the appendix) or all other voxels in the brain (seed-based ISFC, Figure A3.2A).

We focused on anterior hippocampus (aHPC) and VTA/SN as seeds because previous research showed that the two brain areas form a loop in the context of motivated learning where the encoding in the hippocampus is modulated by dopaminergic activity stemming from the midbrain (Lisman et al., 2011; Shohamy & Adcock, 2010). To compute ROI-to-ROI ISFC, i.e., the ISFC between aHPC and VTA/SN (aHPC-VTA/SN-ISFC thereafter), the averaged aHPC time course in subject A was correlated with the averaged VTA/SN time course in subject B. Likewise, the averaged VTA/SN time course of subject A was correlated with the averaged aHPC time course of subject B. To determine aHPC-VTA/SN-ISFC for participant pair A-B, the two correlation coefficients were averaged after Fisher's z-

transformation. This procedure was repeated for all pairs of subjects and is illustrated in Figure A3.2A in the appendix.

Firstly, we were interested in whether there was significant aHPC-VTA/SN-ISFC during the magic trick watching task, and whether this was influenced by the incentives manipulation. Data was analysed using LME-CRE models predicting aHPC-VTA/SN-ISFC with a fixed effect for group (deviation coded) accounting for the interrelatedness using crossed random intercepts for both subjects in each pair. Similar to ISC analysis, this approach cancels out any spontaneous response that is unrelated to the stimuli or any idiosyncratic patterns.

We also expanded the model to link idiosyncratic aHPC-VTA/SN-ISFC patterns to curiosity, memory, and CMLE. A separate LME-CRE model was specified with crossed random intercepts for both subjects in each pair, where the incentive effect together with all three behavioural effects of interest were added as fixed effects into the same model. More specifically, the deviated coded group variable as well as grand-mean centred pairwise curiosity rating and memory encoding correlations as well as grand-mean centred pairwise mean values of the extracted individual curiosity beta values were used.

To examine the interaction between the incentives manipulation and the behavioural effects of interest, another LME-CRE model was specified to include the interaction terms between monetary incentives and each behavioural effect of interest as fixed effects in addition to the fixed effects described above. Interaction effects were computed by multiplying each main effect with the deviation coded incentives effect and all main and interaction effects were combined into one model. Like previous models, interrelatedness in the pairwise aHPC-VTA/SN-ISFC data was accounted for by defining crossed random intercepts for both subjects in each pair. All three LME-CRE models described here were applied using the *lme4* package in R (`lmer()`).

In addition to the ISFC between the aHPC and VTA/SN ROI, seed-based ISFC was conducted separately for both ROIs as seeds for exploratory purposes. The average time course of each seed in subject A was correlated with the (whole brain) voxel-wise time course subject B and vice versa (using `3dTcorr1D`, Figure A3.2B in the appendix), creating two asymmetric matrices $r(x_A, y_B)$ and $r(x_B, y_A)$ that were averaged after Fisher's z -transformation (Nastase et al., 2019). The pair-averaged seed-based ISFC maps were analysed using LME-CRE models (`3dISC`) akin to those used in ISC and IS-RSA predicting the Fisher's z -transformed pairwise ISFC maps for each seed (rather than Fisher's z -transformed pairwise ISC maps) to (a) determine overall seed-based ISFC of aHPC and VTA/SN, respectively, during magic trick watching, (b) identify incentives effects therein, and (c) behavioural effects of curiosity, memory, and CMLE and their interaction with incentives.

Thresholding and regions-of-interest approach. All analyses were conducted at whole brain level specifying a grey matter (GM) mask: during pre-processing, each subject's grey matter (GM) mask

based on FreeSurfer parcellation was transformed to echo-planar imaging (EPI) resolution. After averaging the masks across the sample, the mean image was thresholded so that a voxel was included in the group GM mask if it was GM in at least 50% of the sample.

To account for the multiple testing problem due to mass-univariate testing, cluster-extent based thresholding was performed using the recommended initial threshold of p -value = 0.001 (Woo et al., 2014). The resulting map was cluster-extent corrected based on the output of simulations performed using ‘*3dClustSim*’ for first nearest neighbours clustering (NN = 1; faces of voxels touch) and a cluster threshold of $\alpha = 0.05$ resulting in a threshold of $k = 20$ voxels.

In addition to whole-brain analysis, we were also interested in regions previously implicated in motivated learning and *a priori* defined the following regions-of-interest (ROIs): aHPC, NAcc, caudate nucleus (CN), and VTA/SN. The aHPC has been chosen as increased activity for remembered compared to forgotten items is predominantly centred in anterior parts of the HPC (Kim, 2011; Spaniol et al., 2009). The aHPC is also sensitive to the effects of incentives and motivationally relevant information on encoding (Adcock et al., 2006; Poppenk et al., 2013). To create the aHPC ROI, AFNI’s ‘*whereami*’ was used to extract the bilateral hippocampus (HPC) from the Glasser Human Connectome Project atlas (Glasser et al., 2016). Following the recommendations by Poppenk et al. (2013), the aHPC was created by using the MNI coordinate $y = 21P$ to determine the uncal apex as a landmark to divide anterior and posterior HPC (‘*3dZeropad*’). To create ROI masks for NAcc, CN, and VTA/SN; [atlaskit](https://github.com/jmtyszka/atlaskit) (<https://github.com/jmtyszka/atlaskit>) was used to extract the NAcc, CN, Substantia Nigra pars reticulata (SNr), Substantia Nigra pars compacta (SNc), and Ventral Tegmental Area (VTA) from a high-resolution probabilistic subcortical nuclei atlas in MNI space (Pauli et al., 2018) specifying a probability threshold of 15%. This is similar to procedures by others presenting magic tricks inside the fMRI scanner (Lau et al., 2020). To create the VTA/SN mask, the masks for VTA, SNr, and SNc were combined. In total, the aHPC mask contained 162 voxels, the CN mask contained 573 voxels, and the NAcc and VTA/SN mask both contained 60 voxels each (see Figure A3.3 in the appendix). To correct for multiple comparisons within each ROI, False Discovery Rate (FDR) correction was applied at $q = 0.05$. Additionally, clusters were thresholded at $k = 5$ (NN=1).

Results

Behavioural Data

The groups did not differ in their motivation in any TMI scale in any assessments (all $p > 0.09$). Likewise, no difference was observed in the curiosity ratings (all $p > 0.199$). The detailed results for TMI scores and curiosity ratings can be found in Table A3.1 and A3.2 in the appendix, respectively.

Next, we investigated the effects of curiosity, incentives, and their interaction on memory encoding specifying the same gLME model for each data collection and memory measurement (recognition, high confidence recognition, cued recall) to submit the estimates into FE meta-analyses for each memory measurement separately. The results of the FE meta-analyses are shown in Table 3.2. Curiosity had a positive effect on memory encoding: magic tricks for which participants reported higher curiosity were more likely to be encoded. While the overall curiosity effect was not significant for recognition per se, significant effects were observed for high confidence recognition and cued recall. With respect to the effect of monetary incentives on memory encoding, the effects were overall positive, i.e., participants in the incentive group were more likely to encode the magic tricks compared to participants in the control group. However, the overall effect only reached significance for the high confidence recognition memory measurement. The interaction between monetary incentives and curiosity did not reach significance for any of the memory thresholds investigated.

Table 3.2

Integrated results of gLME models predicting memory encoding using curiosity, monetary incentive, and their interaction

	<i>b</i> (SE)	OR [95%-CI]	<i>z</i> value	<i>p</i> value
Curiosity				
Recognition	0.023 (0.023)	1.02 [0.98; 1.07]	0.988	0.323
High confidence recognition	0.084 (0.022)	1.09 [1.04; 1.14]	3.766	< 0.001
Cued recall	0.098 (0.025)	1.10 [1.05; 1.16]	3.842	< 0.001
Monetary incentive				
Recognition	0.084 (0.050)	1.09 [0.99; 1.20]	1.676	0.094
High confidence recognition	0.155 (0.067)	1.17 [1.03; 1.33]	2.336	0.019
Cued recall	0.119 (0.075)	1.13 [0.97; 1.30]	1.599	0.11
Interaction				
Recognition	-0.002 (0.022)	1.00 [0.96; 1.04]	-0.070	0.944
High confidence recognition	-0.010 (0.021)	0.99 [0.95; 1.03]	-0.479	0.632
Cued recall	-0.025 (0.024)	0.98 [0.93; 1.02]	-1.058	0.290

Note. Separate models were run for each memory threshold. gLME = Generalised Linear Mixed Effects.

b = unstandardised regression coefficient, SE = standard error. OR = Odds Ratio, CI = confidence interval.

We then further examined the quality of recognition memory by changing the confidence cut-off threshold gradually ($0 \leq \text{cut-off} \leq 5$). Again, the same gLME model was run for each confidence threshold and each data collection and estimates were integrated using a FE meta-analysis (for detailed

results for each effect on each threshold, see Table A3.3 in the appendix) to extract the integrated b estimates for each effect at each confidence cut-off. Then, to examine how the cut-off is related to memory enhancement effect, the integrated FE b estimates were predicted using the confidence cut-off in a linear model separately for each effect. The cut-off was scaled from 0 to 5 so that the intercept was interpretable.

Results show that when calculating a linear regression to predict the integrated curiosity effect b values based on the confidence cut-off, the confidence cut-off was a significant predictor in the model ($b = 0.021$, 95%-CI [0.011; 0.031], $p = .004$) indicating that the integrated curiosity effect increases as the confidence cut-off increases: the Odds Ratio (OR) of the curiosity effect was 1.02 for confidence cut-off = 0 and 1.12 for confidence cut-off = 5.

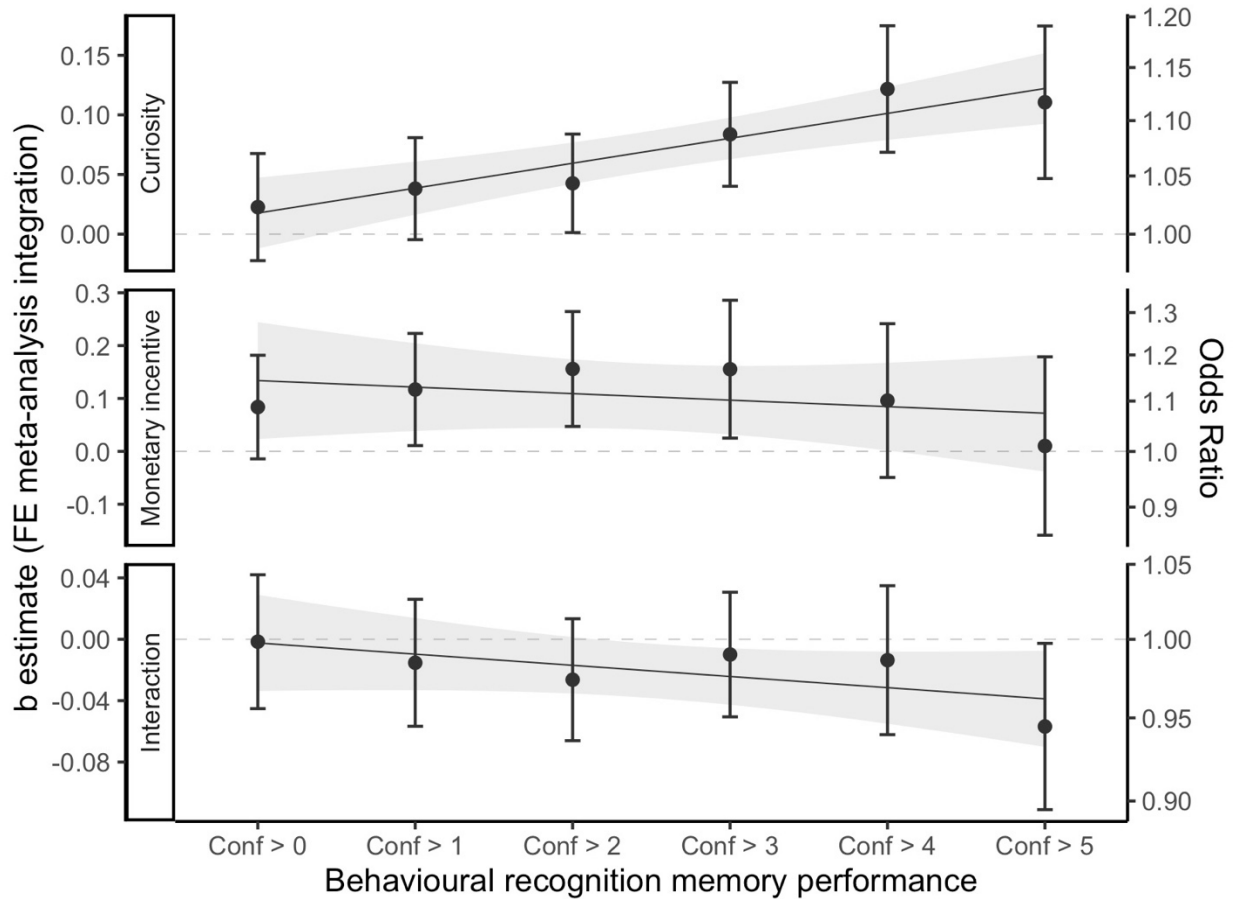
However, in the model predicting the integrated monetary incentives effect b values with the confidence cut-off, the cut-off was not a significant predictor in the model ($b = -0.012$, 95%-CI [-0.049; 0.024], $p = .402$). Likewise, using a linear model to predict the integrated interaction effect b values using the confidence cut-off, confidence cut-off was not a significant predictor ($b = -0.007$, 95%-CI [-0.018; 0.003], $p = .122$).

The results of the exploratory analysis are further illustrated in Figure 3.3 and the detailed regression table can be found in Table A3.6 in the appendix. They suggest that only curiosity but not the monetary incentive or interaction effect is sensitive to the confidence cut-off. More specifically, they show that the more confidently participants recognise the correct answer option, the larger the effect of curiosity on encoding. Monetary incentive and interaction effect, on the other hand, remain invariant regarding the confidence thresholds.

The results of all 21 individual gLME models (seven memory measurements in three data collections) can be found in Table A3.4 in the appendix. Additionally, Figure A3.4 in the appendix contains the equivalent of Figure 3.3 plotting the effects from each data collection individually. Because 8 of 21 gLME models produced a singular fit warning during execution, all analyses were repeated using a simplified gLME model with a reduced RE effects structure omitting the random slopes for the curiosity effect. Applying this reduced gLME model, however, did not affect the results of the meta-analyses and associated confidence cut-off linear model (see Table A3.5, A3.6, and A3.7 as well as Figure A3.5 and A3.6 in the appendix).

Figure 3.3

Integrated fixed effects of curiosity, monetary incentive, and their interaction as a function of confidence cut-off



Note. The x-axis shows the gradual confidence cut-off and y-axis illustrates the integrated effect size (left – unstandardised, right – OR). Each panel shows one of the FE specified in the gLME model. The integrated b estimate for each effect and confidence threshold is plotted and error bars indicate 95%-CI. The regression line illustrates the linear model predicting the effect with the gradual confidence cut-off.

fMRI Data

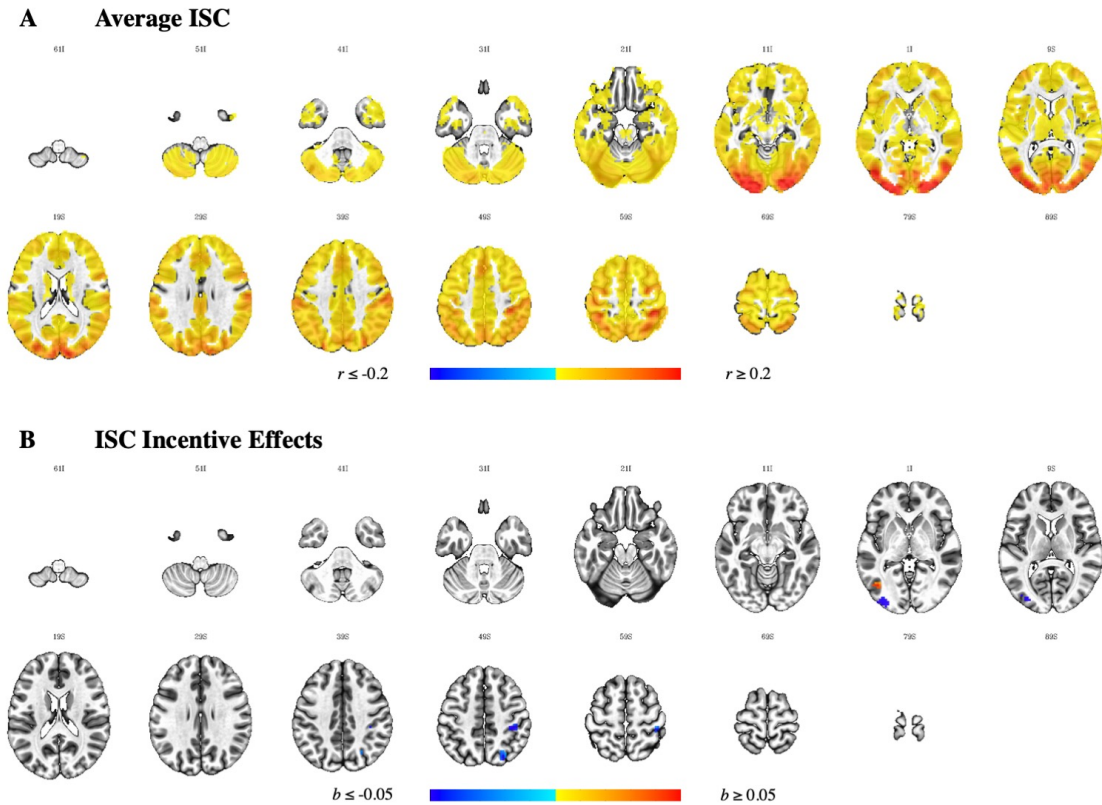
Intersubject Correlation. ISC analyses were carried out to identify brain areas with activity driven by magic trick watching. Significant ISC was found bilaterally in all four ROIs (aHPC, VTA/SN, NAcc, and CN; see Figure A3.7 in the appendix). Shared activity measured as significant ISC in the reward network has previously been observed in naturalistic viewing paradigms when presenting comedy movie clips to participants (Jääskeläinen et al., 2016). At whole brain level, widespread cortical and subcortical synchronisation (Figure 3.4A, Table A3.8 in the appendix) was observed, especially dominant

in the bilateral visual cortex as well as bilateral parietal somatosensory (BA 2, BA 5, BA 40, BA 1/2/3) and attention-related areas (BA 7 and BA 39) as well as bilateral premotor and supplementary motor areas (BA 6, BA 8). Overall, this is in line with other studies showing that dynamic stimuli sync brain activity in visual areas (e.g., Aliko et al., 2020; Baldassano et al., 2017; Hasson et al., 2004; Nguyen et al., 2019), but also with prepositions linking motor and somatosensory areas to the observation of actions (Keysers et al., 2010; Thomas et al., 2018). Likewise, the decline of the ISC from posterior to anterior as well as from lateral to medial areas in the brain can be attributed to higher intersubject variability in the stimulus-induced response in “intrinsic systems” (e.g., prefrontal and cingulate cortices; Ren et al., 2017).

In the next step, we investigated whether the availability of incentives had an effect on the ISC. While no effects were found in the ROIs, four clusters were found at whole-brain level (Figure 3.4B, Table A3.8 in the appendix). More specifically, in the incentive group, we found higher ISC in areas involved in the left middle occipital gyrus, right postcentral gyrus (BA 2), and the right intraparietal sulcus (IPS). Higher ISC in the control group was observed in the left lateral occipital cortex (Area V5/MT+).

Figure 3.4

Whole Brain ISC and Incentive Effects Therein



Note. Results are thresholded at $p < 0.001$, cluster-extent corrected at $k = 20$ (equivalent to per-cluster $\alpha = 0.05$) and plotted on the ICBM 2009c Nonlinear Asymmetric Template. While (A) highlights widespread ISC across cortical and subcortical areas across both groups, (B) shows cluster where the ISC is higher in the incentive group compared to the control group in blue and cluster where ISC is higher in the control group in red.

Intersubject Representational Similarity Analysis (IS-RSA). IS-RSA were carried out to identify brain regions with intersubject temporal dynamics similar to the intersubject variability in our effects of interest as well as brain regions where this association was influenced by the incentive manipulation. For this purpose, for each behavioural effect of interest, a LME-CRE model was specified with fixed effects for group, the behavioural similarity as well as their interaction. The inclusion of the covariate and the interaction effect did not affect the main effect of incentive (all correlations with unthresholded incentive effects reported above ≥ 0.92), hence the incentive effects are not further discussed. Below, the main effects of each behavioural variable are described before discussing the interaction effects and results for the ROI analysis are reported followed by whole-brain analysis.

IS-RSA For Each Behavioural Effect of Interest. Here, the main effects of each behavioural variable are reported highlighting clusters where the behavioural similarity matrix was predictive of the neural similarity matrix. The underlying assumption is that participants similar in behavioural effects of interest (e.g., curiosity ratings) will process the magic trick videos more similarly and regions involved in these processes will reflect this similarity correspondingly and hence are detected in this analysis.

Curiosity Effect. The curiosity effect was defined as the pairwise correlation of trial-by-trial curiosity ratings controlled for the effect of memory at pair level. No activity in the four ROIs survived thresholding. At whole-brain level, seven positive clusters were found (Figure 3.5A, Table A3.9 in the appendix) where idiosyncratic patterns in curiosity were anchored to the brain response. These clusters were located in the left primary visual cortex (V1), right inferior frontal gyrus (pars Opercularis), bilateral supplementary motor area (BA 8), left postcentral gyrus (primary somatosensory cortex), left precuneus (BA 7), right anterior insula cortex (AIC) and right supramarginal gyrus (BA 40).

Memory Effect. The memory effect was defined as pairwise correlation of trial-by-trial encoding performance ratings controlled for the effect of curiosity at pair level. Similarity in brain response could be anchored to similarity in memory encoding in a bilateral cluster in the CN ROI (Figure 3.6, Table A3.9 in the appendix), however, no effects were observed for the other three ROIs. At whole brain level, 21 clusters were found (Figure 3.5B, Table A3.9 in the appendix). More specifically, similarity in memory positively predicted similarly in the brain response in bilateral visual areas as well as the left cerebellum, the bilateral superior (BA 46, BA 9-46, medial BA 8) and middle frontal gyrus (BA 6, BA 8), precuneus

(BA 7) and lateral parietal areas including the right angular gyrus (BA 39) and somatosensory areas (BA 2, BA 40), the left lateral temporal gyrus (BA 37, fusiform and inferior temporal gyrus), right middle occipital gyrus (Area V5/MT+), and the right AIC.

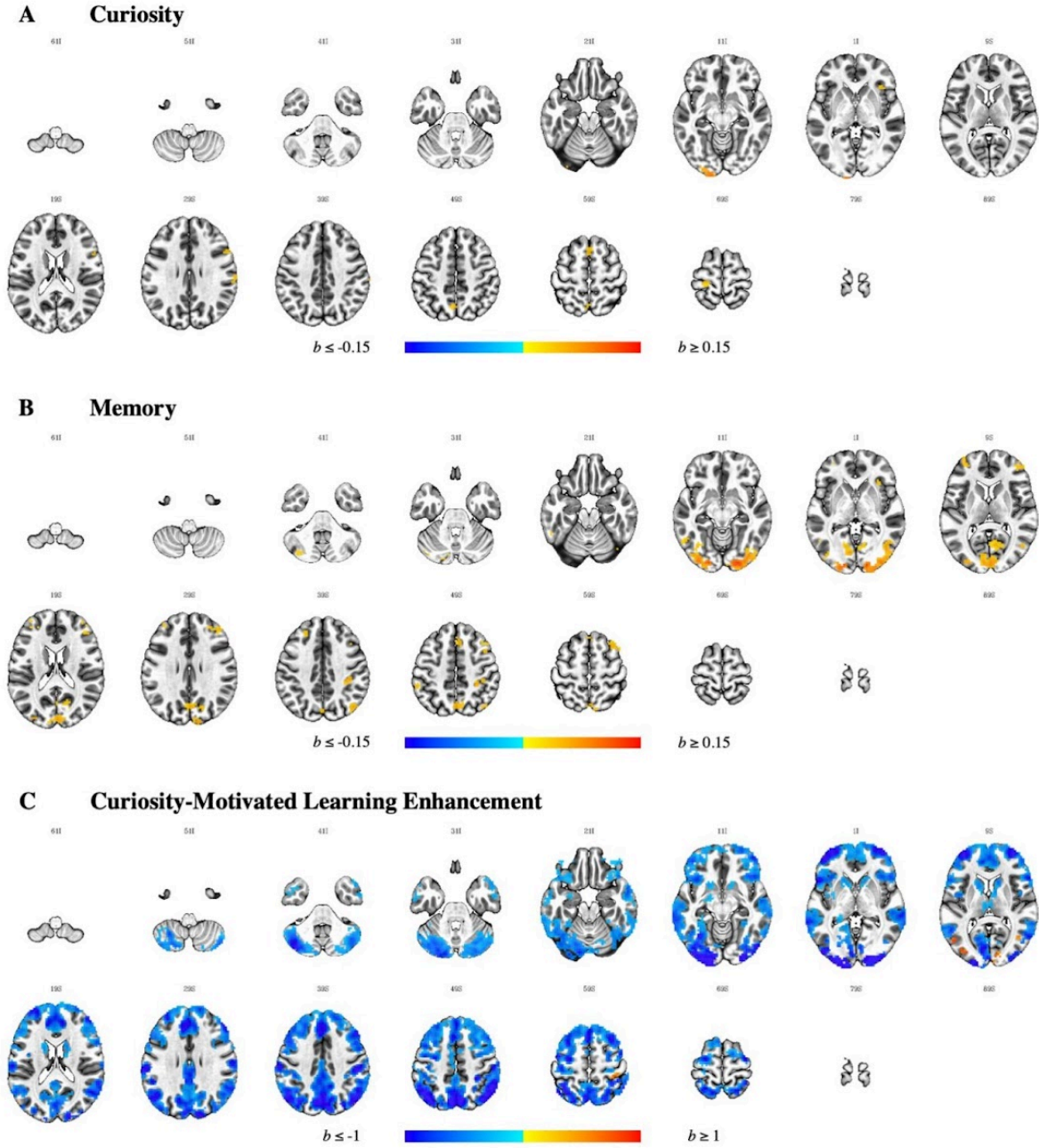
Curiosity-Motivated Learning Enhancement. CMLE was defined based on the random slope predicting memory from curiosity in the gLME model and individual values were extracted. Due to the AnnaK model used to determine the behavioural similarity matrix, the prediction was tested whether participants high in CMLE share similar patterns of brain activity while people low in CMLE show more variability and vice versa (rather than testing for brain areas where similarity is predicted by similarity in CMLE in a linear fashion).

In the ROI analysis, IS-RSA CMLE were found in all 4 ROIs (Figure 3.6B, Table A3.9 in the appendix), all of them negatively directed suggesting that participants with high CMLE scores had less similar brain activity compared to participants with high scores. More specifically, clusters were identified in the right aHPC, right VTA/SN, bilateral CN, and bilateral NAcc. Additionally, 15 clusters survived cluster-extend thresholding at whole brain level out of which 5 were positively and 10 negatively directed (Figure 3.5C, Table A3.9 in the appendix). Positive clusters were located in the bilateral middle temporal gyrus, the left middle occipital gyrus, the right calcarine gyrus, and the right postcentral gyrus. In these positive clusters, subjects high in CMLE are more alike than subjects low in CMLE who are more different in their brain response.

In negative clusters, on the other hand, subjects low in CMLE are more alike and subjects high in CMLE are more different. Negative clusters were spread across large proportions of the brain, in subcortical (e.g., striatum and thalamus) as well as cortical areas along the anterior and posterior midline (e.g., ACC, SMA, superior medial gyrus, precuneus, PCC, and cuneus), visual cortex, cerebellum, postcentral gyrus and posterior parietal cortex (PPC), the bilateral middle temporal gyrus, bilateral AIC, as well as dorsolateral prefrontal cortex (dlPFC; centred around the MFG) and anterior PFC stretching into the frontal operculum/anterior insula (fO/aI).

Figure 3.5

Whole Brain IS-RSA For Each Behavioural Effect of Interest

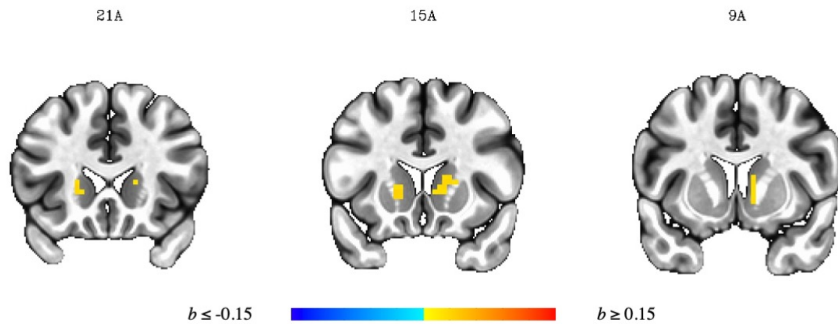


Note. Results are thresholded at $p < 0.001$, cluster-extent corrected at $k = 20$ (equivalent to per-cluster $\alpha = 0.05$) and plotted on the ICBM 2009c Nonlinear Asymmetric Template.

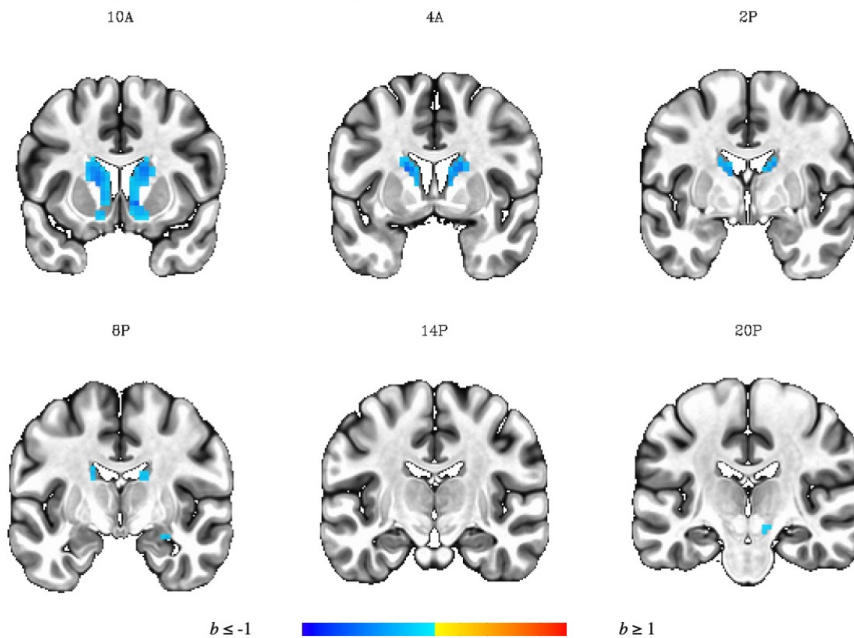
Figure 3.6

Effects of Memory and CMLE in the ROIs

A Memory



B Curiosity-Motivated Learning Enhancement



Note. Results are FDR-corrected at $q < 0.05$, cluster-extent corrected at $k = 5$ and plotted on the ICBM 2009c Nonlinear Asymmetric Template.

IS-RSA For the Interaction Between the Incentive Manipulation and Each Behavioural Effect of Interest. Due to the inclusion of group as a fixed effect in the LME-CRE model, it was further possible to determine brain areas where the behavioural similarity matrix predicted the neural similarity matrix differently depending on the availability of monetary incentives. In doing so, clusters could be identified where the behavioural effect is only predictive in one group or more strongly predictive in one group.

Curiosity Incentive Interaction. When looking at whether the incentive manipulation has an effect on how similarity in curiosity predicts similarity in the brain response in the *a priori* defined ROI, no

clusters survived thresholding. At whole-brain level, two clusters in the bilateral occipital cortex survived thresholding (Figure 3.7A, Table A3.10 in the appendix). In both clusters, similarity in curiosity was more predictive of similarity in the neural responses during magic trick watching in the control compared to the incentive group.

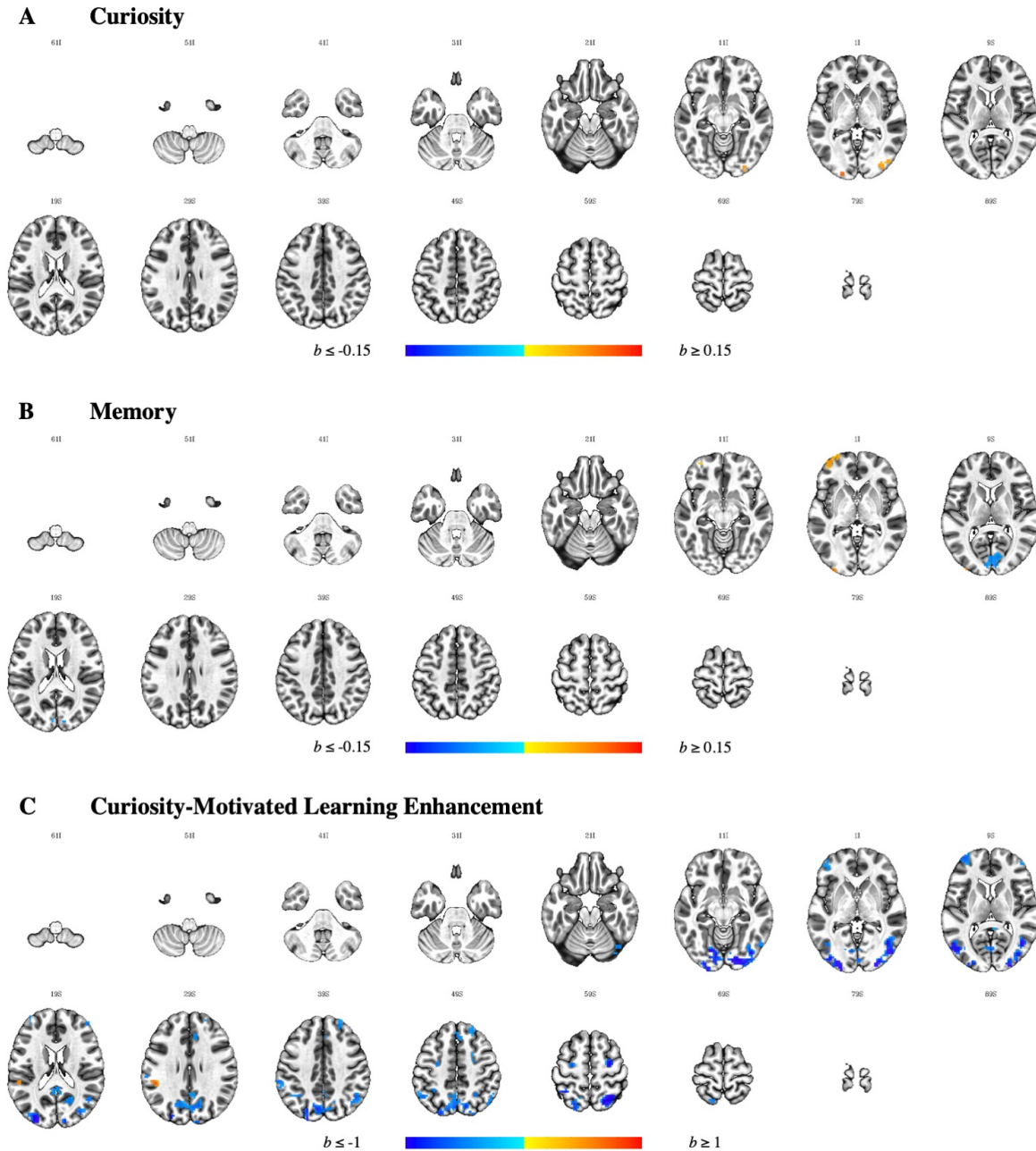
Memory Incentive Interaction. ROI analysis did not reveal any clusters where incentive influenced how similarity in memory predicted the similarity in the neural response. In the whole-brain analysis, three clusters were found (Figure 3.7B, Table A3.10 in the appendix) showing a differential predictive effect of similarity in memory depending on the availability of monetary incentives: One cluster in the bilateral Calcarine gyrus showed a more positive predictive effect of memory in the incentive compared to the control group. Two clusters were found where the predictive effect of memory was larger in the control compared to the incentive group. Those were located in the left dorsolateral prefrontal cortex (dlPFC, BA 10/BA 46) and left lateral middle occipital gyrus.

Curiosity-Motivated Learning Enhancement Incentive Interaction. While effects of curiosity and memory can be understood in a linear manner, the similarity matrix for CMLE was computed based on a non-linear AnnaK model formulation further influencing the interpretation of any effects observed. More specifically, positive clusters represent brain regions where CMLE high scorers share similar patterns and low scorers show variability whereas negative clusters represent regions where CMLE low scorers share similar patterns and high scorers show variability.

As with the effects of curiosity and memory, the availability of monetary incentives did not affect the relationship between the similarity in CMLE and brain activity in any of the ROIs. At whole-brain level, 20 clusters were found (Figure 3.7C, Table A3.10 in the appendix). One cluster showed positive values indicating that values were more positive in the control compared to the incentive group. This cluster was located in the left supramarginal gyrus where values were negative in the incentive group, but weakly positive in the control group. Additionally, 19 clusters showed negative values where the values in the incentives group were more positive compared to the control group. These clusters were predominantly located in posterior regions, stretching from the occipital poles towards the temporo-parietal-occipital junction laterally and the cuneus medially. In the parietal cortex, clusters were found in the precuneus as well as the superior parietal lobe. Frontally, bilateral clusters in the MFG were found as well as in the right superior frontal gyrus and the superior medial gyrus stretching into the ACC.

Figure 3.7

Whole Brain IS-RSA For the Interaction Between the Incentive Manipulation and Each Behavioural Effect of Interest



Note. Results are thresholded at $p < 0.001$, cluster-extent corrected at $k = 20$ (equivalent to per-cluster $\alpha = 0.05$) and plotted on the ICBM 2009c Nonlinear Asymmetric Template. Positive clusters (shown in red) indicate more positive values in the control compared to the incentives groups whereas negative clusters (shown in blue) indicate more positive values in the incentives group.

Intersubject Functional Connectivity (ISFC). In the last set of analysis, the objective was to examine the intersubject dynamics of aHPC and VTA/SN when watching magic tricks.

ROI-to-ROI ISFC Between Anterior Hippocampus and VTA/SN. Previous studies suggested that within-subject FC between aHPC and VTA/SN predicts curiosity- and reward-motivated learning (Gruber et al., 2014, 2016). Here, we were interested in between-subject FC between those two ROIs. More specifically, we investigated (a) whether the availability of monetary incentives influenced the strength of aHPC-VTA/SN-ISFC, and (b) whether the behavioural similarity matrices could predict aHPC-VTA/SN-ISFC and whether this was further affected by the incentive manipulation.

To determine whether the aHPC-VTA/SN-ISFC differed between control and incentive group, a LME-CRE model was specified using the availability of monetary incentives to predict aHPC-VTA/SN-ISFC. There are two observations from the results (Table 3.3). First, the intercept was positive and significant, meaning that there is, in fact, systematic stimulus-driven communication between VTA/SN and aHPC activity across subjects when watching magic tricks. Second, the incentive effect was not significant, suggesting that the availability of monetary incentives did not affect the ISFC between VTA/SN and aHPC.

In a next step, we examined whether the behavioural effects of interest could predict aHPC-VTA/SN-ISFC. All three behavioural effects of interest were entered as covariates into the same LME-CRE model; however, no statistically significant effects were found and only the main effect of curiosity reached trend level (see Table 3.3).

To explore whether the incentive manipulation influenced the relationship between the behavioural effects of interest and aHPC-VTA/SN-ISFC, a last LME-CRE model was specified to include the interaction effects together with the main effects of incentive and behavioural covariates. As indicated in Table 3.3, no effects reached statistical significance, despite the fact that the curiosity effect remained at trend level.

Seed-Based ISFC of Anterior Hippocampus and VTA/SN. In addition to the ISFC between aHPC and VTA/SN, their respective whole brain ISFC was examined by specifying them as seeds creating seed-based ISFC maps where each voxel value represents the between-subject correlation of that voxel's time course with the averaged time course of the seed region. To identify inter-regional correlations of aHPC and VTA/SN when exposed to magic tricks, LME-CRE models were used. These analyses revealed large clusters where shared information about the magic trick stimuli is encoded in a similar manner as in the respective seeds (Figure A3.8A and A3.8B, Table A3.11 in the appendix), suggesting that they encode shared information about the magic trick stimuli. Overall, maps for both seeds were highly similar (correlation unthresholded effect size map = .855, correlation unthresholded statistics map = .819, dice coefficient of masked cluster-extend thresholded results = .627), but ISFC for

the VTA/SN seed is spread further and values are numerically higher compared to the aHPC seed. More specifically, using the 7-Network parcellation proposed by Yeo and colleagues (2011) as reference, cortically, the seeds show positive ISFC with the medial Visual (Vis), Somatosensory, Limbic, Default Mode (DMN), Frontoparietal (FPN), Ventral Attention (VAN) networks whereas negative clusters were located in lateral parts of the Vis and the Dorsal Attention network (DAN). Positive clusters were further found in the striatum, midbrain, medial temporal lobe, and thalamus. While the incentive manipulation did not affect ISFC patterns of the aHPC seed, two clusters were found for the VTA/SN seed (Figure A3.8C, Table A3.11). More specifically, a cluster in the Vis (left occipital pole stretching into inferior occipital gyrus laterally) was found where the VTA/SN seed ISFC was more negative in the incentive compared to the control group, whereas ISFC values were larger in the incentive compared to the control group in the left VAN, more specifically in the left superior temporal gyrus.

To determine brain regions where similarity in the behavioural effects of interest covaries with similarity in the seed-based connectivity with aHPC and VTA/SN, the IS-RSA framework was extended to predict pairwise seed-based ISFC maps rather than the pairwise ISC maps. Separate LME-CRE models were run for each effect as well as each seed and the detailed results can be found in the supplementary material (for main effects, see Figure A3.9 and Table A3.12; for interaction effects, see Figure A3.10 and Table A3.13 in the appendix).

For the aHPC seed, no main effects of curiosity or memory were found. When trying to relate the behavioural effects of interest to VTA/SN ISFC, on the other hand, clusters could be found for all three variables. Similarity in curiosity predicted similarity in the VTA/SN FC in the bilateral superior medial gyrus (BA 8), left AIC, IPL (BA 39), and the dorsal pons. Similarity in memory could positively predict similarity in FC with the VTA/SN in the bilateral medial visual cortex, bilateral frontal cortex (BA 9, BA 46, BA 9-46, BA 6, BA 8), anterior cingulate cortex, left somatosensory cortex, bilateral angular gyrus (BA 39), supramarginal gyrus (BA 40), right AIC, right middle (BA 21) and inferior temporal gyrus (BA 37), the left CN, and left cerebellum. Additionally, in one cluster in the left occipital pole, similarity in memory negatively predicted similarity in FC with the VTA/SN.

Looking at how effects of similarity in CMLE and how this predicts similarity in ISFC with both seeds, respectively, the resulting maps for aHPC (6 positive and 4 negative clusters) and VTA/SN (10 positive and 7 negative clusters) again looked very similar (correlation unthresholded effect size map = .890, correlation unthresholded statistics map = .888, dice coefficient of masked cluster-extend thresholded results = .754). For both seeds, positive clusters were predominantly located in the DAN and Vis (the latter laterally) whereas negative clusters were found in medial areas of the Vis, DMN, FPN, Limbic, and VAN. Intriguingly, the maps found for the CMLE ISFC-RSA effects appeared like a “flipped” version of the ISFC obtained during magic trick watching (correlation unthresholded effect size

maps \leq -.850, correlation unthresholded statistics map \leq -.811, dice coefficient of masked cluster-extend thresholded results \geq .616).

When investigating whether the availability of monetary incentives influenced the association between similarity in behavioural effects of interest and VTA/SN and aHPC ISFC, respectively, no clusters were found for curiosity in either seed. Likewise, no clusters were found for the memory incentive interaction for the aHPC seed. Looking at the VTA/SN seed, however, in total 3 clusters were found: one cluster in the right occipital pole was found where the predictive effect was larger in the incentive compared to the control group. For the opposite effect, two clusters located in the posterior cingulate cortex (PCC) and left dlPFC were identified. With respect to CMLE, one cluster in the left inferior occipital gyrus was found for the aHPC seed where values were more positive in the control compared to the incentive group. For the incentive CMLE interaction on VTA/SN seed-based ISFC, in total 16 clusters were found. The two positive clusters (control > incentive) were located in the right superior parietal lobe and right superior frontal gyrus. The 14 negative (incentive > control) clusters were located in the superior parietal lobe, right precuneus, bilateral MFG, bilateral inferior parietal lobe, left supramarginal gyrus, right middle temporal gyrus, the superior medial gyrus, left superior frontal gyrus, and left aI/FO.

Table 3.3

Results of LME-CRE models predicting aHPC-VTA/SN-ISFC

	Estimate	SE	<i>t</i> value
Incentive Effect			
Intercept	0.010	0.003	3.638
Incentive effect	-0.002	0.003	-0.962
Main Effects			
Intercept	0.010	0.003	3.757
Incentive effect	-0.002	0.003	-0.803
Curiosity effect	0.013	0.007	1.805
Memory effect	-0.003	0.007	-0.361
CMLE effect	-0.073	0.066	-1.102
Main and Interaction Effects			
Intercept	0.010	0.003	3.7
Incentive effect	-0.002	0.003	-0.84
Curiosity effect	0.013	0.007	1.705
Curiosity incentive interaction	0.002	0.011	0.172
Memory effect	-0.003	0.007	-0.417
Memory incentive interaction	0.015	0.011	1.362

CMLE effect	-0.071	0.067	-1.048
CMLE incentive interaction	-0.031	0.09	-0.343

Note. Three different models were computed targeting different effects. Each LME specified crossed random intercepts for both subjects in each pair. Incentive effect was effect-coded (control = -1, incentive = 1). Rather than residualized values, Fisher’s *z*-transformed and grand-mean centred pairwise correlation values were used. *p* values are omitted as the *lme4* package does not compute them by default. SE = standard error. CMLE = Curiosity-motivated learning enhancement.

Discussion

The goal of the present chapter was to examine the effects of curiosity on incidental encoding using different stimuli and a new way to elicit curiosity compared to the well-established trivia question paradigm. Further, we were interested in the combined effects of curiosity and monetary incentives on memory. Results from a set of three experiments showed that curiosity – induced by the violation of expectations and surprise using magic trick videos – as well as the availability of monetary incentives facilitated incidental encoding independently, but did not interact with another with respect to behavioural measures of learning. When the incidental encoding was performed inside the fMRI scanner, analysis accounting for the dynamic nature of the stimuli revealed that effects of curiosity elicitation, memory encoding, curiosity-motivated learning enhancement (CMLE) as well as monetary incentives effects therein were associated with activity across widespread cortical areas. Additionally, while the effects of memory encoding and CMLE were supported by activity within the often implicated mesolimbic regions within the HPC-VTA loop, we did not find any indication that the effects of curiosity elicitation and monetary incentives were supported by shared, stimulus-induced activity in those regions.

Effects of Curiosity and Incentives on Memory

In contrast to the previous studies manipulating monetary reward within the trivia question paradigm (Murayama & Kuhbandner, 2011; Swirsky et al., 2021), we did not find a significant interaction between curiosity and incentives on any of our main measures of interest (recognition, high confidence recognition, cued recall). While the non-significant interaction effect may be explained by the differences in the design (e.g., materials, memory measures, and procedure to manipulate incentives compared to rewards), we also found an interesting dissociation between the effect of curiosity and that of incentives on memory. Specifically, the effects of curiosity on encoding were only found in recollection-based memory measurements (i.e., high confidence recognition and cued recall), but not on recognition regardless of confidence that is assumed to reflect familiarity and recollection (Yonelinas, 2002). On the other hand, the effect of incentives on memory does not seem to be influenced by confidence. These

findings suggest that curiosity only affects recollection-based, but not familiarity-based processes whereas the influence of monetary rewards is less selective.

These findings were unexpected but on scrutiny of the literature, they were somewhat consistent with the previous findings. For example, Gruber and colleagues (2014) reported that the curiosity-related recognition advantage in a delayed memory test was specific to confidently recognised faces and did not emerge in overall recognition rates. These results were replicated with short delays (Galli et al., 2018 (Exp. 1, but not in Exp. 2); Murphy, Dehmelt, et al., 2021), and it has been suggested that curiosity-related memory facilitation is specific to recollection (Gruber et al., 2019; Murayama & Elliot, 2011; cf. Stare et al., 2018 for an exception). On the other hand, studies on incentives/rewards and memory have suggested that rewards may influence both recollection and familiarity components of memory (Bunzeck et al., 2010, 2012; Patil et al., 2017; cf. Wittmann et al., 2011). Although not specifically about reward effects on memory, the findings are also consistent with a meta-analysis showing that extrinsic rewards better predicted the quantity of performance whereas quality was better explained by intrinsic motivation, which is a critical source of curiosity (Cerasoli et al., 2014). Future studies should examine more in detail whether curiosity and incentives have dissociable effects on these distinct aspects of memory.

Neural Correlates of Curiosity- and Incentive-Motivated Learning Within Reward-related Areas and the Hippocampus

fMRI research on the effects of curiosity (Gruber et al., 2014) and monetary reward (Murty & Adcock, 2014; Wittmann et al., 2005, 2008) on incidental encoding has repeatedly implicated the striatum, VTA/SN and hippocampus in curiosity- and reward-motivated learning. While we found that watching magic tricks led to significant synchronisation of brain activity across subjects in these areas, the incentives manipulation did not lead to differential synchronisation in these brain areas, the effects of interest (curiosity, memory, CMLE) and their interaction with the effects of monetary incentives were (partly) located outside our *a priori* defined ROI (aHPC, VTA/SN, NAcc and CN).

The biggest difference between this work and previous studies on the effects of curiosity and monetary incentives/rewards on encoding lies in the nature of stimuli used. Previous studies have used simplistic material like, for instance, blurred images (Jepma et al., 2012; Oosterwijk et al., 2020), lotteries (van Lieshout et al., 2018), or trivia questions (Duan et al., 2020; Gruber et al., 2014; Kang et al., 2009; Ligneul et al., 2018) to elicit curiosity inside the fMRI scanner. In comparison, in the present study, videos of magic tricks were used as stimuli. Compared to the simplistic, static stimuli used by others, magic tricks have added complexity due to their dynamic nature. Critically, we analysed the fMRI data from dynamic stimuli based on intersubject synchronisation (or intersubject correlation (ISC); Hasson et al., 2004), focusing on the intrinsic correlation of the voxel-wise time courses across participants to determine (clusters of) voxels exhibiting a consistent response to the naturalistic stimuli (Nastase et al.,

2019). The obtained ISC maps were further contrasted between different types of participant pairs in terms of incentive condition, curiosity rating, memory encoding, etc. As such, the current analysis captures different types of brain dynamics from the classical GLM approach.

For instance, the lack of ISC effects of monetary incentives in reward-related structures does not necessarily imply that there is no difference in brain activation in response to incentives. In fact, it is very well possible that the activation in reward-related structures was overall increased in the reward compared to the control group, but such an overall increase would not affect the correlation. In the ISC analysis, we rather tested whether the manipulation of incentives increased or reduced the individual differences in time-course patterns within a voxel (e.g., voxels within the reward-related structures). In other words, significant differences in ISC are expected when incentives made participants similarly (or differently) attend and comprehend the magic tricks (Hasson, Furman, et al., 2008), and should manifest in brain areas that are responsible for the synchronised psychological functions (e.g., attention, comprehension). Indeed, the effects of rewards and incentives on attentional processes have previously been discussed (Gottlieb & Oudeyer, 2018; Gruber & Ranganath, 2019). Value-modulated encoding has previously been linked to cortical areas associated with the strategic engagement of deep semantic processing rather than with mesolimbic activity (M. S. Cohen et al., 2014). Hence, we do not have a strong reason to believe that the reward network plays such a role. Similar logic should apply to our IS-RSA analysis of the effects of curiosity and memory performance and the incentive effects therein.

Importantly, while initial fMRI research using the trivia question paradigm suggested that the elicitation of curiosity is supported in dopaminergic regions in the striatum and midbrain (Gruber et al., 2014; Kang et al., 2009; Poh et al., 2021), other studies failed to replicate this effect and instead found striatal activity at curiosity relief (Duan et al., 2020; Ligneul et al., 2018). While these studies differed in various aspects from one another (e.g., intentional vs. incidental encoding; general knowledge- vs. cinema-related trivia questions), the latter studies included a jittered period between cue and target presentation whereas the initial studies did not. As such, the elicitation of curiosity is confounded with the anticipation of rewarding information. Hence, it is possible that the dopaminergic brain activity found was due to the anticipation of rewarding information rather than due to the elicitation of curiosity per se. Indeed, in the context of fully-predictable extrinsic rewards, it has been shown that dopaminergic neurons have signalled the reward-predicting stimuli rather than the reward itself (Knutson, Adams, et al., 2001; Schultz, 1998; Tobler et al., 2005). In a similar manner, if perceptual curiosity is relieved in only half of the trials, striatal activity is found at relief and not at elicitation (Jepma et al., 2012). Taken together, this suggests that when the elicitation of curiosity is not confounded with the anticipation of rewarding information, the curiosity-related effects can be found during curiosity relief and not as previously suggested merely during elicitation. Because in our paradigm, curiosity was elicited but never relieved

and no rewarding information was anticipated, this could potentially further explain the absence of curiosity effects in reward-related structures.

An interesting observation from the ROI analysis, however, is that the memory effect was found in the bilateral CN, replicating previous studies linking declarative memory to the CN (Blumenfeld et al., 2011; Schott, 2006). While meta-analyses have linked the CN to reward processing (Diekhof et al., 2012; Sescousse et al., 2013), the CN has also been implicated in goal-directed action and learning (for a review, see Grahn et al., 2008), and more specifically, in error learning (Delgado et al., 2005) and reward-motivated learning (Wittmann et al., 2005). However, even in the absence of feedback or reward, enhanced activity in the CN has also been found when expectations are violated in a movement observation paradigm (Schiffer & Schubotz, 2011), hence linking the CN to perceptual PEs (when “what is happening now” differs from the internally generated prediction; Zacks et al., 2007). Enhanced CN activity has further been found when participants watch magic tricks compared to matched control scenes not violating expectations (Danek et al., 2015) suggesting that magic tricks because they violate expectations, trigger perceptual PEs, signalled in the CN. We here found that similarity in encoding magic tricks predicts similarity in CN activity. This suggests that the CN is not only important in signalling perceptual PEs but might also play a role in updating internal models and schemas by supporting the encoding of incongruent events. Moreover, the CN has been found to linearly track curiosity ratings (Gruber et al., 2014; Kang et al., 2009) and also support the subsequent memory effect modulated by curiosity (Duan et al., 2020), further stressing its role in generating PEs eliciting curiosity, but also in updating the knowledge base.

Lastly, significant CMLE effects were observed in all four ROIs, but importantly, these effects were negative. Negative clusters essentially indicate that participants who have low beta values (i.e., participants in which curiosity did not predict memory performance) showed more similar brain activation time courses in response to the magic trick stimuli. Put differently, in negative clusters, the response in the low scorers is more exogenous and stimulus-driven whereas the response in high scorers is more endogenous and individual — participants who have high curiosity-memory association have more divergent and diverse time courses between individuals. Using the trivia question paradigm, Gruber and colleagues (2014) were the first to link the effects of curiosity on incidental encoding (i.e., the interaction between curiosity and memory) to activity in the bilateral NAcc and the right HPC (but not the left). Likewise, activity in the CN and NAcc supports the effects of curiosity on intentional encoding (Duan et al., 2020). The current study also not only replicates the critical roles of these brain areas in the effects of curiosity on encoding using dynamic stimuli, but our findings suggest that they do so in a variable manner. Specifically, we found that participants with high CMLE compared to those with low scores show less exogenous shared (i.e., stimulus-driven) activation in these regions. In alignment with

previous findings that intrinsically-oriented processes are less consistent, causing a unique and variable response to dynamic stimuli (Ren et al., 2017), our findings indicate that the effect of curiosity on memory is supported by rather individualised and variable processes across subjects in response to the magic tricks. As such, this echoes previous findings relating the successful encoding of answers in the trivia question paradigm to an individual hippocampal “convergence” state of optimal encoding (Poh et al., 2021).

Curiosity- and Incentive-Motivated Learning Outside Reward-Related Areas and the Hippocampus

In addition to the results within the *a priori* ROIs (the reward-related areas and the hippocampus), our whole-brain IS-RSA showed the broad network of the brain supporting curiosity, memory, and curiosity-motivated learning enhancement (CMLE). To better understand the IS-RSA results, the resulting clusters for each effect of interest were compared with the 7-Network parcellation proposed by Yeo and colleagues (2011) dividing the brain into Visual (Vis), Somatosensory, Dorsal Attention (DAN), Ventral Attention (VAN), Limbic, Frontoparietal (FPN), and Default Mode (DMN) networks.

Curiosity. With respect to the effects of curiosity elicitation, we found that similarity in the curiosity ratings predicted similarity in the brain response in visual areas, the inferior frontal gyrus (IFG), the supplementary motor area (SMA), the postcentral gyrus, precuneus, anterior insula, and the supramarginal gyrus. The elicitation of curiosity has repeatedly been linked to a state of uncertainty, potentially due to a violation of expectations (Gruber & Ranganath, 2019; Murayama, FitzGibbon, et al., 2019). Such violations of expectations have previously been linked to – amongst other regions – dlPFC, premotor cortex, posterior parietal cortex (PPC), and ventral visual stream (Murty & Adcock, 2014). In alignment with this proposal, our findings show that the IS-RSA effect of curiosity is located in the SMA, an area that has been implicated in the processing of uncertainty (Cheung et al., 2019; Volz et al., 2005) and in the IFG – part of the lateral PFC. The IFG has been linked to the elicitation of curiosity in the trivia question paradigm (Gruber et al., 2014; Kang et al., 2009). According to the Prediction, Appraisal, Curiosity, and Exploration (PACE) framework explaining how curiosity enhances HPC-dependent memory (Gruber & Ranganath, 2019), the IFG is involved in the appraisal processes determining whether PEs and associated uncertainty elicit curiosity or anxiety. The IFG has also been linked to the violation of expectations (Danek et al., 2015) and causal relationships (Parris et al., 2009) in magic tricks. This suggests that as participants watch magic tricks, the curiosity IS-RSA effect in the SMA and the IFG could reflect that uncertainty-related signals and their appraisal processes of the experienced PEs share a similar signature when experienced curiosity is similar.

Curiosity IS-RSA effects were also observed in the PPC – a region anteriorly responding to motoric and perceptual representations of actions and candidate for mirror neuron system areas (Chong et al., 2008; Dinstein et al., 2007; Ishida et al., 2010). This could reflect attentional processes. The dorsal

part of the PPC (lateral and medial parts of BA7) has been implicated in top-down attention together with dorsal frontal regions, whereas the ventral part (corresponding to BA 39 and BA 40, often referred to as inferior parietal lobe (IPL)) together with ventral frontal regions are involved in bottom-up attentional processes (Corbetta et al., 2008; Corbetta & Shulman, 2002). Because IS-RSA curiosity effects were located in dorsal (i.e., precuneus) and ventral (i.e., right supramarginal gyrus) PPC regions, as well as in the IFG – part of the wider ventral attention system – this suggests that curiosity is associated with top-down goal-directed attention related to the judgement task or the re-direction of attention in response to the ventral system signalling the violation of expectations and causal relationships as salient events in a bottom-up manner. Indeed, the PPC and more specifically, the IPL was previously linked to signalling the moment of expectation violation in magic tricks (Danek et al., 2015), but also to signalling surprise and model update thereafter in other tasks (J. X. O’Reilly et al., 2013). Overall, these attentional mechanisms could further be related to uncertainty underlying curiosity and exploration and information seeking to resolve it. In fact, investigating the effects of curiosity on eye movements, Baranes and colleagues (2015) suggested that curiosity is associated with prioritisation and allocation of attention which could be supported by “priority maps” in the parietal cortex (Bisley & Goldberg, 2010). The induction of curiosity has also been linked to increased activity in the IPL in a lottery task (van Lieshout et al., 2018) as well as within the trivia question paradigm (Duan et al., 2020). Overall, this suggests that, when the state of curiosity is high, people tend to show shared activity of areas related to (re-)directing attention and processing uncertainty triggered by salient events that violate predictions — people in a curious state may have similar time courses of attention (re-)direction and experience of uncertainty.

Memory. The IS-RSA memory effect was found in broadly distributed cortical areas including visual cortices, medial and lateral parietal lobe, lateral temporal areas and dorsal PFC. Overall, the IS-RSA memory effects reported here replicate previous findings obtained using dynamic stimuli. Nguyen and colleagues (2019) also used IS-RSA to anchor similarity in encoding (immediate recall) to similarity in brain response and reported clusters in the DMN (e.g., angular gyrus) and the FPN (e.g., bilateral MFG). Both networks have been found to be co-activated during movie watching which could be related to mentalizing, emotional processes and social reasoning (Dixon et al., 2018; Nguyen et al., 2019) and ISFC within the DMN during naturalistic narrative comprehension highly correlates with subsequent recall (Simony et al., 2016). Likewise, connectivity between HPC and the posterior medial networks (e.g., angular gyrus, PCC, precuneus) during naturalistic viewing supports learning of the temporal structure in narratives (Aly et al., 2018). This is in alignment with previous studies implicating the DMN in the processing of complex narratives, suggesting that the DMN might accumulate information over longer time scales to integrate them at higher levels of the processing hierarchy (Hasson et al., 2015; Hasson, Yang, et al., 2008). The FPN, on the other hand, supports top-down adaptive, online control (Dosenbach

et al., 2007). This suggests that adaptive control mechanisms in the FPN triggered by the cognitive conflict caused by observing the violation of causal relationships in magic tricks could facilitate successful encoding thereof.

It has previously been proposed that in addition to the MTL, cortical systems or networks support memory encoding (Bastin et al., 2019; Fuster, 1997; Kim, 2011; Ranganath & Ritchey, 2012; Spaniol et al., 2009). As such, different components in the encoding process have been proposed (Kim, 2011): storage, content processing, and attention. While the MTL is implicated in the storage function (Squire et al., 2004), other brain areas mediate the other components. Critically, while the IS-RSA effects during the incidental encoding of magic tricks were not located in the classical storage regions within the MTL, we found clusters in areas of the brain involved in other components of the memory process — content processing and attention. For example, we observed significant IS-RSA memory effects in IFG and fusiform gyrus. Evidence suggests that the lateral PFC is involved in control processes where ventrolateral regions select goal-relevant item information and dorsolateral regions support the organisation of information within working memory to form associations (Blumenfeld & Ranganath, 2007). Also, other IS-RSA memory clusters in the parietal cortex are located in more posterior regions, supporting top-down and bottom-up attentional control (Shomstein, 2012). An attention-driven involvement of the PPC in memory has predominantly been discussed in the context of retrieval (for reviews, see Cabeza et al., 2008; Shimamura, 2011), potentially explaining why the PPC is more activated during recollection- compared to familiarity-based recognition (Kim, 2010) and is further involved in autobiographical memory retrieval (Cabeza et al., 2004). However, other proposals have also suggested that increased activity in the PPC, especially the dorsal, goal-directed regions, increases the likelihood for an event to be later remembered (Uncapher & Wagner, 2009).

These findings are consistent with the idea that memory is not solely supported by the MTL, but rather memory output is a consequence of the complex interaction of different mental processes. For example, the hierarchy of process memory framework (Hasson et al., 2015) posits that each cortical circuit along the processing hierarchy can accumulate information over time, but the temporal receptive windows (time spans in which prior information can impact current processing) increase as the information travels from sensory to high-order cognitive regions. This suggests that memory of recent events (for instance, the events of the magic trick that is currently viewed) are not stored in dedicated areas in e.g., the MTL, but are organised hierarchically across the cortical regions processing the information, enabling the online processing of continuous, dynamic, complex stimuli by retaining information independent of MTL involvement. The widespread cortical IS-RSA effects with the visual cortex in its centre suggest that as participants view the magic tricks, neurons process and retain the

information within their respective temporal receptive windows at each level of hierarchy which in turn also supports later memory for the magic trick.

Curiosity-Motivated Learning Enhancement. In addition to the ROI results discussed above, significant CMLE effects were observed in broad cortical areas but most importantly, these effects were mostly negative. Indeed, negative clusters were found across largely distributed cortical and subcortical areas including large parts of the DMN (e.g., bilateral ACC, angular gyrus, middle temporal gyrus), FPN (e.g., bilateral MFG, SMA), DAN (e.g., bilateral posterior superior parietal lobe), VAN (e.g., anterior insula/frontal operculum (aI/fO)) as well as Vis. A recent re-analysis of the dataset from Gruber and colleagues (2014) showed that the DMN and a subnetwork within the FPN (i.e., lateral PFC, posterior inferior temporal gyrus, and superior parietal lobe) show a curiosity-by-memory interaction (Murphy, Ranganath, et al., 2021). Replicating and expanding on these results and in alignment with the ROI analysis discussed above, we found that participants with high CMLE compared to those with low scores show a more individualised and variable activation in these brain networks.

These observations have various implications. For example, it has been shown that during naturalistic viewing, the anterior (e.g., medial PFC) and lateral DMN (e.g., angular gyrus) are strongly intrinsic whereas the precuneus shows more extrinsic responses that correlate between subjects, making the DMN a prime candidate to integrate extrinsic, stimulus-driven activity with internal processes due to the interconnectivity between these regions (Ren et al., 2017). A recent perspective proposes that the DMN is highly implicated in the processing of the dynamic structure of external, naturalistic stimuli, regardless of modality, by integrating inputs across longer temporal receptive windows with idiosyncratic, internal prior dispositions (e.g., prior knowledge or beliefs) to form models of the experienced situation (Yeshurun et al., 2021). This perspective can explain the role of the DMN in curiosity-motivated learning: In the context of the trivia question paradigm, the involvement of the DMN has been discussed in light of the successful accumulation and integration of new information into prior knowledge and schemas (Murphy, Ranganath, et al., 2021), however, the DMN has also been implicated in processing surprise in naturalistic viewing due to its ability to detect the mismatch between incoming information and internal models (Brandman et al., 2021). Any internal models shaped by prior experiences could be supported by unique firing patterns within the brain and communication across brain regions, hence explaining why curiosity-motivated learning is accompanied by endogenous responses within the DMN, further supporting the update of internal models in the context of curiosity-motivated learning.

Regarding the negative cluster in the FPN, previous work has argued that the FPN exerts cognitive control, especially in the context of multiple demands, allowing the brain to remain flexible and adaptive (Dosenbach et al., 2007). A potential mechanism to achieve cognitive control is to maintain task-relevant information and suppress irrelevant information. In naturalistic conditions, the FPN, showing

high variability in FC, may be involved in shifts in the broader processing of stimuli (Vanderwal et al., 2017). Our findings – that participants with high CMLE scores are less similar in their stimulus-induced brain response in the FPN compared to low scorers – shed further light on the mechanisms by which the FPN is involved in the enhancing effects of curiosity on memory reported by others (Duan et al., 2020; Murphy, Ranganath, et al., 2021). The FPN de-synchronises across participants suggesting individualised, internal processes by which the FPN – previously described as a flexible hub (M. W. Cole et al., 2013) – supports curiosity-motivated learning, potentially by integrating external sensory information with internal representations by transferring information between DMN and DAN, especially in the context of stimulus-related conflict (Vincent et al., 2008) as caused by the violation of cause and effect relationships in magic tricks.

Intersubject Functional Connectivity (ISFC)

We conducted exploratory ISFC analysis using aHPC and VTA/SN as seed regions. There were a few observations. First, we found significant ISFC between aHPC and VTA/SN during magic trick watching. Second, both seeds showed widespread seed-based ISFC within similar cortical and subcortical areas including the striatum and thalamus, while the ISFC of the VTA/SN seed seems to descriptively span across larger regions. Overall, both seeds were positively correlated across subjects with the DMN, VAN, FPN, medial Vis, Limbic, and Somatosensory Network and negatively correlated with the lateral Vis and DAN. Given that previous studies have linked the DAN and Vis to extrinsic, exogenous systems, whereas all other networks support endogenous and exogenous processing, the pattern observed here suggests that aHPC and VTA/SN belong to the latter category.

However, our further analysis showed that this pattern was modulated by some behavioural indices. For example, similarity in curiosity and memory predicted similarity in seed-based ISFC with the dopaminergic midbrain in various regions belonging predominantly to the DMN or FPN. One interesting finding was that ISFC-RSA memory effects were also found in the left CN, overlapping with the cluster where the IS-RSA memory effect was found in the ROI analysis, implying that the effect could at least partly have been driven by dopamine. In addition, similarity in CMLE predicted similarity in whole-brain ISFC for the aHPC and the VTA/SN seed, resulting in positive and negative clusters. The ISFC-RSA CMLE effects were highly similar across both seeds. Positive clusters were located in the Vis around the occipital pole partly stretching laterally as well as in the DAN (e.g., posterior superior parietal cortex and superior frontal gyrus) bordering the Somatosensory network (pre- and postcentral gyrus). Negative clusters were found in the DMN (e.g., ACC, PCC, angular gyrus), FPN (e.g., MFG, inferior temporal gyrus), VAN (e.g., aI/fo), Vis medially (e.g., cuneus) as well as in the Limbic network (e.g., temporal pole, entorhinal and perirhinal cortex) and subcortical regions including the striatum and thalamus. Importantly using the aHPC seed, voxels showing negative ISFC-RSA CMLE effects in the VTA/SN

were found, and vice versa. These results indicate that, while aHPC and VTA/SN show positive correlations with endogenous systems during naturalistic viewing, in the context of curiosity-motivated learning, the communication of both seeds and other members of the endogenous systems (e.g., in the DMN, FPN, or Limbic network) becomes more variable and less stimulus-driven in participants with high compared to low CMLE. In comparison, the communication between both seeds and members of the exogenous system (DAN and Vis) becomes more similar for participants with high compared to low CMLE scores. Overall, this suggests that CMLE is supported by stimulus-driven communication between the aHPC and VTA/SN seed and predominantly exogenous regions and unique ISFC patterns with more endogenous systems.

One critical factor that helps us explain these results is PE. Magic tricks violate expectations, predictions, and cause-effect relationships. Such (unsigned) PEs often create a sense of surprise (Antony et al., 2021; J. X. O'Reilly et al., 2013). Surprise, in turn, can trigger curiosity (Lau et al., 2020; Ligneul et al., 2018; Ozono et al., 2021; Vogl et al., 2019). Importantly, the HPC does not only represent space and context in form of cognitive maps (O'Keefe & Nadel, 1978), but also more generally predictive maps of future states, encoding expectations thereof to support subsequent learning (Stachenfeld et al., 2017). As such, the HPC plays a role in information processing by weighing expectations and novel evidence (Rigoli et al., 2019) and in the detection and encoding of unexpected events (Axmacher et al., 2010). Some also suggest that the HPC signals uncertainty or predictability of events (Harrison et al., 2006) reflecting a more generic context-sensitivity to the probabilistic structure of the environment observed events. A PE also signals saliency, warning that a belief update is necessary to improve the internal model and future predictions. Indeed, PEs have been found to disrupt hippocampal representations to update episodic memories (Sinclair et al., 2021). The saliency of PE is signalled by a dopaminergic response and research suggests that this is not only the case for reward PEs, but PEs in general (Antony et al., 2021; Horvitz, 2000; Pine et al., 2018; Ungless, 2004). Therefore, the ISFC between aHPC and VTA/SN may be explained by the common stimulus-induced responses that signal salient information in the context of uncertainty and PEs elicited by the magic tricks, replicating previous results of increased FC between both brain regions in the context of unexpected, salient single images (Murty & Adcock, 2014).

Similarly, the results of the ISFC-RSA of curiosity and memory using the VTA/SN as seed could reflect the interplay between the PE-related dopaminergic response of the VTA, curiosity and memory during naturalistic viewing. In both cases, parts of the VAN (more specifically, aI/fO) were activated, assumed to play a major role in processing salient events (Corbetta et al., 2008; Corbetta & Shulman, 2002; Menon & Uddin, 2010). The salience-related signal could further recruit FPN as an adaptive control mechanism to ensure cognitive flexibility in the context of PE processing. Indeed, the fronto-insular cortex, where the effects found here are located, is involved in switching between the FPN and the

DMN (Sridharan et al., 2008). Likewise, the DMN recruitment could reflect activity associated with the update of internal models. In each case, it seems reasonable to assume that these networks hence anchor idiosyncratic patterns of curiosity and memory, respectively.

We found that curiosity-motivated learning (as the difference in similarity in ISFC between participants with a high CMLE compared to a low CMLE score) is supported by more individualised, endogenous patterns in ISFC in response to the stimuli between both seeds and the DMN, FPN, and VAN, respectively, but more exogenous responses in the DAN. These findings can be contrasted and interpreted with the findings by Murphy, Ranganath, and Gruber (2021). Using Psychophysiological Interaction (PPI) analysis, the authors showed that coupling between HPC and subparts of the DMN during the relief, but not the elicitation, of curiosity supports curiosity-enhanced learning. Taking a more fine-grained approach, they further showed that during relief, the HPC correlates with the medial PFC and the VTA/SN with the PCC to support curiosity-motivated learning. However, no FC between the FPN and the subcortical structures (HPC and VTA/SN) was found to support curiosity-motivated learning, whereas FC between DMN and FPN during both elicitation and relief supported curiosity-motivated learning.

Intriguingly, in conjunction with the results by Murphy and colleagues (2021), we also identify ISFC between aHPC and medial PFC as well as between the VTA/SN and the PCC as neural substrates of CMLE. Our results extend their findings by showing that the stimulus-induced communication between subcortical and cortical areas in support of CMLE is individualised and endogenous. While subcortical structures and FPN did not show an interaction between curiosity and memory in the PPI analysis, our results suggest that participants with high CMLE scores show more individualised, endogenous ISFC patterns between the FPN and both seeds in response to the stimuli compared to participants with low scores. This might reflect the engagement of cognitive appraisal and control mechanisms in support of the ongoing information-seeking following the encounter with a PE (Gruber & Ranganath, 2019). Lastly, while Murphy et al. (2021) did not include the VAN and DAN, we found that ISFC patterns for both seeds were more exogenous and driven-driven in the DAN, but more endogenous and variable in the VAN in support of curiosity-motivated learning. Assuming that stimulus-induced responses in the aHPC and VTA/SN are indeed related to signalling salient information in the context of uncertainty and PEs, this indicates that salience and bottom-up attentional processes in the VAN are signalled in an endogenous, variable manner across participants in response to the stimulus, whereas top-down attentional processes to redirect attention in response to the unexpected events in DAN are more exogenous and stimulus-driven to support curiosity-motivated learning.

Taken together, the results of the ISFC analysis suggest that while the time course of aHPC and VTA/SN synchronise with the response in large cortical networks across subjects when presented with

magic tricks, these patterns of functional connectivity overall flip to support curiosity-motivated learning where higher CMLE scores are associated with more endogenous, unique ISFC patterns, not only between both seeds but also to cortical networks. As unexpected events and PEs are appraised in a way eliciting curiosity, curiosity in turn enhances encoding by individualised ISFC patterns between subcortical and cortical areas. As such, curiosity-motivated learning is potentially related to or dependent on the higher-order response to unexpected events described by Brandmann and colleagues (2021) in the context of surprise. But curiosity-motivated learning also extends beyond that by further also recruiting ISFC connections between VTA/SN and aHPC and FPN, VAN, and DAN, respectively; partly by stimulus-induced synchronisation of ISFC patterns across participants, but predominantly by desynchronisation in response to the stimulus across participants.

Influences of the Availability of Extrinsic Incentives

While we did not find effects of extrinsic incentives in the HPC-VTA loop or other dopaminergic regions, effects were found at whole-brain level. For instance, we found that monetary incentives are associated with increased synchronisation in the early visual areas, the postcentral gyrus and the intraparietal sulcus (IPS). Overall, these areas have been implicated in top-down spatial attention and form the DAN (Corbetta & Shulman, 2002; Vossel et al., 2014) in general, but also in value-driven attentional processes in the context of monetary rewards (Anderson, 2017) and memory-guided attention (Salsano et al., 2021) in particular. This suggests that participants in the incentives group might have attended the magic tricks in a more similar manner because they have the common goal of maximising their bonus payments in the orientation task, perhaps attending to similar parts of the video clip. Indeed, the idea that rewards or incentives would affect attentional processes is not new (Gottlieb & Oudeyer, 2018). In the control group, on the other hand, increased ISC was found in Area V5/MT+ which is critically involved in motion perception and has feed-forward connections to the parietal cortex (Zeki, 2015). Likewise, the IPS is also more activated during the encoding of items compared to their associations (Kim, 2011), suggesting that the IPS supports familiarity-based compared to recollection-based recognition. Hence, the difference in ISC depending on the availability of monetary incentives provides further support for the proposition regarding the dissociation between curiosity and monetary incentives discussed above.

We further found IS-RSA clusters for each behavioural effect of interest where the second-order similarity between behaviour and brain response differed depending on the availability of monetary incentives, indicating that the incentive manipulation influenced not only the degree of synchronisation during the naturalistic viewing per se but also the way how similarity in the stimulus-elicited brain response could be anchored to the similarity in each of the behavioural variables of interest. The clusters showing an interaction between the behavioural effects of interest and the incentive manipulation are

primarily located in the Vis or the DAN, further suggesting that the incentive manipulation influenced attentional mechanisms during incidental encoding. Of note, for the memory-incentive interaction, we found lower synchronisation in the incentives group compared to the control group on the left lateral PFC, an area in the FPN previously implicated in the neural basis of the undermining effect (Murayama et al., 2010), but also in SME in general (Kim, 2011). Further evidence regarding the idea of an undermining effect was found in CMLE. Overall, our analysis showed that CMLE in and of itself is supported by endogenous rather than exogenous responses to the magic tricks in participants with high CMLE scores compared to those with low scores (reflected in negative effects). Investigating the interaction between CMLE and the incentive manipulation, most clusters were negative, meaning that the values in the incentive group were more positive compared to the control group. This suggests that in the incentive groups, participants' tendency to prioritise internal over external processes was less pronounced in support of curiosity-motivated learning.

Limitations

In the current study, we investigated the effects of curiosity on memory encoding using dynamic, naturalistic stimuli, thereby trying to address some of the shortcomings in the trivia paradigm, e.g., by testing the encoding of the stimuli that elicited curiosity rather than the stimuli that satisfied it. However, the use of magic tricks as stimuli also bears some limitations. First, in the trivia question paradigm, a screening phase is often included (Gruber et al., 2014; Murphy, Dehmelt, et al., 2021; Poh et al., 2021; Stare et al., 2018) to create an individual set of trivia questions featuring the same amount of high and low curiosity questions, ensuring within-person variability and enabling analyses based on a factorial design. Such a pre-screening phase was not possible within the magic trick paradigm and the ISC analysis because the ISC framework requires the same sensory input across participants. Yet, we tried to induce sufficient within-subject variance by including magic tricks spanning a broad range of curiosity ratings based on data from the Magic-CAT stimulus collection (Ozono et al., 2021). To further increase variance or to be able to contrast high and low curiosity conditions, future research could include control clips not violating causal relationships as used by others (Danek et al., 2015; Parris et al., 2009). The inclusion of within-subject control scenes would further allow to contrast brain activity between conditions, especially within the HPC-VTA loop.

Second, analyses in the ISC framework highly depend on the time course that is used to compute the ISC maps (Jääskeläinen et al., 2016) as it has been shown that the degree of ISC can vary from moment-to-moment as a function of emotional states (Nummenmaa et al., 2012). Each magic trick also displays events that might be partially unrelated to our effects of interest. Hence, by computing the ISC across the whole time course of the magic tricks, our analysis could have missed brain areas that show high ISC during certain moments of the magic trick (e.g., the moment of an unexpected event). For

instance, different results in the reward network were observed depending on how the events of the magic trick were specified within the GLM to contrast them with control scenes (Danek et al., 2015): If events were modelled time-locked with the moment of expectation violation with the event duration set to zero compared, the results differed from when the events were modelled by using the onset of the video clip and the corresponding duration. Differences were attributed to the idea that the former models only the incongruency, but the latter the expectation itself (Danek et al., 2015). We computed ISC using the entire course across magic tricks to ensure the sufficient reliability of ISC, but future studies may want to examine potential time-dependent changes of ISC as people watch magic trick videos.

Finally, while the magic tricks videos had varying lengths, curiosity was assessed in only one rating collected at the end of the trick. As such, the behavioural measure spans the whole duration of the trick whereas neural activity was sampled more frequently ($TR = 2s$). Related to what has been discussed above, curiosity likely varied throughout the magic trick presentation. While others have obtained behavioural ratings of cognitive and emotional states for shorter time intervals (Brandman et al., 2021) or even on a moment-by-moment basis (Nummenmaa et al., 2012), such ratings were obtained either by a separate sample or in a second viewing following scanning. However, curiosity ratings show high individual differences (Fastrich et al., 2018; Ozono et al., 2021), making ratings by a separate sample less feasible. Likewise, a second viewing would have interfered with memory measurements and ratings of curiosity would likely have been affected by the fact that the moment of surprise has previously been revealed. Collecting dynamic curiosity ratings during scanning could have increased the attentional load and working memory requirements given that participants were already engaged in an incentive orientation task, which could have impacted encoding (Fernandes & Moscovitch, 2000). As such, while future research on the effects of curiosity on the encoding of dynamic stimuli would benefit from online measures of curiosity, finding ways to measure curiosity during naturalistic viewing in a continuous, yet uninterrupted manner remains challenging, both behaviourally as well as physiologically (cf. Antony et al., 2021 for an example on measuring pupil dilation in the context of surprise during naturalistic viewing).

Overall Conclusion

We found that the curiosity effect of memory can be replicated using naturalistic stimuli. Using analysis approaches to account for the dynamic nature of the magic trick stimuli, the effects of curiosity and incentives were not located within the reward network of the brain per se, but across distributed cortical areas. While effects of memory and CMLE were found within the HPC-VTA loop, they too showed widely distributed cortical clusters. This supports the claim that the effects of motivated incidental encoding of dynamic stimuli are actually more distributed across higher-order cortices. This adds to previous research by showing that the effects extend beyond mesolimbic structures often

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identified using reductionist simple stimuli that do not reflect everyday perception and cognition and analysis approaches based on rigorous modelling of the hemodynamic response. This suggests that a too stringent focus on narrow ROIs could lead to an oversimplification and might miss important insights in how the brain works when processing and encoding naturalistic stimuli. To derive a better understanding of how curiosity influences memory and to inform practitioners in educational settings, more research with various stimuli and tasks is needed.

Chapter 4: The Availability of Extrinsic Monetary Incentives Re-Configures Resting-State Networks in Support of Memory Formation During Early Consolidation

The current chapter examines the effects on whether the post-learning resting state network, which is supposed to reflect consolidation processes, is related to the effects of curiosity and incentives on learning performance. As reviewed in the introductory chapter, consolidation describes processes during which a newly formed memory trace becomes increasingly stabilised and thereby transformed into long-term memory (Dudai, 2012). Consolidation occurs on two levels (S.-H. Wang & Morris, 2010): cellular consolidation describes intracellular mechanisms that give rise to lasting changes in the (synaptic) structure of a neuron in support of information storage, e.g., synthesis of plasticity-related proteins. Systems consolidation, on the other hand, refers to intercellular and interregional mechanisms that enable activity in one area of the brain to influence activity in another brain area in relation to information storage.

Consolidation and Dopamine

As reviewed in earlier chapters, dopamine is exerting its effect on memory encoding by influencing late long-term potentiation (LTP) processes. Behavioural studies often report enhancing effects of monetary rewards on encoding only in delayed, but not immediate memory tests (Murayama & Kitagami, 2014; Murayama & Kuhbandner, 2011; Patil et al., 2017; Wittmann et al., 2005). Indirect evidence supporting this idea was also found in an fMRI by Wittmann and colleagues (2005): while no subsequent memory (SM) effect¹⁰ for reward-predicting items was observed when using data from an immediate memory test to define remembered and forgotten items, SM effects for reward-predicting items were found in dopaminergic brain areas (substantia nigra (SN) and caudate nucleus) as well as the hippocampus (HPC) and parahippocampal gyrus when using data from a delayed memory test carried out 3 weeks after encoding. Crucially, the same voxels in the dopaminergic brain areas were active during reward anticipation and in relation to reward-motivated learning. This suggests that while activity during encoding is associated with later memory encoding, their activity only predicts delayed memory, i.e., encoding that relies on consolidation. Altogether, these studies show that dopaminergic reward effects are supported by consolidation processes that rely on the expression of late LTP and associated protein syntheses and hence can only be measured behaviourally after a sufficient delay. As reviewed earlier, dopamine has indeed been found to influence the expression of late-LTP and evidence suggests that the

¹⁰ Subsequent memory (SM) effects are calculated by contrasting brain activation during the encoding of later remembered trials with that of later forgotten trials.

effects of dopamine on late LTP might bias replay activity favouring events associated with the release of dopamine (e.g., reward and novelty), potentially by mechanisms of synaptic tagging (Atherton et al., 2015). Additionally, pharmacological manipulations in rodents have shown that the application of a dopamine antagonist during encoding prevents the selective consolidation of stimuli associated with the release of dopamine (S.-H. Wang et al., 2010), an effect also observed in humans (Feld et al., 2014).

Due to the important role of the HPC in encoding and the dopaminergic midbrain in the release of dopamine, studies have directly targeted these brain areas in the context of consolidation (i.e., awake rest period after learning). In fact, more sharp wave ripples were recorded in the rodent HPC following reward-motivated learning compared to the absence of reward, implying that the reactivation patterns in the HPC might reflect experiences associated with reward (A. C. Singer & Frank, 2009). Intriguingly, reactivation has also been observed in recordings in the ventral tegmental area (VTA) during awake rest and sleep after receiving different rewards (Valdés et al., 2015). In addition, following appetitive spatial learning, replay in the HPC coincided with reward-responsive neurons in the VTA during an awake rest, but not during sleep (Gomperts et al., 2015). If dopaminergic projections to the HPC are stimulated during the exploring of novel environments or encoding spatial encoding using optogenetics, this is associated with enhanced reactivation of pyramidal cells in the HPC and better recall indicating that activity in dopaminergic cells can enhance hippocampal replay (McNamara et al., 2014). Taken together, these results illustrate dopaminergic effects on consolidation processes within the HPC that can be found during an awake rest following a task and predicts encoding.

In a similar vein, human fMRI studies also suggest a dopaminergic influence on consolidation as measured by BOLD activity in HPC, VTA/SN and their interaction. For instance, after participants performed an associative learning task, cerebral blood flow changes from pre- to post-learning rest were found in a large cluster located in the right MTL spanning HPC and parahippocampal gyrus stretching into VTA/SN that correlated with encoding (Groen et al., 2011). Tomparny and colleagues (2015) also used an intentional associative learning task with separate assessments of item and associative memory (i.e., familiarity and recollection) and collected high-resolution fMRI data before, during, and after learning enabling them to differentiate the functional connectivity (FC) between VTA/SN and CA1 or perirhinal cortex, respectively and how they relate to behavioural encoding performance. Importantly, the authors used an active rest condition during which participants engaged in a maths task. To determine FC during the maths task, background connectivity (Al-Aidroos et al., 2012) was calculated by regressing the stimulus-evoked responses from the data and computing FC based on the residuals. The authors found that while there was no overall increase in VTA-CA1 FC from pre- to post-learning active rest, the individual differences therein predicted long-term associative memory, but not item memory. In contrast, individual differences in the change of VTA-perirhinal cortex FC predicted long-term item memory, but

not associative memory. Importantly, no predictive effects were found on immediate recall, hinting that these effects might be dopaminergic in nature. When accounting for background FC during encoding using partial correlations, effects of change in VTA-HPC FC on long-term associative memory remained significant, however, this was not replicated for VTA-perirhinal cortex FC and item memory. Their results suggest that VTA-MTL consolidation mechanisms facilitate learning and that distinct MTL regions support different memory processes (Tomparry et al., 2015).

While these two studies suggest that post-encoding activity in and between VTA/SN and HPC are predictive of learning in general, others have also targeted their role in reward learning. More specifically, Gruber and colleagues (2016) presented a reward-manipulated incidental item-associative encoding task to participants inside the fMRI and also collected fMRI data during pre- and post-learning rest. Results of the immediate memory test showed that reward enhanced encoding of associative information. They trained a classifier to distinguish between high and low monetary reward contexts during encoding and showed that HPC activity can successfully distinguish between them. Applying the same classifier to pre- and post-learning data, the results showed that only during post- but not pre-learning rest, more volumes would be classified as high-reward than expected by chance, suggesting that high reward items might be preferably reactivated. Indeed, individual differences in the “high-reward reactivation index” (i.e., the change in the number of classifications of high-reward contexts from pre- to post-learning) positively predicted the reward-driven associative memory effect. With respect to resting-state functional connectivity (RSFC) between HPC and midbrain, the authors showed that in the absence of an overall increase in RSFC from pre- to post-learning rest, individual differences therein also positively predicted the reward-driven associative memory effect. Lastly, when predicting the individual reward-driven associative memory effect using HPC activity during encoding, high-reward reactivation index, and RSFC change, the model explained 52% of the variance in the data. However, only the latter two as measures of consolidation activity significantly contributed to the model. That interindividual differences in changes in RSFC between HPC and midbrain can predict later associative memory for information presented in high-reward contexts was recently replicated in an intentional encoding paradigm with a memory test after 24h (A. O. Cohen et al., 2021). In sum, the results provide evidence that monetary rewards influence neural post-encoding processes supporting the preferred consolidation of stimuli associated with rewards.

Trying to understand the mechanisms for the observed effects of changes in HPC-VTA RSFC on encoding, Murty and colleagues (2017) investigated how reward motivation influences post-encoding markers of systems-level consolidation. To this end, participants completed a motivated intentional encoding task inside the fMRI scanner. During each trial, a cue indicating high or low reward in the subsequent immediate memory test was followed by a picture-adjective pairing. The pictures used in the

study showed faces of celebrities or famous houses and the high and low reward conditions were associated with either stimuli category, counterbalanced across participants. Additionally, the study protocol included pre- and post-learning rests as well as a surprise memory test 24h after encoding where participants' associative cued recall was tested. Behavioural results showed enhanced memory for pairs presented during high- compared to low-reward motivation. The fMRI analysis focused on changes in RSFC from pre- to post-learning between HPC or VTA and the category-selective cortex, i.e., fusiform face area or parahippocampal place area depending on whether faces or houses were used in the high-reward condition. The authors showed that changes in RSFC changes between category-selective cortex and aHPC or VTA, respectively, positively predicted high-reward associative memory, but had no effect on low-reward associative memory. These effects observed for VTA remained significant even after controlling for background FC between VTA and category-selective cortex during encoding. Taken together, their results suggest that memory for high-value information (high compared to low reward trials) is supported by mechanisms that specifically target the sensory cortex in which the information was initially processed. This provides evidence for systems-level consolidation whereby hippocampal memory traces enable new connections in relevant modules in the relevant neocortex (Morris, 2006; S.-H. Wang & Morris, 2010), but also extend these proposals by showing the role of the VTA to facilitate valuable information, potentially via neuromodulation of relevant cortices that might have received a behavioural tag during encoding (Moncada et al., 2015; Murty et al., 2017).

Curiosity and Memory Consolidation

In sum, literature on rewarded memory (i.e., high-value memory, often operationalised using monetary rewards or incentives) indicates a critical role of consolidation processes to stabilise the memories over time. These consolidation processes seem to partly depend on the neurotransmitter dopamine that is released during rewarded trials. While dopaminergic activity in the context of extrinsic rewards is well-studied (for a review, see Schultz, 2001), more recent studies have also shown that the same midbrain neurons that respond to the anticipation of primary extrinsic rewards also respond to the anticipation of non-instrumental information (Bromberg-Martin & Hikosaka, 2009) – a concept closely related to curiosity (Gottlieb & Oudeyer, 2018) – suggesting that information is an intrinsic reward (FitzGibbon et al., 2020; Marvin & Shohamy, 2016) that can modify behaviour in a similar vein to extrinsic rewards. The literature reviewed in previous chapters demonstrates a general overlap between the effects of curiosity and extrinsic rewards/incentives on encoding as (1) both are associated with the release of dopamine, (2) both show behavioural memory enhancement effects, that are (3) both supported by activity in the HPC and the VTA/SN as well as the interaction between them during the encoding of new information.

However, the evidence also suggests potential differences of curiosity and extrinsically motivated learning. For example, behavioural evidence showed that they have different time courses for the effects to be manifested. More specifically, incentive/reward effects on encoding are frequently found after long, but not short, delays between encoding and retrieval as evidenced by studies comparing the effects in immediate and delayed memory tests (Murayama & Kitagami, 2014; Murayama & Kuhbandner, 2011; Patil et al., 2017; Wittmann et al., 2005). This is in line with proposals that the effects of monetary reward on encoding are dopaminergic, influencing late LTP and are hence only apparent in delayed, but not immediate encoding (cf. Gruber et al., 2016; Murty & Adcock, 2014). The effects of curiosity on encoding, on the other hand, have consistently been found after short (Brod & Breitwieser, 2019; Galli et al., 2018; Gruber et al., 2014; Jepma et al., 2012; Ligneul et al., 2018; Mullaney et al., 2014; Murphy, Dehmelt, et al., 2021; Poh et al., 2021) and long (Duan et al., 2020; Fastrich et al., 2018; Gruber et al., 2014; Halamish et al., 2019; Kang et al., 2009; Marvin & Shohamy, 2016; Murayama & Kuhbandner, 2011; Swirsky et al., 2021) delays between encoding and retrieval. A study examining the effects of curiosity levels on later memory by testing half of the items after a short and the other half of the items after a long delay found that curiosity correlated with encoding at both time intervals (McGillivray et al., 2015). Likewise, another study did not observe any effects of delay on curiosity-motivated learning (Stare et al., 2018).

These findings are somewhat different from the effects observed in the context of monetary rewards where the reward effect of encoding is larger after sleep (Igloi et al., 2015). This is puzzling because if the effect of curiosity on encoding was purely/predominantly dopaminergic as it is assumed to be the case for monetary rewards (Miendlarzewska et al., 2016; Shohamy & Adcock, 2010), cellular models of learning and the effects of dopamine and late LTP reviewed above would predict that the effects of curiosity on memory should only be seen after long delays (allowing for the expression of late LTP) or that they would at least be more pronounced after long compared to short delays. Hence, the presence of memory-facilitating effects of curiosity after short and long delays indicates that reward- and curiosity might be supported by differential neural mechanisms. Overall, research investigating brain activity during encoding, i.e., when the later tested items are presented, suggests that the effects of monetary reward and curiosity (when tested in separate studies) on encoding are located in overlapping areas in HPC and VTA/SN (Adcock et al., 2006; Gruber et al., 2014; Wittmann et al., 2005; Wolosin et al., 2012). However, the brain activity after encoding, i.e., following the presentation of later tested items, has not been investigated yet.

Current Research

The current chapter aims to investigate whether curiosity-motivated learning is supported by similar post-encoding systems-level consolidation processes (i.e., change in RSFC between HPC and

VTA/SN) as have been reported for extrinsically motivated learning. Likewise, to further understand the interaction between extrinsically and curiosity-motivated learning, a between-subject incentives manipulation was used. While post-encoding mechanisms of reward-motivated learning have been studied and related to the reactivation of local activation patterns within HPC and VTA/SN (Gomperts et al., 2015; Gruber et al., 2016; McNamara et al., 2014; Murty et al., 2017; A. C. Singer & Frank, 2009; Valdés et al., 2015), to the best of our knowledge, research on post-encoding mechanisms of curiosity-motivated learning is thus far lacking. Due to the involvement of overlapping brain regions during encoding, it is tempting to assume that post-encoding processes would also be overlapping. However, the different temporal contingencies of curiosity and incentive/reward effects allow for the possibility that different consolidation processes support both effects or that curiosity does not rely on consolidation mechanisms. The latter seems unlikely given insights into post-encoding effects in support of learning in the context of novelty. Because curiosity and novelty overlap in their conceptualisation (Berlyne, 1950; Ryan & Deci, 2000a), it appears more likely that curiosity-motivated learning is also supported by consolidation processes. For instance, it has been found that novel compared to familiar video clips are associated with an increased offline response (i.e., brain activity at the offset of the stimulus) in the HPC that was predictive of subsequent recall (Ben-Yakov et al., 2014). Likewise, in rodents, the effects of novelty on memory are dependent on plasticity-related proteins as well as on synaptic/behavioural tagging and only emerge after delays, hence suggesting consolidation-related processes (Moncada & Viola, 2007; S.-H. Wang et al., 2010).

Given the role of dopamine, VTA/SN, and HPC during curiosity-motivated encoding as well as its conceptual partial overlap with monetary incentives/rewards and novelty, we investigated whether similar post-encoding mechanisms previously reported in the context of reward and novelty can also be found for curiosity and were interested in post-encoding systems-level interactions between HPC and VTA/SN. More specifically, we focused on the aHPC because the aHPC has previously been implicated in post-encoding processes of high-value information (Murty et al., 2017). To elicit curiosity, magic trick video stimuli from a validated stimulus database (Ozono et al., 2021) were used that participants incidentally encoded during an incentive orientation task inside the fMRI scanner, accompanied by pre- and post-learning resting state scans. The availability of monetary incentives was manipulated in a between-subject design, thereby allowing us to compare differential effects on consolidation processes. We hypothesised an increase in RSFC between VTA/SN and aHPC as a function of learning, which would differ depending on the availability of extrinsic incentives, and that individual differences therein would predict behavioural measures of learning.

Methods

As in the chapter focusing on the task data, here we will analyse data from the Magic, Memory, and Curiosity (MMC) Dataset described earlier¹¹. The methods used will be briefly described below (for a more detailed description, please refer to previous chapters).

Participants and Design

The sample included data from 50 healthy adults aged 18-37 ($M = 25.32$, $SD = 5.19$), randomly assigned to incentives and control groups. Participants were recruited using leaflets distributed across campus and leisure centres. All participants had normal or corrected-to-normal vision using contact lenses, were right-handed, fluent in English, did not suffer from any chronic illness, psychiatric disorders or cognitive impairments and did not take any psychoactive drugs. Women were only included if they were not pregnant or nursing.

The data collection consisted of three sessions: a pre-scanning session conducted online (not described here), an incentive- and/or curiosity-motivated incidental encoding and consolidation session inside the fMRI scanner, and a surprise memory test online approximately a week later. The study used a between-subject design where the availability of extrinsic, monetary incentives for the performance in an incentive orientation task was manipulated: in the incentive group, participants were instructed that each correct answer in the orientation task was worth an additional, performance-dependent bonus of £0.80 for each correct answer per trial (see below). Such instructions were not provided to participants in the control group. Importantly, performance feedback was not provided in either group.

Participants were compensated £30 for their participation and received an additional bonus payment of £7.20 (chance level performance in four-alternative forced choice orientation task across 36 trials), regardless of the group they are assigned to and regardless of their performance in the orientation task. The study design was approved by the University Research Ethics Committee (UREC) of the University of Reading (UREC 18/18).

Material

To induce curiosity inside the fMRI scanner, short videos of magic tricks from a publicly available stimulus collection (“Magic Curiosity Arousing Tricks (MagicCATs)”; Ozono et al., 2021) were used. These stimuli reliably induce curiosity and other epistemic emotions with sufficient within-person variability. For the purpose of this study, 36 magic tricks were selected as stimuli to be presented in the

¹¹ Some of the information might be redundant due to the overlap with previous chapters. However, it was included here to allow readers to understand the chapters independently of one another.

incidental incentive- and/or curiosity-motivated learning task based on the following criteria: (1) duration between 20 and 60s, (2) various range of distinguishable materials and features, (3) broad range of average curiosity ratings as reported in the stimulus collection. The final selection of stimuli was edited using Adobe®Premiere Pro CC® (2015) software. The aim was to hide the faces of the four magicians performing the tricks as much as possible and to ensure similar viewing foci and dark backgrounds across videos. Where needed, additional editing was performed, e.g., removing subtitles. Importantly, all videos were muted, but still understandable due to the non-verbal nature of magic tricks. An individual mock video (duration 6s) was created and added to the beginning of each magic trick where the first frame of the trick was displayed, overlaid with a black video. The viewing focus of that black video slowly opened up to match the viewing focus of the video. The final magic trick files (1280x720 pixels) were on average 38.5s long ($SD = 8.63$, $min = 26.6s$, $max = 58.64$).

For the surprise cued memory test, a frame from each magic trick was extracted as a cue image (1920x1080 pixels). A frame was chosen, ensuring that it was prior to the moment of expectancy violation/surprise to not reveal the trick entirely, yet distinct enough to cue memory of the magic trick.

Task Procedures

The paradigm consisted of different phases (see Figure 4.1): (1) a pre-learning rest phase (i.e., baseline), (2) an incentive- and/or curiosity-motivated incidental learning phase, (3) a post-learning rest phase (i.e., consolidation), and (4) a delayed, surprise memory test. While phase 1-3 happened consecutively during the same session inside the fMRI scanner (using Psychophysics Toolbox; Brainard, 1997 implemented in Matlab (2018b)), the fourth phase took place approximately a week later ($M = 7d$ 10h 19min, $SD = 13h$ 41min) in a separate session.

Pre- and Post-Learning Rest Phases. During the rest phases (10min each), participants were lying inside the MRI scanner and were monitored with an eye-tracking camera. A white rectangle spanning 90% of the height and width of the black screen was presented. Participants were asked to try and keep as still as possible while simply looking at the white screen, allowing usual blinking. They were instructed that their brain activity at rest was measured and that they should hence try to not think about anything at all.

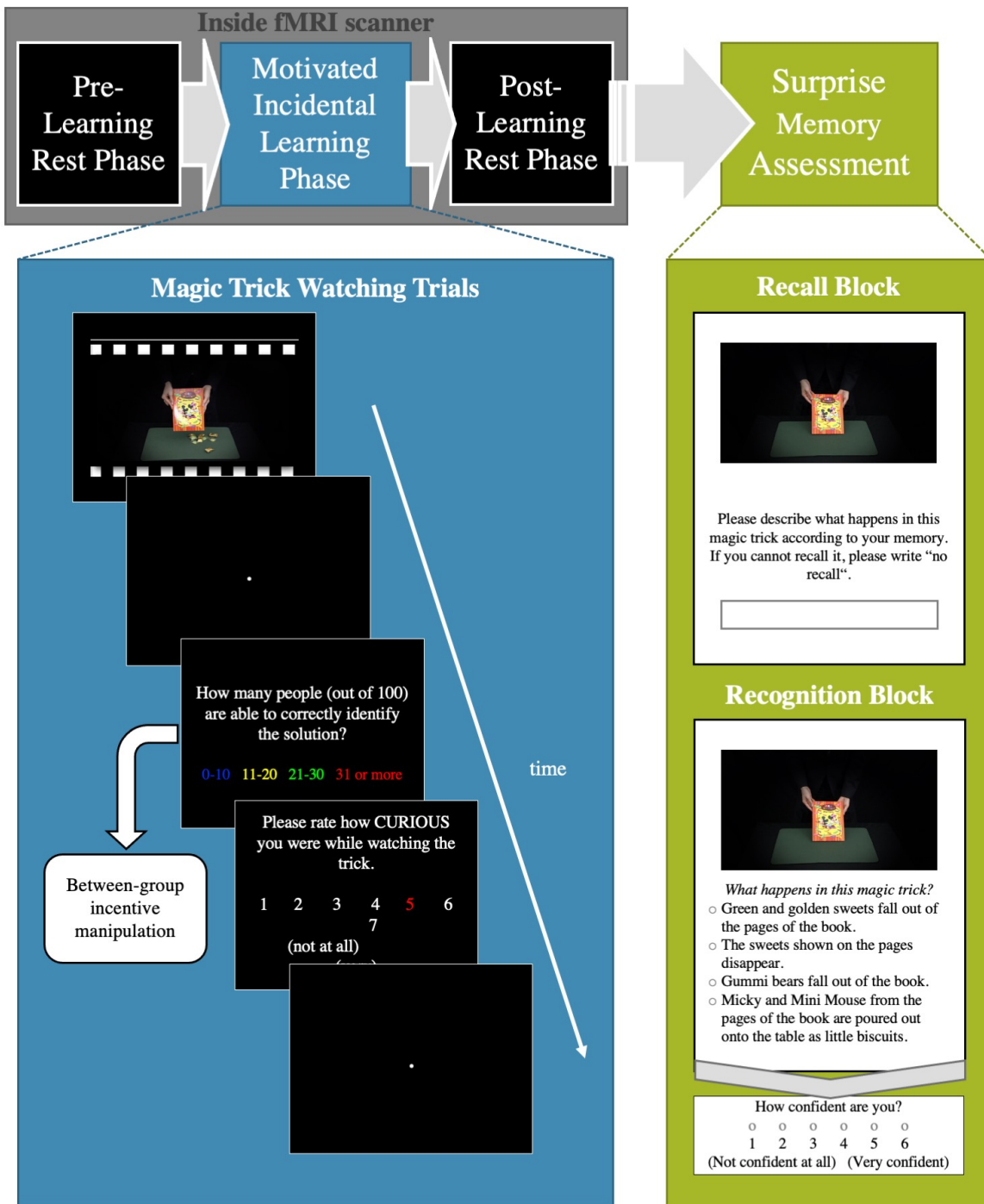
Motivated Incidental Learning Phase. During the incidental learning phase, participants viewed in total 36 magic tricks in pseudo-randomised order distributed across three blocks. Self-paced breaks were offered in between each block. The magic tricks and subsequent ratings were presented on a black background. The display of each magic trick was aligned with the scanner's TTL (transistor-transistor logic) pulse. Each magic trick presentation was followed by a fixation (jittered between 4 and 10s; start TTL pulse aligned). Then participants were asked to give an estimate of how many people (out of 100) would be able to correctly figure out the solution to the magic trick and were presented with four options

(“0-10”, “11-20”, “21-30”, and “31 and more”) each one corresponding to a button on the four-button MRI compatible response device and the printed in the corresponding colour. Importantly, participants in the incentive group were instructed before the start of each task block (but after the pre-learning rest) that each correct estimate would translate into an additional bonus of £0.80. This instruction was not presented to the control group and did not affect the trial structure itself which was the same in both groups. Participants’ response window was fixed to a duration of 6s. If a response was given before the end of the response window, all coloured writing was removed from the screen. After a fixed fixation (0.05s), participants were asked to rate how curious they were while watching the magic trick on a scale from 1 (“not curious at all”) to 7 (“very curious”) by moving a randomly highlighted number on the curiosity scale to the left or right until it represented the chosen rating. This was then confirmed via a button press. The fixed response window here was 5.95s and the font would again turn white if the rating was collected before the end of the response window. After another fixation was presented (jittered between 4 and 10s), the next trial began.

Surprise Memory Assessment. During recruitment, participants were informed that there would be a follow-up assessment, taking place online (implemented using a developmental version of Collector; Haffey et al., 2020) a week after scanning. However, the purpose (i.e., memory test) was not communicated. When asked regarding their guess about the hypothesis behind the study at the end of the fMRI session, no participant mentioned learning, memory, or encoding. Reminders of the assessment were sent out two days in advance and participants received the link for the surprise memory assessment at the same time as their initial slot. The surprise memory test consisted of a recall and recognition block during which the same cue images were displayed in random order. In the cued recall block (not described here), participants were asked to describe what had happened in this magic trick according to their memory but were also instructed to enter “no recall” if they could not remember a trick. During the cued recognition, they were presented with four descriptions of what could have happened in the magic trick and asked to select one and afterwards rate their confidence in the answer on a scale from 1 (“not confident at all”) to 6 (“very confident”).

Figure 4.1

Task Procedures



Note. The figure illustrates the structure of the different phases. Inside the fMRI scanner, resting-state data was collected before the incidental encoding task (trial structure shown in the blue box). This was

followed by another resting-state scan. A week later, memory was accessed in a surprise test online (trial structure illustrated in the green box).

Behavioural Analysis

Behavioural analyses were conducted in R version 3.6.3 (R Core Team, 2020). The recognition data was dummy-coded by comparing the chosen answer against the correct answer, creating a recognition measurement regardless of confidence. Recognition performance was further combined with the confidence ratings (i.e., correct answer chosen with a confidence larger than three) creating a high confidence recognition measurement reflecting recollection-based recognition memory (Yonelinas, 2001b, 2002) that was used as the main measurement.

To relate FC measurements (see below) to behavioural measures of learning, two indices per subject were computed: The absolute number of items encoded was determined by calculating the sum of magic tricks encoded.¹² To create a measurement of curiosity-motivated learning enhancement (CMLE), a Generalised Linear Mixed Effects (gLME) model¹³ (implemented using the *lme4* package; Bates et al., 2015) was used. In the gLME, encoding was predicted using fixed effects for curiosity (ratings centred within clusters, i.e., each participant), group (effect coded; -1 = control, 1 = incentive) and their interaction, and random intercepts for participant and stimulus as well as random slopes for the curiosity effects. The individual slopes from the gLME models were extracted as a measurement for CMLE.

¹² In alignment with previous studies (Duncan et al., 2014; Tompary et al., 2015), we also computed a corrected memory score for each subject [high-confidence correct - (high-confidence incorrect)/4] to account for a larger proportion of incorrect response options in the four-alternative forced choice recognition memory test. Uncorrected and corrected number of items recognised were highly correlated, $r = 0.986$, $t(48) = 40.49$, $p < 0.001$. The use of an uncorrected or corrected absolute number of items encoded did not impact the results (see Figure A4.3).

¹³ This model produced a singular fit warning. By specifying a simplified RE structure where the random intercepts for subject and random slopes for the curiosity effect were specified, but random intercepts for stimuli were removed allowing the model to converge without warnings. The individual curiosity beta values from both models were highly correlated, $r = 0.992$, $t(48) = 55.01$, $p < 0.001$. The gLME model specification did not affect any results reported here (see Figure SA4.3) and the results from the full gLME model are reported in the interest of consistency with previous chapters.

fMRI Acquisition and Pre-processing

A 3.0T Siemens Magnetom Prisma scanner with a 32-channel head coil was used to acquire anatomical and functional images as well as a B_0 field map. To restrict excessive head motion, the participants' head was padded inside the head coil. A Echo-Planar Imaging (EPI) sequence was used to obtain whole-brain (37 axial slices, 3 x 3 x 3 mm, interslice gap of 0.75mm) T2*-weighted images (repetition time (TR) = 2000ms, echo time (TE) = 30ms, field of view (FoV): 1,344 x 1,344 mm², flip angle (FA): 90°; phase encoding direction: P>>A). Additionally, B_0 data were acquired immediately after the pre-learning rest on the same image matrix and the same geometric prescription as the functional data, using a dual-TE 2D gradient-echo sequence (TR = 488 ms, TE1/TE2 = 5.19/7.65 ms, FA = 60°). Lastly, a high-resolution T1-weighted whole-brain image (192 x 1-mm slices) was acquired using an MPRAGE-gradient sequence (in-plane resolution of 1 x 1 x 1 mm; TE: 2.29 ms; TR: 2300 ms; inversion time (TI): 900 ms; FOV: 240 x 240; FA : 8°). Instructions and stimuli were displayed via back projection using a mirror attached to the head coil above the eyes. While being inside the MRI scanner, an MRI compatible eye tracker was used to allow the experimenter to monitor whether the participants kept their eyes open during the rest phases and whether they attended the stimuli during the motivated incidental learning phase.

Imaging data were pre-processed using AFNI (version 21.2.03; Cox, 1996) and the same pipeline was applied to data collected during rest and encoding. Steps included B_0 distortion correction, despiking, slice-timing and head motion correction and normalisation to MNI space using the ICBM 2009c Nonlinear Asymmetric Template. Pre-processed data from the MMC Dataset was smoothed to achieve an approximate, uniform smoothness of full width half maximum (FWHM) kernel of 8mm using AFNI's '*3dBlurToFWHM*'. Compared to conventional smoothing where a Gaussian kernel with a specific FWHM is applied, 3dBlurToFWHM iteratively smooths the EPI time series until the images have reached the desired uniform smoothness within the specified mask (Scheinost et al., 2014).

In fMRI pre-processing, smoothing is usually carried out to increase the temporal signal-to-noise ratio (tSNR), however, with resting-state data, separating signal from noise remains challenging, making smoothing in the context of FC analysis a topic of debate. Investigating the impact of smoothing on RSFC, Molloy and colleagues (2014) did not find a significant effect of smoothing comparing an FWHM of 5.5mm to unsmoothed data, while Wu and colleagues (2011) reported that RSFC increased with increasing smoothing kernels with a significant jump between FWHM kernels of 4mm and 6mm. Recently, in a comparison between no smoothing and FWHM kernels of 4mm and 8mm, it has been shown that ROI-to-ROI-RSFC is not affected by the size of the kernel whereas effects were observed in seed-to-voxel analyses (Alahmadi, 2021). In all cases, conventional smoothing algorithms were applied. Critically, however, it has been pointed out that smoothing might be needed when the normalisation to

template space involves non-linear transformations as this might introduce additional spatial effects and the usage of ‘*3dBlurToFWHM*’ together with a small kernel to target small brain areas or a slightly larger kernel than the original imaging resolution to target cortical networks has been recommended (Wu et al., 2011). Importantly, increased head motion is correlated with intrinsic smoothness of the data, but smoothing using ‘*3dBlurToFWHM*’ and an FWHM kernel of 6mm has also been shown to reduce motion confounds in RSFC (Scheinost et al., 2014). Due to conflicting results and recommendations to analyse data with different smoothing kernels to confirm the robustness of obtained results (Alahmadi, 2021), we here use ‘*3dBlurToFWHM*’ with three different FWHM kernels (4, 6, and 8) as well as unsmoothed data to investigate the generalizability of results. In the interest of readability, results with a smoothing kernel with an FWHM of 4mm will be reported in the main text, while other results can be found in the appendix.

Following smoothing (or following normalisation for the unsmoothed data), time series were scaled to a mean of 100. Local white matter time series, the first three principal components of the lateral ventricles as well as motion estimates were included as regressors of no interest to denoise the data. During linear regression, time courses were also band-pass filtered for frequencies between 0.01 and 0.1 Hz. Time points were censored (i.e., set to zero) if the Euclidean norm of per-slice motion exceeded 0.3mm or if more than 10% of brain voxels were outliers.

During the motivated incidental learning phase, the beginning of magic tricks and fixations following them were aligned with the beginning of a TR. The duration of any fixations and response windows were multiples of the TR. While the fixation after the magic trick was jittered, the minimum duration was set to 4s (or 2 TRs). Because magic tricks were presented in pseudo-randomised order, the task time series was concatenated to remove volumes of no interest (e.g., ratings) and to reorder the volumes so that the final concatenated time series would be the same across subjects (see Thomas et al., 2018) while accounting for the delay in the HRF by shifting the time course by a lag of 4 TRs (for details, see the previous chapter). This was done to create two separate time series: the online encoding time series covered only volumes acquired during the presentation of magic tricks (without the mock video) whereas the offline encoding time series included the last volume of each magic trick as well as the first two volumes of fixation after the end of the magic trick. The online time series consisted of 594 volumes and the offline time series consisted of 108 volumes with 36 volumes overlapping in both time series. The time series acquired during the rest phases consisted of 300 volumes each. For each of the four resulting time series (online and offline encoding as well as pre- and post-learning rest), the global correlation (GCOR; Saad et al., 2013) was computed using AFNI’s ‘*@compute_gcor*’. GCOR represents a single value for each dataset, created by computing the average correlation over all possible combinations of voxels within the grey matter mask, and then averaging all values within the mask. As such, GCOR

captures brain-wide correlations and between-subject fluctuations therein are assumed to be driven by sources of noise.

Functional Connectivity Analysis

Similar to Gruber and colleagues (2016), the main focus of this work was to determine how communication between the aHPC and VTA/SN (i.e., RSFC) changes from pre- to post-learning. For each rest time series separately, AFNI's *'3dSetupGroupInCorr'* was specified, loading in the respective time series of all subjects into an object to be used as input for *'3dGroupInCorr'*, a program that in turn computes the average time series within the specified input mask (i.e., aHPC) to then compute the Pearson correlation between the averaged time course within the input mask and the time course of each voxel in the brain. GCOR was included as a subject-level covariate to further account for nuisance sources. *3dGroupInCorr* does not only calculate seed-based FC at group level, but also outputs the individual Fisher's *z*-transformed results. From the individual seed-based maps, the values within the VTA/SN mask were extracted and averaged as a measurement of RSFC between aHPC and VTA/SN at pre- and post-learning, respectively. Change in RSFC was computed by calculating the difference between both to then be correlated with behavioural measures of learning (Gruber et al., 2016). This was done across the whole sample and within each group separately. To test differences in brain-behaviour-correlations between groups for significance, the *corcor* package (Diedenhofen & Musch, 2015) was used.

Previous research showed that FC between HPC and VTA/SN during encoding is related to memory performance (Adcock et al., 2006; Duncan et al., 2014; Gruber et al., 2014; Shohamy & Wagner, 2008). However, these studies have used static stimuli like pictures or trivia questions. In the context of dynamic stimuli like video clips, however, a distinction can be made between online (intra-stimulus) encoding processes, i.e., processes during stimulus presentation, and offline (post-stimulus) encoding processes, i.e., processes during the period immediately following the event offset (Ben-Yakov & Dudai, 2011). In the majority of studies in cognitive neuroscience investigating the neural underpinnings of encoding, both processes are overlapping due to the use of discrete stimuli; however, the processes are more distinct in the context of dynamic stimuli. Indeed, it has been suggested that offline activity in the HPC following the offset of video clips can predict their encoding, either because the post-stimulus activity represents activity that binds the events of the clip into a single episode or because it reflects early consolidation (Ben-Yakov et al., 2013, 2014; Ben-Yakov & Dudai, 2011).

To determine whether any effects in changes in RSFC between aHPC and VTA/SN and behavioural measurements of encoding were unique to the early consolidation phase rather than reflecting general patterns during online and offline encoding, we also computed FC between aHPC and VTA/SN for each subject using the concatenated time series representing online and offline encoding, respectively,

as input. For each denoised time series, FC between aHPC and VTA/SN was determined akin to what has been described in the context of pre- and post-learning rest phases (i.e., by using ‘*3dSetupGroupInCorr*’ and ‘*3dGroupInCorr*’ accounting for the GCOR measurement obtained for each time series). As such, the FC measurements obtained for the online and offline encoding time series are similar to what others described as background functional connectivity¹⁴ (Duncan et al., 2014; Murty et al., 2017, 2019; Tomparry et al., 2015) which has been shown to reveal processes beyond typical task-based functional connectivity measures (Duncan et al., 2014) like beta-series correlation (Rissman et al., 2004). Importantly, however, no difference was calculated. Lastly, all FC measures (change in RSFC, online FC and offline FC), as well as the availability of extrinsic incentives and the interaction thereof with change in RSFC were used to predict each behavioural measure of learning to determine the robustness of effects.

The main analysis focused on FC between aHPC and VTA/SN. However, whole-brain seed-based RSFC were conducted for exploratory purposes. For this, data from pre- and post-learning rest phases from each subject were loaded into ‘*3dGroupInCorr*’, specifying aHPC and VTA as seeds, respectively, to compute two seed-based FC maps, one for each ROI as seed, while accounting for GCOR to further account for sources of noise at group level, creating two seed-based maps where the value in each voxel represents the Fisher’s z -transformed correlation coefficient with the averaged time series of each seed, respectively.

Individual Fisher’s z -transformed maps were extracted for pre- and post-learning resting phase to compute the RSFC as the difference between post- and pre-learning rest. These individual difference maps were then used as input for One-Sample t -tests carried out across the whole sample as well as a Two Sample t -test to determine any differences between the groups. To determine clusters of voxels exhibiting a significant change in RSFC with either of the seeds, a cluster-defining threshold of $p = 0.001$ was used. Cluster size threshold was determined using AFNI’s ‘*3dttest++*’ with the ‘*ClustSim*’ option and the corresponding cluster size to achieve a cluster-extent threshold of $\alpha = 0.05$ was used.

Regions-of-Interest Approach

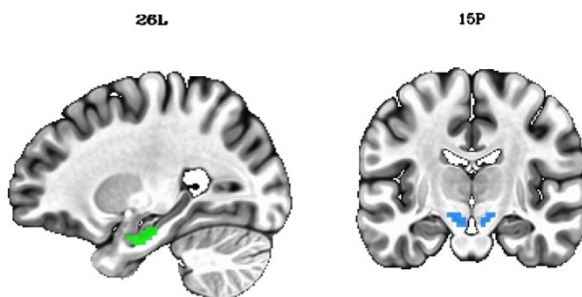
Due to the established roles of HPC and VT/SN as well as their connectivity in motivated learning in the context of incentives and curiosity have previously been established (Adcock et al., 2006;

¹⁴ Studies using background functional connectivity typically apply event-related fMRI with simple, static stimuli. To remove stimulus- or response-induced neural activity, trial-evoked activity is removed using a Generalised Linear Model. This step was omitted due to the added complexity of modelling stimulus onset and duration in the context of naturalistic stimuli like video clips.

Gruber et al., 2014, 2016; Kahn & Shohamy, 2013; Murphy, Ranganath, et al., 2021; Murty & Adcock, 2014; Wolosin et al., 2012), we aimed to determine how their functional connectivity during online and offline encoding as well as during post-encoding rest predicts behavioural measures of learning. Because meta-analytic evidence suggests that increased activity for remembered compared to forgotten items is predominantly centred in anterior parts of the HPC (Kim, 2011; Spaniol et al., 2009), the analysis focused on the anterior HPC (aHPC) and the same masks were used as described in the previous chapter. The bilateral HPC mask was extracted from the Glasser Human Connectome Project atlas (Glasser et al., 2016) and the aHPC was determined based on the uncus apex using MNI coordinate $y = 21P$ (Poppenk et al., 2013). The mask for the VTA/SN was created using atlaskit (<https://github.com/jmtyszka/atlaskit>) by (1) extracting SN pars reticulata (SNr), SN pars compacta (SNc), and VTA from a high-resolution probabilistic subcortical nuclei atlas in MNI space (Pauli et al., 2018) specifying a probability threshold of 15% and then (2) combining all three into a single mask. The masks are shown in Figure 4.2.

Figure 4.2

aHPC and VTA/SN Seeds



Note. aHPC is shown in green, whereas VTA/SN is shown in blue.

Results

Behavioural Measures of Learning

To determine whether participants' performance in the recognition memory test exceeded chance level (i.e., 25% of 36 items), the sum score in recognition performance regardless of confidence was calculated for each participant. A one-tailed t-test showed that the performance in the recognition test ($M = 22.54$, $SD = 4.12$, $\min = 15$, $\max = 32$) was significantly above chance level, $t(49) = 23.26$, $p < 0.001$, $d = 3.29$, 95% CI [2.42; 4.16] and no subject showed individual sum scores below chance level. Together, this suggests participants indeed incidentally encoded the magic tricks.

Encoding was measured as high confidence recognition, (i.e., recognition with a confidence rating > 3), which is a recollection-based recognition memory measurement (Yonelinas, 2001b, 2002). This threshold was chosen as it showed the strongest between-group effect on encoding in behavioural pilot studies (Meliss & Murayama, 2019). Across both groups, the average absolute number of items encoded was 15.14 ($SD = 5.35$, $\min = 3$, $\max = 27$) and no significant differences ($M_c = 15.52$, $SD_c = 4.65$, $M_i = 14.76$, $SD_i = 6.04$) were observed, $t(45.03) = 0.50$, $p = 0.621$, $d = 0.42$, 95% CI [-0.15; 0.99]. To derive individual coefficients quantifying each participant's CMLE score, a gLME was specified predicting high confidence recognition with curiosity, the incentive manipulation, and their interaction as fixed effects, stimulus and participant as random intercepts and the curiosity effects as random slope. As shown in Table 4.1 below, no fixed effects reached statistical significance. The intercepts and slopes are highly correlated indicating a positive definite variance-covariance matrix; however, excluding the covariance term had little impact on the results. From the model, the individual beta values were extracted as an index of the curiosity-motivated learning enhancement (CMLE).

Table 4.1

Fixed effects results of gLME predicting high confidence recognition

	OR	95% CI	<i>p</i> value
Intercept	0.64	[0.21; 1.07]	0.044
Incentives	0.94	[0.72; 1.16]	0.590
Curiosity	1.06	[0.98; 1.14]	0.129
Incentives * curiosity	0.99	[0.92; 1.06]	0.699

Note. OR = Odds Ratio, CI = Confidence Interval, gLME = Generalised Linear Mixed Effects.

Resting-State Functional Connectivity Between aHPC and VTA/SN

RSFC between aHPC and VTA/SN was quantified separately for pre- and post-learning rest. While RSFC values increased slightly numerically from pre- ($M = 0.035$, $SD = 0.025$) to post-learning rest ($M = 0.039$, $SD = 0.030$), the change from pre- to post-learning (aHPC-VTA/SN-RSFC change; $M = 0.004$, $SD = 0.031$) was not significantly larger than zero, $t(49) = 0.931$, $p = 0.178$, $d = 0.14$, 95% CI [-0.44; 0.70]. Likewise, while the difference was numerically larger in the control ($M = 0.007$, $SD = 0.032$) compared to the incentive group ($M = 0.006$, $SD = 0.030$), the effect was not significant, $t(47.816) = 0.785$, $p = 0.435$, $d = 0.22$, 95% CI [-0.35; 0.79]. Similar results were obtained with other FWHM kernels (see Table A4.1 and Figure A4.1 in the appendix).

Brain-Behaviour Correlations

The primary objective of our analysis was to determine whether changes in RSFC between aHPC and VTA/SN were associated with behavioural measures of learning and whether this was influenced by the availability of extrinsic incentives. We, therefore, correlated behavioural measures of learning (i.e., absolute number of items encoded and CMLE) with aHPC-VTA/SN-RSFC change, across the whole sample and within each group separately. Because Shapiro-Wilk tests indicated that all variables were normally distributed across the sample as well as within each group (all $p \geq 0.053$), **Pearson's correlation coefficient was used. The patterns were illustrated in Figure 4.3.**

While the correlation between the absolute number of items encoded and aHPC-VTA/SN-RSFC change was close to zero across the whole sample, $r = 0.08$, $t(48) = 0.557$, $p = 0.581$, 95% CI [-0.20; 0.35], the correlation coefficient was numerically positive within the incentives group, $r_i = 0.39$, $t(23) = 2.028$, $p = 0.054$, 95% CI [-0.01; 0.68], but numerically negative in the control group, $r_c = -0.31$, $t(23) = -1.579$, $p = 0.128$, 95% CI [-0.63; 0.09]. While none of the correlation coefficients reached significance, the difference in correlation between both groups was significant, $\Delta r_{c-i} = 0.70$, $z = 2.436$, $p = 0.015$, 95% CI [0.13; 1.13].

Opposite patterns were observed in the correlation between CMLE and aHPC-VTA/SN-RSFC change. Here, the correlation coefficient was numerically positive within the control group, $r_c = 0.29$, $t(23) = 1.458$, $p = 0.158$, 95% CI [-0.12; 0.62], but numerically negative in the incentives group, $r_i = -0.39$, $t(23) = -2.005$, $p = 0.057$, 95% CI [-0.68; 0.01], and again close to zero across the whole sample, $r = -0.08$, $t(48) = -0.546$, $p = 0.581$, 95% CI [-0.35; 0.20]. As above, the difference in correlation between both groups was significant, $\Delta r_{c-i} = -0.68$, $z = -2.342$, $p = 0.019$, 95% CI [-1.11; -0.11].

Overall, these results suggest that there is an interaction between the incentive manipulation and aHPC-VTA/SN-RSFC change in how they relate to behavioural measures of learning. To confirm the robustness of these results, we controlled for aHPC-VTA/SN-FC during encoding in a linear regression predicting each behavioural variable of interest using online and offline aHPC-VTA/SN-FC¹⁵, group, aHPC-VTA/SN-RSFC change and the interaction between the latter two. As shown in Table 4.3, after accounting for all other variables, the interaction term between group and aHPC-VTA/SN-RSFC change

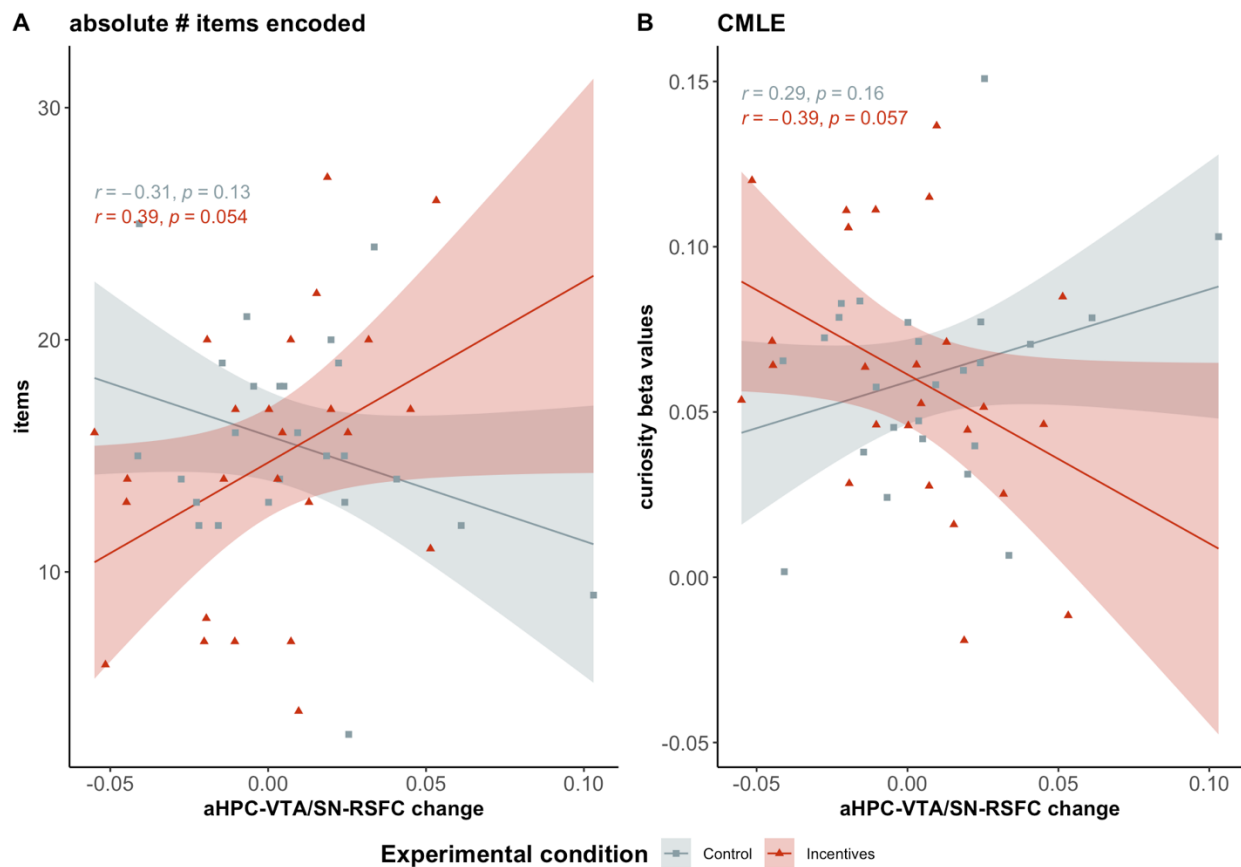
¹⁵ While online and offline FC between aHPC and VTA/SN were significantly correlated, $r = 0.47$, $t(48) = 3.673$, $p = 0.006$, 95% CI [0.22; 0.66], the correlation coefficient does not exceed critical thresholds in the context of multicollinearity in multiple regression.

remained the only significant predictor. To further understand the interaction term, separate linear regression models were run for each group separately predicting the behavioural measures of learning using aHPC-VTA/SN-FC during online and offline encoding and aHPC-VTA/SN-RSFC change. Only in the incentives group, aHPC-VTA/SN-RSFC change reached trend level (see Table 4.2).

Importantly, these patterns of results were observed independent of smoothing kernels (see Table A4.2, Table A4.3, and Figure A4.2 in the appendix). Of note, when an FWHM kernel of 6 or 8mm was used, correlation coefficients within the incentives group reached significance and aHPC-VTA/SN-RSFC change became a significant predictor in the linear model predicting learning only in the incentives group.

Figure 4.3

Correlation Between aHPC-VTA/SN-RSFC Change and Behavioural Measures of Learning



Note. The scatter plots above show the association between changes in FC between aHPC and VTA/SN from pre- to post-learning rest on the x-axis and behavioural measures of learning on the y-axis. Data is shown separately for the absolute number of items encoded (A) and the curiosity-motivated learning enhancement (B). Different colours were used for the control and the incentives group, respectively. Regression lines with 95% confidence have been added to illustrate the relationship between the

behavioural measures of learning and aHPC-VTA/SN-RSFC change within each group together with the corresponding correlation coefficients.

Table 4.2

Results of Linear Regression Predicting Behavioural Measures of Learning

	Whole sample		Control group		Incentives group	
	<i>b</i> (SE)	<i>p</i> value	<i>b</i> (SE)	<i>p</i> value	<i>b</i> (SE)	<i>p</i> value
	absolute # items encoded					
Intercept	15.75 (1.06)	< 0.001	15.52 (0.94)	< 0.001	14.76 (1.16)	< 0.001
Online FC	-20.1 (41.51)	0.631	15.36 (48.47)	0.755	-74.39 (74.79)	0.331
Offline FC	16.59 (29.85)	0.581	0.15 (37.75)	0.997	30.12 (47.37)	0.532
Incentives	-0.77 (1.5)	0.611				
RSFC change	-49.44 (34.18)	0.155	-45.68 (31.55)	0.162	84.79 (42.11)	0.057
Incentives * RSFC change	127.24 (49.12)	0.013				
	CMLE					
Intercept	0.06 (0.01)	< 0.001	0.06 (0.01)	< 0.001	0.06 (0.01)	< 0.001
Online FC	0.12 (0.28)	0.66	-0.12 (0.32)	0.726	0.49 (0.49)	0.337
Offline FC	-0.13 (0.2)	0.53	-0.02 (0.25)	0.947	-0.21 (0.31)	0.501
Incentives	0 (0.01)	0.984				
RSFC change	0.31 (0.23)	0.176	0.29 (0.21)	0.187	-0.55 (0.28)	0.061
Incentives * RSFC change	-0.82 (0.33)	0.016				

Note. The table above shows the results of the linear regressions predicting each behavioural measures of learning using the availability of extrinsic incentives (“Incentives”, effect-coded using 1 for incentives and -1 for control group), aHPC-VTA/SN-RSFC change (“RSFC change”), and their interaction (“Group * RSFC change”) after controlling for the FC between aHPC and VTA/SN during encoding (“Online FC” and “Offline FC”) across the whole sample. Given the significant interaction term for both measures, a linear regression was run within each group using Online and Offline FC as well as RSFC change as predictors to further understand the interaction effects. *b* = unstandardised beta coefficient. SE = standard error.

Explorative Whole-Brain FC Analysis

Exploratory whole-brain seed-to-voxel FC analysis was run to identify voxels showing a significant change from pre- to post-learning rest in FC with the aHPC seed and the VTA/SN seed, respectively. To achieve this, the change in RSFC across the whole sample, as well as within each group separately, was examined together with the effect of the incentive manipulation therein. For the aHPC

seed, across the whole sample, four clusters survived cluster-extend thresholding based on permutation testing. In all clusters, values were positive, indicating an increase in RSFC from pre- to post-learning. Those clusters were located in the bilateral anterior insula/frontal operculum, the left supramarginal gyrus and the right superior temporal gyrus (see Table A4.4 and Figure A4.4 in the appendix). When looking within each group separately, on the other hand, no clusters survived thresholding. Likewise, no clusters were identified where the change in RSFC with the aHPC seed differed between the groups. When using the VTA/SN seed, no clusters were identified that showed significant changes in RSFC from pre- to post-learning, neither across the whole sample nor in each group individually and no effects of the incentive manipulation were found.

When comparing the results across different smoothing kernels, the number and size of clusters showing a significant change in RSFC with the aHPC seed numerically increased as the smoothing kernel increased. However, results were overall not robust as different FWHM kernels led to variations in the cluster locations. Notably, across all used smoothing kernels, a significant cluster in the left anterior insula/frontal operculum was found (see Figure A4.4 in the appendix). However, consistently across smoothing kernels, no effects were found within each group separately or between them. Likewise, using the VTA/SN seed, the null results were robust across different smoothing kernels when looking at changes in RSFC across the whole sample and within each group separately. Conversely, with respect to the group effect therein, a cluster survived thresholding when data was smoothed to achieve an FWHM kernel of 8mm. This cluster was located in the left inferior parietal lobe (size = 33 voxels; coordinates 46.5R, 37.5P, 52.5S; z value = 4.329). Given the overall lack of previous studies investigating the effects of the availability of monetary incentives at changes in RSFC, leniently thresholded results ($p = 0.05$, $k = 10$; following recommendations by G. Chen et al., 2021) were added for each seed to guide future hypothesis generation (see Figure A4.5 and A4.6 in the appendix).

Discussion

To investigate early levels of systems-level consolidation in support of curiosity-motivated learning in interaction with the availability of extrinsic incentives, two approaches were used: First, we were interested in systems-level interactions between the aHPC and VTA/SN and how they relate to behavioural measures of learning. Second, we run exploratory analyses to identify systems-level interactions across the whole brain using aHPC and VTA/SN as seeds.

No Statistically Significant Overall Change in aHPC-VTA/SN-RSFC or Incentive Effects

We found that overall, there was no significant increase in aHPC-VTA/SN-RSFC change from pre- to post-learning rest, neither across the whole sample nor as a function of the availability of incentives. The lack of overall change in RSFC between the aHPC and VTA/SN is somewhat surprising

given the general assumption that changes in interregional FC from pre- to post-learning rest are related to the encoding, due to the post-learning rest being contrasted against the pre-learning rest baseline (Tambini & Davachi, 2019). While the lack of significant changes could imply that the encoding did not alter patterns of functional connectivity between the two areas that could reflect patterns of replay during consolidation processes (Josselyn et al., 2015), the absence of an overall shift in RSFC with encoding experience aligns with previous studies investigating changes in RSFC between MTL and dopaminergic midbrain (Gruber et al., 2016; Tompariy et al., 2015). The absence of any effects of the incentive manipulation upon changes in RSFC suggests that providing additional extrinsic incentives in and of itself does not impact post-encoding communication between aHPC and VTA/SN. This is therefore somehow contradicting electrophysiological recordings in rodents showing an increase in hippocampal ripples after rewarded trials (A. C. Singer & Frank, 2009). However, it is important to note that electrophysiological recordings of hippocampal sharp wave ripples and aHPC-VTA/SN-RSFC change measured using fMRI BOLD responses are very different measures. For instance, in the absence of an overall aHPC-VTA/SN-RSFC change from pre- to post-learning, Gruber and colleagues (2016) found an increase in hippocampal reactivation activity as a function of encoding, suggesting that overall local activation patterns can change without necessarily impacting systems-level interactions.

Brain-Behaviour-Correlations are Affected by the Availability of Extrinsic Incentives

In the absence of effects of the incentives manipulation on RSFC changes between aHPC and VTA/SN, we found that the availability of extrinsic monetary incentives significantly impacted how intersubject variability in RSFC changes is associated with behavioural measures of learning. In other words, brain-behaviour-correlations were significantly different in both groups. More specifically, the correlation between the absolute number of items encoded and RSFC change between aHPC and VTA/SN differed significantly between both groups with larger brain-behaviour-correlations in the incentivised group (numerically positive correlation coefficient) compared to the control group (numerically negative correlation coefficient). For the curiosity-motivated learning enhancement (CMLE; i.e., the effect of curiosity on memory encoding estimated for each participant by specifying random intercepts in the gLME), the opposite pattern was observed where brain-behaviour-correlations were larger in the control (numerically positive correlation coefficient) compared to the incentives group (numerically negative correlation coefficient).

The incentive effects on how individual differences in the aHPC-VTA/SN-RSFC change are associated with behavioural measures of learning were still observed after accounting for FC between aHPC and VTA/SN during online (i.e., during stimulus presentation) and offline (i.e., during the last volume of magic trick presentation and the first two volumes of fixation thereafter) encoding as indicated by the significant interaction term. As such, this suggests that the association between aHPC and VTA/SN

FC in early consolidation during quiet awake rest posits a unique mechanism supporting learning rather than a continuation of FC processes observed during encoding. This observation is thereby in line with others deriving similar conclusions about the unique contribution of systems-level interaction during early consolidation to memory formation (Gruber et al., 2016; Murty et al., 2017; Tompary et al., 2015).

Overall, our result adds to previous results showing that individual differences in systems-level interactions differentially or selectively predict high-reward memory, in comparison to low-reward memory, where these effects were interpreted in light of a selective stabilisation of high-value memories (A. O. Cohen et al., 2021; Gruber et al., 2016; Murty et al., 2017). While no data was collected here to determine the subjective value of each trial, it has been demonstrated that curiosity can be measured indirectly using willingness-to-wait (e.g., van Lieshout et al., 2018) or willingness-to-pay (e.g., Fastrich & Murayama, 2018) paradigms and is also reflected in an increased willingness to take risks (Lau et al., 2020). These findings suggest that also in our study, events during which participants experienced higher curiosity might also have a higher value. Assuming that to be the case, our result—that the availability of extrinsic incentives significantly influences correlations between dopaminergic consolidation activity (i.e., aHPC-VTA/SN-RSFC change) and behavioural measures of learning, could imply that the availability of extrinsic incentives affects which events (only a subset or all of them) are deemed motivationally salient or valuable. In fact, while curiosity can be described as a source of intrinsic motivation (Ryan & Deci, 2000b), a plethora of research has demonstrated that additional extrinsic rewards and incentives can undermine intrinsic motivation as well as activity in the reward network (Cerasoli et al., 2014; Deci et al., 1999; Murayama et al., 2010; Murayama, Sakaki, et al., 2019). More specifically, extrinsic rewards and incentives, as drivers of extrinsic motivation, are associated with the quantity of performance whereas intrinsic motivation is associated with the quality of performance (Cerasoli et al., 2014).

While this argumentation is very indirect and requires further investigation, our results are in line with the idea that extrinsic motivation is associated with a focus on quantity rather than quality. Indeed, the significant effects of the availability of incentives on how aHPC-VTA/SN-RSFC change (a potential neural marker for the selective encoding of motivationally salient information; Gruber et al., 2016) predicts overall as well as curiosity-driven learning could be seen as in line with the idea proposed by Cerasoli and colleagues (2014) if overall learning is seen as a quantitative measure of learning whereas curiosity-motivated learning might be a more qualitative one.

Other studies (A. O. Cohen et al., 2021; Gruber et al., 2016; Murty et al., 2017) investigating consolidation processes supporting memories for high-value information have manipulated value (i.e., incentives for intentional encoding or rewards in an unrelated task during incidental encoding) using within-subject manipulations. In such designs, it is likely that the cue indicating high- or low-value trials

elicits a phasic dopamine response, i.e., a burst of activity in dopaminergic neurons. Such bursts facilitate the encoding of the dopamine-releasing events by cellular mechanisms of learning through the synthesis of plasticity-related protein during the expression of late LTP, which are then captured by tagged synapses, thereby enhancing their strength. These processes are then reflected in enhanced memory at the behavioural level (Düzel et al., 2010; Shohamy & Adcock, 2010). Importantly, similar phasic dopamine responses have been surmised to underlie curiosity (Bromberg-Martin & Hikosaka, 2009; Gruber et al., 2014; Gruber & Ranganath, 2019). Comparatively, in our study, we used a between-subject manipulation where half of the participants were informed that correct responses would be associated with additional monetary bonus payments — thus possibly impacting the amount of effort that participants would invest into the task by incentivising their performance. These effects are nonetheless assumed to be related to dopamine, but more particularly, to sustained changes in dopamine release, also known as tonic dopamine responses (Shohamy & Adcock, 2010). Such tonic dopaminergic responses are also assumed to be related to the effects of novelty exposure on encoding: Viewing novel scenes for 5 min has prolonged enhancement effects on the encoding of words studied afterwards (Fenker et al., 2008). However, rather than directly providing plasticity-related proteins to tagged synapses, prolonged tonic upregulation of dopamine might enhance the salience of environmental stimuli by making the dopaminergic neurons more likely to engage in phasic responses, increasing the likelihood that a presented stimulus will lead to a phasic response that then triggers plasticity-dependent protein synthesis processes (Düzel et al., 2010). Likewise, tonic dopaminergic activity might also influence hippocampal encoding processes within its own merits (Shohamy & Adcock, 2010). Overall, it is likely that the effects of dopamine on encoding cannot fully be attributed to phasic or tonic dopaminergic activity and are likely to be relying on a combination of these processes (Düzel et al., 2010; Shohamy & Adcock, 2010). In any case, if the incentive manipulation is indeed associated with tonic upregulation of dopaminergic activity as has been observed in the context of novelty, this might be the underlying mechanism that lead to the group effects observed and reported here.

Curiosity-Motivated Learning is not Significantly Related to aHPC-VTA/SN-RSFC Change

While we found that brain-behaviour-correlations were significantly different as a function of the availability of extrinsic incentives, it is important to note that brain-behaviour-correlation coefficients within each group did not reach significance for neither behavioural measure of learning, despite trend effects found in the incentives group. This contradicts previous studies that found significant correlations between post-encoding connectivity between MTL and dopaminergic midbrain and behavioural measures of learning. Tomparry and colleagues (2015) observed a double-dissociation whereby VTA-CA1 post-encoding connectivity correlated with associative, but not item memory; whereas VTA-perirhinal cortex post-encoding connectivity correlated with item, but not associative memory. While associative memory

and high-confidence recognition are both measures of hippocampal recollection-based memory (Diana et al., 2007), implying that aHPC-VTA/SN-RSFC change should support both of them in a similar manner, work by others (A. O. Cohen et al., 2021; Gruber et al., 2016) suggests that aHPC-VTA/SN-RSFC change prioritises the consolidation of motivationally salient information.

More specifically, Gruber and colleagues (2016), found that RSFC change between HPC and VTA/SN correlated with the extent to which associative memory was enhanced in high- compared to low-reward contexts, thereby extending previous results by showing that RSFC between HPC and VTA/SN selectively supports the consolidation of items presented in high-reward contexts. Importantly, curiosity is often described as a motivation to reduce novelty and uncertainty or sometimes even as a motivation “for its own sake” (Silvia, 2012). As such, stimuli that elicit curiosity can have a motivational salience within their own merit that can be similar to that found in the context of extrinsic incentives and rewards (FitzGibbon et al., 2020; Lau et al., 2020). Given previous studies showing that aHPC-VTA/SN-RSFC change supports memory for motivationally salient events in the context of extrinsic rewards (A. O. Cohen et al., 2021; Gruber et al., 2016), and proposals that extrinsic rewards and curiosity share features of incentive salience (FitzGibbon et al., 2020; Lau et al., 2020), it is tempting to predict that curiosity- and reward-motivated learning would use similar neural post-encoding mechanisms. Despite the prediction, we did not find that aHPC-VTA/SN-RSFC change predicted CMLE, neither across the whole sample nor within each group separately. This suggests that curiosity-motivated learning might be relying on, at least partially, post-encoding mechanisms other than dopaminergic influences on hippocampal activity measured using aHPC-VTA/SN-RSFC change. This is in line with behavioural results suggesting that the facilitating effects of curiosity on encoding occur independently of delay (Stare et al., 2018).

Hopefully, future research, potentially in combination with data-driven machine learning approaches, may help identify new candidates for supporting the consolidation of curiosity-motivated learning. Change in FC between various ROIs (even stemming from a whole-brain parcellation) could be used as features to train a model to predict behavioural measures of learning. More generally, because the MMC Dataset is openly available, other researchers can analyse the post-encoding resting-state data using a plethora of alternative methods. As reviewed in earlier chapters, besides investigating systems-level interactions using experience-dependent changes in FC measures from pre- to post-learning, another common approach in analysing such data applies multivoxel pattern analysis (MVPA; Norman et al., 2006) to probe the reactivations of event patterns within a pre-determined search light or brain region (Tambini & Davachi, 2019): fMRI data during encoding is used to determine “template patterns” that could represent either specific stimuli or events or connectivity patterns (e.g., multivoxel correlation structures). If there is a greater level of similarity between multivoxel patterns during encoding and post-learning rest compared to pre-learning rest, this is interpreted as reactivation (Deuker et al., 2013; Gruber

et al., 2016; Schapiro et al., 2018; Schlichting & Preston, 2014; Schuck & Niv, 2019; Staresina et al., 2013; Tambini & Davachi, 2013). In the MMC Dataset, the multivoxel correlation structure of e.g., the HPC could be used.

However, it is important to note that the absence of significant correlations between aHPC-VTA/SN-RSFC change and CMLE needs to be interpreted with caution given the lack of behavioural effects (for a discussion on potential explanations for the lack of effects, please see below). Likewise, the absence of effects could also be related to a lack of statistical power.

Exploratory Whole-Brain Analysis

As a first step aiming to assist such discoveries, exploratory analyses were run using aHPC and VTA/SN as seeds for whole-brain RSFC to identify any clusters showing different RSFC with either of the seeds as a function of learning. For the aHPC seed, a cluster in the left anterior insula/frontal operculum was found that showed increases in RSFC with the aHPC seed after learning. In a study that observed increased interaction between aHPC and perirhinal cortex after the intentional encoding of objects, this was attributed to the role of the perirhinal cortex in object encoding and information transfer between HPC and perirhinal cortex following learning (Murty et al., 2019). While the anterior insula/frontal operculum is not directly associated with a specific function, but is part of higher-order cortices and might be involved in many functions (e.g., Craig, 2009), the aI/fO is part of the salience network. By using videos of magic tricks to elicit curiosity – stimuli showing impossible or implausible events – the associated violation of expectation is likely a salient event that could be signalled by activity in the aI/fO. Hence, increases in RSFC between aHPC and anterior insula/frontal operculum could be related to the salience of the events shown in the magic trick themselves. Such functional connectivity could be supported by bilateral connections between insular cortices and HPC (Fanselow & Dong, 2010).

For the VTA/SN seeds, on the other hand, no clusters were found that showed stronger FC with the seed after learning. While previous research found that connectivity between VTA and category-selective visual cortices processing the stimuli presented during encoding increases (Murty et al., 2017), such results were obtained with very distinct stimulus categories (i.e., images of faces and places) that were associated with high or low value. With dynamic stimuli as used here, on the other hand, there was no clear association between certain inputs (e.g., the use of specific objects) and their value. This could explain the lack of clear associations between VTA and other areas in the brain in general and sensory areas in particular.

Lastly, when testing whether the incentives manipulation was associated with differential changes in RSFC with either seed, no effects were found. It is important to note, however, that the absence of overall changes in RSFC or group effects therein suggest that no consolidation processes were identified or that consolidation did not differ as a function of the availability of extrinsic incentives. In fact, it is

important to keep in mind that studies more often than not fail to identify overall changes as a result of learning, but yet find that individual differences in neural processes associated with systems-level consolidation can predict behavioural measures of learning. As such, identifying consolidation mechanisms in support of curiosity-motivated learning remains a promising target for future research.

Effects of Smoothing

Some of the previous research on systems-level consolidation applied spatial smoothing with an FWHM of 5mm (A. O. Cohen et al., 2021; Murty et al., 2017, 2019), or used unsmoothed data (Gruber et al., 2016; Tompary et al., 2015). Due to mixed recommendations in systematic investigations of the effects of smoothing within the correlation-based analysis of resting-state data reviewed earlier (Alahmadi, 2021; Molloy et al., 2014; Scheinost et al., 2014; Wu et al., 2011), data presented in the main text used an FWHM smoothing kernel of 4mm, but in the appendix (Table A4.1-A4.4, Figure A4.1-A4.6), results are presented obtained with pre-processed data where the smoothing step was either omitted (FWHM = 0) or where a different FWHM smoothing kernel was applied (6 and 8mm, respectively). AFNI's '3dBlurToFWHM' smoothing algorithm was used, also referred to as uniform or adaptive smoothing, because data is smoothed in an iterative process until the specified level of smoothness has been reached across the data rather than simply applying a Gaussian filter, thereby "adding" smoothness that makes data smoother in comparison to the output of 3dBlurFWHM (Scheinost et al., 2014). Regardless of the specific pre-processing pipeline, the same analyses were applied to the data, but the cluster-defining threshold was adjusted depending on cluster size simulations.

Results showed that overall aHPC-VTA/SN-FC estimates (e.g., during online encoding) numerically increased as the smoothing kernel increased and that smoothing increased the variability within the FC estimates as well as for the change in RSFC. However, the overall results (e.g., whether a significant RSFC change or group effects therein were observed) were not affected. When looking at brain-behaviour correlations, the results showed robust patterns. This suggests that while the chosen smoothing kernel might influence the FC estimates, the individual differences therein seem to be preserved. It is important to note that while the brain-behaviour-correlations within the incentives group reached trend level, but were not significant when no smoothing or an FWHM of 4mm was used, the correlations were significant with kernels of 6 or 8mm. Indeed, the graphs (Figure A4.2-3 in the appendix) show a small shift within the incentives group as smoothness increases from 4 to 6mm. This mirrors previous findings investigating the effects of different smoothing kernels (0,2, 4, 6, 8, 10mm) whereby a significant difference in correlation coefficients can be found between 4 and 6mm, but not between any other stepwise increases (Wu et al., 2011). During smoothing, the similarity of adjacent voxels is enhanced, hence, while speculative, it is possible that at larger smoothing FWHM kernels (6 and 8mm), the time series within the aHPC ROI could have become more similar to that of surrounding MTL

cortices, e.g., the perirhinal cortex. Previous research shows that individual differences in changes in VTA-perirhinal cortex FC correlates with item memory, a familiarity-based measurement (Tomparry et al., 2015). As discussed in the previous chapter, the incentive manipulation affected both, familiarity- and recognition-based recollection measurements and the perirhinal cortex is traditionally associated with familiarity-based or item memory (Davachi, 2006; Diana et al., 2007). Thereby, the shift from a FWHM kernel of 4mm compared to 6mm might be due to the fact that at 6mm, activity from the perirhinal cortex was blended into the HPC ROI and that effect is only visible in the incentives group because the incentive manipulation is indifferent to the type of memory, i.e., HPC-based recollection and perirhinal cortex-based familiarity.

In line with previous reports (Wu et al., 2011), more and larger clusters were observed during whole-brain seed-based FC analysis when larger FWHM kernels were applied (Figure A4.4-A4.6 and Table A4.4 in the appendix). In the absence of ground truth, it is difficult to judge which FWHM is most appropriate or trustworthy. However, comparing the results across different smoothing kernels might represent a fruitful approach to gain more confidence in whether changes in RSFC are meaningful or an artefact of smoothing/pre-processing. Likewise, analysing whether individual differences in RSFC between seed and identified cluster can provide a further indication of whether the effects are meaningful or not. Overall, our results suggest that brain-behaviour-correlations as well as group effects therein are fairly robust across different smoothing kernels, whilst this is less the case in the context of seed-based FC analysis. This result was somehow surprising to us given that the dependent variable was the change in RSFC from pre- to post-learning. We would have therefore expected that any (increasing) effects of smoothing on RSFC coefficients at pre-learning rest would affect RSFC coefficients at post-learning rest in a similar manner, hence cancelling each other out. However, this assumption does not seem to hold based on the observations described here. Therefore, we would echo recommendations by others (Alahmadi, 2021) to analyse data using multiple FWHM kernels to increase confidence in the results.

Lack of Behavioural Effects

Contrary to predictions based on two behavioural studies using the same paradigm showing positive effects of curiosity and the availability of incentives on encoding (Meliss & Murayama, 2019), the fMRI study failed to replicate these effects. As shown in the previous chapter, the confidence intervals of the effects obtained in each of the three studies separately were overlapping, hence the absence of effects in the fMRI study could be due to sampling error. However, additional explanations are possible. For instance, the sample size in the behavioural studies was larger (n per group = 38-40) compared to the fMRI study (n per group = 25), hence leading to a larger power in the behavioural studies. Additionally, the underlying motivation of participants in the behavioural study might have been different compared to the fMRI sample. More specifically, the behavioural studies were conducted online using the recruitment

portal Prolific whereas the fMRI was advertised to interested individuals on campus using leaflets. Hence, an incentive manipulation offered to participants that were participating due to monetary reimbursement for their time (as in the online participant pool) could result in different effects compared to when the same manipulation is applied to participants that were interested in participating in fMRI research. Indeed, for the latter, the incentive manipulation might have undermined their intrinsic motivation. Importantly, ratings for intrinsic motivation obtained in all three samples did not lend support for the claim of an undermining effect in neither sample nor did the samples differ in their ratings of intrinsic motivation. Because participants for the fMRI study were not recruited using SONA, most of them were likely research-naïve and have not previously undergone fMRI scanning (for the sake of research). Hence, the fMRI environment and experience would have been a novel experience to the participants. As reviewed above and by others (Düzel et al., 2010; Shohamy & Adcock, 2010), novel experiences are associated with an upregulation of tonic dopaminergic responses making it more likely for dopaminergic cells to engage in phasic responses enhancing the encoding of events that elicited it. On a note of caution, it has been suggested that the relationship between increases tonic and phasic dopaminergic activity might indeed be quadratic rather than linear where phasic responses lose their value if tonic dopamine levels are too high (Alcaro et al., 2007; Di Domenico & Ryan, 2017). It is therefore possible that the fMRI environment itself has raised tonic dopamine levels so that (a) the incentive motivation could not additionally raise the tonic dopamine levels to the same extent as it might have in behavioural studies, and (b) the phasic bursts associated with high states of curiosity were less effective in signalling their motivational salience.

It is important to note that the presence of behavioural effects cannot guarantee neural correlates. For instance, when extracting CMLE from a gLME model predicting recognition with the highest confidence (i.e., equal to 6) that showed an effect of curiosity (see previous chapter), aHPC-VTA/SN-RSFC change and CMLE still do not show a significant correlation, in neither of the groups nor across the whole sample (analysis not reported here¹⁶). This suggests that the lack of correlations between aHPC-VTA/SN-RSFC change and curiosity-motivated learning cannot solely be explained by a lack of behavioural effects. Instead, curiosity-motivated learning might be supported by other consolidation mechanisms compared to extrinsically motivated learning that showed clear correlations with aHPC-VTA/SN-RSFC change (A. O. Cohen et al., 2021; Gruber et al., 2016). Additionally, in studies on systems-level consolidation of extrinsically motivated learning, value was manipulated as binary (i.e.,

¹⁶ The analysis was not reported here because the dependent variable of interest (i.e., recognition with confidence ratings above 3) was determined *a priori* based on the behavioural studies.

high and low) categories (\$15.00 vs. \$1.00, A. O. Cohen et al., 2021; \$2.00 vs. \$0.02, Gruber et al., 2016; \$20.00 vs. \$1.00, Murty et al., 2017). Likewise, studies on the encoding processes in support of curiosity-motivated learning often implement a screening procedure during which participants rate their curiosity for the stimuli to create equally large sets of high- and low-curiosity stimuli to be used in the encoding session (Duan et al., 2020; Gruber et al., 2014; Murphy, Dehmelt, et al., 2021; Stare et al., 2018), thereby increasing the variance and contrast in the data. Importantly, the dichotomisation of high- compared to low-curiosity trials has previously been used to calculate a “curiosity-driven memory benefit” (i.e., memory for information presented in the state of high compared to low curiosity; Gruber et al., 2014) akin to the reward-driven associative memory effect (i.e., memory for associations learned in high- compared to low-reward contexts; Gruber et al., 2016). These motivated learning facilitation indices were associated with FC between HPC and VTA during task (Gruber et al., 2014) or their change during rest (Gruber et al., 2016). In our design, on the other hand, a screening was not possible (e.g., due to repetition suppression effects), which is why a direct comparison between memory for magic tricks eliciting high or low states of curiosity was not feasible and curiosity ratings were hence operationalised as a continuous predictor in the model. While the curiosity-driven memory benefit captures the effects of high compared to low (intrinsic) value, CMLE represents a metric on how much the likelihood to remember an item increases as curiosity increases. When computing the curiosity-driven memory benefit in adapted form to account for a lack of a clear distinction between high and low curiosity as well as an unequal number of trials¹⁷, the non-significant correlations with aHPC-VTA/SN-RSFC change were replicated (analysis not reported here). Taken together, the results suggest that the lack of a correlation between behavioural measures of curiosity-motivated learning and aHPC-VTA/SN-RSFC change could be a robust result, hinting to the conclusion that curiosity-motivated learning differs from extrinsically motivated learning in terms of its consolidation mechanisms, but more research is needed.

¹⁷ To calculate curiosity-driven memory benefits, clusterwise mean-centered curiosity ratings were used to define high and low curiosity trials. The sum of trials remembered from the high curiosity condition were divided by the total number of high curiosity trials. The same procedure was applied to the low curiosity condition to then subtract both quotients from one another. Any trials that received average curiosity ratings were excluded. The analysis with this index is not reported here due to concerns about its validity due to a smaller number of trials compared to prior work (Gruber et al., 2014 used 56 trials in each condition).

Limitations

The design of the study has satisfactory face validity to draw the conclusion that changes in activity from pre- to post-learning are related to the encoding per se and do not reflect intrinsic properties of the brain at baseline (Tambini & Davachi, 2019). However, when interpreting the results, it is important to keep certain limitations in mind.

First, we aimed to investigate dopaminergic consolidation processes in the context of curiosity-motivated learning and how this is influenced by the availability of extrinsic incentives. Our analysis hence focused on the interaction between aHPC and VTA/SN because these regions are key players in models of motivated learning and have been implicated in the context of curiosity and extrinsic rewards/incentives (Gruber & Ranganath, 2019; Lisman et al., 2011; Lisman & Grace, 2005; Murty & Dickerson, 2016; Shohamy & Adcock, 2010). Effects within and between HPC and VTA/SN are often seen as an indication of dopaminergic activity. Indeed, it has been shown that dopamine release in the VTA/SN is reflected in the BOLD response (D'Ardenne et al., 2008). However, the VTA/SN also contains GABAergic and glutamatergic neurons (Nair-Roberts et al., 2008), which could be a source of the BOLD response (Düzel et al., 2009). Concluding with certainty that observed changes in the BOLD responses and FC are dopaminergic is hence impossible. Overall, the approach taken here is correlational in nature. It points towards the co-existence of learning and changes in RSFC, but it does not allow causal inferences regarding the role of dopamine. For this purpose, other methods are needed, including neurostimulation or pharmacological interventions. While pharmacological studies have been conducted in the context of reward and learning, most prominently in the context of instrumental learning (for a review, see Webber et al., 2021), pharmacological studies in the context of curiosity-motivated learning are thus far lacking and more research is needed in this area.

Second, in a related manner, studies targeting the dopaminergic midbrain and HPC also suffer from an overall poorer signal-to-noise ratio in these compared to cortical areas, making it even more challenging to capture effects in these areas. Indeed, as shown in the chapter describing and validating the MMC Dataset, the temporal signal-to-noise ratio is lower in MTL and midbrain compared to e.g., the visual cortex. Likewise, prior literature has also found evidence for reactivation within the entorhinal cortex (Staresina et al., 2013), systems-level consolidation between HPC and perirhinal cortex interacting with striatal activity (Murty et al., 2019), but also memory-reward interactions during encoding in the parahippocampal gyrus (Wolosin et al., 2012). Overall, this suggests that in addition to the HPC, other MTL structures might be involved in consolidation processes in the context of motivated learning. High-resolution fMRI studies (e.g., Duncan et al., 2014; Tompariy et al., 2015; Wolosin et al., 2012) could help further disentangle the contributions of regions within the MTL, not only during consolidation but also during encoding, to enhance our understanding of motivated learning. More fine-grained approaches

could also help to identify unique mechanisms in the context of curiosity- and extrinsically motivated learning.

Third, the sample size of the study needs to be taken into consideration. While the sample size used here reflects those of typical fMRI studies (Szucs & Ioannidis, 2020), the sample size does not allow for reliable effect estimates in the context of brain-wide association studies, i.e., studies mapping individual differences in (f)MRI measures to cognitive function (Marek et al., 2022). Hence, the robustness of the results needs to be confirmed in future studies.

Fourth, based on our design, we cannot exclude that observed effects are a result of intentional, spontaneous rumination/rehearsal. However, systems-level consolidation effects between dopaminergic midbrain and MTL have previously been observed during active rest (A. O. Cohen et al., 2021; Tompariy et al., 2015), hence reducing the likelihood that our results here are solely driven by rumination/rehearsal. Likewise, when asked about the hypothesis of the study after fMRI scanning, none of the participants suspected that the aim was to investigate memory, further rebutting the idea that the effects are a mere result of intentional rumination/rehearsal. Crucially, even if the effects found here were fully attributable to spontaneous rehearsal, this might (a) be part of the consolidation process and (b) it would nevertheless suggest that the availability of extrinsic incentives influences spontaneous rehearsal as measured in this paradigm. To further shed light on the question of whether the effects can better be explained by rehearsal, future research could implement a distractor task between encoding and resting-state scan to further control for rehearsal effects.

Conclusion

Taken together, our results suggest that aHPC-VTA/SN-RSFC change does not predict learning in the context of curiosity, potentially suggesting that curiosity- and extrinsically motivated learning do not rely on the same mechanisms during consolidation and that their effects on encoding might thereby be additive. Indeed, the availability of extrinsic incentives influenced brain-behaviour correlations, suggesting that the availability of extrinsic incentives is associated with a large-scale switch in neural processes. In the absence of behavioural effects, however, we were unable to determine whether this switch is adaptive or maladaptive in nature and more research is needed to inform educational policies.

Chapter 5: General Discussion

Summary of the Work

The present work aimed to investigate the behavioural and neural effects of curiosity on memory using a new paradigm and stimuli. In the introductory chapter, the scientific study of memory was discussed, highlighting the core neuroanatomical structures involved as well as the cellular mechanisms in support of learning. Because human memory is selective, the effects of dopamine on encoding were reviewed, followed by the effects of reward/incentives and curiosity on learning, which are both associated with the release of dopamine in the dopaminergic midbrain. This revealed that both reward/incentives and curiosity are associated with similar behavioural effects which are located in overlapping brain regions. Importantly, the research on motivated learning is still fairly young and has studied the effects of curiosity and rewards/incentives on memory in isolation.

In the context of the effects of curiosity and memory, a single paradigm has dominated the field. While curiosity is central to the human condition in general and knowledge acquisition in particular, research aimed at understanding this powerful force is still in its infancy. This could be because it is challenging to induce curiosity reliably in an experimental setting. Indeed, previous studies often used simplistic, reductionist stimuli, often in the context of the trivia question paradigm. While valuable, these are not sufficient to reach a full understanding of ‘real-life’ curiosity as encountered in, e.g., classrooms. This is why after discussing the accomplishments of the trivia question paradigm, the focus was shifted towards its limitations. In doing so, we provided a rationale why the effects of curiosity on memory should be investigated using a new paradigm to gain insights in the effects of curiosity on encoding outside the trivia question paradigm. Additionally, to better understand the combined effects of extrinsic incentives and curiosity, a between group incentives manipulation was included into the paradigm to be able to study the effects of curiosity, monetary incentives, and their interaction on learning and memory.

In Chapter 2, we describe and validate the Magic, Memory, and Curiosity (MMC) Dataset. More specifically, after behavioural studies were used to design and pilot a new paradigm to investigate the effects of curiosity on memory – the magic trick paradigm – 50 participants underwent fMRI before, during, and after the incentive- and/or curiosity-motivated learning paradigm. Curiosity was elicited using short videos of magic tricks taken from a validated stimuli database (Ozono et al., 2021) that reliably induced curiosity. Encoding performance was measured in a surprise, delayed memory test consisting of cued recall and cued recognition. Additionally, survey data of potentially relevant constructs was collected. After a detailed description of the methods used to generate the MMC Dataset, we showed that the behavioural data had high timing accuracy and good inter-individual differences in encoding performance and curiosity ratings. To evaluate the quality of the fMRI data, standardised tools and basic

validation analyses were used, overall showing that all image quality metrics are comparable with other publicly available datasets and that well-established effects in the expected locations associated with video watching and resting-state could be replicated in the MMC Dataset. The MMC Dataset allows researchers to explore cognitive and motivational processes adding to the emerging, multidisciplinary science of curiosity and its neural effects on learning during encoding and consolidation.

In Chapter 3, the data from the two behavioural studies used to pilot the magic trick paradigm together with the behavioural data from the MMC Dataset were analysed using a meta-analytic approach integrating the effects across all three studies. In doing so, a robust memory-enhancing effect of curiosity on recollection-based memory was found in the absence of an effect for familiarity-based measurements. We also found positive effects of the availability of extrinsic incentives, however, only on one, not both measures of recollection-based memory with a trend for effects for the familiarity-based measurements. No interaction effects between curiosity and monetary incentives on memory were found. Exploratory analyses revealed that while the effects of curiosity on memory increased as the confidence in the recognition memory test increased, no such effects were found for the incentives or interaction effects, overall suggesting that curiosity and incentives might affect memory using different mechanisms. Further, in that chapter, the fMRI data acquired during encoding was analysed using the intersubject correlation (ISC) framework to account for the dynamic nature of the stimuli. To compute pairwise ISC maps, the voxelwise time courses were correlated across participants, revealing far-reaching synchronisation of brain responses in cortical and subcortical areas during magic trick watching. To link these ISC maps to the behavioural data acquired during the magic trick watching paradigm, the Representational Similarity Analysis (RSA; Kriegeskorte et al., 2008) was applied to the ISC maps using the intersubject (IS)-RSA framework (Finn et al., 2020; Nummenmaa et al., 2012). These behavioural effects of interest were curiosity, memory, and the curiosity-motivated learning enhancement (CMLE). For each effect, a behavioural similarity matrix was computed to identify clusters where the similarity in the behavioural response predicted the similarity in the brain response. We found that while the effects of curiosity and monetary incentives were only located outside the often implicated loop between hippocampus (HPC) and ventral tegmental area (VTA) or substantia nigra (SN), the effects of memory were mirrored by similarity in the caudate nucleus. The CMLE effects were found within the HPC-VTA/SN loop. However, importantly, all effects also showed significant clusters surviving conventional thresholding at whole-brain level, overall suggesting that the effects of curiosity or incentives on memory as well as their interaction might be reflected by a large number of brain areas. Indeed, functional connectivity (FC) analysis applied to the ISC context revealed that the behavioural effects of interest are supported by communication between HPC and VTA/SN and various brain areas. Taken together, the results suggest that, during encoding, the effects of curiosity on memory and their interaction with monetary reward

might be supported by broad brain networks, rendering a too narrow focus on often implicated regions-of-interest (ROI) insufficient to understand the effects.

In Chapter 4, we focused on the neural mechanism in support of motivated learning during early consolidation. The resting-state data from the MMC Dataset was analysed whereas the pre-learning rest data was used as a baseline to identify significant changes from pre- to post-learning that occurred due to learning and/or could predict individual differences in learning. We focused on post-encoding resting-state FC (RSFC) between HPC and VTA/SN to reward-motivated learning because previous literature had established a link in the context of reward-motivated learning. While neither an overall change in HPC-VTA-RSFC was found nor a significant correlation between HPC-VTA-RSFC change and individual differences of learning, the availability of extrinsic incentives significantly influenced brain-behaviour correlations. Overall, this suggests that curiosity- and extrinsically motivated learning might be accompanied by differential mechanisms during early consolidation and that the availability influences neural post-encoding mechanisms in support of learning.

Replicating and Expanding the Effects of Curiosity on Memory

The primary aim of this thesis was to examine the effects of epistemic curiosity on incidental encoding outside the predominantly used trivia question paradigm (Gruber & Ranganath, 2019) by using other methods and materials to elicit curiosity. More specifically, within the trivia question paradigm, curiosity arises from the awareness of a knowledge gap or an information-based prediction error (PE) (Gruber & Ranganath, 2019; Loewenstein, 1994), but research suggests that curiosity is a multifaceted construct and can be triggered by different factors, potentially related to different psychological and neural mechanisms (Gruber & Ranganath, 2019; Jach et al., 2021; Kobayashi et al., 2019; Sharot & Sunstein, 2020). In addition to the question of generalisability, the trivia question paradigm also has other limitations: the stimuli are reductionist and static, the elicitation of curiosity is confounded with the anticipation of rewarding information, and the effects of curiosity on memory are tested using the information that satisfied curiosity rather than information that elicited it. We here developed a new paradigm to investigate the effects of curiosity on encoding: curiosity was induced by magic tricks videos that violated expectations and created a sense of surprise. Memory for the magic tricks were then tested in a delayed, surprise memory test a week later. As such, this “magic trick paradigm” tries to address some of the limitations of the trivia question paradigm and thereby, contributing to the question of robustness of effects.

Effects of epistemic curiosity on delayed incidental memory encoding within the trivia question paradigm are well established in the literature (Fastrich et al., 2018; Gruber et al., 2014; Kang et al., 2009; Marvin & Shohamy, 2016; Murayama & Kuhbandner, 2011; Stare et al., 2018; Swirsky et al., 2021), and

we were able to support our hypothesis that curiosity elicited when watching magic tricks also positively predicts their encoding. This demonstrates that the effects of curiosity on encoding can be found when curiosity is induced using dynamic, more complex stimuli, further generalising the effects found in previous studies. According to the prediction-appraisal-curiosity-encoding (PACE) framework (Gruber & Ranganath, 2019), curiosity arises from PEs and an associated state of uncertainty.

Trivia questions trigger the awareness of a gap in one's knowledge and a PE is triggered because this violates one's expectations about one's knowledge (i.e., information-based PE). Magic tricks, on the other hand, show implausible, if not impossible events (Kuhn et al., 2008; Rensink & Kuhn, 2014). This might also lead to the awareness of an information gap because the viewer experienced the effect (e.g., an object vanished) without knowing the method (i.e., how the trick works). More importantly, however, because the viewer generates predictions as the magic trick unfolds, any violation of causal relationships would also violate the viewer's expectations (i.e., context-based or perceptual PE; Zacks et al., 2007). Indeed, previous research has shown that magic tricks are rated as surprising, violate cause and effect relations, and lead to unexpected outcomes (Danek et al., 2015; Parris et al., 2009), trigger epistemic emotions (surprise in response to the trick, interest in the trick, and curiosity in the solution; Ozono et al., 2021), and elicit curiosity to motivate risky decision making in a similar way as trivia questions do, supported by the ventral striatum (Lau et al., 2020). Likewise, magic tricks have been used to investigate effects of age and anxiety on encoding (Shen et al., 2021), and prior research has shown that the content of videos that include magic tricks are better remembered than videos matched in content that do not include magic (Subbotsky & Mathews, 2011).

However, to the best of our knowledge, no research has previously linked curiosity elicited by magic tricks to their encoding. While previous research has shown that curiosity enhances the encoding of the information that satisfied the curiosity (e.g., Fastrich et al., 2018; Kang et al., 2009) and incidental information presented in the context of high curiosity states (e.g., Gruber et al., 2014), we here show that self-reported trial-by-trial curiosity ratings also predict the encoding of the material that elicited curiosity. This further stresses the critical role of curiosity in learning. It should further be noted that the effects of curiosity on encoding were only found in recollection-based memory measurements (i.e., high confidence recognition and cued recall), but not on recognition regardless of confidence that is assumed to reflect familiarity and recollection (Yonelinas, 2002). While we did not predict such a dissociation, these results are in somewhat of an alignment with results on the recognition rate of incidental information presented in states of high compared to low curiosity. For instance, Gruber and colleagues (2014) reported that the curiosity-related recognition advantage was specific to confidently recognised faces and did not emerge in overall recognition rates. These results were replicated and extended for short delays by showing that curiosity enhances recollection of incidental information, but only if presented in close temporal

proximity, whereas no effects were found on familiarity-based measurements (Murphy, Dehmelt, et al., 2021). Indeed, it has been suggested that curiosity-related memory facilitation is specific to recollection (Gruber et al., 2019). While this has previously only been shown using incidental information presented in the context of high vs low curiosity, here we show that this “recollection-only” memory effect can also be found for the material eliciting curiosity. However, it is important to mention that some studies found effects of curiosity on memory for incidental material regardless of whether all confidence responses were collapsed or not (Galli et al., 2018 Exp. 1; Stare et al., 2018) whereas others did not find an effect of curiosity on neither recollection- nor familiarity-based measures of the encoding of incidental information (Fandakova & Gruber, 2021; Galli et al., 2018 Exp. 2; Swirsky et al., 2021). In summary, this illustrates that more research is needed to fully understand the effects of curiosity on recollection and familiarity.

While we replicated previously reported effects of curiosity on recollection-based measurements of memory, it should be noted that our effect sizes are somewhat smaller compared to studies using the trivia question paradigm. More specifically, the integrated effect of curiosity on high confidence recognition and cued recall expressed as Odds Ratio (OR) was 1.09, 95% CI [1.04; 1.14], and 1.10, 95% CI [1.05; 1.16] suggesting that as curiosity increases by one unit, the odds of encoding increased by the factor 1.09 and 1.10, respectively. In comparison, a recent study (Swirsky et al., 2021) that used the trivia paradigm to investigate effects of curiosity as well as monetary rewards on incidental, delayed encoding and also analysed the data using a gLME, reported an OR of 1.25, 95% CI [1.17; 1.32], for the curiosity effect on cued recall. Yet, in the trivia paradigm, the effects of curiosity to know the answer on its encoding are inherently intertwined with effects of prior knowledge as well as with interest and other epistemic emotions triggered by the answer (Fastrich et al., 2018; Halamish et al., 2019; Ligneul et al., 2018; Mullaney et al., 2014; Wade & Kidd, 2019) and previous research has been somewhat inconclusive regarding the extent of the purely curiosity-related effects in encoding.

In our paradigm, on the other hand, the effects of interest (defined as the rewarding experience upon knowledge acquisition) have been eliminated because no resolving knowledge was presented. In a similar vein, because we presented magic tricks to participants with little to no experience in producing magic tricks, prior knowledge would have little to no effect on encoding. Indeed, the differences between our results and those by Swirsky and colleagues (2021) could potentially be explained by the fact that they did not control for effects related to prior knowledge or interest. For instance, in a saturated structural equation model predicting incidental, delayed recall of answers in the trivia question paradigm with confidence in knowing the answer and curiosity about the answer as distal factors and interest as proximal factor, Fastrich and colleagues (2018) found that curiosity was only a very weak predictor of recall ($\beta = .018$, or when exponentiated to calculate OR = 1.018; Murayama et al., 2014). Therefore, while it is true that the effects of curiosity on encoding are weaker in our paradigm, this might partly be

due to the fact that the curiosity effect is not or at least to a lesser extent confounded with prior knowledge or interest within the trivia question. Overall, our results replicate previous results and further the contribution of curiosity to learning.

Effects of Extrinsic Motivation on Encoding

In line with our hypothesis and other studies investigating the role of monetary rewards/incentives on incidental delayed encoding (Bunzeck et al., 2010, 2012; Murayama & Kitagami, 2014; Patil et al., 2017; Stanek et al., 2019; Wittmann et al., 2005, 2008, 2011), we found that participants in the incentives group showed better memory performance. While the direction of the OR of the integrated effects across all three studies for all main measurements of memory (recognition, high confidence recognition, and cued recall) suggests that additional monetary reward facilitates encoding, only the effect for high confidence recognition reached significance whereas the effect for recognition reached trend level. Again, we did not formulate an *a priori* hypothesis for any dissociative effects. Research studying the effects of monetary rewards on incidental encoding often tests the recognition for target items by displaying them together with unseen new targets to determine the corrected hit rate as a measure of recognition based on old/new judgements. This is often combined with judgements of confidence or by applying the remember/know technique (Diana et al., 2007) to differentiate recollection-compared to familiarity-based recognition. In doing so, it has been shown that reward is associated with improved recognition when confidence is not considered (Murayama & Kitagami, 2014; Stanek et al., 2019; Wittmann et al., 2008), but reward effects can also be found when only focusing at high confidence recognition or source memory (Wittmann et al., 2005). Even though one study found that reward only enhances recollection, but not familiarity (Wittmann et al., 2011), most studies find effects on measures of both (Bunzeck et al., 2010, 2012; Patil et al., 2017). In the magic trick paradigm, we used a four-alternative forced choice recognition paradigm and asked participants to select the answer indicating what happened in the magic trick according to their memory and afterwards, rate their confidence. While these measurements are quite different from one another, our results show that incentives enhance high confidence recognition and, at trend level, also enhance recognition regardless of confidence. This finding aligns well with the previous literature. However, the fact that no effects of incentives on recall were found is surprising given that recall and high confidence recognition are both assumed to be supported by processes of recollection (Yonelinas, 2002). This suggests that the effects of reward on encoding could be weaker or less specific compared to the effects of curiosity.

In contrast, previous studies manipulating monetary rewards within the trivia question paradigm by asking participants to guess the correct answers and offering performance-dependent rewards to half of the participants found that participants in the monetary reward condition recalled more answers than those

in the control group during a surprise memory test (Murayama & Kuhbandner, 2011; Swirsky et al., 2021). While speculative, it is possible that we did not replicate those effects because we used an incentive rather than a reward manipulation, potentially making the manipulation more indirect in comparison. In lay terms, the difference between incentives and rewards is the difference between “do well” and “well done”. In the magic trick paradigm, participants in the incentives group were told that they could earn additional monetary bonus payments if they estimated correctly how many people will be able to find the solution to the magic trick rather than asking them to guess the solution to the magic trick themselves. In comparison, in the trivia question paradigm, participants made guesses regarding the correct answer when the question was presented and could receive monetary bonus payments if the guess was correct. As such, in both paradigms, participants were incentivised to “do well”, but only in the trivia question paradigm, there was a mapping between “do well” and “well done” when the answer was presented. While participants receive direct feedback on their guesses in form of the answer being presented, no feedback regarding the correctness of the estimate was provided in our task – not only because it was a mock judgement task but also – to eliminate any neural effects related to processing success or failure feedback or effects of feedback on memory. However, the lack of feedback during the magic trick watching task meant that the participants in the incentives group were incentivised, but not rewarded. Future research will have to determine whether providing feedback, e.g., randomly generated number reflecting change level performance (25% of 36 trials, so nine “correct” trials in total, distributed across three blocks) at the end of each block counterbalanced between groups would have resulted in more stable effects for extrinsically motivated learning.

On a related note, providing an estimate for the number of people who would be able to solve the magic trick and guessing the correct answer are different tasks used to embed the incentives or rewards manipulation in. We decided not to ask participants to generate a solution themselves to prevent any effects of insight in the solution to the magic trick on memory (Danek & Wiley, 2020). Similarly to what has been discussed in the context of the effects of curiosity on encoding, it is also possible that better memory performance in the reward group in the trivia paradigm can at least partially be explained by increased retrieval attempts during guessing or by more pronounced hyper-correction effects compared to the control group (Butler et al., 2011; Kornell et al., 2009). Both effects were eliminated in our paradigm, potentially contributing to the fact that the reward effects on recall found in the trivia paradigm were not replicated here.

Crucially, however, this is not to suggest that the incentives manipulation did not work as intended because in the fMRI, in the absence of behavioural effects, neural effects were observed during encoding as well as during early consolidation. Critically, the effects of the incentive manipulation were not found in the reward network, but instead in cortical areas that have previously been implicated in

attentional processes. Likewise, while changes in RSFC from pre- to post-learning did not directly predict individual differences in learning, the incentives manipulation significantly impacted brain-behaviour correlation. Overall, this suggests that the incentives manipulation impacted neural mechanisms in support of learning during encoding and consolidation. However, it is crucial to note that the influence of extrinsic motivation on learning does not have to be purely caused by neural mechanisms associated with reward-related processes, but could also reflect attentional processes as previously discussed (Gottlieb & Oudeyer, 2018; Gruber & Ranganath, 2019).

Interaction Between Curiosity and Monetary Incentives

In addition to replicating the effects of curiosity on memory, we were further interested in determining whether curiosity interacts with extrinsic motivation, as manipulated with the availability of monetary incentives. Previous research suggested that curiosity- and extrinsically motivated behaviour and learning might rely on overlapping underlying neural mechanisms (Gruber & Ranganath, 2019; Miendlarzewska et al., 2016; Murayama, 2019; Murty & Dickerson, 2016). If the systems overlapped, this would imply sub-additive (or undermining) effects whereas additive effects would be expected if the systems differed.

Our hypothesis was in line with evidence from neural studies suggesting involvement of similar regions for curiosity- and reward-motivated effects on delayed, incidental encoding (Gruber et al., 2014; Wittmann et al., 2005) and previous research on the interaction between curiosity and monetary reward within the trivia question paradigm (Murayama & Kuhbandner, 2011; Swirsky et al., 2021). We hypothesised to find an interaction effect showing that both effects are sub-additive because they are supported by shared neural mechanisms. In fact, previous studies showed that monetary reward only enhanced the encoding of trivia answers to questions eliciting low, but not high curiosity ratings. Put differently, as curiosity increases, the likelihood of recalling the answer increases more in the non-rewarded compared to the rewarded group, which has previously been interpreted in the light of an undermining effect of monetary reward on the memory-facilitating effects of curiosity (Murayama & Kuhbandner, 2011). Contrary to our predictions, we did not find a significant interaction on any of our main measures of interest (recognition, high confidence recognition, cued recall).

However, visual inspection indicated that, descriptively, data for recollection-based measures followed a similar trend where the effects of curiosity appear smaller in the context of additional monetary rewards, suggesting that potentially our design was not sufficiently powered to detect small interaction effects. This is further amplified by the fact that there are good reasons to believe that the interaction effect, if present, would have been smaller in the magic trick compared to the trivia question paradigm. In the reward-motivated version of the trivia question paradigm where participants in the

reward condition can earn additional monetary rewards for correctly guessing the correct answer to the trivia question, the presentation of the answer to the trivia question does not only satisfy any curiosity they have experienced but also serves as de facto performance feedback. The analyses on the memory effect excluded correct guesses, revealing the answer in the reward condition would also signal failure in the guessing task or a missed opportunity to earn additional rewards. Research has shown that loss and missed opportunity are associated with a decrease in activity in the striatum (Büchel et al., 2011). In our paradigm, on the other hand, no performance feedback was provided, hence reducing the likelihood of failure-related activity that could have interacted with the brain activity related to not only the relief of curiosity (Duan et al., 2020), but potentially might also influence brain activity related to incorrect guesses (Kang et al., 2009). In fact, this view can also explain the lack of an interaction effect in reward-motivated versions of the trivia question paradigm to measure the effects of curiosity and monetary rewards on intentional encoding (Duan et al., 2020; Halamish et al., 2019) where participants can earn additional monetary rewards for recalling an answer during the delayed memory test rather than correctly guessing during encoding. In that instance, there would also be no performance feedback during encoding, potentially impacting the curiosity-related activity. However, it is important to note that both studies also found that, on a descriptive level, the effects of curiosity were smaller in the context of monetary rewards, allowing the speculation that the interaction effect was present but too small to be detected. Indeed, large sample sizes are required to reliably detect interactions (Rohrer & Arslan, 2021). While our sample sizes within each group were comparable, if not larger to previous studies reporting a significant interaction between curiosity and monetary reward on incidental memory (Murayama & Kuhbandner, 2011; Swirsky et al., 2021), they were not sufficient to detect large interaction effects with high power. This is supported by recent meta-analytic results showing that if extrinsic rewards are only indirectly salient to performance, intrinsic motivation is a better predictor of task performance compared to situations where extrinsic rewards are directly salient to performance (Cerasoli et al., 2014). Arguably, the reward contingencies were more salient in the incidental reward-motivated trivia question paradigm compared to its intentional counterpart and our incentive-motivated magic trick paradigm which could have led to smaller interaction effects. Hence, more studies sufficiently powered to detect small interaction effects are needed to fully understand the interplay between curiosity and monetary rewards in incidental as well as intentional encoding to derive conclusions to inform educational policies.

Another possibility for the absence of interaction effects is that in our design, the effects of curiosity and monetary rewards were additive rather than sub-additive. As such, it is possible that the elicitation of curiosity (when independent of the anticipation and reception of information satisfying it) enhances incidental memory via different processes compared to performance-dependent incentive/reward for an unrelated task during encoding. In fact, our exploratory analysis of the

behavioural data showed that the memory-enhancement effect of curiosity linearly increased as the confidence in the recognition response increased whereas such relationships were not found for the effects of monetary incentives. This might indeed suggest a dissociation: curiosity only affects recollection-based, but not familiarity-based processes, whereas the influence of monetary incentives is less selective. A recent meta-analysis on the combined effects of intrinsic and extrinsic motivation on task performance showed that extrinsic rewards better predicted the quantity of performance whereas quality was better explained by intrinsic motivation (Cerasoli et al., 2014). According to dual-process models of recognition memory, successful recognition memory judgements can be based on a “quantitative” memory strength as captured by familiarity measurements. However, if additional “qualitative” information (e.g., where and when the item was presented) can be retrieved, this is referred to as recollection (Diana et al., 2007; Yonelinas, 2002). It is further assumed that recollection supports higher confidence judgments during recognition compared to familiarity (Yonelinas, 1994). Therefore, it could be argued that the distinctive aspects of intrinsic and extrinsic motivation in their effects on task performance, in general, could also apply to encoding specifically.

While more research is needed to determine whether familiarity and recollection are affected differentially by monetary incentives and curiosity and if so, how such findings could be explained, a premature proposition is that in the magic trick watching task described here, curiosity and monetary incentives capture external attention differently (for a review, see Chun et al., 2011). As reviewed elsewhere (Gottlieb & Oudeyer, 2018), rewards can affect attention in a potentially maladaptive fashion. It is thereby possible that participants in the incentivised group could have attended the stimuli more or differently in a manner that aligns with the task goals (i.e., identifying cues that help to provide the “correct” estimate of how many people would be able to identify the solution). However, this top-down adaptive attention directed to some aspects of the magic tricks and related to the task goal does not guarantee subsequent memory for said magic tricks. In fact, the incentive manipulation could have been dysfunctional with respect to deep, incidental encoding because attentional resources were removed from the processing of the magic trick itself and focused on the identification of cues related to succeeding in the incentivised task. The increased top-down attentional processes in the monetary incentive group could have led to increased familiarity with the stimulus, but at the same time hampered elaborate encoding to a certain extent due to a shift of attentional resources. In actuality, it has been shown that divided attention impairs recollection, but not familiarity (Yonelinas, 2001a). This could explain the absence of incentive effects in the cued recall. Curiosity, on the other hand, might encourage processing of the stimuli in a deeper, more elaborate fashion due to the PE involved in eliciting curiosity, capturing attention in a more bottom-up manner compared to the availability of extrinsic incentives further promoting learning (Gruber & Ranganath, 2019).

Differential Underlying Mechanisms for Extrinsically and Curiosity-Motivated Learning?

It is often argued that the effects of rewards/incentives and as well as states of curiosity are associated with dopaminergic activity, thereby influencing synaptic plasticity processes – the cellular mechanisms of learning – via dopaminergic effects on late LTP (Gruber & Ranganath, 2019; Miendlarzewska et al., 2016; Murty & Dickerson, 2016; Shohamy & Adcock, 2010). More specifically, dopamine is necessary for the synthesis of plasticity-related proteins used to strengthen existing synapses or build new ones (Kandel et al., 2014; Lisman et al., 2011). This is why dopamine-related memory enhancements (depending on late LTP) would only occur after delays between encoding and retrieval because they are dependent on consolidation. In line with this, enhancing effects of reward on memory are found after long, but not short delays (Murayama & Kitagami, 2014; Murayama & Kuhbandner, 2011; Patil et al., 2017; Wittmann et al., 2005). However, some studies have also reported reward effects after short delays (Gruber et al., 2013, 2016; Gruber & Otten, 2010; Murty & Adcock, 2014; Wolosin et al., 2012). In a similar vein, the facilitating effect of curiosity on encoding has been found after short and long delays (Galli et al., 2018; Gruber et al., 2014; Stare et al., 2018).

Such findings conflict with the proposal that these effects are purely dopaminergic in nature and suggest that other neurotransmitters such as noradrenaline or acetylcholine could be involved as well (Atherton et al., 2015; Gruber & Ranganath, 2019; Lisman et al., 2011; Sakaki et al., 2018; Shohamy & Adcock, 2010). For instance, in a placebo-controlled double-blind study targeting the effects of noradrenaline and dopamine on incidental memory (tested after a short delay), *arousal* was manipulated by randomly rewarding 25% of all stimuli with £0.50 (Hauser et al., 2019). Results showed that selective blockage of noradrenaline, but not dopamine, suppressed the effects of arousal (i.e., random rewards in 25% of stimuli) on memory. Importantly, while the authors of the study referred to this effect as arousal, others (including us) would refer to it as a reward manipulation. While a discussion of the appropriate linguistics and terms is beyond the scope, it is important to note that the effects of random rewards on memory after short delays could be supported by noradrenaline, not dopamine.

It is thereby possible that the memory-enhancing effects of rewards/incentives and curiosity found at short delays between learning and memory tests are not dopaminergic but rather mediated by attention (Gruber & Ranganath, 2019). Attentional processes are associated with various neurotransmitters including acetylcholine, dopamine, noradrenaline, glutamate, and GABA (Burk et al., 2018). Besides attention and arousal, noradrenaline has also been implicated in the processing of uncertainty (for a review, see Sakaki et al., 2018), and curiosity is conceptualised as driven by a state of uncertainty (Gruber & Ranganath, 2019; van Lieshout et al., 2018). Indeed, states of curiosity are associated with increased pupil dilation (Brod & Breitwieser, 2019; Kang et al., 2009), a marker of the release of noradrenaline from the locus coeruleus (LC) located in the brain stem (Aston-Jones & Cohen,

2005). Intriguingly, neurons in the LC not only release noradrenaline, but also dopamine (C. C. Smith & Greene, 2012). Dopaminergic LC neurons do not only signal novelty, but also enhance memory (Takeuchi et al., 2016), further highlighting the possible interplay between noradrenaline and dopamine in motivated learning. On a broader scale, both noradrenaline and dopamine might be signalling salience (Bromberg-Martin et al., 2010; Totah et al., 2019), thereby assigning priority to certain events or information to support enhanced memory for them, either by neural processes during encoding or consolidation (Atherton et al., 2015; Mather & Sutherland, 2011). The salience of (primary) rewards to an organism is quite obvious due to a direct link to survival. However, curiosity also involves an inherent salience because current theories assume that curiosity is elicited via PEs, potentially signalling that internal models need to be updated to reduce uncertainty (Gottlieb & Oudeyer, 2018; Gruber & Ranganath, 2019).

Whether the salience differs between both is still an open question and salience in and of itself cannot fully explain the effects. A popular model within the literature on the effects of salience and arousal to explain their respective effects on memory is the arousal-biased competition (ABC) theory (Mather & Sutherland, 2011): According to the ABC theory, arousal has a modulating effect on the competing mental representations and their strength. More specifically, arousal, elicited e.g., by salient stimuli, biases the competition, favouring the most salient (conspicuous) or goal-relevant stimuli, creating high- and low-priority representations. This bias is then associated with selective attention during perception and memory afterwards. These competition- and prioritisation-related processes have been linked to noradrenergic activity originating from the LC (Mather et al., 2016). If we were to assume that the effects of curiosity were purely noradrenergic, the ABC model would predict greater memory selectivity during high compared to low states of curiosity. However, this account is contradicted by findings showing that incidental information presented after curiosity has been elicited is better encoded during states of high compared to low curiosity (Galli et al., 2018; Gruber et al., 2014; Murphy, Dehmelt, et al., 2021; Swirsky et al., 2021). The ABC theory would predict that memory for goal-irrelevant incidental information would be suppressed during states of high arousal, hence predicting better memory for incidental information during low states of curiosity (or arousal). Instead, memory is enhanced for incidental information during high states of curiosity, which is in line with the proposal of a dopaminergic penumbra (Miendlarzewska et al., 2016).

Taken together, it seems as if a purely dopaminergic account is not suitable to explain the effects of motivated memory because this would imply a delayed encoding effect which seems to be more prevalent in the context of extrinsic rewards compared to curiosity. Likewise, an account focused on noradrenaline also does not fit the data given consistent evidence of penumbra effects in motivated

learning. This suggests that it is most likely an interplay of both transmitters and possibly others as well that support motivated learning.

Indeed, the effects of CMLE observed in the IS-RSA analysis were far spread across subcortical and cortical regions and networks including the HPC-VTA/SN loop, making it unlikely to be only associated with one single neurotransmitter. Thus, more research aiming to dissociate not only incentive/reward- and curiosity-motivated learning, but also the contributions of dopamine and noradrenaline (as well as other neurotransmitters like acetylcholine) is needed, ideally using more causal pharmacological manipulations. While speculative, it is possible that both effects are supported by the same neurotransmitters, but perhaps to a different extent, thereby also explaining why we did not find support for dopaminergic systems-level consolidation processes in support of curiosity-motivated learning.

The Surprising Role of the Anterior Insula

As a surprising result, we found that IS-RSA effects of curiosity, memory, and CMLE all anchored their similarity onto similarity in the right anterior insula/frontal operculum (aI/fO) with clusters overlapping in the right anterior insula cortex (AIC). The AIC is part of the putative "salience network" (Seeley et al., 2007), but also of the cingulo-opercular task maintenance network (Dosenbach et al., 2007) suggesting the AIC to be involved in both, tonic and phasic alertness supporting the detection of salient as well as homeostatically relevant signals and their integration into awareness (Craig, 2009) and has been found to be co-activated in thousands of studies (Chang et al., 2012; Craig, 2009; Droutman et al., 2015; Seeley, 2019; Yarkoni et al., 2011). As such, the AIC has been linked to urge generation and addiction (Naqvi & Bechara, 2010), as well as attention, cognitive control and executive functioning (Dosenbach et al., 2006; Mayer et al., 2007; Sridharan et al., 2008). The AIC is also associated with the processing of reward, punishment and subjective value of choice alternatives regardless of their valence (Bartra et al., 2013) and is recruited during the anticipation of rewards (Diekhof et al., 2012; Liu et al., 2011; R. P. Wilson et al., 2018) where the AIC might play a specific role in reward-based attention (L. Wang et al., 2015) or the cognitive expectations expressing causal relations regarding act-outcome representations of incentive value (Berridge, 2000). Investigating the basis of motivational decision-making under uncertainty in the field of neuroeconomics (reviewed by Platt & Huettel, 2008), research has observed increased activity in the AIC associated with risky decision-making (Paulus et al., 2003), risk prediction and risk prediction errors (Preuschoff et al., 2008). Likewise, the AIC has been implicated in error processing (Ullsperger et al., 2010), information update (van Lieshout et al., 2018), prediction errors (Weilnhammer et al., 2017) and their magnitude (Pine et al., 2018), the violation of expectations (Danek et al., 2015; Schiffer & Schubotz, 2011), uncertainty (Grinband et al., 2006; Huettel et al., 2005, 2006;

Volz et al., 2003), and surprise (Loued-Khenissi et al., 2020), but also the elicitation (Jepma et al., 2012) and relief of curiosity (W. Lee & Reeve, 2017). Moreover, the AIC not only signals the magnitude of unsigned prediction errors but is further involved in memory updates thereafter (Pine et al., 2018). Prestimulus activity in the AIC before the onset of movie clips has been shown to positively predict the encoding thereof and further influences memory performance by increased activity in temporal regions, but decreased activity in the posterior precuneus, cingulate, and striatum during stimulus presentation (N. Cohen et al., 2020). The AIC has further been implicated in the subsequent memory effects (Kim, 2011) in general, and curiosity-motivated learning in particular (Duan et al., 2020).

On a broader level, curiosity is often seen as an element or a source of intrinsic motivation (Deci & Ryan, 1985). In an attempt to identify the neural mechanisms of intrinsic motivation, the AIC has been discussed as a basis thereof (Di Domenico & Ryan, 2017; W. Lee, 2016). As such, the AIC has been found to be more activated when participants imagined doing a task out of intrinsic rather than extrinsic reasons (W. Lee et al., 2012; W. Lee & Reeve, 2013). Likewise, higher activity was found when participants performed intrinsically motivating tasks compared to non-intrinsically motivating tasks, and activity in the AIC not only predicted trial-level interest but also interacted with the striatum, thereby potentially forming the intrinsic motivation system by combining intrinsic reward processing in the striatum with feelings of inherent satisfaction in the AIC (W. Lee & Reeve, 2017).

In another account linking the AIC to intrinsic motivation, Di Domenico & Ryan (2017) discussed the AIC as the hub in the bilateral salience network (Menon & Uddin, 2010) involved in the bottom-up detection of subjectively important events to support goal-directed behaviour by providing attentional resources and flexible control. Importantly, because the overlap here is found on the right hemisphere during encoding, the activity observed here could also reflect the right-lateralized ventral attention network described by Corbetta and colleagues (2008) – a bottom-up ‘alerting system’ or ‘circuit breaker’ to shift attention in the top-down DAN. More specifically, the AIC plays a central role in switching between default-mode and central-executive networks (Sridharan et al., 2008) as well as the DAN (Z. Huang et al., 2021), potentially making the AIC a candidate to represent a gateway for sensory information to enter consciousness, together with other structures like the thalamus.

Furthermore, the AIC has anatomical and functional connections with the HPC (Fanselow & Dong, 2010) as well as the dopaminergic striatum (Chikama et al., 1997; Cho et al., 2013; Flynn, 1999). Dopamine depletion is associated with reduced connectivity between the salience network and other parts of the brain (Shafiei et al., 2019), altogether suggesting that the AIC is innervated by dopamine and modulated. Importantly, dopamine does not only signal reward, but in addition to value-coding dopamine neurons, there are also salience-coding dopamine neurons (Bromberg-Martin et al., 2010). Additionally, there is also evidence for noradrenergic effects in the AIC, not only because noradrenaline is associated

with salience (Totah et al., 2019), but ISC in the salience network is dependent on noradrenaline and pharmacologically blocking it during movie watching decreased ISC in the salience network including the aI/FO (Hermans et al., 2011). Noradrenaline has in fact been linked to the reward effect on memory, potentially mediated via surprise (Hauser et al., 2019). On the other hand, surprise during naturalistic viewing has also been linked to dopaminergic activity (Antony et al., 2021). Likewise, while the role of dopamine in curiosity has long been discussed, studies suggest that noradrenaline is additionally involved in curiosity (Sakaki et al., 2018). Traditionally, it was assumed that dopamine is released in the VTA/SN and noradrenaline in the locus coeruleus, however, recent evidence suggests that catecholamine pluripotent neurons in the LC also release dopamine affecting hippocampal consolidation processes (Kempadoo et al., 2016; Takeuchi et al., 2016). Overall, this suggests that both dopamine and noradrenaline could be important in the context of curiosity and curiosity-motivated learning, making the AIC a potential candidate in signalling the effects of both neurotransmitters.

How can this rich and diverse literature on the AIC be integrated theoretically? Sterzer and Kleinschmidt (2010) proposed a framework according to which the AIC plays a central role in perception: AIC activity represents the recruitment of processing resources during “challenging” sensory stimulation to mediate states of sensitivity and reactivity to the environment through reciprocal connections with all sensory cortices. The challenge may arise in a bottom-up manner related to salient aspects of the stimuli or in a top-down manner due to task demands requiring cognitive effort as found in the context of uncertainty or ambiguity. Watching magic tricks whilst performing a judgement task is likely to recruit processing resources in a top-down as well as bottom-up manner. Especially in the context of ISC analysis, it has been suggested that certain brain areas – amongst them the AIC – are more likely to represent information that has been derived from the stimuli (rather than the stimuli themselves) and is hence more idiosyncratic across individuals (Ren et al., 2017). Using IS-RSA, we were able to link variations in the stimulus-induced response in the AIC to fluctuations in curiosity, memory, and CMLE. Hence, our results showing that similarities in our behavioural effects of interest are reflected by similarities in the stimulus-evoked responses in the AIC could reflect recruitment of cognitive resources during their naturalistic viewing that can potentially have an impact on all behavioural effects of interest.

Moving beyond perception and extending computational models of the AIC on risk-taking, Singer and colleagues (2009) postulated a unifying model of various fMRI evidence linking the AIC to feelings, empathy, and the processing of uncertainty in decision-making. According to their model, the AIC signals representations about predicted feeling states, current feeling states, and feeling state prediction errors that in combination support error-based learning, especially in the context of uncertainty. Information about these states is then integrated into a dominant subjective feeling state modulated by individual characteristics (e.g., sensation seeking) as well as contextual appraisal processes. Together,

these mechanisms can not only motivate behaviour and guide decision-making in complex and uncertain environments, but also facilitate learning. Applying this framework to curiosity-motivated learning where curiosity can be conceptualised as a state of uncertainty (Gruber & Ranganath, 2019), the AIC might support representations of the predicted state of knowledge, the actual state of knowledge, and knowledge state prediction errors in light of that uncertainty where the latter is used to inform future predicted knowledge states to reduce uncertainty in the future, hence functioning as learning.

A recent fMRI study (Ligneul et al., 2018) further supported the idea that curiosity and curiosity-motivated learning might be better explained within the framework of predictive coding and uncertainty than using reward-maximization. Predictive coding theories (Friston, 2010; Friston et al., 2012) propose that organisms strive towards minimizing uncertainty and surprise levels associated with sensory inputs by optimising the internal generative model of the environment. However, this maxim is somewhat conflicting with curiosity-related behaviour that might lead to transient increases in uncertainty (Schwartenbeck et al., 2013). This is why second-order expectations regarding an optimal amount of uncertainty have been proposed (Clark, 2013) functioning homeostatically to maintain uncertainty around an expected value. Trying to link these concepts to curiosity and curiosity-motivated learning, Ligneul and colleagues (2018) tested the hypothesis of whether a large (or low) estimate of average surprise (and thus uncertainty) experienced in a given context will down- (or up-) regulate situational epistemic curiosity levels. Indeed, using a modified version of the trivia question paradigm, behavioural data showed an inverse relationship between average surprise triggered in previous trials and epistemic curiosity ratings. Analysis of the fMRI data indicated that average surprise was monitored and updated during answer presentation by deactivation in the rostralateral PFC – a region previously linked to uncertainty-driven exploration – to regulate (i.e., reduce) upcoming curiosity levels. Likewise, during question presentation, high average surprise levels reduced the amplitude of responses in the salience (e.g., AIC) and executive control network (e.g., dlPFC, IPL) that might potentially signal post-processing activity or depletion of attentional resources according to the authors. Although some have argued that curiosity is a reward-seeking process where “information is reward” (Marvin & Shohamy, 2016), the predictive coding framework tested by Ligneul and colleagues (2018) characterises curiosity in terms of uncertainty. As such, high states of curiosity during the question presentation would not reflect the anticipation of more pleasurable outcomes, but the experience of more uncertainty. Likewise, activity during the answer presentation would be interpreted as relief- and/or surprise-related rather than in terms of reward processing. The authors further argue that stochastic relief of curiosity might be associated with a dopaminergic response whereas average surprise levels are likely to be signalled by noradrenaline which is well suited to mediate the interplay between surprise and memory. Intriguingly, both noradrenaline (Lawson et al., 2021) as well as dopamine (Gershman & Uchida, 2019) have not only been

discussed in the context of signalling uncertainty, but also in respect to curiosity-motivated learning (Sakaki et al., 2018).

If uncertainty is a key driver behind curiosity as indicated in previous fMRI studies as well as our findings (Duan et al., 2020; Jepma et al., 2012; Ligneul et al., 2018; van Lieshout et al., 2018), could curiosity-motivated learning also be better characterised in terms of learning under uncertainty than as reward-based learning? To answer this question, more research is needed. Information reducing uncertainty is likely associated with a dopaminergic neural response (Duan et al., 2020; Jepma et al., 2012; Ligneul et al., 2018). However, as discussed elsewhere (Ligneul et al., 2018), such a dopaminergic response in and of itself cannot be interpreted as evidence favouring reward over predictive coding frameworks. Indeed, recent results (Duan et al., 2020; Murphy, Ranganath, et al., 2021) have linked curiosity-motivated learning to brain areas associated with the update of internal models of the environment (e.g., anterior cingulate cortex and precuneus), further supporting the idea that curiosity-motivated learning can (partly) be explained using the predictive coding framework. Because the AIC is not only linked to uncertainty through lack of knowledge but also associated subjective feelings (T. Singer et al., 2009), it might be a promising candidate in signalling curiosity and supporting curiosity-motivated learning.

While more research is necessary to fully understand the role of the AIC in curiosity-motivated learning, our results suggest that the IS-RSA could be caused by similar brain activity related to the context-based prediction errors and surprise triggered by the violation of expectation in magic tricks as a state of uncertainty, creating a salient signal that could be mirrored in the curiosity ratings and influence encoding. Importantly, the AIC might also be a hub where dopaminergic and noradrenergic signals converge, potentially supporting curiosity-motivated learning. Future research is needed to determine whether similar processes also apply in the context of information-based prediction errors within the trivia question paradigm.

There is More to it than Meets the ROIs

In the analysis of data stemming from the task reflecting encoding processes as well as from the post-encoding rest reflecting early consolidation processes, a hypothesis-driven approach was applied by focusing on *a priori* defined regions-of-interest (ROIs). Based on previous research (Gruber & Ranganath, 2019; Lisman et al., 2011; Miendlarzewska et al., 2016), we primarily focused on the anterior HPC (aHPC) and VTA/SN, together forming the HPC-VTA-loop, but also included the caudate nucleus and the nucleus accumbens in part of the analysis of the encoding data. Research on curiosity is still fairly young and models trying to explain its effects on memory are scarce. However, Gruber and Ranganath (2019) made a compelling attempt to summarise the literature on the effects of curiosity on memory

within the PACE framework whereby curiosity is elicited by PEs (signalled by HPC and anterior cingulate cortex) and a state of uncertainty. This uncertainty triggers appraised processes of coping abilities in the lateral prefrontal cortex that determine actions and subjective feelings in response to uncertainty (i.e., anxiety or curiosity). The lateral PFC is then assumed to stimulate dopamine release in the VTA/SN associated with curiosity, in turn stimulating information seeking and encoding. In fact, the idea that curiosity *per se* is associated with the release of dopamine has stabilised itself since the first finding of a linear increase of activity in the striatum as curiosity increases (Kang et al., 2009). However, in line with the information gap theory of curiosity (Loewenstein, 1994), Kang and colleagues (2009) operationalised curiosity in a manner that is associated with the anticipation of rewarding information. While amounts of literature suggest that information indeed is an intrinsic reward with similar motivating properties as found for extrinsic rewards (Bromberg-Martin & Hikosaka, 2009; FitzGibbon et al., 2020; Lau et al., 2020; Marvin & Shohamy, 2016), a too narrow fixation on curiosity as anticipation of rewarding information might be an oversimplification.

However, subsequent fMRI research in the field of curiosity-motivated learning continued to conceptualise curiosity implicitly in this manner (Gruber et al., 2014; Poh et al., 2021). These studies have led to valuable insights on how *anticipatory* dopaminergic activity in the HPC-VTA-loop during high states of curiosity benefits the later encoding of information. Because information is a reward (FitzGibbon et al., 2020; Marvin & Shohamy, 2016), it is not surprising that brain areas active during the anticipation of information overlap with brain areas activated during the anticipation of extrinsic rewards (Knutson, Adams, et al., 2001; Knutson et al., 2000). Crucially, this anticipatory dopaminergic activity can be found because the rewarding information will indeed be delivered and the dopaminergic response is transferred to the earliest reliable cue of reward delivery (Schultz, 1998; Tobler et al., 2005), i.e., the presentation of the curiosity-eliciting cue.

This “artefact” of the design, a mere result of conceptualising curiosity as associated with the anticipation of rewarding information and hence a dopaminergic response, should not be confused with a characteristic of curiosity in and of itself as done in influential work in the field (Gruber et al., 2019; Gruber & Ranganath, 2019). In fact, doing so intermixes distinct components of the reward-learning framework of autonomous knowledge acquisition (Murayama, FitzGibbon, et al., 2019) proposing that the subjective feeling of curiosity (i.e., state of uncertainty related to a perceived gap in one’s knowledge) is different from subjective feelings associated with acquiring the knowledge that satisfies the curiosity (often termed interest). If curiosity is operationalised as the anticipation of rewarding information, delivered in 100% after a fixed/predicted interstimulus interval (as done by Gruber et al., 2014; Kang et al., 2009; Poh et al., 2021), the rewarding response associated with the delivery of information is transferred to the time point of curiosity elicitation, thereby facilitating premature or incomplete

conclusions about the nature of curiosity. Indeed, other research that either implemented variable delays between the elicitation and satisfaction of curiosity (Duan et al., 2020) or relieved curiosity in a stochastic manner (Jepma et al., 2012; Ligneul et al., 2018) found dopaminergic activity, not during the elicitation, but instead during the satisfaction of curiosity.

Overall, this suggests that curiosity *per se* might not be associated with the release of dopamine, but rather that certain circumstances when curiosity is associated with the anticipation of rewarding information may elicit this response. In fact, the elicitation of curiosity has repeatedly been linked to other, non-dopaminergic brain areas like the inferior parietal cortex or more broadly the default mode and fronto-parietal network (Duan et al., 2020; Murphy, Ranganath, et al., 2021; van Lieshout et al., 2018). In line with that, we also found that curiosity, in absence of effects within the HPC-VTA-loop, is mirrored by activity in brain areas that could be more closely associated with a state of uncertainty. As such, this interpretation might be closer to the current working definition of curiosity as a motivational state towards reducing uncertainty (Gruber & Ranganath, 2019). However, the PACE framework, whilst based on this working definition of curiosity, could further be extended by including brain areas that process (rather than detect or appraise) the uncertainty underlying curiosity. Since there is still so much we do not know about curiosity and its neural mechanisms, a premature focus on a single underlying mechanism related to dopamine and associated brain regions in ROI analysis bears the danger that other contributing brain areas and mechanisms will be overlooked that could drive further advances and re-conceptualisations in the field. The same applies to curiosity-motivated learning: our results suggest that while curiosity-motivated learning is supported by activity in the HPC-VTA/SN loop during encoding, many more brain regions and networks are involved, further replicating findings by others (Duan et al., 2020; Murphy, Dehmelt, et al., 2021).

Curiosity is not the only source of intrinsic motivation and other factors, e.g., a sense of agency, have been discussed (Deci & Ryan, 1985). When manipulating agency using self-determined or forced choice in an intentional encoding paradigm, the opportunity to choose is associated with enhancements in declarative memory (Murty et al., 2015, 2019). Analysing fMRI data acquired during encoding, it has been shown that choice is associated with anticipatory activity in the striatum, that this anticipatory activity correlated with behavioural memory-facilitation effects, and also interacted with hippocampal activity during the presentation of stimuli that are later remembered compared to those that are later forgotten (Murty et al., 2015). This suggests that a sense of agency is associated with mesolimbic and hence possibly dopaminergic activity that facilitates encoding via mechanisms of consolidation. Indeed, it has been shown that while an effect of choice can be found in both, immediate as well as delayed memory, forgetting rates (a behavioural measure of consolidation) were lower in the choice compared to the forced condition (Murty et al., 2019). Further investigations showed that FC between HPC and

perirhinal cortex (a region important for object memory and object-based memory consolidation; Davachi, 2006; Vilberg & Davachi, 2013) did not increase following encoding, but was also correlated with striatal activity during the anticipation of choice trials (but not fixed trials); that increases in FC between HPC and perirhinal cortex predict the number of objects encoded in the choice condition; and that changes in FC between both regions mediated the relationship between choice-related striatal activity and memory (Murty et al., 2019). These results show that mesolimbic striatal activity (presumably dopaminergic in nature) is related to systems-level interactions during early consolidation between HPC and perirhinal cortex in support of the encoding of the stimuli that elicited the increased striatal (dopaminergic) engagement. This suggests that while neurobiological/cellular models of motivated learning implicate the memory-facilitation effects of items associated with the release of dopamine into the HPC-VTA/SN loop by dopaminergic influences on late LTP, (Lisman et al., 2011; Lisman & Grace, 2005; Shohamy & Adcock, 2010), the actual resulting effects on system-level consolidation (i.e., changes in FC between brain areas following or in prediction of learning) supporting the selective encoding of information associated with the increased dopaminergic response are not limited to HPC-VTA interaction, but could be reflected in changes in FC between other brain areas. Indeed, results showing that selective memory for incentivised items is supported by changes in FC between VTA and visual areas as well as HPC and visual areas (Murty et al., 2017) together with results that choice memory is supported by changes in FC between HPC and perirhinal cortex (Murty et al., 2019) allow for the exciting opportunity of involvement of other regions in curiosity-motivated learning than the FC between aHPC and VTA/SN investigated here. Indeed, ISFC using both regions as seeds revealed far-reaching interregional communication during encoding, not only during magic trick watching, but also in support of the effects of curiosity, memory, and CMLE, providing a long list of candidates that might support early consolidation processes.

Given the multiple-testing problem in fMRI research, an ROI approach is still vital to be able to identify effects in *a priori* ROIs that would otherwise not survive thresholding at whole-brain level to control for the false positive rate. Yet, this should not replace exploratory whole-brain analysis that can guide hypothesis generation in future research, especially when rather lenient thresholds are applied here to reduce informational waste in fMRI research (G. Chen et al., 2021). Similarly, data sharing, especially when accompanied by thorough description and validation together with the methods used to generate the datasets allows other researchers to reuse data for their respective research questions. Especially in the context of naturalistic stimuli, this is proven highly valuable because such complex, dynamic data can be analysed with a myriad of different approaches (DuPre et al., 2020; Sonkusare et al., 2019). We hope that by sharing the high-quality MMC Dataset produced and used in the course of this work will spark future

discoveries, both theory- as well as data-driven, related to curiosity and its effects on memory, both within and outside the HPC-VTA/SN loop.

The Blessing and the Curse of Naturalistic Stimuli

The aim of this work was to develop a new paradigm to investigate the effects of curiosity on encoding as well as its interaction with extrinsic motivation to (1) address some of the limitations of the trivia question paradigm, (2) contribute to the generalizability of effects, and related (3) use naturalistic, complex stimuli to reduce the gap between the laboratory settings and real-world cognition. The use of such dynamic stimuli, compared to “classic” static, reductionist ones, promises a better approximation to the complexity of the world we are living in, thereby offering insights into how the brain integrates stimuli and events in real life that do not occur in isolation but are embedded into a perceptual stream (Shamay-Tsoory & Mendelsohn, 2019; Sonkusare et al., 2019).

Because of these characteristics, naturalistic stimuli can be used to study cognitive concepts and functions that accumulate information over longer time scales as they improve the sensitivity of the fMRI signal to temporal patterns. (Hasson & Honey, 2012). Likewise, it has been argued that real-life cognition and information processing could be too complex to be captured with static, reductionist stimuli that are traditionally linked to the functional labelling of different brain regions. Using more complex stimuli, however, research may be able to better identify the distributed network architecture of cognitive functions (Bottenhorn et al., 2019). As such, naturalistic stimuli could be preferable when investigating cognitive functions that require information integration over given time spans. Indeed, it has long been argued that real-life memory is one of these functions (Neisser, 1991; Sonkusare et al., 2019). Naturalistic stimuli not only evoke complex, multimodal cognitive processing but also elicit strong emotions (Saarimäki, 2021), making them prime candidates to investigate the interplay between affect and cognition. Indeed, using tightly controlled stimuli with short presentation times and static content, many core questions in neuroscience are difficult to answer (Nastase et al., 2019).

To elicit curiosity, we used short video clips showing magic tricks rather than presenting static trivia questions. In trivia questions, the elicitation of curiosity constitutes a single, isolated event (Murayama, 2022) independent of previous events (cf. Fastrich & Murayama, 2018). In magic tricks, on the other hand, curiosity is elicited as events unfold which may be closer to how curiosity is experienced in real life where curiosity can be seen as a dynamic process (Murayama, 2022). Put differently, naturalistic stimuli allow studying the evolution of curiosity over time that is potentially supported by many brain areas (Gruber & Ranganath, 2019). Additionally, because curiosity can be conceptualised as an epistemic emotion (Ozono et al., 2021; Pekrun et al., 2017; Vogl et al., 2019), it is tempting to

hypothesize that naturalistic stimuli also evoke epistemic emotions more strongly than their static counterpart as has been reported for other emotions (Saarimäki, 2021).

The use of naturalistic stimuli with higher complexity goes hand in hand with added complexity in the analysis of neural data acquired during their presentation. When using simple, static stimuli, the traditional univariate general linear model (GLM) analysis approach is often used. The GLM aims to model the time course of the experiment (i.e., the onset and duration of different events as well as of responses with regressors) to create a design matrix that is then convolved with the hemodynamic response function to estimate the slopes associated with each regressor for each subject individually. These regressors are then contrasted (e.g., for the contrast of remembered compared to forgotten trials) to create contrast maps for each subject that are used as input for analysis at the group or sample level. This approach is powerful if (a) the time course of the experiment including its stimuli can be modelled and (b) the hemodynamic response function fits the response brain response well.

This GLM approach is well suited for parametric experimental designs where stimuli are well controlled. In the trivia question paradigm, during each trial, a trivia question followed by its answer is presented. As such, when contrasting trials eliciting high vs. low states of curiosity or those that were later remembered vs. forgotten, in the GLM analysis, the high level of control with respect to the stimuli (in both cases, written words presented at the centre of the screen are compared), allows attributing any differential brain activity to the construct in question (i.e., curiosity or encoding) because the stimuli are designed to not differ in other aspects. With dynamic stimuli like the magic tricks used in this research, however, the individual videos might differ considerably from each other (e.g., in terms of the materials used in the trick) in addition to the degree to which they elicit curiosity or are encoded and are hence less suited for a 'localist' approach based on trial averaging (Hasson & Honey, 2012; Nastase et al., 2019; Sonkusare et al., 2019).

Likewise, in the context of naturalistic stimuli modelling the onset and duration of events embedded in a dynamic stream can be challenging, partly because of the mere definition of what actually constitutes an event and what associated onsets and durations are. A core benefit of using naturalistic stimuli lies in their underlying narrative where events somewhat seamlessly transition. Indeed, the lack of sufficiently sparse events that can be clearly separated further limits the applicability of traditional GLM approaches because overlapping events cannot be statistically separated, further limiting the design efficiency and statistical power of the experiment (Sonkusare et al., 2019; Wager & Nichols, 2003). Further complicating such matters, different brain areas along the cortical hierarchy have been found to process events in dynamic stimuli on different time scales (Baldassano et al., 2017). Hence, the way events are defined might favour the detection of activity in certain brain areas because the modelled

BOLD time course would fit the brain areas better that process events on a time scale more similar to what has been used to model the experiment in the GLM approach.

While others have used short videos of magic tricks and analysed the data using GLM approaches where the whole video clip is considered a single event (Danek et al., 2015; Lau et al., 2020), potentially to circumvent such issues, modelling the whole magic trick as a single event can be problematic as noise follows 1/f distribution, making longer sequences (> 20s) noisier (Nastase et al., 2019). Importantly, the magic tricks videos used here range from 20 - 60 s in duration. Taken together, the usage of GLM approaches did not seem to constitute an appropriate analysis strategy for the magic trick stimuli used in this work and more broadly show why model-free, data-driven approaches often dominate when analysing fMRI data stemming from naturalistic paradigms (Sonkusare et al., 2019).

One of these model-free frameworks is intersubject synchronisation (Hasson et al., 2004; Nastase et al., 2019; Nummenmaa et al., 2018): it is based on the assumption that given the same external input, brain areas associated with its processing would synchronise (i.e., linearly correlate) across subjects. More specifically, the time course of each voxel in a participant is correlated with the time course of the same voxel in all other participants. As such, ISC analysis can be seen as a specific case of the GLM approach where the response in a given brain area in one subject is used to predict the response in the same brain area in another subject (Nastase et al., 2019). However, there are some conceptual limitations to be taken into consideration. Firstly, because ISC is stimulus-driven, it is strongest in the associated sensory cortices. However, if a narrative is present, higher-order cortices supporting higher-order cognitive functions like semantic processing also show significant ISC (Kauttonen et al., 2018). As such, ISC can also identify “similarity of the contents of consciousness across individuals” potentially promoting a shared understanding of the environment (Nummenmaa et al., 2018, p. 12). In either case, significant ISC does not mean that a region is activated by the stimulus but instead that the region encodes information about the stimulus in a consistent manner across subjects that can be caused by increases or decreases in brain activation (Nastase et al., 2019). As such, ISC only captures consistent, shared responses. More specifically, brain activity and fluctuations therein have to roughly align temporally (i.e., fluctuations share onset, phase, and amplitude) as well as spatially (i.e., anatomical-functional mapping of voxels) across participants in order to result in significant ISC. This means that brain regions that encode information about the stimuli will not be picked up in ISC analysis if they do so in a way that is individualised rather than consistent. Further complicating such matters, ISC is limited to shared responses that can be described in a linear fashion, but not non-linear shared responses. This limitation can partially be overcome using IS-RSA (Finn et al., 2020; Nummenmaa et al., 2012) where idiosyncratic response patterns are linked to behavioural measures (however, again in a linear manner).

Another issue arises from the fact that ISC is computed using correlation coefficients that are inherently unsuitable to establish causality. Using traditional event-related fMRI designs and GLM approaches, on the other hand, it is possible to identify brain regions that respond to the experimental manipulation where a change in condition (e.g., treatment vs. control) is causally related to a change in the brain response. Importantly though, as discussed above, the inverse effect that activity in a brain area is causally linked to the phenomenon or cognition in question, is not possible without neurostimulation or pharmacological studies.

To link these ISC maps to behavioural data, the similarity of behavioural effects is computed across participants to identify clusters where the similarity in brain response is predicted by similarity in the behavioural response (using IS-RSA). As such, the overall analysis approach is vastly different for static compared to dynamic stimuli, making it challenging to attribute differential effects to the mere nature of the stimuli as it is confounded with the analysis approach. Indeed, studies that used a GLM and ISC approach to analyse the same dataset found different effects (Hasson, Furman, et al., 2008; Jääskeläinen et al., 2016). Further complicating such matters, there are large degrees of freedom associated with both approaches in terms of how the experimental time course is modelled within the GLM (Botvinik-Nezer et al., 2020) but also in terms of which time course or volumes are selected to compute the ISC (Jääskeläinen et al., 2016) as ISC can vary from moment-to-moment as a function of internal states (Nummenmaa et al., 2012). It is hence likely that the results would have been different if rather than selecting the whole time course of the magic trick, our analysis would have focused on e.g., the occurrence of surprising, unpredicted events.

In a similar vein, activity in the brain supporting encoding might only occur during parts of the magic tricks and could differ throughout its time course. For instance, when encoding dynamic stimuli, early and late online encoding processes have been identified (Ben-Yakov & Dudai, 2011). Likewise, it has been shown that surprise during naturalistic viewing predicts neural event segmentation (Antony et al., 2021) and event boundaries in higher order cortices including the PCC and angular gyrus, in turn, predict an increase in hippocampal activity starting already slightly before the event boundaries (Baldassano et al., 2017), potentially reflecting the transfer of information from short- into long-term memory (Kurby & Zacks, 2008). The hippocampal response during an event boundary increases with boundary salience and also occurs independent of the angular gyrus event boundaries and hippocampal response is specific to event boundaries in continuous narratives over multiple minutes to hours (Ben-Yakov & Henson, 2018). According to the Event Segmentation Theory (Zacks et al., 2007), such event boundaries correspond to perceptual PEs in the narrative and information presented at event boundaries is more likely to be encoded. Such considerations have inspired research focusing on offline activity, i.e., brain activity following the presentation of dynamic stimuli (compared to online activity during the

stimulus presentation). To investigate offline hippocampal activity and its relation to successful encoding, Ben-Yakov and Dudai (2011) presented short video clips (4-16s) to participants, followed by short rests (8-16s) and showed that that increased activity in the HPC (as well as the dorsal striatum) following the offsets of short video clips (4-16s), which predicted the encoding thereof rather than online activity during encoding. Subsequent studies linked the degree of hippocampal offline activity to overall memory performance and showed that the offset activity is triggered by the offset of a cohesive event regardless of whether this is followed by rest or another short video clip. However, hippocampal offset activity is attenuated by subsequent events compared to rest, suggesting that event boundaries trigger encoding in a manner sensitive to retroactive – but not proactive – interference (Ben-Yakov et al., 2013). The offset response in the HPC further decreases when the same short clip is viewed multiple times, suggesting that the offset activity might be novelty-related (Ben-Yakov et al., 2014) which could interact with curiosity-motivated learning. In our analysis, we focused on online activity during encoding, ignoring activity prior to and following encoding, allowing us to focus on the same time course across all behavioural effects of interest, making them comparable across each other. However, investigating these “peri-encoding” time windows (reviewed by N. Cohen et al., 2015) is a promising target for future research to further enhance our understanding of the effects of curiosity on memory as it seems likely that clusters at (partly) different locations could have been observed in the IS-RSA for each behavioural effect of interest. The endless possibilities in which the task, but also the rest data could be analysed to enhance our understanding of curiosity and its influence on learning during encoding and consolidation motivated us to share the MMC Dataset for others to re-use.

Curiosity as an epistemic emotion is often highly correlated with other epistemic emotions like interest. It is therefore not surprising that curiosity and interest ratings are highly correlated, both in response to trivia questions (Fastrich et al., 2018) and also in response to magic tricks (Ozono et al., 2021). This is further amplified by the fact that there are no widely agreed upon distinct definitions for both constructs yet (Murayama, FitzGibbon, et al., 2019). It should be further pointed out that the operationalisation of curiosity assessment used here differs from what has been used previously: in previous studies using trivia questions and magic tricks, the curiosity assessments were directed towards the answer (e.g., Gruber et al., 2014) and solution (Ozono et al., 2021), respectively. Here, we focused more on assessing curiosity as a subjective feeling (i.e., “How curious were you while watching the magic trick?”) unrelated to the information resolving uncertainty. Likewise, no definition of curiosity was supplied to the participants, so the curiosity measures here are based on the participants’ naïve concepts of curiosity, i.e., an innate, positive, and active feeling related to an urge to think actively and differently, especially in the context of uncertainty (Aslan et al., 2021). As such, it is possible that curiosity could be confounded with other variables (e.g., surprise or interest) that could have influenced encoding on their

own merits. In fact, within the trivia question paradigm, it has repeatedly been shown that the effects of curiosity on memory are mediated by interest and surprise (Fastrich et al., 2018; Halamish et al., 2019; Ligneul et al., 2018). However, compared to the magic trick paradigm, an important distinction arises: in the trivia question paradigm, curiosity is measured in response to the question eliciting it whereas surprise and interest are measured in response to the answer satisfying curiosity. While still correlated, the elicitation of curiosity and the relief thereof are distinct, dissociable aspects of the knowledge acquisition process (Murayama, FitzGibbon, et al., 2019). The former captures the awareness of a knowledge gap and associated uncertainty and information-seeking behaviour, the latter refers to the actual knowledge acquisition and rewarding feeling associated with it. While curiosity, interest and surprise in relation to magic tricks have been shown to be highly correlated within and between participants (Ozono et al., 2021), we would argue that they all capture the same aspect in the knowledge acquisition framework. As has been said above, the use of naturalistic stimuli might come with accepting certain confounding issues because they offer less control to disentangle them. However, in the context of epistemic emotions, correlations between them are frequently observed (Fastrich et al., 2018; Ozono et al., 2021; Pekrun et al., 2017), so any confoundedness might be less of a problem, but more so reflect inherent characteristics of the construct, especially if derived from real-life curiosity. Nevertheless, future research should aim to assess related or confounded constructs to explore their influence on memory and knowledge acquisition more broadly.

The use of dynamic stimuli is beneficial in that they are less artificial and abstract compared to the well-controlled stimuli often used in event-related fMRI studies to isolate and localise targeted functions. But there is also weakness in that strength: magic tricks are less controlled, but thereby also less controllable within the analysis. Static trivia questions and their answers resemble learning lists (Stare et al., 2018). This kind of stimuli is often found in experimental research because it is fairly easy to control for in terms of, e.g., presentation time, number of words, or how frequent or common words are. Their downside is that learning in real life is more complex than this (Shamay-Tsoory & Mendelsohn, 2019; van Atteveldt et al., 2018). In the magic tricks, however, there are noticeable differences in between the videos, e.g., related to the duration of the tricks, the objects used, or whether only the magician or another person was shown, making them less well controlled. At the same time, because all magic tricks were taken from the same stimulus database and background as well as expression and clothing of the magician, has been controlled for and only magic tricks were selected specifically for the purpose of this study, e.g., by excluding any tricks relying on subtitles. Other aspects might be more difficult to account for because magic trick videos could be more prone to confounders compared to trivia questions. For instance, it is possible that the presence of a person picking a card – due to the social interaction aspect thereof – affects self-reported curiosity ratings and/or the encoding of that magic trick. Similarly, it might

be more difficult to induce large variances in the data with naturalistic stimuli, potentially because they are more engaging (Sonkusare et al., 2019). The trivia question paradigm lends itself well to pre-screening procedures to select stimuli eliciting high and low states of curiosity. In the magic trick paradigm, such procedures were not possible. While the fMRI data showed sufficient participant x stimulus variance as determined by variance decomposition of the behavioural data, there is yet less control compared to creating participant-specific stimulus sets containing high and low curiosity trivia questions. Likewise, the experienced curiosity might vary over the course of the magic trick, but only one rating was obtained per trick. In comparison, in the trivia question paradigm, a single rating for a static stimulus might portray the subjective curiosity experienced in a better manner. The use of dynamic stimuli inherently involves a trade-off between higher complexity of stimuli and experimental control. There is no one-fits-all solution to this conundrum, however, the kind of research question that is to be answered might give a reference point on where to position the design within this trade-off. If the aim is to localise specific cognitive functions with a narrow definition or to understand their mechanisms, it might be better to put a high emphasis on tightly controlled paradigms that bear little to no resemblance to cognition in the real world. If the aim is to test for the generalizability of effects found in controlled stimuli to less controlled stimuli or if we can accept that our effect of interest might be confounded with other effects to a certain extent (maybe because they often do co-occur and their strict distinction is not relevant for the practical application of this research), then naturalistic stimuli might be a better choice. Importantly, conducting studies on all ends of the spectrum of the trade-off is what will facilitate a well-rounded theory of cognitive function, both within the laboratory as well as in real life.

The question arises though whether tightly controlled or more naturalistic stimuli are better suited to investigate the interaction between intrinsic and extrinsic motivation on learning and memory. When developing the paradigm, our aim was to contribute to translational research that can hopefully inform policy-makers in the future. The research on curiosity and its effects on memory, including the underlying neural mechanisms, are tightly linked to educational neuroscience, i.e., the cognitive study of learning and development that applies neuroimaging methods to (in)directly provide valuable insights to improve learning and teaching practices (van Atteveldt et al., 2018). To strengthen the relevance of such studies within the educational context, the use of naturalistic stimuli has been discussed, especially in the context of research targeting long-term memory and the integrating of new information into existing knowledge (van Atteveldt et al., 2018; van Kesteren et al., 2010). We used naturalistic stimuli that reliably elicit various degrees of curiosity combined with an incentive manipulation for a task associated with the material, hoping to reflect some contingencies of real-life educational learning that, due to its reliance on grades, is largely incentivised. It is important to note, however, that while magic trick videos as stimuli are more naturalistic than static trivia questions, they are not close to educational material either. Hence,

their ability to capture the knowledge acquisition process might be limited as knowledge acquisition does not have a clearly defined start and end point as newly acquired information is integrated into the existing knowledge and influences future information-seeking (Murayama, 2022). Future research could benefit from using full-length documentaries as stimuli to better track the acquisition of knowledge over a longer narrative. Indeed, first attempts in this area have been made: Cohen and colleagues (2018) presented educational videos to participants and used electroencephalogram recordings to compute ISC, showing that higher ISC was associated with better memory. Such approaches could also be used in the research of curiosity on memory by obtaining dynamic curiosity ratings throughout the presentation of documentaries or shorter educational video clips. While this study is a great example of how research can utilise material that is used in teaching contexts to investigate the neural underpinnings of its encoding, it did not offer insights on the mechanisms beyond assuming that neural engagement as a measure of attention correlates with learning. However, such stimuli combined with measurements of epistemic emotions show promising potential in understanding knowledge acquisition in the classroom.

Concluding Remarks

We would argue that the magic trick paradigm can be found more towards the naturalistic side of the continuum between controlled laboratory settings and real-life cognition, at least compared to the trivia question paradigm. However, the associated lack of tight experimental control when working with naturalistic stimuli means that they are less suitable to localise the underlying mechanisms of cognitive functions at a neural level. As such, if the focus of the research is to compare extrinsically and intrinsically motivated learning, static stimuli might be a better choice. However, it is important to note that inducing epistemic curiosity reliably within experimental settings is not trivial and only a limited amount of stimuli are suited for this (Ozono et al., 2021). As discussed, while trivia questions can reliably induce curiosity, the trivia question paradigm has inherent limitations, not only in terms of how it can be used to measure the effects of curiosity on memory but also in terms of how the interaction with extrinsic motivation can be studied because this either requires intentional encoding paradigms (Duan et al., 2020; Halamish et al., 2019) or the manipulation is combined with guessing tasks (Murayama & Kuhbandner, 2011; Swirsky et al., 2021).

Overall, it seems challenging to compare the effects of different kinds of rewards with each other, even outside the memory domain. Indeed, as we discussed elsewhere (Matyjek et al., 2020), rewards are multidimensional constructs and often differ in more than one domain. For instance, Lau and colleagues (2020) compared the effects of curiosity (elicited using trivia questions and magic tricks) and food items on risky decision-making. While curiosity and food as incentives differ in their source (intrinsic vs extrinsic), they also differ in their tangibility. This makes it difficult to attribute any differential effects to

the domain of interest because that domain is often confounded with other domains. With respect to their effects on learning, this means any unique neural effects for intrinsic and extrinsic rewards in support of encoding could be related to (partially) non-overlapping systems supporting both kinds of learning, but that does not mean that this is related to their source, but could also reflect their e.g., tangibility. If such confounders cannot be eliminated by design, researchers should at least acknowledge and discuss them.

As such, a lot more research and new paradigms are needed to investigate the commonalities and differences between curiosity- and extrinsically motivated learning. While the effects of curiosity on memory might be more straightforward, the effects of extrinsic motivation could depend more on the encoding strategy (intentional or incidental) and the actual contingencies (incentives or rewards) and temporal time frames between them. Hence, focusing on curiosity as an intrinsic driver of knowledge acquisition could present a safer, more generalisable recommendation towards policy-makers whereas the use of extrinsic motivation – due to the risk of undermining the effects of curiosity on encoding (Murayama & Kuhbandner, 2011; Swirsky et al., 2021) – should potentially be reserved to cases and situations where curiosity cannot be elicited.

That being said, at the same time, our western education system relies on grades, a form of extrinsic motivation, further complicating the matter. However, even if learning to solve mathematical equations was purely extrinsically motivated, succeeding therein (i.e., acquiring knowledge) would likely also generate intrinsic rewards (Murayama, 2022). On the other hand, due to the evolutionary benefit of intrinsic motivation, it is debatable whether pure intrinsic motivation exists (Kidd & Hayden, 2015; Murayama, 2022) and if so, whether it could be measured or manipulated in the lab. All in all, this suggests that a focus on the differences between extrinsic and intrinsic motivation might be misguided as the processes are not fully distinct, yet also not fully overlapping either. Therefore, to inform and improve learning and teaching practices, it might be beneficial to investigate how curiosity and other epistemic emotions can be used in conjunction with extrinsic incentives and rewards to maximise knowledge acquisition in students across the lifespan, potentially in personalised learning settings and approaches rather than a one-fits-all solution.

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Appendix

Appendix

Supplemental Experimental Procedures for MMC Dataset

Pre scanning online session

The following questions, questionnaires, and instructions for the working memory (WM) assessment were presented to the participants during the pre scanning online session implemented using PsyToolkit (Stoet, 2010, 2017) version 2.5.3 (<https://www.psychtoolkit.org/cgi-bin/psy2.5.3/survey?s=Y9a>).

Information on how this information is referred to in the dataset is added in square brackets and italics.

1. Before you proceed, please confirm that you fulfil the inclusion criteria by ticking all boxes. If you do not fulfil a criteria, please do not proceed and get in touch with the researchers (email: memo.pcls.phd@gmail.com).

[inclusioncheck.[1-7] in MAGMOT_raw_quest_data.csv]

- I am aged between 18 and 45.
- I am healthy and do not suffer from any chronic illness or psychiatric disorder.
- I am not taking any psychoactive drugs.
- I am not currently nursing, pregnant, or intending to become pregnant.
- I do not have cognitive impairments.
- I have normal or corrected hearing and vision (using contact lenses).
- I speak English fluently.

Demographics

1. How old are you? *[age in MAGMOT_demographics.csv]*
2. What is your date of birth? (DD/MM/YYYY) *[DOB in MAGMOT_demographics.csv]*
3. What sex has been assigned at birth? *[sex in MAGMOT_demographics.csv]*
 - Male
 - Female
4. What is your gender? *[gender in MAGMOT_demographics.csv]*
 - Male
 - Female
 - I describe my gender differently
5. What is your ethnic origin? *[ethnicity in MAGMOT_demographics.csv]*
 - White - British
 - Other White
 - Asian or Asian British - Bangladeshi
 - Asian or Asian British - Indian
 - Asian or Asian British - Pakistani
 - Asian or Asian British - Chinese
 - Other Asian background
 - Black or Black British - Caribbean
 - Other Black background
 - Mixed - White and Asian
 - Mixed - White and Black African
 - Mixed - White and Black Caribbean

Appendix

- Other Mixed background
 - Other Ethnic background
 - Not known
 - Information refused
6. Is English your first language? [*english in MAGMOT_demographics.csv*]
- yes
 - no
- a. At what age did you start learning English? [*ageEnglishAcquisition in MAGMOT_demographics.csv*]
7. What is the highest level of education you have completed? [*education in MAGMOT_demographics.csv*]
- Primary school
 - GCSEs or equivalent
 - A-Levels or equivalent
 - University undergraduate program
 - University post-graduate program
 - Doctoral degree
8. How many years of education have you received, including primary school? (12 = HS diploma, 15 = Bachelor's degree) [*yearsOfEducation in MAGMOT_demographics.csv*]
9. What is your employment status? [*employment in MAGMOT_demographics.csv*]
- Unemployed
 - Self-employed part-time
 - Self-employed full-time
 - Part-time employment within organisation/company
 - Full-time employment within organisation/company
 - Full-time student
 - Part-time student
- a. Which subject do you study? [*studySubject in MAGMOT_demographics.csv*]
10. Please specify your handedness. [*handedness in MAGMOT_demographics.csv*]
- left
 - right
 - both
11. Do you have normal or corrected vision? [*vision in MAGMOT_demographics.csv*]
- I have normal vision and do not need glasses or contact lenses.
 - I have corrected vision and am using glasses or contact lenses.
- a. You mentioned before that you have corrected vision. We are doing eye tracking inside the scanner which means that we cannot provide you with MRI goggles as wearing them

prevents us from being able to track your eyes. This means that you are only able to participate in the MRI study if your vision is corrected using contact lenses.

- I have corrected vision and CAN wear contact lenses for the MRI experiment.
- I have corrected vision and CANNOT wear contact lenses for the MRI experiment.

12. Please select the number that describes your health best. How would you describe your overall health, on a scale from 1 to 9 (1 = very poor health, 9 = excellent health)? *[health in MAGMOT_demographics.csv]*

13. Are you currently under a doctor's care for any of the following *[health_current.[1-4] in MAGMOT_raw_quest_data.csv]*

- Heart disease (including coronary artery disease, angina, and arrhythmia)
- Vascular disease
- Diabetes
- I am not under a doctor's care for any of the items listed above.

14. Have you EVER been told by a doctor or other health professional that you had... (please tick any that applies) *[health_ever.[1-4] in MAGMOT_raw_quest_data.csv]*

- Hypertension, also called high blood pressure
- Coronary heart disease
- A heart attack (also called myocardial infarction)
- Multiple sclerosis
- Parkinson's disease
- Neuropathy
- Seizures
- Any kind of heart condition or heart disease
- A stroke
- Arthritis, rheumatoid arthritis, gout, lupus, or fibromyalgia
- Emphysema
- Cancer or a malignancy of any kind
- High cholesterol
- Diabetes or sugar diabetes
- Poor circulation in your legs
- Irregular heartbeats
- Congestive heart failure
- Asthma
- Osteoporosis or tendonitis
- Ulcers
- Varicose veins or haemorrhoids
- Narcolepsy
- Sleep Apnoea or other sleep disorder
- I have never been told by a doctor or other health professional that I have any of the items listed above.

MRI screening

[screening_MRI.[1-19] in MAGMOT_raw_quest_data.csv]

Thank you for providing some demographical information. As next step, we would like you to go through the MRI screening form. Please make sure to give these questions due considerations.

Please read the following questions CAREFULLY and provide answers. For a very small number of individuals, being scanned can endanger comfort, health or even life. The purpose of these questions is to make sure that you are not such a person.

You have the right to withdraw from the screening and subsequent scanning if you find the questions unacceptably intrusive. The information you provide will be treated as strictly confidential and will be held in secure conditions.

If you answer "yes" to any of the questions, please email memo.pcls.phd@gmail.com the specific details. If you answer "yes" to any of the questions 1 to 7, you **cannot** be scanned without risking your health and safety and hence have to be excluded as study participant. Please do not proceed in that case.

- | | |
|--|--------|
| 1. Have you been fitted with a pacemaker or artificial heart valve? | YES/NO |
| 2. Have you any active implants, such as cochlear, ocular, penile implant? | YES/NO |
| 3. Have you ever had any metal fragments in your eyes? | YES/NO |
| 4. Have you ever had any metal fragments, e.g. shrapnel in any other part of your body? | YES/NO |
| 5. Do you have any drug infusion pump installed? | YES/NO |
| 6. Do you have any stimulators for nerves, brain or bone installed? | YES/NO |
| 7. Is there any possibility that you might be pregnant? | YES/NO |
| 8. Have you ever been diagnosed with any form of heart disease or thermoregulatory problem? | YES/NO |
| 9. Have you any surgically implanted metal in any part of your body, other than dental fillings and crowns (e.g. joint replacement or bone re construction)? | YES/NO |
| 10. Have you ever had any surgery that might have involved metal implants? | YES/NO |
| 11. Have you ever suffered from epilepsy? | YES/NO |
| 12. Do you have an intrauterine contraceptive device (IUD) installed? | YES/NO |
| 13. Do you wear transdermal patches that contain metal? | YES/NO |
| 14. Do you wear a filling, crown, dental post (entirely within the tooth) associated with root canal treatment, retainer, bridge, or braces? | YES/NO |
| 15. Are you using coloured contact lenses? | YES/NO |

- | | |
|--|--------|
| 16. Do you wear a hearing aid? | YES/NO |
| 17. Do you have any body piercings that you cannot, or are unwilling to, remove? | YES/NO |
| 18. Do you have any tattoos or permanent make-up? | YES/NO |
| 19. Are you claustrophobic? | YES/NO |

Questionnaires

Thank you for filling in the MRI screening form and providing some demographical information. Next we have some questionnaires. Please read all questions carefully and choose the answer that describes best how you feel. There are no correct or incorrect answers, so please just answer the questions as honestly as possible.

BIS BAS scale (Carver & White, 1994)

[BISBAS.[1-20] in MAGMOT_raw_quest_data.csv; BISBAS [score] in MAGMOT_scores.csv with scores [score] = inhibition, rewardresponsiveness, drive, funseeking]

Each item of this questionnaire is a statement that a person may either agree with or disagree with. For each item, indicate how much you agree or disagree with what the item says. Please respond to all the items; do not leave any blank. Choose only one response to each statement. Please be as accurate and honest as you can be. Respond to each item as if it were the only item. That is, don't worry about being "consistent" in your responses.

[options]

- very true for me
- somewhat true for me
- somewhat false for me
- very false for me

1. I worry about making mistakes.
2. Even if something bad is about to happen to me, I rarely experience fear or nervousness.
3. I go out of my way to get things I want.
4. When I'm doing well at something I love to keep at it.
5. I'm always willing to try something new if I think it will be fun.
6. It would excite me to win a contest.
7. When I get something I want, I feel excited and energised.
8. Criticism or scolding hurts me quite a bit.
9. When I want something I usually go all-out to get it.
10. I will often do things for no other reason than that they might be fun.
11. If I see a chance to get something I want I move on it right away.
12. I feel pretty worried or upset when I think or know somebody is angry at me.

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13. When I see an opportunity for something I like I get excited right away.
14. I often act on the spur of the moment.
15. If I think something unpleasant is going to happen I usually get pretty "worked up."
16. When good things happen to me, it affects me strongly.
17. I feel worried when I think I have done poorly at something important.
18. I crave excitement and new sensations.
19. When I go after something I use a "no holds barred" approach.
20. I have very few fears compared to my friends.

Need for cognition (Cacioppo et al., 1984)

[NeedForCognition.[1-18] in MAGMOT_raw_quest_data.csv, NeedForCognition in MAGMOT_scores.csv]

Please describe the extent to which you agree with each statement using a 9-point scale ranging from very strong agreement to very strong disagreement.

[options]

- very strong agreement
- strong agreement
- moderate agreement
- slight agreement
- neither agreement nor disagreement
- slight disagreement
- moderate disagreement
- strong disagreement
- very strong disagreement

1. I would prefer complex to simple problems.
2. I like to have the responsibility of handling a situation that requires a lot of thinking.
3. Thinking is not my idea of fun.
4. I would rather do something that requires little thought than something that is sure to challenge my thinking abilities.
5. I try to anticipate and avoid situations where there is likely a chance I will have to think in depth about something.
6. I find satisfaction in deliberating hard and for long hours.
7. I only think as hard as I have to.
8. I prefer to think about small, daily projects to long-term ones.
9. I like tasks that require little thought once I've learned them.
10. The idea of relying on thought to make my way to the top appeals to me.
11. I really enjoy a task that involves coming up with new solutions to problems.
12. Learning new ways to think doesn't excite me very much.
13. I prefer my life to be filled with puzzles that I must solve.
14. The notion of thinking abstractly is appealing to me.
15. I would prefer a task that is intellectual, difficult, and important to one that is somewhat important but does not require much thought.
16. I feel relief rather than satisfaction after completing a task that required a lot of mental effort.

17. It's enough for me that something gets the job done; I don't care how or why it works.
18. I usually end up deliberating about issues even when they do not affect me personally.

Fear of failure (Spence & Helmreich, 1983)

[FearOfFailure.[1-9] in MAGMOT_raw_quest_data.csv, FearOfFailure in MAGMOT_scores.csv]

For each statement, please indicate your level of agreement or disagreement.

[options]

- strongly disagree
- disagree
- uncertain
- agree
- strongly agree

1. When I start doing poorly on a task, I feel like giving up.
2. If given a choice, I have a tendency to select a relatively easy task rather than risk failure.
3. When I fail at a task, I am even more certain that I lack the ability to perform the task.
4. I often find that I am well prepared for success on a task, but I do not perform the task well under pressure.
5. I tend to put forth a great deal of effort into a task, but I often know that this effort is of poor quality.
6. Sometimes I think it is better not to have tried at all, then to have tried and failed.
7. When I am tackling a challenging task, I find that I am reminded of my previous failures.
8. I often avoid a task because I am afraid that I will make mistakes.
9. I find that I can learn to perform a task very well, but I "crack" under the pressure of the situation and often do not perform anywhere close to my potential.

Approach and avoidance temperament (Elliot & Thrash, 2010)

[ApproachAndAvoidanceTemperament.[1-9] in MAGMOT_raw_quest_data.csv, ApproachTemperament and AvoidanceTemperament in MAGMOT_scores.csv]

Please indicate how much you agree or disagree with each of the following statements by writing a number in the space provided. All of your responses are anonymous and confidential. Please select numbers according to the following scale:

1 = strongly disagree, 4 = neither agree nor disagree, 7 = strongly agree.

1. By nature, I am a very nervous person.
2. Thinking about the things I want really energizes me.
3. It doesn't take much to make me worry.
4. When I see an opportunity for something I like, I immediately get excited.
5. It doesn't take a lot to get me excited and motivated.
6. I feel anxiety and fear very deeply.

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7. I react very strongly to bad experiences.
8. I'm always on the lookout for positive opportunities and experiences.
9. When it looks like something bad could happen, I have a strong urge to escape.
10. When good things happen to me, it affects me very strongly.
11. When I want something, I feel a strong desire to go after it.
12. It is easy for me to imagine bad things that might happen to me.

Melbourne Curiosity Inventory – Trait form (Naylor, 1981)

[TraitCuriosity.[1-18] in MAGMOT_raw_quest_data.csv, TraitCuriosity in MAGMOT_scores.csv]

A number of statements which people have used to describe themselves are given below. Read each statement and then circle the appropriate number to the right of the statement to indicate how you generally feel.

There are no right or wrong answers. Do not spend too much time on any one statement but give the answer which seems to describe how you generally feel.

[options]

- almost never
 - sometimes
 - often
 - almost always
-
- I think learning “about things” is interesting and exciting
 - I am curious about things
 - I enjoy taking things apart to “see what makes them tick”
 - I feel involved in what I do
 - My spare time is filled with interesting activities
 - I like to try to solve problems that puzzle me
 - I enjoy exploring new places
 - I feel active
 - New situations capture my attention
 - I feel inquisitive.
 - I feel like asking questions about what is happening.
 - The prospect of learning new things excites me.
 - I feel like searching for answers.
 - I like speculating about things.
 - I like to experience new sensations.
 - [I fee] interested in things.

- I like to enquire about things I don't understand.
- I feel like seeking things out.
- I want to probe deeply into things.
- I feel absorbed in things I do.

Corsi

[corsiSpan in MAGMOT_scores.csv]

Introduction

Thank you for filling in the questionnaires.

As last part, we would like get a measurement of your cognitive abilities. First, we would like you to do the Corsi block tapping task.

In this implementation, we start with a sequence of 2 blocks. Once the sequence has been shown, you hear the word "go" (if you have your speakers on). You need to click with the mouse on the blocks in exactly the same order as shown before. When you are done, you click the green block "done". You get feedback (smiley face means you did it correct, or frowny face if you made a mistake). If you do it correctly, you go the the next higher number of blocks. If you do it wrong, you get once more chance. If you do it then wrong again, you get your score (the Corsi block span) and the task is over.

Instructions

In this task, you need a mouse.

You will see 9 blocks.

Some will "light" up (yellow) in a sequence. Once you hear "go", you need to click the same blocks in the same sequence. The sequences will increasingly get longer,

Press space bar when ready.

[Corsi task]

2-back

[nBack [score] in MAGMOT_scores.csv with scores [score] = hits, misses_inclTooSlow, misses_exclTooSlow, correctrejections, falsealarms_inclTooSlow, falsealarms_exclTooSlow, hitrate, falsealarmrate, accuracy]

Introduction

Thank you for doing the Corsi task. The last thing to do is a 2-back task.

There will be letters presented to you. You need to press the **m key** if the stimulus is the same as two trials ago, and the **n key** if not. The letters m and n are chosen for practical reasons (they can be easily remembered: m=memory, n=no).

You will start with a practice block followed by 4 task blocks in total. You will get feedback within the practice block, but not for the task blocks. You can take a break for as long as you like to between each of the blocks.

Once you are done with this task, please send an email to stefanie.meliss@pgr.reading.ac.uk with the completion code.

Instructions

1. 2-back working memory task

In this task, you will see a sequence of letters. Each letter is shown for a few seconds. You need to decide if you saw the same letter 2 trials ago, that is, this is a n=2-back task.

If you saw the same letter 2 trials ago, please press **M** (M for Memory). If it was not a letter shown two trials ago, please press **N** (N for No).

You need to press a button starting from the first letter presented.

press the space bar for next info screen

2. 2-back working memory task

We are going to start with a practice block with 20 trials. Afterwards, you will get some feedback on your performance.

The actual task consists of 4 blocks with 20 trials each.

Please feel free to take a break in between.

press the space bar for next info screen

3. 2-back working memory task

For example, these could be the letters and below the correct key press:

A B L B T R H R I
n n n **m** n n n **m** n

This is actually very difficult! So you need some time to get good at it. When you respond correctly, you see the bars around the letter turning green and red, if wrong.

press Q to start or arrow up to go back

Feedback after practice

Percentage of missed 2-back items: xx % of all presented 2-backs

Percentage false alarms of 2-back item: xx % of all presented non 2-backs

Press space to finish practice and start first task block.

There will be no more red and green feedback.

The instructions will be shown once more.

Break

2-back working memory task

Please take a break.

You need to decide if you saw the same letter 2 trials ago. If so, please press M (M for Memory). If it was not a letter shown 2 trials ago, please press N (N for no).

press Q for the next block

[2-back task]

Instructions for the magic trick watching task for the MRI session in the lab

Different sets of instructions were presented to the participant during (1) practice, (2) while they were inside the MRI scanner, and (3) an assessment outside the MRI scanner. The instructions during practice and inside the MRI scanner were presented using PsychToolBox (Brainard, 1997) on a black screen using “Courier” font in white (unless indicated differently). The assessment outside the MRI scanner was implemented using PsyToolkit (Stoet, 2010, 2017) version 2.5.3 (<https://www.psychtoolbox.org/cgi-bin/psy2.5.3/survey?s=JDPGx>). Instructions presented on the same screen are grouped together and in ascending order. Instructions were the same for both groups unless indicated differently. Text in square brackets was added to enhance readability, but not presented to the participant. They also contain information on additional communication with participants using the intercom from the scanner control room or when sequences were started.

Instructions presented during practice

1. 'Hello and welcome!

Thank you very much
for participating in the experiment.'

'(press any key to continue)'

2. 'We are going to practice
the actual task.

Do you feel ready?

We will show you the instructions.'

'(press any key to continue)'

3. 'In this experiment you will be presented
with a series of magic tricks.
The videos are without audio.

Your task is to carefully watch the videos
and try to figure out what has happened.'

'(press any key to continue)'

4. 'Before the start of each magic trick
you will see a fixation point.'

'(press any key to continue)'

5. 'Afterwards, you are asked to give an estimate of how many people (out of 100) are able to correctly figure out the solution to the trick.

Possible answers are the following:

0 - 10 people
11 - 20 people
21 - 30 people
31 or more people'

'(press any key to continue)'

6. 'In addition to that, we would like you to rate how curious you were while watching the magic tricks on a scale

from 1 (not curious at all) to 7 (very curious)'

'(press any key to continue)'

7. 'For each of the answers, you have 6 seconds.'

'(press any key to continue)'

8. 'To select the estimate you think is correct, you have to press the corresponding button on the button box.

Your INDEX finger is lies on the blue button corresponding to the answer "0 to 10 people".
Your MIDDLE finger is on the yellow button corresponding to "11 to 20 people".
Your RING finger lies on the green button corresponding to "21 to 30 people"
and your PINKIE lies on the red button corresponding to "31 and more people".'

'(press any key to continue)'

9. 'For the curiosity rating, you have to move the red number to the number representing your curiosity.

To move it to the left,
please use your index finger (blue button).

To move it to the right,
please use your middle finger (yellow button).

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To confirm your selection,
please use your pinkie (red button).'

'(press any key to continue)'

10. 'You will see both the answer and
the rating screen to show you
how it looks like.

After you have indicated your answer and
your rating, the coloured ink will turn white
and you simply wait for the task to continue.'

'(press any key to continue)'

11. 'This is how it is going to look like:'

[Example rating answer]

'How many people (out of 100)
are able to correctly figure out the solution?'

'0 - 10	11 - 20	21 - 30	31 or more
[in blue	in yellow	in green	in red]
'(index finger)	(middle finger)	(ring finger)	(pinkie)'

'(press any key to continue)'

12. 'This is how it is going to look like:'

[Example rating curiosity]

'Please rate how CURIOUS
you were while watching the trick.'

'1	2	3	4	5	6	7'
(not at all)						(very)

'(press any key to continue)'

13. 'Do you have any questions?

Please just ask.'

'(press any key to continue)'

14. 'You will see two magictricks
during the practice.

In the actual experiment,
there will be 36 magic tricks.'

'(press any key to continue)'

15. 'The practice starts NOW.'

You are asked to estimate
how many people are able to correctly find
the solution to the magic trick.'

'(press any key to continue)'

[practice]

16. 'The practice is over now.'

Do you have any questions?'

'(press any key to EXIT)'

Instructions presented during the MRI scanning

Introduction

[check in with participant via intercom to tell them to read and follow the instructions on the screen]

1. 'Hello and welcome!

Thank you very much
for participating in the experiment.'

'(press any key to continue)'

2. 'Do you feel comfortable?

If you would like to, you can have
a little wiggle to make
yourself even more comfortable.

For the scanning, it is very important
that you do not move your head.

So please try to find a position
that is as convenient as possible.'

'(press any key to continue)'

3. 'We are going to run
a short localizer sequence.

Please keep your head as still as possible
and continue reading.'

'(press any key to continue)'

[Localizer scan starts]

4. 'With the next sequence,
we are measuring your brain activity at rest.

The scan will last for approximately 10 min.
You will see a white screen.

Please keep your eyes open
and simply look at the white screen.
You are allowed to blink as usual.

Please try to NOT think about anything at all.'

- '(press any key to continue)'
5. 'Do you have any questions?'

Please just ask.'

'(press any key to continue)'

[check in with participant via intercom to repeat the instructions verbally and clarify any questions]

6. 'To remind you:

Please keep your head as still as possible
and do not cross your legs or your arms.'

'(press any key to continue)'

Pre-learning rest

1. 'The screen will turn white shortly.

Please keep your eyes open
and try not to think about anything.'

'scanning is starting, waiting for trigger'

[white screen presented for 10 minutes; EPI sequence]

2. 'EXPERIMENTER INPUT:
continue or abort'

Task

[check in with participant via intercom and offer of a break]

1. 'Do you feel okay?'

Next, we are going to do
the actual experiment.

Do you feel ready?'

We will show you the instructions again.

It is going to be the same task

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we practised earlier.'

'(press any key to continue)'

2. 'While you are reading the instructions, we are running the fieldmap. So please keep your head as still as possible. There will be a screen asking you to wait so that someone can talk to you. Please do so once you get there.'

'(press any key to continue)'

[field map scan starts]

3. 'In this experiment you will be presented with a series of magic tricks. Your task is to carefully watch the videos and try to figure out what has happened.'

'(press any key to continue)'

4. 'Afterwards, you are asked to give an estimate of how many people (out of 100) are able to correctly figure out the solution to the trick.

Possible answers are the following:

0 - 10 people
11 - 20 people
21 - 30 people
31 or more people'

'(press any key to continue)'

5. 'In addition to that, we would like you to rate how curious you were while watching the magic tricks on a scale

from 1 (not curious at all) to 7 (very curious)'

'(press any key to continue)'

6. 'For each of the answers, you have 6 seconds. '

'(press any key to continue)'

7. *[Reward manipulation (presented in experimental group only)]*

'We ask you to answer the question
"how many people are able to find
the solution?" and you can get'
' an additional 50% bonus payment on top
of your payment for both tasks (GBP 30.00)
if you answer all questions correctly.
That means each correct answer
is worth an additional GBP 0.80' [presented in green]¹⁸

'Please press GREEN key (ring finger)
to confirm that you read this statement.'

- Block 1

1. 'Please wait.

Someone will talk to you shortly.'

'(press any key to continue)'

[check in with participant via intercom to repeat the instructions and reward manipulation in experimental group only verbally and clarify any questions]

2. 'In total, you will see 36 magic tricks.
These will be presented in 3 blocks.

There will be two breaks in between
so that you can rest and relax.

Please try not to move at all
while you do the task.'

'(press any key to continue)'

3. 'The experiment is ready to START.

You are asked to estimate
how many people are able to correctly find
the solution to the magic trick.'

¹⁸ 50% additional bonus payment should have translated to £0.40 per correct answer. However, no participant reported to notice this error.

- '(press any key to continue)'
4. 'To remind you:

Please keep your head as still as possible

and do not cross your legs or your arms.'

- '(press any key to continue)'
5. 'The fixation point will show up shortly.'

'scanning is starting, waiting for trigger'

[12 trials of magic trick watching task; EPI sequence]

- Block 2

1. 'Thank you,
the first block of the task is finished.

WELL DONE!

- '(press any key to continue)'
2. 'Please wait.

Someone will talk to you shortly.'

'(press any key to continue)'

[check in with participant via intercom and offer of a break]

3. 'Take a break for as long as you need to.

The next part of the experiment
will start as soon as you are ready.

The task is going to be
the same as in the previous block.'

- '(press any key to continue)'
4. 'Do you have any questions?

Please just ask.'

- '(press any key to continue)'
5. 'The experiment is ready to CONTINUE.'

You are again asked to estimate
how many people are able to correctly
find the solution to the magic trick.'

[Reward manipulation (presented in experimental group only)]
'[You can get] an additional 50% bonus payment on top
of your payment for both tasks (GBP 30.00)
if you answer all questions correctly.
That means each correct answer
is worth an additional GBP 0.80' *[presented in green]*

'Please press GREEN key (ring finger)
to confirm that you read this statement.'

- [presented in control group only]*
'(press any key to continue)'
6. 'To remind you:

Please keep your head as still as possible
and do not cross your legs or your arms.'

'(press any key to continue)'

*[check in with participant via intercom to repeat the instructions and reward manipulation in
experimental group only verbally and clarify any questions]*

6. 'The fixation point will show up shortly.'

'scanning is starting, waiting for trigger'

[12 trials of magic trick watching task; EPI sequence]

- Block 3

1. 'Thank you,
the second block of the task is finished.

WELL DONE!'

- '(press any key to continue)'
2. 'Please wait.'

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Someone will talk to you shortly.'

'(press any key to continue)'

[check in with participant via intercom and offer of a break]

3. 'Take a break for as long as you need to.

The next part of the experiment
will start as soon as you are ready.

The task is going to be
the same as in the previous block.'

'(press any key to continue)'

4. 'Do you have any questions?

Please just ask.'

'(press any key to continue)'

5. 'The experiment is ready to CONTINUE.

You are again asked to estimate
how many people are able to correctly
find the solution to the magic trick.'

[Reward manipulation (presented in experimental group only)]

'[You can get] an additional 50% bonus payment on top
of your payment for both tasks (GBP 30.00)
if you answer all questions correctly.

That means each correct answer
is worth an additional GBP 0.80' [presented in green]

'Please press GREEN key (ring finger)
to confirm that you read this statement.'

[presented in control group only]

'(press any key to continue)'

6. 'To remind you:

Please keep your head as still as possible

and do not cross your legs or your arms.'

'(press any key to continue)'

[check in with participant via intercom to repeat the instructions and reward manipulation in

experimental group only verbally and clarify any questions]

7. 'The fixation point will show up shortly.'

'scanning is starting, waiting for trigger'

[12 trials of magic trick watching task; EPI sequence]

Post-learning rest

1. 'The task is done, GOOD JOB!

Thank you very much for completing it.'

'(press any key to continue)'

2. 'Please wait.

Someone will talk to you shortly.'

'(press any key to continue) '

[check in with participant via intercom and offer of a break]

3. 'With the next sequence,
we are measuring your brain activity at rest.

The scan will last for approximately 10 min.
You will see a white screen.

Please keep your eyes open
and simply look at the white screen.
You are allowed to blink as usual.

Please try to NOT think about anything at all.'

'(press any key to continue)'

4. 'Do you have any questions?

Please just ask.'

'(press any key to continue)'

[check in with participant via intercom to repeat the instructions verbally and clarify any

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questions]

5. 'To remind you:

Please keep your head as still as possible
and do not cross your legs or your arms.'

'(press any key to continue)'

6. 'The screen will turn white shortly.

Please keep your eyes open
and try not to think about anything.'

'scanning is starting, waiting for trigger'

[white screen presented for 10 minutes, EPI sequence]

7. 'EXPERIMENTER INPUT:
continue or abort'

Questionnaire

1. 'Thank you.

We are nearly done.'

'(press any key to continue)'

[check in with participant via intercom, offer of a break and verbal explanation of how to do the questionnaire, start of T1 scan]

2. 'We will start the last scan now.
This is a structural image of your brain.
That means you do not have to do
anything at all.

It will take approximately 6 minutes.'

'(press any key to continue)'

3. 'To remind you:

Please keep your head as still as possible
and do not cross your legs or your arms.'

- '(press any key to continue)'
4. 'To prevent you from being too bored, we have prepared a questionnaire.

This questionnaire is about your opinion of the experiment.'

- '(press any key to continue)'
5. 'Each question can be answered on a scale from 1 (definitely disagree) to 7 (definitely agree). Similar to the curiosity ratings, you have to move the red number to the number reflecting your opinion.

To move it to the left, please use your index finger (blue button).

To move it to the right, please use your middle finger (yellow button).

To confirm your selection, please use your pinkie (red button).'

- '(press any key to continue)'
6. *[24-item questionnaire; each question presented on a single screen in random order; PostExpAssessment[1-24] in MAGMOT_raw_quest_data.csv; IMI [score] in MAGMOT_scores.csv with scores [score] = intrinsicMotivation, interest, taskEngagement, boredom, effort, pressure; compliance and ableToSee in MAGMOT_other_information.csv]*

[intrinsic motivation (from Elliot & Harackiewicz, 1996): items 1-3

task engagement (from Elliot & Harackiewicz, 1996): items 4-6

interest (adopted from Wigfield & Eccles, 2000): items 7-9

boredom (adopted from Pekrun et al., 2002): items 9-12

effort (Ryan, 1982): items 13-17

pressure (Ryan, 1982): items 18-22]

[answer scale]

1 2 3 4 5 6
7

Appendix

definitely	somehow	slightly	neither	slightly	somehow	definitely
disagree	disagree	disagree	disagree	disagree	agree	agree
	agree					
				nor	agree'	

'It was fun to do the experiment.'

'It was boring to do the experiment.'

'It was enjoyable to do the experiment.'

'I was totally absorbed in the experiment.'

'I lost track of time.'

'I concentrated on the experiment.'

'The task was interesting.'

'I liked the experiment.'

'I found working on the task interesting.'

'The experiment bored me.'

'I found the experiment fairly dull.'

'I got bored.'

'I put a lot of effort into this.'

'I did not try very hard\nto do well at this activity.'

'I tried very hard on this activity.'

'It was important to me to do well at this task.'

'I did not put much energy into this.'

'I did not feel nervous at all while doing this.'

'I felt very tense while doing this activity.'

'I was very relaxed in doing this experiment.'

'I was anxious while working on this task.'

'I felt pressured while doing this task.'

'I tried to find out how many people will be able to find the solution.'

'I was able to see the magic tricks properly.'

Instructions presented outside the scanner after scanning

Melbourne Curiosity Inventory – State form (Naylor, 1981)

[StateCuriosity[1-20] in MAGMOT_raw_quest_data.csv, StateCuriosity in MAGMOT_scores.csv]

A number of statements which people have used to describe themselves are given below. Read each statement and then circle the appropriate number to the right of the statement to indicate how you generally feel.

There are no right or wrong answers. Do not spend too much time on any one statement but give the answer which seems to describe how you generally feel.

[options]

- not at all
- somewhat
- moderately so
- very much so

1. I want to know more.
2. I feel curious about what is happening.
3. I am feeling puzzled.
4. I want things to make sense.
5. I am intrigued by what is happening.
6. I want to probe deeply into things.
7. I am speculating about what is happening.
8. My curiosity is aroused.
9. I feel interested in things.
10. I feel inquisitive.
11. I feel like asking questions about what is happening.
12. Things feel incomplete.
13. I feel like seeking things out.
14. I feel like searching for answers.
15. I feel absorbed in what I am doing.
16. I want to explore possibilities.
17. My interest has been captured.
18. I feel involved in what I am doing.
19. I want more information.
20. I want to enquire further.

Other post-experimental assessments

1. How many hours did you sleep last night? [*sleepLastNight* in *MAGMOT_other_information.csv*]
2. How many hours do you sleep on average each night? [*sleepAverage* in *MAGMOT_other_information.csv*]
3. Did you drink alcohol in the last 24 hours? [*alcohol* in *MAGMOT_other_information.csv*]
 - a. How much alcohol did you drink during the last 24 hours? [*alcoholAmount* in *MAGMOT_other_information.csv*]
4. Please share some of your thoughts and opinions regarding the study with us. [*comment_task[1-3]* in *MAGMOT_other_information.csv*]
 - Did you like the experiment? Why? Why not?
 - What do you think is the hypothesis behind the experiment?

Appendix

- Is there anything else you would like us to know?

Comments added by the experimenters after data collection added as comment_exp in MAGMOT_other_information.csv

[Items presented to experimental group only]

Choose one response that best describes how strongly each item applies to you:

1. I tried hard to increase my reward. [*rewardEffort in MAGMOT_other_information.csv*]
 - Strongly disagree
 - Somehow disagree
 - Slightly disagree
 - Neither agree nor disagree
 - Slightly agree
 - Somehow agree
 - Strongly agree
2. How much additional bonus for correct answers do you expect? [*rewardExpectations in MAGMOT_other_information.csv*]

Instructions presented in the memory test

Introduction

Dear participant

Thank you very much for accepting the invitation to participate in the second part of the MAGMOT study.

During this part, you will be asked to try to remember the magic tricks you have seen inside the MRI scanner a week ago.

This includes a cued recall where we will present you still images of each of the 36 magic tricks and ask you to briefly describe what has happened in the magic trick. Depending on your answers in the recall tests, we will categorize each magic trick you have seen in the first experiment as either remembered or forgotten. To enable us to do that, please try to be as distinct, specific and descriptive as possible when referring to the magic tricks.

Further, there will be a recognition test where you will see the same 36 still images and offered four choices to answer the question, "what happens in this magic trick?". You are asked to pick the correct answer and to indicate afterwards how confident you feel regarding your answer.

We estimate the duration of the task to be 45 min. You will receive additional course credit/monetary reward for your participation in this part of the study.

Recall

In the following trials, we will present you still images of the 36 magic tricks you have seen in random order. Please write down what has happened in the trick cued by the picture.

Again, please try to write down your answer as descriptive as possible, so that we are able to judge whether you recalled a specific magic trick or not.

If you cannot recall what has happened in the magic trick cued by the still image, please insert "no recall".

[36 cued recall trials]

Recognition

Thank you for completing the cued recall task.

Appendix

Next, there will be a recognition memory test. You will see the same images as before in random order and again, you are asked to correctly recall what has happened in the magic trick. This time, however, you will be offered with four answers and we would kindly ask you to pick the correct one. Afterwards, please indicate how confident you are regarding your answer. That means if you are certain that this is the correct answer, your confidence will be high whereas it is low in case you are guessing.

[36 recognition trials]

Questionnaire

Thank you for completing the recognition task.

You are nearly at the end of the experiment.

On the next page, there will be a short questionnaire. Afterwards, you will be debriefed and directed to the completion code.

Choose one response that best describes how strongly each item applies to you:

1. I slept between my participation in the first and second part of the study. *[sleepBeforeMemoryTest in MAGMOT_other_information.csv]*
 - Yes
 - No
 - a. If yes, how many hours did you approximately sleep in total between your first and second participation? *[sleepHours in MAGMOT_other_information.csv]*
2. When watching the magic tricks, I was aware that my memory of them will be tested later. *[memoryTestKnown in MAGMOT_other_information.csv]*
 - Definitely agree
 - Somehow agree
 - Slightly agree
 - Slightly disagree
 - Somehow disagree
 - Definitely disagree
3. When watching the magic tricks, I tried to encode them. *[memoryIntention in MAGMOT_other_information.csv]*
 - Definitely agree
 - Somehow agree
 - Slightly agree
 - Slightly disagree
 - Somehow disagree
 - Definitely disagree
4. Please answer the following statement **ONLY IF** you have been offered **additional £0.80 bonus per correct answer**. If you have not been offered additional bonus, please select "not applicable."

Did you believe that you would receive a bonus payment based on your performance? [*rewardBelief* in *MAGMOT_other_information.csv*]

- Definitely agree
 - Somehow agree
 - Slightly agree
 - Slightly disagree
 - Somehow disagree
 - Definitely disagree
 - Not applicable
5. I have experiences in producing magic tricks. [*magictrickExperience* in *MAGMOT_other_information.csv*]
- Very frequently
 - Frequently
 - Occasionally
 - Rarely
 - Very rarely
 - Never
6. There were no problems with the internet connection while I participated in the experiment. [*connection* in *MAGMOT_other_information.csv*]
- Definitely agree
 - Somehow agree
 - Slightly agree
 - Slightly disagree
 - Somehow disagree
 - Definitely disagree
7. Is there anything else you would like us to know? [*comment_memory* in *MAGMOT_other_information.csv*]

Debrief

Dear participant,

Thank you for completing the task.

The purpose of this study was to find out how curiosity and the availability of reward can influence memory performances. We hypothesise that both, reward and high levels of curiosity will have enhancing effects and lead to the magic tricks being better encoded. We further investigate the neural underpinnings of this phenomena which we expect to be mirrored in the reward network, medial temporal lobe and mid brain.

We manipulated the availability of reward in the following ways: Some participants were not offered any reward for finding the correct estimate on how many people are able to find the solution, while other participants were offered an additional £0.80 for each correct estimate on how many people are able to find the solution to the magic trick.

Appendix

We offered money to some of the participants to be able to look at the effect of the availability of monetary reward on memory. We asked you to rate your curiosity to determine how curiosity influences memory performances. We asked you to provide an estimate on how many people will be able to solve the magic trick to make sure that you are engaged in the task and pay attention to it. However, we never collected data on how many people are able to find the solution - therefore, there are no right or wrong answers to this question, and this was our cover story. We would like to apologise for any inconveniences caused by this. Out of courtesy, we pay the same bonus to all participants.

We would like to thank you again for participating in this experiment and supporting our research. If you have any additional questions, please do not hesitate to contact us.

Kind regards,

Stef Meliss (email: stefanie.meliss@pgr.reading.ac.uk) and Kou Murayama (email: k.murayama@reading.ac.uk)

Supplementary Analysis to Determine the Optimal Hemodynamic Response Function (HRF) Lag

Previous research has discussed different lags to account for the delay in the HRF (Hasson et al., 2004; Nastase et al., 2019; Zadbood et al., 2017), so there is no commonly applied correction to shift the time course by in the context of ISC. Here, intersubject pattern correlation (ISPC; J. Chen et al., 2017) - a data-driven approach was applied to determine the optimal lag (see Figure A3.1). In ISPC (also referred to as spatial ISC (Nastase et al., 2019)), the correlation of a spatially distributed response pattern (e.g., within a searchlight or ROI) at a given time point is computed across subjects. Computing ISPC leads to a time point by time point correlation matrix where the diagonal captures the reliability of the spatial response across subjects (isolating the stimulus-driven component that is shared across subjects) at each moment in time and the off-diagonal values represent intersubject reinstatement of response patterns from time point $t(i)$ at time point $t(j)$ (Nastase et al., 2019). Because the time course of what was displayed on the screen is known, the reinstatement patterns of certain critical volumes can be used to validate which HRF lag is most appropriate. More specifically, after applying different HRF lags, the observed reinstatement patterns can be compared to expected reinstatement patterns: if a fixation was shown at the consecutive time points $t(i)$ and $t(j)$, the intersubject reinstatement of $t(i)$ at $t(j)$ should be high. On the other hand, if a fixation volume at $t(i)$ was not followed by another fixation volume at $t(j)$, the intersubject reinstatement of $t(i)$ at $t(j)$ should be low.

To apply ISPC to our data, an initial concatenation step was carried out to reorder the volumes across subjects (Figure A3.1A). For each magic trick, four additional volumes before (1 TR fixation, 3 TRs mock video) and six additional volumes after the magic trick presentation (depending on jitter, 2-5 TRs fixation and 2-4TRs of rating, respectively) were selected (Figure A3.1B) and concatenated so that the final concatenated order of volumes remained invariant regardless of the pseudo-randomised order in which trials were presented (cf. Thomas et al., 2018). After the initial concatenation step, the timeseries consisted of 954 volumes. To determine the optimal HRF response lag, we were interested in the reliability and reinstatement of responses in the visual cortex (V2). The V2 mask was created based on the atlas by Glasser and colleagues (2016) of which the left and right second visual area were extracted before combining both and resampling them to EPI grid. The final V2 mask included 706 voxels. A leave-one-out approach was applied to compute ISPC where the response pattern in V2 in a subject at a single time point was correlated with the mean response pattern of all other subjects at all timepoints (Figure A3.1C, left). This procedure was repeated for all time points and subjects to create a 954 x 954 time point by time point correlation matrix for a given subject and the mean of all other subjects. The matrices were Fisher's z -transformed before computing the sample mean time point by time point correlation matrix (Figure A3.1C, right).

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The k^{th} upper and lower off-diagonals were extracted for $1 \leq k \leq 2$, hence values represent the intersubject reinstatement of the pattern observed at a given time point in the next volume or the after next volume. The upper off-diagonal shows the correlation between the subject response at volume $t(i)$ and the mean response of all other subjects at volume $t(i + k)$ whereas the lower off-diagonal shows the correlation between the mean response of all other subjects at volume $t(i)$ and the subject response at volume $t(i + k)$. In a next step (Figure A3.1D), each value extracted from the off-diagonal was labeled and categorised in correspondence to the selected volumes shown in Figure A3.1A. Additionally, the labels were shifted assuming different lags in the HRF response ($1 \text{ volume} \leq \text{HRF lag} \leq 6 \text{ volumes}$) and for each event category and HRF lag, data was averaged.

Analysis to determine the optimal lag focused on two events (outlined in black in Figure A3.1B): the fixation before the beginning of the video (one volume) and the first volume of fixation after the video. We predicted that the reinstatement of the fixation before the video (“pre fixation volume”) should be small at $k = 1$ (first volume of the mock video) and even smaller at $k = 2$ (second volume of the mock video). For the first volume of fixation after the video (“post fixation volume”), we hypothesized a high reinstatement at $k = 1$ (second volume of fixation after the magic trick) decreasing at $k = 2$ (either third volume of fixation or first volume of rating). As shown in Figure A3.1E, applying an HRF lag of 4 volumes when labelling the data best matches the predictions. Additionally, patterns in the upper and lower diagonal were largely similar ($r = .90$).

Supplementary Tables

Appendix

Table A2.1

Description of the magic tricks used as stimulus in the study

E/P?	Stim ID	Description	Recognition option 1	Recognition option 2	Recognition option 3	Recognition option 4
E	H10	Card that's split into four pieces is magically put back together.	The magician magically repairs split card.	The magician is able to split and put back together a card.	Without touching it, the magician is able to move the pieces of the cards further and further away from each other.	The magician places his hand over the card multiple times and each time a piece disappears.
E	H15	Magician is able to balance a toothpick on a deck of cards but the volunteer cannot.	The magician balances a toothpick on a deck of cards.	The magician pierces the deck of cards with a toothpick, but afterwards there is no hole.	The magician lets a card picked by the volunteer appear in the card box.	When the magician starts to shake the card box, toothpicks start to fall out of the box and the cards have vanished.
E	H16	Magician pours coke into glass from an empty can.	The magician pours coke into a glass from an empty can.	The magician is able to remove the dents from the can without touching it.	The magician pours coke into a glass and makes it disappear.	Although the can seems empty, the magician is able to pour sparkling water.
E	H17	The magician uses a guillotine to slice breadsticks, then asks the volunteer to put her finger in. He slices the breadstick but not her finger.	The magician uses a guillotine to slice breadsticks, but not the volunteer's finger.	The magician rejoins bread sticks which the volunteer sliced with the guillotine.	The magician places the bread sticks in the bag, when the volunteer looks into the bag the bread sticks have transformed into a bun.	The volunteer tries to slice breadsticks with the guillotine, but cannot do it.
E	H19	Magician places ball of paper in participants hand and sets it alight, revealing a red sponge ball.	The magician places paper in volunteer's hand and sets it alight, revealing a red sponge ball.	The magician lights matches without touching them.	The magician transforms matches into a lighter.	The magician presses a lit match into volunteer's hand without hurting her.

How Curiosity and Incentives Shape Memory Formation

E	H35	Volunteer signs card which the magician ends up pulling out of a Ziploc bag.	The volunteer signs a card which the magician subsequently pulls from a Ziploc bag.	While the magician is shuffling the deck of cards, all four aces start to appear in the Ziploc bag.	The magician puts all the cards into the Ziploc bag. After snapping their fingers the cards appear in the box and the bag is empty again.	The volunteer signs a card that is placed into the Ziploc bag, but then appears in the card box.
E	H36	Screw and bolt unscrew itself.	The nut is placed on the middle of the bolt by the volunteer and magically unscrews itself.	The magician shrinks the bolt, so that the nut does not stay on it any longer.	The magician places the nut in the middle of the bolt and it magically screws itself.	The magician bends the bolt by hand.
E	H37	Magician unscrews his finger and then shakes it back into place.	The magician unscrews his own finger and then shakes it back into place.	The magician claps his gloved hands, the gloves disappear leaving his hands bare.	The magician turns his gloves into mittens.	The magician detaches his thumb, but when he turns his hands, the thumb is reattached.
E	H7	Coin appears everywhere around the salt case.	The magician lets a coin appear everywhere around the salt shaker.	The magician changes the salt to water.	The magician wraps the salt shaker in the cloth and makes it disappear.	The salt shaker turns into a bottle.
E	K10	Safety pins magically interlock without breaking the seal.	The safety pins magically interlock without breaking the seal.	The safety pins magically double in size.	Although there are two safety pins at the beginning, they are magically melt together.	The magician uses the safety pins to create a little star.
E	K16 (s)	Volunteer selects and signs a card. Magician put it inside the deck and the signed card appeared on the top repeatedly.	The volunteer selects and signs a card that is placed in the middle of the deck, but then appears on the top of it.	The magician shuffles the cards and places them in front of him. When he taps the card with the pen, they spread out.	The magician covers the unsorted cards with a silk handkerchief. When the handkerchief is removed, each of the cards is marked.	The magician asks the volunteer to mark the cards using the pen. After he shuffles them, the volunteer's writing has disappeared from all of the cards.

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E	K18	Pack of cards comes out of a piece of paper.	A pack of cards appears from a single piece of paper.	The magician folds the sheet of paper smaller and smaller until it transforms into a pack of cards.	The magician splays out the cards more and more until they resemble bunting.	The magician turns the sheet of paper which now shows a bouquet of flowers.
E	K19 (1)	balls in a cup warps and turns into a toy rabbit.	The balls magically change their location and become a toy rabbit.	The print on the mug changes from a black Q10 to a red B2.	The red balls are placed under the mug and merge to become a form a larger ball.	The magician covers the mug and the red balls with a handkerchief. When he removes it, there is a tea pot with a red lid.
E	K2	The sweets from a page in a children's story book are poured out onto the table from it.	Green and golden sweets fall out of the pages of the book.	The sweets shown on the pages disappear.	Gummi bears fall out of the book.	Micky and Mini Mouse from the pages of the book are poured out onto the table as little biscuits.
E	K21 (1)	A card flips with a short hand gesture.	The magician flips the middle card over with a slight gesture and then changes the colour of the back of the card from blue to red.	The magician reduces a full deck of cards to only three cards.	The magician places a card between two other cards and makes it disappear.	The magician transforms three cards into a full deck.
E	K24	£10 note is transformed into a £2.	A £10 note is transformed into a £20 note.	The note is folded so small that it disappears.	The magician makes a note out of a flower.	The magician folds the →£10 note in a piece of paper and tears it. He reveals that the note is still intact afterwards.
E	K3	A magician has a leaf on which two ladybirds appear on either side before	The magician makes ladybirds appear and then disappear again.	The magician changes the shape of the leaf.	The magician takes the leaf and turns it into a box of flowers.	The magician changes the colour of the leaf several times.

E	K4	magically disappearing. The magician magically solves the rubix cube by spinning it in the air.	The magician solves the rubix cube by spinning it in the air.	The rubix cube levitates.	The rubix cube turns into a ball.	The magician shakes the rubix cube and it becomes all white.
E	S11	Magician pushes a cigarette through a coin and then reveals that there is no hole.	The magician pushes a cigarette through a coin and then reveals that there is no hole.	The coin and the cigarette melt into another, so that the cigarette becomes metal.	The magician pushes a cigarette through a coin, but after he has pushed it through, he reveals that the cigarette is a £10 note.	The magician uses the coin to slice the cigarette, but it is still intact afterwards.
E	S12	A hole is hole-punched into the corner of a card. The magician then moves the hole to a different corner and then reveals that it's actually a black spot on the card.	The magician punches a hole in the card. He then moves the hole from one corner to another before finally revealing that it is actually a black spot on the card.	The magician punches a hole into the card. This hole expands as the magician opens his fist.	The magician punches circular holes into the card, but after the card is turned, the punched holes have a square shape.	The magician punches a hole into the card, which then becomes a toy ladybird.
E	S15	Magician places ring on the stem of a glass without breaking it.	The magician places a ring on the stem of the glass without breaking it.	The magician places the glass upside down on the ring and covers it with a piece of silk. When he removes it, the ring is placed on the stem.	The magician puts the ring into the glass and starts tossing it around until the ring is around the stem.	The magician removes the glass and puts a ring on the stem before reattaching it.
E	S18	Magician pulls out 3 boxes with flowers in from a paper bag.	The magician pulls three boxes containing flowers from a paper bag.	The magician is able to hide his whole arm inside the blue paper bag.	The magician produces a rabbit out of the empty paper bag.	When the magician turns the bag inside-out the bag folds into a paper aeroplane.

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E	S21	Magician bends a spoon using fingers.	The magician detaches the head of a spoon by moving the handle up and down.	The magician detaches the head of a spoon by turning the handle clockwise and counter clockwise.	The magician bends the spoon only using his pinkie as a force.	The magician covers the spoon with a handkerchief. When he removes it, the spoon is bent.
E	S25	Handkerchief appears from bread.	The magician makes a silk handkerchief appear inside a bread roll.	The magician makes bread rolls appear in his hands.	The magician holds a bread roll in his left hand, which then appears in his right hand.	The magician makes a signed coin appear inside a bread roll.
E	S27	Magician pours water into cup from bottle and then pours the water into another cup but when he tips it upside down, no water spills out.	The magician pours water into a cup from the bottle and then pours the water into another cup but when he tips it upside down, no water spills out.	The magician pours water into a cup from the bottle, but when he tips it upside down, no water spills out.	Although the magician pours water into both cups, the water bottle seems to refill itself magically whenever the magician snaps his fingers.	The magician pours water into one cup, but the other cup is magically refilled.
E	S30	Magician pulls strings through a stick which makes the other string in the other stick move.	The magician pulls string through two sticks which appear to be connected. However he then reveals the two sticks are not connected at all.	The magician is able to join the two separated parts of the stick.	Without any movement, the magician lets the strings in the sticks dance in little circles around him.	The magician cuts a piece of string in several places and then magically puts it back together again.
E	S31	Magician places a pair of chopsticks into envelope and proceeds to crush the envelope and its contents into a paper ball.	The magician places chopsticks into an envelope, but is still able to crush the envelope and its contents into a paper ball.	The magician transforms the envelope into a -£10 note.	As the magician turns around the envelope, writing appears on it.	The magician folds the envelope multiple times until he reveals that it is a pair of chopsticks.

E	S9	Magician turns a deck of cards into a blank deck.	The cards magically change their appearance.	The magician covers the cards with a silk handkerchief. After the silk is removed, the cards are blank.	The magician shows a card and then pulls the correct card from a shuffled deck.	The cards spread across the table into a circle without being touched.
E	Trick20 (s)	The magician shows a metal nut and rope. It doesn't matter how many times he secures the nut with the rope, it always escape.	The magician shows the volunteer metal nut and rope. Although he secures the nut with the rope, it repeatedly escapes.	The magician ties a knot around the volunteer's wrist using the rope. After snapping his finger, the nut is tied in the rope, too.	The volunteer holds the nut in her hands which are then tied with the rope. When the magician removes the rope, the nut is no longer in the volunteer's hand but appears in the magician's pocket.	The magician ties rope around the nut, but is not able to remove it afterwards as it seems that the nut has shrunk.
E	Trick28	Magician links and unlinks several silver rings.	The magician links and unlinks several silver rings while they keep their shape.	Starting with small rings, the magician merges them so that there are less rings in total, but they are larger in size.	The magician firstly puts the rings around his arms, but after he turns around, the volunteer has them around their arms.	The magician links and unlinks several silver rings while the rings shape their appearance once they get linked.
E	Trick32 (l)	The magician makes a silver coin disappear and reappear several times.	The magician makes a silver coin disappear and reappear several times before it is transformed into a large coin.	The magician has a coin in each of his hands. They both end up in one hand.	The magician shows a silver and a copper coin. Every time he puts a coin in his pocket, the coin appears again in his hand.	The magician asks the volunteer for a coin. Then the coin magically bends inside the closed fist of the volunteer.
E	Trick37	An elastic band visually travels from finger to finger, then it travels again even when the fingers are	An elastic band visually travels from finger to finger.	The magician has an elastic band on his hand, which then magically ends up around the volunteer's hand.	The magician makes several star shapes using the two elastic bands and then produces a star shaped elastic band.	The magician has two elastic bands and tangles them up. They then become untwisted.

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		secured with another elastic band.				
E	Trick38	The magician closes his left fist around a silk, and makes it disappear. Then, he makes it appear from his right fist.	The magician closes one fist around a silk handkerchief and makes it disappear. Then, he makes it appear in his other hand.	The magician makes a little bird figure appear under the silk handkerchief.	The magician takes a coin from the volunteer and freezes it in the silk.	The magician closes his hand around a green silk handkerchief, but when he opens his hand, the silk is blue.
E	Trick4	The magician puts a mobile phone inside a balloon with a simple gesture of his hands.	The magician puts the mobile phone inside the balloon with a simple gesture of his hands.	As the magician blows up the balloon, the phone increases in size.	The magician blows up an orange balloon, then the phone flashes and the balloon turns yellow.	As the balloon deflates, the phones starts moving across the surface without the magician touching it.
E	Trick6 (s)	The classic cup and ball routine using only 1 cup and an egg.	The magician puts a ball under the cup, which then turns into a larger ball and then becomes an egg.	The magician puts the ball under the cup which then turns into an egg and then becomes a chicklet.	The magician puts the ball under the cup and makes it disappear.	The magician places a red ball underneath the cup, but when he lifts it up, it is an orange balloon.
E	Trick7 (s)	The magician gets the volunteer to hold a foam ball which then doubles in to two. He repeats the trick and they then turn into three.	The magician gets the volunteer to hold a foam ball, which he then transforms into two balls.	The magician places two foam balls in volunteer's hands. The foam balls then start to jump up and down of their own accord.	The magician places two foam balls in volunteer's hand and sets them alight, revealing two paper balls.	Two sponge balls turn into a cube.
P	H4 (l)	Magician has four coins and two cards. He places the coins in each corner of the table and places two cards on top of the two top coins. He picks up one of the two remaining coins and makes it disappear from his hand. and then reveals it is now underneath one of the cards with the other coin.				
P	K23	Magician puts a hole through the money bill but then reveals that the hole disappears.				

Note. “E/P?” specifies whether the trick has been presented during the experiment (E) or during practice (P). “Stim ID” refers to the unique name of each magic trick. In cases where long (l) and short (s) versions of the same magic trick exists, the version used here is indicated. The description

of the magic tricks stems from Ozono and colleagues (2021) where more information (e.g., name, credit, phenomena category, and materials) can be found and descriptions were taken there. The wording of the options for the recognition task has been piloted and tested in behavioural samples.

Appendix

Table A2.2

Description of video files used in this study

Stim ID	Duration	Marker	Timing	Description	Notes
H10	36.84 (30.84)	Time stamp of cue image	7.17	H10_cue.png	
		1. moment of surprise	18.2	The magician fixes 3/4 bits of the broken card.	
		2. moment of surprise	25.18	The magician fixes remaining bit of card.	
H15	37.88 (31.88)	Time stamp of cue image	7.15	H15_cue.png	
		1. moment of surprise	15.11	The magician balances a toothpick on a deck of cards.	
H16	39.6 (33.6)	Time stamp of cue image	7.2	H16_cue.png	Main moment of surprise is the third moment of surprise
		1. moment of surprise	19.22	The crushed can is brought back to its original shape.	
		2. moment of surprise	25.23	Metal lid of can is closed.	
		3. moment of surprise	29.23	The magician pours a drink out of the can into the glass.	
H17	52.6 (46.6)	Time stamp of cue image	6.24	H17_cue.png	
		1. moment of surprise	41.16	The magician cuts the bread sticks with a guillotine whilst the volunteer has a finger in there as well.	
		additional marker for 1. moment of surprise	43.19	The magician presents the volunteer's finger.	
H19	28.6 (22.6)	Time stamp of cue image	9.21	H19_cue.png	
		1. moment of surprise	21.22	The magician places ball of paper in volunteer's hand and sets it alight, revealing a red sponge ball.	
H35	43.64 (37.64)	Time stamp of cue image	9.05	H35_cue.png	
		1. moment of surprise	40.02	The volunteer signs a card which the magician subsequently pulls from a Ziploc bag.	
H36	42.4 (36.4)	Time stamp of cue image	8.09	H36_cue.png	

		1. moment of surprise	29.03	The nut is placed on the middle of the bolt by the volunteer and magically unscrews itself.
		additional marker for 1. moment of surprise	27.22	The nut is unscrewing itself.
H37	34.76 (28.76)	Time stamp of cue image	7.17	H37_cue.png
		1. moment of surprise	14.03	The magician "breaks" his finger.
		2. moment of surprise	19.03	The magician unscrews his finger.
		3. moment of surprise	24.03	The magician screws his finger back on.
		4. moment of surprise	30.22	The magician's finger appears normal again.
H4 (1)	63.04 (57.04)	Time stamp of cue image	7	H4_long_cue.png
		1. moment of surprise	25.03	The coin disappears.
		2. moment of surprise	26.23	The coin reappears under the card.
		3. moment of surprise	35.23	The coin disappears again.
		4. moment of surprise	37.05	The coin appears again.
		5. moment of surprise	54.22	The coin disappears.
		6. moment of surprise	59.16	All coins appear.
H7	39.84 (33.84)	Time stamp of cue image	7.08	H7_cue.png
		1. moment of surprise	15.2	The coin appears in the magician's hand.
		2. moment of surprise	22.21	The coin disappears from the magician's hand.
		3. moment of surprise	25.12	The coin appears beneath the saltshaker.
		4. moment of surprise	31.22	The coin disappears from magician's hand again.
		5. moment of surprise	35.23	The coin appears on the top of the saltshaker.
K10	29.4 (23.4)	Time stamp of cue image	7.22	K10_cue.png
		1. moment of surprise	9	The safety pins magically interlock.
		2. moment of surprise	11.1	The safety pins magically unlink.

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		3. moment of surprise	14.05	The safety pins magically interlock again.
		4. moment of surprise	16.11	The safety pins magically unlink again.
		5. moment of surprise	17.05	The safety pins magically interlock again.
K16 (s)	37.4 (31.4)	Time stamp of cue image	7	K16_short_cue.png The card that was marked by the volunteer appears on the top of the deck.
		1. moment of surprise	36.07	
K18	28.2 (22.2)	Time stamp of cue image	12.2	K18_cue.png
		1. moment of surprise	17.14	The magician makes a deck of cards fall from the pictures.
K19 (l)	37.8 (31.8)	Time stamp of cue image	9.11	K19_long_cue.png
		1. moment of surprise	19.08	A ball disappears from underneath the mug.
		2. moment of surprise	23.03	The ball appears in volunteer's hand.
		3. moment of surprise	31.01	Both balls disappear from magician's hand.
		4. moment of surprise	33.23	A bunny appears when the mug is lifted.
K2	33.2 (27.2)	Time stamp of cue image	6.1	K2_cue.png Main moment of surprise is the first moment of surprise
		1. moment of surprise	19.01	The magician makes fall candy out a book.
		additional marker for 1. moment of surprise	18.23	The first piece of candy falls out of the book.
		2. moment of surprise	26.21	The pictures of candy have disappeared from the book pages.
K21 (l)	49.76 (43.76)	Time stamp of cue image	38.1	K21_long_cue.png
		1. moment of surprise	22.08	The magician flips the cards so that the one in the middle is facing up while the others are facing down.
		2. moment of surprise	42.08	The magician changes the colour of one of the cards from blue to red.
K23	41.4 (35.4)	Time stamp of cue image	7	K23_cue.png
		1. moment of surprise	36.15	The magician puts a pen through the note and the hole disappears.
K24	30.2 (24.2)	Time stamp of cue image	8.15	K24_cue.png

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		1. moment of surprise	23.09	A £10 note is transformed into a £20 note (partially visible)
		additional marker for 1. moment of surprise	24.22	Notes is almost completely unfolded and visible.
K3	31.88 (25.88)	Time stamp of cue image	8.14	K3_cue.png
		1. moment of surprise	22.02	The magician makes ladybirds appear on a leaf.
		2. moment of surprise	27.15	Ladybirds disappear.
K4	37.16 (31.16)	Time stamp of cue image	11.15	K4_cue.png
		1. moment of surprise	21.2	The magician solves the rubix cube by spinning it in the air.
S11	30.4 (24.4)	Time stamp of cue image	6.13	S11_cue.png
		1. moment of surprise	16.13	The magician pushes a cigarette through a coin.
		2. moment of surprise	26.06	It is revealed that the coin is not damaged.
S12	47.88 (41.88)	Time stamp of cue image	8.24	S12_cue.png
		1. moment of surprise	24	The hole is moved from the top left to bottom left corner.
		2. moment of surprise	32.03	The magician moves the hole to the bottom left to bottom right corner.
		3. moment of surprise	44.19	The hole turns into a black dot and the magician shakes it off.
S15	37.96 (31.96)	Time stamp of cue image	7.1	S15_cue.png
		1. moment of surprise	34.08	The magician places a ring on the stem of the glass without breaking it.
S18	37.92 (31.92)	Time stamp of cue image	14.16	S18_cue.png
		1. moment of surprise	17.22	The magician pulls out first box from the bag.
		2. moment of surprise	23.08	The magician pulls out second box from the bag.
		3. moment of surprise	32.06	The magician pulls out third box from the bag.
S21	27.8 (21.8)	Time stamp of cue image	7.15	S21_cue.png
		1. moment of surprise	16.1	The magician bents a spoon without applying force. It is more clear moment.

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		additional marker for 1. moment of surprise	13.2	This is the first movement of finger and spoon.
		2. moment of surprise	24.05	The spoon breaks into two pieces.
S25	58.64 (52.64)	Time stamp of cue image	29.07	S25_cue.png
		1. moment of surprise	35.13	A red cloth disappears from magicians hand.
		2. moment of surprise	48.23	The cloth appears inside the bread roll.
S27	37.56 (31.56)	Time stamp of cue image	7.03	S27_cue.png
		1. moment of surprise	33.04	The magician pours the cup, but no water is coming out.
S30	31.16 (25.16)	Time stamp of cue image	23.01	S30_cue.png
		1. moment of surprise	27.08	The magician manipulates one string and with that also manipulates a second string that is not connected to the first one.
S31	27 (21)	Time stamp of cue image	18.01	S31_cue.png
		1. moment of surprise	19.23	The Magician can scrunch an envelope although chopsticks are inside it.
		additional marker for 1. moment of surprise	20	You can clearly see that the envelope is crushed.
S9	38.44 (32.44)	Time stamp of cue image	6.22	S9_cue.png
		1. moment of surprise	29.07	The front side of the deck changes from colourful to white.
		additional marker for 1. moment of surprise	30.11	The whole deck is visible.
Trick20 (s)	32.12 (26.12)	Time stamp of cue image	12.18	Trick20_short_cue.png
		1. moment of surprise	30.01	Although the magician secures the nut with a rope, it escapes.
Trick28	46.44 (40.44)	Time stamp of cue image	16.06	Trick28_cue.png
		1. moment of surprise	17.06	The magician links one ring to another.
		2. moment of surprise	25	The magician unlinks the previously linked rings.
		3. moment of surprise	31	The magician links two rings again.

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		4. moment of surprise	36.03	The magician links four rings together.
		5. moment of surprise	40.15	The magician links more rings together.
		6. moment of surprise	45.06	The magician displays all rings in a vertical line.
Trick32 (l)	52.92 (46.92)	Time stamp of cue image	10.24	Trick32_long_cue.png
		1. moment of surprise	15.22	The coin disappears.
		2. moment of surprise	18.17	The coin appears in the other hand.
		3. moment of surprise	24.24	The coin changes hands again.
		4. moment of surprise	31.19	The coin disappears again.
		5. moment of surprise	33.11	The coin appears other hand.
		6. moment of surprise	42.15	The coin appears in the magician's hand.
		7. moment of surprise	47.12	The coin turns into a bigger coin.
Trick37	52.28 (46.28)	Time stamp of cue image	11.18	Trick37_cue.png
		1. moment of surprise	24.2	An elastic band visually travels from finger to finger.
		2. moment of surprise	47.15	An elastic band visually travels from finger to finger, passing through the barrier.
Trick38	33.4 (27.4)	Time stamp of cue image	8.15	Trick38_cue.png
		1. moment of surprise	21	A green tissue disappears from the magician's hand.
		2. moment of surprise	26	The tissue reappears in other hand.
Trick4	53.8 (47.8)	Time stamp of cue image	37.15	Trick4_cue.png
		1. moment of surprise	40.23	The phone appears inside the balloon.
		additional marker for 1. moment of surprise	41.23	Here it can be seen fully.
Trick6 (s)	43.64 (37.64)	Time stamp of cue image	8.19	Trick6_short_cue.png
		1. moment of surprise	21.14	The ball appears under the cup.
		2. moment of surprise	32.18	A bigger ball appears under the cup.

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		3. moment of surprise	39.09	An egg appears under the cup.	
Trick7 (s)	26.6 (20.6)	Time stamp of cue image	9.03	Trick7_short_cue.png	Main moment of surprise is the second moment of surprise
		1. moment of surprise	22.04	A foam ball disappears from the magician's hand.	
		2. moment of surprise	24.17	The ball appears in volunteer's hand.	
		additional marker for 2. moment of surprise	25.07	Two balls are clearly visible.	

Note. For each magic trick, we included the duration (duration without the mock video), the marker and their associated timings, and descriptions for the moment(s) of surprise. The onsets of each of them have been added as markers in the PsychophysicsToolbox script and the experimental data files. All durations and timings are measured in seconds. As in the previous table, “Stim ID” refers to the unique name of each magic trick. In cases where long (l) and short (s) versions of the same magic trick exists, the version used here is indicated.

Table A2.3

Variable Dictionary for Behavioural Dataset

Variable	Explanation
ID	subject ID
BIDS	BIDS identifier
group	group: exp = experimental, cont = control
orderNumber	number of trial order task
block	task block
acq	acquisition within block
startBlock	time stamp (in secs) start of block
endBlock	time stamp (in secs) end of block
timingCorrection	half of the flip interval applied as timing correction (in secs) in PTB script
jitterVideo_trial	intended jitter interval (in secs) after magic trick display
jitterRating_trial	intended jitter interval (in secs) after curiosity rating
stimID	magic trick stimulus ID
vidFileName	file name of magic trick video
trial	trial number in magic trick task
tTrialStart	time stamp (in secs) start of trial
tTrialEnd	time stamp (in secs) end of trial
durationTrial	duration of trial (in secs)
fixationInitialDuration	duration of initial fixation at start of each block
displayVidOnset	time stamp (in secs) of magic trick onset; collected before the video was opened
displayVidOffset	time stamp (in secs) of magic trick offset; collected after the video was closed
displayVidDuration	observed display duration (in secs) of magic trick
displayBlankDuration	duration of blank presentation (in secs) between end of magic trick and onset of fixation
fixationPostVidOnset	time stamp (in secs) of onset of fixation after magic trick display
fixationPostVidDuration	duration (in secs) of display of fixation after magic trick display
displayAnswerOnset	time stamp (in secs) of onset of estimate rating
displayAnswerDuration	duration (in secs) of display of estimate rating
timeoutAnswer	response time window for estimate rating
responseAnswer	response given in estimate rating
timestampAnswer	time stamp (in secs) of response in estimate rating
timestampAnswerWhite	time stamp (in secs) of estimate rating being displayed in white ink
rtAnswer	response time for estimate rating
answer_tooSlow	1 if time stamp response estimate > response time window for estimate rating - 3 * timing correction; else 0; subject sum score in other_information.csv ('answer_tooSlow')
fixationPostAnswerOnset	time stamp (in secs) of onset of fixation after estimate rating

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fixationPostAnswerDuration	duration (in secs) of display of fixation after estimate rating
betweenRatingFixation	intended duration (in secs) for fixation after estimate rating
displayCuriosityOnset	time stamp (in secs) of onset of curiosity rating
displayCuriosityDuration	duration (in secs) of display of curiosity rating
timeoutCuriosity	response time window for curiosity rating
responseCuriosity	response given in curiosity rating
timestampCuriosity	time stamp (in secs) of response in curiosity rating
timestampCuriosityWhite	time stamp (in secs) of curiosity rating being displayed in white ink
rtCuriosity	response time for curiosity rating
startValueCuriosity	number that was highlighted in red at the beginning of the curiosity rating
clicksCuriosity	number of button presses to move the number to the left and right in the curiosity rating
fixationPostCuriosityOnset	time stamp (in secs) of onset of fixation after curiosity rating
fixationPostCuriosityDuration	duration (in secs) of display of fixation after curiosity rating
curiosity_tooSlow	1 if time stamp response curiosity > response time window for curiosity rating - 3 * timing correction; else 0; subject sum score in other_information.csv ('curiosity_tooSlow')
mockOffset	time stamp (in secs) of offset of mock video
cueImage	time stamp (in secs) of cue image presentation
momentOfSurprise_1	time stamp (in secs) of first moment of surprise
momentOfSurprise_2	time stamp (in secs) of second moment of surprise
momentOfSurprise_3	time stamp (in secs) of third moment of surprise
momentOfSurprise_4	time stamp (in secs) of fourth moment of surprise
momentOfSurprise_5	time stamp (in secs) of fifth moment of surprise
momentOfSurprise_6	time stamp (in secs) of sixth moment of surprise
momentOfSurprise_7	time stamp (in secs) of seventh moment of surprise
additionalMarker_momentOfSurprise_1	time stamp (in secs) of first additional marker for moment of surprise
additionalMarker_momentOfSurprise_2	time stamp (in secs) of second additional marker for moment of surprise
trialRecall	trial number in recall block of memory task
responseRecall	response given in cued recall block of memory task
cuedRecallStrict	dummy coding of cued recall performance according to strict criteria: 1 if recalled; else 0; subject sum score and percentage out of 36 trials in scores.csv ('cuedRecallStrict_abs and cuedRecallStrict_rel')
cuedRecallLenient	dummy coding of cued recall performance according to lenient criteria: 1 if recalled; else 0 subject sum score and percentage out of 36 trials in scores.csv ('cuedRecallLenient_abs and cuedRecallLenient_rel')
Flagging	1 if cued recall response required further discussion during coding; else 0
Comments	comments related to flagging

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trialRecognition	trial number in recognition block of memory task
responseRecognition	response selected in recognition block of memory task
rtRecognition	response time for recognition response
responseConfidence	response given in confidence rating
rtConfidence	response time for response response
recognition	dummy coding of recognition (regardless of confidence): 1 if correct answer chosen; else 0; subject sum score and percentage out of 36 trials in scores.csv ('allConf_abs and allConf_rel
recognitionConfLevel_4_5_6	1 if recognition = 1 & confidence > 3; else 0; subject sum score and percentage out of 36 trials in scores.csv ('highConf_abs and highConf_rel
rememberedStrictHigh	1 if cuedRecallStrict = 1 or recognitionConfLevel_4_5_6 = 1; else 0; subject sum score and percentage out of 36 trials in scores.csv ('rememberedStrictHigh_abs and rememberedStrictHigh_rel
rememberedLenientHigh	1 if cuedRecallLenient = 1 or recognitionConfLevel_4_5_6 = 1; else 0; subject sum score and percentage out of 36 trials in scores.csv ('rememberedLenientHigh_abs and rememberedLenientHigh_rel

Note. Variable dictionary referencing the variables included in the MMC_experimental_data.csv file. An explanation of each variable is given to enhance usability for other researchers.

Appendix

Table A3.1

Welch's Two-Sample t-test for between-group differences in the TMI scales

	Intrinsic motivation	Task engagement	Interest	Boredom	Effort	Pressure
Behavioural study						
Control group	5.32 (1.88)	5.28 (1.39)	5.54 (1.86)	2.98 (2.14)	5.78 (1.20)	1.89 (1.06)
Incentive group	[1.00; 7.00]	[2.33; 7.00]	[1.00; 7.00]	[1.00; 7.00]	[2.00; 7.00]	[1.00; 5.25]
Group comparison	$t(69.774) = -0.603$, $p = 0.548$	$t(67.698) = -0.648$, $p = 0.519$	$t(69.181) = -0.732$, $p = 0.467$	$t(69.156) = 0.824$, $p = 0.413$	$t(74.599) = 0.567$, $p = 0.572$	$t(74.619) = 0.749$, $p = 0.456$
Cohen's d	0.14 [-0.31; 0.59]	0.15 [-0.30; 0.60]	0.17 [-0.28; 0.62]	-0.19 [-0.64; 0.26]	-0.13 [-0.58; 0.32]	-0.17 [-0.62; 0.28]
Replication						
Control group	5.58 (1.20)	5.40 (1.01)	5.87 (1.00)	2.69 (1.48)	5.62 (1.03)	2.53 (1.22)
Incentive group	[2.67; 7.00]	[3.33; 7.00]	[3.67; 7.00]	[1.00; 5.67]	[3.00; 7.00]	[1.00; 5.20]
Group comparison	$t(74.589) = -0.758$, $p = 0.451$	$t(75.944) = -0.911$, $p = 0.365$	$t(70.803) = -0.314$, $p = 0.754$	$t(75.855) = 0.180$, $p = 0.857$	$t(75.979) = -0.738$, $p = 0.463$	$t(75.412) = -1.720$, $p = 0.090$
Cohen's d	0.17 [-0.27; 0.62]	0.21 [-0.24; 0.65]	0.07 [-0.37; 0.52]	-0.04 [-0.49; 0.40]	0.17 [-0.28; 0.61]	0.40 [-0.06; 0.85]
fMRI study						
Control group	5.24 (1.16)	5.35 (0.88)	5.32 (1.12)	2.87 (1.10)	4.93 (0.93)	2.89 (1.41)
Incentive group	[2.33; 7.00]	[4.00; 6.67]	[3.00; 7.00]	[1.00; 5.00]	[3.00; 6.40]	[1.00; 5.40]
Group comparison	$t(47.470) = 0.000$, $p = 1.000$	$t(45.947) = 0.059$, $p = 0.953$	$t(45.296) = -1.502$, $p = 0.140$	$t(46.682) = -1.097$, $p = 0.278$	$t(47.092) = -1.661$, $p = 0.103$	$t(45.866) = 0.199$, $p = 0.843$
Cohen's d	0.00 [-0.55; 0.55]	-0.02 [-0.57; 0.54]	0.43 [-0.14; 1.00]	0.32 [-0.25; 0.88]	0.48 [-0.10; 1.05]	-0.06 [-0.61; 0.50]

Note. For each TMI scale, the table shows mean (standard deviation) [minimum; maximum] separately for each group and data collection. To test for differences, Welch Two Sample t-tests were used, and the table reports *t* statistics and *p* values. Effects were quantified using Cohen's *d* [95%-confidence interval]. TMI = Task Motivation Inventory.

Table A3.2

Results of LME models predicting curiosity ratings by group

	Estimate	SE	<i>t</i> value
Behavioural study			
Intercept	4.408	0.157	28.098
Incentive effect	0.058	0.148	0.393
Replication			
Intercept	4.793	0.136	35.164
Incentive effect	0.152	0.118	1.284
fMRI study			
Intercept	4.407	0.14	31.502
Incentive effect	-0.056	0.119	-0.465

Note. The LME model specified random intercepts for subject and stimulus ID. Incentive effect was effect coded (control = -1, incentive = 1). *p* values are omitted as the *lme4* package does not compute them by default. LME = Linear mixed effects. SE = standard error.

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Table A3.3

Integrated results of gLME models predicting recognition memory with gradual increase in confidence using curiosity, monetary incentive, and their interaction

Effect	<i>b</i> (SE)	OR [95%-CI]	<i>z</i> value	<i>p</i> value
Recog [Conf > 0]				
Curiosity	0.023 (0.023)	1.02 [0.98; 1.07]	0.988	0.323
Monetary incentive	0.084 (0.050)	1.09 [0.99; 1.20]	1.676	0.094
Interaction	-0.002 (0.022)	1.00 [0.96; 1.04]	-0.070	0.944
Recog [Conf > 1]				
Curiosity	0.038 (0.022)	1.04 [1.00; 1.08]	1.747	0.081
Monetary incentive	0.117 (0.054)	1.12 [1.01; 1.25]	2.161	0.031
Interaction	-0.015 (0.021)	0.98 [0.94; 1.03]	-0.725	0.468
Recog [Conf > 2]				
Curiosity	0.043 (0.021)	1.04 [1.00; 1.09]	2.021	0.043
Monetary incentive	0.156 (0.055)	1.17 [1.05; 1.30]	2.811	0.005
Interaction	-0.026 (0.020)	0.97 [0.94; 1.01]	-1.300	0.194
Recog [Conf > 3]				
Curiosity	0.084 (0.022)	1.09 [1.04; 1.14]	3.766	< 0.001
Monetary incentive	0.155 (0.067)	1.17 [1.03; 1.33]	2.336	0.019
Interaction	-0.010 (0.021)	0.99 [0.95; 1.03]	-0.479	0.632
Recog [Conf > 4]				
Curiosity	0.122 (0.027)	1.13 [1.07; 1.19]	4.496	< 0.001
Monetary incentive	0.096 (0.074)	1.10 [0.95; 1.27]	1.294	0.196
Interaction	-0.014 (0.025)	0.99 [0.94; 1.04]	-0.549	0.583
Recog [Conf > 5]				
Curiosity	0.111 (0.033)	1.12 [1.05; 1.19]	3.388	0.001
Monetary incentive	0.010 (0.086)	1.01 [0.85; 1.20]	0.118	0.906
Interaction	-0.057 (0.028)	0.94 [0.89; 1.00]	-2.056	0.040

Note. The same model specifying the full random effects structure was run for each recognition memory threshold. Please note that Recog [Conf > 0] and Recog [Conf > 3] are equal to Recognition and High confidence recognition in Table 3.2, respectively. gLME = Generalised Linear Mixed Effects. *b* = unstandardised regression coefficient. SE = standard error. OR = Odds Ratio, CI = confidence interval. Recog = recognition. Conf > [0:5] = confidence above given threshold.

Table A3.4

Results of gLME models for each data collection specifying the full RE structure

Fixed Effect	Behavioural study			Replication			fMRI study			
	<i>b</i> (SE)	OR	95%-CI	<i>b</i> (SE)	OR	95%-CI	<i>b</i> (SE)	OR	95%-CI	
				Recog [Conf > 0]						
Curiosity	0.026 (0.037)	1.03	[0.96; 1.10]	0.024 (0.039)	1.02	[0.95; 1.11]	0.016 (0.044)	1.02	[0.93; 1.11]	
Monetary incentive	0.158 (0.094)	1.17	[0.98; 1.41]	0.229 (0.083)	1.26	[1.07; 1.48]	-0.130 (0.085)	0.88	[0.74; 1.04]	
Interaction	0.027 (0.036)	1.03	[0.96; 1.10]	-0.048 (0.038)	0.95	[0.89; 1.03]	0.018 (0.043)	1.02	[0.94; 1.11]	
				Recog [Conf > 1]						
Curiosity	0.042 (0.036)	1.04	[0.97; 1.12]	0.047 (0.038)	1.05	[0.97; 1.13]	* 0.024 (0.040)	1.02	[0.95; 1.11]	
Monetary incentive	0.161 (0.108)	1.18	[0.95; 1.45]	0.257 (0.084)	1.29	[1.10; 1.52]	* -0.096 (0.094)	0.91	[0.75; 1.09]	
Interaction	0.006 (0.035)	1.01	[0.94; 1.08]	-0.046 (0.036)	0.95	[0.89; 1.02]	* -0.005 (0.039)	1.00	[0.92; 1.07]	
				Recog [Conf > 2]						
Curiosity	0.013 (0.037)	1.01	[0.94; 1.09]	* 0.075 (0.034)	1.08	[1.01; 1.15]	* 0.034 (0.039)	1.03	[0.96; 1.12]	
Monetary incentive	0.247 (0.118)	1.28	[1.02; 1.62]	* 0.265 (0.084)	1.30	[1.11; 1.54]	* -0.044 (0.095)	0.96	[0.79; 1.15]	
Interaction	0.009 (0.036)	1.01	[0.94; 1.08]	* -0.058 (0.033)	0.94	[0.89; 1.01]	* -0.024 (0.038)	0.98	[0.91; 1.05]	
				Recog [Conf > 3]						
Curiosity	* 0.048 (0.038)	1.05	[0.97; 1.13]	0.136 (0.037)	1.15	[1.07; 1.23]	* 0.061 (0.040)	1.06	[0.98; 1.15]	
Monetary incentive	* 0.298 (0.128)	1.35	[1.05; 1.73]	0.245 (0.106)	1.28	[1.04; 1.57]	* -0.062 (0.114)	0.94	[0.75; 1.18]	
Interaction	* 0.006 (0.036)	1.01	[0.94; 1.08]	-0.021 (0.034)	0.98	[0.92; 1.05]	* -0.015 (0.038)	0.99	[0.91; 1.06]	
				Recog [Conf > 4]						
Curiosity	0.088 (0.043)	1.09	[1.00; 1.19]	0.138 (0.044)	1.15	[1.05; 1.25]	0.152 (0.057)	1.16	[1.04; 1.30]	
Monetary incentive	0.280 (0.140)	1.32	[1.01; 1.74]	0.192 (0.123)	1.21	[0.95; 1.54]	-0.148 (0.124)	0.86	[0.68; 1.10]	
Interaction	0.004 (0.039)	1.00	[0.93; 1.08]	-0.038 (0.040)	0.96	[0.89; 1.04]	-0.002 (0.053)	1.00	[0.90; 1.11]	
				Recog [Conf > 5]						
Curiosity	* 0.118 (0.051)	1.13	[1.02; 1.24]	0.071 (0.055)	1.07	[0.96; 1.19]	0.158 (0.068)	1.17	[1.03; 1.34]	
Monetary incentive	* 0.255 (0.149)	1.29	[0.96; 1.73]	0.053 (0.165)	1.05	[0.76; 1.46]	-0.227 (0.137)	0.80	[0.61; 1.04]	
Interaction	* -0.003 (0.042)	1.00	[0.92; 1.08]	-0.148 (0.047)	0.86	[0.79; 0.95]	-0.019 (0.060)	0.98	[0.87; 1.10]	

Appendix

	Recall									
Curiosity	0.033 (0.052)	1.03	[0.93; 1.14]	* 0.107 (0.038)	1.11	[1.03; 1.20]	* 0.135 (0.046)	1.14	[1.05; 1.25]	
Monetary incentive	0.096 (0.171)	1.10	[0.79; 1.54]	* 0.228 (0.105)	1.26	[1.02; 1.54]	* -0.043 (0.134)	0.96	[0.74; 1.25]	
Interaction	-0.015 (0.048)	0.99	[0.90; 1.08]	* -0.063 (0.036)	0.94	[0.88; 1.01]	* 0.019 (0.043)	1.02	[0.94; 1.11]	

Note. For each data collection and memory measurement, the same gLME model was run. Full RE structure indicates random intercepts for participant and stimulus, as well as random slopes for the curiosity effect. If the model produced a singular fit error, an asterisk was added before reporting the coefficients. gLME = generalised linear mixed effects. RE = random effects. *b* = unstandardised regression coefficient. SE = standard error. OR = Odds Ratio. CI = confidence interval. Recog = recognition. Conf > [0:5] = confidence above given threshold.

Table A3.5

Integrated results of gLME models with reduced RE structure predicting memory encoding using curiosity, monetary incentive, and their interaction

Effect	<i>b</i> (SE)	OR [95%-CI]	<i>z</i> value	<i>p</i> value
Recog [Conf > 0]				
Curiosity	0.024 (0.021)	1.02 [0.98; 1.07]	1.152	0.249
Monetary incentive	0.083 (0.050)	1.09 [0.99; 1.20]	1.675	0.094
Interaction	-0.005 (0.020)	0.99 [0.96; 1.03]	-0.264	0.792
Recog [Conf > 1]				
Curiosity	0.038 (0.021)	1.04 [1.00; 1.08]	1.838	0.066
Monetary incentive	0.116 (0.054)	1.12 [1.01; 1.25]	2.156	0.031
Interaction	-0.017 (0.020)	0.98 [0.95; 1.02]	-0.849	0.396
Recog [Conf > 2]				
Curiosity	0.042 (0.021)	1.04 [1.00; 1.09]	2.041	0.041
Monetary incentive	0.155 (0.055)	1.17 [1.05; 1.30]	2.803	0.005
Interaction	-0.026 (0.020)	0.97 [0.94; 1.01]	-1.295	0.195
Recog [Conf > 3]				
Curiosity	0.085 (0.021)	1.09 [1.04; 1.13]	4.002	< 0.001
Monetary incentive	0.155 (0.066)	1.17 [1.03; 1.33]	2.336	0.019
Interaction	-0.011 (0.020)	0.99 [0.95; 1.03]	-0.541	0.589
Recog [Conf > 4]				
Curiosity	0.111 (0.022)	1.12 [1.07; 1.17]	4.968	< 0.001
Monetary incentive	0.092 (0.073)	1.10 [0.95; 1.27]	1.251	0.211
Interaction	-0.015 (0.021)	0.99 [0.94; 1.03]	-0.702	0.483
Recog [Conf > 5]				
Curiosity	0.115 (0.026)	1.12 [1.07; 1.18]	4.456	< 0.001
Monetary incentive	0.005 (0.085)	1.00 [0.85; 1.19]	0.054	0.957
Interaction	-0.060 (0.025)	0.94 [0.90; 0.99]	-2.448	0.014
Recall				
Curiosity	0.102 (0.024)	1.11 [1.06; 1.16]	4.335	< 0.001
Monetary incentive	0.119 (0.074)	1.13 [0.97; 1.30]	1.606	0.108
Interaction	-0.024 (0.023)	0.98 [0.93; 1.02]	-1.063	0.288

Note. The reduced RE structure specifies random intercepts for participant and stimulus, but it omits random slopes for the curiosity effect. Recog [Conf > 0] and Recog [Conf > 3] are the same as Recognition and High confidence recognition in Table 2, respectively. gLME = Generalised Linear Mixed Effects. RE = random effects. *b* = unstandardised regression coefficient. SE = standard error. OR = Odds Ratio, CI = confidence interval. Recog = recognition. Conf > [0:5] = confidence above given threshold.

Appendix

Table A3.6

Predicting integrated effects using the gradual confidence cut-off

	Full gLME model					Reduced gLME model				
	<i>b</i> (SE)	95%-CI	<i>t</i> value	<i>p</i> value	Fit	<i>b</i> (SE)	95%-CI	<i>t</i> value	<i>p</i> value	Fit
Curiosity										
Intercept	0.018 (0.011)	[-0.012; 0.047]	1.652	0.174	$R^2 = 0.898$	0.018 (0.008)	[-0.004; 0.041]	2.23	0.09	$R^2 = 0.935$
Slope	0.021 (0.004)	[0.011; 0.031]	5.92	0.004		0.020 (0.003)	[0.013; 0.028]	7.562	0.002	
Monetary Incentive										
Intercept	0.134 (0.040)	[0.023; 0.244]	3.361	0.028	$R^2 = 0.180$	0.134 (0.041)	[0.021; 0.247]	3.297	0.03	$R^2 = 0.197$
Slope	-0.012 (0.013)	[-0.049; 0.024]	-0.937	0.402		-0.013 (0.013)	[-0.051; 0.024]	-0.99	0.378	
Interaction										
Intercept	-0.002 (0.011)	[-0.034; 0.029]	-0.213	0.842	$R^2 = 0.488$	-0.004 (0.012)	[-0.037; 0.028]	-0.362	0.735	$R^2 = 0.473$
Slope	-0.007 (0.004)	[-0.018; 0.003]	-1.954	0.122		-0.007 (0.004)	[-0.018; 0.003]	-1.895	0.131	

Note. For each fixed effect, a linear model was used to predict the integrated effect using the confidence cut-off value. The integrated results are based on the full and reduced gLME model, respectively. The confidence cut-off value was defined from 0 to 5 so that the intercept can be interpreted. gLME = Generalised Linear Mixed Effects. *b* = unstandardised regression coefficient, SE = standard error. CI = confidence interval.

Table A3.7

Results of gLME models for each data collection specifying the reduced RE structure

Fixed Effect	Behavioural study			Replication			fMRI study		
	<i>b</i> (SE)	OR	95%-CI	<i>b</i> (SE)	OR	95%-CI	<i>b</i> (SE)	OR	95%-CI
				Recog [Conf > 0]					
Curiosity	0.026 (0.035)	1.03	[0.96; 1.10]	0.023 (0.035)	1.02	[0.96; 1.10]	0.023 (0.039)	1.02	[0.95; 1.10]
Monetary incentive	0.158 (0.093)	1.17	[0.98; 1.41]	0.227 (0.082)	1.25	[1.07; 1.47]	-0.129 (0.084)	0.88	[0.75; 1.04]
Interaction	0.024 (0.034)	1.02	[0.96; 1.10]	-0.052 (0.034)	0.95	[0.89; 1.01]	0.018 (0.037)	1.02	[0.95; 1.10]
				Recog [Conf > 1]					
Curiosity	0.041 (0.035)	1.04	[0.97; 1.12]	0.045 (0.035)	1.05	[0.98; 1.12]	0.026 (0.038)	1.03	[0.95; 1.11]
Monetary incentive	0.161 (0.108)	1.18	[0.95; 1.45]	0.255 (0.083)	1.29	[1.10; 1.52]	-0.096 (0.094)	0.91	[0.76; 1.09]
Interaction	0.005 (0.035)	1.01	[0.94; 1.08]	-0.049 (0.033)	0.95	[0.89; 1.02]	-0.002 (0.037)	1.00	[0.93; 1.07]
				Recog [Conf > 2]					
Curiosity	0.015 (0.036)	1.02	[0.95; 1.09]	0.075 (0.034)	1.08	[1.01; 1.15]	0.032 (0.038)	1.03	[0.96; 1.11]
Monetary incentive	0.247 (0.118)	1.28	[1.02; 1.61]	0.265 (0.084)	1.30	[1.11; 1.54]	-0.044 (0.094)	0.96	[0.80; 1.15]
Interaction	0.008 (0.035)	1.01	[0.94; 1.08]	-0.058 (0.032)	0.94	[0.89; 1.01]	-0.022 (0.037)	0.98	[0.91; 1.05]
				Recog [Conf > 3]					
Curiosity	0.058 (0.037)	1.06	[0.99; 1.14]	0.132 (0.035)	1.14	[1.07; 1.22]	0.055 (0.039)	1.06	[0.98; 1.14]
Monetary incentive	0.298 (0.128)	1.35	[1.05; 1.73]	0.244 (0.106)	1.28	[1.04; 1.57]	-0.062 (0.114)	0.94	[0.75; 1.18]
Interaction	0.004 (0.036)	1.00	[0.94; 1.08]	-0.021 (0.033)	0.98	[0.92; 1.04]	-0.015 (0.037)	0.99	[0.92; 1.06]
				Recog [Conf > 4]					
Curiosity	0.089 (0.038)	1.09	[1.01; 1.18]	0.139 (0.036)	1.15	[1.07; 1.23]	0.101 (0.043)	1.11	[1.02; 1.20]
Monetary incentive	0.279 (0.140)	1.32	[1.01; 1.74]	0.193 (0.123)	1.21	[0.95; 1.54]	-0.148 (0.121)	0.86	[0.68; 1.09]
Interaction	0.002 (0.037)	1.00	[0.93; 1.08]	-0.038 (0.034)	0.96	[0.90; 1.03]	-0.003 (0.040)	1.00	[0.92; 1.08]
				Recog [Conf > 5]					
Curiosity	0.107 (0.043)	1.11	[1.02; 1.21]	0.130 (0.042)	1.14	[1.05; 1.24]	0.102 (0.050)	1.11	[1.00; 1.22]
Monetary incentive	0.256 (0.149)	1.29	[0.96; 1.73]	0.064 (0.165)	1.07	[0.77; 1.47]	-0.234 (0.133)	0.79	[0.61; 1.03]
Interaction	-0.003 (0.042)	1.00	[0.92; 1.08]	-0.141 (0.040)	0.87	[0.80; 0.94]	-0.021 (0.048)	0.98	[0.89; 1.08]

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	Recall								
Curiosity	0.068 (0.041)	1.07	[0.99; 1.16]	0.109 (0.038)	1.12	[1.04; 1.20]	0.134 (0.045)	1.14	[1.05; 1.25]
Monetary incentive	0.096 (0.169)	1.10	[0.79; 1.53]	0.229 (0.105)	1.26	[1.02; 1.55]	-0.043 (0.134)	0.96	[0.74; 1.25]
Interaction	-0.015 (0.040)	0.99	[0.91; 1.06]	-0.062 (0.036)	0.94	[0.88; 1.01]	0.020 (0.043)	1.02	[0.94; 1.11]

Note. For each data collection and memory measurement, the same gLME model was run. The reduced RE structure specifies random intercepts for participant and stimulus, but it omits random slopes for the curiosity effect. gLME = generalised linear mixed effects. RE = random effects. b = unstandardised regression coefficient. SE = standard error. OR = Odds Ratio. CI = confidence interval. Recog = recognition. Conf > [0:5] = confidence above given threshold.

Table A3.8

ROI and Whole Brain Results of ISC and Incentive Effects Therein

Cluster	Macro Label	Direction	Cluster Size	Maximum Intensity			
				t value	x	y	z
Average ISC							
Regions-of-Interest Approach							
1	R aHPC	positive	62	7.1708	22.5	-1.5	-19.5
2	L aHPC	positive	45	5.8873	-31.5	-7.5	-19.5
1	L VTA/SN	positive	30	6.927	-7.5	-13.5	-10.5
2	R VTA/SN	positive	29	4.9475	4.5	-16.5	-16.5
1	R NAcc	positive	31	6.8451	16.5	7.5	-10.5
2	L NAcc	positive	27	6.0561	-13.5	10.5	-10.5
1	R CN	positive	273	13.686	13.5	22.5	4.5
2	L CN	positive	270	12.944	-19.5	16.5	10.5
Whole Brain Approach							
	R Middle Frontal Gyrus						
	L Middle Frontal Gyrus						
	L Middle Temporal Gyrus						
	R Middle Temporal Gyrus						
	R Superior Frontal Gyrus						
	L Precuneus						
	L Precentral Gyrus						
	L Middle Occipital Gyrus						
	R Precuneus8						
	L Postcentral Gyrus						
	L Superior Frontal Gyrus						
	L Superior Medial Gyrus						
	R Postcentral Gyrus						
	R Precentral Gyrus						
	R Inferior Temporal Gyrus						
	R Superior Temporal Gyrus						
	L Inferior Parietal Lobule						
	L Cerebellum (Crus 1)						
	L Calcarine Gyrus						
	R Cerebellum (Crus 1)						
	R Lingual Gyrus						
	L Inferior Frontal Gyrus (p. Triangularis)						
	L Lingual Gyrus						
	L SMA						
	R Middle Occipital Gyrus						
	L Inferior Temporal Gyrus						
	R Fusiform Gyrus						
	R Superior Parietal Lobule						
	L Superior Parietal Lobule						
1	R SMA	positive	45359	18.783	46.5	-70.5	-7.5

Appendix

R Supramarginal Gyrus
L Middle Cingulate Cortex
L Cerebellum (Crus 2)³
R Superior Medial Gyrus
L Superior Temporal Gyrus
R Middle Cingulate Cortex
R Angular Gyrus
R Cerebellum (Crus 2)
R Cerebellum (VI)
R Calcarine Gyrus
L Fusiform Gyrus
R Inferior Frontal Gyrus (p.
Triangularis)
R Insula Lobe
L Cuneus
L Cerebellum (VI)
R Cerebellum (VIII)
R Inferior Parietal Lobule
R Cuneus
L Inferior Frontal Gyrus (p.
Orbitalis)
L Insula Lobe
R Inferior Frontal Gyrus (p.
Orbitalis)
L Anterior Cingulate Cortex
R Superior Occipital Gyrus
L Superior Occipital Gyrus
R Inferior Frontal Gyrus (p.
Opercularis)
R Rolandic Operculum
L Supramarginal Gyrus
L Angular Gyrus
R Inferior Occipital Gyrus
L Cerebellum (VIII)
L Thalamus
R Anterior Cingulate Cortex
L Rolandic Operculum
L Inferior Occipital Gyrus
R Middle Orbital Gyrus
L Putamen
L Inferior Frontal Gyrus (p.
Opercularis)
R Putamen
L Paracentral Lobule
R Caudate Nucleus
R Temporal Pole
L Caudate Nucleus
R Thalamus
L Middle Orbital Gyrus
L Mid Orbital Gyrus
R Medial Temporal Pole

R Mid Orbital Gyrus
 L Temporal Pole
 R Paracentral Lobule
 L Hippocampus
 L Cerebellum (VII)
 R Cerebellum (IV-V)
 R Superior Orbital Gyrus
 R Cerebellum (VII)
 R Hippocampus
 L Posterior Cingulate Cortex
 Cerebellar Vermis (6)
 L Superior Orbital Gyrus
 R Parahippocampal Gyrus
 Cerebellar Vermis (4/5)
 R Heschls Gyrus
 L Cerebellum (IX)
 L Heschls Gyrus
 L Medial Temporal Pole
 R Cerebellum (IX)
 L Cerebellum (IV-V)
 L Parahippocampal Gyrus
 R Pallidum
 R Amygdala
 R Posterior Cingulate Cortex
 L Amygdala
 L Olfactory cortex
 Cerebellar Vermis (7)
 L Rectal Gyrus
 L Pallidum
 R Rectal Gyrus
 R Olfactory cortex
 R Cerebellum (X)
 Cerebellar Vermis (8)
 Cerebellar Vermis (3)
 L Cerebellum (X)

ISC Incentive Effects

Regions-of-Interest Approach

no clusters survive thresholding

Whole Brain Approach

1	L Middle Occipital Gyrus	I > C	85	-8.0421	-43.5	-91.5	-1.5
2	R Postcentral Gyrus	I > C	53	-11.744	37.5	-31.5	49.5
	Superior Parietal Lobule						
3	R Superior Occipital Gyrus	I > C	38	-6.101	25.5	-70.5	46.5
	L Middle Occipital Gyrus						
4	L Inferior Occipital Gyrus	I < C	28	6.0377	-43.5	-67.5	-1.5

Note. Results are thresholded at $q < 0.05$ and $k = 5$ for the regions-of-interest approach and at $p < 0.001$, cluster-extent corrected at $k = 20$ (equivalent to per-cluster $\alpha = 0.05$) for whole brain analysis. The table corresponds to Figure 3.4 and A3.7. (x, y, and z) denote MNI coordinates of the peak voxel. Cluster size

Appendix

is given in voxels. ISC = Intersubject correlation, aHPC = anterior hippocampus, VTA/SN = ventral tegmental area/substantia nigra, NAcc = nucleus accumbens, CN = caudate nucleus, L = left, R = right.

Table A3.9

ROI and Whole Brain Results of IS-RSA For Each Behavioural Effect of Interest

Cluster	Macro Label	Direction	Cluster Size	Maximum Intensity			
				t value	x	y	z
Curiosity							
Regions-of-Interest Approach							
<i>no clusters survive thresholding</i>							
Whole Brain Analysis							
	L Inferior Occipital Gyrus						
	L Lingual Gyrus						
1	L Calcarine Gyrus	positive	63	6.2884	-13.5	-106.5	-4.5
	R Inferior Frontal Gyrus						
2	(p. Opercularis)	positive	34	4.9267	52.5	16.5	25.5
3	R SMA	positive	33	4.9359	1.5	13.5	61.5
4	L Postcentral Gyrus	positive	29	4.9618	-25.5	-31.5	73.5
5	L Precuneus	positive	23	4.2003	-1.5	-64.5	61.5
6	R Insula Lobe	positive	20	5.2905	37.5	22.5	1.5
7	R Supramarginal Gyrus	positive	20	4.202	67.5	-25.5	37.5
Memory							
Regions-of-Interest Approach							
1	R CN	positive	30	4.1269	13.5	19.5	4.5
2	L CN	positive	20	4.253	-19.5	22.5	4.5
Whole Brain Analysis							
	R Inferior Occipital Gyrus						
	R Middle Occipital Gyrus						
	R Lingual Gyrus						
1	R Middle Temporal Gyrus	positive	455	7.9417	34.5	-85.5	-10.5
	R Calcarine Gyrus						
	L Lingual Gyrus						
	R Lingual Gyrus						
	L Cuneus						
2	R Cuneus	positive	320	5.5756	7.5	-64.5	4.5
	L Middle Occipital Gyrus						
	L Inferior Occipital Gyrus						
3	L Fusiform Gyrus	positive	270	7.7376	-34.5	-64.5	-13.5
	L Calcarine Gyrus						
	L Cuneus						
	R Cuneus						
4	R Calcarine Gyrus	positive	233	7.1555	4.5	-94.5	10.5
5	L Middle Frontal Gyrus	positive	81	5.1844	-34.5	52.5	7.5
	R Precuneus						
6	L Precuneus	positive	75	5.5491	1.5	-70.5	55.5
7	R Middle Frontal Gyrus	positive	59	5.5209	49.5	46.5	13.5
8	R Middle Frontal Gyrus	positive	55	4.973	31.5	43.5	31.5
9	R Angular Gyrus	positive	50	5.3212	43.5	-70.5	43.5
10	R Postcentral Gyrus	positive	45	6.2064	31.5	-34.5	43.5
11	R Middle Frontal Gyrus	positive	42	5.2976	31.5	19.5	58.5

Appendix

12	R SMA	positive	42	5.2509	7.5	19.5	49.5
	L Cerebellum (Crus 1)						
13	L Cerebellum (Crus 2)	positive	34	4.5986	-16.5	-82.5	-28.5
	L Cerebellum (Crus 2)						
14	L Cerebellum (Crus 1)	positive	33	5.0131	-31.5	-76.5	-37.5
	L Inferior Temporal						
15	Gyrus	positive	33	5.3724	-55.5	-58.5	-7.5
16	R Insula Lobe	positive	33	5.2887	31.5	25.5	-4.5
17	L Middle Occipital Gyrus	positive	32	5.7279	-46.5	-85.5	4.5
18	R Middle Frontal Gyrus	positive	29	4.8888	43.5	16.5	43.5
19	L Cerebellum (Crus 1)	positive	22	5.3657	-43.5	-73.5	-25.5
20	L Middle Frontal Gyrus	positive	22	5.0285	-25.5	37.5	37.5
21	L Inferior Parietal Lobule	positive	20	4.7087	-55.5	-40.5	52.5

Curiosity-Motivated Learning Enhancement

Regions-of-Interest Approach

1	R aHPC	negative	8	-4.456	31.5	-4.5	-19.5
2	R VTA/SN	negative	5	-3.401	13.5	-22.5	-10.5
1	R NAcc	negative	25	-5.5516	10.5	10.5	-4.5
2	L NAcc	negative	11	-4.4598	-13.5	13.5	-10.5
1	R CN	negative	188	-8.0879	13.5	16.5	7.5
2	L CN	negative	176	-8.9741	-16.5	4.5	16.5

Whole Brain Analysis

					0	0	
1	R Calcarine Gyrus	positive	42	6.7942	16.5	-88.5	7.5
2	L Middle Occipital Gyrus	positive	33	8.1115	-37.5	-82.5	7.5
3	R Postcentral Gyrus	positive	26	7.1842	40.5	-31.5	58.5
4	L Middle Temporal Gyrus	positive	22	5.8015	-49.5	-64.5	7.5
	R Middle Temporal						
5	Gyrus	positive	20	6.9451	43.5	-61.5	7.5
	L Middle Frontal Gyrus						
	R Middle Frontal Gyrus						
	L Superior Medial Gyrus						
	L Precuneus						
	R Superior Frontal Gyrus						
	L Middle Temporal Gyrus						
	R Precuneus						
	R Middle Temporal						
	Gyrus						
	L Superior Frontal Gyrus						
	L Cerebellum (Crus 1)						
	L Precentral Gyrus						
	L Inferior Frontal Gyrus						
	(p. Triangularis)						
	R Superior Medial Gyrus						
	R Angular Gyrus						
	R Cerebellum (Crus 1)						
	L Cerebellum (Crus 2)						
6	L Inferior Parietal Lobule	negative	20326	-16.137	49.5	-55.5	49.5

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	L Calcarine Gyrus						
	L Cuneus						
	L Superior Parietal Lobule						
	R Superior Parietal Lobule						
	R Cerebellum (Crus 2)						
	L Middle Occipital Gyrus						
	R Inferior Parietal Lobule						
	L Lingual Gyrus						
	R Inferior Frontal Gyrus (p. Orbitalis)						
	L Inferior Frontal Gyrus (p. Orbitalis)						
	L Angular Gyrus						
	R Inferior Frontal Gyrus (p. Triangularis)						
	L Fusiform Gyrus						
	R Supramarginal Gyrus						
	L SMA						
	L Middle Cingulate Cortex						
	L Inferior Temporal Gyrus						
	R Middle Occipital Gyrus						
	L Postcentral Gyrus						
	L Anterior Cingulate Cortex						
	R Cuneus						
	L Inferior Occipital Gyrus						
	R Postcentral Gyrus						
	R Inferior Temporal Gyrus						
	R Precentral Gyrus						
	R Caudate Nucleus						
	L Thalamus						
	R Thalamus						
7	R Putamen	negative	208	-8.0879	13.5	16.5	7.5
	L Caudate Nucleus						
8	L Putamen	negative	183	-8.9741	-16.5	4.5	16.5
	L Rolandic Operculum						
9	L Insula Lobe	negative	60	-10.656	-40.5	-1.5	16.5
	L Amygdala						
10	L Hippocampus	negative	57	-6.7116	-16.5	-7.5	-13.5
11	L Putamen	negative	42	-6.1443	-28.5	-4.5	4.5
	R Postcentral Gyrus						
12	R Precentral Gyrus	negative	37	-6.0096	28.5	-25.5	58.5
	R Rolandic Operculum						
13	R Insula Lobe	negative	36	-8.0841	43.5	-1.5	16.5
	R Lingual Gyrus						
14	R Calcarine Gyrus	negative	33	-7.401	7.5	-79.5	1.5

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15	L Supramarginal Gyrus	negative	28	-8.1472	-52.5	-43.5	28.5
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Note. Results are thresholded at $q < 0.05$ and $k = 5$ for the regions-of-interest approach and at $p < 0.001$, cluster-extent corrected at $k = 20$ (equivalent to per-cluster $\alpha = 0.05$) for whole brain analysis. The table corresponds to Figure 3.5 and 3.6. (x, y, and z) denote MNI coordinates of the peak voxel. Cluster size is given in voxels. IS-RSA = Intersubject Representational Similarity Analysis, aHPC = anterior hippocampus, VTA/SN = ventral tegmental area/substantia nigra, NAcc = nucleus accumbens, CN = caudate nucleus, L = left, R = right.

Table A3.10

ROI and Whole Brain Results of IS-RSA For the Interaction Between the Incentive Manipulation and Each Behavioural Effect of Interest

Cluster	Macro Label	Direction	Cluster Size	MI			
				<i>t</i> value	x	y	z
Curiosity							
Regions-of-Interest Approach							
<i>no clusters survive thresholding</i>							
Whole Brain Analysis							
	R Inferior Occipital Gyrus						
1	R Middle Occipital Gyrus	I < C	60	4.9726	31.5	-88.5	-4.5
2	L Middle Occipital Gyrus	I < C	36	5.4253	-22.5	-97.5	1.5
Memory							
Regions-of-Interest Approach							
<i>no clusters survive thresholding</i>							
Whole Brain Analysis							
	R Calcarine Gyrus						
	L Calcarine Gyrus						
	L Cuneus						
1	R Cuneus	I > C	120	-5.3723	10.5	-82.5	13.5
	L Middle Orbital Gyrus						
2	L Middle Frontal Gyrus	I < C	76	5.7046	-37.5	58.5	1.5
3	L Middle Occipital Gyrus	I < C	25	5.4122	-34.5	-97.5	4.5
Curiosity-Motivated Learning Enhancement							
Regions-of-Interest Approach							
<i>no clusters survive thresholding</i>							
Whole Brain Analysis							
	R Middle Occipital Gyrus						
	R Inferior Occipital Gyrus						
	R Middle Temporal Gyrus						
	L Lingual Gyrus						
	R Lingual Gyrus						
1	L Calcarine Gyrus	I > C	711	-9.0868	40.5	-79.5	-7.5

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	R Inferior Temporal Gyrus						
	R Fusiform Gyrus						
	R Calcarine Gyrus						
	L Precuneus						
	R Precuneus						
	R Cuneus						
	L Cuneus						
2	L Superior Parietal Lobule	I > C	544	-7.0127	13.5	-67.5	46.5
	L Middle Occipital Gyrus						
	L Middle Temporal Gyrus						
3	L Inferior Occipital Gyrus	I > C	297	-8.1443	-31.5	-91.5	16.5
	R Superior Parietal Lobule						
4	R Inferior Parietal Lobule	I > C	131	-9.7247	25.5	-64.5	64.5
	L Middle Frontal Gyrus						
5	L Middle Orbital Gyrus	I > C	120	-6.1818	-37.5	58.5	10.5
	R Angular Gyrus						
6	R Inferior Parietal Lobule	I > C	86	-5.9831	46.5	-58.5	37.5
	R Superior Frontal Gyrus						
7	R Precentral Gyrus	I > C	54	-6.5473	25.5	-7.5	55.5
8	R Superior Frontal Gyrus	I > C	51	-5.7977	22.5	43.5	43.5
	R Middle Cingulate Cortex						
	R Superior Medial Gyrus						
	L Superior Medial Gyrus						
9	R Anterior Cingulate Cortex	I > C	48	-4.9674	4.5	28.5	43.5
	L Inferior Parietal Lobule						
10	L Angular Gyrus	I > C	46	-6.486	-46.5	-55.5	46.5
	R Precuneus						
	R Middle Cingulate Cortex						
11	R Posterior Cingulate Cortex	I > C	45	-5.0203	4.5	-49.5	34.5
	L Superior Parietal Lobule						
12	L Superior Occipital Gyrus	I > C	41	-7.5829	-22.5	-79.5	46.5
	L Supramarginal Gyrus						
13	L Inferior Parietal Lobule	I > C	31	-4.7041	-64.5	-34.5	40.5

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	R Cuneus						
14	R Superior Occipital Gyrus	I > C	29	-6.81	13.5	-94.5	22.5
15	R Middle Frontal Gyrus	I > C	28	-6.4763	46.5	46.5	16.5
	R Posterior Cingulate Cortex						
	R Precuneus						
16	L Posterior Cingulate Cortex	I > C	27	-4.9755	4.5	-43.5	19.5
	L Inferior Parietal Lobule						
17	L Superior Parietal Lobule	I > C	27	-6.4452	-34.5	-49.5	58.5
	L Precentral Gyrus						
18	L Superior Frontal Gyrus	I > C	24	-5.4886	-25.5	-13.5	55.5
	L Inferior Occipital Gyrus						
	L Inferior Temporal Gyrus						
	L Middle Temporal Gyrus						
19	L Middle Occipital Gyrus	I > C	23	-6.4189	-43.5	-64.5	-4.5
	L Supramarginal Gyrus						
20	L Superior Temporal Gyrus	I < C	31	5.331	-49.5	-37.5	28.5

Note. Results are thresholded at $q < 0.05$ and $k = 5$ for the regions-of-interest approach and at $p < 0.001$, cluster-extent corrected at $k = 20$ (equivalent to per-cluster $\alpha = 0.05$) for whole brain analysis. The table corresponds to Figure 3.7. (x, y, and z) denote MNI coordinates of the peak voxel. Cluster size is given in voxels. IS-RSA = Intersubject Representational Similarity Analysis, L = left, R = right, C = control group, I = incentive group.

Appendix

Table A3.11

Whole Brain Results of ISFC and Incentive Effects Therein Specifying aHPC and VTA/SN as Seeds

Cluster	Macro Label	Direction	Cluster Size	Maximum Intensity			
				<i>t</i> value	x	y	z
Average ISFC							
aHPC seed							
	L Middle Temporal Gyrus						
	L Middle Frontal Gyrus						
	L Superior Medial Gyrus						
	L Superior Frontal Gyrus						
	R Middle Temporal Gyrus						
	R Superior Medial Gyrus						
	L Precuneus						
	L Calcarine Gyrus						
	L Lingual Gyrus						
	R Superior Frontal Gyrus						
	L Middle Cingulate Cortex						
	L Cuneus						
	R Precuneus						
	R Calcarine Gyrus						
	L Inferior Frontal Gyrus (p. Orbitalis)						
	R Lingual Gyrus						
	L SMA						
	R Superior Temporal Gyrus						
	L Inferior Temporal Gyrus						
	L Insula Lobe						
	L Anterior Cingulate Cortex						
	R Middle Cingulate Cortex						
	L Angular Gyrus						
	L Inferior Frontal Gyrus (p. Triangularis)						
	R Inferior Temporal Gyrus						
	L Thalamus						
	R Cuneus						
	R Anterior Cingulate Cortex						
	R Insula Lobe						
	L Fusiform Gyrus						
	L Putamen						
	R Hippocampus						
	R Inferior Frontal Gyrus (p. Orbitalis)						
	R Thalamus						
	L Hippocampus						
	R Medial Temporal Pole						
	R Middle Frontal Gyrus						
	L Temporal Pole						
	R Temporal Pole						
1	R Parahippocampal Gyrus	positive	17870	9.9588	19.5	13.5	-7.5

L Superior Temporal Gyrus
L Inferior Parietal Lobule
R Caudate Nucleus
L Mid Orbital Gyrus
R Putamen
L Caudate Nucleus
R Mid Orbital Gyrus
R Cerebellum (IV-V)
R Fusiform Gyrus
L Cerebellum (IV-V)
L Rolandic Operculum
L Superior Occipital Gyrus
L Parahippocampal Gyrus
L Posterior Cingulate Cortex
L Medial Temporal Pole
R Rolandic Operculum
R SMA
R Middle Orbital Gyrus
L Middle Occipital Gyrus
L Superior Orbital Gyrus
L Inferior Frontal Gyrus (p.
Opercularis)
R Heschls Gyrus
R Cerebellum (VI)
R Superior Orbital Gyrus
L Middle Orbital Gyrus
L Heschls Gyrus
R Superior Occipital Gyrus
R Amygdala
R Olfactory cortex
L Olfactory cortex
R Posterior Cingulate Cortex
L Amygdala
R Pallidum
L Cerebellum (VI)
L Precentral Gyrus
L Rectal Gyrus
L Pallidum
L Postcentral Gyrus
R Inferior Frontal Gyrus (p.
Opercularis)
Cerebellar Vermis (4/5)
L Paracentral Lobule
L Superior Parietal Lobule
L Supramarginal Gyrus
R Rectal Gyrus
R Paracentral Lobule
L Inferior Occipital Gyrus
R Inferior Frontal Gyrus (p.
Triangularis)
Cerebellar Vermis (3)

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	L Cerebellum (III)						
	L Cerebellum (Crus 1)						
	R Cerebellum (III)						
	L Postcentral Gyrus						
2	L Precentral Gyrus	positive	535	8.5217	-16.5	-34.5	64.5
	R Angular Gyrus						
	R Inferior Parietal Lobule						
3	R Middle Occipital Gyrus	positive	531	7.0422	58.5	-58.5	28.5
	R Precentral Gyrus						
4	R Postcentral Gyrus	positive	305	7.3448	22.5	-25.5	61.5
	L Cerebellum (Crus 2)						
5	L Cerebellum (Crus 1)	positive	241	5.837	-40.5	-82.5	-34.5
	R Cerebellum (Crus 1)						
6	R Cerebellum (Crus 2)	positive	155	6.2307	40.5	-76.5	-34.5
7	Brainstem	positive	69	5.9908	-4.5	-28.5	-40.5
	R Middle Frontal Gyrus						
8	R Middle Orbital Gyrus	positive	40	4.2492	40.5	52.5	7.5
	Cerebellar Vermis (8)						
9	L Cerebellum (VIII)	positive	22	4.8611	1.5	-70.5	-37.5
	R Superior Parietal Lobule						
	R Postcentral Gyrus						
	R Inferior Parietal Lobule						
10	R Precuneus	negative	713	-7.6371	13.5	-55.5	70.5
	L Superior Parietal Lobule						
	L Inferior Parietal Lobule						
	L Postcentral Gyrus						
11	L Precuneus	negative	495	-6.4146	-22.5	-61.5	58.5
	L Middle Occipital Gyrus						
	L Inferior Occipital Gyrus						
	L Lingual Gyrus						
12	L Calcarine Gyrus	negative	488	-6.6946	-28.5	-94.5	-16.5
	R Superior Frontal Gyrus						
	R Precentral Gyrus						
13	R Middle Frontal Gyrus	negative	343	-7.03	34.5	-7.5	55.5
	R Supramarginal Gyrus						
14	R Postcentral Gyrus	negative	334	-6.3619	52.5	-37.5	28.5
	R Precentral Gyrus						
	R Inferior Frontal Gyrus (p. Opercularis)						
15	R Rolandic Operculum	negative	208	-7.545	64.5	10.5	16.5
	R Inferior Occipital Gyrus						
	R Lingual Gyrus						
16	R Calcarine Gyrus	negative	196	-5.0473	22.5	-100.5	-13.5
	L Precentral Gyrus						
17	L Superior Frontal Gyrus	negative	159	-6.6714	-25.5	-10.5	58.5
	L Supramarginal Gyrus						
18	L Postcentral Gyrus	negative	97	-5.0521	-58.5	-25.5	28.5
	L Supramarginal Gyrus						
19	L Superior Temporal Gyrus	negative	69	-6.7032	-52.5	-37.5	25.5
	L Precentral Gyrus						
20	L Postcentral Gyrus	negative	44	-5.9077	-58.5	1.5	43.5

VTA/SN seed

	L Middle Frontal Gyrus						
	R Middle Frontal Gyrus						
	L Middle Temporal Gyrus						
	R Middle Temporal Gyrus						
	R Superior Frontal Gyrus						
	L Cerebellum (Crus 1)						
	L Inferior Temporal Gyrus						
	L Superior Medial Gyrus						
	L Superior Frontal Gyrus						
	L Inferior Frontal Gyrus (p. Triangularis)						
	R Cerebellum (Crus 1)						
	R Inferior Temporal Gyrus						
	L Lingual Gyrus						
	R Lingual Gyrus						
	L Precuneus						
	L Calcarine Gyrus						
	R Inferior Frontal Gyrus (p. Triangularis)						
	L Cerebellum (Crus 2)						
	R Superior Medial Gyrus						
	R Angular Gyrus						
	R Precuneus						
	R Superior Temporal Gyrus						
	L Inferior Frontal Gyrus (p. Orbitalis)						
	R Inferior Frontal Gyrus (p. Orbitalis)						
	L Inferior Parietal Lobule						
	R Cerebellum (Crus 2)						
	L Cuneus						
	L Middle Cingulate Cortex						
	R Calcarine Gyrus						
	L Insula Lobe						
	R Cuneus						
	R Middle Cingulate Cortex						
	R Cerebellum (VI)						
	L Precentral Gyrus						
	R Insula Lobe						
	R Fusiform Gyrus						
	L Angular Gyrus						
	L SMA						
	L Thalamus						
	L Fusiform Gyrus						
	R Inferior Parietal Lobule						
	R Middle Orbital Gyrus						
	R Temporal Pole						
	L Anterior Cingulate Cortex						
	L Temporal Pole						
1	L Putamen	positive	32507	16.502	-10.5	-85.5	4.5

Appendix

R Inferior Frontal Gyrus (p.
Opercularis)
R Thalamus
R Anterior Cingulate Cortex
L Inferior Frontal Gyrus (p.
Opercularis)
R Caudate Nucleus
R Medial Temporal Pole
L Postcentral Gyrus
L Middle Orbital Gyrus
L Superior Temporal Gyrus
L Superior Occipital Gyrus
L Caudate Nucleus
R Parahippocampal Gyrus
R SMA
R Putamen
R Cerebellum (VIII)
R Superior Orbital Gyrus
R Supramarginal Gyrus
R Cerebellum (IV-V)
L Middle Occipital Gyrus
R Hippocampus
R Superior Occipital Gyrus
L Hippocampus
L Medial Temporal Pole
L Cerebellum (VI)
R Middle Occipital Gyrus
L Superior Orbital Gyrus
L Parahippocampal Gyrus
Cerebellar Vermis (4/5)
R Cerebellum (VII)
R Pallidum
L Cerebellum (IV-V)
L Superior Parietal Lobule
L Pallidum
L Posterior Cingulate Cortex
L Cerebellum (VII)
L Supramarginal Gyrus
L Amygdala
R Amygdala
L Cerebellum (IX)
L Rolandic Operculum
L Cerebellum (VIII)
R Olfactory cortex
R Superior Parietal Lobule
R Precentral Gyrus
R Posterior Cingulate Cortex
L Olfactory cortex
L Cerebellum (III)
R Rectal Gyrus
R Cerebellum (IX)

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	Cerebellar Vermis (8)						
	R Rolandic Operculum						
	Cerebellar Vermis (3)						
	Cerebellar Vermis (9)						
	Cerebellar Vermis (6)						
	L Inferior Occipital Gyrus						
	R Heschls Gyrus						
	R Mid Orbital Gyrus						
	Cerebellar Vermis (7)						
	L Rectal Gyrus						
	L Heschls Gyrus						
	R Cerebellum (III)						
	Cerebellar Vermis (1/2)						
	Cerebellar Vermis (10)						
	L Paracentral Lobule						
	R Paracentral Lobule						
	L Mid Orbital Gyrus						
	R Precentral Gyrus						
2	R Postcentral Gyrus	positive	33	7.5112	37.5	-16.5	37.5
	L Middle Occipital Gyrus						
	L Inferior Occipital Gyrus						
	L Lingual Gyrus						
	L Middle Temporal Gyrus						
3	L Calcarine Gyrus	negative	2676	-12.85	37.5	-37.5	58.5
	R Inferior Occipital Gyrus						
	R Middle Occipital Gyrus						
	R Middle Temporal Gyrus						
	R Lingual Gyrus						
4	R Calcarine Gyrus	negative	890	-11.985	-19.5	-103.5	4.5
	R Inferior Occipital Gyrus						
	R Middle Occipital Gyrus						
	R Middle Temporal Gyrus						
	R Lingual Gyrus						
5	R Calcarine Gyrus	negative	806	-13.049	22.5	-97.5	-4.5
	L Postcentral Gyrus						
	L Supramarginal Gyrus						
6	L Precentral Gyrus	negative	196	-6.3416	-61.5	-16.5	37.5
	L Supramarginal Gyrus						
7	L Superior Temporal Gyrus	negative	82	-7.1019	-49.5	-40.5	28.5
	L Mid Orbital Gyrus						
	L Rectal Gyrus						
	R Rectal Gyrus						
8	R Mid Orbital Gyrus	negative	78	-4.9271	-1.5	52.5	-13.5
	R Precentral Gyrus						
9	R Postcentral Gyrus	negative	65	-7.109	61.5	10.5	34.5
10	L Cerebellum (VIII)	negative	58	-6.1588	-28.5	-52.5	-46.5
	R Superior Occipital Gyrus						
11	R Superior Parietal Lobule	negative	52	-7.9278	28.5	-82.5	43.5
	L Superior Occipital Gyrus						
	L Middle Occipital Gyrus						
12	L Superior Parietal Lobule	negative	50	-6.8917	-25.5	-85.5	40.5

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13	R Supramarginal Gyrus R Rolandic Operculum L Cerebellum (Crus 2) L Cerebellum (VII)	negative	41	-5.4704	40.5	-25.5	22.5
14	Cerebellar Vermis (7) R Rolandic Operculum	negative	25	-5.8236	1.5	-76.5	-31.5
15	R Insula Lobe	negative	21	-6.0122	40.5	1.5	16.5
ISFC Incentive Effects							
aHPC seed							
<i>no clusters survive thresholding</i>							
VTA/SN seed							
1	L Superior Temporal Gyrus L Supramarginal Gyrus L Calcarine Gyrus L Inferior Occipital Gyrus L Middle Occipital Gyrus	I > C	23	-4.3753	-55.5	-28.5	16.5
2	L Lingual Gyrus	I < C	56	5.1537	-10.5	-100.5	-4.5

Note. Results are thresholded at $p < 0.001$, cluster-extent corrected at $k = 20$ (equivalent to per-cluster $\alpha = 0.05$) for whole brain analysis. The table corresponds to Figure A3.8. (x, y, and z) denote MNI coordinates of the peak voxel. Cluster size is given in voxels. ISFC = Intersubject Functional Connectivity, aHPC = anterior hippocampus, VTA/SN = ventral tegmental area/substantia nigra, L = left, R = right, C = control group, I = incentive group.

Table A3.12

Whole Brain Results of ISFC-RSA For Each Behavioural Effect of Interest Specifying aHPC and VTA/SN as Seeds

Cluster	Macro Label	Direction	Cluster Size	Maximum Intensity			
				t value	x	y	z
Curiosity							
aHPC seed							
<i>no clusters survive thresholding</i>							
VTA/SN seed							
1	R Superior Medial Gyrus L Superior Medial Gyrus L Inferior Frontal Gyrus (p. Orbitalis)	positive	49	5.1764	4.5	40.5	52.5
2	L Insula Lobe L Inferior Parietal Lobule	positive	44	5.288	-31.5	25.5	-7.5
3	L Middle Occipital Gyrus	positive	31	4.4912	-34.5	-82.5	37.5
4	Dorsal pons	positive	30	5.7828	-1.5	-22.5	-25.5
5	R Superior Medial Gyrus R SMA	positive	26	4.9863	10.5	22.5	58.5
Memory							
aHPC seed							
<i>no clusters survive thresholding</i>							
VTA/SN seed							
1	L Cuneus L Calcarine Gyrus R Calcarine Gyrus R Cuneus	positive	480	5.3752	4.5	-85.5	25.5
2	R Middle Frontal Gyrus R Superior Frontal Gyrus R Anterior Cingulate Cortex L Superior Medial Gyrus R Middle Cingulate Cortex R Superior Medial Gyrus	positive	227	5.7297	28.5	40.5	34.5
3	L Anterior Cingulate Cortex L Postcentral Gyrus	positive	205	5.3584	4.5	28.5	34.5
4	L Precentral Gyrus R Angular Gyrus	positive	82	4.8762	-46.5	-22.5	55.5
5	R Inferior Parietal Lobule	positive	77	4.5695	43.5	-70.5	46.5
6	R Insula Lobe	positive	65	5.1114	31.5	28.5	4.5
7	R Inferior Parietal Lobule R Supramarginal Gyrus	positive	52	4.7107	55.5	-43.5	43.5
8	R Middle Frontal Gyrus L SMA	positive	47	5.2007	40.5	13.5	58.5
9	R SMA L Angular Gyrus	positive	42	4.3257	-4.5	16.5	58.5
10	L Inferior Parietal Lobule	positive	39	4.7107	-43.5	-64.5	46.5
11	R Middle Frontal Gyrus	positive	35	4.7809	43.5	19.5	43.5
12	R Inferior Temporal Gyrus	positive	32	4.8716	58.5	-55.5	-13.5

Appendix

13	L Middle Frontal Gyrus	positive	32	4.5784	-37.5	52.5	19.5
14	R Middle Temporal Gyrus	positive	28	4.719	64.5	-34.5	-13.5
	R Cuneus						
15	R Superior Occipital Gyrus	positive	27	4.4552	16.5	-91.5	28.5
	L Caudate Nucleus						
16	L Putamen	positive	23	5.1853	-16.5	16.5	-1.5
17	L Cerebellum (Crus 2)	positive	20	5.2813	-46.5	-64.5	-52.5
	L Middle Occipital Gyrus			-			
18	L Inferior Occipital Gyrus	negative	21	4.4753	-22.5	-97.5	-1.5

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aHPC seed

	R Lingual Gyrus						
	R Calcarine Gyrus						
	R Fusiform Gyrus						
	R Cuneus						
1	R Superior Occipital Gyrus	positive	377	6.7356	16.5	-79.5	-7.5
	L Calcarine Gyrus						
	L Superior Occipital Gyrus						
	L Cuneus						
2	L Lingual Gyrus	positive	144	6.2075	-7.5	-94.5	13.5
	L Middle Frontal Gyrus						
	L Inferior Frontal Gyrus (p. Triangularis)						
3	L Inferior Frontal Gyrus (p. Opercularis)	positive	137	5.858	-43.5	28.5	34.5
	L Inferior Parietal Lobule						
4	L Angular Gyrus	positive	112	6.1657	-28.5	-76.5	49.5
	L Superior Parietal Lobule						
	L Inferior Frontal Gyrus (p. Orbitalis)						
	L Inferior Frontal Gyrus (p. Triangularis)						
	L Middle Orbital Gyrus						
5	L Middle Frontal Gyrus	positive	105	4.7188	-49.5	34.5	-7.5
	R Angular Gyrus						
	R Superior Occipital Gyrus						
6	R Superior Parietal Lobule	positive	93	5.3644	37.5	-67.5	49.5
7	R Middle Temporal Gyrus	positive	71	4.6236	-61.5	-55.5	19.5
	R Middle Temporal Gyrus						
8	R Superior Temporal Gyrus	positive	55	4.5192	58.5	-34.5	-1.5
	L Lingual Gyrus						
9	L Cerebellum (Crus 1)	positive	53	5.3504	-13.5	-85.5	-13.5
	L SMA						
10	R SMA	positive	51	4.6741	-1.5	19.5	55.5
11	R Inferior Parietal Lobule	positive	49	4.6818	46.5	-49.5	49.5
12	L Middle Frontal Gyrus	positive	45	4.657	-28.5	49.5	19.5
	R Fusiform Gyrus						
13	R Lingual Gyrus	positive	35	5.2247	22.5	-58.5	-10.5
	L Superior Orbital Gyrus						
	L Middle Orbital Gyrus						
14	L Superior Frontal Gyrus	positive	33	4.731	-22.5	61.5	-7.5

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15	R Precuneus	positive	26	4.306	7.5	-73.5	49.5
	L Superior Frontal Gyrus						
16	L Superior Medial Gyrus	positive	20	4.4976	-16.5	64.5	13.5
	L Inferior Occipital Gyrus			-			
17	L Middle Occipital Gyrus	negative	112	6.9394	-19.5	-100.5	-10.5
VTA/SN seed							
	L Precentral Gyrus						
	R Superior Frontal Gyrus						
	L SMA						
	R SMA						
	R Precentral Gyrus						
1	L Superior Frontal Gyrus	positive	804	10.396	-25.5	-13.5	58.5
	L Superior Parietal Lobule						
	L Postcentral Gyrus						
	L Inferior Parietal Lobule						
2	L Supramarginal Gyrus	positive	749	9.5435	-25.5	-67.5	64.5
	R Postcentral Gyrus						
	R Superior Parietal Lobule						
	R Supramarginal Gyrus						
3	R Inferior Parietal Lobule	positive	407	9.5024	31.5	-40.5	49.5
	R Inferior Occipital Gyrus						
	R Calcarine Gyrus						
4	R Middle Occipital Gyrus	positive	193	8.7441	25.5	-103.5	1.5
	L Middle Occipital Gyrus						
5	L Inferior Occipital Gyrus	positive	155	7.9807	-22.5	-103.5	-7.5
	L Precentral Gyrus						
6	L Postcentral Gyrus	positive	90	6.7871	-61.5	7.5	28.5
7	L Middle Occipital Gyrus	positive	42	5.9038	-37.5	-70.5	4.5
8	R Precentral Gyrus	positive	42	6.2684	64.5	7.5	25.5
9	L Cerebellum (VIII)	positive	29	5.3834	-25.5	-64.5	-52.5
10	L Rolandic Operculum	positive	28	6.5409	-52.5	-4.5	13.5
	L Middle Frontal Gyrus						
	R Middle Frontal Gyrus						
	L Superior Medial Gyrus						
	R Superior Frontal Gyrus						
	L Cerebellum (Crus 1)						
	L Inferior Frontal Gyrus (p. Triangularis)						
	R Superior Medial Gyrus						
	R Cerebellum (Crus 1)						
	R Inferior Frontal Gyrus (p. Triangularis)						
	R Inferior Frontal Gyrus (p. Orbitalis)						
	R Middle Temporal Gyrus						
	L Calcarine Gyrus						
	L Cerebellum (Crus 2)						
	L Cuneus						
	L Superior Frontal Gyrus						
	R Angular Gyrus						
11	L Middle Temporal Gyrus	negative	18122	-11.71	49.5	-52.5	52.5

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	R Inferior Temporal Gyrus						
	L Inferior Frontal Gyrus (p. Orbitalis)						
	R Precuneus						
	R Cuneus						
	L Precuneus						
	L Lingual Gyrus						
	R Inferior Parietal Lobule						
	R Calcarine Gyrus						
	R Lingual Gyrus						
	L Inferior Temporal Gyrus						
	R Middle Orbital Gyrus						
	R Cerebellum (Crus 2)						
	R Caudate Nucleus						
	L SMA						
	R Anterior Cingulate Cortex						
	R Inferior Frontal Gyrus (p. Opercularis)						
	L Middle Orbital Gyrus						
	L Anterior Cingulate Cortex						
	L Superior Occipital Gyrus						
	L Inferior Parietal Lobule						
	L Angular Gyrus						
12	L Middle Occipital Gyrus	negative	951	-9.872	-46.5	-58.5	55.5
13	L Inferior Temporal Gyrus	negative	112	-5.771	-43.5	4.5	-40.5
	R Parahippocampal Gyrus						
	R Amygdala						
14	R Hippocampus	negative	81	-5.083	25.5	-10.5	-34.5
	Fusiform Gyrus						
	Inferior Temporal Gyrus						
15	Parahippocampal Gyrus	negative	55	-5.485	-31.5	-7.5	-34.5
	L Insula Lobe						
16	L Superior Temporal Gyrus	negative	22	-5.464	-37.5	-4.5	-7.5
	R Parahippocampal Gyrus						
17	R Hippocampus	negative	21	-4.646	28.5	-19.5	-22.5

Note. Results are thresholded at $p < 0.001$, cluster-extent corrected at $k = 20$ (equivalent to per-cluster $\alpha = 0.05$) for whole brain analysis. The table corresponds to Figure A3.9. (x, y, and z) denote MNI coordinates of the peak voxel. Cluster size is given in voxels. ISFC-RSA = Intersubject Functional Connectivity Representational Similarity Analysis, aHPC = anterior hippocampus, VTA/SN = ventral tegmental area/substantia nigra, L = left, R = right.

Table A3.13

Whole Brain Results of ISFC-RSA For the Interaction Between the Incentive Manipulation and Each Behavioural Effect of Interest Specifying aHPC and VTA/SN as Seeds

Cluster	Macro Label	Direction	Cluster Size	Maximum Intensity			
				t value	x	y	z
Curiosity							
aHPC seed	<i>no clusters survive thresholding</i>						
VTA/SN seed	<i>no clusters survive thresholding</i>						
Memory							
aHPC seed	<i>no clusters survive thresholding</i>						
VTA/SN seed	<i>no clusters survive thresholding</i>						
1	R Middle Occipital Gyrus R Superior Occipital Gyrus R Calcarine Gyrus R Inferior Occipital Gyrus L Posterior Cingulate Cortex L Middle Cingulate Cortex R Middle Cingulate Cortex	I > C	20	-4.2192	28.5	-100.5	1.5
2	R Precuneus L Middle Frontal Gyrus	I < C	79	4.7595	1.5	-49.5	25.5
3	L Middle Orbital Gyrus	I < C	31	5.3363	-43.5	55.5	1.5
Curiosity-Motivated Learning Enhancement							
aHPC seed	<i>no clusters survive thresholding</i>						
VTA/SN seed	<i>no clusters survive thresholding</i>						
1	L Inferior Occipital Gyrus	I < C	28	5.2033	-43.5	-70.5	-4.5
1	L Precuneus R Precuneus	I > C	264	-5.5263	-13.5	-73.5	46.5
2	R Middle Frontal Gyrus R Middle Orbital Gyrus L Middle Frontal Gyrus	I > C	149	-5.7355	37.5	61.5	7.5
3	L Middle Orbital Gyrus	I > C	110	-4.9382	-40.5	49.5	-1.5
4	R Inferior Parietal Lobule	I > C	98	-5.4174	49.5	-49.5	58.5
5	L Supramarginal Gyrus	I > C	93	-6.7075	-64.5	-49.5	31.5
6	R Middle Temporal Gyrus	I > C	67	-4.9715	61.5	-28.5	-4.5
7	L Inferior Parietal Lobule L Superior Medial Gyrus	I > C	67	-4.7524	-37.5	-52.5	40.5
8	R Superior Medial Gyrus R Cuneus	I > C	51	-4.3063	1.5	25.5	37.5
9	R Precuneus	I > C	47	-4.633	19.5	-70.5	28.5
10	R Angular Gyrus L Superior Frontal Gyrus	I > C	47	-4.6916	43.5	-73.5	46.5
11	L SMA	I > C	39	-5.4058	-19.5	16.5	67.5
12	R Middle Frontal Gyrus	I > C	33	-5.2262	40.5	10.5	55.5
13	L Middle Frontal Gyrus	I > C	22	-4.6668	-52.5	28.5	34.5

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14	L Inferior Frontal Gyrus (p. Orbitalis)	I > C	20	-4.2697	-40.5	22.5	-10.5
15	R Superior Parietal Lobule	I < C	50	4.9234	25.5	-67.5	64.5
16	R Superior Frontal Gyrus R Precentral Gyrus	I < C	30	5.3659	25.5	-10.5	55.5

Note. Results are thresholded at $p < 0.001$, cluster-extent corrected at $k = 20$ (equivalent to per-cluster $\alpha = 0.05$) for whole brain analysis. The table corresponds to Figure A3.9. (x, y, and z) denote MNI coordinates of the peak voxel. Cluster size is given in voxels. ISFC-RSA = Intersubject Functional Connectivity Representational Similarity Analysis, aHPC = anterior hippocampus, VTA/SN = ventral tegmental area/substantia nigra, L = left, R = right, C = control group, I = incentive group.

Table A4.1

Functional Connectivity Between aHPC and VTA/SN at Different Phases For Different Pre-processing Pipelines

	Whole sample		Control group		Incentives group		Difference C < I	
	Mean (SE)	t-test	Mean (SE)	t-test	Mean (SE)	t-test	Mean (SE)	t-test
	Change [pre < post]							
FWHM = 0	0.003 (0.004)	$t(49) = 0.86,$ $p = 0.196$	0.007 (0.006)	$t(24) = 1.14,$ $p = 0.132$	0 (0.006)	$t(24) = 0.04,$ $p = 0.483$	-0.007 (0.008)	$t(47.81) = 0.8,$ $p = 0.426$
FWHM = 4	0.004 (0.004)	$t(49) = 0.93,$ $p = 0.178$	0.008 (0.006)	$t(24) = 1.18,$ $p = 0.125$	0.001 (0.006)	$t(24) = 0.10,$ $p = 0.46$	-0.007 (0.009)	$t(47.82) = 0.79,$ $p = 0.435$
FWHM = 6	0.006 (0.007)	$t(49) = 0.9,$ $p = 0.186$	0.011 (0.01)	$t(24) = 1.15,$ $p = 0.132$	0.001 (0.01)	$t(24) = 0.12,$ $p = 0.452$	-0.01 (0.014)	$t(48) = 0.72,$ $p = 0.473$
FWHM = 8	0.007 (0.009)	$t(49) = 0.83,$ $p = 0.207$	0.014 (0.013)	$t(24) = 1.07,$ $p = 0.147$	0.001 (0.013)	$t(24) = 0.09,$ $p = 0.465$	-0.012 (0.018)	$t(48) = 0.69,$ $p = 0.49$
	Online encoding							
FWHM = 0	0.027 (0.003)	$t(49) = 9.92,$ $p < 0.001$	0.029 (0.004)	$t(24) = 6.74,$ $p < 0.001$	0.025 (0.003)	$t(24) = 7.49,$ $p < 0.001$	-0.005 (0.005)	$t(44.62) = 0.87,$ $p = 0.39$
FWHM = 4	0.032 (0.003)	$t(49) = 10.74,$ $p < 0.001$	0.034 (0.005)	$t(24) = 7.26,$ $p < 0.001$	0.029 (0.004)	$t(24) = 8.17,$ $p < 0.001$	-0.005 (0.006)	$t(44.63) = 0.87,$ $p = 0.387$
FWHM = 6	0.071 (0.005)	$t(49) = 13.59,$ $p < 0.001$	0.075 (0.009)	$t(24) = 8.57,$ $p < 0.001$	0.068 (0.006)	$t(24) = 11.45,$ $p < 0.001$	-0.007 (0.011)	$t(42.21) = 0.67,$ $p = 0.507$
FWHM = 8	0.112 (0.007)	$t(49) = 15.28,$ $p < 0.001$	0.117 (0.012)	$t(24) = 9.42,$ $p < 0.001$	0.107 (0.008)	$t(24) = 13.45,$ $p < 0.001$	-0.01 (0.015)	$t(40.92) = 0.66,$ $p = 0.516$
	Offline encoding							
FWHM = 0	0.026 (0.004)	$t(49) = 7.02,$ $p < 0.001$	0.026 (0.006)	$t(24) = 4.46,$ $p < 0.001$	0.026 (0.005)	$t(24) = 5.55,$ $p < 0.001$	0 (0.008)	$t(45.81) = 0.01,$ $p = 0.994$
FWHM = 4	0.031 (0.004)	$t(49) = 7.53,$ $p < 0.001$	0.031 (0.006)	$t(24) = 4.93,$ $p < 0.001$	0.031 (0.006)	$t(24) = 5.69,$ $p < 0.001$	0 (0.008)	$t(47.17) = -0.04,$ $p = 0.972$
FWHM = 6	0.072 (0.007)	$t(49) = 10.01,$ $p < 0.001$	0.072 (0.011)	$t(24) = 6.69,$ $p < 0.001$	0.072 (0.01)	$t(24) = 7.38,$ $p < 0.001$	0 (0.014)	$t(47.55) = 0,$ $p = 0.997$
FWHM = 8	0.111 (0.01)	$t(49) = 11.5,$ $p < 0.001$	0.112 (0.015)	$t(24) = 7.63,$ $p < 0.001$	0.111 (0.013)	$t(24) = 8.55,$ $p < 0.001$	0 (0.020)	$t(47.37) = 0.02,$ $p = 0.988$

Note. The tables shows M = mean and SE = standard error of measures of functional connectivity (FC) between anterior hippocampus (aHPC) and dopaminergic midbrain (VTA/SN), computed across the whole sample as well as within each group separately. T-tests (one-tailed) were used to

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determine whether the FC was larger than zero. Additionally, the difference between both groups was computed and group effects were tested using Two-Sample t-test (two-sided) not assuming equal variances. FC was computed for pre- and post-learning rest to determine the change therein, as well as during online (volumes obtained during magic trick presentation) and offline (last volume of magic trick presentation and two consecutive volumes of fixation) encoding. The same analysis was applied to data from different pre-processing pipelines using different FWHM kernels where 0 is equivalent to unsmoothed data and the other numbers represent the input for AFNI's 3dBlurToFWHM algorithm. $t = t$ value. $p = p$ value.

Table A4.2

Robust Correlation Coefficients Between aHPC-VTA/SN-RSFC Change and Behavioural Measures of Learning Irrespective of Pre-processing

	Whole sample		Control group		Incentives group		Difference C < I	
	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>	<i>r</i>	<i>p</i>
	absolute # items encoded							
FWHM = 0	0.069	0.633	-0.335	0.102	0.388	0.055	0.723	0.012
FWHM = 4	0.08	0.580	-0.313	0.128	0.389	0.054	0.702	0.015
FWHM = 6	0.134	0.353	-0.342	0.094	0.492	0.013	0.834	0.003
FWHM = 8	0.165	0.253	-0.328	0.11	0.536	0.006	0.864	0.002
	CMLE							
FWHM = 0	-0.067	0.645	0.314	0.126	-0.383	0.058	-0.698	0.016
FWHM = 4	-0.079	0.588	0.291	0.158	-0.386	0.057	-0.677	0.019
FWHM = 6	-0.136	0.348	0.322	0.116	-0.494	0.012	-0.816	0.004
FWHM = 8	-0.167	0.245	0.311	0.131	-0.542	0.005	-0.853	0.002

Note. Correlation coefficients were computed using data from the whole sample as well as for each group individually and the difference in correlation between both groups. The same analysis was applied to data from different pre-processing pipelines using different FWHM kernels where 0 is equivalent to unsmoothed data and the other numbers represent the input for AFNI's 3dBlurToFWHM algorithm. *r* = Pearson correlation coefficient. *p* = p value.

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Table A4.3

Results of Linear Regression Predicting Behavioural Measures of Learning Using Different Pre-processing Pipelines

	Whole sample		Control group		Incentives group	
	Beta (SE)	<i>p</i>	Beta (SE)	<i>p</i>	Beta (SE)	<i>p</i>
FWHM = 0						
absolute # items encoded						
Intercept	15.8 (1.05)	< 0.001	15.52 (0.94)	< 0.001	14.76 (1.15)	< 0.001
Online FC	-38.02 (44.2)	0.394	0.45 (52.49)	0.993	-91.19 (78.68)	0.26
Offline FC	20.68 (32.37)	0.526	-0.13 (40.32)	0.997	36.99 (53.04)	0.493
Incentives	-0.85 (1.49)	0.574				
RSFC change Incentives *	-59.01 (36.92)	0.117	-52.49 (34.3)	0.141	95.19 (45.42)	0.048
RSFC change	146.8 (53.39)	0.009				
CMLE						
Intercept	0.06 (0.01)	< 0.001	0.06 (0.01)	< 0.001	0.06 (0.01)	< 0.001
Online FC	0.24 (0.29)	0.424	-0.02 (0.35)	0.958	0.59 (0.52)	0.269
Offline FC	-0.15 (0.22)	0.484	-0.01 (0.27)	0.96	-0.26 (0.35)	0.468
Incentives	0 (0.01)	0.977				
RSFC change Incentives *	0.37 (0.25)	0.135	0.33 (0.23)	0.164	-0.62 (0.3)	0.053
RSFC change	-0.94 (0.35)	0.011				
FWHM = 6						
absolute # items encoded						
Intercept	15.7 (1.01)	< 0.001	15.52 (0.92)	< 0.001	14.76 (1.11)	< 0.001
Online FC	-1.8 (25.78)	0.945	13.19 (29.32)	0.657	-32.15 (51.16)	0.536
Offline FC	10.12 (18.61)	0.589	0.79 (24.2)	0.974	21.49 (29.26)	0.471
Incentives	-0.65 (1.44)	0.652				
RSFC change Incentives *	-35.06 (21.47)	0.11	-35.03 (19.99)	0.094	64.17 (25.5)	0.02
RSFC change	94.35 (29.97)	0.003				
CMLE						
Intercept	0.06 (0.01)	< 0.001	0.06 (0.01)	< 0.001	0.06 (0.01)	< 0.001
Online FC	0.01 (0.17)	0.971	-0.09 (0.2)	0.64	0.21 (0.34)	0.541
Offline FC	-0.08 (0.12)	0.528	-0.02 (0.16)	0.905	-0.15 (0.19)	0.442
Incentives	0 (0.01)	0.919				
RSFC change Incentives *	0.22 (0.14)	0.122	0.22 (0.13)	0.107	-0.42 (0.17)	0.02
RSFC change	-0.61 (0.2)	0.003				

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FWHM = 8

absolute # items encoded						
Intercept	15.68 (1)	< 0.001	15.52 (0.93)	< 0.001	14.76 (1.08)	< 0.001
Online FC	-1.07 (19.97)	0.958	10.24 (23.2)	0.663	-26.23 (39.81)	0.517
Offline FC	6.85 (14.62)	0.642	0.19 (19.49)	0.992	15.86 (22.71)	0.493
Incentives	-0.62 (1.42)	0.665				
RSFC change	-25.68 (16.43)	0.125	-26.92 (15.63)	0.1	54.25 (19.12)	0.01
Incentives *						
RSFC change	75.42 (22.51)	0.002				
CMLE						
Intercept	0.06 (0.01)	< 0.001	0.06 (0.01)	< 0.001	0.06 (0.01)	< 0.001
Online FC	0.01 (0.13)	0.97	-0.07 (0.15)	0.658	0.17 (0.26)	0.512
Offline FC	-0.06 (0.1)	0.57	-0.01 (0.13)	0.914	-0.11 (0.15)	0.458
Incentives	0 (0.01)	0.899				
RSFC change	0.17 (0.11)	0.134	0.17 (0.1)	0.108	-0.36 (0.13)	0.009
Incentives *						
RSFC change	-0.5 (0.15)	0.002				

Note. The table above shows the results of the linear regressions predicting each behavioural measures of learning using the availability of extrinsic incentives (“Incentives”, effect-coded using 1 for incentives and -1 for control group), aHPC-VTA/SN-RSFC change (“RSFC change”), and their interaction (“Group * RSFC change”) after controlling for the FC between aHPC and VTA/SN during encoding (“Online FC” and “Offline FC”) across the whole sample. Given the significant interaction term for both measures, a linear regression was run within each group using Online and Offline FC as well as RSFC change as predictors to further understand the interaction effects. This table is equivalent to Table 2 in the main text, but using different smoothing kernels during pre-processing where 0 is equivalent to unsmoothed data and the other numbers represent the input for AFNI’s 3dBlurToFWHM algorithm. Beta = unstandardised Beta coefficient. *SE* = standard error. *p* = *p* value.

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Table A4.4

Significant Changes in RSFC from Pre- to Post-Learning Rest Across Both Seeds and Different Pre-processing Pipelines

Cluster	Macro Label	Direction	Cluster Size	Maximum Intensity			
				z value	x	y	z
FWHM = 0							
aHPC seed							
1	L Inferior Frontal Gyrus (pars Orbitalis)	positive	7	4.2973	-34.5	31.5	4.5
2	R Insula Lobe	positive	7	4.0047	34.5	25.5	7.5
3	R Postcentral Gyrus	positive	5	4.0041	58.5	-19.5	43.5
VTA/SN seed							
<i>no clusters survive thresholding</i>							
FWHM = 4							
aHPC seed							
1	L Supramarginal Gyrus	positive	8	4.3465	-49.5	-43.5	25.5
2	L Inferior Frontal Gyrus (pars Orbitalis)	positive	7	4.3031	-34.5	31.5	4.5
3	R Insula Lobe	positive	7	4.0265	34.5	22.5	10.5
4	R Superior Temporal Gyrus	positive	6	4.0113	52.5	-19.5	10.5
VTA/SN seed							
<i>no clusters survive thresholding</i>							
FWHM = 6							
aHPC seed							
1	R Superior Temporal Gyrus						
1	R Temporal Pole	positive	61	4.658	55.5	-1.5	-1.5
2	L Inferior Frontal Gyrus (pars Orbitalis)	positive	34	4.5569	-37.5	25.5	-7.5
3	Left Middle Frontal Gyrus	positive	26	4.2229	-28.5	7.5	61.5
4	L Inferior Frontal Gyrus (pars Orbitalis)	positive	25	4.187	-58.5	7.5	13.5
5	R Postcentral Gyrus						
5	R Precentral Gyrus	positive	24	4.7927	58.5	-16.5	43.5
6	L Supramarginal Gyrus	positive	22	4.4761	-52.5	-43.5	25.5
7	L Superior Temporal Gyrus	positive	21	3.8818	-55.5	-22.5	7.5
VTA/SN seed							
<i>no clusters survive thresholding</i>							
FWHM = 8							
aHPC seed							
1	R Temporal Pole						
1	R Superior Temporal Gyrus	positive	138	4.9612	55.5	-1.5	-1.5
2	L/R SMA	positive	135	4.4827	-10.5	7.5	55.5
3	L Inferior Frontal Gyrus (pars Orbitalis)	positive	132	4.4482	-58.5	7.5	13.5
4	L Middle Frontal Gyrus						
4	L Precentral Gyrus	positive	79	4.3677	-31.5	-10.5	61.5
5	L Superior Temporal Gyrus						
5	L Middle Temporal Gyrus	positive	61	4.4129	-67.5	-16.5	4.5

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6	L Inferior Frontal Gyrus (pars Orbitalis)	positive	53	4.5471	-34.5	25.5	-7.5
7	R Inferior Frontal Gyrus (pars Orbitalis)	positive	49	4.4046	34.5	22.5	7.5
8	R Insula Lobe	positive	47	4.3851	58.5	-16.5	43.5
	R Precentral Gyrus						
	R Postcentral Gyrus						
	VTA/SN seed						

no clusters survive thresholding

Note. Results are thresholded at $p < 0.001$, cluster-extent corrected at the threshold k equivalent to per-cluster $\alpha = 0.05$, as the cluster extent threshold has been simulated separately ($k_{0mm} = 5$, $k_{4mm} = 6$, $k_{6mm} = 18$, $k_{8mm} = 37$). The results presented in this table are shown in Figure A4.4. (x , y , and z) denote MNI coordinates of the peak voxel. Cluster size is given in voxels. aHPC = anterior hippocampus, VTA/SN = ventral tegmental area/substantia nigra, L = left, R = right.

Appendix

Supplementary Figures

Figure A3.1

Methodology to Determine the Optimal Lag to Apply During Concatenation



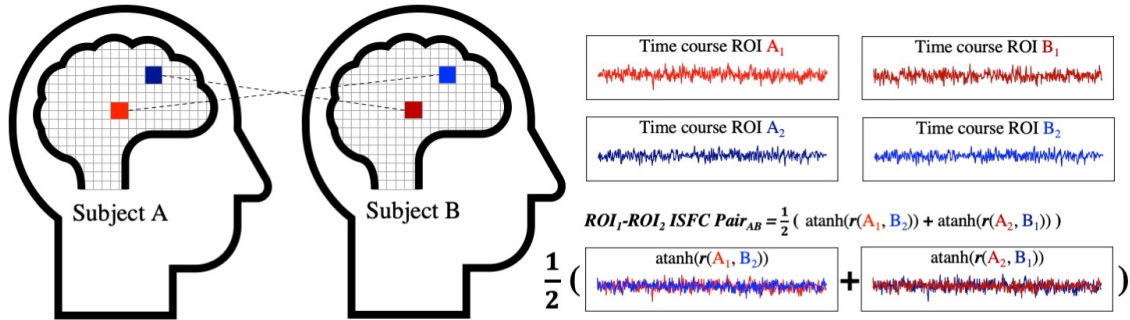
Appendix

Note. Due to inconsistencies in the literature, the optimal HRF lag was determined based on data. (A) To reverse the pseudo-randomisation of stimuli, an initial concatenation step was applied. (B) During the initial concatenation, volumes before and after the magic trick video were selected and categorised depending on events in the experimental task. (C) The concatenated time series were used to extract the time course of the second visual cortex (V2) for each voxel at each time point. The data in time point $t(i)$ in a given subject was correlated with time points from the mean time series of all other subjects creating a time point by time point intersubject pattern correlation (ISPC) matrix for each subject that was Fisher's z-transformed before computing the mean sample ISPC matrix. In the matrix, the k^{th} off-diagonal represents the intersubject reinstatement of time point $t(i)$ at time point $t(i + k)$. The upper diagonal shows the reinstatement of the subject's response in the sample mean of all other subjects whereas the lower diagonal represents the reinstatement of the sample mean of all other subjects in the subject's response. (D) For $1 \leq k \leq 2$, the upper and lower off-diagonals were extracted and labelled in correspondence to (B) without applying any HRF lags. Labels were also shifted for $1 \text{ volume} \leq \text{HRF lag} \leq 6 \text{ volumes}$. (E) For the events "Fixation pre video" and "Fixation post video (volume 1)" (both highlighted in (B)), intersubject reinstatement (measured as correlation) data was averaged and plotted for each HRF lag and k . Error bars represent standard errors.

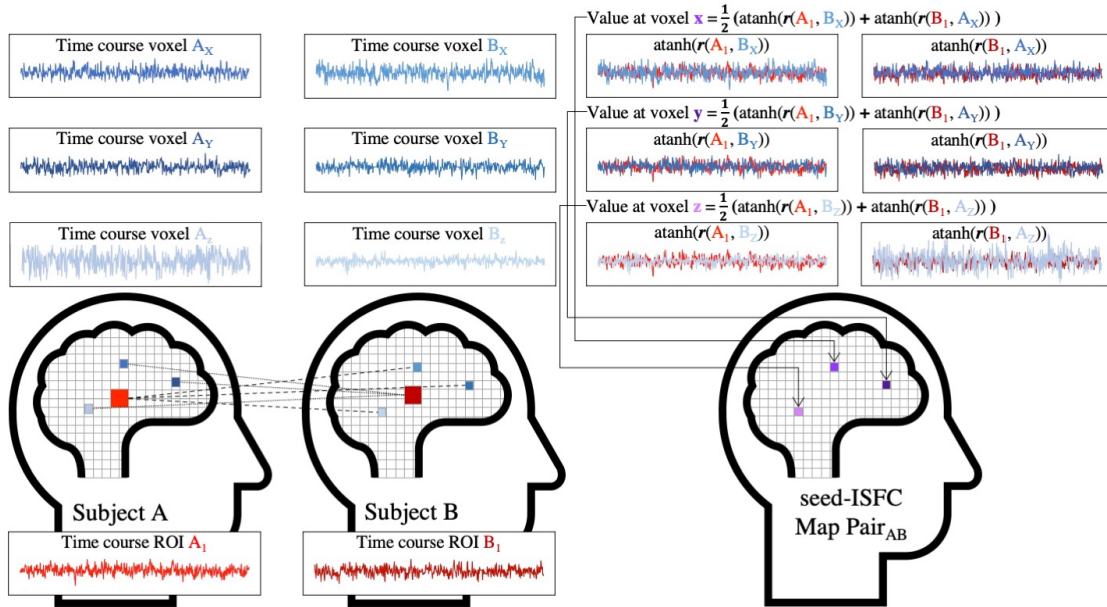
Figure A3.2

Schematic Illustration of Intersubject Functional Connectivity (ISFC)

A ROI-to-ROI



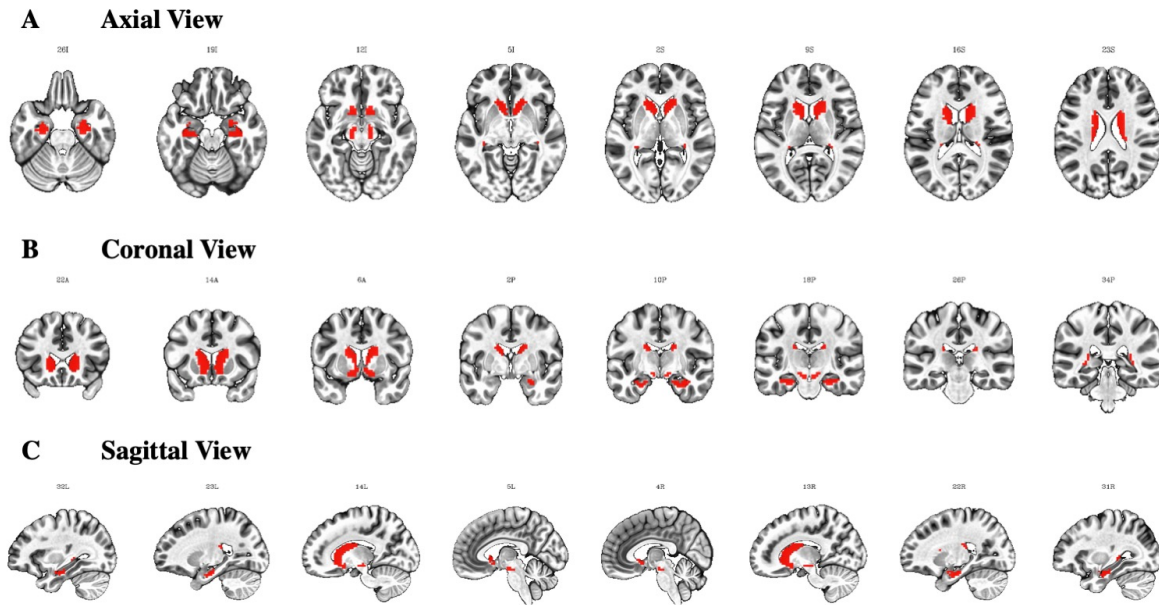
B seed-based



Note. Intersubject functional connectivity (ISFC) was computed as a measurement of consistency of responses between different regions. (A) To compute ISFC between ROIs, the averaged time course of ROI 1 was correlated with the averaged time course of ROI 2 between subjects for each pair of participants. The ROI-to-ROI ISFC for a given pair was determined as the mean of both correlations after Fisher’s z-transformation (indicated as *atanh()*). (B) To compute seed-based ISFC, the averaged ROI time course was correlated with the time course of all other voxels between subjects for each pair of subjects creating a seed-ISFC map for each subject of the pair. Both maps were averaged after Fisher’s z-transformation (indicated as *atanh()*) to determine the seed-ISFC map for the pair.

Figure A3.3

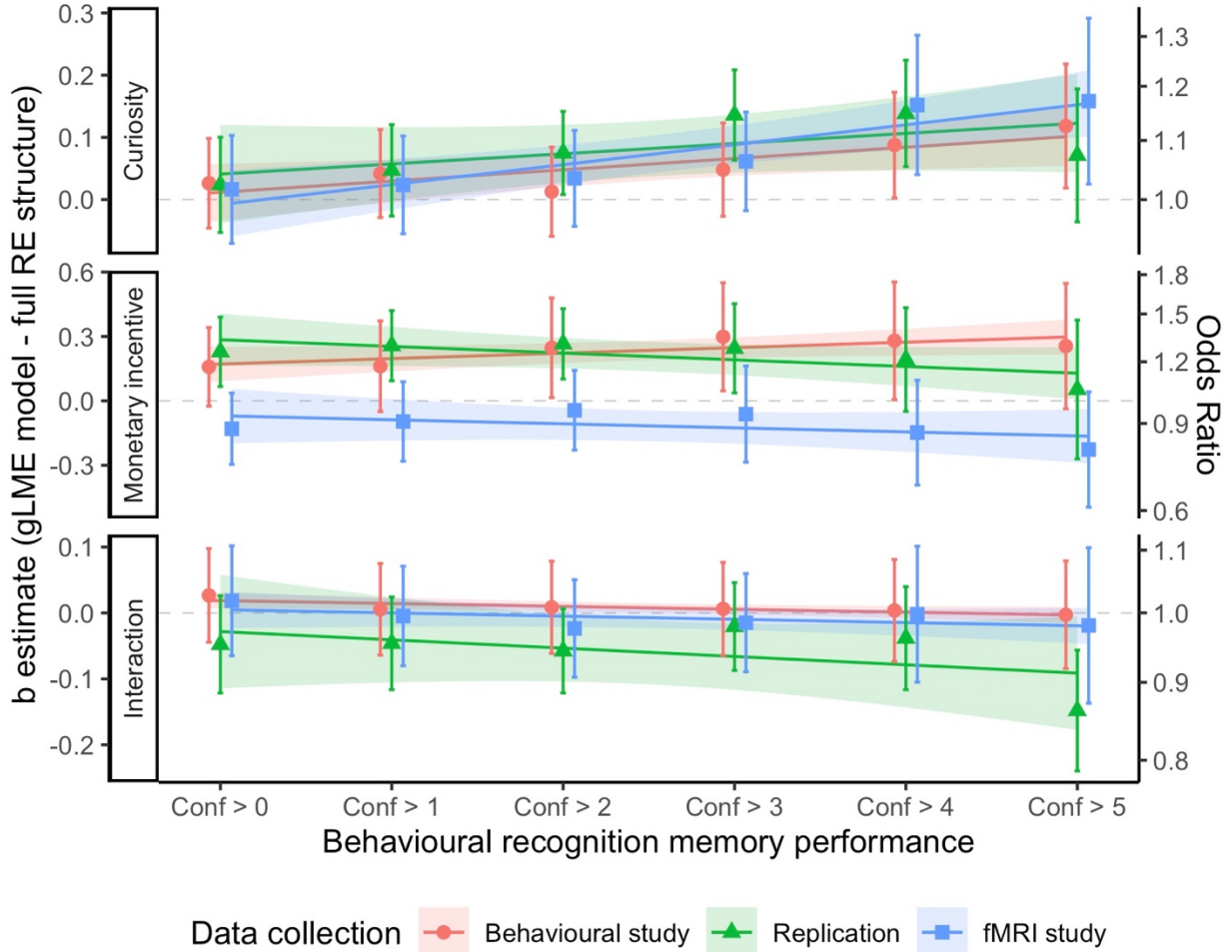
Regions-of-interest (ROIs)



Note. The *a priori* defined ROIs were anterior hippocampus (aHPC), nucleus accumbens (NAcc), caudate nucleus (CN), and dopaminergic midbrain (VTA/SN) in (A) axial, (B) coronal, and (C) sagittal view. For details on how they were created, please refer to the main text. ROIs are shown on the ICBM 2009c Nonlinear Asymmetric Template and resampled to the EPI grid.

Figure A3.4

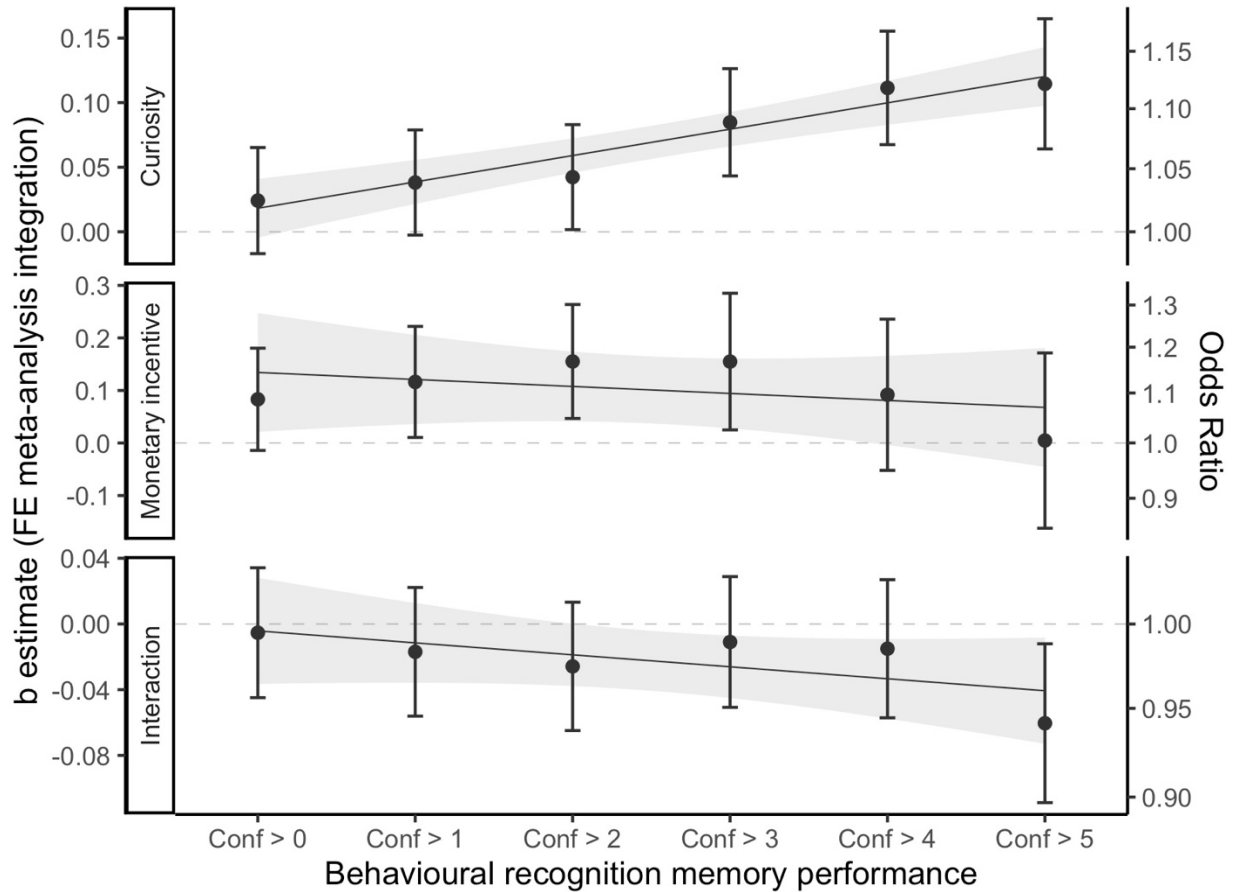
Fixed effects estimates of curiosity, monetary incentive, and their interaction as a function of confidence cut-off separately for each data collection



Note. The x-axis shows the gradual confidence cut-off and y-axis illustrates the integrated effect size (left - unstandardised, right - OR). Each panel shows one of the FE specified in the gLME model. The b estimate from each data collection for each effect and confidence threshold is plotted and error bars indicate 95%-CI. The regression line illustrates the linear model predicting the effect with the gradual confidence cut-off. The data shown here was integrated and plotted in Figure 3.3 in the main text.

Figure A3.5

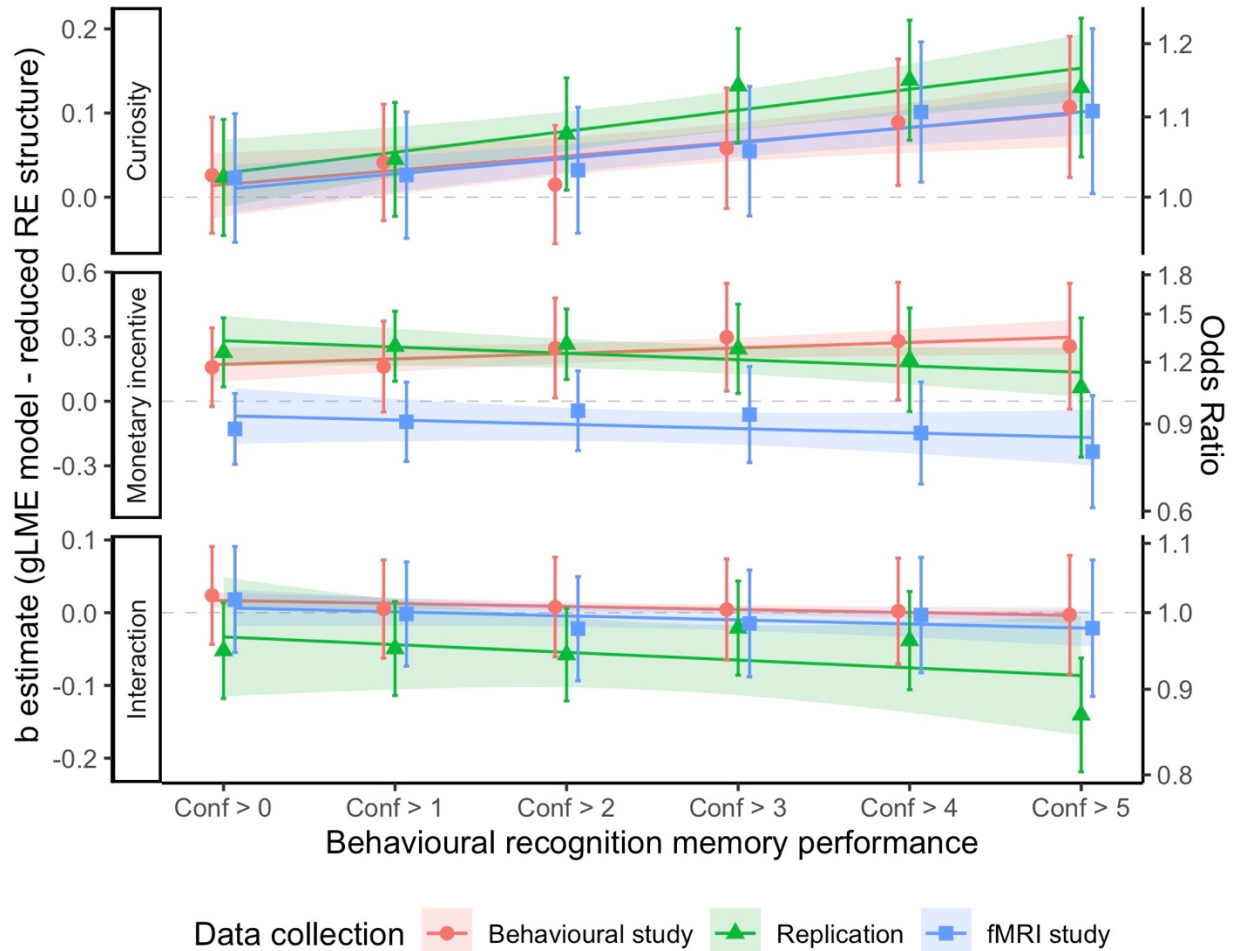
Integrated fixed effects of curiosity, monetary incentive, and their interaction as a function of confidence cut-off



Note. The x-axis shows the gradual confidence cut-off and y-axis illustrates the integrated effect size (left - unstandardised, right - OR). Each panel shows one of the FE specified in the gLME model. Importantly, a gLME model with reduced RE structure (no random slope for the curiosity effect) was used to analyse the data from each data collection before integrating the results. The integrated b estimate for each effect and confidence threshold is plotted and error bars indicate 95%-CI. The regression line illustrates the linear model predicting the effect with the gradual confidence cut-off. This figure corresponds to Figure 3.3 in the main text where a gLME model with full RE structure was specified to analyse the data before FE meta-analysis integration.

Figure A3.6

Fixed effects estimates of curiosity, monetary incentive, and their interaction as a function of confidence cut-off separately for each data collection

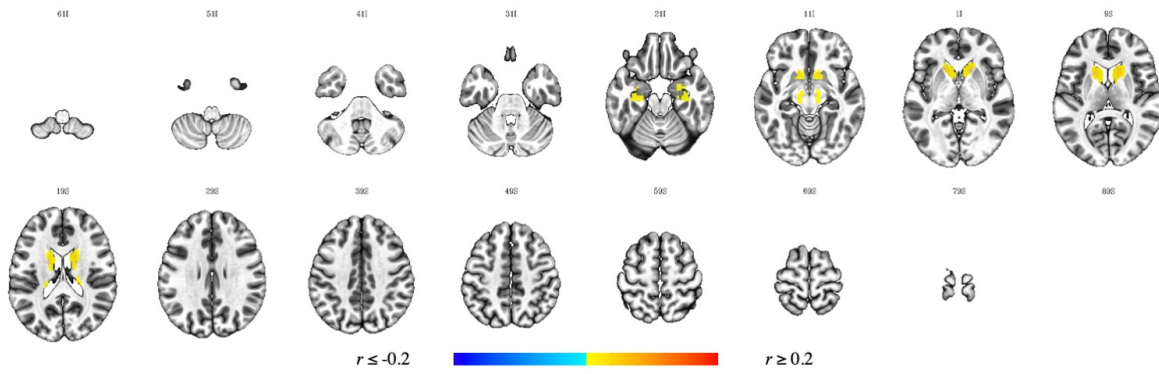


Note. The x-axis shows the gradual confidence cut-off and y-axis illustrates the integrated effect size (left - unstandardised, right - OR). Each panel shows one of the FE specified in the gLME model. Importantly, a gLME model with reduced RE structure (no random slope for the curiosity effect) was used. The b estimate from each data collection for each effect and confidence threshold is plotted and error bars indicate 95%-CI. The regression line illustrates the linear model predicting the effect with the gradual confidence cut-off. The data shown here was integrated and plotted in Figure A3.5 and this figure corresponds to Figure A3.4 where a gLME model with full RE structure was specified.

Appendix

Figure A3.7

ISC in the a priori defined ROIs

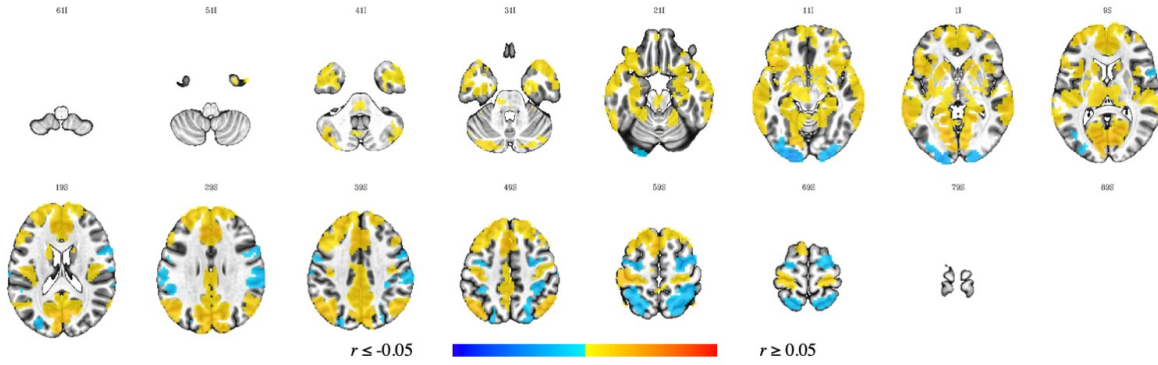


Note. Results are FDR-corrected at $q < 0.05$, cluster-extent corrected at $k = 5$ and plotted on the ICBM 2009c Nonlinear Asymmetric Template. ISC = Intersubject correlation.

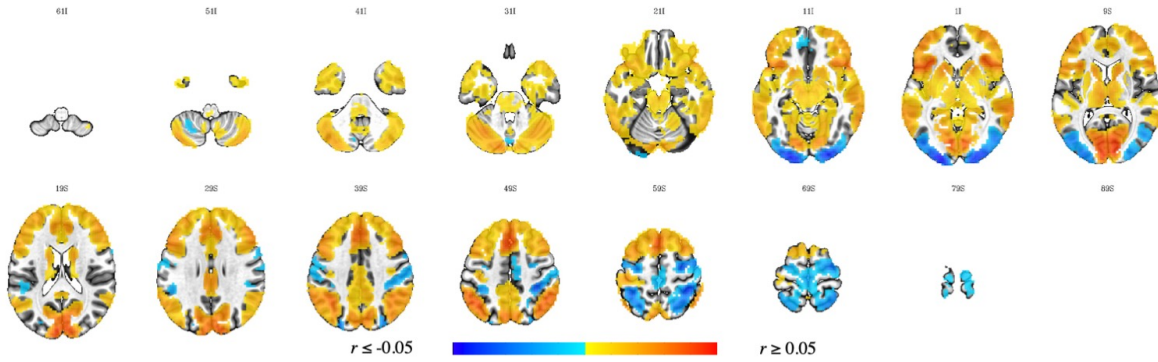
Figure A3.8

ISFC and Incentive Effects Therein Specifying aHPC and VTA/SN as Seeds

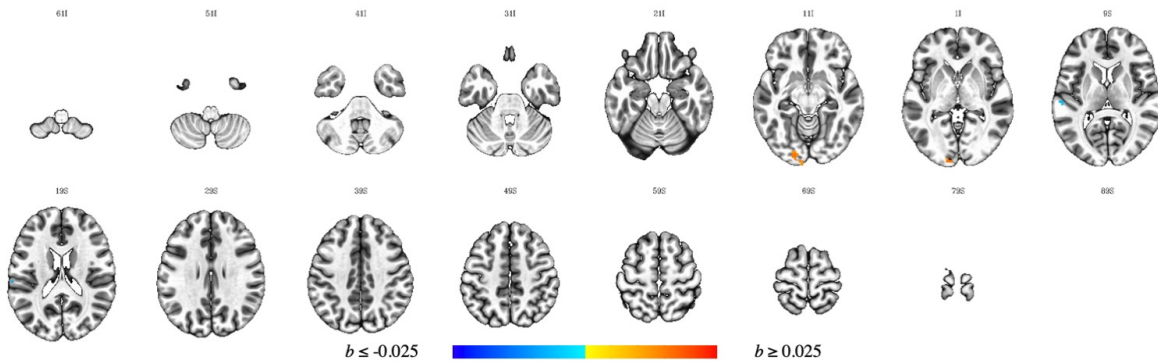
A Average ISFC: aHPC



B Average ISFC: VTA/SN



C ISFC Incentive Effects: VTA/SN



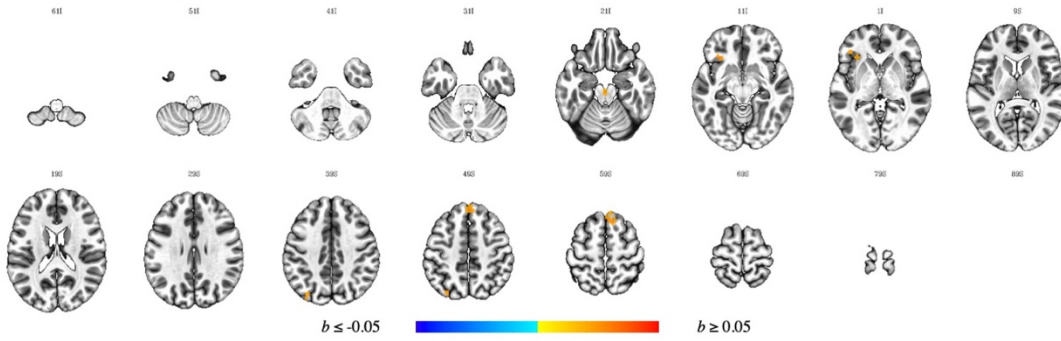
Note. Results are thresholded at $p < 0.001$, cluster-extent corrected at $k = 20$ (equivalent to per-cluster $\alpha = 0.05$) and plotted on the ICBM 2009c Nonlinear Asymmetric Template. ISFC = Intersubject Functional Connectivity, aHPC = anterior hippocampus, VTA/SN = ventral tegmental area/substantia nigra.

Appendix

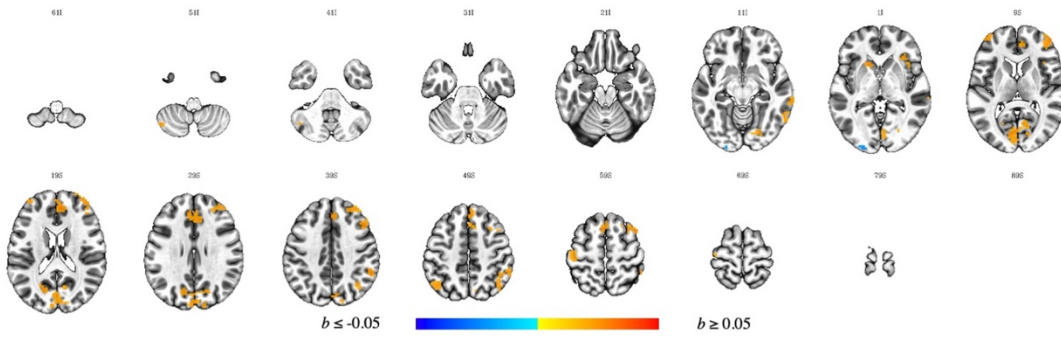
Figure A3.9

ISFC-RSA For Each Behavioural Effect of Interest Specifying aHPC and VTA/SN as Seeds

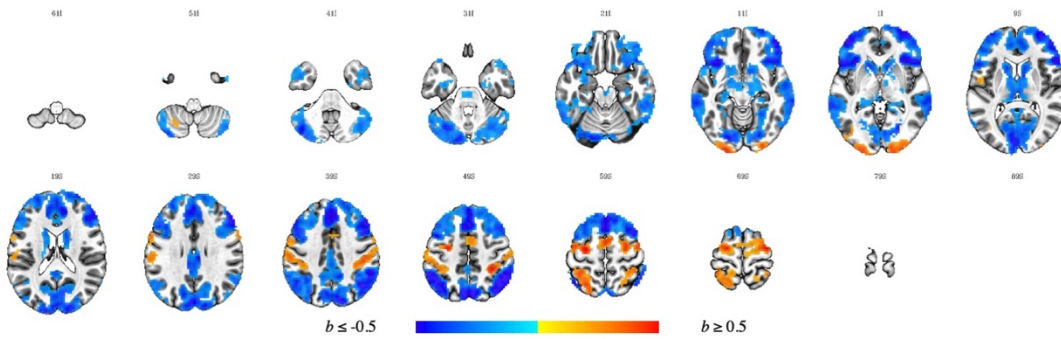
A Curiosity: VTA/SN



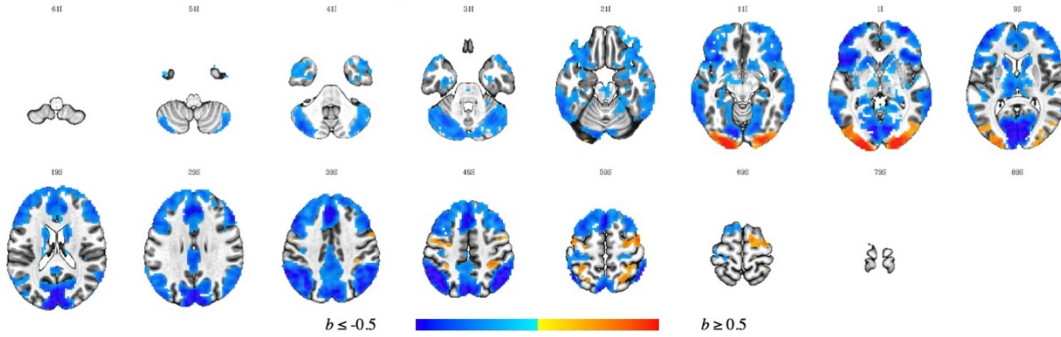
B Memory: VTA/SN



C Curiosity-Motivated Learning Enhancement: VTA/SN



D Curiosity-Motivated Learning Enhancement: aHPC



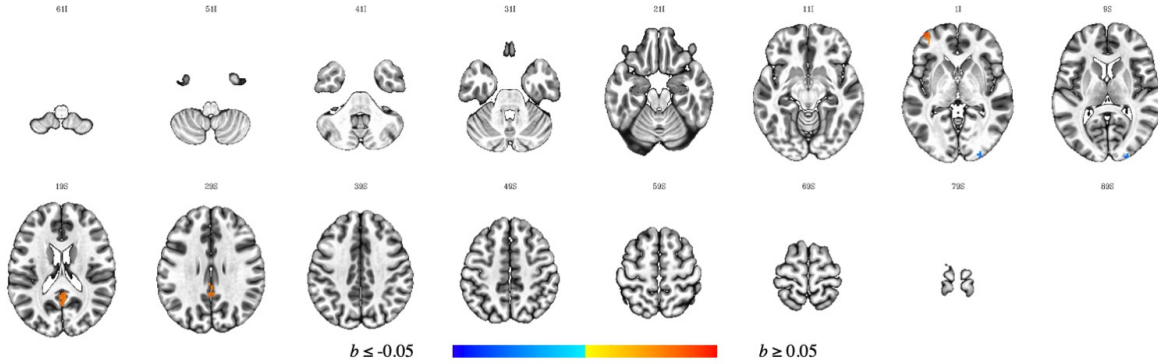
How Curiosity and Incentives Shape Memory Formation

Note. Results are thresholded at $p < 0.001$, cluster-extent corrected at $k = 20$ (equivalent to per-cluster $\alpha = 0.05$) and plotted on the ICBM 2009c Nonlinear Asymmetric Template. ISFC-RSA = Intersubject Functional Connectivity Representational Similarity Analysis, aHPC = anterior hippocampus, VTA/SN = ventral tegmental area/substantia nigra.

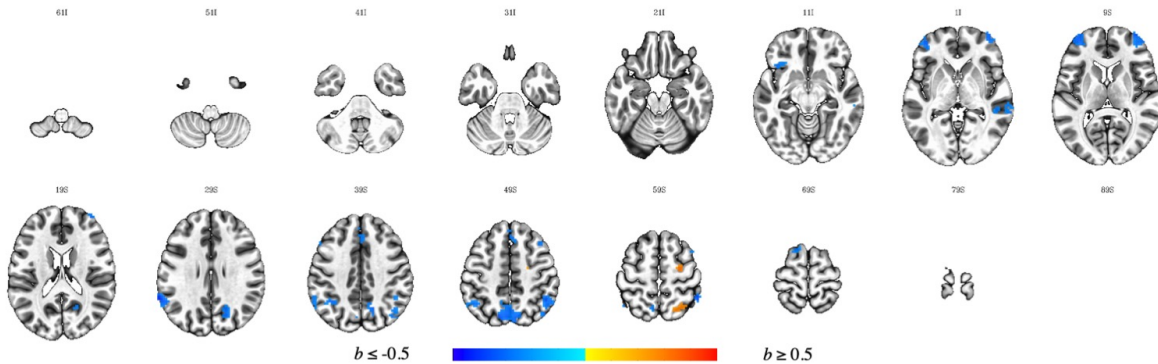
Figure A3.10

ISFC-RSA For The Interaction Between The Incentive Manipulation and Each Behavioural Effect of Interest Specifying aHPC and VTA/SN as Seeds

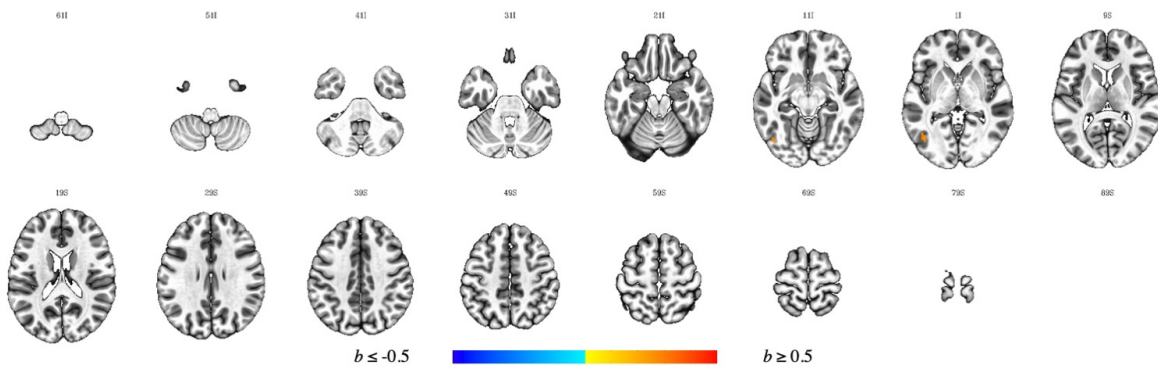
A Memory: VTA/SN



B Curiosity-Motivated Learning Enhancement: VTA/SN



C Curiosity-Motivated Learning Enhancement: aHPC



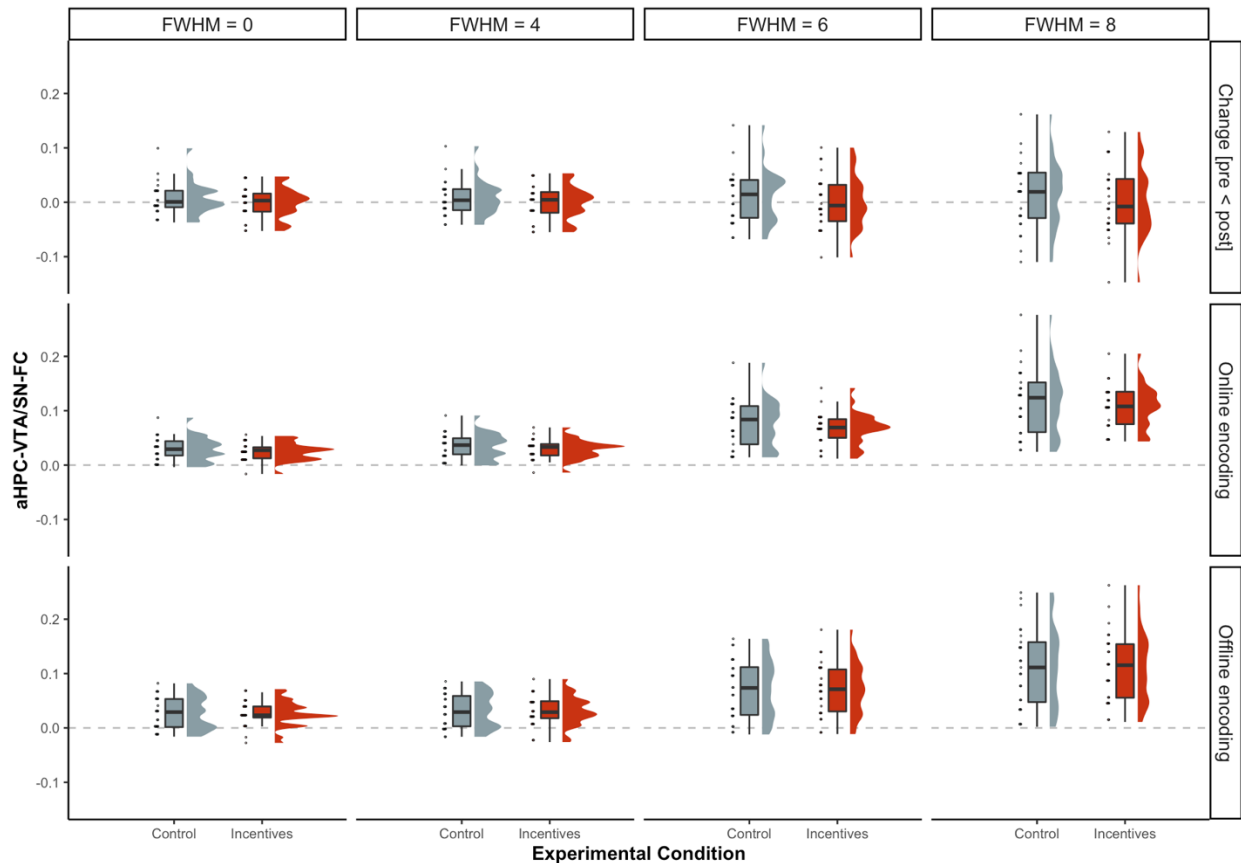
Note. Results are thresholded at $p < 0.001$, cluster-extent corrected at $k = 20$ (equivalent to per-cluster $\alpha = 0.05$) and plotted on the ICBM 2009c Nonlinear Asymmetric Template. Positive clusters (shown in red) indicate more positive values in the control compared to the incentives groups whereas negative clusters (shown in blue) indicate more positive values in the incentives group. ISFC-RSA = Intersubject

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Functional Connectivity Representational Similarity Analysis, aHPC = anterior hippocampus, VTA/SN = ventral tegmental area/substantia nigra.

Figure A4.1

Functional Connectivity (FC) Between Anterior Hippocampus (aHPC) and Dopaminergic Midbrain (VTA/SN) as a Function of Learning Phase and Pre-processing

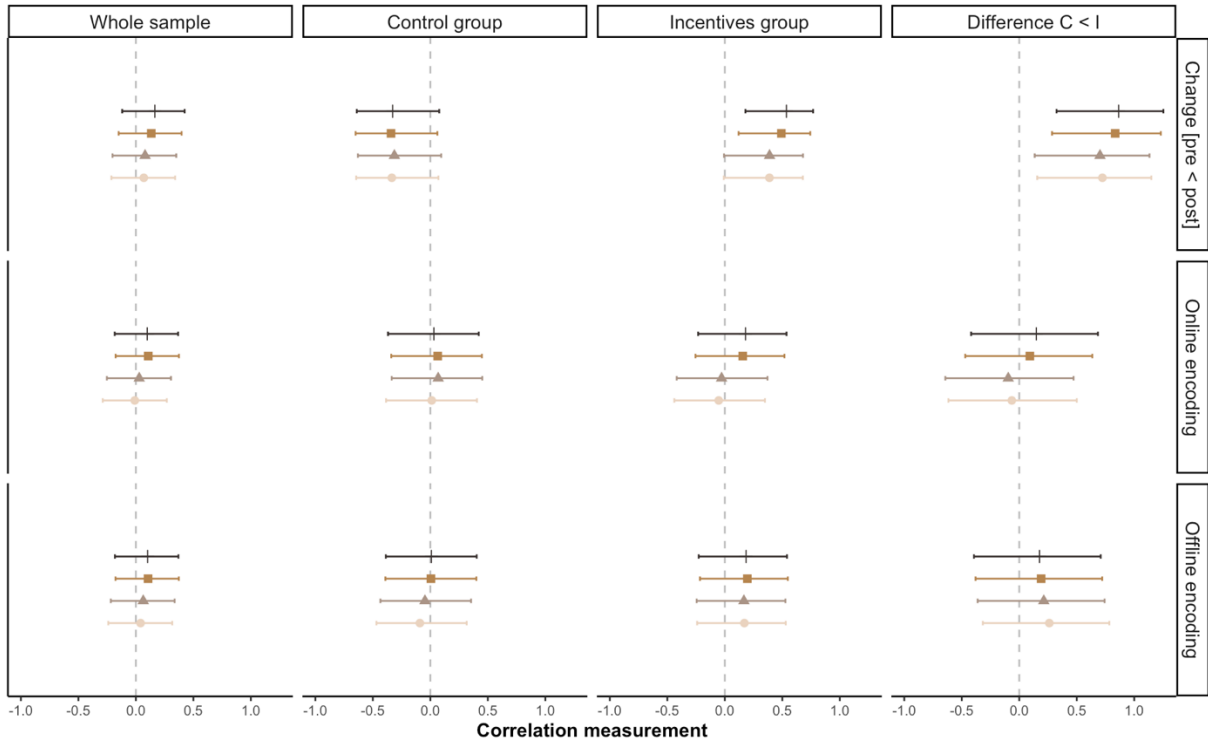


Note. Functional connectivity (FC) between anterior hippocampus (aHPC) and dopaminergic midbrain (VTA/SN) was calculated by using the bilateral aHPC as seed region and then averaging the obtained Fisher's z -transformed correlation values among the voxels in the VTA/SN mask. FC measures between aHPC and VTA/SN were computed separately for each pre- and post-learning rest phase to determine the change therein (top panel). Additionally, the correlation was computed for volumes covering the presentation of magic tricks (online encoding, middle panel) as well as the last volume of magic trick presentation and the following two volumes of fixation (offline encoding, bottom panel). Different full-width half maximum (FWHM) kernels were specified during pre-processing as input for 3dBlurToFWHM where 0 is equivalent to unsmoothed data and the other numbers represent the input for AFNI's 3dBlurToFWHM algorithm. Data is shown as a raincloud plot separately for each group. The dashed horizontal line indicates zero.

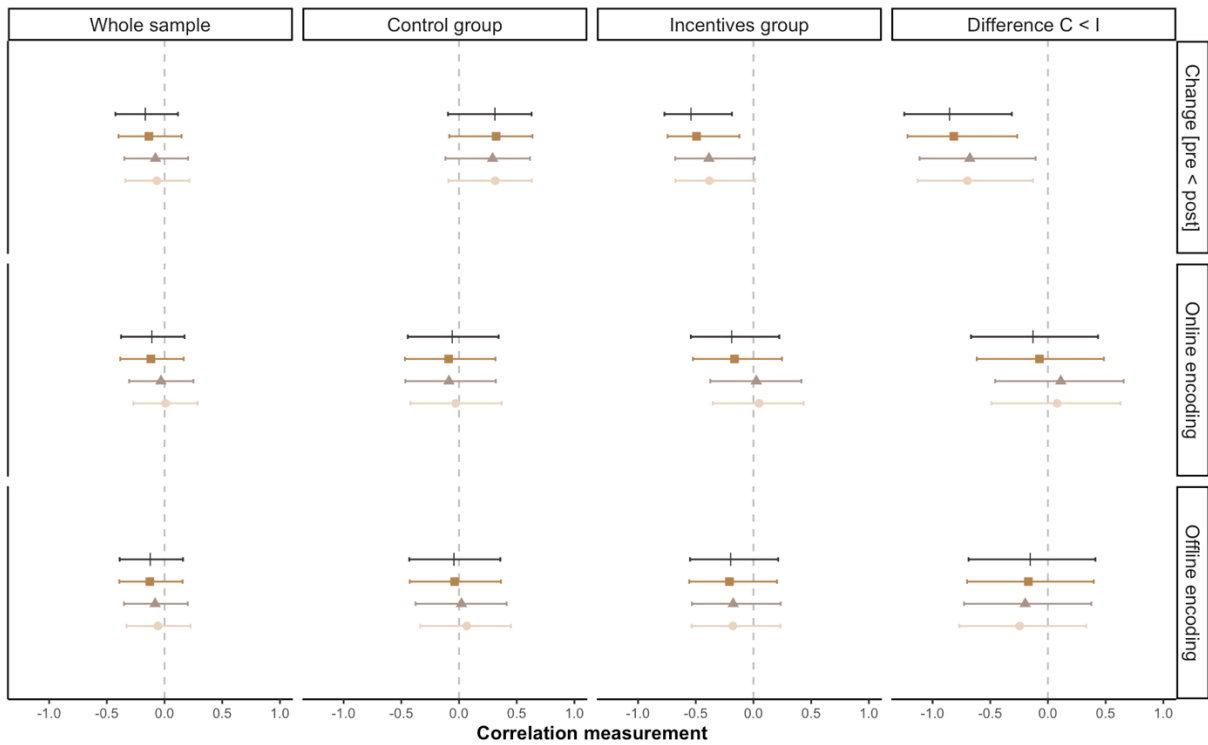
Figure A4.2

Brain-Behaviour Correlation Coefficients as a Function of Learning Phase and Pre-processing

A absolute # items encoded



B CMLE



3dBlurToFWHM — FWHM = 0 — FWHM = 4 — FWHM = 6 — FWHM = 8

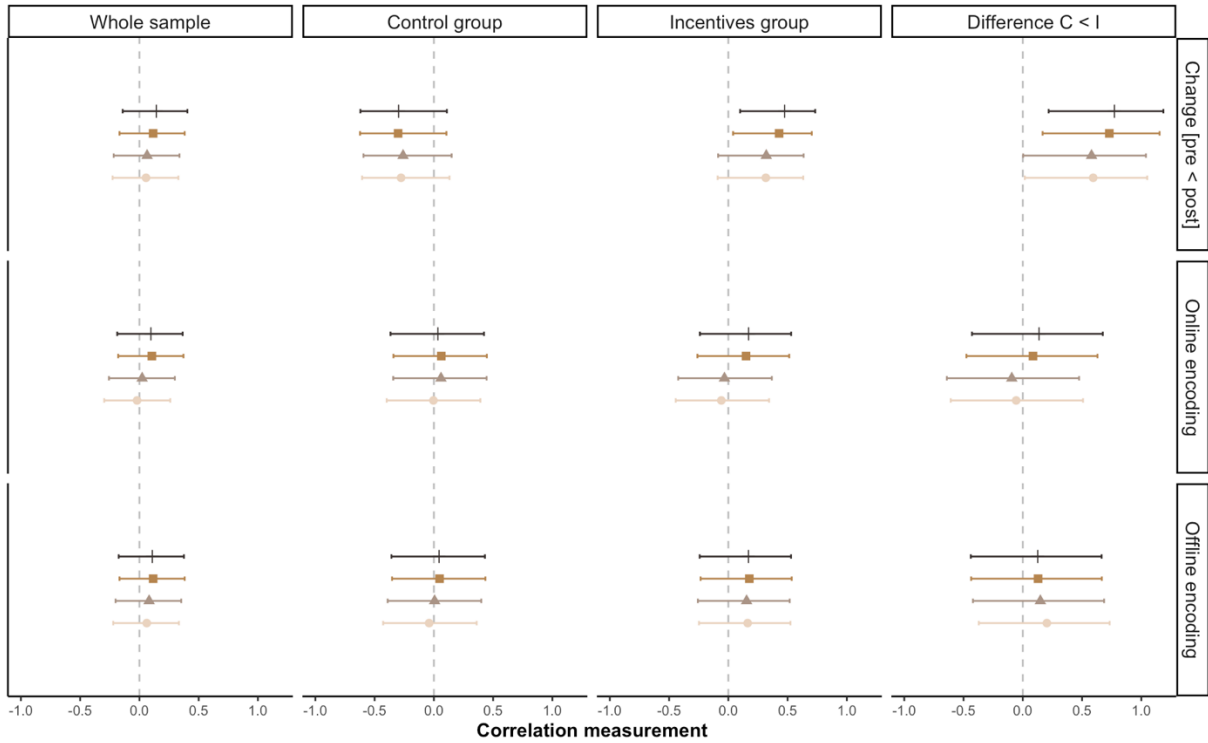
Appendix

Note. The plot shows the computed correlation between behavioural measures of learning and aHPC-VTA/SN-FC measures obtained during different phases of the task. Correlation coefficients are computed using data from the whole sample as well as for each group individually and the difference in correlation between both groups. Error bars represent the 95% CI. As behavioural measures of learning the absolute number of items encoded (A) and curiosity-motivated learning enhancement (B) were used. FC measures between aHPC and VTA/SN were computed separately for each pre- and post-learning rest phase to determine the change therein (top panel). Additionally, the correlation was computed for volumes covering the presentation of magic tricks (online encoding, middle panel) as well as the last volume of magic trick presentation and the following two volumes of fixation (offline encoding, bottom panel). Different colours denote FWHM kernels used in the pre-processing where 0 is equivalent to unsmoothed data and the other numbers represent the input for AFNI's 3dBlurToFWHM algorithm.

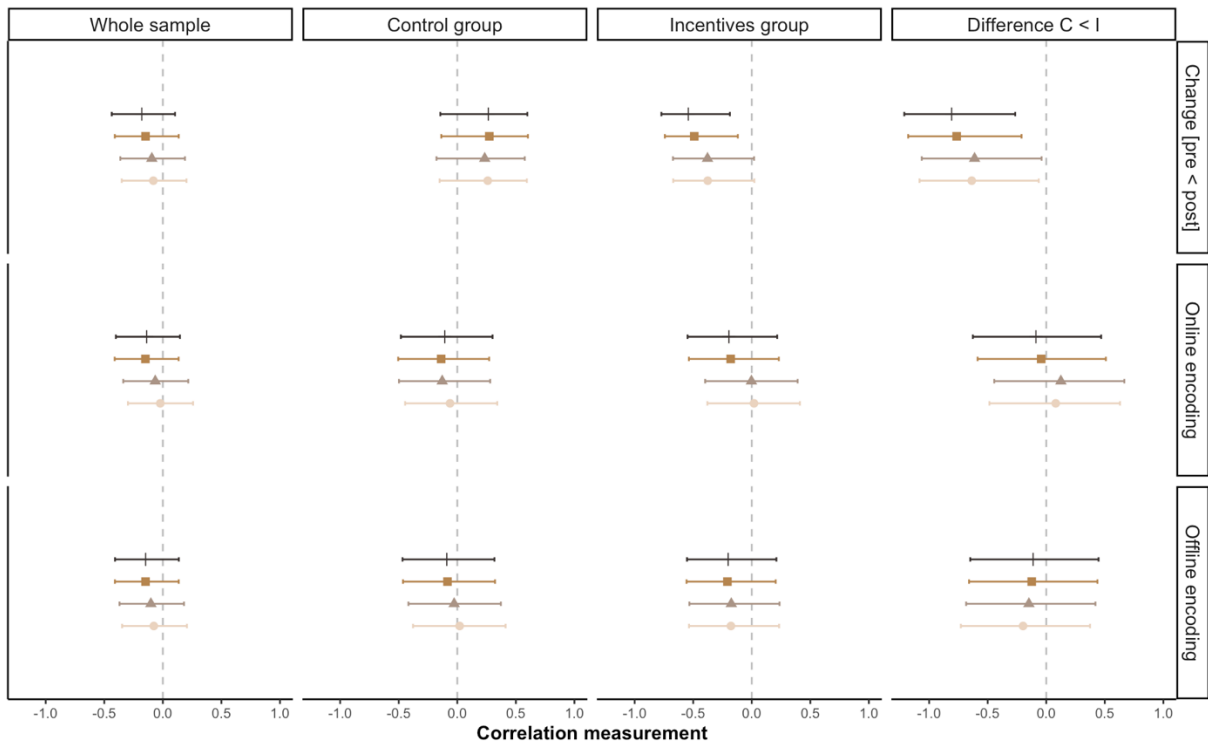
Figure A4.3

Brain-Behaviour Correlation Coefficients as a Function of Learning Phase and Pre-processing

A absolute # items encoded (corrected)



B CMLE (reduced model)



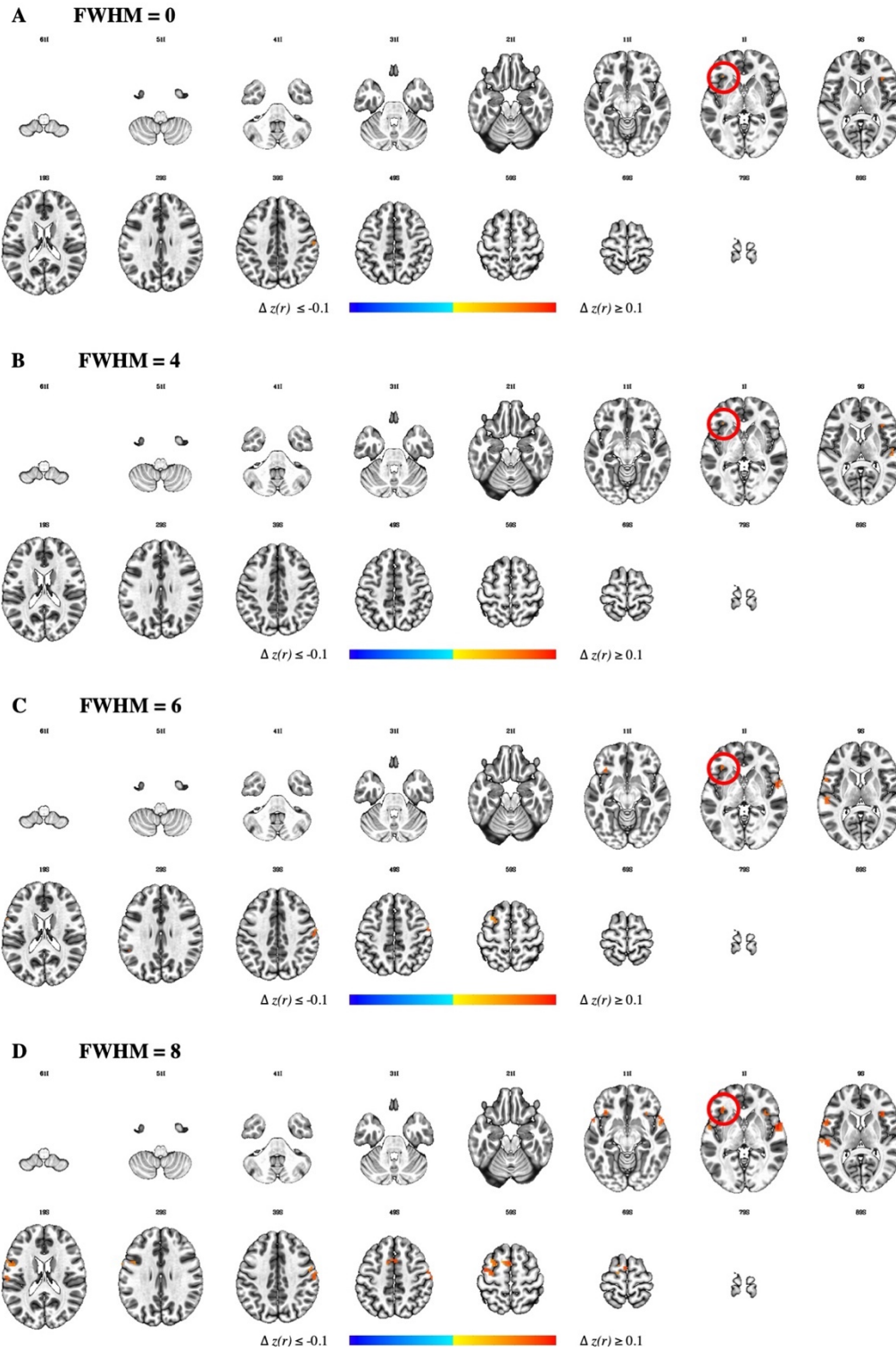
3dBlurToFWHM — FWHM = 0 — FWHM = 4 — FWHM = 6 — FWHM = 8

Appendix

Note. The plot shows the computed correlation between behavioural measures of learning and aHPC-VTA/SN-FC measures obtained during different phases of the task. Correlation coefficients are computed using data from the whole sample as well as for each group individually and the difference in correlation between both groups. Error bars represent the 95% CI. In comparison to Figure A4.2, the behavioural measures of learning were calculated differently. More specifically, when determining the absolute number of items encoded (corrected) (A), wrong answers given with high confidence were accounted for and a simplified generalised linear mixed effects model was used to extract curiosity-motivated learning enhancement (reduced) (B) from (for details, please refer to the main text). FC measures between aHPC and VTA/SN were computed separately for each pre- and post-learning rest phase to determine the change therein (top panel). Additionally, the correlation was computed for volumes covering the presentation of magic tricks (online encoding, middle panel) as well as the last volume of magic trick presentation and the following two volumes of fixation (offline encoding, bottom panel). Different colours denote FWHM kernels used in the pre-processing where 0 is equivalent to unsmoothed data and the other numbers represent the input for AFNI's 3dBlurToFWHM algorithm.

Figure A4.4

Clusters Showing Significant Changes in RSFC With the aHPC Seed From Pre- to Post-Learning Rest Across Different Pre-processing Pipelines

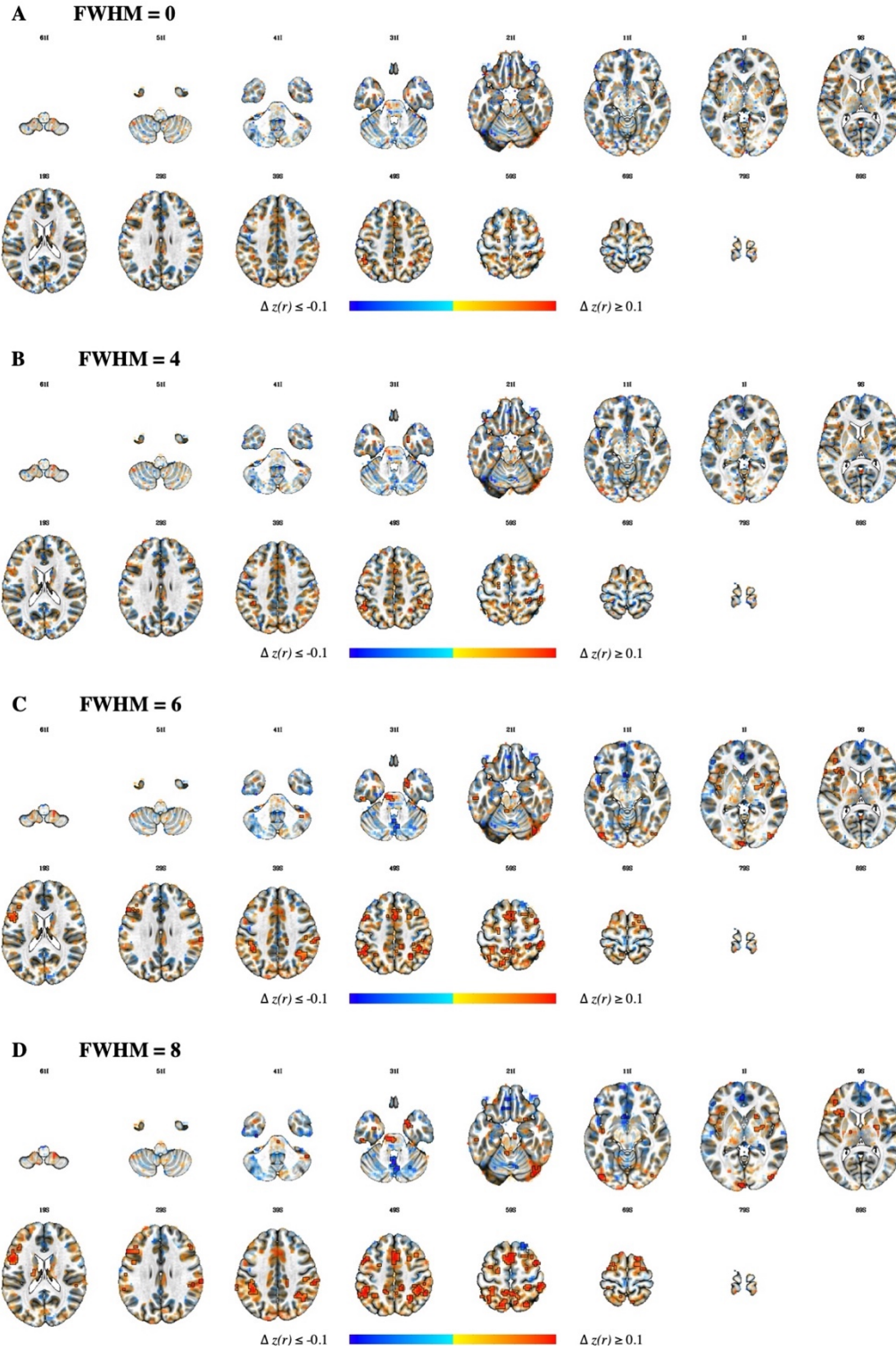


Appendix

Note. The results above highlight clusters that show a significant change in RSFC with the aHPC seed from pre- to post-learning rest across the whole sample. As cluster-defining threshold, $p = 0.001$ was used. For each smoothing kernel, the cluster extent threshold was defined based on permutation tests using $\alpha = 0.05$ as threshold. We here show the effect estimates (i.e., Fisher's z -transformed difference in correlation; $\Delta z(r)$) rather than the statistical map. Positive values (shown in red) indicate an increase in RSFC from pre- to post-learning rest. One cluster in the left anterior insula/frontal operculum was found consistently and is circled in red.

Figure A4.5

Clusters Showing Effects of the Incentive Manipulation on Changes in RSFC With the aHPC Seed From Pre- to Post-Learning Rest Across Different Pre-processing Pipelines

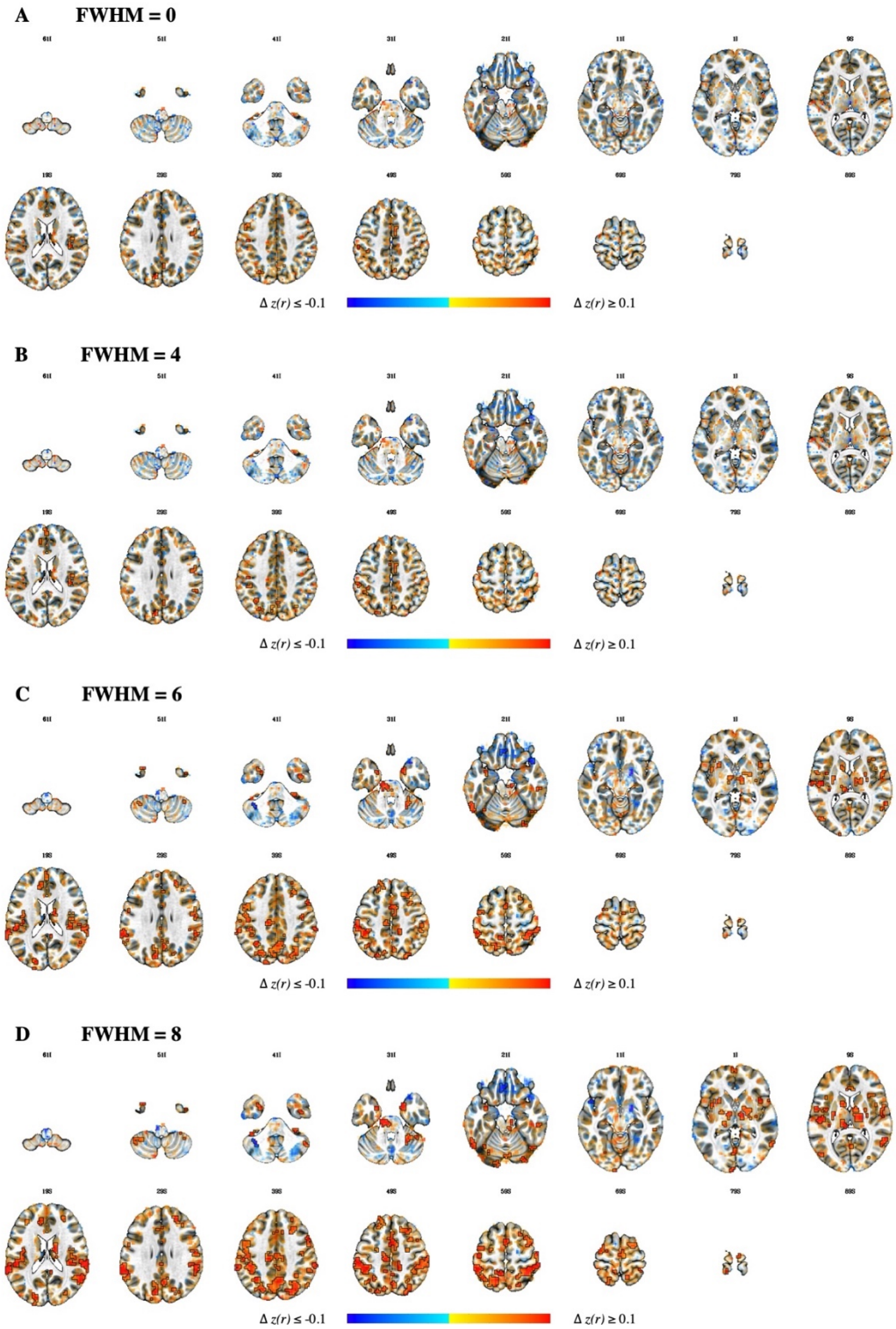


Appendix

Note. The results above highlight clusters where the change in RSFC with the aHPC seed differed as a function of the availability of extrinsic incentives. As cluster-defining thresholds, $p = 0.05$ and $k = 10$ were used. Lenient thresholds were used to guide future research. The effect of thresholding was further softened by applying opacity information so that values closer to the threshold would be shown with higher opacity and a box was added around supra-threshold voxels only. The same threshold is applied across FWHM kernels. We here show the effect estimates (i.e., Fisher's z -transformed difference in correlation; $\Delta z(r)$) rather than the statistical map. Positive clusters indicate higher values in the control compared to the incentives group whereas in negative clusters, the change in RSFC from pre to post is more positive in the incentives compared to the control group.

Figure A4.6

Clusters Showing Effects of the Incentive Manipulation on Changes in RSFC With the VTA/SN Seed From Pre- to Post-Learning Rest Across Different Pre-processing Pipelines



Appendix

Note. The results above highlight clusters where the change in RSFC with the VTA/SN seed differed as a function of the availability of extrinsic incentives. As cluster-defining thresholds, $p = 0.05$ and $k = 10$ were used. Lenient thresholds were used to guide future research. The effect of thresholding was further softened by applying opacity information so that values closer to the threshold would be shown with higher opacity and a box was added around supra-threshold voxels only. The same threshold is applied across FWHM kernels. We here show the effect estimates (i.e., Fisher's z -transformed difference in correlation; $\Delta z(r)$) rather than the statistical map. Positive clusters indicate higher values in the control compared to the incentives group whereas in negative clusters, the change in RSFC from pre to post is more positive in the incentives compared to the control group.