Brain bases of meaningful and meaningless action imitation: a neurostimulation and two-person motion-tracking approach

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DECLARATION

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

Chapter 1 contains text from a published review article (Reader & Holmes, 2016), in which both authors were involved in writing and editing, and of which I estimate my contribution to be 80%.

The experiment discussed in Chapter 3 has since been accepted for publication (Reader, Royce, Marsh, Chivers & Holmes, in press). Data collection by Reader, Royce, Marsh, Chivers. Data analysis and writing by Reader and Holmes. Proofing by all authors. I estimate my contribution to be 80%.

Signed:

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ABSTRACT

Humans can imitate both meaningful and meaningless actions. However, the behavioural and neural processes underlying the imitation of these different action types are still not fully understood. It is difficult to link imitation performance to brain regions commonly associated with imitation due to the limitations on movement imposed by the brain scanning environment. Furthermore, claims made about areas commonly associated with imitation are often imitation-general, despite experiments generally testing single action types. However, evidence from apraxia (a disorder of complex movement) suggests both common and specific brain regions may be involved in meaningful and meaningless action imitation. For example, damage to the left inferior parietal lobule (IPL) is frequently associated with deficits in meaningless action imitation. In order to address these concerns, we used motion-tracking, transcranial magnetic stimulation (TMS), and ecologically valid two-person experimental paradigms. In experiment 1, we found that imitating meaningless actions increased the reaction time for performing a subsequent action, supporting theories of different processing routes to meaningless and meaningful action imitation. In addition, we discovered that the hallmark of meaningless action imitation is a strategy designed to maximise correction time at the end of the action, ensuring accurate completion of actions that may be unfamiliar. Using TMS and two-person motion-tracking, we then examined three brain areas often associated with imitation. In experiment 2 we found that the left IPL is involved in matching observed kinematics. In experiment 3 we found that the left ventral premotor cortex (PMv) has a general role in hand shaping for imitation. In experiment 4 we found that the left posterior middle temporal gyrus (pMTG) is involved in meaningful, but not meaningless, hand gesture imitation. Overall, these results provide causal evidence for previous claims that meaningful and meaningless action imitation are subserved by common (IPL, PMv) and specific (pMTG) neural pathways.

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LIST OF ABBREVIATIONS AND ACRONYMS

AG	angular gyrus
fMRI	functional magnetic resonance imaging
IFG	inferior frontal gyrus
IPL	inferior parietal lobule
M1	primary motor cortex
MEP	motor-evoked potential
MNS	mirror neuron system
MO	movement onset time
MT	movement time
MTG	middle temporal gyrus
MV	mean velocity
PA	peak acceleration
PD	peak deceleration
PET	positron emission tomography
PMd	dorsal premotor cortex
PMv	ventral premotor cortex
PV	peak velocity

RMS	root mean squared
RMT	resting motor threshold
RT	reaction time
SMG	supramarginal gyrus
STS	superior temporal sulcus
TMS	transcranial magnetic stimulation
TPA	time to peak acceleration
TPD	time to peak deceleration
TPV	time to peak velocity
VLSM	voxel-based lesion-symptom mapping

SUPPLEMENTAL MATERIAL

1 INTRODUCTION

Action imitation is an essential element of social interaction. By copying the behaviour of another individual, we develop new skills and better connect with other people (Heyes, 2009; Jones, 2009). But imitation is not as simple as just doing what we see. In order to accurately replicate an observed action, we might need to recognise the action, account for differences between our own body and that of the actor, create an appropriate motor code for performing the action, and also consider the social context and how the motivations of the actor and ourselves interact.

This complexity is similarly reflected in the broad variety of actions that we can imitate, and the different ways in which (imitative) action can be distinguished. We can consider action in terms of familiarity: we can copy actions that we are familiar with (i.e., that we recognise, through frequent observation or performance), as well as new actions that we have never seen before. We can imitate actions that involve objects (transitive) or are goal-directed, as well as empty-handed (intransitive) actions with no purpose whatsoever. These distinctions mean that there is still a lot to understand about how different types of actions are imitated (Hamilton, 2015), both behaviourally, and in relation to the neural components underlying these behaviours.

Another way in which we can consider the various types of action we can imitate is in terms of semantic content, or action meaning. Actions that are meaningful are actions that can be categorised based on their function, and linked to either a concept (i.e., thumbs up = “good”), or an object. For example, brushing one’s teeth requires the movement of a clenched fist parallel to the mouth, and is easy to categorise regardless of the actual presence of a toothbrush (i.e., if that action is ‘pantomimed’). How do our brains process meaningful and meaningless actions for the purpose of imitation? Do we imitate meaningful and meaningless actions differently?

Whilst semantic content is not the only way to consider action, answering these questions is important. By considering action imitation in this way we can begin to link semantic aspects of action to their recognition and performance. In doing so, we can see how performance might differ in novel scenarios where actions are meaningless, which might be important for imitation learning. Furthermore, better understanding of meaningful and meaningless action imitation in healthy people might assist us in learning more about neuropsychological disorders where these skills are defective. Here we will provide an overview of the motivations for this thesis. We will discuss neuroimaging, neuropsychological, and behavioural research in meaningful and meaningless action imitation, and how these relate to models of imitation. We will also explain how naturalistic approaches to action imitation may allow us to deepen our knowledge, and how combining ecologically valid testing methods with non-invasive neurostimulation may allow us to link specific brain regions to imitative behaviour in healthy people.

1.1 Neuroimaging studies of imitation

A great deal of research has been done in the last 20 years to try and uncover the neural processes underlying imitation in healthy individuals. Whilst this has allowed the field to begin to reach some agreement, there is still more work to be done to fully understand the role of different brain areas in processing different imitative abilities. The majority of studies on the neural bases of imitation have used functional magnetic resonance imaging (fMRI) or positron emission tomography (PET). These studies highlight the importance of frontoparietal regions in the imitation of various types of action (Caspers *et al.*, 2010; Hamilton, 2015; Iacoboni, 2005; Molenberghs *et al.*, 2009). In particular, the inferior parietal lobule (IPL), premotor cortex, and inferior frontal gyrus (IFG) are frequently considered to make up part of a core imitation network.

Because it is difficult to perform complex arm and hand movements in a brain scanning environment, many neuroimaging studies of action imitation have used simple finger tapping tasks or stereotyped actions (e.g., Bien *et al*., 2009; Iacoboni *et al*., 1999, 2001; Jonas *et al*., 2007; Koski *et al*., 2002, 2003; Williams *et al*., 2007). This means that the results of these experiments do not allow us to draw strong conclusions regarding the role of different brain areas in meaningful or meaningless action imitation. The few exceptions to these paradigms, where researchers have directly compared the brain regions associated with meaningful and meaningless action imitation, are worth some consideration.

An early PET study by Decety *et al*. (1997) revealed that when participants observed actions with the intention to imitate, meaningful actions were associated with greater cortical activity in the left middle temporal gyrus (MTG), left IFG, right medial frontal gyrus, and right parahippocampal gyrus, when contrasted with meaningless actions. Compared to meaningful actions however, meaningless actions were associated with increased cortical activity in the right IPL, precuneus, precentral gyrus, and occipitotemporal junction. This right-lateralised activity associated with meaningless action imitation was not shown in a later experiment by Tanaka *et al*. (2001), though their contrasts were mainly focused on comparing activity versus rest. Their direct comparison between meaningless and meaningful actions showed that meaningless actions were associated with greater activity in the left primary motor cortex (M1), primary somatosensory cortex (S1), supramarginal gyrus (SMG), and right SMG. They suggested that the SMG is particularly important for imitating meaningless actions.

A later PET study by Peigneux *et al*. (2004) revealed that compared to meaningful actions, meaningless actions were associated with greater cortical activity in the left IPL, precuneus, and postcentral gyrus, and right precuneus, superior parietal lobule, postcentral gyrus, and IPL. Compared to meaningless actions, meaningful actions were associated with greater cortical activity in the left IPL, middle temporal gyrus, superior temporal gyrus, precuneus, middle frontal gyrus, and superior frontal gyrus, and right IPL, inferior temporal gyrus, middle temporal gyrus, inferior frontal gyrus, middle frontal gyrus, medial frontal gyrus, superior frontal gyrus, and orbital gyrus. Finally, Rumiati *et al*. (2005) found that meaningful actions were associated with greater activity in the left inferior temporal gyrus, angular gyrus, and parahippocampal gyrus. Meaningless actions, by contrast, were associated with greater activity in the left superior temporal gyrus, along with the right occipitoparietal junction and occipitoparietal junction, and bilateral superior parietal cortex.

Whilst these few studies implementing direct comparisons between meaningful and meaningless action imitation provide little consensus, they do suggest that there may be common and specific brain regions involved in mediating meaningful and meaningless action imitation. Attempts to decompose neural activity related to separable elements of imitation may be highly informative, but are rare. For example, Menz *et al*. (2009) used fMRI to record brain activity during the delayed imitation of object-directed actions and abstract (meaningless) gestures. They split trials into distinct epochs, relating to the onset of the observed action, the onset of imitation, and the delay period between action observation and performance. By using independent components analysis they were able to decompose recorded brain activity relating to these epochs into four components.

They found that both types of action shared common activation in bilateral lateral occipital cortex, right intracalcarine cortex, and left fusiform gyrus during action observation (a component they referred to as ‘action perception’), bilateral primary sensorimotor regions, (pre)supplementary motor area, bilateral MTG, bilateral putamen, right cerebellum, bilateral superior parietal lobule, and bilateral IFG during action performance (‘motor preparation and action execution’), and in the anterior cingulate, posterior cingulate, frontal pole, precuneus, bilateral intraparietal sulcus, right inferior lateral occipital cortex, and bilateral superior temporal sulcus during the delay between action observation and performance (‘encoding and retrieval into and from working memory’). A fourth component, related specifically to object-directed actions, was also observed, showing activity in the bilateral superior parietal cortex, anterior and posterior cingulate, bilateral middle frontal gyrus, and bilateral lateral prefrontal cortex. Menz *et al*. (2009) suggested that this component reflected the ‘dynamic integration of object affordances’.

Though the statistical approach taken by Menz *et al*. (2009) is informative, as far as we are aware there are no published papers performing such fine-grained decomposition for meaningful and meaningless action. Such an endeavour is likely to be useful in informing us of the different neural processes underlying imitation. In addition, very little has been done to link the brain regions associated with imitation with actual imitative performance. Luckily, neuroimaging studies in healthy individuals are not the only source of information we have about the brain regions involved in meaningful and meaningless action imitation. Lesion studies can assist in our understanding of the role of different brain regions in different types of behaviour by providing more causative links.

1.2 Apraxia

Evidence from neuropsychological patients seems to reflect a possible dissociation between brain regions involved in imitating different action types. Patients with apraxia, a disorder of complex movement, can show deficits in, among other skills, the ability to imitate meaningful or meaningless actions (Canzano *et al*., 2016; Petreska *et al*., 2007; Rumiati *et al*., 2009). Selective deficits in meaningless action imitation are frequently associated with damage to the left parietal lobe (Goldenberg, 2009). Deficits in meaningful action imitation are more commonly associated with damage to the temporal lobe (Buxbaum *et al*., 2014; Tessari *et al*., 2007).

Unlike neuroimaging studies in healthy people, studies examining patients with apraxia allow a more detailed examination of specific regions-of-interest (within the lesion limits), without necessarily removing individual variability by registering brain images to a template brain. These case studies can also be useful in examining whether different brain areas are associated with *performance* in meaningful and meaningless action imitation. This has led to discussions regarding the differential contribution of postural, kinematic, and stored semantic information in different types of action imitation, and of course the brain regions associated with each of these elements of movement (Buxbaum *et al.*, 2014; Dressing *et al.*, 2016), which are discussed in more detail in Chapters 3 and 5. Notably, the consideration of action imitation in terms of meaning by neuropsychologists has led to a useful model: the dual-route model.

1.3 Models of imitation

The dual-route model was first formalised by Rothi *et al.* (1991), and, following this, the model has seen developments and adaptations (Buxbaum *et al.*, 2000; Cubelli *et al.*, 2000; Roy & Square, 1995; Rumiati & Tessari, 2002). Put simply, the model suggests that for imitation, meaningful actions are processed through a semantic, or indirect, route which draws on pre-existing representations of the movements stored in long term memory. By contrast, meaningless actions are processed using a direct route which relies on a direct mapping between the observed action and the performed copy (visuomotor matching). Damage to the brain regions underlying these routes can result in different performance deficits for different types of action and action imitation in apraxia.

The dual-route model is supported by the dissociation of deficits in meaningful and meaningless action imitation, along with the different brain regions reported in neuroimaging contrasts. For example, one could suggest that the left IPL is involved in direct processing for imitation (Tessari *et al*., 2007), since damage to this area frequently results in specific deficits in meaningless action imitation (Goldenberg, 2009). The dual-route model is also supported by behavioural evidence (Rumiati *et al*., 2009). Notably, placing experimental demands on cognitive load tends to have a greater influence on the imitation of meaningless gestures compared to meaningful ones (Tessari & Rumiati, 2004), which seems to support the idea that the imitation of meaningless gestures is more cognitively demanding. Supporters of the dual-route approach point to this fact as evidence for the more intensive ‘direct’ route for meaningless action imitation (Tessari *et al*., 2007), and this idea is discussed in more detail in Chapter 2. Generally speaking, the dual-route model provides a feasible explanation for the imitation of both action types, particularly in light of the clear dissociations observed in apraxia, but it is less clear on how the matching process of the direct route is implemented.

Another explanation for imitation is provided by the goal-directed theory of imitation (GOADI, Bekkering *et al*., 2000; Wohlschlager *et al*., 2003), an extension of ideomotor theories of imitation (e.g., Greenwald, 1970; Prinz, 1997, 2002) which assume a common representational framework for perception and action. For imitation, the observation of an action can trigger the representation of movements that would be necessary to repeat that action. Supporters of this approach often point to the phenomenon of automatic imitation, whereby, for example, observing a congruent finger movement can speed performance of the same action compared to an incongruent finger movement (e.g. Brass *et al*., 2000).

Like the dual-route model, GOADI attempts to make sense of the processes that must necessarily occur in order to perform both known and unknown actions, but treats these actions as goal-directed and non-goal-directed, rather than meaningful or meaningless. Specifically, GOADI suggests that observed actions can be decomposed into separate goals for imitation, and these goals are ranked with regards to their functional importance. For example, in order to copy an action moving an object from one position to another, one can simply focus on the functional aspect of moving the object, as if we were performing this action outside of an imitative context. The kinematics and posture of the actor's body can be ignored in order to complete the most important goal (moving the object from point A to point B). On the other hand, if an action is observed that does not have a goal, the movement itself can be considered the goal and so the movements of the actor can be closely followed. In support of these ideas, proponents point to results indicating that children tend to make less errors in copying distal compared to proximal goals (Bekkering *et al*., 2000), stating that "when multiple goals compete for capacity, one goal is more likely to be preserved than another, leading to specific and consistent errors in imitative behaviour" (p. 157).

Clearly, there is substantial overlap in the treatment of imitation by the dual-route model and GOADI - both models posit the importance of visuomotor matching for non-goal or meaningless actions. However, GOADI appears to provide a more concrete explanation for the way in which meaningless actions can be copied, and there is some suggestion that the goal-related processes it focuses on are impaired in apraxia. Bekkering *et al*. (2005) found that when apraxia patients had to perform multi-level goal-directed actions, they showed defective performance of proximal (the effector to use) but not distal (the object to reach to) goals, suggesting a reduced ability for action goal-related processing. However, the dissociation between defective meaningful and meaningless action imitation in apraxia do not strongly support a broad deficit in goal-processing. In addition, the fact that apraxia frequently co-occurs with aphasia (Goldenberg & Randerath, 2015) indicates that there are substantial semantic elements of action that need to be considered to fully comprehend the neural control of imitation. Specifically, the co-occurrence of defective meaningful action imitation (apraxia) and semantic processing for language (aphasia) suggest that goal-processing may not provide a sufficient explanation for different types of action imitation.

A further model of meaningful and meaningless action imitation is provided by Subiaul (2010): the multiple imitation mechanisms (MIM) hypothesis. MIM suggests that “the imitation faculty consists of multiple, dissociable imitation systems that specialize in copying specific types of information. Some of these systems process broad content types (e.g., familiar vs. novel imitation), while other systems process narrower content types (e.g., motor, vocal, and cognitive imitation)” (p. 223, Subiaul, 2010). Particularly useful is the recognition that experimental tasks can assess the imitation of a single action type in ways that may be dissociable. For example, a task may assess both the ability to copy motor behaviour and the ability to copy temporal goals (which may be more generalised).

Generally speaking, the MIM does not posit a strong and distinct assertion regarding *how* the imitation of meaningful and meaningless action is processed, only that they are served by different systems. Of interest is the suggestion that there are specific, dissociable systems for meaningful (familiar) and meaningless (novel) action imitation. Whilst the dissociation of these abilities is evident in apraxia, there is also evidence suggesting that it is the kinematic or postural *components* of these skills that are actually defective (Buxbaum *et al.*, 2014; Dressing *et al.*, 2016), and that the differential reliance on kinematic and postural information is why dissociations can be observed. This is discussed in more detail in the following chapters and general discussion.

The dual-route model and GOADI provide the most well-known explanations for distinguishing between meaningful and meaningless action imitation. Also worth mentioning are models that posit more broad explanations for imitation as a whole. One example of this type of model is provided by the associative sequence learning (ASL) framework (Heyes, 2001). ASL suggests that actions are encoded both in visual and somatosensory terms, and that these representations become linked through Hebbian learning. These associations can be used to inform the way in which observed actions should be copied, and can be developed through normal observation of one's own actions.

Like GOADI, the phenomenon of automatic imitation may also support ASL, and there is evidence that the learning of new associations between observed and performed actions can change the influence of anatomical congruence on subsequent action performance (e.g., Heyes *et al*., 2005; Press *et al*., 2007). Learning is important to ASL, since the model suggests that the accuracy of imitation is dependent on the opportunity to develop links between visual and motor aspects of a given action (Brass & Heyes, 2005). Broadly speaking, the ASL is better considered as a model highlighting how the imitative capacity develops, rather than informing the specific dissociation between meaningful and meaningless action imitation skills. In these terms, like GOADI, it is not strongly suited to address distinctions in action driven by semantic categorisation.

The AIM (active intermodal mapping) model also attempts to explain the general development of imitative capacity and, by contrast, indicates that when an action is observed for the purpose of imitation, visual information about that action is converted into a multimodal representation regarding the relationship between specific body parts (Meltzoff & Moore, 1979, 1997). This representation is then matched with a stored motor code that can replicate the perceived action. This approach is derived from claims that the ability to perform (facial) imitation is innate. The model suggests that in imitation an infant attempts to make the felt relationship between their own body parts match the observed one in an adult, by using a 'proprioceptive feedback loop' to match the observed and performed action. The claim that imitation is an innate ability has recently received considerable criticism (e.g., Oostenbroek *et al.*, 2016) beyond the scope of this introduction, and the AIM model's derivation from facial mimicry make it unclear how informative it may be regarding meaningful and meaningless hand action imitation.

One way to bring together broader models, like ASL and AIM, and models that more specifically cover the imitation of meaningful and meaningless actions (dual-route, GOADI, MIM), is to consider the lowest level at which they may share consistent processes. *A priori* we know that imitation requires the assessment of visual information about the observed action, and the creation of the correct motor code in order to replicate it (the 'correspondence problem', Brass & Heyes, 2005). With this in mind, the suggestion that imitative abilities can be broadly considered as a bidirectional visuomotor stream, undergoing moderation through top-down cognitive processes, might provide a suitable general explanation. This approach is referred to as social top-down response modulation (STORM, Wang & Hamilton, 2012), and was originally developed as a way to explain the control of mimicry (unconscious imitation) in social scenarios.

Under this approach, imitation is like any other visuomotor skill (Hamilton, 2015), which relies on the integration of various other processes to inform successful performance (e.g., object affordances, social context, semantic content). Unlike other models, STORM clearly posits brain regions that might map onto the processes it suggests (Hamilton, 2014, 2015), pointing to the common association of these areas with imitation (Caspers *et al*., 2010) – top-down control may be performed by the medial prefrontal cortex and tempoparietal junction, whilst the premotor cortex, supramarginal gyrus, and anterior intraparietal sulcus form part of the visuomotor stream. The mapping of brain regions onto these supposed processes is further considered in the general discussion, in light of our results.

Whilst it is yet unclear whether all types of imitation can be considered in the terms posited by the STORM model and its proposed brain regions, direct comparisons of different types of action imitation, as this thesis aimed to perform, are likely to be useful in assessing this (Hamilton, 2015). It is likely that there are dissociable and overlapping elements in the visuomotor stream for imitation (Hamilton, 2014). For example, for actions that are more reliant on kinematics (meaningless), or semantics (meaningful), or, more generally, between voluntary imitation and mimicry (Hamilton, 2008).

1.4 The putative human mirror neuron system

Many models of imitation propose processes that might help solve the ‘correspondence problem’ (Brass & Heyes, 2005) – how it is possible to convert the visual image of someone else’s action into a motor code for our subsequent imitative performance. Outside of the models highlighted above, the most popular explanation for the way in which the brain solves this problem is provided by a neurobiological approach: the putative human mirror neuron system. Mirror neurons are bimodal neurons first discovered in the macaque premotor cortex (area F5), which were found to be active during the performance of an object-directed action, and when the monkey observed an experimenter performing the same or similar action (di Pellegrino *et al*., 1992). Neurons with similar properties were later observed in the macaque parietal lobe (Fogassi *et al*., 2005). Some have suggested that these visuomotor properties could reflect a neural basis for human imitative capacity (e.g., Iacoboni, 2009).

Indeed, inferior frontal and parietal areas of the human brain do appear to be strongly activated by imitation (see section 1.1) and appear to show complementary activity for both action observation and imitation in neuroimaging experiments (e.g., Iacoboni *et al*., 1999). Whilst only one experiment has reported actual neuronal activity in keeping with the mirror neuron findings in macaques (Mukamel *et al.*, 2010), these responses were observed in the supplementary motor area and the medial temporal lobe, not the areas typically associated with mirror neuron processing in humans. Further work would be necessary to replicate these findings.

Instead, the most common support for a human mirror neuron system (MNS) comes from fMRI experiments. Typically, these have used repetition suppression, which allows one to infer brain regions similarly involved in different tasks based on the reduction of neural firing rate following the exposure to preferred stimuli. That is, by examining which areas of the brain show a reduction in activity when an action is observed following execution (or vice versa), one can infer that these regions are involved in both tasks. These experiments indicate common processing for action observation and execution in the ventral premotor cortex and intraparietal sulcus (Dinstein *et al.*, 2007), IPL (Chong *et al.*, 2008), and IFG (de la Rosa *et al.*, 2016; Kilner *et al.*, 2009). Though not every experiment using repetition suppression has found evidence for brain regions that adapt to action observation following action execution (Lingnau *et al.*, 2009), other experiments using fMRI methods such as multivoxel pattern analysis (MVPA), which can show the degree to which activity related to one sensory modality can predict the other, provide converging evidence for frontal and parietal regions performing bimodal processing for action observation and execution (Oosterhof *et al.*, 2010).

What is still unclear, and is addressed more thoroughly in Chapters 3 and 4, is whether the mirror neuron system can provide a holistic explanation for multiple types of imitation, including intransitive meaningful and meaningless actions. The sensory and motor field properties of mirror neurons in macaques are almost exclusively reported as being related to object-directed action. Whilst there is some evidence that macaque premotor mirror neurons are responsive to intransitive actions (Kraskov *et al.*, 2009; Papadourakis & Raos, 2017), in these cases the actions observed were always contextualised in a familiar scenario for the monkeys, and involved pantomimed grasping in the absence of an object, or flat-handed reaching towards the experimental workspace. Such actions are qualitatively very different from the intransitive emblematic or entirely novel hand actions that can be imitated by humans, and suggests that more can be done to confirm whether activity in the human brain related to intransitive gesturing is reflective of mirror neuron processing, or different functions.

It is worth noting here that the general aim of this thesis was not to distinguish between different theories of imitation, or provide evidence for or against mirror system-based imitation hypotheses. Instead, we hoped to examine different brain areas commonly associated with imitation in order to better understand how these regions may or may not be involved in meaningful and meaningless action imitation. However, this exploratory approach was also grounded in a broader interest in naturalistic approaches to social neuroscience, such that we hoped to develop ecologically valid methods that would allow us to link specific brain regions to the performance of meaningful and meaningless imitation tasks.

1.5 Objective assessment and naturalistic approaches in imitation

Neuroimaging studies tend to limit the imitative capacity afforded by the entire arm and hand, and in both research in healthy individuals and apraxia patients imitation is often assessed using subjective rating measures (with some exceptions, e.g., Campione & Gentilucci, 2011; Hermsdörfer *et al*., 1996; Pan & Hamilton, 2015; Reader & Holmes, 2015; Sacheli *et al*., 2012, 2013, 2015a, 2015b; Wild *et al*., 2010). However, kinematics are an important element of realistic social interactions (Krishnan-Barman, *et al*., 2017), which contribute to our ability to accurately assess the behaviour of other individuals, suggesting that we might be able to better understand imitation by taking them into account. In addition, is not yet clear to what degree the finger tapping movements frequently used in studies of imitation reflect realistic social behaviour, and whether or not these actions can be considered meaningful or meaningless.

The dual-route model posits that meaningless actions may be more reliant on matching the spatial or kinematic elements of the observed movement, and some recent apraxia research supports the idea that there may also be postural and kinematic dissociations for apraxic imitation deficits (Buxbaum *et al*., 2014). It seems, then, that there is a need for objective kinematic measurements of healthy participant imitation behaviour, in order to better link actual motor behaviour to brain regions associated with imitation. In addition, most previous experiments on meaningful and meaningless action imitation typically used a single participant responding to pre-recorded stimuli, which may limit the ecological validity of the task (Reader & Holmes, 2015). Specifically, there are at least three potential confounds that might occur from examining social behaviour in single participant designs, which we highlighted in a recent review (Reader & Holmes, 2016), and will provide a brief overview of here. These confounds stem from differences in visual fidelity of the stimuli, gaze, and social potential, between naturalistic and laboratory-based interactions.

Single-participant experimental designs often rely on video stimuli. However, some have suggested that the social relevance of a task is likely to be different in “reel” (recorded) and “real” (live) scenarios (Risko *et al.*, 2012). This is not surprising, since in most cases social interaction is a dynamic experience, where each of the individuals involved influence, and are influenced by, each other. Unfortunately, little work has been done to test how video stimuli might change participant behaviour compared to more ecologically valid approaches, and what the implications of this might be for imitation. One possibility is that the reduced visual fidelity of video stimuli (compared to real interactions) could influence imitative performance. In a recent experiment (Reader & Holmes, 2015) we showed that imitation accuracy was reduced when participants had to copy an actor through a live video feed, compared to face-to-face. The 2D video stimuli reduced performance in a 3D, object-directed imitation task, which we suggested was due to differences in visual fidelity between the two conditions. In particular, visuomotor responses to video stimuli might be different than those observed face-to-face, since the treatment of 3D and 2D visual information by the visual system is different (Patterson, 2009). For example, 3D stimuli afford more cues to depth than 2D stimuli, and so action responses to these stimuli are likely to be guided by sub-optimal visual information. This means that imitation in response to 2D stimuli may be less accurate than in naturalistic scenarios.

Another potential issue for assessing realistic imitation is that of gaze. During social interactions, gaze can provide a useful cue to attention for an observer (Friesen & Kingstone, 1998), and provide a strong influence on the observer's own gaze (Gallup *et al.* 2012). Particularly important for imitation is the fact that gaze and kinematics are complementary during social action, such that an observed actor's gaze influences the speed of attending to a target for action, whilst the actor's kinematics influence the accuracy of that attention (Letesson *et al.*, 2015). However, the separation of kinematic and gaze cues is common in social interaction research, and many articles do not control for gaze in pre-recorded stimuli (e.g., Campione & Gentilucci 2011; Fernando & Rob, 2015). It is unclear to what extent the failure to control for gaze might influence participant performance, but it is possible that behaviour is impoverished without the information provided by another's gaze.

It seems that there is some evidence for the idea that differences in visual fidelity or gaze behaviour could change the way in which participants respond to social scenarios. In addition to this, experiments that focus on testing a single individual may also suffer from a reduction of 'social potential'. By this, we mean that the potential for a meaningful two-way interaction is reduced, possibly changing participant behaviour compared to what might be observed in a normal interaction with another human being. It is well-established that there are differences between how people act in isolation and social contexts (e.g., Becchio *et al*., 2010), and the intentions, actions, and locations of other individuals can change how we interact with them. In one interesting example of this, Quesque *et al*., (2013) found that the kinematics of a participant's object-directed actions were changed by the presence and proximity of an observer, along with the observer's ability to intervene with the participant's actions. These effects were observed *even when it was not possible for the observer to directly influence the action outcome*, suggesting that even just having an individual in the same room can have important effects on behaviour.

Each of these confounds (changes in visual fidelity, gaze, social potential) have the potential to influence participant imitative behaviour to an unknown degree, such that we cannot be sure how close the recorded experimental data is to what we might observe in a more realistic scenario, or to what degree experimental power might be reduced by these extraneous variable. With this in mind, we wanted to better understand imitation as a dynamic social experience.

Motion-tracking may provide one way to find objective measures for examining imitation, and examine the performance of participants' relative to the person they are imitating. This prompted us to plan experiments that allowed objective measurement of whole arm movements and dynamic interactions with another individual, which is hard to do in a scanning environment. Because of this, we decided to implement non-invasive neurostimulation, in order to flexibly integrate natural social behaviour with a neuroscience-driven approach to imitation. By doing this we also hoped that we would be able to directly link specific areas of the brain with imitation performance. Integrating neuroimaging with motion-tracking in order to test imitation fidelity is a highly valuable approach (Hamilton, 2015), that very few neuroimaging experiments have attempted (e.g., Krüger *et al.*, 2014), likely due to the difficulties inherent in recording action kinematics or complex goal-directed movements in the scanning environment.

1.6 Transcranial magnetic stimulation

In order to link imitation kinematics with brain regions commonly associated with imitation, we decided to use transcranial magnetic stimulation (TMS). TMS is a non-invasive neurostimulation method that interferes with cortical activity under the scalp through means of an electromagnetic pulse. In particular, the strong magnetic field is believed to depolarise neurons, initiating action potentials (Rossini *et al.*, 2015). Repetitive application of TMS pulses over the cortex can be used to perturb cortical excitability (Rossi *et al*., 2009), which can be used to infer the functions of specific cortical areas when combined with behavioural tests. The ability to develop causal links between stimulated brain regions and subsequent behaviour means that TMS provides a valid way of testing the relationship between (imitative) behaviour and brain.

We hoped that TMS would allow us to ascertain the relative roles of different brain regions in meaningful and meaningless action imitation, whilst maintaining the ability to examine whole arm actions outside of the confined scanning environment. This would allow us to better match cortical locations to imitation behaviour, since lesion evidence from apraxia is rarely focussed on a single parcellated region. By interfering with specific areas of the brain associated with imitation, then examining the effects on imitative performance, we can infer the role of those areas. As such, TMS can provide a unitary approach, bringing research in healthy individuals and neuropsychological patients together, allowing us to examine the healthy brain outside of the scanner, and providing the opportunity to test meaningful and meaningless action imitation using objective motion-tracking measures and naturalistic two-person paradigms.

1.7 Aims

Whilst we did not have strong hypotheses to test, we expected that meaningful and meaningless actions would be reflected in different kinematics, and that these kinematics would be differentially influenced by TMS over different parts of the imitation network. Generally, we hoped that by perturbing activity in selected areas of the brain using TMS, then testing participant behaviour in realistic meaningful and meaningless imitation tasks, we would be able to see if the brain regions are differentially involved in these tasks. In particular, we chose to stimulate the left premotor cortex, IPL, and posterior temporal lobe. The reasons for these choices are discussed in detail in their relevant chapters.

In sum, the following experiments will address three broad aims, each of which attempts to build upon gaps in the aforementioned literature. We aimed to:

a) Use motion-tracking to better characterise the kinematic elements of meaningful and meaningless action imitation
b) Use two-person experiments in order to examine imitation in a more ecologically valid fashion, and better link actor and imitator behaviour
c) Examine the role of brain areas frequently associated with imitation by using TMS, in combination with the methods described in a) and b)

2 EXPERIMENT 1 (BEHAVIOURAL)

2.1 Introduction

In order to use motion-tracking to better understand the role of certain brain areas in meaningful and meaningless action imitation, we first needed to find basic kinematic markers that are sensitive to action meaning, and could be used as variables in later TMS experiments. Previous behavioural work on dual-route imitation processing in healthy participants (Press & Heyes, 2008; Tessari & Rumiati, 2004) appeared to provide a good starting point for this endeavour.

As mentioned in the introduction, the dual-route model has been very informative in understanding imitation deficits in apraxia. What is less clear, however, is how these different routes manifest themselves in healthy individuals. Whilst imitation has been much studied in healthy individuals, compared to work in apraxia, relatively little has been done to tease apart the ways in which different types of action are imitated. Tessari & Rumiati (2004) examined this issue by testing healthy individuals' ability to imitate meaningful or meaningless actions in blocks of only one type of action, or in mixed blocks. Using a subjective rating measure, they found that performance for meaningful actions was significantly more accurate than meaningless actions when presented in blocks with only the same type of action, but that, when meaningful and meaningless actions were presented together in mixed blocks, accuracy was not significantly different. They claimed that this supports a strategic selection of the dual-routes used for imitation: when participants could not be sure of the composition of the list of gestures to be imitated, they chose to imitate solely using the direct route, in order to avoid the cognitive cost of switching between the routes.

Press & Heyes (2008) replicated this experiment, and added a reaction time (RT) measure. As in the experiment by Tessari & Rumiati (2004), Press & Heyes found that accuracy was better for meaningful actions in a blocked condition, but that this effect was not present in mixed conditions. The effect was also shown with RT, such that meaningful actions had a shorter RT. To discover why this effect was not evident in the mixed blocks, they then looked at how imitation in the mixed blocks was affected by the action performed in the previous trial. Interestingly, they found that RTs were longer, and movements less accurate when actions of either type followed a meaningless action in the mixed block. They suggested that this result supports a stimulus selection hypothesis - participants always used the processing route best suited to the action type, but the working memory demand of the direct route (i.e., the cognitive demands of matching the observed and performed actions) interferes with the speed of reactions to the following actions. This reduces the advantage that meaningful actions have over meaningless actions.

In these previous experiments, the primary dependent variable was either RT or a subjective rating of accuracy. However, the dual-route model posits that meaningless actions may be more reliant on matching the spatial or kinematic elements of the observed movement, and some recent apraxia research supports the idea that there may also be postural and kinematic dissociations for apraxic imitation deficits (Buxbaum et al., 2014). Despite this, little research has been done to objectively characterise the kinematics of meaningful and meaningless action imitation. As discussed in the general introduction, using objective motion-tracking measures to examine how kinematics vary in different types of imitation may help develop our understanding of the behavioural differences in performing these types of action.

In this experiment we wanted to examine dual-route processing of imitation, and to confirm the nature of route selection using both RT measures and motion-tracking. This was done by examining the coarse-grained wrist movement, which we believed would provide a basic measure for how participants were approaching the final hand posture in meaningful and meaningless actions. In particular, we took an exploratory approach to see if the RT effects would similarly be observed in any common kinematic parameters, with the hope that this would improve understanding of the underlying mechanisms of imitation of different action types, and provide variables to test in later TMS experiments. We also hypothesised that we would replicate the RT findings of Press & Heyes (2008), and find further support for stimulus selection. We aimed to do this using a typical single-person design, which could then be built upon in later two-person experiments.

2.2 Experiment 1A

2.2.1 Methods

2.2.1.1 Participants

Sample size was based on Press & Heyes (2008). 24 participants were recruited from the University of Reading and the surrounding area (mean±SE age = 24.4±1.08 years, 11 males, 3 left handed). The experimental procedures were approved by the local ethics committee (ref: 2016-059-AC); participants gave written, informed consent; and the experiments were conducted in accordance with the Declaration of Helsinki (as of 2008).

2.2.1.2 Materials and stimuli

The position of each participant's right wrist was recorded during action imitation using a wired Polhemus Fastrak (Polhemus Inc., Colchester, VT, USA) 120Hz motion tracking system with six degrees of freedom (x, y, z, azimuth, elevation, and roll). The tracker was attached to the pisiform using adhesive medical tape and Velcro™.

The experiment was controlled and data were acquired using custom software written in MATLAB 2014a (Mathworks, Inc.). We used the HandLabToolbox to control experiments and analyse data. The associated repositories are, or will be, freely available at https://github.com/TheHandLaboratory, whilst raw data are available on request.

A total of twenty gestures were used as stimuli. This included five meaningful hand gestures (“salute”, “shock”, “stop”, “I’m listening”, “looking into the distance”), five meaningful finger gestures (“peace”, “thumbs up”, “okay”, “gun”, “silence”), and ten matched meaningless gestures. For each meaningful gesture, a matched meaningless gesture was created (Figure 2-1). In the case of finger gestures, this was done by changing the fingers used to create the gesture and/or the orientation of the hand. In the case of hand gestures, this was done by either changing the orientation and/or position of the hand. Meaningful gestures were chosen based on empty-handed emblematic gestures that have meaning in the UK. Stimuli were first assessed for suitability by asking 12 individuals (not tested in this experiment) whether a list of 30 actions were meaningful or meaningless, and excluding any that did not reach a 75% agreement with our categorisation. 5 actions were excluded based on this assessment, along with 5 others very near this threshold, and the above 20 gestures were maintained.

Gestures were presented as videos with a mean±SD duration of 1573±16.1ms, in which a male actor raised his left hand from the table in front of him, created the gesture, and held it until the end of the video. The actor's gaze was fixed on the camera. In each video the mean±SD time to perform the initial action was 948±35.4ms, after which the gesture was held in position until the end of the video. Videos were presented in the centre of a monitor at a resolution of 709 x 591 (18 x 15cm at 100ppi) and ~30 frames-per-second. During the task, participants sat opposite a 40cm (diagonal measure) computer screen approximately 110cm away. A start point was placed on a table in front of the participant using Blu Tack®, 20cm away from their right-hand side.


salute
peace


shock
thumbs up


stop
okay


I'm listening
gun

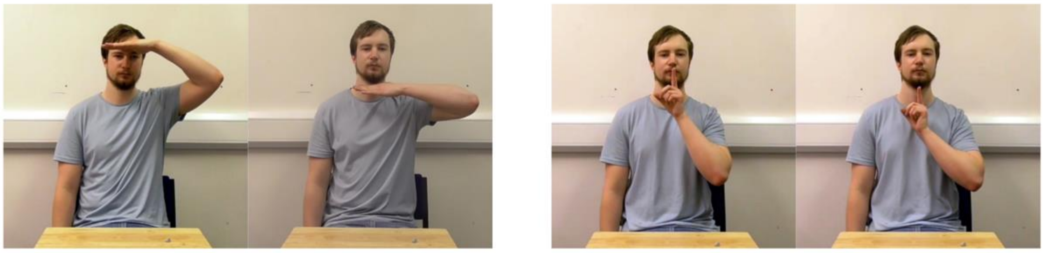
looking into the distance
silence

Figure 2-1: Experimental stimuli

For each meaningful emblematic gesture (left), a matched meaningless gesture was created (right).

2.2.1.3 Procedure

Participants took part in four separate blocks of imitation, each with 80 trials. Two of the blocks contained only meaningful or meaningless gestures, each repeated eight times and randomly ordered (the blocked condition). The other two mixed blocks contained 50% meaningful and 50% meaningless gestures, with each gesture repeated four times and randomly ordered (the mixed condition). The order of these four blocks was counterbalanced across participants.

In a single trial, participants observed the action stimulus until the video finished. The screen then turned black, and a 100ms tone signalled participants to repeat the action and maintain the gesture until they heard a further, lower-frequency tone (lasting 250ms) 1250ms later, at which point they were to return their hand to the start point. From the start of the second tone, participants had 750ms to return their hand to the start point before the next trial began. Once the four blocks were finished, participants completed a short questionnaire showing a pseudorandomised list of the gestures they had performed. For each gesture, they were, asked to state whether they thought the action was meaningful, and if so what that action meaning was.

Participants were excluded if they failed to adequately perform 25% of their trials in all blocks. Failures were counted as false starts (i.e., starting before the tone), or non-completion of the gesture in the given time (i.e., their wrist velocity did not drop below 10cm/s before returning their hand to the start point). Participants were also excluded if their subjective rating of the action meanings failed to meet a 60% accuracy criterion (mean±SE accuracy=82.1±2.03%). These criteria resulted in one participant excluded due to their questionnaire results, and six due to the percentage of false starts. The excluded participants were replaced until a total of 24 participants were available for analysis.

2.2.1.4 Data analysis

For each participant, the data for meaningful and meaningless gestures in the mixed blocks was extracted and split into blocks of 80 meaningful and 80 meaningless trials. This meant that the four crossed conditions for the final analysis, with 80 trials each, were blocked meaningful, blocked meaningless, mixed meaningful, and mixed meaningless.

An automated script was used for pre-processing and extraction of variables. The analysis routines processed the position data from each trial of each participant and rejected artefacts before filtering with a bidirectional low-pass 4th order Butterworth filter (cutoff frequency 15Hz). Kinematic variables were extracted from the imitator's primary movements (i.e., from movement onset to the point at which the hand gesture was maintained using a 5cm/s velocity criterion): RT, movement time (MT), peak acceleration (PA), time to peak acceleration (TPA), TPA/MT, peak velocity (PV), time to peak velocity (TPV), TPV/MT, peak velocity/mean velocity (TPV/MV), peak deceleration (PD), time to peak deceleration (TPD), TPD/MT, and root mean squared jerk (RMS jerk). A schematic highlighting peak values can be observed in Figure 2-2.

11.3% of trials were removed due to false starts or failure to finish the gesture before the end of the action period, and a further 1.7% of trials were removed due to remaining electromagnetic artefacts based on visual inspection. We decided post-hoc to use the percentage of trials in which the actions were incomplete within the time limit as a further variable for analysis, to examine whether participants' ability to adequately complete the action was significantly reduced in any condition.

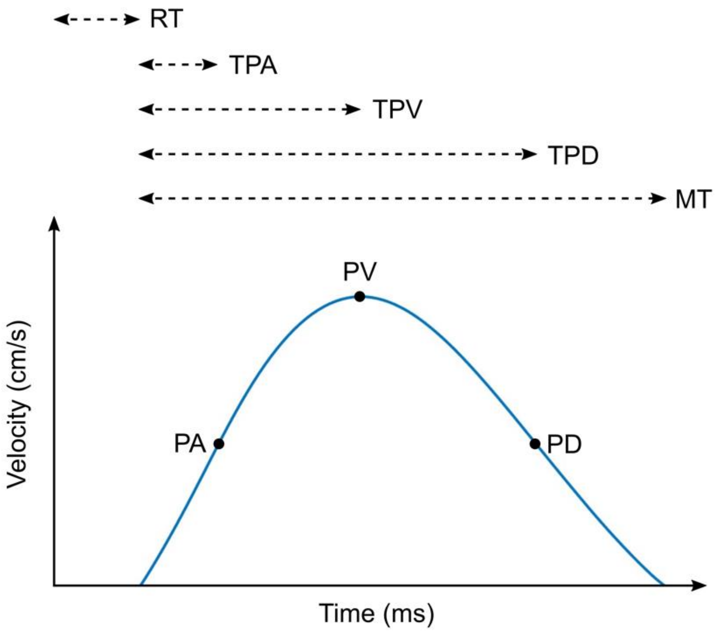

Figure 2-2: Example velocity plot and kinematic markers

RT = reaction time, TPA = time to peak acceleration, TPV = time to peak velocity, TPD = time to peak deceleration, MT = movement time, PA = peak acceleration, PV = peak velocity, PD = peak deceleration

For each of the extracted variables, two-way repeated measures ANOVAs were run to compare the across-trial mean values per participant over the four conditions resulting from crossing block type and meaning. To examine how the prior action (i.e., meaningful or meaningless) influenced the present action within the mixed block, we ran further two-way repeated measures ANOVAs. In these ANOVAs, prior and present action type were used as levels in a within-participant variable. The percentage of incomplete actions was not examined in this instance since the number of congruent and incongruent trials varied across blocks and participants.

2.2.2 Results

When comparing all block types (Table 2-1), blocked trials had a significantly longer MT, but a significantly earlier time to peak velocity and time to peak acceleration as a proportion of the MT, as compared to mixed trials. Meaningless trials had a significantly greater PV compared to meaningful trials. Meaningless trials also had a significantly longer MT, and were found to have a significantly earlier time to peak velocity, time to peak acceleration, and time to peak deceleration as a proportion of the entire MT.

These differences between meaningful and meaningless actions (MT, TPV/MT, TPA/MT, TPD/MT) were maintained in the present action comparison in the mixed block analysis (Table 2-1). There were no significant block type*meaning interactions, notably in RT, suggesting that there was no effect of changing the block type on meaningful or meaningless action performance. This was against what we had originally hypothesised, and what was shown for RT by Press & Heyes (2008).

Table 2-1: Group means and ANOVA results

Significant p-values are in bold.

Variable	Mean(±SE) value				Main effect						Block type*meaning interaction		
	Block type		Meaning		Block type			Meaning			F (1, 23)	p	η^2
	Blocked	Mixed	Meaningful	Meaningless	F (1, 23)	p	η^2	F (1, 23)	p	η^2			
RT (ms)	315 (11.7)	317 (11.5)	320 (12.7)	312 (10.2)	0.124	.728	.005	1.67	.209	.068	1.00	.328	.042
TPA (ms)	120 (4.66)	124 (5.93)	123 (5.28)	121 (5.08)	2.16	.155	.086	1.98	.173	.079	1.41	.247	.058
TPA/MT (0-1)	.178 (.00757)	.188 (.00831)	.188 (.00809)	.178 (.00757)	6.45	**.018**	.219	18.3	**<.001**	.443	1.63	.215	.066
PA (cm/s^2)	565 (27.4)	568 (28.0)	560 (27.9)	572 (26.9)	0.100	.756	.004	2.11	.160	.084	0.292	.594	.013
TPV (ms)	305 (5.95)	307 (7.83)	306 (7.02)	306 (6.61)	0.228	.637	.010	0.148	.704	.006	0.018	.894	.001
TPV/MT (0-1)	.454 (.00844)	.465 (.00883)	.467 (.00852)	.452 (.00798)	6.25	**.020**	.214	20.4	**<.001**	.469	0.220	.643	.009
PV (cm/s)	89.9 (3.42)	90.6 (3.44)	89.3 (3.44)	91.2 (3.35)	0.349	.560	.015	8.76	**.007**	.276	1.44	.242	.059
PV/MV (cm/s)	1.75 (0.0132)	1.76 (0.0136)	1.75 (0.0135)	1.76 (0.0131)	0.475	.498	.020	4.12	.054	.152	0.139	.713	.006
TPD (ms)	515 (11.9)	510 (13.6)	509 (12.5)	517 (12.6)	0.484	.493	.021	2.25	.147	.089	0.004	.949	<.001
TPD/MT (0-1)	.762 (.00835)	.768 (.00931)	.773 (.00894)	.756 (.00858)	1.09	.308	.045	9.58	**.005**	.294	0.050	.825	.002
PD (cm/s^2)	-410 (19.9)	-422 (20.0)	-414 (18.8)	-418 (20.5)	1.80	.193	.073	0.647	.429	.027	0.808	.378	.034
MT (ms)	678 (11.8)	665 (11.8)	659 (11.9)	684 (11.2)	4.39	**.047**	.160	44.4	**<.001**	.659	0.444	.512	.019
RMS jerk (cm/s^3)	4979 (195)	5139 (259)	5003 (209)	5114 (230)	0.781	.386	.033	0.595	.448	.025	0.160	.693	.007
Incomplete actions (%)	9.45 (2.53)	9.22 (1.92)	8.05 (1.80)	10.6 (2.49)	0.018	.895	.001	3.78	.064	.141	0.171	.683	.007

Table 2-2: Group means and ANOVA results for mixed blocks only (prior action vs. present action)
Significant p-values are in bold.

Variable	Mean(±SE) value				Main effect						Prior*present interaction		
	Prior action		Present action		Prior action			Present action			F (1, 23)	p	η^2
	Meaningful	Meaningless	Meaningful	Meaningless	F (1, 23)	p	η^2	F (1, 23)	p	η^2			
RT (ms)	316 (11.4)	318 (12.0)	318 (12.2)	316 (11.2)	0.562	.461	.024	0.560	.462	.024	0.007	.934	<.001
TPA (ms)	123 (5.82)	127 (6.36)	125 (6.27)	124 (5.90)	3.08	.092	.118	0.155	.697	.007	0.702	.411	.030
TPA/MT (0-1)	.185 (.00830)	.191 (.00879)	.192 (.00908)	.184 (.00787)	2.92	.101	.113	8.51	**.008**	.270	0.329	.572	.014
PA (cm/s^2)	569 (29.3)	566 (26.9)	564 (27.7)	570 (28.6)	0.406	.531	.017	1.30	.265	.054	0.118	.734	.005
TPV (ms)	306 (7.93)	309 (7.94)	306 (7.87)	308 (8.12)	2.42	.134	.095	0.371	.549	.016	0.178	.677	.008
TPV/MT (0-1)	.463 (.00814)	.467 (.00858)	.472 (.00861)	.458 (.00816)	1.62	.216	.066	18.8	**<.001**	.450	0.647	.429	.027
PV (cm/s)	90.3 (3.48)	90.9 (3.43)	90.3 (3.50)	90.9 (3.41)	1.10	.304	.046	1.98	.173	.079	0.016	.901	.001
PV/MV (cm/s)	1.76 (0.0136)	1.76 (0.0140)	1.75 (0.0137)	1.76 (0.0144)	0.172	.682	.007	2.61	.120	.102	0.002	.964	<.001
TPD (ms)	509 (14.2)	511 (13.3)	507 (13.6)	514 (14.1)	0.252	.621	.011	2.77	.109	.108	5.21	**.032**	.185
TPD/MT (0-1)	.766 (.0101)	.769 (.00878)	.775 (.0101)	.759 (.00995)	0.485	.493	.021	4.36	**.048**	.159	5.64	**.026**	.197
PD (cm/s^2)	-422 (20.2)	-422 (20.0)	-422 (19.8)	-422 (20.4)	0.002	.968	<.001	0.082	.777	.004	0.183	.672	.008
MT (ms)	666 (11.8)	666 (12.1)	654 (12.0)	678 (12.0)	0.016	.901	.001	63.0	**<.001**	.732	0.005	.946	<.001
RMS jerk (cm/s^3)	5142 (263)	5129 (259)	5109 (254)	5162 (266)	0.035	.853	.002	0.783	.386	.033	0.633	.434	.027

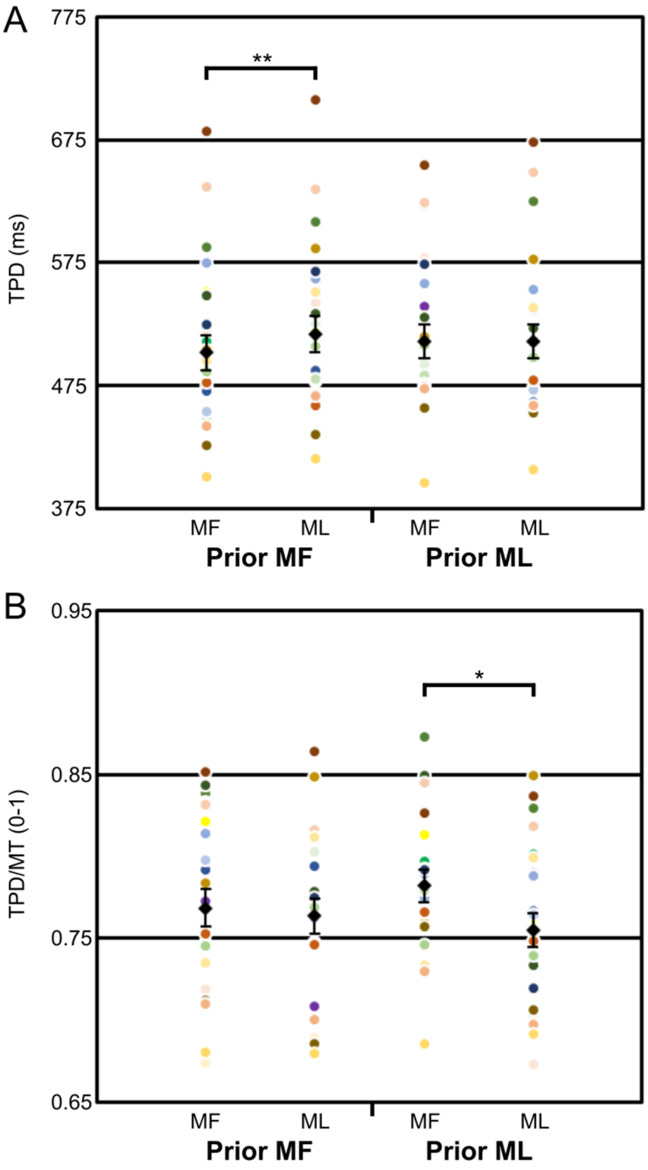

Figure 2-3: Paired comparisons for significant prior*present interactions

A) TPD B) TPD/MT; Coloured points represent single participant values, black diamonds represent mean values with between-subjects SE bars; MF = meaningful, ML = meaningless; * = p<.025, ** = p<.01.

Despite this, there were significant prior*present interactions (Table 2-2) in time to peak deceleration and TPD/MT, suggesting that the type of prior action may have influenced the following action performance. To examine these further we used two-tailed t-tests for post-hoc paired comparisons (Figure 2-3). Since comparisons could be run at either the level of the prior action or the present action, we used a Bonferroni corrected alpha cutoff of .025 for assessing statistical significance.

When the prior action was meaningful, time to peak deceleration was significantly later in meaningless trials compared to meaningful trials (t(23)=-2.88, p=.008), but there was no significant difference between time to peak deceleration in meaningful and meaningless trials that followed a meaningless action (t(23)=-0.019, p=.985). However, when examining TPD/MT we found that when the prior action was meaningless, TPD/MT was significantly later in meaningful trials compared to meaningless trials (t(23)=2.81, p=.010), but there was no significant difference between TPD/MT in meaningful and meaningless trials that followed a meaningful action (t(23)=0.592, p=.560).

2.2.3 Discussion

We found several interesting differences in kinematic parameters between performance for meaningful and meaningless actions. First, meaningless trials had a significantly greater MT and proportionally earlier time to peak acceleration, time to peak velocity, and time to peak deceleration compared to meaningful actions, despite the absolute values of time to peak acceleration, time to peak velocity, and time to peak deceleration showing no significant difference. Such a result indicates that the difference in MT reflects a difference in time between PD and the end of the action. It took longer for participants to settle into the final posture in meaningless actions, possibly because they were less familiar with the correct end point in these instances. The increased PV observed in meaningless trials may also reflect this, such that participants performed less familiar actions more rapidly to be certain of their completion within the given time, and allowing themselves more time for correction. However, this was not reflected in a significant difference in PA, nor was this finding repeated when we examined mixed blocks alone. Overall, this finding seems to indicate that the correction period in gesture imitation is dependent on whether the imitator is familiar with the action.

Movements in the blocked condition were significantly longer in duration than in the mixed condition, with proportionally earlier time to peak velocity and time to peak acceleration. The longer MT in this case may indicate that when the entire block of trials was similar in familiarity, participants could better regulate the time they spent performing the actions to optimise their performance given the time constraints.

When we examined the mixed trials in terms of prior and present actions to test the stimulus selection hypothesis, we found that time to peak deceleration was significantly later for meaningless (but not meaningful) actions when the prior action was meaningful, and that TPD/MT was significantly later in meaningful (but not meaningless) actions when the prior action was meaningless. It is not entirely clear what could be driving this surprising result. If imitation of meaningless and meaningful actions is reliant on a stimulus selected dual-route, as posited by Press & Heyes (2008), we would indeed expect action performance to depend on the type of action performed in the previous trial, as they had observed in RT. However, it is hard to tell why a meaningful action would delay the deceleration of a subsequent meaningless trial, whilst a meaningless action would cause the PD of the following meaningful trial to occur at a later portion of the MT. In both cases it may just be a side-effect of switching between the two routes, such that when the following action was different, participants focused more on forming the action quickly than correcting it.

Contrary to our hypothesis, and out of line with Press & Heyes (2008), we did not observe any significant interactions in RT. In particular we did not observe any increased RT for trials following meaningless actions. In this experiment, participants were required to watch the stimuli (~1573ms), before they were given 1250ms to perform and maintain the gesture, then 750ms to return their hand before the next trial started. This meant that the time between action onset in consecutive trials (i.e., the trial length) was ~3573ms. This was more than the trial lengths in which effects were found in the experiments of Tessari & Rumiati (2004) and Press & Heyes (2008): 1750ms and 2750ms, respectively.

As emphasised in the general introduction, Press & Heyes (2008) suggest that since the direct route for processing meaningless actions is more cognitively demanding, the increased working memory load associated with performing these sorts of actions can negatively influence the performance of the following action in the mixed block. We decided that participants may have had too much time to recover from the constraints imposed on working memory load by the direct route following meaningless action imitation in the mixed blocks. This may have removed the potential for interaction effects, and reducing our likelihood of observing the effects of RT discovered by Press & Heyes (2008).

We attempted to rectify this in two further experiments, reducing the trial length by increasing durations. We did this by manipulating our original stimuli of ~1573ms duration. In experiment 1B we examined ~948ms stimuli, showing the movement start to gesture position being held. In experiment 1C we examined ~553ms stimuli, simply showing the gesture position being held. We hypothesized that we would at least observe the RT interaction effect found in previous work, possibly in experiment 1B, but more likely in experiment 1C.

2.3 Experiment 1B

2.3.1 Methods

The methods were the same as experiment 1A, except where indicated.

2.3.1.1 Participants

24 new participants were recruited (mean±SE age = 20.2±0.54 years, 1 male, 1 left-handed). None of the participants had taken part in the previous experiment. As in experiment 1A, participants were excluded if their subjective rating of the action meanings failed to meet a 60% accuracy criterion (mean±SE accuracy = 82.7±2.17%). They were also excluded if every block had a greater than 25% failure rate (false starts or non-completions). Only the false start criteria resulted in exclusion (seven participants). These participants were replaced until 24 total participants were available for analysis.

2.3.1.2 Materials, stimuli, and procedure

These were the same as experiment 1A, except in this case the videos presented to participants had a mean±SD length of 948±35.4. These videos were identical to those in experiment 1A, the only change being that they ended as soon as the posture was complete (i.e., excluding the period in which the gesture was held statically).

2.3.1.3 Data analysis

This was the same as experiment 1A. In this instance 4.44% of trials were removed due to false starts or failure to finish the gesture before the end of the action period, and a further 1.69% of trials were removed due to electromagnetic artefacts as defined by visual inspection.

One participant showed unusually low RTs (below 150ms, dark green points in Figure 2-4A). However, since RT was cued in this experiment, with the videos finishing prior to the tone signalling movement, it is likely that participants were more prepared to rapidly act compared a RT without cue. In addition, since our RT measures are based on the movement of the wrist, rather than a button press or release, we have low RT values in general. Finally, this participant did not show outlying values on any other variable, suggesting that they were completing the task as expected.

2.3.2 Results

When examining both block types (Table 2-3) we found that, compared to meaningful trials, meaningless trials had a significantly larger peak acceleration, peak velocity, PV/MV, MT, and RMS jerk, and significantly smaller RT, TPV/MT and TPD/MT. The effects on peak velocity, MT, TPA/MT, TPV/MT, and TPD/MT were replicated from experiment 1A. The effects on peak acceleration, TPV/MT, TPD/MT, and MT were maintained for present trials in the mixed block analysis (Table 2-4). This analysis also revealed that TPV/MT was significantly greater for present meaningful versus present meaningless trials, and that RT was significantly greater for prior meaningless versus prior meaningful trials, in line with Press & Heyes (2008).

To examine significant block type*meaning interactions (Table 2-3) we used two-tailed t-tests for post-hoc pairwise comparisons (Figure 2-4). Since comparisons could be run at either the level of the block type or the action meaning, we used a Bonferroni corrected alpha cutoff of .025 for assessing statistical significance. Meaningful trials had a significantly later RT than meaningless trials in the blocked condition (t(23)=2.58, p=.017), but there was no significant difference between meaningful and meaningless trials in the mixed condition (t(23)=-0.048 p=.962). This effect was also observed for PV, where meaningful actions had a significantly smaller PV than meaningless actions in the blocked condition (t(23)=-3.78, p<.001), whilst there was no significant difference in PV between meaningless and meaningful trials in the mixed blocks (t(23)=1.19, p=.248).

Examining the interaction in PV/MV (a measure of movement 'shape', or kurtosis) revealed that PV/MV was significantly greater in meaningless versus meaningful trials in the blocked condition (t(23)=4.23, p<.001), but there was no significant difference between meaningless and meaningful trials in the mixed condition (t(23)=0.856, p=.401). Meaningful trials had a significantly greater peak acceleration in the mixed versus blocked conditions (t(23)=2.79, p=.010), whilst there was no significant difference in peak acceleration between meaningless trials in the mixed and blocked conditions (t(23)=0.083, p=.935).

Table 2-3: Group means and ANOVA results

Significant p-values are in bold.

Variable	Mean(±SE) value				Main effect						Block type*meaning interaction		
	Block type		Meaning		Block type			Meaning					
	Blocked	Mixed	Meaningful	Meaningless	F (1, 23)	p	η^2	F (1, 23)	p	η^2	F (1, 23)	p	η^2
RT (ms)	309 (10.7)	311 (8.97)	317 (9.48)	304 (9.53)	0.061	.808	.003	4.44	**.046**	.162	9.52	**.005**	.293
TPA (ms)	128 (6.78)	127 (6.13)	126 (5.58)	129 (7.47)	0.083	.775	.004	.635	.434	.027	2.23	.149	.088
TPA/MT (0-1)	.199 (.00908)	.199 (.00825)	.202 (.00806)	.197 (.00940)	<.001	.985	<.001	1.42	.245	.058	1.76	.198	.071
PA (cm/s^2)	498 (22.2)	512 (21.1)	493 (20.5)	518 (22.1)	2.34	.140	.092	19.5	**<.001**	.459	6.376	**.019**	.217
TPV (ms)	297 (7.71)	297 (7.71)	298 (6.74)	296 (8.61)	0.052	.822	.002	0.210	.651	.009	0.166	.687	.007
TPV/MT (0-1)	.470 (.00772)	.471 (.00761)	.481 (.00756)	.460 (.00778)	0.019	.891	.001	37.7	**<.001**	.621	2.147	.156	.085
PV (cm/s)	75.6 (2.09)	77.3 (1.92)	75.3 (1.92)	77.6 (1.97)	2.14	.157	.085	12.5	**.002**	.351	9.25	**.006**	.287
PV/MV (cm/s)	1.75 (0.0117)	1.76 (0.0113)	1.74 (0.0118)	1.76 (0.0111)	1.09	.307	.045	11.4	**.003**	.332	10.8	**.003**	.320
TPD (ms)	474 (10.5)	470 (10.0)	471 (9.23)	473 (11.3)	0.842	.368	.035	0.11	.742	.005	0.002	0.967	<.001
TPD/MT (0-1)	.749 (.00889)	.746 (.00904)	.761 (.00934)	.734 (.00853)	0.308	.584	.013	34.8	**<.001**	.602	1.58	.221	.064
PD (cm/s^2)	-349 (12.7)	-362 (12.0)	-356 (12.0)	-355 (11.9)	2.71	.113	.105	0.059	.811	.003	1.98	.172	.079
MT (ms)	637 (11.1)	633 (10.5)	622 (10.4)	648 (11.4)	0.659	.425	.028	20.3	**<.001**	.469	0.991	.330	.041
RMS jerk (cm/s^3)	3943 (156)	4053 (135)	3943 (141)	4053 (135)	1.11	.304	.046	6.10	**.021**	.210	3.77	.065	.141
Incomplete actions (%)	4.79 (1.20)	3.83 (1.00)	3.39 (0.624)	5.23 (1.46)	1.14	.298	.047	3.49	.074	.132	0.336	.568	.014

Table 2-4: Group means and ANOVA results for mixed blocks only (prior action vs. present action)

Significant p-values are in bold.

Variable	Mean(±SE) value				Main effect						Prior*present interaction		
	Prior action		Present action		Prior action			Present action			F (1, 23)	p	η^2
	Meaningful	Meaningless	Meaningful	Meaningless	F (1, 23)	p	η^2	F (1, 23)	p	η^2			
RT (ms)	307 (9.22)	314 (9.12)	311 (9.11)	310 (9.20)	5.97	**.023**	.206	0.019	.893	.001	2.59	.121	.101
TPA (ms)	128 (6.04)	127 (6.56)	128 (6.23)	127 (6.53)	0.121	.731	.005	0.117	.735	.005	0.154	.699	.007
TPA/MT (0-1)	.201 (.00807)	.198 (.00887)	.204 (.00882)	.194 (.00833)	0.421	.523	.018	5.12	**.033**	.182	0.404	.531	.017
PA (cm/s^2)	508 (21.5)	513 (20.6)	505 (20.7)	516 (21.4)	1.25	.276	.051	7.67	**.011**	.250	2.76	.110	.107
TPV (ms)	297 (7.68)	296 (8.07)	297 (7.61)	296 (8.14)	0.121	.731	.005	0.106	.748	.005	2.51	.127	.099
TPV/MT (0-1)	.472 (.00742)	.469 (.00811)	.479 (.00826)	.462 (.00737)	2.70	.114	.105	36.4	**<.001**	.613	5.37	**.030**	.189
PV (cm/s)	76.8 (1.92)	77.5 (1.91)	76.9 (1.97)	77.5 (1.87)	3.02	.096	.116	1.31	.265	.054	3.32	.082	.126
PV/MV (cm/s)	1.76 (0.0112)	1.75 (0.0120)	1.75 (0.0128)	1.76 (0.0107)	0.604	.445	.026	0.616	.440	.026	0.80	.381	.034
TPD (ms)	470 (10.3)	472 (10.2)	470 (9.82)	472 (10.7)	0.295	.592	.013	0.194	.664	.008	0.193	.665	.008
TPD/MT (0-1)	.747 (.00950)	.746 (.00926)	.758 (.0104)	.735 (.00843)	0.007	.932	<.001	21.0	**<.001**	.478	1.19	.287	.049
PD (cm/s^2)	-359 (12.8)	-362 (11.1)	-364 (12.0)	-356 (11.9)	0.481	.495	.020	4.23	.051	.155	1.84	.188	.074
MT (ms)	632 (10.7)	635 (10.6)	623 (10.9)	645 (10.7)	1.18	.288	.049	28.0	**<.001**	.549	1.16	.292	.048
RMS jerk (cm/s^3)	4036 (143)	4045 (127)	4035 (135)	4046 (137)	0.048	.828	.002	0.059	.810	.003	4.62	**.042**	.167

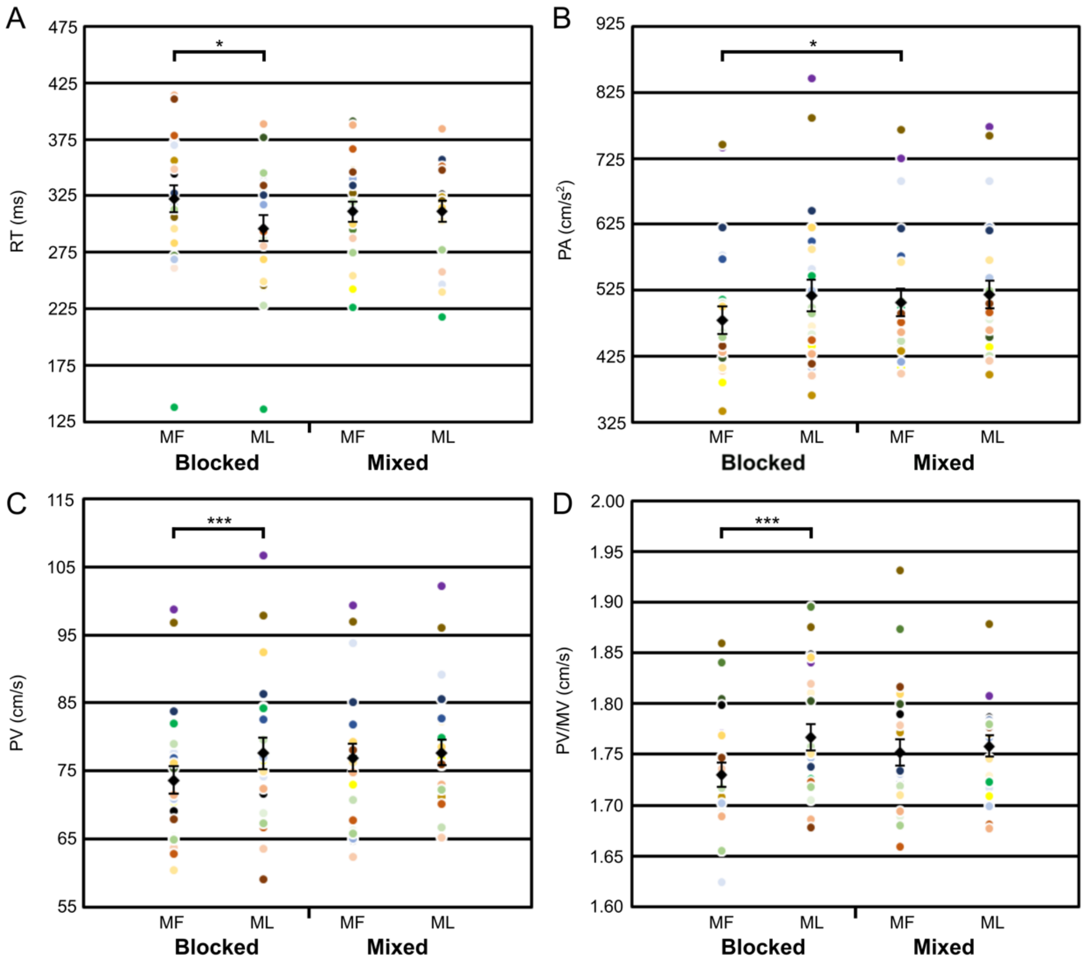

Figure 2-4: Paired comparisons for significant block type*meaning interactions

A) RT B) PA C) PV D) PV/MV; Coloured points represent single participant values, black diamonds represent mean values with between-subjects SE bars; MF = meaningful, ML = meaningless; * = p<.025, *** = p<.001.

Table 2-4 shows significant prior*present interactions in TPV/MT and RMS jerk, which we examined using post-hoc two-tailed paired t-tests (Figure 2-5) with a Bonferroni corrected alpha cutoff of .025 for assessing statistical significance. Meaningful trials had a significantly greater TPV/MT when they followed a meaningful action compared to a meaningless action (t(23)=3.46, p=.002), but there was no significant difference between meaningless trials following a meaningful or meaningless action (t(23)=-0.603, p=.552). There was no significant difference in RMS jerk between meaningful (M±SE=3989±147cm/s^3) and meaningless (4083±144cm/s^3) trials that followed a meaningful action (t(23)=-1.74, p=.096), nor between meaningful (4080±127cm/s^3) and meaningless (4009±136cm/s^3) trials that followed a meaningless action (t(23)=1.08, p=.291).

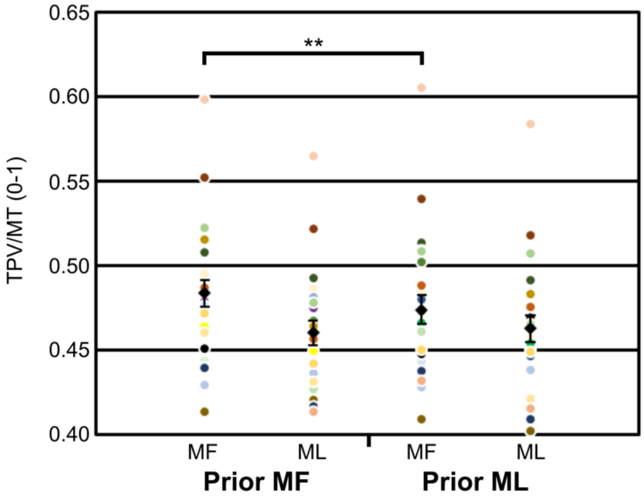

Figure 2-5: Prior*present paired comparison for TPV/MT

Coloured points represent single participant values, black diamonds represent mean values with between-subjects SE bars; MF = meaningful, ML = meaningless; ** = p<.01.

2.3.3 Discussion

As in experiment 1A, we observed that meaningless trials had a significantly larger MT and peak velocity, and significantly smaller TPV/MT and TPD/MT than trials with a meaningful action. This suggested that participants' behaviour in terms of meaningful and meaningless action performance was similar to that observed in experiment 1A. Participants increased their PV to ensure a greater correction time in meaningless actions, reflected by a longer period of MT following peak deceleration. We also observed that meaningless actions had a significantly greater PA, and this is again likely to reflect a more rapid performance of the action to allow for greater correction time in meaningless gestures. Meaningless actions were found to have a significantly larger PV/MV, indicating a narrower velocity curve which could be suggestive of a more rapid transition between acceleration and deceleration, further supporting this claim. The block type*meaning interaction revealed that this effect in PV/MV was driven by a significant difference between meaning in the blocked condition only, possibly indicating a normalisation of this variable in situations where the actions to imitate are mixed.

We also found that PA was significantly greater in mixed versus blocked conditions for meaningful actions, and that PV was significantly greater in meaningless compared to meaningful trials in the blocked condition only. In mixed trials, meaningful actions had an increased PV, and this could explain the absence of an effect. One possibility is that these effects reflect the increased uncertainty in the mixed trials, which may provide a greater sense of urgency, as a result of the time required to complete the action. This is a feasible explanation in the absence of evidence for a dual-route effect (i.e., an influence of prior action in the mixed trials).

The analysis of RMS jerk data suggested that meaningful actions were performed significantly smoother than meaningless actions. This is in line with the idea that participants maintained better control over their arm movement when they were familiar with the action to be imitated. Interestingly, meaningful actions only had a significantly greater TPA/MT when examining the mixed blocks in terms of prior and present action, though it is unclear why this would be the case. The reduced time available for switching between trial types may have influenced this, but the fact that no block type*meaning interaction was present suggests that this could just have been the result of larger participant variability in TPA/MT for this experiment compared to experiment 1A. The SD of this variable in experiment 1A was 0.0379, whilst it was 0.0417 in the current experiment, perhaps lending credence to this explanation.

Importantly, and somewhat surprisingly, RT was found to be significantly slower in meaningful compared to meaningless actions. The block type*meaning interaction indicated that meaningful and meaningless actions were only significantly different in the blocked condition. When examining only the mixed blocks, the cause of this RT effect was explained. Trials following a meaningless action were found to have a significantly greater RT compared to those following a meaningful action. This is in line with the findings of Press & Heyes (2008). This supports the idea that, following the decreased inter-trial trial interval in this experiment, the cognitive load associated with direct processing of meaningless gestures was so great as to interfere with the speed with which the following action was initiated, as has been posited by Press & Heyes (2008).

Despite the replication of this effect, the fact that meaningful actions had a greater RT than meaningless actions (the opposite direction of effect to that in Press & Heyes, 2008) is worth discussion. One possibility, which is discussed in more detail in the general discussion section, is that this results from our choice of stimuli. Press & Heyes (2008) used empty-handed pantomimes, which implied the use of an object. Considering the functional nature of object-directed action, information regarding these types of action may be more frequently accessed than for emblematic gestures, indicating that emblematic gestures could require greater 'search time' for accessing their motor representation. Put simply, the retrieval of emblematic gestures from long term memory may take longer than the retrieval of pantomimed gestures, but the cognitive load associated with this retrieval may be similar. Evidence suggesting different approaches to the retrieval of concrete versus conceptual information may support this (Noppeney & Price, 2004).

Finally, we found a significant interaction between the meaningfulness of the prior action and the present trial, indicating that meaningful trials had a later TPV/MT when they followed another meaningful action than a meaningless action. This may again reflect a compensatory measure, whereby participants would speed their action following a meaningless action to ensure timely completion.

Overall, the results of experiment 1B support the fact that meaningless actions use a greater correction time after peak deceleration, and also supports the stimulus selection hypothesis posited by Press & Heyes (2008): imitating a meaningless action increases the RT of the following action, suggestive of a greater stress placed on working memory by the direct route. In order to better understand the effects of a reduced trial time on RT, we performed a further experiment with the stimuli duration reduced to ~553ms, as previously discussed in section 2.2.3. We expected to once again observe increased RTs following meaningless actions in the mixed block, though possibly with a greater effect size than experiment 1B.

2.4 Experiment 1C

The methods were the same as for Experiment 1B, except where indicated.

2.4.1 Methods

2.4.1.1 Participants

24 new participants were recruited (mean±SE age = 22.8±0.88 years, 7 male, 3 left-handed). None of the participants had taken part in the previous experiments. Participants' mean±SE accuracy was 78.3±1.75%. None were excluded on accuracy or false start criteria.

2.4.1.2 Materials, stimuli, and procedure

The videos presented to participants had a mean±SD length of 553±9.62ms. These videos were identical to those in the previous experiments, the only change being that they did not show the actor moving their hand to the gesture location, only holding the gesture in place for the full video.

2.4.1.3 Data analysis

9.41% of trials were removed due to false starts or failure to finish gesture before the end of the action period, and a further 2.07% of trials were removed due to electromagnetic artefacts as defined by visual inspection.

2.4.2 Results

In the analysis of both block types (Table 2-5) we observed that meaningless actions had a significantly greater time to peak deceleration and MT, and significantly smaller TPA/MT, TPV/MT, TPD/MT, and peak deceleration when compared to meaningful actions. These effects on MT, TPA/MT, TPV/MT, and TPD/MT were replicated from the previous experiments. In the mixed block analysis (Table 2-6) the effects of meaning on TPA/MT, TPV/MT, TPD/MT, peak deceleration, and MT were maintained.

Table 2-5: Group means and ANOVA results

Significant p-values are in bold.

Variable	Mean(±SE) value				Main effect						Block type*meaning interaction		
	Block type		Meaning		Block type			Meaning			F (1, 23)	p	η^2
	Blocked	Mixed	Meaningful	Meaningless	F (1, 23)	p	η^2	F (1, 23)	p	η^2			
RT (ms)	298 (12.8)	291 (9.48)	302 (11.3)	288 (10.8)	1.12	.302	.046	6.23	**.020**	.213	0.042	.840	.002
TPA (ms)	129 (7.29)	129 (7.82)	129 (7.80)	130 (7.12)	<.001	.987	<.001	0.043	.837	.002	2.78	.109	.108
TPA/MT (0-1)	.198 (.00944)	.198 (.0104)	.203 (.0105)	.193 (.00918)	0.029	.867	.001	6.27	**.020**	.214	0.469	.500	.020
PA (cm/s^2)	496 (23.1)	511 (28.4)	506 (25.3)	502 (25.9)	1.83	.189	.074	0.256	.618	.011	0.149	.703	.006
TPV (ms)	305 (9.30)	302 (9.84)	301 (9.10)	305 (9.75)	0.665	.423	.028	3.00	.097	.115	2.42	.134	.095
TPV/MT (0-1)	.469 (.00923)	.467 (.0102)	.479 (.00948)	.456 (.0100)	0.621	.439	.026	43.4	**<.001**	.653	0.536	.471	.023
PV (cm/s)	77.8 (2.37)	78.8 (2.83)	77.9 (2.54)	78.6 (2.66)	1.09	.308	.045	0.601	.446	.025	1.30	.267	.053
PV/MV (cm/s)	1.75 (0.0111)	1.76 (0.0118)	1.75 (0.0104)	1.76 (0.0129)	1.33	.261	.054	3.80	.063	.142	.137	.714	.006
TPD (ms)	483 (12.3)	480 (13.1)	476 (12.2)	487 (12.6)	0.209	.652	.009	14.3	**<.001**	.384	6.74	**.016**	.227
TPD/MT (0-1)	.741 (.00931)	.740 (.0102)	.754 (.00984)	.726 (.00979)	0.056	.815	.002	34.3	**<.001**	.598	0.210	.651	.009
PD (cm/s^2)	-348 (14.8)	-356 (18.2)	-360 (16.2)	-344 (16.9)	1.01	.325	.042	5.85	**.024**	.203	0.235	.633	.010
MT (ms)	654 (11.4)	651 (12.3)	631 (11.1)	673 (12.1)	0.270	.608	.012	107	**<.001**	.823	6.16	**.021**	.211
RMS jerk (cm/s^3)	3927 (155)	3965 (180)	3970 (169)	3921 (167)	0.268	.609	.012	0.470	.500	.020	.562	.461	.024
Incomplete actions (%)	6.30 (1.63)	4.66 (1.02)	5.60 (1.28)	5.36 (1.18)	1.36	.256	.056	0.086	.772	.004	0.199	.660	.009

Table 2-6: Group means and ANOVA results for mixed blocks only (prior action vs. present action)

Significant p-values are in bold.

Variable	Mean(±SE) value				Main effect						Prior*present interaction		
	Prior action		Present action		Prior action			Present action			F (1, 23)	p	η^2
	Meaningful	Meaningless	Meaningful	Meaningless	F (1, 23)	p	η^2	F (1, 23)	p	η^2			
RT (ms)	288 (10.3)	293 (9.06)	298 (10.1)	284 (9.50)	2.54	.124	.100	13.1	**.001**	.363	0.166	.687	.007
TPA (ms)	128 (7.94)	131 (7.90)	131 (8.74)	128 (7.21)	2.80	.108	.108	0.956	.338	.040	0.439	.514	.019
TPA/MT (0-1)	.196 (.0107)	.201 (.0104)	.205 (.0116)	.192 (.00956)	2.88	.103	.111	9.59	**.005**	.294	0.591	.450	.025
PA (cm/s^2)	508 (27.7)	512 (29.4)	514 (29.3)	505 (27.8)	0.519	.478	.022	2.57	.122	.101	0.279	.602	.012
TPV (ms)	480 (13.5)	480 (13.0)	478 (13.4)	482 (13.0)	0.025	.877	.001	0.095	.761	.004	0.008	.929	<.001
TPV/MT (0-1)	.466 (.00996)	.467 (.0107)	.478 (.0100)	.456 (.0107)	0.298	.590	.013	43.5	**<.001**	.654	0.138	.714	.006
PV (cm/s)	78.2 (2.75)	78.9 (2.97)	78.8 (2.95)	78.3 (2.74)	0.900	.353	.038	0.955	.339	.040	0.408	.529	.017
PV/MV (cm/s)	1.75 (0.0117)	1.76 (0.0128)	1.75 (0.0125)	1.76 (0.0123)	0.683	.417	.029	1.91	.180	.077	1.74	.200	.070
TPD (ms)	480 (13.5)	480 (13.0)	478 (13.4)	482 (13.0)	<.001	.990	<.001	2.14	.157	.085	.726	.403	.031
TPD/MT (0-1)	.738 (.0104)	.742 (.0107)	.754 (.0104)	.726 (.0107)	1.09	.308	.045	33.8	**<.001**	.595	.220	.643	.009
PD (cm/s^2)	-351 (17.8)	-357 (18.4)	-365 (19.4)	-343 (17.0)	3.36	.080	.127	16.0	**<.001**	.410	0.078	.782	.003
MT (ms)	652 (12.5)	649 (12.3)	634 (12.6)	667 (12.0)	0.647	.429	.027	122	**<.001**	.841	0.044	.835	.002
RMS jerk (cm/s^3)	3948 (175)	3957 (187)	4041 (188)	3894 (177)	0.044	.836	.002	3.03	.095	.116	.256	.618	.011

To examine the significant block type*meaning interactions shown in Table 2-5 we used post-hoc two-tailed paired t-tests (Figure 2-6). Since comparisons could be run at either the level of the block type or the action meaning, we used a Bonferroni corrected alpha cutoff of .025 for assessing statistical significance. Meaningless trials had a significantly greater TPD than meaningful trials in the blocked condition (t(23)=3.44, p=.002), but there was no significant difference between meaningful and meaningless trials in the mixed condition (t(23)=-1.21, p=.240). There was no significant difference in MT for meaningless actions between the blocked (mean±SE=680±12.6ms) and mixed (667±12.2ms) conditions (t(23)=2.18, p=.040), nor between meaningful trials in the mixed (634±12.5ms) and blocked (628±11.2ms) conditions (t(23)=0.705, p=.488).

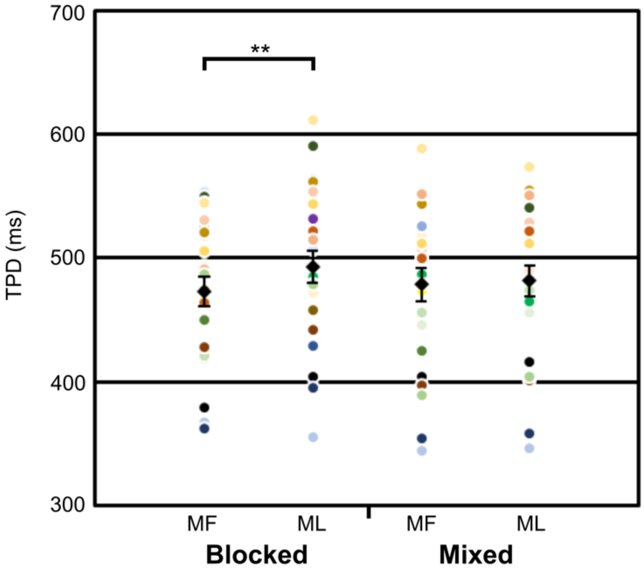

Figure 2-6: Block type*meaning paired comparison for TPD

Coloured points represent single participant values, black diamonds represent mean values with between-subjects SE bars; MF = meaningful, ML = meaningless; ** = p<.01.

2.4.3 Discussion

In experiment 1C we continued to find a significantly smaller TPA/MT, TPV/MT, and TPD/MT, and a greater MT for meaningless actions. We also observed that meaningless actions had a significantly later time to peak deceleration (despite earlier TPD/MT) and significantly smaller peak deceleration. The later time to peak deceleration might reflect an attempt by participants to reduce the correction time in the face of a shorter trial duration (despite the time available for performing actions remaining the same). Since the task was shorter, this may have biased participant behaviour such that those in experiment 1C felt a greater need to complete the actions more rapidly. However, since MT continued to be longer in meaningless actions, it is possible that this explicit attempt did not assist in reducing the correction time. On the other hand, the smaller peak deceleration in meaningless trials may reflect a reduction in the speed with which participants slowed to enter the correction phase, making these effects hard to explain. An interaction effect showed that time to peak deceleration was found to be significantly later only for meaningless actions versus meaningful actions in blocked trials, which may suggest that participant attempts to delay their peak deceleration may have been abandoned in the mixed blocks.

Whilst we found that meaningless actions had a significantly smaller RT compared to meaningful actions (as in experiment 1B), there was no longer any interaction between the block type and the meaningfulness of actions, or an effect of prior action in the mixed block. The absence of effect in this instance is discussed in more detail in the general discussion below.

2.5 Behavioural discussion

We hoped to reveal information about the kinematic differences between meaningful and meaningless action imitation which would provide us with behavioural markers for future experiments, and attempted to replicate previous findings in measures of RT from a previous experiment (Press & Heyes, 2008). In terms of the movements' kinematics, we found that meaningless action imitation was associated with a longer time spent in the 'correction' phase, at the end of the movement, as compared to meaningful actions, and that this effect possibly reflects an explicit strategy by participants.

When the previously observed RT effect was not evident in our original experiment (with stimuli of ~1573ms in length, and ~3573ms between movement onsets), we hypothesised that reducing the duration of stimuli could place greater stress on the direct route for matching observed and performed action kinematics. This would result in greater cognitive demand for performing the action and make it more likely that a RT cost would be incurred for the following action. We observed a similar effect to that revealed by Press & Heyes (2008) when we used a ~948ms stimulus duration (and with ~2948ms between movement onsets). Actions of either type, when they followed a meaningless action in the mixed condition, resulted in significantly greater RT. A stimulus of ~553ms (with ~2553ms between movement onsets) failed to show the same effect.

2.5.1 Kinematics in meaningful and meaningless action imitation

The most consistent kinematic effect, found in all three experiments, was that meaningless actions were associated with a longer MT, and proportionally earlier time to peak acceleration, time to peak velocity, and time to peak deceleration, strongly indicative of a longer time spent in the final, corrective phase, as compared to meaningful actions. One possible explanation of this is that participants purposely maintained a greater correction time in actions they did not know, to give themselves more time to confirm the final posture was accurate. The increased peak velocity and peak acceleration for meaningless actions in experiments 1A and 1B could then reflect an increase in speed at the start of these actions to allow for this. However, unlike experiments 1A and 1B, in experiment 1C meaningless actions were associated with a reduced peak deceleration rather than an increased peak velocity and peak acceleration. This suggests that the shorter trial time was associated with a lesser reduction in speed prior to the correction phase. Participants were still allowing themselves greater correction time in meaningless actions in experiment 1C, but through a reduction in the deceleration at the end of the movement, rather than an increase in velocity or acceleration at the start. This could reflect a reduced ability to adequately prepare for the correction phase under the increased pressure of the short trial time.

Whilst previous work has quantitatively examined the kinematic elements of imitative behaviour in both healthy people (e.g., Campione & Gentilucci, 2011; Pan & Hamilton, 2015; Reader & Holmes, 2015; Sacheli *et al.*, 2012; Sacheli *et al.*, 2013; Sacheli *et al.*, 2015a; Sacheli *et al.*, 2015b; Wild *et al.*, 2010) and brain damaged patients (Hermsdörfer *et al.*, 1996), as far as we are aware no previous experiments have looked at so many components of the velocity profile in order to compare the coarse-grained (i.e., wrist) kinematic approach to meaningful and meaningless actions. Much informative work has been done to examine kinematic aspects of meaningful and meaningless action imitation (e.g., Buxbaum *et al.*, 2014; Carmo & Rumiati, 2009; Goldenberg & Hagmann, 1997; Mengotti *et al.*, 2013; Rumiati & Tessari, 2002), but frequently using subjective rating measures.

Fine-grained kinematic differences between the imitation of these types of action are yet to be fully clarified, particularly as they relate to different body parts. Further work using motion-tracking will be essential to expand on these findings, particularly if we want to understand how gesture imitation differs from more commonly examined point-to-point movements (i.e., reaching-to-grasp). This is emphasised by a recent discussion by Wong *et al.* (2016), suggesting that differences in planning different types of action trajectories may be useful for distinguishing between types of action (e.g., meaningful versus meaningless, or transitive versus intransitive).

Beyond the consistent effects in the correction period discussed above, it is worth briefly considering some of the more inconsistent effects of action meaning between the three experiments reported here, which could inform us further as to how the change in trial timing might have influenced different movement parameters. Table 2-7 provides a summary of all significant effects in each experiment.

Table 2-7: Summary of significant effects reported in each experiment

Effects replicated in two or three experiments are in bold.

Variable	Block analysis							Prior action analysis					
	Effect of block type		Effect of meaning		Block type*meaning interaction			Effect of prior action	Effect of present action		Prior* present interaction		
	Blocked > mixed	Mixed > blocked	MF > ML	ML > MF	Blocked: MF > ML	Blocked: ML > MF	MF: Mixed > Blocked	ML > MF	MF > ML	ML > MF	Prior MF: ML > MF	Prior ML: MF > ML	Present MF: MF > ML
RT			**B, C**		B			B	C				
TPA/MT		A	**A, C**						**A-C**				
PA				B			B			B			
TPV/MT		A	**A-C**						**A-C**				B
PV				**A, B**		B							
PV/MV				B		B							
TPD				C		C					A		
TPD/MT			**A-C**						**A-C**			A	
PD			C						C				
MT	A			**A-C**						**A-C**			
RMS jerk				B									

Only in experiment 1A did we observe that TPD was significantly later in meaningless actions when the prior action was meaningful, and that TPD/MT was significantly later in meaningful actions when the prior action was meaningless. The fact that these effects disappeared with a shorter trial time is hard to explain, especially considering the replication of previous RT effects in experiment 1B. It is possible that these results are false positives, or that they reflect differing effects of trial time that would need further work to tease apart.

Only in experiment 1B did we observe that RMS jerk was significantly greater in meaningless compared to meaningful actions, and that TPV/MT was significantly greater in meaningful trials when they followed a meaningful action compared to a meaningless action. In experiment 1A the mean RMS jerk was 5059cm/s^3, reducing to 3998cm/s^3 in experiment 1B, and 3946cm/s^3 in experiment 1C, suggesting that actions performed in the reduced trial times were generally smoother than in the original experiment. Bonferroni-corrected post-hoc t-tests confirm this, showing significant between-subjects differences in RT between experiment 1A and experiment 1B (t(46)=4.24, p<.001), experiment 1A and experiment 1C (t(46)=4.17, p<.001), but not experiment 1B and experiment 1C (t(46)=0.245, p=.807). It is possible that meaningless actions were less sensitive to changes in time constraints for this variable. As emphasised previously, the effect of TPV/MT in experiment 1B may reflect a compensatory measure, where participants increased the speed of action performance after a meaningless action to ensure completion during the available time. This may have been harder to do under the increased time pressure in experiment 1C.

Only in experiment 1C did we observe that TPD was significantly later in meaningless as compared to meaningful trials in the blocked condition, but without a significant difference in the mixed condition. As highlighted in the discussion of experiment 1C, this may reflect an attempt to reduce the correction time, under greater time pressure, which disappeared when there was uncertainty regarding the composition of the mixed block.

2.5.2 Reaction time effects

Our results go some way to support the stimulus selection hypothesis posited by Press & Heyes (2008), which suggests that in mixed blocks actions are always imitated by way of their associated route (i.e., the route is *selected* based on the *stimulus*). Since meaningless actions are copied through visuomotor matching by the direct route, actions following a meaningless action trial show an increased RT due to the greater working memory load associated with matching observed to performed kinematics. The fact that in experiment 1B participants were significantly slower to initiate both meaningful and meaningless actions following a meaningless trial could indeed be suggestive of lingering working memory load effects following direct processing of meaningless actions. The fact that this was only observed after meaningless actions makes it likely that the direct route was only used in these instances, for the purpose of matching observed and performed kinematics (but see Rumiati & Tessari, 2002; Tessari *et al*., 2007; Tessari *et al*., 2009; Tessari & Cubelli, 2014; Tessari & Rumiati, 2004). More importantly, it appears that there is a temporal limit (in either direction) for direct route working memory interference to take effect. Reducing the trial length by ~625ms was enough to create this interference, possibly by reducing the time available to overcome the working memory effect.

What is less clear is why reducing the time available between movements by a further ~395ms would then negate this prior action effect, despite the maintained significant RT slowing between meaningful and meaningless conditions. In experiment 3, meaningless actions continued to have a significantly lower RT than meaningful actions, but this effect did not interact with the block type. In the mixed blocks there was no longer any negative influence on performance following a prior meaningless action. One explanation for this is that working memory interference on RT in this task is not linear. The semantic route may be the dominant and automatic route for imitation (Tessari *et al*., 2009) – when we have to imitate an action we know if is more efficient to recall it from memory than to match the observed kinematics as if we did not already know how to perform the action. With this in mind, it is possible that under such intense time constraints the accuracy of the meaningless (but not meaningful) action performance suffered to ensure task completion. This could in turn reduce the working memory interference related to meaningless action performance in the mixed trials – fewer cognitive resources would be dedicated to accurate visuomotor matching of the observed meaningless action, meaning less working memory interference to overcome in the following trial. Unfortunately we did not record participant accuracy, but certainly this would provide a feasible explanation.

Interestingly, we generally failed to observe potential dual-route (i.e., effects of prior action in the mixed block) evidence in kinematics. The most likely possibility is that these effects are simply not observable at the level of the wrist – they may be specific to the more fine-grained contributors to the action (i.e., the digits). The reported results for accuracy by Tessari & Rumiati (2004) and Press & Heyes

(2008) support this. However, in future work it may be beneficial to objectively examine the kinematics of the fingers to provide a more objective measure of imitation accuracy.

Also worth mentioning is the general finding that meaningful actions were performed with a slower RT than meaningless actions in this experiment, contrary to Press & Heyes (2008). As mentioned above, it is possible that this is due to the difference in actions used in our experiment. Since we were aiming to examine kinematics, we desired actions with a static endpoint such that we could extract velocity curves and their associated parameters. Pantomimes rarely meet these criteria, since they imply object use which is generally dynamic. The question then is whether this experiment is examining the same effect observed by Press & Heyes (2008). It certainly seems feasible that semantic information for imitation is in general processed in a similar fashion, and the differences between emblematic and pantomimed gestures may help to explain such findings.

As stated earlier, one possibility is that emblematic gestures have a greater semantic 'search time' compared to object-directed pantomimes. In fact, emblematic gestures may be processed similarly to language (Bernardis & Gentilucci, 2006; Xu *et al.*, 2009). Whilst object-directed pantomimes directly infer the object portrayed simply through their motion (which remains the same even though the hand is empty), emblematic gestures may require an extra step to be associated with semantic meaning. That is, they may take a longer processing time to be ‘linked’ with the concept (i.e., “thumbs up” = good) in the absence of an implied object. The fact that such gestures still show a similar effect as revealed by Press & Heyes (2008) seems to suggest that the semantic processing route is effective for these types of movement. This implies that the speed of commencing performance (RT) does not provide the strongest distinction between the semantic and direct routes. Rather, it is the intensity of processing that matters. Though the retrieval of emblematic gestures may take longer than the retrieval of pantomimed actions, the cost in cognitive terms remains comparable. Hence we see the results reported here, whereby working memory load from meaningless action processing is still the hardest to overcome. Whilst it is certainly possible that that these distinctions are reflective of three routes to imitation, rather than two, such a claim would require further work to better test and understand the differences between emblematic and pantomimed actions.

2.5.3 Behavioural conclusions

We found that the time spent in the terminal, 'correction' phase of movement is a distinguishing factor between the imitation of meaningful and meaningless actions. This effect was found in each of the three experiments reported here. In addition, our results broadly support a stimulus selection hypothesis for dual-route processing of imitation, though only under inter-movement intervals of ~2948ms. The effect was evident for reaction time measures, but not wrist kinematics. Importantly, this experiment provided some kinematic variables that distinguished between meaningful and meaningless action imitation, which we used in the following experiments.

3 EXPERIMENT 2 (INFERIOR PARIETAL LOBULE)

3.1 Introduction

Following our discovery of correction time markers that distinguish between wrist movements in meaningful and meaningless action imitation, we wanted to use these to test the role of a brain region commonly associated with action observation and imitation: the IPL (Caspers et al., 2010; Molenberghs et al., 2009). This region is frequently discussed as being part of the putative human mirror neuron system (MNS), which may support imitation by creating direct visuomotor links between an observed action and a stored motor representation of that action (Brass & Heyes, 2005; Rizzolatti et al., 2014). The IPL could contain a human homologue of monkey area PFG, which appears to encode action intention-related information during action observation (Fogassi *et al*., 2005; Rizzolatti *et al*., 2014).

Evidence that the parietal lobe may have mirror properties comes from a number of studies which show similar activity in this region for both observation and performance of the same actions (Caspers *et al*., 2010). Early work on imitation used fMRI to examine changes in brain activation during simple finger action observation, imitation, and execution (Iacoboni *et al*., 1999). Iacoboni *et al*. (1999)

observed that the anterior parietal lobe showed activity for both observed and performed finger movements, which increased during imitation. Further research confirmed that the IPL shows increased activity for action imitation versus action observation or control motor tasks (Jack *et al*., 2011; Jackson *et al*., 2006; Mainieri *et al*., 2013). Such effects may possibly reflect shared activity in the IPL for action observation and performance, and greater recruitment of this area in scenarios where matching is required – i.e., where mirror neurons could ostensibly link the action that was observed with the corresponding one in the observer's motor repertoire, coding both visual and motor aspects of the observed action (Iacoboni *et al*., 1999; Iacoboni, 2009).

Some have suggested that during imitation, the parietal lobe supports the matching of motor-related aspects of action, rather than goal-related aspects (Iacoboni & Dapretto, 2006; Iacoboni, 2009). However, the evidence for these claims comes from experiments using simple finger movements (i.e., Iacoboni *et al*., 1999), which may not accurately reflect more commonly used object-directed movements or gesturing. Some have suggested the contrary (Hamilton, 2008, 2014), pointing to the fact that parietal lobe activity may be better associated with encoding the goals of observed object-directed hand actions. In this case, there is the possibility that the IPL can subserve imitation by linking observed goals to the necessary action that needs to be performed to replicate the goal, though how this could be reflected in intransitive gestural imitation is uncertain.

In addition, in most neuroimaging work discussing the putative human MNS, there is more to be done to account for the specific role of IPL subregions (supramarginal gyrus, SMG; angular gyrus, AG), or how different types of action are processed by this area for imitation. Notably, there is no clear evidence regarding exactly which area of the IPL is engaged in mirror neuron processing. There is some suggestion that the SMG may be more frequently associated with action observation and imitation (Caspers *et al*., 2010; Molenberghs *et al*., 2009), but activity in the AG has also been observed in response to imitative tasks (e.g., Rumiati *et al*., 2005).

More generally, reporting of activity in the parietal lobe as belonging to simply ‘the IPL’ may make it hard to reconcile differences between disparate findings in neuroimaging studies of imitation, inform us of which exact area is potentially ‘mirroring’, or help us better understand different contributions of the IPL to different types of imitation. The IPL is a large region, which can be parcellated into at least 7 distinct cytoarchitectonic areas (Caspers *et al*., 2006, 2008), and it is unlikely that all of these areas support imitation. Further compounding the problem is a concern common to most neuroimaging publications: assessing individual brain activity fitted to a mean template is likely to undermine differences in individual gross neuroanatomy, making it harder to comprehend specific contributions of smaller subregions.

Furthermore, mirror-based discussions of the IPL are generally derived from object- or target-directed action imitation paradigms (Molenberghs *et al*., 2009), which may not adequately reflect the potential role of this area in empty-handed (intransitive) meaningful or meaningless gestures. Indeed, most direct evidence for mirror neurons in the monkey parietal cortex come from an examination of object-directed actions (Rizzolatti *et al*., 2014). Whilst there is some evidence from monkeys that mirror neurons in the premotor cortex might respond to intransitive hand actions (Kraskov *et al*., 2009; Papadourakis & Raos, 2017), similar effects have not yet been observed in the parietal lobe. In humans, the IPL does appear to be active during the imitation of meaningless actions (e.g., Tanaka *et al*., 2001). However, for meaningless (intransitive) actions, whether the processes supporting imitation in the IPL are driven by mirror neurons, or can be better explained by alternative possibilities, is yet to be established.

The uncertainty surrounding how the left or right IPL might support intransitive (meaningless) action imitation is important, since neuropsychologists studying apraxias suggest that the left parietal lobe controls kinematic or spatial aspects of imitation, and that the left IPL in particular is critical for imitating meaningless actions (Achilles *et al*., 2016; Goldenberg, 2009). Though both the left and the right IPL have been associated with action imitation (Caspers *et al*., 2010), some neuroimaging experiments in healthy individuals (Hermsdorfer *et al*., 2001; Peigneux *et al*., 2004; Tanaka *et al*., 2001) and clinical studies support this claim.

For example, damage to the left AG has been associated with disturbed imitation of meaningless, but not meaningful gestures (Goldenberg & Hagmann, 1997).

One explanation for the role of the IPL in imitation is provided by Goldenberg (2001, 2009), who suggests that the IPL supports ‘body part coding’, that is, the decomposition of observed actions into spatial relationships between different body parts, which can then be replicated. Finding that damage to the left IPL could be associated with non-motor and non-imitative tasks led Goldenberg & Randerath to suggest that this coding may reflect a more general role of the IPL in the “categorical apprehension of spatial and visual relationships”, which can not be easily reconciled with the claims made for a mirror-role of this region. This could only be done if the IPL is playing multiple roles in imitation, the confirmation of which requires more finely examining specific subregions of the IPL as we suggest.

Recently, large scale voxel-based lesion-symptom mapping (VLSM) studies, like that performed by Goldenberg & Randerath (2015), has enhanced our understanding of neuropsychological disorders by allowing the variability in patient deficits to be associated with the variability in lesion locations. VLSM approaches thus allow researchers to make stronger claims regarding the role of damaged areas associated with deficits across large samples. However, results using this approach are not always consistent. Some studies have suggested that the left SMG might be more important for meaningful actions, whilst the left AG is more important for meaningless actions (Mengotti *et al.*, 2013). Other experiments implicate the left IPL as being involved in kinematic, rather than semantic, elements of action imitation (Buxbaum *et al.*, 2014). It seems then that our objective motion-tracking approach might be useful to better understand the role of the IPL in realistic imitation tasks, particularly if we do or do not observe dissociations between meaningful and meaningless action performance.

One particularly useful aspect of this approach is that it allows more focussed assessment of specific subregions of the IPL (the SMG and AG), and their relation to imitative behaviour. This may allow us to assess specific subregions in a way that is not possible in VLSM, since like fMRI they rely heavily on shifting individual brain images to a template, which may reduce the accuracy of assessing the contributions of specific parcellated brain regions to imitation. Such an approach may be useful for helping us understand differences between results from apraxia and neuroimaging studies in healthy individuals. By deriving our TMS sites from individual brain images, we hoped that we would be able to make more concrete claims regarding any differences between parts of the IPL, which could feasibly subserve different processes during imitation. The utility of such an approach has been commented on before by Weiss *et al.*, (2013), who used non-invasive brain stimulation to assess the role of different IPL subregions in gesture processing.

In this experiment we aimed to use TMS over the left hemisphere to arbitrate between the roles of the two broad IPL subregions (SMG and AG) in imitation, and to test whether these regions are differentially involved in meaningful and meaningless action imitation. This was an exploratory approach, focussed on providing information that might allow us to better understand the role of the IPL, rather than distinguishing between mirror neuron and apraxia theories *per se*. In particular, we were interested in examining our previously observed correction markers, imitation accuracy, and kinematics in an exploratory fashion. We applied repetitive TMS (rTMS) over the SMG, AG, or during a no-rTMS baseline, then asked participants to imitate a confederate's actions in a two-person, ecologically valid and naturalistic motion-tracking paradigm.

3.2 Methods

3.2.1 Participants

We recruited 12 participants from the University of Reading (mean±SE age = 23.2±1.1 years, 5 males, 2 left handed). Left-handed participants were not excluded since, in the SMG at least, praxis representation is not related to handedness (Króliczak *et al*., 2016). The experiment was approved by the University of Reading ethics committee (ref: UREC 15/49); participants gave written, informed consent; the experiments were conducted in accordance with the Declaration of Helsinki (as of 2008). Sample size was based on previous TMS experiments performed by our group, and provides statistical power of 80% for a Cohen's d of 0.8 and alpha of

.05. This sample size also takes into account the relatively long testing duration for this experiment.

3.2.2 Materials and stimuli

Positions of the participant's right arm and hand and a confederate's left arm and hand were recorded using a Polhemus Liberty motion tracking system (Polhemus Inc., Colchester, VT, USA) recording 16 channels (8 per person) with 6 degrees of freedom (x, y, z, azimuth, elevation, and roll) at 240Hz. Trackers were attached to the shoulder (acromial end of the clavicle), elbow (olecranon), wrist (pisiform), and the thumb and finger tips, using adhesive medical tape or Velcro™. rTMS was applied using a PowerMAG 100 (Mag & More GmbH, Munich, Germany) with a 70mm figure-of-eight coil.

The experiment was controlled and data acquired using custom software written in MATLAB 2014b (Mathworks, Inc.) and using the ProkLiberty interface (https://code.google.com/p/prok-liberty/). We used LabMan and the HandLabToolbox to document and control experiments and analyse data. The associated repositories are, or will be, freely available at https://github.com/TheHandLaboratory, whilst raw data are available from the HandLaboratory's website (http://neurobiography.info and/or on request).

Thirty gestures were used as stimuli. This included five meaningful hand, five meaningful finger, and twenty matched meaningless gestures. For each meaningful gesture, two matched meaningless gestures were created. Meaningless gestures were matched to meaningful ones as in experiment 1. We used more meaningless than meaningful gestures to reduce the number of times participants were exposed to these actions, reducing the likelihood that they would associate them with a particular meaning. The finger gestures signified "okay", "thumbs up", "gun", "peace", and "silence". The hand gestures signified "salute", "stop", "shock", "looking into the distance", and "I'm listening" (Figure 3-1).

During the imitation task, participants sat opposite a confederate at a round plastic table (diameter=85cm), approximately 100cm apart (Figure 3-1). A Blu Tack® start point was located 20cm away from each person’s abdomen. To inform the confederate of the actions they needed to perform, a computer screen (unobservable by the participant imitator) was placed parallel to the table, approximately 50cm left of the actor.

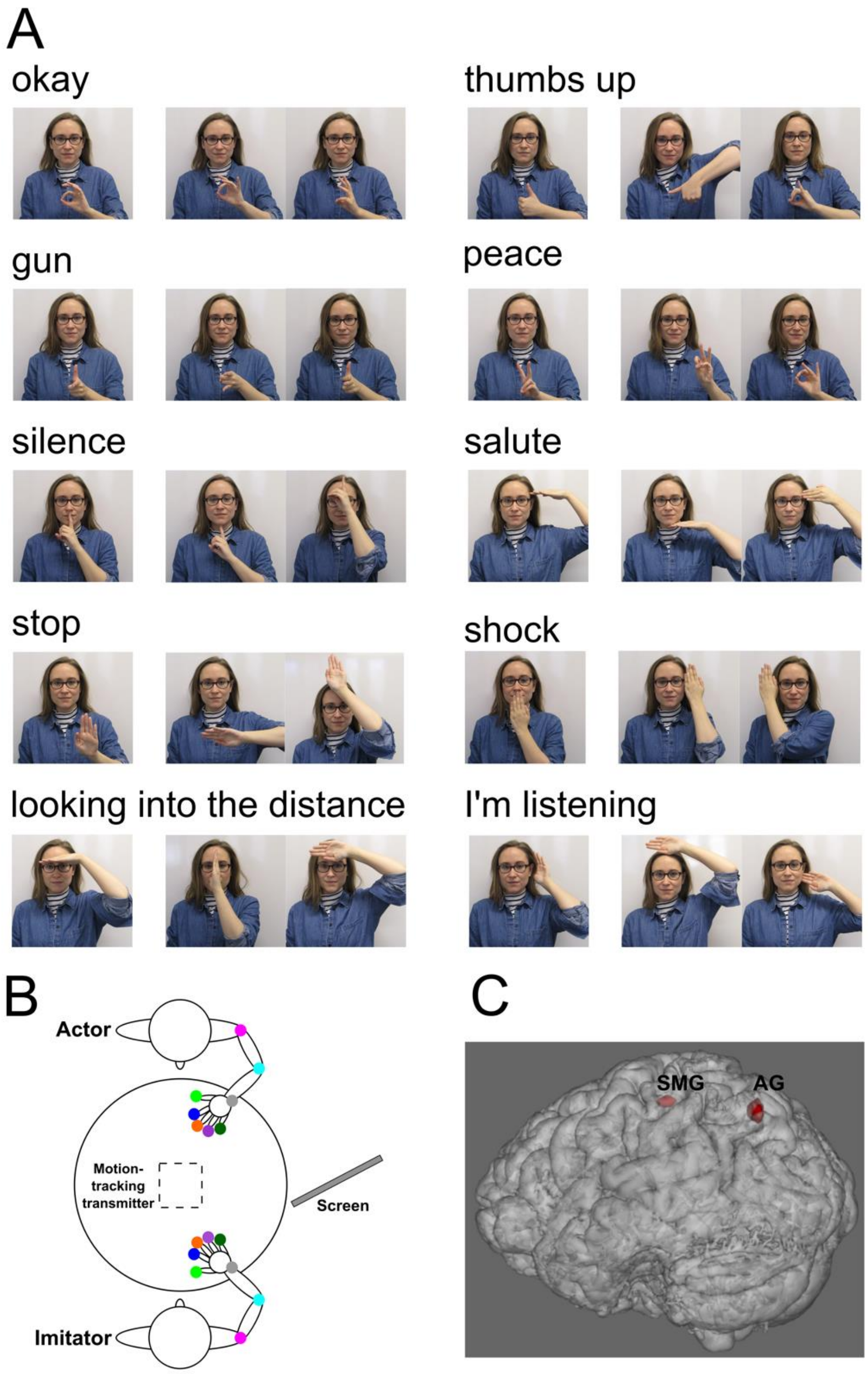

Figure 3-1: Experimental stimuli, setup, and rTMS stimulation sites

A) Meaningful finger and hand gestures alongside their matched meaningless counterparts. B) Experimental set-up. Dots indicate the location of motion trackers. The tracking box was placed under the table, and the actor's actions were cued through images displayed on a computer screen that was not observable to the imitator. C) 95% confidence ellipsoids for the rTMS target sites shown on a representative participant's brain.

3.2.3 Selection of TMS sites

Visualisation of the participant's brain used T1 weighted MR images alongside Brainsight 2.2.13 (Rogue Research Inc., Montreal, Canada). T1 scans were retrieved from the PI of a previous fMRI experiment which the participant had taken part in, following their consent to this retrieval. Due to SMG and AG size, stimulation locations were based on guidance from previous experimental activation and cytoarchitectonic maps (Caspers *et al*., 2006, 2008). The stimulation site for SMG was area PF, located by finding the dorsal extension of the posterior end of the Sylvian fissure and the anterior end of the intraparietal sulcus (IPS), drawing an imaginary line between them, and stimulating the centre of this line. Evidence suggests that area PF always falls within these limits (Caspers *et al*. 2006). Since AG activation in neuroimaging studies of imitation is less frequent than SMG activation, the stimulation site was the centre of the AG, aiming to cover both PGa and PGp. The AG site was located half way between the dorsal extension of the posterior superior temporal sulcus and the IPS.

Mean±95% CI locations are shown in Figure 3-1. For both AG and SMG the coil was oriented orthogonal to the main orientation of the gyrus limits, approximately perpendicular to axons. The location of the coil in the no-rTMS baseline condition was placed directly between the AG and SMG positions, but held parallel against the head, such that no or minimal stimulation of the brain should occur.

3.2.4 TMS parameters

Monophasic rTMS was applied to SMG, AG, and in the no-rTMS condition (coil angled away from the head) at 1Hz and 110% of distance adjusted resting motor threshold (RMT, Stokes *et al.*, 2007). RMT (Rossini *et al.*, 1994) was obtained at the start of the first session. Mean±SE RMT was 69±4.1% of maximum stimulator output. The distance from M1, SMG, and AG, to the scalp was measured using Brainsight. The no-rTMS site distance was measured from the cortical tissue directly underlying the no-rTMS site to the scalp. Stimulation intensity was limited to a maximum of 85% of maximum stimulator output in order to prevent the coil overheating. Mean±SE stimulation intensity (as a percentage of machine output) in each condition was as follows: SMG=70±4.1%, AG=72±4.4%, no-rTMS=71±3.9%.

3.2.5 Design and procedure

Participants took part in three sessions split at least a week apart. On a single day rTMS was applied twice (once for meaningless, once for meaningful) for 15 minutes (900 pulses at 1Hz) to either the left SMG, AG, or in the no-rTMS baseline condition, in counterbalanced order across participants. After each rTMS application, participants took part in either a meaningful or meaningless action imitation task. Meaningless and meaningful actions were segregated into their own separate trials (each following a single rTMS application). Task order was counterbalanced across stimulation sites.

Both confederate and imitator began with their thumb and forefinger gripping their start points. In both meaningful and meaningless imitation tasks, action images (in a random order) appearing on a computer screen signalled the confederate to perform the displayed action, which they performed and maintained briefly before returning their hand to the start point. Five seconds after presentation of the image to the confederate, a tone indicated the participant to imitate the action they had observed, which they performed in a mirror fashion (i.e., using their right hand to copy the confederate’s left hand). After completing the action, they returned their hand to the start point before the next trial. Following a single application of rTMS, each meaningful action was presented six times, or each meaningless action was presented three times, giving a total of 60 trials per condition and TMS site. Imitation was performed in same-sex dyads, with either a male confederate or one of two female confederates. Confederates were trained prior to the task by performing the actions until they felt that they could accurately and rapidly reproduce them. Good performance was maintained throughout the task through observation by a second confederate present in every session. The same confederate was used as actor for every condition of a given participant.

Following the third rTMS session, participants were presented with a questionnaire featuring the meaningful and meaningless images in pseudorandom order. They were asked to state whether they thought each gesture had a meaning, and if it did, to provide an explanation. As in experiment 1, this was done with the aim of excluding participants if they failed to meet a 60% agreement with our meaningful and meaningless action categorisation, but no participants failed this criterion. Mean±SE agreement on the meaningful gestures was 75.8±7.83%, and the mean percentage of meaningless gestures described as meaningful was 5.83±1.83%.

3.2.6 Data analysis

An automated script was used for pre-processing and extraction of variables. The analysis routines processed the position data from each trial of each participant and rejected artefacts (e.g., trials with missing samples or spikes resulting from electromagnetic interference) before filtering with a bidirectional low-pass 4th order Butterworth filter (cutoff frequency 15Hz). 5.3% of trials were removed due to incorrect start times or artefacts.

We extracted kinematic variables from the participant wrist marker in order to assess participant behaviour in relation to the correction markers found previously: movement onset (MO, similar to RT but this was not a speeded task), time to peak acceleration, TPA/MT, peak acceleration, time to peak velocity, TPV/MT, peak velocity, time to peak deceleration, TPD/MT, peak deceleration, and MT. These were analysed using two-way repeated measures ANOVAs (stimulation site, meaning).

The imitator's and actor's 3D velocity over their primary movement (MO to MT, mean±SE duration=1021±34.3ms) were then resampled to 240 samples and correlated with the actor data to provide a measure of imitation accuracy (Reader & Holmes, 2015). The 3D velocity profiles for each of the imitator's trackers were correlated with each of the actor's corresponding trackers: shoulder (SH), elbow (EL), wrist (WR), thumb (TH), index finger (IN), middle finger (MI), ring finger (RI), little finger (LI). In order to use parametric statistics, the resulting r-values were converted into Z-values using Fisher's transformation $Z = \frac{1}{2}\ln\left(\frac{1+r}{1-r}\right)$, where ln is the natural logarithm.

3D velocity profiles were used since these provide a measure of the change in the 3D position of the trackers over time, and thus the formation of the final gesture posture over time. This was considered preferable to using the x, y, and z values for two reasons. Firstly, because this approach reduces the number of statistical comparisons that have to be performed, reducing the likelihood of reporting false positives. Secondly, using 3 dimensions for this analysis was unlikely to provide further information regarding the accuracy of imitation, considering that the actual position in space is only informative in relation to the other trackers. That is, some individuals may have ways of imitating which are clearly correct, but do not exactly conform to the spatial characteristics of the actor’s action. For example, one can choose to make the “okay” sign with the middle, ring, and little fingers extended straight or slightly curled. In both cases the gesture is recognisable as matching what is observed. Whilst these issues could potentially be addressed with a greater number of trackers, alongside analytical methods using dimensionality reduction, using the 3D velocity as a marker for the change in the position in space over time represents an effective, and computationally efficient, compromise.

Two-way repeated measures ANOVAs were also performed on the means of all relevant trials for each of these variables across each crossed condition. Preliminary analysis indicated that hand gestures were biasing the results (i.e., the mean Z-values for all digits were similar since the digits generally moved together). Because of this we split the hand and finger gestures before examining accuracy, then corrected for multiple comparisons using Bonferroni correction, reducing our alpha used to determine a statistically significant result to .025. We then performed the following analysis on the hand and finger data separately.

In order to assess whether there were time-dependent significant differences in the main effects or interaction, t-statistic plots of the resampled data were created for each instance (see Figure 3-2 as an example). We took this time-series-driven approach in order to inform us of possible differences in peak kinematic values in separate trackers, without the inflated type 1 error that would occur were we to examine multiple kinematic parameters in multiple trackers. In cases where the t-value was at a significant level for any sequence of samples in the time-series, we performed permutation testing on the relevant data.

Permutation testing was performed over 10,000 iterations to create a custom empirical null distribution of the length of samples with significant t-statistics, which was then used to decide whether an observed sequence was significantly long. This is similar to the use of cluster based statistics in fMRI, where a fixed, arbitrary threshold is used for creating clusters, then a second threshold is calculated for determining how large a cluster needs to be before it is statistically significant. On each iteration, the condition labels for each participant's data were pseudorandomised, and the original analyses were then repeated exactly, in order to obtain t-statistics, and sequences of significant t-statistics for the difference between 'SMG' and 'AG' conditions, under the null hypothesis. From this we were able to assign a p-value to our actual results by seeing what proportion of the tail of the distribution was greater (or lesser) than or equal to the actual result. We examined the minimum length of sequences of continuous values in which $|t|>2.201$ (i.e., statistically significant at a samplewise, $p<.05$), and also the p-values associated with the sequences of timepoints in our recorded data where $|t|>2.201$.

Where significant sequences were found, we examined the standard kinematic parameters that occurred during that period to confirm whether the differences were derived from the SMG-AG comparison, or if there was further information to be gained from the no-rTMS baseline. Imitator peak kinematic parameters were examined using one-tailed post-hoc paired t-tests. To check that any differences were derived from imitator rather than actor performance, we ran the same analysis on the actor peak values using two-tailed paired t-tests.

3.3 Results

3.3.1 Wrist kinematics

There were no significant differences in wrist kinematics between stimulation sites (Table 3-1). However, meaningless actions had a significantly smaller MO, time to peak acceleration, TPA/MT, peak acceleration, TPV/MT, and peak velocity, and a significantly greater time to peak deceleration and MT when compared to meaningful actions.

There was a significant site*meaning interaction in TPV, but paired comparisons revealed no significant difference between meaningful and meaningless actions for the SMG (mean±SE = 357±14.5ms versus 370±12.6ms, F(1,11)=2.27, p=.160, η^2=.171), AG (365±16.7ms versus 379±19.9ms, F(1,11)=2.98, p=.113, η^2=.213), or no-rTMS control (373±16.4ms versus 358±13.8ms, F(1,11)=2.13, p=.173, η^2=.162). There was also a significant site*meaning interaction in TPV/MT, though in this case paired comparisons revealed significant differences between meaningful and meaningless actions at every level of stimulation site: SMG (mean±SE = .372±.0144 versus .352±.0124, F(1,11)=6.05, p=.032, η^2=.355), AG (.384±.0102 versus .361±.00875, F(1,11)=15.8, p=.002, η^2=.589), no-rTMS control (.387±.0125 versus 344±.0110, F(1,11)=66.3, p<.001, η^2=.858).

Table 3-1: Mean values, main effects, and interactions for wrist kinematic variables

Significant p-values are in bold.

Variable	Mean(±SE) value					Main effect							Site*meaning interaction			
	Site			Meaning		Site				Meaning			F	df	p	η^2
	SMG	AG	No-rTMS	MF	ML	F	df	p	η^2	F (1, 11)	p	η^2				
MO (ms)	864 (23.1)	863 (25.1)	867 (18.1)	876 (22.7)	853 (20.2)	0.053	2, 22	.949	.005	6.37	**.028**	.367	0.041	1.24, 13.7	.889	.004
TPA (ms)	167 (9.91)	176 (13.5)	167 (12.0)	177 (10.8)	163 (10.1)	0.508	1.24, 13.6	.527	.044	6.97	**.023**	.388	0.615	2, 22	.550	.053
TPA/ MT (0 – 1)	.166 (.00984)	.175 (.0105)	.167 (.0111)	.183 (.0104)	.156 (.00947)	1.02	1.30, 14.3	.353	.085	30.6	**<.001**	.735	0.781	2, 22	.470	.066
PA (cm/s^2)	485 (31.2)	513 (44.6)	513 (30.5)	518 (31.8)	489 (34.3)	0.719	1.27, 14.0	.444	.061	6.03	**.032**	.354	0.350	2, 22	.709	.031
TPV (ms)	364 (12.8)	372 (17.9)	365 (14.3)	365 (12.9)	369 (12.8)	0.184	1.18, 12.9	.715	.016	0.460	.512	.040	4.16	2, 22	**.029**	.275
TPV/ MT (0 – 1)	.362 (.0128)	.373 (.00903)	.365 (.0115)	.381 (.0111)	.353 (.00981)	0.966	1.24, 13.6	.363	.081	41.9	**<.001**	.792	4.32	2, 22	**.026**	.282
PV (cm/s)	79.5 (4.47)	82.9 (6.20)	83.7 (4.22)	83.6 (4.87)	80.5 (4.72)	1.15	2, 22	.334	.095	5.40	**.040**	.329	0.335	2, 22	.719	.030
TPD (ms)	440 (12.0)	439 (17.5)	436 (10.2)	422 (12.6)	453 (11.7)	0.056	2, 22	.946	.005	10.6	**.008**	.491	0.008	2, 22	.992	.001
TPD/ MT (0 – 1)	.429 (.00735)	.433 (.00724)	.430 (.00822)	.435 (.00836)	.427 (.00636)	0.163	2, 22	.851	.015	1.04	.330	.086	0.247	2, 22	.738	.022
PD (cm/s^2)	-177 (13.4)	-193 (21.0)	-189 (15.2)	-186 (16.9)	-187 (15.4)	1.30	1.22, 13.4	.286	.105	0.015	.904	.001	1.369	2, 22	.275	.111
MT (ms)	1030 (33.6)	1015 (47.2)	1019 (30.7)	972 (31.6)	1071 (38.6)	0.166	2, 22	.848	.015	36.4	**<.001**	.768	0.454	2, 22	.641	.040

3.3.2 Actor-imitator correspondence

No significant effects of stimulation site, nor interaction between stimulation site and meaning were observed in imitation accuracy (full results shown in supplemental sections S3-1 and S3-2). In hand gestures, shoulder positions were significantly more correlated for meaningless (mean±SE Z-value = 0.622±0.0669) versus meaningful (0.388±0.0514) actions ($F(1,11)=39.2$, $p<.001$, $\eta^2=.781$). Elbow positions were also significantly more correlated for meaningless (1.04±0.0679) versus meaningful (0.753±0.0862) actions ($F(1,11)=28.8$, $p<.001$, $\eta^2=.723$). This effect was also significant in the same direction for the shoulder in finger gestures (0.187±0.0277 versus 0.0486±0.0309, F(1,11)=37.1, p<.001, η^2=.771), and, only when uncorrected (i.e., p<.025), in the elbow (0.488±0.0710 versus 0.386±0.0791, F(1,11)=6.54, p=.027, η^2=.027).

3.3.3 t-statistic plots and permutation testing

Figure 3-2A shows the t-statistic plots for the main effect of SMG versus AG in hand gestures. Figure 3-2B shows the t-statistic plots for the interaction between stimulation site and meaning in hand gestures. Figure 3-2D shows the t-statistic plots for the interaction between stimulation site and meaning in finger gestures. No significantly long sequences were observed in these data.

Figure 3-2C shows the t-statistic plots for SMG versus AG in meaningful and meaningless actions for finger gestures. Permutation test statistics for the thumb revealed a significant sequence between 59 and 108 samples (p=.035). The index finger showed a significant sequence between 65 and 119 samples (p=.022). The ring finger showed a significant sequence between 72 and 116 samples (p=.041). The little finger showed a significant sequence between 67 and 114 samples (p=.036). The middle finger sequence between 70 and 106 samples was not significantly long (p=.054).

The mean peak velocity (PV) for the digits in finger gestures was examined post-hoc since the above significant sequences overlapped with this kinematic parameter. Figure 3-3 emphasises this difference in the original data for the thumb. One-tailed t-tests for imitator mean digit PV (Figure 3-4) indicated a Bonferroni-corrected significant ($p<.025$) difference where stimulation over the AG resulted in a greater mean digit PV stimulation over the SMG ($t(11)=2.23$, $p=.024$, $g_{rm}=0.207$), and a significant uncorrected difference where stimulation over the AG resulted in a greater mean digit PV than the sham baseline ($t(11)=2.10$, $p=.030$, $g_{rm}=0.182$). There was no significant difference in mean digit PV between stimulation over the SMG and the sham baseline $t(11)=-0.503$, $p=.303$, $g_{rm}=0.0465$).

We then used two-tailed t-tests to perform the same analysis on the PV of the actor in their finger gestures (Figure 3-4), which revealed a Bonferroni-corrected significant ($p<.025$) difference between mean digit PV in the AG condition and sham baseline ($t(11)=2.91$, $p=.014$, $g_{rm}=0.529$). There was no significant difference in mean digit PV following stimulation over the SMG and the sham baseline ($t(11)=1.89$, $p=.086$, $g_{rm}=0.331$), or between the SMG and AG conditions ($t(11)=-1.71$, $p=.115$, $g_{rm}=0.222$). This suggested that actor behaviour was not unbiased, and so we also decided post-hoc to examine the imitator PV relative to the actor PV to try and control for the effects of this bias.

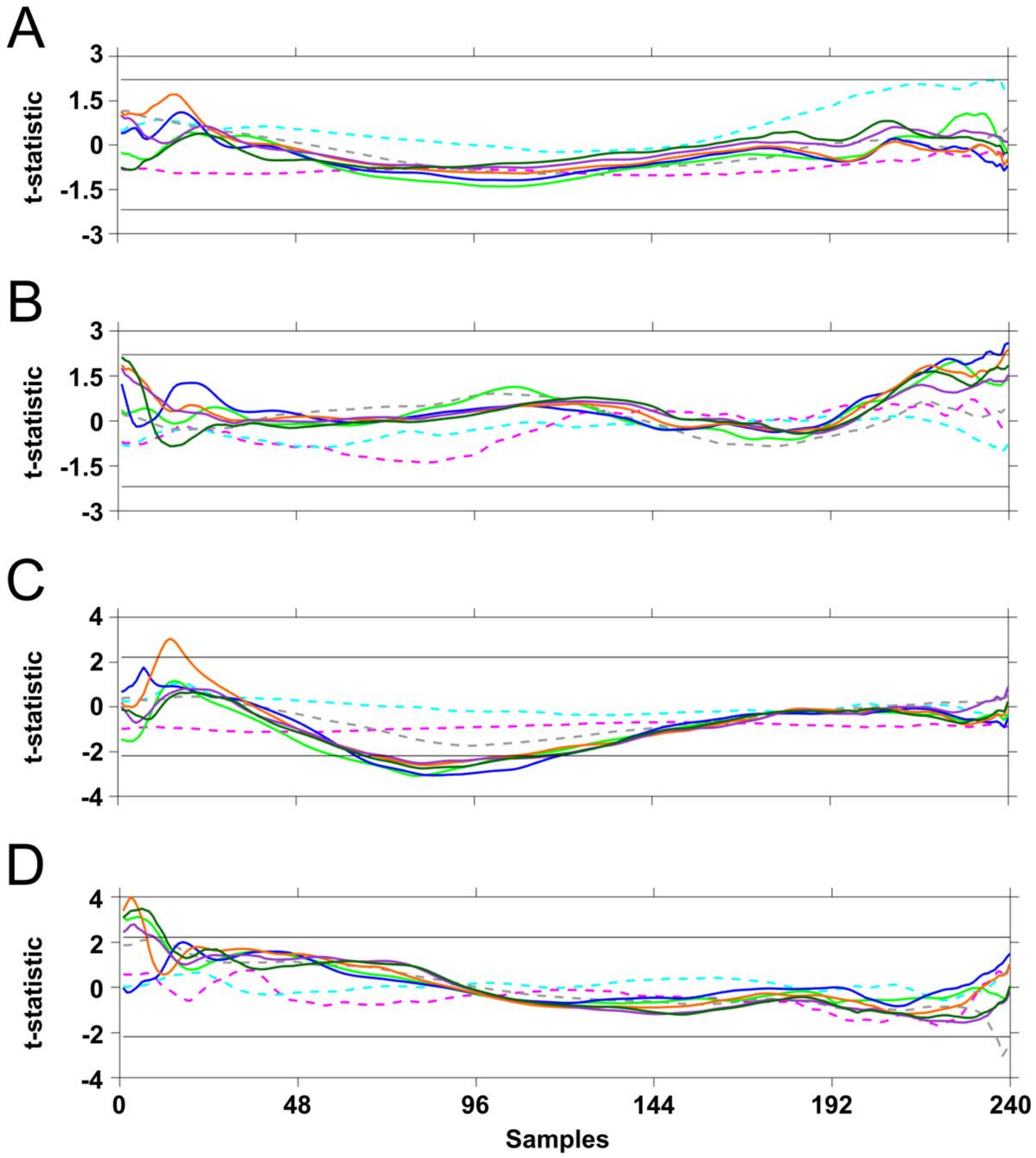

Figure 3-2: t-statistic plots for resampled comparisons in all trackers

A) SMG versus AG in hand gestures B) stimulation site*meaning interaction in hand gestures C) SMG versus AG in finger gestures (significantly long sequence for the thumb between samples 59 and 108, index finger between samples 65 and 119, ring finger between samples 72 and 116, little finger between samples 67 and 114) D) site*meaning interaction in finger gestures; In all plots the black horizontal lines indicate positive and negative critical t-values. Dashed magenta = shoulder, dashed cyan = elbow, dashed grey = wrist, light green = thumb, blue = index finger, orange = middle finger, purple = ring finger, dark green = little finger.

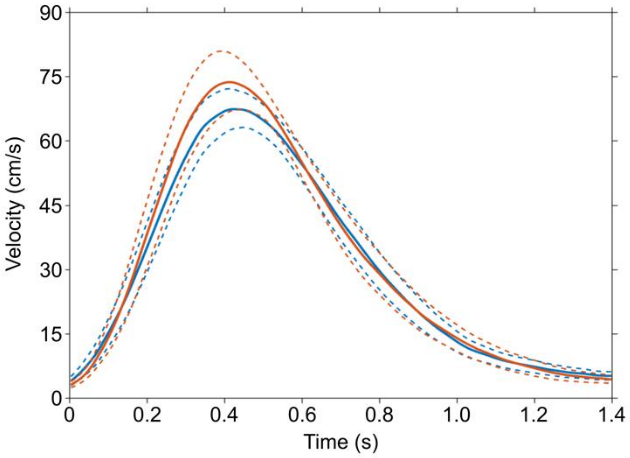

Figure 3-3: Original mean velocity curve for the thumb comparing SMG and AG in finger gestures

Blue = SMG, red = AG; Dashed lines = between-subjects SE.

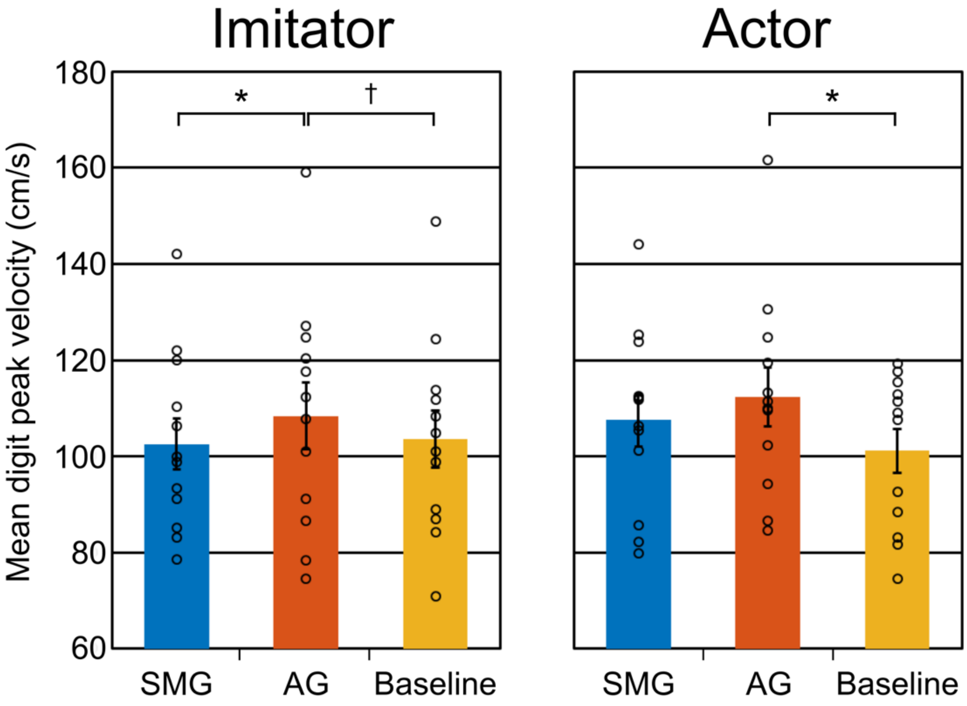

Figure 3-4: Mean digit peak velocity for finger gestures in imitator and actor data

Error bars indicate between-subjects standard error, whilst single points show individual participant values. * = p<.05 corrected, † = p<.05 uncorrected.

We examined the imitator mean digit PV relative to the actor mean digit PV in finger gestures using two-tailed t-tests with a Bonferroni-corrected alpha criterion of .025 (Figure 3-5). There were two uncorrected significant differences such that mean digit relative PV was significantly reduced following stimulation over the SMG compared to the sham baseline (t(11)=-2.37, p=.037, g_{rm}=0.335), and also following stimulation over the AG compared to the sham baseline (t(11)=-2.31, p=.041, g_{rm}=0.281). There was also no significant difference in mean digit relative PV between the SMG and AG conditions (t(11)=-0.316, p=.758, g_{rm}=0.0424).

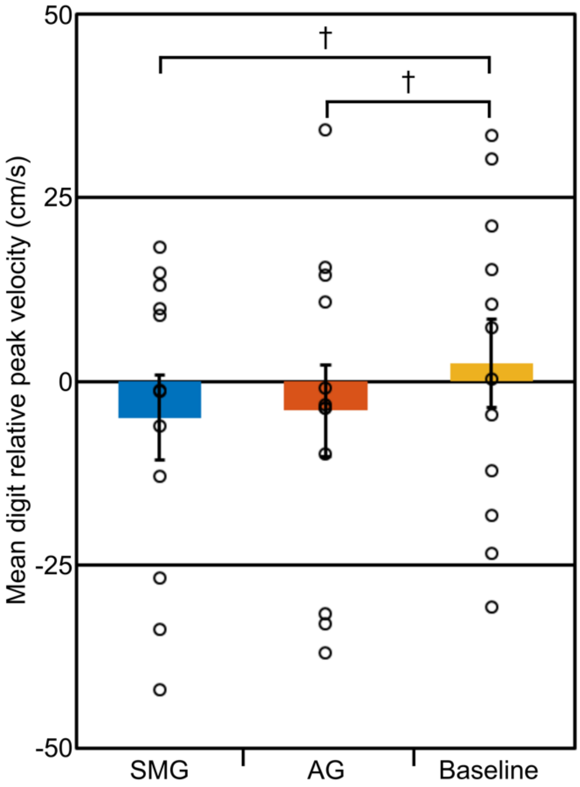

Figure 3-5: Mean digit relative peak velocity for finger gestures in imitator relative to actor data

Error bars indicate between-subjects standard error, whilst single points show individual participant values. † = p<.05 uncorrected.

3.4 Inferior parietal lobule discussion

We tested participants' ability to imitate meaningful and meaningless actions following rTMS over the left SMG, AG, or after a no-rTMS baseline. Whilst there were no significant differences in correction time markers or imitation accuracy between stimulation sites, we observed that participant digit PV was lower relative to the actor in finger gestures following SMG or AG stimulation, though with a larger effect size in the SMG condition.

3.4.1 Variability in wrist kinematics

Wrist kinematic analysis revealed that meaningless actions had a significantly smaller MO, time to peak acceleration, TPA/MT, peak acceleration, TPV/MT, and peak velocity, and a significantly greater time to peak deceleration and MT when compared to meaningful actions. The MO, TPA/MT, TPV/MT, and MT effects were in keeping with experiment 1, suggesting that participants were once again spending a longer time correcting actions following PV. Unlike our previous findings though, PA and PV were now greater for meaningful actions. The most feasible explanation is that since this was not a speeded task as in experiment 1, participants did not need to strategically increase the speed of performance to maintain enough correction time at the end of the action. Rather, they performed as we might naturally expect: quicker performance for actions that they knew. The fact that we did not observe site*meaning interactions in any correction time markers suggests that the IPL is not involved in the (possibly explicit) approach towards meaningless gesture imitation.

3.4.2 Effects of meaning on imitation accuracy

Whilst stimulation did not influence imitation accuracy, there was some evidence for differences between accuracy in meaningful and meaningless action performance. Interestingly, participants matched the confederates shoulder and elbow movements to a significantly greater degree in meaningless actions. Meaningless actions are likely to rely more on matching action kinematics (e.g., Tessari & Rumiati, 2004) than meaningful actions. The fact that effects were only observed in the shoulder and elbow may reflect the fact that the differences in accuracy were easier to detect in proximal effectors with lower degrees of freedom.

3.4.3 The role of the IPL in imitation kinematics

Examining t-statistics over time, we found significantly long periods during which imitator finger velocity was significantly lower following rTMS over SMG compared to AG during imitation of finger gestures, but regardless of action meaning. These significant differences overlapped with PV. When we examined mean digit PV in a paired fashion between the two active rTMS sites, and the baseline sham, we found that stimulation over the AG resulted in a significantly greater PV compared to SMG or baseline. However, when we ran the same analysis in the actor's data to confirm that their behaviour was not driving this effect, we found a similar significant difference. In order to tease apart possible confederate bias and imitator behaviour, we examined imitator mean digit PV relative to the actor mean digit PV, and found that participants showed significantly reduced digit PV relative to the actor following SMG and AG stimulation compared to baseline.

This result seems to indicate that during the imitation of finger gestures, rTMS to the SMG or AG reduces digit velocity relative to the observed actor. These results provide the first causal evidence, using brain stimulation in healthy individuals, for a role of the left IPL in controlling the kinematics of finger movements during imitation. Further study is necessary to understand the underlying processes altered in this experiment, but these results have the potential to bring together both findings from apraxia and discussions of the putative MNS in healthy individuals. Under a mirror system interpretation, disturbed visuomotor matching following IPL stimulation could reduce the velocity with which the fingers shape complex postures relative to the actor. Whilst areas of the putative human mirror neuron system do respond strongly to observed kinematics (Becchio *et al.*, 2012), visuomotor matching makes the assumption that there is a pre-existing representation of the observed movement. This would not explain why our observed velocity effects did not interact with action meaning. Rather, recent discussions in the apraxia literature seem to explain these results better, given that they emphasise the importance of individual elements of movement, which may be partly dissociable from deficits relating to action meaning.

Buxbaum *et al*. (2014) found that damage to the left IPL was associated with deficits in kinematic (rather than postural) aspects of movement for novel and tool-related actions. Similar results were found in a more recent VLSM study by Dressing *et al*. (2016). Buxbaum *et al*. (2014) suggested that the IPL computes "movement plans [as] dynamic changes in the relative spatial positions of body parts needed to reach a goal configuration" (p. 13). If this is the case, changes in effector movement relative to the goal (the actor movement) following IPL stimulation are a likely consequence. We found that our observed effect occurred regardless of action meaning, which seems to be at odds with the fact that IPL damage may disproportionately affect imitation of meaningless actions (Goldenberg, 2009). One possible explanation is that IPL damage in apraxia also damages connectivity to other areas involved in action imitation, whilst our stimulation was more focussed. In relation to this, previous research has discussed the importance of considering cytoarchitectonically defined regions of the IPL in gesture imitation (Weiss *et al*., 2013). Another feasible possibility is that, since meaningless action imitation may be more reliant on matching the movement information in the observed action (Rumiati & Tessari, 2002; Wild *et al*., 2010), it would be more affected by permanent damage to the left IPL.

To expand on this point, we posit that dissociating deficits in meaningful and meaningless action imitation following left IPL damage may reflect the action type's relative reliance on the kinematic information portrayed in the observed movement. Even in the case of meaningful actions, kinematic information is still relevant to the way in which one must replicate the action. For example, the imitator is not likely to ignore explicit but irrelevant kinematics, such as a particularly slow or rapid action which does not assist in the development of the final hand posture (see Forbes & Hamilton, 2017, for evidence in support of this claim). However, should the IPL be irreversibly damaged, and the ability to match the observed kinematic information reduced, information about the movement requirements for a meaningful action can still be retrieved from memory – something that is not possible for meaningless actions. It is possible that in such cases there is still an influence of IPL damage on the kinematics of the meaningful action in relation to the observed movement, but since previous research has not examined this using motion-tracking, such a result has not been forthcoming. One way to confirm such a hypothesis in apraxia patients would be to examine the degree to which patients with left IPL damage and a specific deficit in imitating meaningless actions match irrelevant kinematics in meaningful actions. However, subjective measures may not be sensitive enough to detect fine-grained differences in kinematics, particularly between two interacting individuals. This information could only be confirmed following motion-tracking and comparative analysis of both the actor and imitator, as we have done.

3.4.4 Distinguishing between the SMG and AG

Our results seem, then, to confirm the importance of the left IPL in asserting kinematic control during imitation, particularly as it relates to meeting the kinematic requirements of the observed action, over and above the meaning of that action. Since movement necessarily contains kinematic features, our results help to explain why left IPL activity is frequently reported during imitation in healthy individuals, regardless of the type of action imitated (e.g., Jack *et al*., 2011; Molenberghs *et al*., 2010; Mühlau *et al*., 2005; Tanaka *et al*., 2002).

Unfortunately, our study was not able to reveal more about the possible division of labour between the SMG and AG. The existence of similar effects in both the SMG and AG may not necessarily reflect similar roles for each of these regions, but perhaps the connectivity between them. For example, the AG stimulation may have had an effect on information processing between the AG and SMG, with the greater effect size observed following SMG stimulation (Hedge's g_{rm} = 0.335 versus 0.281) partially supportive of this claim. Since the AG is anatomically connected to the posterior SMG (Seghier, 2013), rTMS over both areas might induce a reduction in efficient SMG functioning if information regarding the kinematic constraints of the observed action is passed in a posterior-anterior (AG to SMG) fashion. It is also worth noting that a previous study indicated that the AG could be involved in both meaningful and meaningless action imitation (Vanbellingen *et al*., 2014). However, the location of AG in that experiment was more ventral and anterior to ours.

3.4.5 Hand and finger gestures

It is interesting that the above result was found specifically for finger gestures, rather than hand gestures. This is somewhat at odds with previous findings in apraxia, though our stimuli were not modelled on previous distinctions between hand and finger gestures – our main aim was to ensure there was a sufficient number of different emblematic stimuli for participants to copy. There is evidence to suggest that defective finger gesture imitation is more associated with left IFG damage, compared to defective hand gesture imitation, which is more associated with left IPL damage (Goldenberg & Karnath, 2006). This is discussed in terms of 'body part coding', where hand gesture imitation is related to the spatial mapping of the hand in relation to other body parts, whilst finger gesture imitation is reliant on serial positioning of uniform elements (fingers). Previous neuroimaging results are mixed, with some experimental results indicating no difference between neural processing of hand and finger gesture imitation (Mühlau *et al.*, 2005), and others finding the contrary (Tanaka & Inui, 2002).

It is possible that the movement to attain the posture, rather than the final hand position alone may be an important factor. For example, whilst Goldenberg & Karnath (2006) considered only performance on the final gesture posture, Buxbaum *et al*. (2014) examined dynamic movements, hence their suggestion that dynamic change in body part position is important. It is possible that the difference between kinematic and postural elements of movement may take precedence over the difference between hand and finger gestures, though further research would be needed to clarify this. If this is the case, the fact we only observed kinematic effects in the finger velocities for finger-specific gestures may reflect the fact that the dynamic change of each of the fingers independently is more complex than the movement of the hand as a whole. We decided to better account for differences between hand and finger gestures in the following experiments.

3.4.6 Inferior parietal lobule conclusions

We found in this experiment that the left IPL is involved in matching observed digit velocity in action imitation, regardless of action meaning. However, we did not observe effects on correction time markers or imitation accuracy. It is possible that the apparent role of the IPL in kinematic processing is not related to the correction time markers observed in experiment 1. The absence of any effect of TMS on imitation accuracy seems to suggest that TMS, over the IPL at least, is not strong enough to influence imitation accuracy in the way in which wide-ranging and permanent lesions can.

In conclusion, more work is needed to expand on how imitation kinematics are processed in the left IPL, and the relative contributions of the SMG and AG. These nuances may not be observable following large lesions, but can be examined using neuronavigated TMS. Our results confirm that brain stimulation may help close the gap in understanding imitation in apraxia and in healthy people, particularly if it is combined with motion-tracking. As such, we continued to use this approach to examine two further brain regions associated with action imitation.

4 EXPERIMENT 3 (PREMOTOR CORTEX)

4.1 Introduction

The premotor cortex is, like the IPL, often associated with imitation. It is generally discussed in terms of two constituent parts: the dorsal (PMd) and ventral (PMv) regions. The premotor cortex contributes to numerous functions, from speech perception (Iacoboni, 2008) to multisensory integration (Gentile *et al*., 2015). Importantly, the PMd and PMv play a number of essential roles in motor control (Kantak *et al*., 2012; Schubotz & von Cramon, 2003), integrating visual, somatosensory, and cognitive functions for the purpose of goal-directed action.

The PMd is involved in planning reach trajectories (Beurze *et al*., 2007; Lee *et al*., 2006; Ohbayashi *et al*., 2016; Nakayama *et al*., 2008; Pesaran *et al*., 2006) and action selection in response to cues (Chouinard *et al*., 2005). TMS over this region in humans can result in increased RTs during motor planning (Mochizuki *et al*., 2005). The PMv is often associated with hand movements, particularly grasping and object manipulation (Davare *et al*., 2006, 2008, 2009; Fogassi *et al*., 2001; Majdandžić *et al*., 2009; Vingerhoets *et al*., 2013), though the PMd may assist in such processing (Fattori *et al*., 2010; Filimon *et al*., 2015; Grafton *et al*., 1996; Raos *et al.*, 2004). The PMv is also possibly involved in encoding the location and properties of targets to be acted upon, regardless of the hand used to reach (Hoshi & Tanji, 2002).

Perhaps more importantly for imitation, the PMv has been associated with cognitive elements of motor control, particularly for goal-directed action. The PMv has also been suggested to be part of the putative human MNS, and some claim that the PMv is the human homologue for macaque area F5 (Ferri *et al.*, 2015; Grèzes *et al.*, 2003; Morin & Grèzes, 2008), where mirror neurons were originally observed (di Pellegrino *et al.*, 1992). F5 has been shown to contain neurons that code for specific hand-object interactions, rather than their single constituent movements (Rizzolatti *et al.*, 2002). Put simply, mirror neurons in area F5 may code hand-object oriented action (rather than action intention, as has been suggested for the IPL), regardless of their visual or motor modality (Rizzolatti *et al.*, 2014). In this case, the PMv could possibly assist in imitation by providing the scaffolding for linking observed and to-be-performed actions. If this region is involved in action goal recognition (Urgesi *et al.*, 2014; Wurm *et al.*, 2014, but see Kalénine *et al.*, 2010), we might feasibly expect it to play a role in imitating actions that are meaningful (but see Koski *et al.*, 2002 for evidence that bilateral PMd might also be encoding goals for imitation).

As emphasised previously, neuroimaging studies on action observation, understanding, and imitation are heavily focussed on goal-directed or object-directed behaviour (Caspers *et al.*, 2010), which may not encompass the same processes involved in imitation from a semantic standpoint (i.e., meaningful versus meaningless actions). This is particularly important considering that the PMv may be specifically involved in processing action goals rather than hand movements alone (Agnew *et al.*, 2012; Johnson-Frey *et al.*, 2003). Both the PMd and PMv have been implicated in numerous studies of imitation (Hamilton, 2015; Molenberghs *et al.*, 2009), but the results are not consistent, particularly when it comes to distinguishing between meaningful and meaningless actions. However, research implicating the premotor cortex in imitation does exist, regardless of the presence or absence of object interaction portrayed in the stimuli.

Some research strongly supports the claim that bilateral, but particularly left lateralised premotor regions are involved in meaningless (Carmo *et al.*, 2012; Rumiati *et al.*, 2005) and meaningful (Montgomery *et al.*, 2007; Rumiati *et al.*, 2005) action imitation. The few studies that have focussed on meaningful and/or meaningless actions have found activity related to meaningless action imitation in the left PMd (Grèzes *et al.*, 1999; Tanaka *et al.*, 2001), right PMv (Decety *et al.*, 1997; Krüger *et al.*, 2014), and right PMd (Grèzes *et al.*, 1999). Activity related to meaningful action imitation has been found in the left PMd (Tanaka *et al.*, 2001). Such variability in both results and experimental approaches (i.e., fMRI contrasts testing imitation versus rest, imitation versus observation, or meaningful action imitation versus meaningless action imitation) suggests that the causal inference provided by TMS might be useful to better clarify the role of the premotor cortex in imitation.

We chose to examine the left PMv and PMd, considering that activity in these regions in the left hemisphere has been found for meaningful and meaningless action imitation. In addition, apraxia has also been associated with left inferior frontal damage (Buxbaum *et al.*, 2014). We had no strong hypotheses considering the large variability in results from previous experiments. Mainly, we hoped that our categorisation of action in semantic, rather than goal-directed terms, along with large-scale motion-tracking would develop understanding of the PMd and PMv in different types of action imitation. We were particularly interested in better clarifying the role of these regions as they relate to our correction time markers (i.e., as observed in the wrist tracker as in experiments 1 and 2), and imitation accuracy (actor-imitator correspondence).

4.2 Methods

Except where stated, the experimental setup was the same as in experiment 2.

4.2.1 Participants

We recruited 12 right-handed participants from the University of Nottingham and the surrounding area (mean±SE age = 25.1±1.7 years, 4 males). The experimental procedures were approved by the local ethics committee (ref: SoPEC 853); participants gave written, informed consent; and the experiments were conducted in accordance with the Declaration of Helsinki (as of 2008).

4.2.2 Materials and stimuli

The position of participant's right arm and hand and a confederate's left arm and hand were recorded using the same motion-tracking setup as experiment 2. rTMS was applied using a Magstim Rapid^2 (The MagStim Company, Cardiff, UK) with one of two 70mm outer diameter figure-of-eight precision coils. To ensure any TMS effects were not due to motor cortical stimulation, muscle activity was recorded continuously in the right first dorsal interosseus and brachioradialis using an AD Instruments Powerlab 16/30 at 2kHz via a Dual Bioamp/stimulator and LabChart software, with 10-500Hz bandpass filtering.

The experiment was controlled and data were acquired using custom software written in Labview (National Instruments). We used LabMan to document experiments, and the HandLabToolbox and MATLAB 2016b (Mathworks, Inc.) to analyse data.

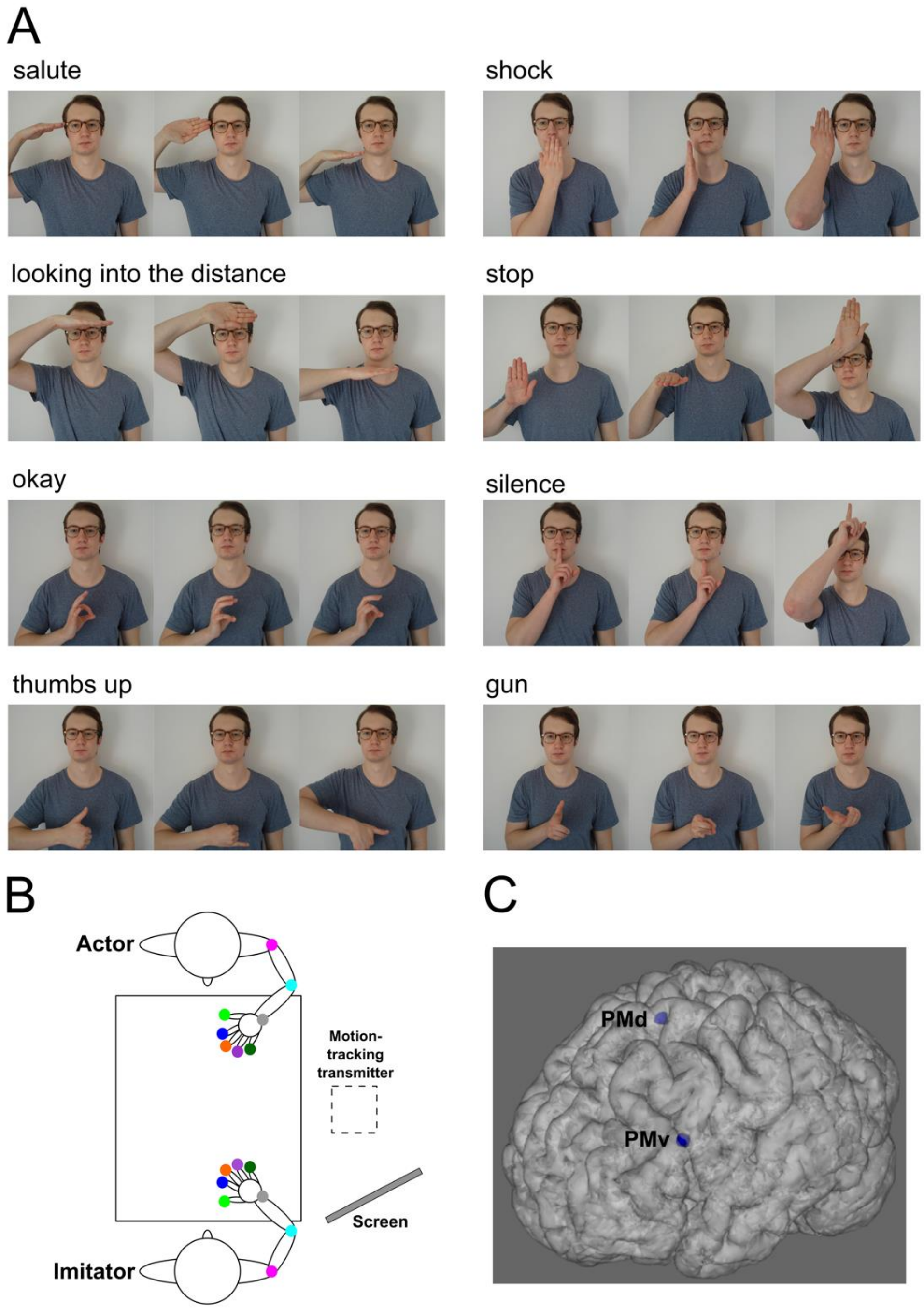

Figure 4-1: Stimuli, experimental setup and rTMS stimulation sites

A) Stimuli: for each meaningful emblematic gesture, two matched meaningless gestures were created. B) Experimental set-up. Dots indicate the location of motion trackers. The tracking box was placed under the table, and the actor's actions were cued through images displayed on a computer screen that was not observable to the imitator. C) 95% confidence ellipsoids for the rTMS target sites shown on a representative participant's brain.

A total of twenty-four gestures were used as stimuli (Figure 4-1A). This included four meaningful hand gestures (“salute”, “looking into the distance”, “shock”, “stop”), four meaningful finger gestures (“okay”, “thumbs up”, “silence”, “gun”), and sixteen matched meaningless gestures. For each meaningful gesture, two matched meaningless gestures were created as in experiment 2. A male confederate actor performed these actions for every participant.

During the imitation task, participants sat opposite a confederate at a rectangular plastic table, approximately 76cm away from each other (Figure 4-1B). A start point was located 20cm away from each individual’s abdomen using Blu Tack®. In order to inform the confederate actor of the action they needed to perform, a computer screen was placed behind the imitator. This was unobservable by the participant imitator.

4.2.3 Selection of TMS sites

Visualisation of the participant’s brain was performed using T1 weighted MR images alongside the Brainsight stereotactic system (Rogue Research Inc., Montreal, QC, Canada), as in the previous experiment. To account for differences in individual anatomy, experimental stimulation locations were based on gross neuroanatomy, rather than atlas coordinates (Figure 4-1C). The PMd location was defined as the anterior portion of the precentral gyrus, above the posterior limit of the superior frontal sulcus. The PMv location was defined as the anterior portion of the precentral gyrus, below the posterior limit of the inferior frontal sulcus. The vertex was used as a control site, the location of which was found using normal measures (i.e., halfway between both the two ears and the inion and nasion).

During stimulation over the PMd the coil was angled such that the wings did not overlap with the primary motor cortex, as measured by motor-evoked potential (MEP) presence in EMG. In the case of MEPs being observed with rTMS applied during natural finger-thumb opposition movements, stimulation was reduced by 5% of the maximum stimulator output. If MEPs were still observed, the coil was moved medially by up to 1cm until no MEPs could be observed.

rTMS over PMv is uncomfortable (Meteyard & Holmes, 2018), so during stimulation over the PMv the coil was angled with the handle pointed towards the posterior of the skull, but manipulated to maximally reduce facial twitching and discomfort for the participant. If participant discomfort was still too great, stimulation was reduced by 5% of the maximum stimulator output.

4.2.4 TMS parameters

Biphasic repetitive transcranial magnetic stimulation (rTMS) was applied to the PMv, PMd, and over the vertex in a control condition for 3 seconds per trial at 3Hz, and at 110% of distance adjusted resting motor threshold (RMT, Stokes *et al.*, 2007). In each condition, stimulation intensity was limited to 80% of machine output to reduce coil overheating. Stimulation was applied during either action observation or imitation, to more finely examine the role of each area (i.e., in case a region was involved in either action observation or action performance during imitation). RMT was obtained using the Rossini *et al.* (1994) method at the start of the first session. Mean RMT was 68±2.9% of machine output. The distance from M1, PMv, and PMd to the outside of the skull was measured using the Brainsight neuronavigation software. Vertex stimulation intensity was taken as the mean of PMd and PMv. Mean±SE stimulation intensity (as a percentage of machine output) in each condition was as follows: PMv = 65±2.6%, PMd = 74±2.4%, Vertex = 72±2.1%.

4.2.5 Design and procedure

Participants took part in three sessions separated by at least 24 hours. In each session a single brain region was stimulated. In every session, participants took part in both meaningful and meaningless action imitation tasks. Meaningless and meaningful actions were segregated into their own separate blocks, counterbalanced across participants and stimulation sites.

At the start of each of the three sessions, we requested participants to perform a finger-thumb opposition task whilst their finger and arm movements were tracked and EMG was recorded in the right first dorsal interosseus and brachioradialis. Participants were requested to perform this task as quickly and as accurately as possible for 15 seconds. During the middle section of this task, rTMS was applied at 3Hz (15 pulses, from 5.00 to 9.67s) at the chosen intensity for that session's brain region. The purpose of this motor task was twofold. Firstly, we wanted a measure of performance in a control motor task to examine the role of the stimulated regions in a general fine-motor control. Additionally, by observing the EMG data online during the finger-thumb opposition task, we could make changes to the angle of the coil or intensity of stimulation in the case of unwanted M1 stimulation (i.e., TMS-evoked MEPs).

During the imitation task, both confederate and participant imitator began with their thumb and forefinger gripping their start points. In both meaningful and meaningless imitation tasks, action images appearing on a computer screen informed the confederate of which action to perform. Action images (in a random order) were cued on the screen opposite the confederate and unobservable by the imitator. A tone 1000ms after image presentation signalled the actor to begin the action, which they performed and maintained until a second, lower tone was played 2000ms later. They then returned their hand to the start point. 1000ms after the signal for the actor to return their hand, a tone played to signal the imitator to imitate the action which they performed and maintained until a second, lower tone was played 2000ms later. They then returned their hand to the start point. 64 trials were presented in this way, and the imitator was provided with a break at the halfway point. rTMS occurred during action observation or imitation, in order to more finely examine the role of each stimulated area (i.e., in case a region was involved in either action observation or action performance during imitation). Stimulation during observation started 333ms after the point at which the new image appeared on the screen. Stimulation during imitation started 1000ms before the imitator was cued to begin their action. There was a 10 second gap between the end of one, and the start of the following train of stimulation, with trial timings matched to this criterion.

Following the completion of all TMS sessions, participants were presented with a questionnaire featuring the meaningful and meaningless images in a random order, again with the aim to exclude participants if they were less than 60% consistent with our own categorisation of the actions. No participants met this criterion. Mean±SE rating accuracy was 75.0±6.15% for meaningful actions and 86.5±2.86% for meaningless actions.

4.2.6 Data analysis

As in previous experiments, an automated script was used for pre-processing and extraction of variables. The analysis routines processed the position data from each trial of each participant and rejected artefacts (e.g., trials with missing samples or spikes resulting from electromagnetic interference). Single timepoint spikes (>3SD from the mean), in each trial's double-differentiated time-series were deemed electromagnetic artefacts and removed by interpolation across three adjacent samples either side. Since this approach was not thorough enough, we then used a locally weighted scatter plot smoothing method. With the MATLAB “smooth” function we used weighted linear least squares and a 1^{st} degree polynomial model over a moving window of five samples to identify outliers which were then removed. The data including and surrounding TMS artefacts were finally visually inspected, and then manually removed.

The largest continuous series of removed points in any instance for the actor data was 53 samples (221ms). The mean±SE sum of the removed samples in each trial for the actor data was 165±9 (688±37.5ms) participant-wise, whilst the mean±SE length of any single removed period for the actor data was 28±1 (117±4.17ms). The largest continuous series of removed points in any instance for the imitator data was 33 samples (138ms). The mean±SE sum of the removed samples in each trial for the imitator data was 110±5 (458±20.8ms) participant-wise, whilst the mean±SE length of any single removed period for the imitator data was 19±1 (79.2±4.17ms). Removed datapoints were interpolated using spline interpolation, and then further inspected to confirm complete removal of artefacts and normal trajectory shape. This pre-processing step examined the entire time-series (effectively 1800ms, the maximum accepted movement time), including data prior to the movement onset and after the movement end (which were not used in final analysis). Data were removed equally across conditions. The data were then filtered with a bidirectional low-pass 4th order Butterworth filter (cutoff frequency 12Hz). Any trials in which the participant started before the starting tone, or failed to finish moving within

200ms of the return tone, were also excluded. Following the above exclusions, a total of 83.4% of trials were maintained for statistical analysis.

To examine wrist kinematic correction components, we ran four-way repeated measures ANOVAs on the participant imitator MO, time to peak acceleration, TPA/MT, peak acceleration, time to peak velocity, TPV/MT, peak velocity, time to peak deceleration, TPD/MT, peak deceleration, and MT, which were extracted from the wrist tracker. The four levels of the ANOVA were stimulation site (PMv, PMd, vertex), stimulation time (observation, imitation), action meaning (meaningful, meaningless), and action effector (hand, finger).

To test participant accuracy, we compared the actor and the imitator 3D velocity for each of the trackers. To do this we ran cross-correlation between the original actor and imitator velocity curves for each trial for each tracker, across lags of the difference between the actor and imitator timeseries length. From this information we took the maximum r-value (i.e., the point at which the imitator was best correlated with the actor), and the associated lag (the time it took for the imitator to reach the optimum (maximum) correlation) for each trial. r-values were converted to Z-values using the Fisher transformation. The means of the Z-value and lag for each condition were analysed using a four-way (stimulation site, stimulation time, meaning, effector) repeated measures ANOVA. We hoped that by using cross-correlation, rather than the correlation approach used in the previous experiment, we would be able to characterise imitator behaviour in terms of both spatial and temporal adherence to the actor behaviour.

To reduce our likelihood of reporting false positives, we divided our alpha value cutoff for assessing statistical significance by 8 (the number of trackers). Therefore in the ANOVAs of max Z-value and associated lag for each tracker, the alpha used to determine a significant result was reduced from 0.05 to 0.0063.

In order to look for dissociations between the two active stimulation sites (PMv and PMd), and whether there were stimulation-related time-dependent significant differences in the main effects or interactions, t-statistic plots were created for the resampled data in each instance. In cases where the t-value was at a significant level for any period of the time-series, we performed permutation testing on the relevant data and, as in experiment 2, examined whether these sequences overlapped with any peak kinematic parameters, which we ran paired t-tests on, Bonferroni-correcting where necessary. Considering the relative velocity results found in experiment 2, we also confirmed that no effects were observed in t-statistic plots for the actor, and ran paired t-tests on the imitator peak values relative to the actor peak values.

The finger-thumb opposition task was pre-processed as above (spike removal and filtering). We took three measures of task performance: the RMS jerk of the thumb (a measure of how much participants were changing their acceleration to switch between touches), the number of touches made between the thumb and other digits, and the percentage of touches that were accurate (i.e., where the thumb came within an arbitrary threshold of 1cm of the other digits). RMS jerk was used as this was the lowest possible differential of the thumb velocity that could capture the oscillating nature of the velocity data in this task (i.e., since the thumb was continuously moving, peak velocity or peak acceleration/deceleration were not appropriate). This information resulted in values for each of the brain stimulation sites for 5 seconds pre-stimulation, 5 seconds stimulation, and 5 seconds post-stimulation. In order to account for the reaction time in the pre-stimulation, we corrected the number of touches and number of accurate touches in relation to the percentage of pre-stimulation time that was not taken up by reaction time. The data were analysed using a two-way repeated measures ANOVA using stimulation site and stimulation time as the within-subjects factors.

4.3 Results

4.3.1 Finger-thumb opposition task

Two-way repeated measures ANOVAs revealed that that for the thumb RMS jerk there was a significant difference between stimulation sites (F(2,22)=5.41, p=.012, η^2=.330). Bonferroni-corrected pairwise comparisons revealed a significant difference between PMv and PMd, and PMv and vertex (F(2,10)=7.00, p=.013, η^2=.583) (Figure 4-2).There was no significant difference between pre-stimulation (mean±SE = 60.1±11.8cm/s^3), stimulation (49.2±4.23cm/s^3), and post-stimulation (45.8±7.15cm/s^3) (F(2,22)=1.15, p=.336, η2=.094). There was also no site*time interaction (F(4,44)=0.58, p=.680, η2=.050).

There was no significant difference between the number of touches made between the thumb and fingers for the PMv (14.7±0.86), PMd (14.6±0.91), and vertex (14.7±0.79) (F(2,22)=0.006, p=.994, η^2=.001). There was also no significant difference between number of touches made during pre-stimulation (14.4±0.73), stimulation (14.8±0.80), and post-stimulation (14.8±0.90) (F(2,22)=0.71, p=.501, η^2=.061). There was no significant site*time interaction (F(4,44)=0.61, p=.660, η^2=.052).

For the percentage touches that were accurate, there was a significant effect of stimulation site (F(2,22)=10.5, p=.001, η^2=.488). Bonferroni-corrected pairwise comparisons revealed that there was a significant difference between PMv and PMd, but not PMv and vertex, or PMd and vertex (F(2,10)=13.5, p=.001, η^2=.730) (Figure 4-3). There was no significant difference between pre-stimulation (60.1±6.90%), stimulation (43.7±6.61%), and post-stimulation (54.3±7.26%) (F(2,22)=1.50, p=.246, η^2=.120). There was also no significant site*time interaction (F(4,44)=0.51, p=.729, η^2=.044).

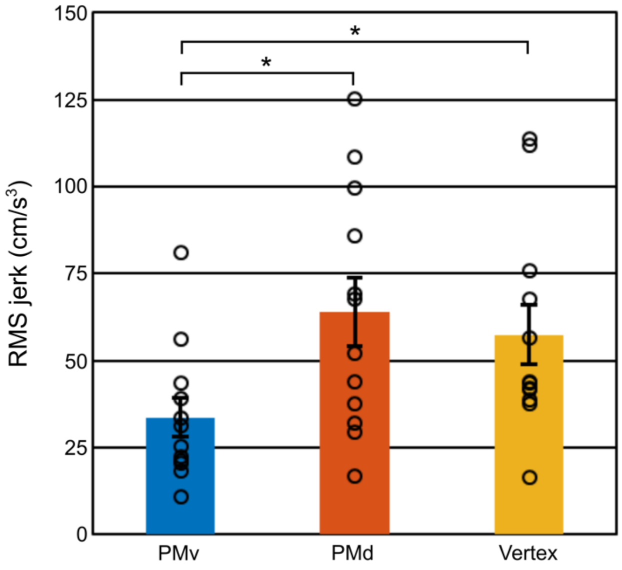

Figure 4-2: Thumb RMS jerk

Single points reflect individual participant values; * = p<.05 (corrected). Error bars indicate between-subjects SE.

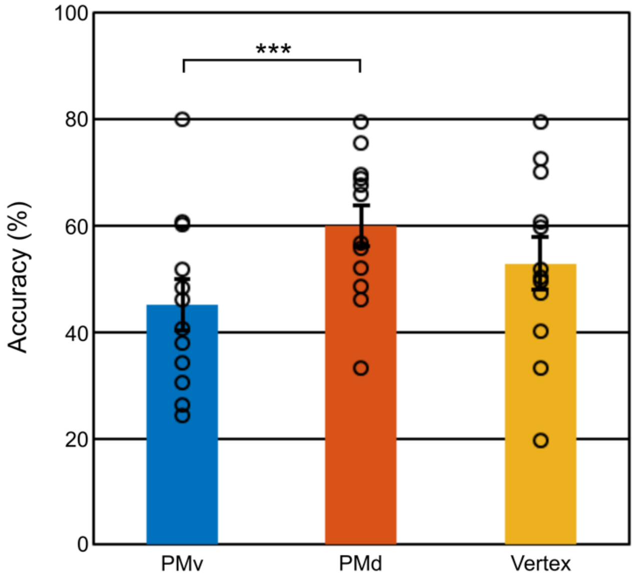

Figure 4-3: Thumb touch accuracy

Single points reflect individual participant values; *** = p=.001 (corrected). Error bars indicate between-subjects SE.

4.3.2 Imitation wrist kinematics

There were a number of significant effects observed in wrist kinematics (Table 4-1 and Table 4-2). Compared to stimulation during imitation, stimulation during observation resulted in a significantly greater MO and MT, and significantly smaller peak velocity and peak deceleration. Compared to meaningful actions, meaningless actions had a significantly greater peak acceleration, time to peak velocity, peak velocity, and MT, and a significantly smaller TPV/MT and TPD/MT. This was in keeping with what we had observed in previous experiments. Compared to hand gestures, finger gestures had a significantly greater MO, and significantly smaller time to peak acceleration, TPA/MT, peak acceleration, time to peak velocity, peak velocity, time to peak deceleration, peak deceleration, and MT.

Table 4-1: Mean values for wrist kinematic variables

Variable	Mean(±SE) value								
	Site			Time		Meaning		Effector	
	PMv	PMd	Vertex	Observation	Imitation	Meaningful	Meaningless	Hand	Finger
MO (ms)	329 (31.5)	310 (35.4)	316 (31.6)	301 (28.5)	336 (33.4)	319 (29.5)	318 (31.8)	312 (30.8)	325 (30.0)
TPA (ms)	137 (6.46)	147 (5.62)	142 (4.30)	142 4.83)	142 (4.30)	141 (5.20)	143 (4.38)	157 (5.94)	127 (3.27)
TPA/MT (0 – 1)	.176 (.0108)	.187 (.00838)	.179 (.00524)	.180 (.00755)	.181 (.00699)	.184 (.00777)	.178 (.00752)	.189 (.00817)	.173 (.00658)
PA (cm/s^2)	387 (24.6)	364 (18.7)	387 (22.1)	380 (21.5)	379 (19.4)	372 (18.6)	387 (22.4)	423 (21.6)	336 (19.7)
TPV (ms)	329 (6.79	335 (8.97)	334 (6.86)	333 (7.06)	332 (6.63)	329 (6.27)	336 (7.54)	352 (7.27)	314 (6.64)
TPV/MT (0 – 1)	.422 (.00926)	.422 (.00728)	.420 (.00580)	.420 (.00672)	.423 (.00719)	.430 (.00678)	.413 (.00751)	.420 (.00781)	.425 (.00668)
PV (cm/s)	72.4 (3.30)	70.2 (1.96)	73.8 (2.22)	71.6 (2.29)	72.7 (2.30)	70.8 (2.19)	73.5 (2.53)	82.4 (2.57)	61.9 (2.15)
TPD (ms)	543 (14.4)	558 (18.4)	550 (16.5)	552 (15.9)	549 (15.3)	541 (13.2)	559 (18.6)	583 (16.6)	517 (15.4)
TPD/MT (0 – 1)	.690 (.00850)	.698 (.0109)	.687 (.0102)	.690 (.00938)	.693 (.00937)	.702 (.00883)	.681 (.0109)	.691 (.00892)	.692 (.0107)
PD (cm/s^2)	-277 (20.1)	-266 (14.6)	-276 (10.7)	-268 (14.7)	-279 (13.0)	-272 (14.4)	-274 (14.2)	-302 (14.7)	-244 (14.0)
MT (ms)	788 (16.2)	799 (18.2)	802 (17.5)	800 (15.9)	793 (15.8)	771 (13.4)	822 (18.8)	845 (18.0)	747 (14.7)

Table 4-2: Main effects for wrist kinematic variables

Significant p-values are in bold.

Variable	Main effect											
	Site			Time			Meaning			Effector		
	F (2, 22)	p	η^2	F (1, 11)	p	η^2	F (1, 11)	p	η^2	F (1, 11)	p	η^2
MO	0.384	.686	.034	7.35	**.020**	.401	0.006	.939	.001	10.4	**.008**	.486
TPA	1.57	.230	.125	0.058	.814	.005	0.409	.536	.036	58.2	**<.001**	.841
TPA/MT	0.881	.428	.074	0.090	.769	.008	1.13	.312	.093	12.1	**.005**	.524
PA	1.79	.191	.140	0.040	.844	.004	5.24	**.043**	.323	137	**<.001**	.925
TPV	0.524	.599	.045	0.223	.646	.020	6.20	**.030**	.360	166	**<.001**	.938
TPV/MT	0.112	.895	.010	2.09	.176	.160	18.8	**.001**	.631	0.403	.538	.035
PV	1.68	.210	.132	5.49	**.039**	.333	5.12	**.045**	.317	255	**<.001**	.959
TPD	1.19	.324	.097	0.675	.429	.058	4.05	.069	.269	70.5	**<.001**	.865
TPD/MT	1.71	.204	.135	0.633	.443	.054	7.62	**.019**	.409	0.008	.931	.001
PD	0.449	.644	.039	11.7	**.006**	.516	0.094	.764	.009	58.0	**<.001**	.841
MT	0.800	.462	.068	8.19	**.015**	.427	36.7	**<.001**	.770	121	**<.001**	.917

In the case of significant interactions (supplemental sections S4-1 and S4-2) we used pairwise comparisons to look at the highest level interaction in each instance. There were significant site*time interactions in MO, TPA/MT, and peak deceleration. For MO (Figure 4-4), stimulation during imitation resulted in a significantly later MO than stimulation during observation over the PMv (F(1,11)=21.0, p=.001, η^2=.657). There was no significant difference between stimulation during observation and imitation over the PMd (F(1,11)=2.59, p=.136, η^2=.191), or between observation and imitation over the vertex (F(1,11)=0.442, p=.520, η^2=.039). For the site*time interaction in TPA/MT there was no significant difference between stimulation during observation (mean±SE = .172±.0115) and imitation (.180±.0105) over the PMv (F(1,11)=3.61, p=.084, η^2=.247), between observation (.189±.00906) and imitation (.184±.00846) over the PMd (F(1,11)=1.10, p=.317, η^2=.091), or between observation (.179±.00584) and imitation (.179±.00558) over the vertex (F(1,11)=0.002, p=.965, η^2<.001).

For the site*time interaction in PD (Figure 4-4), stimulation during imitation resulted in a significantly greater PD than stimulation during observation over the PMv ($F(1,11)=31.0$, $p<.001$, $\eta^2=.738$). There was no significant difference between stimulation during observation and imitation over the PMd ($F(1,11)=1.06$, $p=.326$, $\eta^2=.088$), or between observation and imitation over the vertex ($F(1,11)=2.68$, $p=.130$, $\eta^2=.196$).

There was a significant time*effector interaction in TPV. However this was found to reflect significant differences between hand and finger gestures following stimulation during both observation (351±7.53ms for hand gestures versus 315±6.84ms for finger gestures, $F(1,11)=167$, $p<.001$, $\eta^2=.938$), and imitation (352±7.13ms versus 312±6.54ms, $F(1,11)=142$, $p<.001$, $\eta^2=.928$).

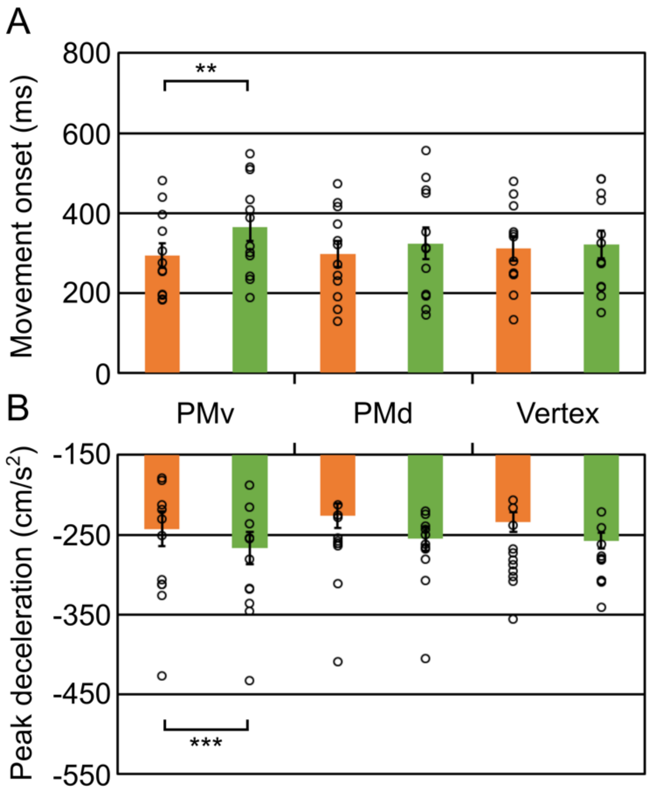

Figure 4-4: Paired comparisons for significant site*time interactions

A) MO B) PD; Error bars indicate between-subjects standard error, whilst single points show individual participant values; Orange = observation, green = imitation; ** = p<.01, *** = p<.001.

There were significant meaning*effector interactions in peak acceleration, peak velocity, time to peak deceleration (Figure 4-5). For the meaning*effector interaction in peak acceleration, meaningless hand gestures had a significantly greater peak acceleration than meaningful hand gestures (F(1,11)=13.6, p=.004, η2=.553), whilst there was no significant difference between meaningless finger gestures and meaningful finger gestures (F(1,11)=0.008, p=.931, η2=.001). For the meaning*effector interaction in peak velocity, meaningless hand gestures had a significantly greater peak velocity than meaningful hand gestures (F(1,11)=17.5, p=.002, η2=.614), whilst there was no significant difference between meaningless finger gestures and meaningful finger gestures (F(1,11)=0.100, p=.757, η2=.009). For the meaning*effector interaction in time to peak deceleration, meaningless hand gestures had a significantly greater time to peak deceleration than meaningful hand gestures (F(1,11)=9.12, p=.012, η2=.453), whilst there was no significant difference between meaningless finger gestures and meaningful finger gestures (F(1,11)=0.023, p=.883, η2=.002).

There were significant time*meaning*effector interactions in TPV/MT, peak deceleration, and MT (Figure 4-6). For the time*meaning*effector interaction in TPV/MT, stimulation during observation resulted in a significant difference between meaningful and meaningless hand gestures (F(1,11)=18.7, p=.001, η^2=.629), but not meaningful and meaningless finger gestures (F(1,11)=1.35, p=.270, η^2=.109), whilst stimulation during imitation resulted in a significant difference between meaningful and meaningless hand gestures (F(1,11)=6.61, p=.026, η^2=.375), and meaningful and meaningless finger gestures (F(1,11)=17.5, p=.002, η^2=.614).

For the time*meaning*effector interaction in PD, there was a significant difference between meaningful and meaningless hand gestures following stimulation during imitation (F(1,11)=6.00, p=.032, η^2=.353), but not between meaningful and meaningless finger gestures following stimulation during imitation (F(1,11)=2.29, p=.158, η^2=.172). Similarly, there was no significant difference between meaningful and meaningless hand gestures (F(1,11)=0.144, p=.711, η^2=.013), or meaningful and meaningless finger gestures (F(1,11)=0.030, p=.866, η^2=.003) following stimulation during observation.

The time*meaning*effector interaction in MT reflected significant differences between meaningful (809±15.7ms) and meaningless (889±23.1ms) hand gestures following stimulation during observation (F(1,11)=37.9, p<.001, η^2=.775), meaningful (741±15.0ms) and meaningless (763±15.5ms) finger gestures following stimulation during observation (F(1,11)=4.95, p=.048, η^2=.310), meaningful (812±14.0ms) and meaningless (873±21.6ms) hand gestures following stimulation during imitation (F(1,11)=31.1, p<.001, η^2=.738), and meaningful (724±13.9ms) and meaningless (762±17.1ms) finger gestures following stimulation during imitation (F(1,11)=30.1, p<.001, η^2=.732).

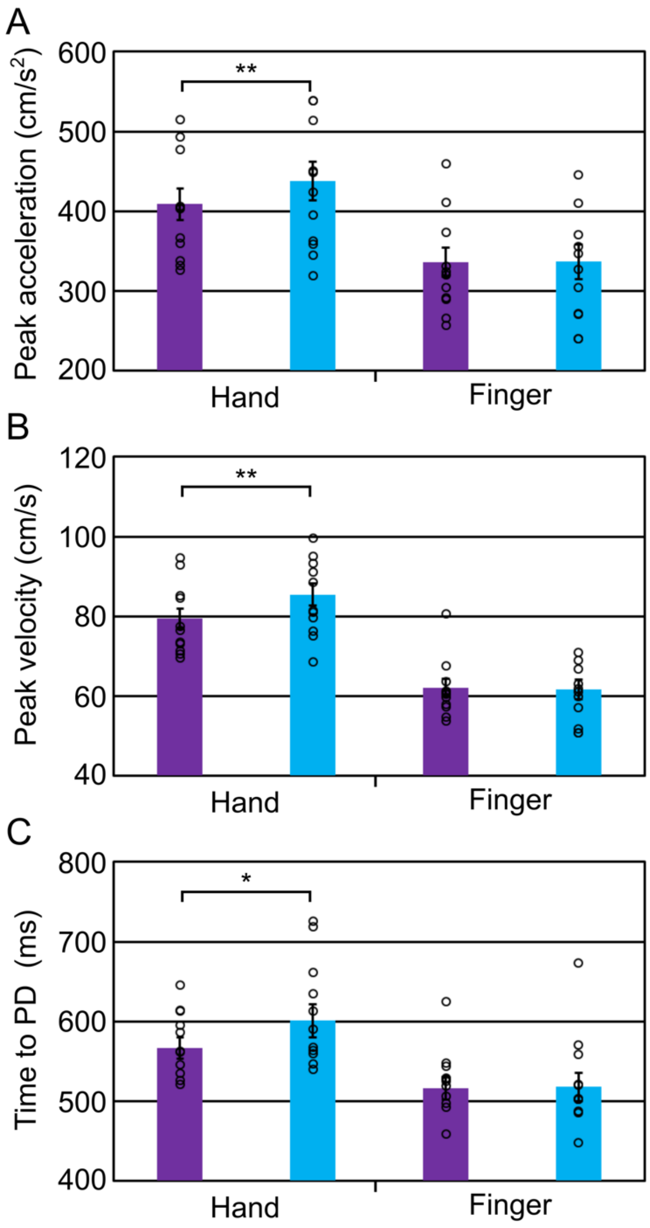

Figure 4-5: Paired comparisons for significant meaning*effector interactions

A) PA B) PV C) TPD; Error bars indicate between-subjects standard error, whilst single points show individual participant values; Purple = meaningful, blue = meaningless; * = p<.025, ** = p<.01.

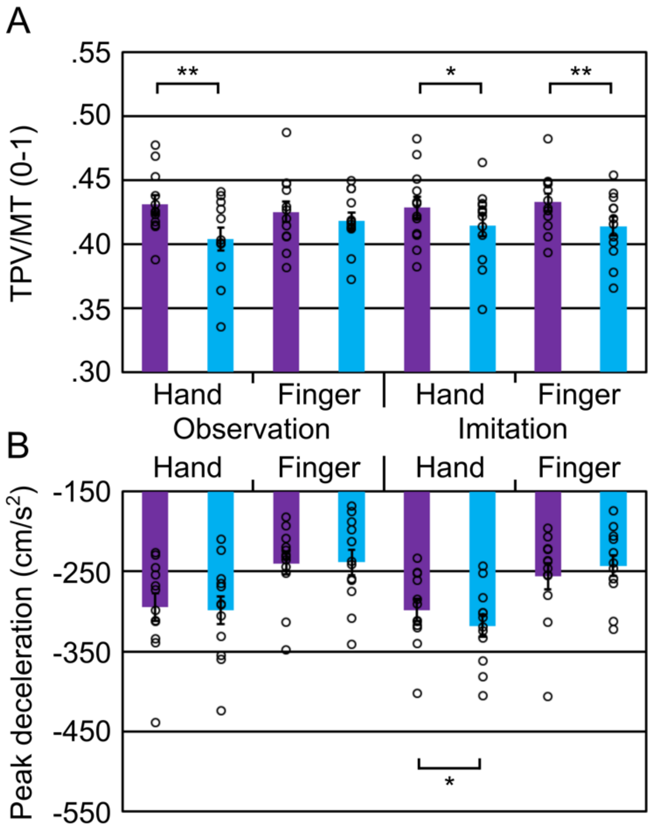

Figure 4-6: Paired comparisons for significant time*meaning*effector interactions

A) TPV/MT B) PD; Error bars indicate between-subjects standard error, whilst single points show individual participant values; Purple = meaningful, Blue = meaningless; * = p<.05, ** = p<.01.

4.3.3 Actor-imitator correspondence

There were no significant effects of stimulation site or stimulation time in the max Z-value analysis (Table 4-3 and Table 4-4). Meaningless actions were significantly better correlated than meaningful actions in the shoulder. A significant uncorrected effect in the same direction was observed in the elbow. Meaningful actions were significantly better correlated than meaningless actions in the index, middle, ring, and little fingers. Significant uncorrected effects in the same direction were observed in the wrist and thumb. Hand gestures were significantly better correlated than finger gestures in the shoulder, elbow, wrist, thumb, index finger, and little finger. A significant uncorrected effect in the same direction was observed in the ring finger. There were no significant interactions in the max Z-value analysis (S4-3 and S4-4).

There were a number of significant main effects in the lag at maximum Z-value analysis (Table 4-5 and 4-6). Stimulation during observation compared to stimulation during imitation resulted in a significantly greater lag at the maximum Z-value in the wrist, thumb, and index finger. Significant uncorrected effects in the same direction were observed in the middle and ring finger. Meaningless actions had a significantly greater lag at the maximum Z-value than meaningful actions in the shoulder. Meaningful actions had a significantly greater lag at the maximum Z-value than meaningless actions in the thumb, index finger, and ring finger. Significant uncorrected effects in the same direction were observed in the middle and little finger. Hand gestures had a significantly greater lag at the maximum Z-value compared to finger gestures in the shoulder, middle, ring, and little fingers. Significant uncorrected effects in the same direction were observed in the wrist and thumb.

A significant meaning*effector interaction (S4-5 and S4-6) was observed in the shoulder. Meaningless hand (19.0±2.88ms) gestures had a significantly greater lag than meaningful hand (9.00±2.18ms) gestures (F(1,11)=19.5, p=.001, η^2=.640), whilst there was no significant difference between meaningless finger (3.15±2.94ms) gestures and meaningful finger (1.56±2.63ms) gestures (F(1,11)=0.697, p=.422, η^2=.060).

Table 4-3: Mean values for max Z-value

SH: shoulder, EL: elbow, WR: wrist, TH: thumb, IN: index finger, MI: middle finger, RI: ring finger, LI: little finger.

Tracker	Mean(±SE) Z-value								
	Site			Time		Meaning		Effector	
	PMv	PMd	Vertex	Observation	Imitation	Meaningful	Meaningless	Hand	Finger
SH	0.779 (0.0438)	0.741 (0.0580)	0.814 (0.0331)	0.785 (0.420)	0.774 (0.0367)	0.687 (0.0444)	0.870 (0.0396)	0.999 (0.0503)	0.557 (0.0323)
EL	1.45 (0.0650)	1.44 (0.0807)	1.44 (0.0797)	1.44 (0.0630)	1.45 (0.0600)	1.34 (0.0815)	1.54 (0.0502)	1.69 (0.0642)	1.19 (0.0616)
WR	2.27 (0.0523)	2.25 (0.0658)	2.33 (0.0512)	2.29 (0.0529)	2.29 (0.0517)	2.33 (0.0601)	2.24 (0.0464)	2.36 (0.0618)	2.21 (0.0451)
TH	1.97 (0.0523)	1.96 (0.0568)	1.92 (0.0478)	1.94 (0.0474)	1.96 (0.0492)	1.99 (0.0521)	1.91 (0.0456)	2.03 (0.0502)	1.87 (0.0496)
IN	1.91 (0.0438)	1.89 (0.0451)	1.88 (0.0386)	1.89 (0.0374)	1.90 (0.0391)	1.94 (0.0397)	1.85 (0.0382)	2.04 (0.0407)	1.75 (0.0423)
MI	1.98 (0.0451)	1.97 (0.0546)	1.98 (0.0496)	1.97 (0.0437)	1.99 (0.0462)	2.04 (0.0445)	1.91 (0.0487)	2.01 (0.0587)	1.94 (0.0380
RI	2.03 (0.0365)	2.02 (0.0462)	2.02 (0.0381)	2.02 (0.0337)	2.03 (0.0335)	2.07 (0.0321)	1.97 (0.0361)	2.07 (0.0413)	1.98 (0.0312)
LI	2.06 (0.0363)	2.05 (0.0461)	2.05 (0.0400)	2.05 (0.0368)	2.06 (0.0333)	2.11 (0.0357)	2.00 (0.0357)	2.11 (0.0441)	2.00 (0.0313)

Table 4-4: Main effects for max Z-value

Significant p-values (<.0063) are in bold; SH: shoulder, EL: elbow, WR: wrist, TH: thumb, IN: index finger, MI: middle finger, RI: ring finger, LI: little finger.

Tracker	Main effect											
	Site			Time			Meaning			Effector		
	F	p	η^2	F (1, 11)	p	η^2	F (1, 11)	p	η^2	F (1, 11)	p	η^2
SH	1.43	.261	.115	0.339	.572	.030	31.0	**<.001**	.738	169	**<.001**	.939
EL	0.016	.985	.001	0.184	.677	.016	10.9	.007	.497	221	**<.001**	.952
WR	1.99	.160	.153	0.008	.929	.001	9.14	.012	.454	24.3	**<.001**	.688
TH	0.715	.500	.061	0.465	.509	.041	10.7	.007	.493	25.7	**<.001**	.700
IN	0.279	.759	.025	0.124	.732	.011	13.6	**.004**	.553	60.9	**<.001**	.847
MI	0.093	.911	.008	1.72	.216	.135	20.5	**.001**	.651	2.97	.113	.213
RI	0.086	.918	.008	0.998	.339	.083	32.0	**<.001**	.744	8.50	.014	.436
LI	0.017	.983	.002	0.135	.720	.012	29.3	**<.001**	.727	12.6	**.005**	.533

Table 4-5: Mean values for lag at max Z-value

SH: shoulder, EL: elbow, WR: wrist, TH: thumb, IN: index finger, MI: middle finger, RI: ring finger, LI: little finger.

Tracker	Mean(±SE) ms								
	Site			Time		Meaning		Effector	
	PMv	PMd	Vertex	Observation	Imitation	Meaningful	Meaningless	Hand	Finger
SH	6.75 (2.28)	6.74 (3.14)	11.0 (2.82)	7.07 (2.24)	9.26 (2.31)	5.28 (2.03)	11.1 (2.50)	14.0 (2.29)	2.35 (2.62)
EL	9.22 (4.56)	13.4 (4.46)	16.2 (3.90)	13.5 (3.52)	12.4 (4.28)	11.0 (3.99)	14.9 (4.04)	18.5 (4.07)	7.40 (5.53)
WR	27.8 (4.99)	31.8 (6.56)	37.0 (5.83)	35.4 (5.13)	29.0 (4.96)	33.8 (4.59)	30.6 (5.57)	38.7 (6.07)	25.7 (5.00)
TH	16.9 (5.39)	20.7 (5.29)	28.8 (5.69)	25.6 (5.36)	18.8 (4.27)	26.5 (4.72)	17.9 (5.10)	29.8 (6.04)	14.5 (5.07)
IN	16.5 (5.98)	18.5 (6.55)	24.8 (6.38)	24.1 (6.05)	15.7 (4.95)	25.8 (5.46)	14.1 (5.65)	26.2 (6.50)	13.6 (5.96)
MI	13.6 (5.85)	16.6 (6.06)	21.2 (6.07)	20.4 (5.84)	13.8 (4.63)	20.3 (5.31)	13.9 (5.18)	28.1 (5.75)	6.12 (5.51)
RI	12.1 (5.56)	17.2 (6.75)	20.5 (6.20)	19.3 (5.75)	13.9 (5.06)	20.5 (5.38)	12.7 (5.41)	20.1 (6.02)	7.16 (5.83)
LI	15.1 (5.20)	17.1 (6.61)	22.5 (5.84)	20.5 (5.27)	16.0 (5.08)	21.0 (5.10)	15.4 (5.30)	27.9 (5.81)	8.56 (5.54)

Table 4-6: Main effects for lag at max Z-value

Significant p-values (<.0063) are in bold; SH: shoulder, EL: elbow, WR: wrist, TH: thumb, IN: index finger, MI: middle finger, RI: ring finger, LI: little finger.

Tracker	Main effect											
	Site			Time			Meaning			Effector		
	F (2, 22)	p	η^2	F (1, 11)	p	η^2	F (1, 11)	p	η^2	F (1, 11)	p	η^2
SH	1.25	.306	.102	1.70	.219	.134	11.5	**.006**	.510	21.0	**.001**	.656
EL	2.19	.135	.166	0.588	.459	.051	3.02	.110	.215	3.55	.086	.244
WR	1.48	.249	.119	12.3	**.005**	.527	1.87	.199	.145	6.75	.025	.380
TH	3.40	.052	.236	13.5	**.004**	.551	12.2	**.005**	.525	6.91	.023	.386
IN	1.24	.308	.101	22.6	**.001**	.673	30.4	**<.001**	.734	4.31	.062	.282
MI	0.979	.392	.082	6.34	.029	.366	6.64	.026	.376	21.5	**.001**	.661
RI	1.16	.331	.096	5.76	.035	.344	14.3	**.003**	.566	12.6	**.005**	.534
LI	1.06	.363	.088	4.87	.050	.307	6.33	.029	.365	14.7	**.003**	.571

4.3.4 t-statistic plots and permutation testing

When comparing the resampled velocity curves between PMv and PMd conditions (Figure 4-7A), there were significantly long sequences for the thumb between 89 and 117 samples (p=.026), middle finger between 102 and 120 samples (p=.048), and little finger between 91 and 110 samples (p=.041) such that the velocity with TMS over the PMv was greater than with TMS over the PMd. Sequences between 93 and 95 samples (p=.204) in the index finger and between 99 and 112 samples (p=.078) in the ring finger were not statistically significant. These periods overlapped with the deceleration phase on resampled velocity curves (S4-7), and no similar effect was observed when we performed the same t-statistic plotting on the actor data (Figure 4-7B).

We decided to examine the original mean digit PD using Bonferroni-corrected t-tests with an alpha cutoff of .025. There was no significant difference in mean digit PD between PMv and PMd (mean±SE = -582±38.0cm/s^2 versus -578±30.4, t(11)=-0.173, p=.044, g_{rm}=0.0228), between PMv and vertex (-564±22.6, t(11)=-0.668, p=.518, g_{rm}=0.135), or between PMd and vertex (t(11)=-0.617, p=.550, g_{rm}=0.137). Considering the significant differences in relative PV observed in experiment 2 analysis, we also examined the imitator mean digit PD relative to the actor mean digit PD. However, there was no significant difference in mean digit relative PD between PMv and PMd (112±41.4cm/s^2 versus 112±46.6, t(11)=0.010, p=.992, g_{rm}=0.00187), between PMv and vertex (155±30.5, t(11)=-1.11, p=.292, g_{rm}=0.312), or between PMd and vertex (t(11)=-1.26, p=.233, g_{rm}=0.273).

In the site*time interaction (Figure 4-8A), there were significantly long sequences present in the index finger from sample 34-55 (p=.044) and ring finger from sample 31-54 (p=.036). These sequences overlapped with the period covering PV in resampled velocity curves (S4-8). Similar effects were not observed in the actor data (Figure 4-8B). Whilst the sequences in the thumb (p=.109), middle finger (p=.126), and index finger (p=.054) were not significantly long, the consistent direction of effects observed prompted us to examine the original mean digit PV using two-tailed t-tests.

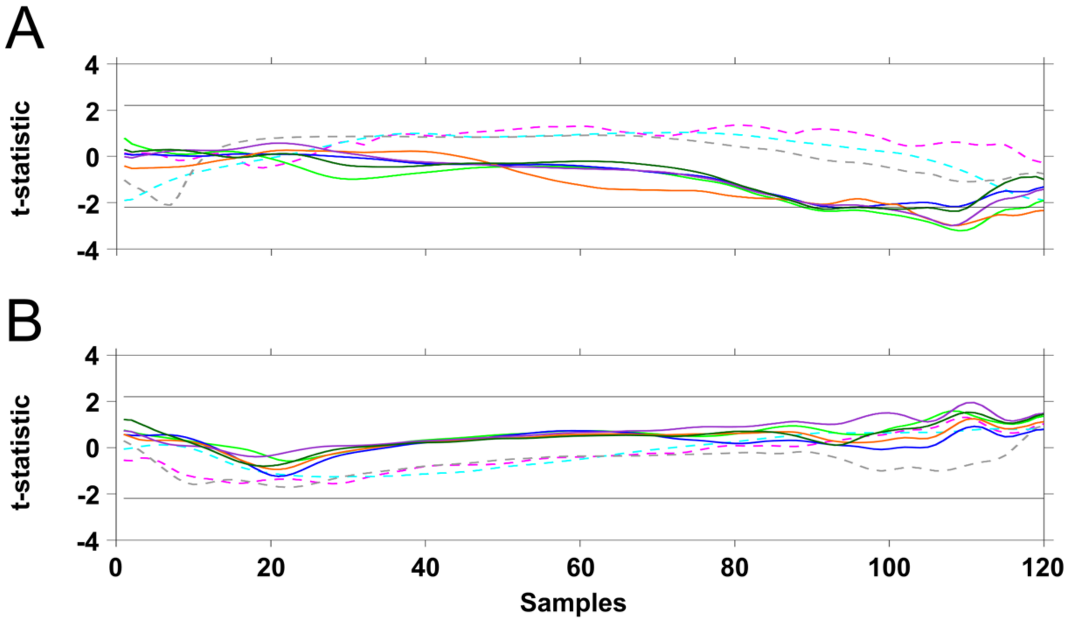

Figure 4-7: t-statistic plots for main effect of stimulation site (PMv versus PMd) in all trackers

A) imitator (significantly long sequence for the thumb between samples 89 and 117, middle finger between samples 102 and 120, little finger between samples 91 and 110) B) actor; Horizontal lines indicate positive and negative critical t-values; Dashed magenta = shoulder, dashed cyan = elbow, dashed grey = wrist, light green = thumb, blue = index finger, orange = middle finger, purple = ring finger, dark green = little finger.

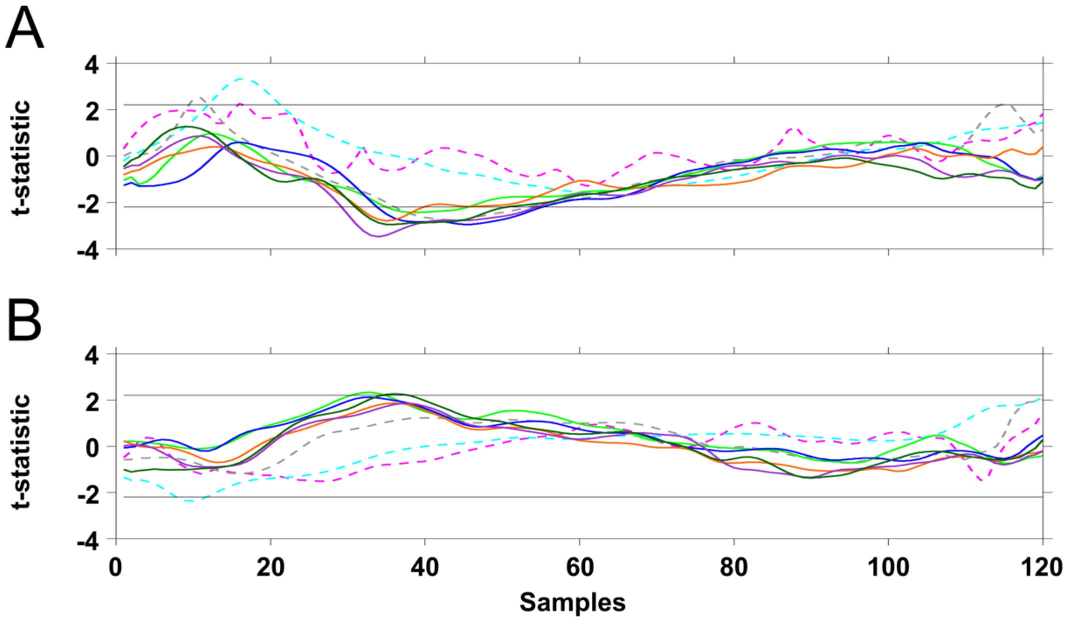

Figure 4-8: t-statistic plots for site*time interaction in all trackers

A) imitator (significantly long sequence for the index finger between samples 34 and 55, ring finger between samples 31 and 54) B) actor; Horizontal lines indicate positive and negative critical t-values; Dashed magenta = shoulder, dashed cyan = elbow, dashed grey = wrist, light green = thumb, blue = index finger, orange = middle finger, purple = ring finger, dark green = little finger.

This revealed that mean digit PV was significantly lower (Figure 4-9) following stimulation over the PMv during observation compared to stimulation over the PMv during imitation (t(11)=-2.31, p=.041, g_{rm}=0.149). There was no significant difference between stimulation over the PMd during observation and imitation (t(11)=-0.622, p=.547, g_{rm}=0.0314), or between stimulation over the vertex during observation and imitation (t(11)=-0.961, p=.357, g_{rm}=0.0633). In order to check for differences in the imitator's velocity relative to the actor's velocity, we performed the same analysis on the imitator mean digit PV relative to the actor mean digit PV (Figure 4-10). There was a significant difference in mean digit relative PV between stimulation over the PMv during observation and stimulation over the PMv during imitation (t(11)=-4.04, p=.002, g_{rm}=0.229). There was also a significant difference in mean digit relative PV between stimulation over the vertex during observation and stimulation over the vertex during imitation (t(11)=-2.83, p=.016, g_{rm}=0.117). There was no significant difference in mean digit relative PV between stimulation over the PMd during observation and stimulation over the PMd during imitation (t(11)=-0.918, p=.379, g_{rm}=0.0537).

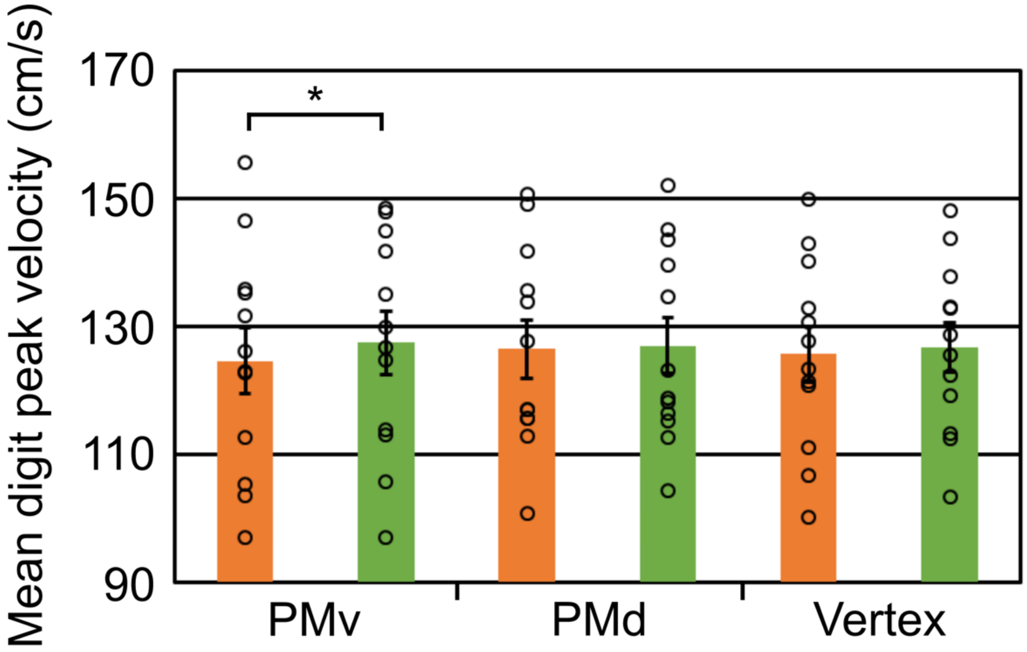

Figure 4-9: Imitator mean digit peak velocity

Error bars indicate between-subjects standard error, whilst single points show individual participant values; Orange = observation, green = imitation; * = p<.05.

Finally, there was a significantly long sequence observed for the site*effector interaction (S4-9) in the elbow from samples 31-69 (p=.022) overlapping peak acceleration, peak velocity, and peak deceleration, though no significant differences were found in elbow peak values when we examined these using Bonferroni-corrected t-tests (S4-10). There were no other significantly long sequences observed in the t-statistic plots (S4-9).

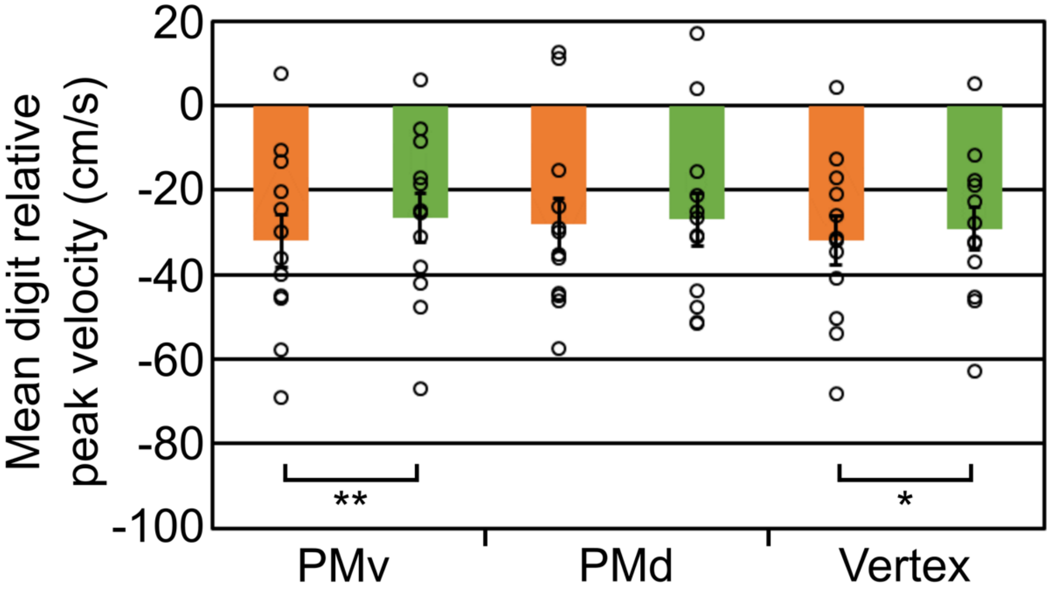

Figure 4-10: Imitator mean digit relative peak velocity

Error bars indicate between-subjects standard error, whilst single points show individual participant values; Orange = observation, green = imitation; * = p<.025, ** = p<.01.

4.4 Premotor cortex discussion

In this experiment we examined the role of the left dorsal and ventral premotor cortices in meaningful and meaningless action imitation. We were interested to see the degree to which these areas might distinguish between meaningful and meaningless actions for the purpose of imitation. We found that stimulating the PMv influenced the movement of the digits, both in our control finger-thumb opposition and our imitation task (regardless of action meaning). We also discovered that meaningless actions are imitated slower but more accurately with the shoulder and elbow, whilst meaningful actions are imitated slower but more accurately with the wrist and digits.

4.4.1 Correction time effects

We continued to observe an influence of action meaning on wrist correction time markers, confirming that participant behaviour was similar here to previous experiments. Participants increased their wrist peak acceleration and peak velocity when performing meaningless actions, ensuring more time was available for correcting the action following peak deceleration (reflected in smaller TPV/MT and TPD/MT, and longer MT). These effects were not influenced by stimulation site, indicating that the premotor cortex does not seem to be involved in moderating this possibly explicit approach to action imitation in scenarios when the gesture is not known.

4.4.2 Effector-specificity and gesture meaning

Following experiment 2 we decided to better account for the differences between hand and finger gestures by including them as a factor in our analysis. This allowed us to better characterise participant performance in actions that required more fine-grained manipulation of the fingers, or the use of the entire hand as a single effector for gestures. Compared to hand gestures, finger gestures had a significantly greater MO, and significantly smaller wrist time to peak acceleration, TPA/MT, peak acceleration, time to peak velocity, peak velocity, time to peak deceleration, peak deceleration, and MT. The effects of time to peak acceleration, TPA/MT, time to peak velocity, and MT most likely reflect the greater variability in hand position required for hand gesture imitation. Whilst finger gestures generally required manipulation of the fingers with the hand in a single location (in front of the torso), hand gestures required placement of the hand in different locations surrounding the upper body. Thus, hand gestures had a longer movement time, and took longer to reach peak kinematic parameters. The greater MO for finger gestures possibly reflects the longer time needed to plan these actions, considering the more complex positioning of the digits required.

Interactions in some of the above variables revealed effects driven by differences between meaningful and meaningless hand gestures. Meaningless hand gestures had a significantly greater peak acceleration, peak velocity, and time to peak deceleration compared to meaningful hand gestures, whilst there were no significant differences between meaningless and meaningful finger gestures in these variables. This may indicate that the explicit approach towards imitating meaningless actions, as characterised by increased peak acceleration and peak velocity in previous experiments, may be more associated with hand gesture than finger gesture imitation. This may again reflect the fact that hand postures required a greater distance to move, such that greater attention needed to be paid to ensure that the unfamiliar action was completed in the required time.

Our new approach to testing actor-imitator correspondence (cross-correlation and associated lag, rather than solely correlation) revealed some interesting effects of both meaning and effector. Meaningless actions were significantly better correlated than meaningful actions in the shoulder. A significant uncorrected effect in the same direction was observed in the elbow. This confirms similar results that were observed in experiment 2. In addition, meaningless actions had a significantly greater lag at max Z-value than meaningful actions in the shoulder.

Meaningful actions were significantly better correlated than meaningless actions in the index, middle, ring, and little fingers. Significant uncorrected effects in the same direction were observed in the wrist and thumb. Meaningful actions also had a significantly greater lag at max Z-value than meaningless actions in the thumb, index finger, and ring finger. Significant uncorrected effects in the same direction were observed in the middle and little finger. The inverse effects of correlation and lag indicate that, unsurprisingly, actions were imitated more accurately when they were performed more slowly.

More interestingly, our results seem to allow one to infer distinctions between proximal (shoulder, elbow) and distal (wrist, digit) recruitment dependent on action meaning. In the case of meaningless action imitation, where adherence to observed kinematics is more useful, it is likely that the shoulder and elbow are easier to imitate than the fingers because they have fewer degrees of freedom. Furthermore, since meaningful actions are already present in the motor repertoire, the proximal effectors may be less accurately imitated in order to perform the action in a preferred fashion. On the other hand, the higher degrees of freedom in the wrist and digits make matching much more difficult, hence imitation is less accurate for meaningless actions.

Hand gestures were significantly better correlated than finger gestures in the shoulder, elbow, wrist, thumb, index finger, and little finger. A significant uncorrected effect in the same direction was observed in the ring finger. In addition, hand gestures had a significantly greater lag compared to finger gestures in the shoulder, middle, ring, and little fingers. Significant uncorrected effects in the same direction were observed in the wrist and thumb. These effects likely reflect the fact that hand gestures were computationally less complex. The hand moves as one single effector to a single point in the body, at a certain orientation, whilst digits require accurately distinguishing the position and orientation of each of the digits.

Finally, a significant meaning*effector interaction was observed in the shoulder. Meaningless hand gestures had a significantly greater lag than meaningful hand gestures, whilst there was no significant difference between meaningless finger gestures and meaningful finger gestures. This probably reflects the greater shoulder recruitment required for hand gestures.

4.4.3 Absence of PMd effects

We did not observe any significant main effects or interactions associated with PMd stimulation in this experiment. This was surprising, considering previous findings associating this area with intransitive or novel action performance (Hamilton & Grafton, 2009; Króliczak & Frey, 2009). Furthermore, there is some evidence to suggest that both the PMd and PMv play a role in encoding hand-shaping kinematics (Takahashi *et al*., 2017), and rTMS over the left PMd has been found to induce inhibition in the hand area of M1 (Gerschlager *et al*., 2001).

Importantly, the more frequent discussion of the PMd in terms of reaching (Beurze *et al*., 2007; Lee *et al*., 2006; Ohbayashi *et al*., 2016; Nakayama *et al*., 2008; Pesaran *et al*., 2006) may not be fully applicable to the gestural actions which we were using as stimuli. In particular, there are likely to be different processing routes underlying point-to-point functional actions like reaching, compared with the less linear trajectories used for abstract action like gesture (Wong *et al.*, 2016). It is still unclear then what PMd activity in previous studies of imitation could represent. It may be that this region is more likely to be involved in the encoding of external (i.e., not part of the body) targets (Koski *et al.*, 2002).

4.4.4 Role of the PMv in hand shaping for gestures

In our imitation task we found that mean digit PV was significantly lower following stimulation over the PMv during observation compared to stimulation over the PMv during imitation. There was no significant difference between stimulation over the PMd during observation and imitation, or between stimulation over the vertex during observation and imitation. Additionally, in our control fine motor task, the finger-thumb opposition task, we found that stimulating the PMv resulted in a reduced thumb RMS jerk (likely reflecting reduced switching between the digits) compared to the PMd and vertex, and lower accuracy when compared to the PMd. These results are suggestive of a general role for the PMv in fine motor control of the digits, which is not specific to imitation.

As discussed in the introduction, the PMv is often associated with hand shaping during grasping (Davare *et al.*, 2006, 2008, 2009; Fogassi *et al.*, 2001; Majdandžić *et al.*, 2009; Vingerhoets *et al.*, 2013). One possibility that arises from our results is that the hand-shaping element is not object-specific, and can be associated with other hand-shaping movements that are directed towards more abstract goal-states (like gesture formation). Hoshi & Tanji (2007) claim that during “direct sensorimotor processing, the PMv receives information on a motor target and sends outputs to achieve an action that directly matches the information” (pg. 240), whilst Vingerhoets & Clauwaert (2015) suggest that the PMv has a role in “matching hand posture configurations in accordance to visual demands” (pg. 3437). However, neither of these popular descriptions are necessarily reliant on a target object. We posit that during both meaningful and meaningless gesture formation, the movement of the digits towards other digits of the (same) hand is enough to constitute an ‘target-directed’ hand shaping action. In this explanation, the other digits or parts of the hand constitute the object/target. As in object-directed action (Davare *et al.*, 2009), the PMv would process target-relevant properties for hand shape, and possibly transmit this information to M1 in a muscle-specific manner. The attenuation of this process following rTMS could therefore result in a reduction in muscle recruitment, leading to the observed decrease in velocity observed here.

We are unaware of any other studies that have causally linked (i.e., using neurostimulation) the PMv to gestural kinematics using motion-tracking (but see Schettino *et al.*, 2015 for a role of the PMv in compensating grip aperture perturbation). However, our claim is broadly in keeping with some previous discussion, and some have made similar claims based on fMRI data (Montgomery *et al.*, 2007). It seems possible then that popular consideration of the PMv in terms of object-directed hand shaping is purely a result of the object-directed experimental paradigms commonly used to examine this region.

The PMv has been found to be associated with both meaningful and meaningless action imitation in neuroimaging (imitation versus observation, Rumiati *et al.*, 2005) and neuropsychological (Buxbaum *et al.*, 2014) studies. Some have suggested that damage to frontal regions overlapping the PMv can be associated with selective deficits in meaningless finger gesture imitation (Goldenberg & Karnath, 2006). However, the specificity of such deficits does not necessarily indicate a specific function. One possibility is that damage to the PMv also damages connectivity from regions associated with meaningless action processing. Another is that damage encompasses regions processing, or connectivity to regions processing, ‘internal’ (i.e., one’s own body) or ‘external’ (objects) goal locations.

It is of course worth noting the specific interaction with stimulation time in the PMv. Since stimulating the PMv during observation (i.e., prior to movement) reduced the speed with which the digits formed the required posture, it is possible that effects observed here are related to a lingering influence of cortical stimulation, prior to the enactment of the required motor code for the observed action. Stimulation during imitation may have been ineffective at influencing the PMv except later in the action, beyond the point of PV, though there was no evidence to suggest this in our results.

A general role for the PMv in hand shaping during action is not the only feasible explanation for our results. The PMv has also been associated with biological motion perception (Saygin, 2007; van Kemenade *et al*., 2012), such that stimulating this area may have influenced accurate apprehension of the observed action kinematics. However, the effects observed in the finger-thumb opposition task, which was non-imitative, do not seem to be in support of this. Furthermore, it is not possible to completely rule out a general influence of TMS. One problem with stimulating the PMv is that it is often uncomfortable (Meteyard & Holmes, 2018). This discomfort may help to explain the significantly slower MO when the PMv was stimulated during imitation rather than during observation. It is somewhat harder to explain why stimulation over the PMv during action imitation would also have resulted in a significantly increased peak deceleration, though this is possibly related to the increased MO such that actions performed later required a greater deceleration in order to perform the action in adequate time.

4.4.5 Mere presence of TMS

We were surprised to observe multiple effects of stimulation timing. We found that regardless of the location, stimulation during action observation, rather than action imitation, resulted in a significantly greater MO and MT, and significantly smaller wrist peak velocity and peak deceleration. In addition, stimulation during observation resulted in a significantly larger TPV/MT for meaningless finger gestures compared to meaningless hand gestures. When we examined actor-imitator correspondence, we found that stimulation during observation compared to stimulation during imitation resulted in a significantly greater lag at max Z-value in the wrist, thumb, and index finger. Significant uncorrected effects in the same direction were observed in the middle, ring, and little fingers.

These results are highly suggestive of a “mere presence” effect of TMS in this experiment. Little has been done to fully research the potential of mere presence effects of TMS, but there is some evidence that TMS can influence RTs regardless of actual cortical stimulation (Duecker *et al.*, 2013). Whilst it is not clear whether our stimulation time-related results reflect an inhibitory effect following offline stimulation, or an excitatory effect during online stimulation, we are inclined to suggest the former. It is possible that the stimulation prior to action performance was distracting, reducing participant preparedness for imitation, and therefore increasing MO, MT, and lag in the hand, and reducing peak velocity and peak deceleration. This may also be supported by the fact that there was a significant difference in mean digit relative PV between stimulation over the PMv during observation and stimulation over the PMv during imitation, and between stimulation over the vertex during observation and stimulation over the vertex during imitation. A distracting influence of stimulation during action observation may have reduced participant focus on the actor kinematics. It is unclear why this same effect was not observed for PMd stimulation, but this could reflect greater variability in this condition (PMd SD=20.1cm/s, PMv=19.8cm/s, vertex=18.0cm/s).

4.4.6 Premotor cortex conclusions

In conclusion, our experiment has revealed new information about the role of the PMv in action imitation, and the general approach taken towards imitating meaningful and meaningless hand and finger gestures. The accuracy of hand and finger gesture performance is not consistent throughout the arm and hand, with proximal and distal effectors supporting meaningful and meaningless action imitation to different degrees. Hand gestures appear to be easier to imitate than finger gestures given the significantly higher actor-imitator correspondence. Our results also indicate that the premotor cortex does not appear to be involved in mediating between explicit strategies for imitating meaningless actions (as expressed by wrist kinematic correction markers), but that the PMv has a general role in hand shaping for gesture.

5 EXPERIMENT 4 (POSTERIOR MIDDLE TEMPORAL GYRUS)

5.1 Introduction

The posterior temporal lobe is involved in high level visual perception, including action observation (Caspers *et al.*, 2010), the recognition of biological motion, tools, and body parts (Lingnau & Downing, 2015). In addition, the left temporal lobe, particularly the middle temporal gyrus, is often considered to play a role in semantic storage (Binder *et al.*, 2009) and retrieval (Davey *et al.*, 2015). These visual and semantic representations have important implications for the observation, recognition, and imitation of another individual's actions. The left pMTG is frequently reported in neuroimaging studies of imitation (Caspers *et al.*, 2010), which possibly reflects the observational aspect of imitation rather than any imitation-specific process. Indeed, meta-analytic evidence suggests the pMTG is more frequently associated with action observation than action performance (Caspers *et al.*, 2010; Grèzes & Decety, 2001), though it is still not clear what this activity could represent.

One explanation is provided by Hamilton (2008), who suggested that the MTG may support imitation by providing a visual representation of an observed action's kinematics. Evidence for this comes from research using repetition suppression (Hamilton & Grafton, 2007). Repetition suppression is an fMRI method based on the fact that repeat exposure to similar stimuli results in reduced activity in brain regions involved in processing those stimuli. As such, this approach allows one to examine brain regions differentially involved in assessing separable components of a stimulus, by presenting repeated stimuli that vary in some features but not others. In particular, Hamilton & Grafton (2007) found that the MTG showed increased activity for novel grasps compared to repeated grasps, and suggested that this might reflect a role of this area in representing observed grasps, rather than any singular grasp or simply visual kinematic information.

Whilst these results do support the idea that the pMTG might be involved in kinematic analysis of observed grasps, no published experiments have yet attempted to directly link the pMTG with expressed kinematics using non-invasive neurostimulation and motion-tracking in healthy individuals. This provides some justification for targeting this area, but further justification is provided by the fact that the pMTG might support also semantic aspects of meaningful action imitation. Indeed, evidence from neuropsychological patients indicates the importance of the pMTG in postural or semantic processing, which may extend beyond the observation of object-directed grasping. Specifically, being able to adequately recognise actions that have meaning to us is likely to be important for imitation, particularly if we consider action in semantic terms (meaningful, meaningless).

Patients with deficits in action recognition strongly suggest that the left posterior middle temporal gyrus (pMTG) is involved in linking action and meaning (Kalénine *et al.*, 2010). Unlike the IPL and PMv however, the role of the pMTG in action observation and action recognition may not be closely tied to object-directed action. In fact, there is evidence to suggest that the left pMTG is also associated with recognising or knowing the meaning of observed *intransitive* actions (Möttönen *et al.*, 2016; Villarreal *et al.*, 2008), which confirms that it may be essential for recognising action in general semantic terms (i.e., possibly related to communicative gesturing), rather than strict object-based interactions. The left pMTG has also been found to distinguish between social and non-social actions (Wurm *et al.*, 2017), further supporting the idea that this region might be important for recognising meaningful gestures.

This is important since the dual-route model indicates that meaningful actions are more accurately and more rapidly performed because there is a pre-existing representation of these actions which we can call on once we have recognised the observed action (Press & Heyes, 2008; Tessari & Rumiati, 2004). This process could feasibly be influenced by an inability to call upon stored action representations. Furthermore, this area could be important for distinguishing between meaningful and meaningless actions in the ways in which we have described in chapter 2. Specifically, since meaningless action imitation might rely on a greater correction time, we could feasibly suggest that a reduced ability to recognise an action as meaningful could extend the correction time of that action when it is performed.

It's worth noting that in addition to observation and recognition, Buxbaum *et al.* (2014) found that damage to the pMTG was associated with deficits in the postural elements of meaningful (in their case tool-related) action imitation. They suggested that the postural element of gesture may be a semantic feature through which action information in the pMTG is organised, which could be true for both transitive and intransitive actions. In this case, the left pMTG may be important for not just observational or recognition aspects of action imitation, but also the actual movement. Such a claim is supported by neuroimaging work in healthy individuals (e.g., Astafiev *et al.*, 2004; Oosterhof *et al.*, 2010), which indicates that this area is active not only for observed but also performed actions.

The different kinematic, postural, and semantic processes that have been associated with the pMTG make it an excellent target for study, since our experimental approach established in the previous chapters allows us to disentangle these different elements of imitation. In particular, we hypothesised that using rTMS over the left pMTG would reduce participant performance in meaningful, but not meaningless, action imitation, which would be reflected in reduced actor-imitator correspondence. We also expected that by stimulating this area, we would reduce the accuracy with which participants could recognise meaningful actions. This would potentially influence our correction time markers, such that following stimulation over the pMTG participants would perform meaningful actions more akin to meaningless actions (i.e., with earlier TPA/MT, TPV/MT, TPD/MT, and greater peak acceleration and peak velocity).

5.2 Methods

Except where stated, the experimental setup and stimuli were the same as in experiment 3.

5.2.1 Participants

We recruited 12 right-handed participants from the University of Nottingham and the surrounding area (mean±SE age = 24.0±1.04 years, 1 male). The experimental procedures were approved by the local ethics committee (ref: SoPEC 904); participants gave written, informed consent; and the experiments were conducted in accordance with the Declaration of Helsinki (as of 2008).

5.2.2 Selection of TMS sites

Left pMTG location was based on individual neuroanatomy rather than a statistical approach (Figure 5-1), as before using structural T1 MR images for each participant. The posterior limit of the MTG was designated by drawing an imaginary line from the pre-occipital notch vertically in the dorsal direction. The stimulation site was located halfway between the superior and middle temporal sulci, and approximately 10mm from the posterior limit of the MTG. A control vertex location was found using normal measures (i.e., halfway between both the two ears and the inion and nasion).

5.2.3 TMS parameters

Biphasic repetitive transcranial magnetic stimulation (rTMS) was applied to the left pMTG and the vertex control condition for 3 seconds per trial at 3Hz and 110% of distance adjusted resting motor threshold (Stokes *et al.*, 2007). Mean±SE RMT was 66±2.9% of machine output. The distance from M1 and pMTG to the outside of the skull was measured using the Brainsight neuronavigation software. Vertex stimulation intensity was the same as pMTG. Mean±SE experimental stimulation intensity (as a percentage of machine output) was 66±2.6%.

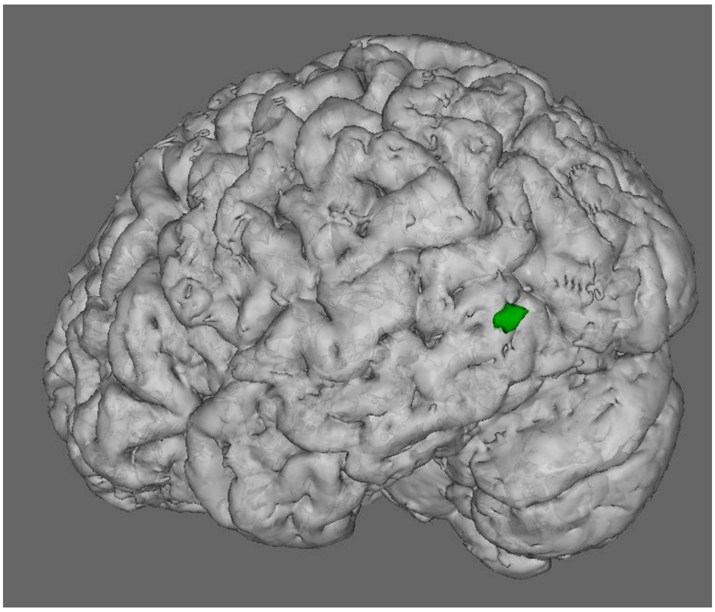

Figure 5-1: rTMS stimulation site

95% confidence ellipsoid for the rTMS target site shown on a representative participant's brain.

5.2.4 Design and procedure

Participants took part in two sessions split at least 24 hours apart. In each session a single brain region was stimulated. Meaningless and meaningful actions were segregated into their own separate blocks, with all blocks counterbalanced across participants and stimulation sites. A trained male and female confederate were used, with each participant being assigned to one confederate for both of their testing sessions.

In both meaningful and meaningless imitation tasks, there were 64 trials, and the imitator was provided with a break at the halfway point. rTMS occurred during action observation, starting 333ms after the point at which the new image appeared on the screen.

Following the completion of both TMS sessions, participants were once again presented with a questionnaire featuring the meaningful and meaningless images in a random order. Mean±SE rating accuracy was 86.5±3.25% for meaningful actions and 82.8±2.89% for meaningless actions, and no participants were excluded based on their answers.

5.2.5 Data analysis

An automated script was used for pre-processing and extraction of variables. The analysis routines processed the position data from each trial of each participant and rejected artefacts. Single timepoint spikes (>3SD from the mean), in each trial's double-differentiated time-series were deemed electromagnetic artefacts and removed by interpolation across three adjacent samples either side.

The data were filtered with a bidirectional low-pass 4th order Butterworth filter (cutoff frequency 12Hz). Trials in which either the actor or imitator moved for less than 400ms, started before the starting tone, or failed to finish the action before the end of the trial, were excluded. Finally, all trials were visually inspected for remaining artefacts and excluded if any remained. Following the above exclusions, a total of 78.7% of trials were maintained for statistical analysis.

Imitator wrist kinematic variables were analysed using a repeated-measures ANOVA with three levels: stimulation site (pMTG, vertex), action meaning (meaningful, meaningless), and action effector (hand, finger). Since some single trackers (other than the wrist) had remaining artefacts, we removed these trackers trial-wise in each instance. This resulted in 157 (~0.81%) tracker-specific time-series removed from the analysis outlined below.

As in experiment 3, we examined actor and imitator correspondence using cross-correlation (max Z-value) and associated lag. We also created t-statistic plots on time-series resampled to 120 samples, and performed permutation testing on the data to find significantly long periods for any relevant plot, then looked at peak kinematic values overlapping significant sequences. In the case of significant sequences in the site*meaning*effector interaction, we also examined paired t-statistic plots.

5.3 Results

5.3.1 Wrist kinematics

There were a number of significant main effects and interactions observed in wrist kinematics (Table 5-1 and Table 5-2). We did not observe any main effects of stimulation site. However, we did find that compared to meaningful actions, meaningless actions had a significantly smaller TPA/MT, TPV/MT, and TPD/MT, along with a significantly greater peak acceleration, peak velocity, and MT. Compared to finger gestures, hand gestures had a significantly greater time to peak acceleration, peak acceleration, time to peak velocity, peak velocity, time to peak deceleration, peak deceleration, and MT, and significantly smaller TPV/MT. These results were all in keeping with previous experiments, confirming that participant behaviour was similar in this experiment. The highest level significant interactions were examined using paired tests. Meaning*effector interactions were observed in peak acceleration, TPV/MT, and MT (Figure 5-2).

Table 5-1: Mean values and main effects for wrist kinematic variables

Significant p-values are in bold.

Variable	Mean(±SE) value						Main effect								
	Site		Meaning		Effector		Site			Meaning			Effector		
	pMTG	Vertex	MF	ML	Hand	Finger	F (1, 11)	p	η^2	F (1, 11)	p	η^2	F (1, 11)	p	η^2
MO (ms)	277 (21.7)	285 (22.3)	288 (20.6)	274 (22.9)	273 (20.0)	289 (23.6)	0.648	.438	.056	3.66	.082	.250	3.97	.072	.256
TPA (ms)	135 (7.60)	136 (7.26)	136 (6.86)	135 (7.69)	148 (8.95)	123 (6.27)	0.126	.730	.011	0.033	.858	.003	17.8	**.001**	.619
TPA/ MT (0 – 1)	.170 (.00923)	.171 (.00837)	.175 (.00886)	.166 (.00855)	.172 (.00863)	.169 (.00918)	0.064	.806	.006	7.20	**.021**	.396	0.631	.444	.054
PA (cm/s^2)	377 (26.3)	402 (29.0)	372 (26.2)	406 (27.5)	452 (32.7)	326 (21.0)	2.41	.149	.180	16.9	**.002**	.605	74.9	**<.001**	.872
TPV (ms)	324 (8.53)	325 (11.2)	326 (10.0)	323 (9.24)	340 (11.5)	310 (8.26)	0.021	.888	.002	0.830	.382	.070	22.8	**.001**	.674
TPV/ MT (0 – 1)	.410 (.00654)	.408 (.00846)	.419 (.00756)	.398 (.00716)	.397 (.00826)	.421 (.00675)	0.231	.640	.021	46.8	**<.001**	.810	29.1	**<.001**	.726
PV (cm/s)	66.4 (3.32)	69.3 (3.00)	66.1 (3.05)	69.5 (3.15)	79.4 (3.80)	56.2 (2.51)	3.84	.076	.258	13.5	**.004**	.551	138	**<.001**	.926
TPD (ms)	545 (13.0)	555 (16.3)	547 (15.8)	553 (13.5)	584 (17.6)	516 (12.9)	1.13	.310	.093	0.409	.536	.036	25.3	**<.001**	.697
TPD/ MT (0 – 1)	.684 (.0102)	.689 (.00839)	.699 (.00977)	.675 (.00860)	.676 (.00793)	.697 (.0115)	0.428	.526	.037	9.02	**.012**	.451	3.56	.086	.245
PD (cm/s^2)	-242 (18.7)	-256 (14.2)	-246 (16.3)	-252 (15.9)	-275 (19.7)	-223 (12.9)	1.89	.196	.147	1.60	.232	.127	27.4	**<.001**	.713
MT (ms)	800 (18.5)	808 (21.7)	785 (19.4)	823 (20.5)	865 (22.7)	743 (18.5)	0.690	.424	.059	22.9	**.001**	.675	79.3	**<.001**	.878

For the meaning*effector interaction in PA, there was a significant difference between meaningful hand and meaningless hand gestures (F(1,11)=22.9, p=.001, η^2=.676), but not between meaningful finger and meaningless finger gestures (F(1,11)=4.06, p=.069, η^2=.269). For the meaning*effector interaction in TPV/MT, there was a significant difference between meaningful hand and meaningless hand gestures (F(1,11)=50.0, p<.001, η^2=.820), but not between meaningful finger and meaningless finger gestures (F(1,11)=4.16, p=.066, η^2=.274). For the meaning*effector interaction in MT, there was a significant difference between meaningful hand and meaningless hand gestures (F(1,11)=42.0, p<.001, η^2=.792), but not between meaningful finger and meaningless finger (750±19.0ms) gestures (F(1,11)=2.27, p=.161, η^2=.171).

Table 5-2: Interactions for wrist kinematic variables

Significant p-values are in bold.

Variable	Site*meaning			Site*effector			Meaning*effector			Site*meaning*effector		
	F (1, 11)	p	η^2	F (1, 11)	p	η^2	F (1, 11)	p	η^2	F (1, 11)	p	η^2
MO	0.044	.837	.004	0.947	.351	.079	2.35	.153	.176	0.001	.976	<.001
TPA	1.92	.194	.148	0.109	.747	.010	0.692	.423	.059	0.023	.882	.002
TPA/MT	0.127	.728	.011	0.002	.965	<.001	0.458	.513	.040	0.001	.979	<.001
PA	0.953	.350	.080	0.064	.805	.006	6.97	**.023**	.388	4.52	.057	.291
TPV	0.734	.410	.063	0.386	.547	.034	0.179	.681	.016	0.445	.518	.039
TPV/MT	0.122	.733	.011	0.666	.432	.057	6.93	**.023**	.386	0.676	.429	.058
PV	1.65	.225	.130	3.85	.076	.259	25.3	**<.001**	.697	8.36	**.015**	.432
TPD	1.90	.196	.147	0.032	.861	.003	3.73	.080	.253	2.66	.132	.194
TPD/MT	0.154	.702	.014	0.061	.810	.005	0.006	.940	.001	4.66	.054	.298
PD	2.73	.126	.199	0.107	.750	.010	4.07	.069	.270	4.50	.057	.290
MT	2.52	.141	.186	0.092	.767	.008	27.8	**<.001**	.717	0.019	.892	.002

We also observed a significant site*meaning*effector interaction in PV (Figure 5-3). In support of our hypothesis that the pMTG is involved in meaningful action imitation, paired comparisons revealed that PV was significantly reduced for meaningful hand gestures following stimulation over the pMTG compared to over the vertex (F(1,11)=17.2, p=.002, η^2=.610), but there was no similar significant difference for meaningful finger gestures (F(1,11)=0.781, p=.396, η^2=.066), meaningless hand gestures (F(1,11)=0.571, p=.466, η^2=.049), or meaningless finger gestures (F(1,11)=0.476, p=.505, η^2=.041).

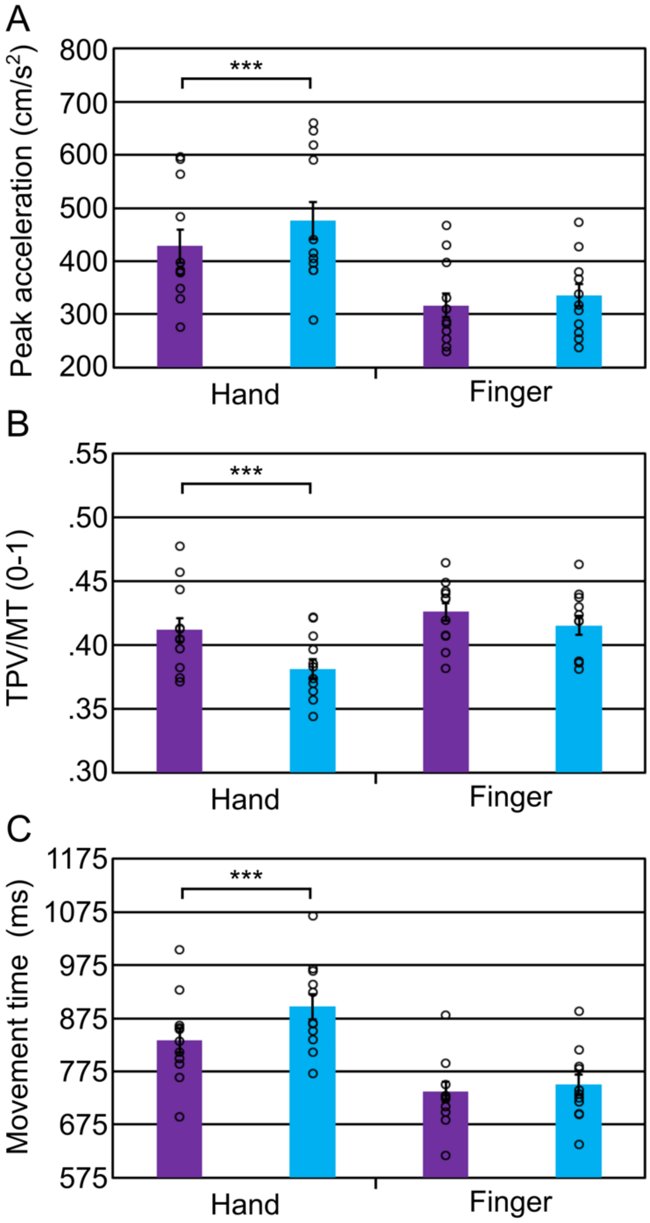

Figure 5-2: Paired comparisons for significant meaning*effector interactions

A) PA B) TPV/MT C) MT; Error bars indicate between-subjects standard error, whilst single points show individual participant values; Purple = meaningful, blue = meaningless; *** = p ≤.001.

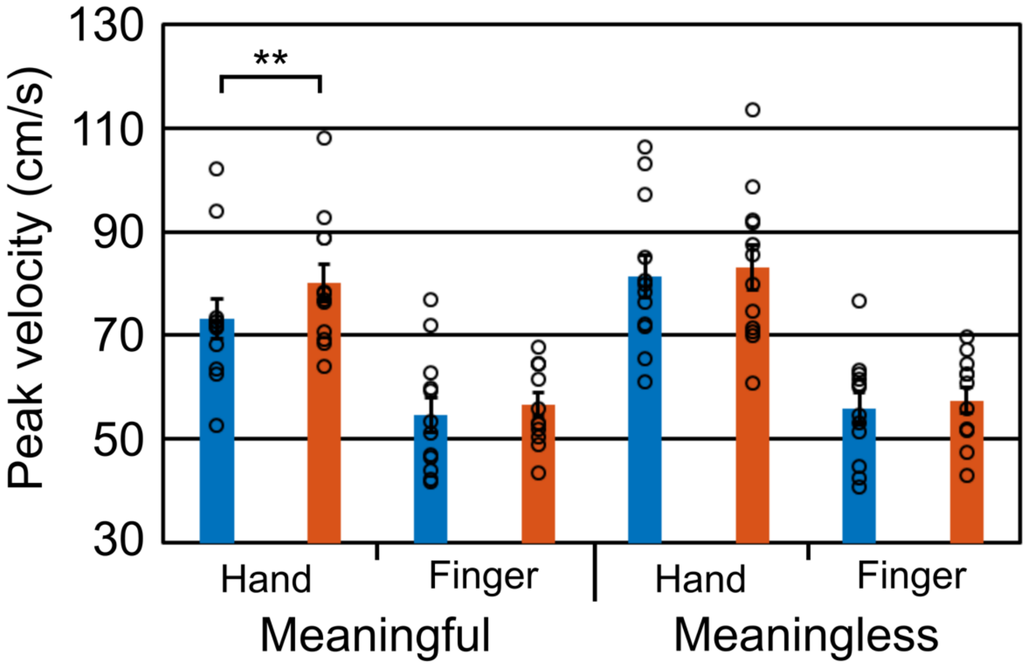

Figure 5-3: Paired comparisons for imitator peak velocity

Error bars indicate between-subjects standard error, whilst single points show individual participant values; Blue = pMTG, red = vertex; ** = p<.01.

5.3.2 Actor-imitator correspondence

There were significant main effects (Table 5-3), but not interactions (supplemental section S5-1) for max Z-value. Hand gestures were significantly better correlated than finger gestures in the shoulder, elbow, wrist, thumb, index, and little fingers. Significant uncorrected differences in the same direction were observed in the middle finger and ring finger. This was in keeping with results from experiment 3. Meaningless gestures were significantly less correlated than meaningful gestures in the little finger. A significant uncorrected difference in the same direction was observed in the ring finger. There were no significant main effects (S5-2) or interactions (S5-3) observed for lag at max Z-value.

Table 5-3: Mean values and main effects for max Z-value

Significant p-values (<.0063) are in bold; SH: shoulder, EL: elbow, WR: wrist, TH: thumb, IN: index finger, MI: middle finger, RI: ring finger, LI: little finger.

Tracker	Mean(±SE) value						Main effect								
	Site		Meaning		Effector		Site			Meaning			Effector		
	pMTG	Vertex	MF	ML	Hand	Finger	F (1, 11)	p	η^2	F (1, 11)	p	η^2	F (1, 11)	p	η^2
SH	0.877 (0.0464)	0.848 (0.0513)	0.817 (0.0448)	0.909 (0.0565)	1.10 (0.0465)	0.626 (0.0535)	1.12	.313	.092	5.34	.041	.327	181	**<.001**	.943
EL	1.62 (0.0825)	1.62 (0.0800)	1.62 (0.0805)	1.62 (0.0760)	1.83 (0.0702)	1.40 (0.0878)	<.001	.986	<.001	0.008	.931	.001	48.5	**<.001**	.815
WR	2.17 (0.0723)	2.19 (0.0727)	2.20 (0.0759)	2.16 (0.0678)	2.27 (0.0698)	2.09 (0.0765)	0.740	.408	.063	3.40	.092	.236	28.1	**<.001**	.719
TH	1.81 (0.0543)	1.88 (0.0516)	1.86 (0.0604)	1.83 (0.0415)	1.95 (0.0541)	1.74 (0.0548)	5.07	.046	.316	2.08	.177	.159	22.9	**.001**	.676
IN	1.76 (0.0562)	1.82 (0.0413)	1.80 (0.0531)	1.78 (0.0402)	1.92 (0.0601)	1.66 (0.0361)	1.43	.257	.115	0.189	.673	.017	36.6	**<.001**	.769
MI	1.81 (0.0597)	1.88 (0.0502)	1.88 (0.0627)	1.82 (0.0453)	1.91 (0.0571)	1.79 (0.0536)	3.80	.077	.257	2.94	.114	.211	10.2	.009	.480
RI	1.91 (0.0611)	1.96 (0.0584)	1.96 (0.0641)	1.90 (0.0516)	1.98 (0.0644)	1.88 (0.0553)	1.69	.221	.133	6.73	.025	.380	7.55	.019	.407
LI	1.94 (0.0600)	1.97 (0.0516)	2.00 (0.0584)	1.90 (0.0506)	2.04 (0.0655)	1.86 (0.0470)	0.770	.399	.065	15.5	**.002**	.585	18.7	**.001**	.630

5.3.3 t-statistic plots and permutation testing

Significantly long sequences were observed in the t-statistic plots comparing velocity following stimulation over the pMTG and vertex (Figure 5-4A). These were present between samples 50 – 79 in the thumb (p=.027), between samples 51 – 89 in the index finger (p=.019), and between samples 50 – 87 in the little finger (p=.020). These effects overlapped with the period of PV and PD in resampled velocity plots (S5-4). Similar effects were not observed in the actor data (Figure 5-4B). The sequence between samples 51 – 65 in the ring finger was not significant (p=.065) but the consistent effects observed in the digits prompted us to use two-tailed paired t-tests to examine mean digit PV and PD. In addition, we also examined imitator mean digit PV and PD relative to the actor considering the relative effects observed in previous experiments.

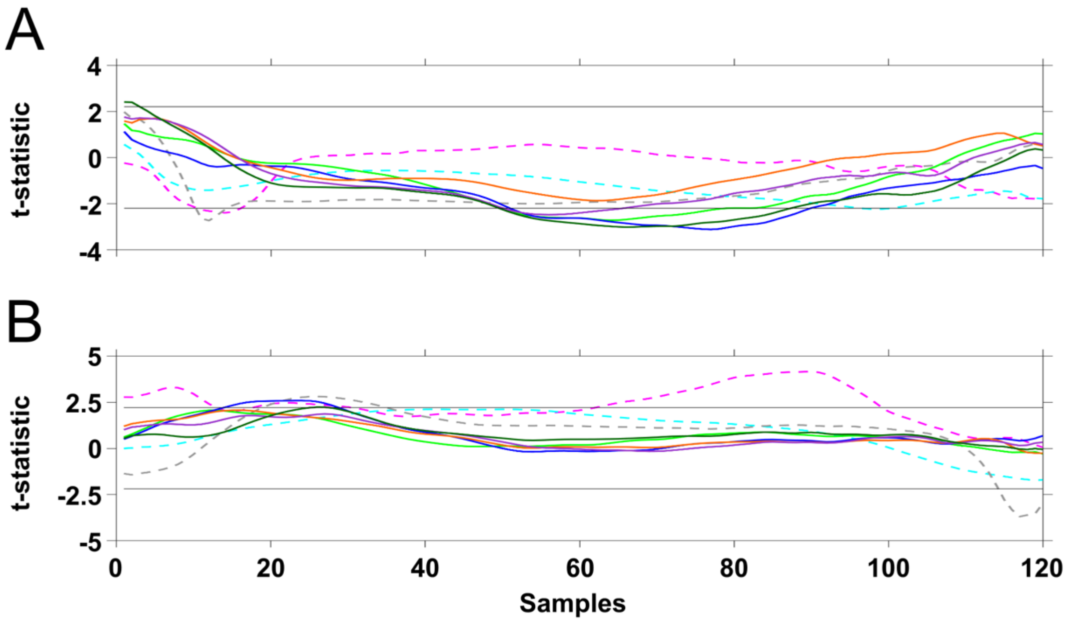

Figure 5-4: t-statistic plots for main effect of stimulation site (pMTG versus vertex) in all trackers

A) imitator (significantly long sequence in the thumb between samples 50 and 79, index finger between samples 51 and 89, little finger between samples 50 and 87) B) actor; Black horizontal lines indicate positive and negative critical t-values; Dashed magenta = shoulder, dashed cyan = elbow, dashed grey = wrist, light green = thumb, blue = index finger, orange = middle finger, purple = ring finger, dark green = little finger.

There was no significant difference in mean digit PD between pMTG (mean±SE = -555±41.5cm/s^2) and vertex (-583±39.5cm/s^2, t(11)=1.70, p=.116, g_{rm}=0.181). There was no significant difference in mean digit relative PD between pMTG (73.4±41.9cm/s^2) and vertex (45.7±41.3cm/s^2, t(11)=1.58, p=.142, g_{rm}=0.178). There was also no significant difference in mean digit PV between pMTG

(117±5.29cm/s) and vertex (122±5.52cm/s, t(11)=1.70, p=.117, g_{rm}=0.241). However, mean digit relative PV was significantly smaller following stimulation over pMTG (-19.6±4.70cm/s) compared to stimulation over the vertex (-13.2±5.19cm/s, t(11)=-2.21, p=.049, g_{rm}=0.338).

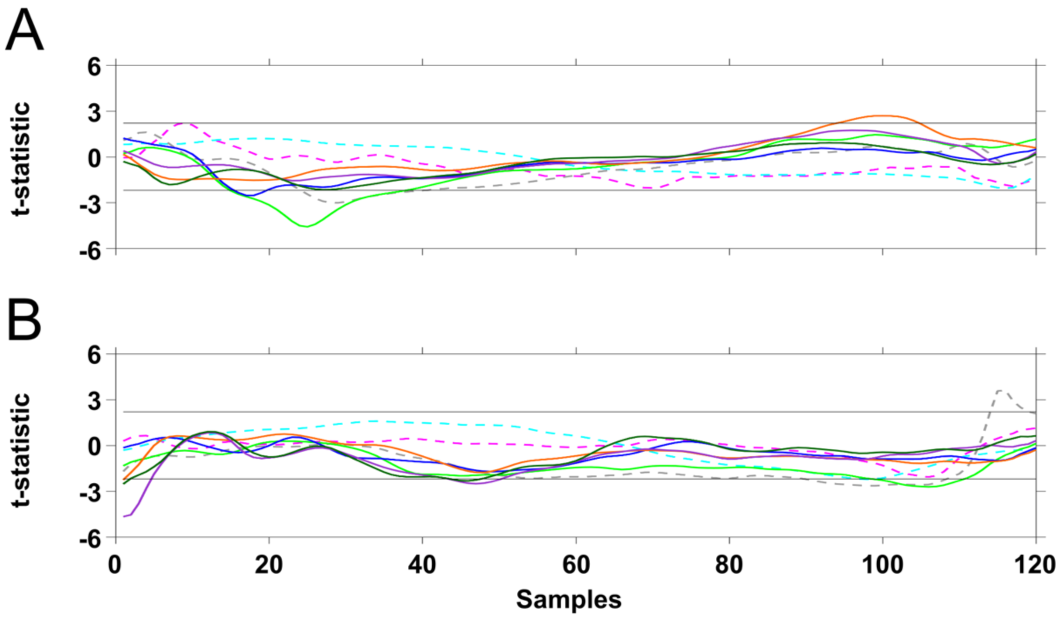

Figure 5-5: t-statistic plots for site*meaning*effector interaction in all trackers

A) imitator (significantly long sequence in the wrist between samples 25 and 40, thumb between samples 15 and 37) B) actor; Black horizontal lines indicate positive and negative critical t-values; Dashed magenta = shoulder, dashed cyan = elbow, dashed grey = wrist, light green = thumb, blue = index finger, orange = middle finger, purple = ring finger, dark green = little finger.

A significantly long sequence (p=.048) was observed for the wrist in the site*effector plot (S5-5). However, since effects in the same direction were observed in the site*meaning*effector plot, and wrist peak values had already been examined in the previous kinematic analysis, we examined in detail only the highest level interaction. The site*meaning*effector plot (Figure 5-5A) contained significantly long sequences between samples 25 – 40 in the wrist (p=.047) and between samples 15 – 37 in the thumb (p=.037). Similar effects were not observed for the actor data (Figure 5-5B).

When we examined this interaction with paired t-statistic plots (Figure 5-6 and S5-7), we found that for meaningful hand gestures (Figure 5-6), there were significantly long sequences observed between pMTG and vertex in the wrist (from samples 19 – 86, p=.004), and the thumb (from samples 50 – 85, p=.003). We took the wrist effect to be reflective of the wrist kinematic effect that we had observed earlier (i.e., where meaningful hand gestures were performed with significantly lower wrist PV following stimulation over the pMTG compared to the vertex). The sequence in the thumb was found to overlap PV and PD in resampled velocity curves (S5-6), which we examined using two-tailed paired t-tests. There was no significant difference in thumb PV between pMTG (116±5.44cm/s) and vertex (123±5.81cm/s) stimulation (t(11)=-2.11, p=.058, g_{rm}=0.304), or in thumb relative PV between pMTG (-28.2±5.44cm/s) and vertex (-22.3±5.09cm/s) stimulation (t(11)=-1.40, p=.188, g_{rm}=0.299). Thumb PD was significantly reduced following pMTG (-490±36.9cm/s^2) compared to vertex (-530±cm/s^2) stimulation (t(11)=3.08, p=.010, g_{rm}=0.297). There was no significant difference in thumb relative PD between pMTG (123±46.7cm/s^2) and vertex (99.9±40.0cm/s^2) stimulation (t(11)=0.879, p=.398, g_{rm}=0.136).

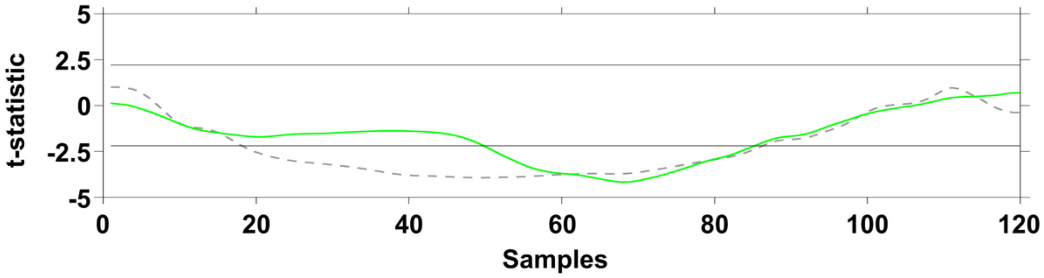

Figure 5-6: t-statistic plot comparing pMTG versus vertex for meaningful hand gestures

Black horizontal lines indicate positive and negative critical t-values; Dashed grey = wrist, light green = thumb.

We also observed a significantly long sequence in the thumb when comparing stimulation over the pMTG and vertex for meaningless hand gestures (S5-7, from 15 – 82 samples, p<.001), which overlapped with PA and PV in resampled velocity curves (S5-8). When we examined these peak parameters using two-tailed paired t-tests, there was no significant difference in thumb PA between pMTG (910±61.8cm/s^2) and vertex (969±98.3cm/s^2) stimulation (t(11)=-0.782, p=.451, g_{rm}=0.177), or in thumb relative PA between pMTG (-367±69.8cm/s^2) and vertex (-284±103cm/s^2) stimulation (t(11)=-1.04, p=.323, g_{rm}=0.238). There was also no significant difference in thumb PV between pMTG (125±6.34cm/s) and vertex (125±6.10cm/s) stimulation (t(11)=-0.144, p=.888, g_{rm}=0.0237), or in thumb relative PV between pMTG (-26.6±5.52cm/s) and vertex (-22.4±6.23cm/s) stimulation (t(11)=-1.13, p=.283, g_{rm}=0.186).

5.4 Posterior middle temporal gyrus discussion

In this experiment we examined the role of the left posterior middle temporal gyrus in meaningful and meaningless action imitation. We hypothesised that rTMS over the pMTG would reduce performance in meaningful, but not meaningless, action imitation, which would be reflected in reduced actor-imitator correspondence. In addition, we expected that following stimulation over the pMTG participants would perform meaningful actions more akin to meaningless actions (i.e., with earlier TPA/MT, TPV/MT, TPD/MT, and greater peak acceleration and peak velocity).

We found that stimulation over the left pMTG significantly reduced the speed with which participants imitated meaningful hand gestures compared to stimulation over the vertex. This effect in wrist velocity was maintained over time, as reflected in t-statistic plots. We also found that stimulating the pMTG significantly reduced mean digit relative peak velocity compared to the vertex regardless of action meaning.

5.4.1 Wrist kinematics and actor-imitator correspondence

Wrist kinematics showed similar effects of meaning and action effector as had been observed in previous experiments. Specifically, meaningless actions had a significantly smaller TPA/MT, TPV/MT, and TPD/MT, along with a significantly greater peak acceleration, peak velocity, and MT compared to meaningful actions (i.e., previously observed correction time markers). Compared to finger gestures, hand gestures had a significantly greater time to peak acceleration, peak acceleration, time to peak velocity, peak velocity, time to peak deceleration, peak deceleration, and MT, and significantly smaller TPV/MT, generally in keeping with experiment 3. Also in keeping with experiment 3, we observed that meaningless hand gestures had a significantly greater PA than meaningful hand gestures, whilst meaningful and meaningless finger gestures were not significantly different. This seems to confirm our previous claim that explicit approaches to maintaining correction time are better captured in hand gestures, perhaps because of the greater distance that the hand must move. We also found that TPV/MT was significantly smaller in meaningless compared to meaningful hand gestures, whilst MT was significantly longer in meaningless hand compared to meaningful hand gestures. Neither of these effects were observed in finger gestures. The implications for these findings are discussed in more detail in the general discussion below.

Notably, we did not observe any interactions with stimulation site and meaning or effector on any correction time markers. In particular, we predicted that stimulating the pMTG would reduce participant's ability to recognise meaningful gestures, resulting in a greater period of movement spent in the correction period as in meaningless actions, but we did not observe any effects of this nature.

As in experiment 3, hand gestures were significantly more accurately imitated (i.e., with greater correlation) compared to finger gestures. However, we did not replicate a number of other effects in actor-imitator correspondence that were observed in the experiment 3, despite an identical experimental setup. Namely, we no longer observed that proximal (shoulder, elbow) effectors were significantly more correlated for meaningless actions, whilst distal (wrist, digits) effectors were significantly more correlated for meaningful actions. In addition, we did not observe any main effects or interactions in lag at max Z-value. Such inconsistency may reflect individual differences in approaches to imitation. Alternatively, the earlier results may be false positives, and more work is necessary to confirm their validity.

The absence of site-related effects in actor-imitator correspondence suggests that, as in our previous experiments, rTMS is not disruptive enough to influence imitation accuracy, compared to the deficits that can be observed following large scale lesion damage.

5.4.2 pMTG and meaningful hand posture

Stimulation over the left pMTG resulted in a significantly reduced speed (PV) with which participants performed meaningful hand gestures compared to stimulation over the vertex, partially supporting our hypothesis that the pMTG is specifically involved in meaningful action imitation. This reduction in velocity was maintained over approximately half of the action, as reflected in paired t-statistic plots. This interesting result allows us to add to the somewhat sparse information that we currently have about the role of the left pMTG in action imitation.

As emphasised in the introduction, the left pMTG may be involved in associating action and meaning (Kalénine *et al.*, 2010). In addition, this area is possibly involved in the postural elements of movement, either in an imitative scenario or to demand (Buxbaum *et al.*, 2014, but see Vingerhoets & Clauert, 2015). One feasible explanation is that by stimulating the left pMTG we reduced the efficiency with which participants could retrieve or use the stored postural information for the meaningful actions they were requested to imitate. This resulted in slower movement for meaningful hand actions.

That this effect was observed solely for hand gestures could be explained by the fact that these results were taken from the wrist tracker, and the wrist tended to move a greater distance for hand gestures than for finger gestures. In general, finger gestures were performed at the front of the body, and did not require the hand to be moved as far from the starting point, thus reducing the movement time and the time in which an effect could be observed. Alternatively, this effect for hand gestures could specifically reflect the approach towards positioning the hand in relation to other parts of the body. The relative importance of the temporal lobe in hand gestures compared to finger gestures has been addressed before by Goldenberg &

Karnath (2006), where they suggest that temporal lobe damage is more likely to be associated with defective hand posture than finger posture performance. However, they tested apraxia patients with defective imitation of meaningless gestures only, and Buxbaum *et al.* (2014) also reported that regions of the pMTG could also be associated with defective meaningless action imitation following lesion damage.

Despite this, previous research has reported pMTG damage associated with postural deficits partially assessed using a hand shape component (Buxbaum *et al.*, 2014), so we might have expected to observe similar effects in the digits for finger gestures in our site*meaning*effector t-statistic plot (Figure 5-5). This was not the case. It seems then that there is a great deal more to be done to tease apart the links between semantic meaning and action effector, and how the pMTG might mediate between these different ways of representing action. In particular, we need to better understand to what degree intransitive hand and finger gestures are dependent on the postural aspects of action or the meaning portrayed by them. Future motion-tracking experiments attempting to delineate the relative contributions of these factors are likely to be useful, particularly if combined with dimensionality reduction methods.

It was also interesting that stimulation over the pMTG was associated with a reduction in PV for meaningful action imitation, rather than an increase. As we have shown in previous experiments, when participants imitate actions that they think are meaningless, they perform the action with a greater peak acceleration and PV, with the end goal of increasing the correction time available prior to the final hand posture formation. We might reasonably expect that interrupting the activity of an area involved in action recognition could lead participants to take an approach more similar to that of meaningless actions. The current finding suggests that the explicit approach to imitating meaningless actions may be a higher level cognitive strategy, and confirms that the left pMTG is not solely involved in passive recognition of familiar actions, but might be storing functionally useful familiar hand postures (as reflected in defective action on demand following damage to this area).

Lastly, we also observed that thumb PD was significantly lower for meaningful hand gestures following stimulation over the pMTG compared to the vertex. It is unclear what this result reflects, though it may be related with the shifting of the thumb away from gripping the starting point. The thumb is the most independent of the digits (Ingram *et al*., 2008), meaning that the movement of the thumb could also be more variable as the hand forms into a flat shape for a hand gesture. Stimulation over the left pMTG prior to imitation of a meaningful hand action may have reduced participant ability to modulate the speed with which they moved their thumb to join the other digits, thus influencing the thumb deceleration phase.

5.4.3 pMTG stimulation and relative digit velocity

Considering the frequency with which the temporal lobe is associated with semantic information, we were surprised to see that stimulation over the left pMTG significantly reduced mean digit relative PV compared to stimulation over the vertex regardless of action meaning. This result (reduced mean digit relative velocity) is similar to what we observed following left IPL stimulation. One explanation for this is that rTMS also influenced the proposed role of the MTG in providing visual representations of observed action kinematics (Hamilton, 2008).

One possibility, discussed in more detail in the general discussion below, is that by reducing the sensitivity of the MTG to observed low-level kinematics, we also influenced the later higher-level processing of the kinematic information portrayed in that motion. As such, we observed a reduction in participant digit velocity relative to the actor, as if we had directly influenced the kinematic matching potentially performed by the IPL. Similar discussion in neuroimaging (Iacoboni *et al.*, 2001; Molenberghs *et al.*, 2010), and the fact that the IPL and MTG are anatomically connected (Burks *et al.*, 2017), suggests that these ideas are feasible, though more work would need to be done to confirm the presence of a functional connection.

5.4.4 Posterior middle temporal gyrus conclusions

In conclusion, our results strongly support the idea that the left pMTG is involved in the imitation of meaningful gestures, particularly gestures that require the positioning of the hand in relation to other parts of the body. However, more work would need to be done to better clarify whether this reflects meaning-related processing, or postural-related processing that is in turn differentially associated with meaningful and meaningless action.

6 GENERAL DISCUSSION

6.1 Summary

We aimed to see whether meaningful and meaningless action imitation are reflected in different kinematics, and if brain regions commonly associated with imitation distinguish between these action types. By using two-person motion-tracking and non-invasive neurostimulation we revealed the following:

a) Under a moderate time constraint, imitating a meaningless action increases the reaction time to imitate a subsequent action

b) In cases where participants imitate a meaningless action, they increase the speed with which they perform the action (greater peak velocity), and spend a greater period of time in the deceleration phase (longer MT, smaller TPA/MT, TPV/MT, TPD/MT)

c) rTMS over the left inferior parietal lobule reduces mean digit peak velocity relative to the actor for finger gestures, regardless of action meaning

d) rTMS over the left ventral premotor cortex during observation reduces mean digit peak velocity compared to rTMS over the left ventral premotor cortex during imitation

e) rTMS over the left posterior middle temporal gyrus reduces wrist peak velocity during the imitation of meaningless hand gestures

f) rTMS over the left posterior middle temporal gyrus also reduces mean digit peak velocity relative to the actor, regardless of action meaning

g) Proximal effectors (shoulder, elbow) show greater actor-imitator correspondence (as measured by cross-correlation), with longer lag (delay for optimal correlation), during meaningless actions, whilst distal effectors (wrist, digits) show greater actor-imitator correspondence, with longer lag, during meaningful actions (though only in experiment 3)

h) Consistent effects of action effector in experiments 3 and 4 revealed that compared to hand gestures, finger gestures have significantly shorter and slower wrist movements (smaller wrist time to peak acceleration, time to peak velocity, peak velocity, time to peak deceleration, peak deceleration, and MT)

i) Consistent meaning*effector interactions in experiments 3 and 4 also revealed that meaningless hand gestures have a significantly greater peak acceleration than meaningful hand gestures, with no significant difference between meaningful and meaningless finger gestures

j) Hand gestures show a greater actor-imitator correspondence compared to finger gestures

6.2 Characterising the kinematic elements of meaningful and meaningless action imitation

The primary aim of this thesis was to better understand the kinematics of meaningful and meaningless action imitation, and whether brain regions often associated with imitation *in general* play different roles in these two action types. The dual-route model provides the most relevant (though not the only) account for discussing meaningful and meaningless action imitation, suggesting that meaningful actions are imitated using pre-existing action representations based in memory, whilst meaningless actions are imitated through a more resource-intensive approach using visuomotor conversion.

Our results in experiment 1 are strongly supportive of previous claims regarding behavioural evidence for a dual-route approach to action imitation (Tessari & Rumiati, 2004). Namely, since meaningless actions require more cognitive resources to imitate, they slow the onset of performance in subsequent trials (Press & Heyes, 2008). In addition to this, we add to these established findings by showing clear distinctions in the expressed wrist kinematics for meaningful and meaningless actions. We observed consistent effects, throughout each of our experiments, suggesting that during meaningless action imitation, participants increase their wrist velocity in order to maintain a greater correction period in the deceleration phase.

We posit that this increase in velocity reflects a strategy aimed at maximising correction time during meaningless action imitation. One possibility is that, once an observed action is classified as meaningless, this top-down strategy takes hold during action planning. Similar effects may be present for other distinctions between action types. Previous evidence also suggests that there may be changes in kinematics between, for example, competitive and cooperative actions (Georgiou *et al*., 2007), or if an individual is the leader or follower in a joint action task (Sacheli *et al*., 2013). To further develop our understanding of the strategies used in different action types it would be useful to see whether such effects are also present for other distinctions between types, such as transitivity.

Interestingly, experiment 3 also revealed that meaningless actions may be better imitated (as reflected in actor-imitator correspondence) using proximal effectors, whilst meaningful actions are better imitated using distal effectors. Whilst some caution is advised regarding results observed in only one experiment, this particular result does provide an interesting source of discussion. This finding seems to suggest that adherence to observed kinematics might vary not just in relation to the action meaning, but also in relation to the effectors used to perform the action. The shape of the hand for emblematic gestures is likely to be more consistent between individuals, but not necessarily the position the hand is held in for those gestures (defined by the shoulder and elbow joint angles).

We hoped that correction markers (increased meaningless action velocity, movement time, and deceleration phase) and actor-imitator correspondence would be useful variables for examining the role of different brain areas in action imitation. However, these variables were not influenced by TMS over any of our experimental stimulation sites. At the most basic level, the absence of correction marker effects indicates that the left IPL, premotor cortex, or pMTG are not involved in modulating strategies for maximising correction time during imitation. These correction time effects could possibly be modulated by frontal brain regions involved in action and outcome monitoring (Amodio & Frith, 2006). The failure to influence actor-imitator correspondence using TMS is likely due to the fact that, unlike the wide-ranging and permanent lesions observed in patients with apraxia, TMS is not strong enough to influence imitation accuracy.

6.3 Linking the brain, action meaning, and kinematics using non-invasive brain stimulation

Whilst we hoped that our research would allow us to clarify the roles of brain areas commonly associated with imitation, our results instead provide stronger links between imitation kinematics and the brain, rather than action meaning and the brain. In fact, our results from stimulating the left IPL and PMv are generally supportive of previous imitation-general claims for these areas (i.e., Iacoboni, 2009). As such, the contribution of this thesis to our understanding of neural processes underlying imitation is to develop these previous findings by directly linking brain regions to realistic imitative performance.

Considering that damage to the left IPL often results in deficits in meaningless action imitation (Goldenberg, 2009), we were surprised to find that in experiment

2 this region did not distinguish between meaningful and meaningless actions, and instead seemed to play a general role in matching the observed kinematics. This is in keeping with some previous neuroimaging experiments (e.g., Mühlau *et al.*, 2005), but it is worth noting that there are no experiments that we are aware of that have attempted to assess kinematic processing for meaningless and meaningful actions in healthy individuals. Our TMS-induced effects were observed for both the SMG and the AG, though since the SMG is more frequently associated with action observation and execution than the AG (Grèzes & Decety, 2001), it is possible that effects on the AG are reflective of this area being part of a processing route to the SMG. As we suggested in the discussion for that chapter, it is possible then that the left IPL is involved in matching observed kinematics for the purpose of imitation, but for both types of action. Previous distinctions in this area for meaningful and meaningless action imitation may therefore not reflect a semantic split *per se*, but rather distinctions between the relative reliance on kinematic information for meaningful and meaningless actions.

Our suggestions are at odds with other claims that during imitation the IPL may be involved in visuospatial descriptions of one's own body (Chaminade *et al.*, 2005), or coding both visual and motor aspects of the observed action (Iacoboni *et al.*, 1999; Iacoboni, 2009). This is possibly due to the fact that these articles do not directly compare meaningful and meaningless action imitation. Other articles also suggest that IPL activity is increased for learned compared to unfamiliar actions

(Bello *et al*., 2013; Grèzes *et al*., 1999), though the constraints of the approach used in these cases is highlighted below.

Our results are, however, supported by experiments showing that IPL activity is greater for novel versus familiar action imitation (Peigneux *et al*., 2004), that IPL damage is often associated with deficits in kinematic aspects of imitation (Buxbaum *et al*., 2014; Dressing *et al*., 2016), that the IPL shows greater activity for imitation tasks versus observation or control motor tasks (Jack *et al*., 2011; Jackson *et al*., 2006; Mainieri *et al*., 2013), or might be involved in preparatory processes for action execution (Krams *et al*., 1999; Tanaka *et al*., 2001). Supporting articles have generally assessed imitation in a similar way to the work reported here – by directly comparing different types of action (Buxbaum *et al*., 2014; Dressing *et al*., 2016; Mainieri *et al*., 2013; Peigneux *et al*., 2004; Tanaka *et al*., 2001), such that our explanation for the role of the left IPL in imitation would be sufficient in explaining these results. Alternatively, in the previous studies that compared action imitation and observation (Jack *et al*., 2011; Jackson *et al*., 2006), it is possible that the increased IPL activity for imitative tasks is reflective of the IPL generally processing kinematics for the purpose of reaching goal-states (i.e., the observed action), as previously suggested by Buxbaum *et al*. (2014).

Some claims made regarding differing roles of the IPL may reflect their focus on singular action types (e.g., Iacoboni *et al*., 1999; Krams *et al*., 1999; Krüger *et al*., 2014), such that the contrasts used in these studies may not be informative regarding differences between the brain regions supporting the imitation of meaningful and meaningless actions. For example, Iacoboni *et al*., (1999) compared brain activity associated with the observation and imitation of simple finger-tapping movements. In this case, their results cannot inform us of how the IPL might differentially or similarly support meaningful and meaningless action imitation, though their claim that the opercular region of the IPL might be preserving body identity during imitation is still feasible (see also Krüger *et al*., 2014, discussed further below). It is also possible that different effects observed in previous experiments, such as the suggestion that IPL activity is increased for learned versus novel actions are the result of inaccurate action classification. For example, Bello *et al*. (2013) classified precision grips formed with fingers further from the index as unfamiliar, but did not directly assess participants' views on this classification. In our work, we used questionnaires to check the degree of correspondence between our own classification of the action stimuli, and the participants' views. In addition, the actions used by Bello *et al*., (2013) were not in keeping with the emblematic gestures we have used, or the tool related pantomimes tested in apraxia. Alternatively, these disparate findings could reflect different roles of the IPL in imitation.

An area as large as the IPL is unlikely to play a singular role in imitation, and it is important to also consider subregions beyond PF and PG. This might be a feasible explanation for previous articles reporting results that seem to contradict our own

– they may refer to another subregion of the IPL. For example, the suggestion that the parietal operculum may play a role in comparing the copied action with the action that was observed (Krüger *et al*., 2014), which would be a complementary process to the kinematic matching element we have suggested, supports the idea that different parts of the IPL may support different elements of imitation. With further regards to the size of the IPL, it is also important to recognise the limits of fMRI work reporting mean brain activations on standardised brain templates. Since individuals' brains can differ in shape, fine-grained detail regarding the exact anatomically-parcellated regions is likely to be lost if not accounted for when presenting mean brain activation. As such, it would be useful for future fMRI-driven work comparing meaningful and meaningless action imitation to also report individual activations for each participant.

Interestingly, stimulating the left pMTG also resulted in a significant reduction in mean digit relative peak velocity as observed in the IPL. We suggested that such an effect could be the result of interference with MTG processing of low-level observed action kinematics (Hamilton, 2008), thus reducing the integrity of observed kinematic information available to the IPL for matching. The sensitivity of both the IPL and the MTG to observed kinematics (Anat & Miriam, 2016) may support this claim. That the effects on mean digit relative velocity were observed for both hand and finger gestures following temporal lobe stimulation, but only finger gestures following IPL stimulation, may reflect more generalised disruption following stimulation earlier in the kinematic analysis process, or more effective stimulation considering the more online approach taken to stimulating pMTG (compared to the offline approach in our IPL experiment). However, our data do not allow us to directly assess this hypothesis.

We also found that the left PMv did not distinguish between meaningful and meaningless actions. Instead, we found that this area had a general role in hand shaping for the purpose of gesture. This is a novel finding for a region most frequently tested using object-directed designs, and the previous consideration of this function of the PMv as being related to object-directed action (e.g., Vingerhoets *et al*., 2013) is likely to reflect the predominantly object-directed paradigms used for previous experiments. It may be more viable to consider the PMv as being concerned with 'target-directed' rather than object-directed movement, such that the rest of the hand can act as a target for the digits to act upon. This role is unlikely to be imitation-specific, considering the effects of PMv stimulation on our control fine motor task. The fact that the PMv does not seem to be involved in distinguishing between different observed gestures (Hermsdörfer *et al*., 2001) suggests that its role in intransitive action imitation may be specifically movement related.

How might we consider this in light of the fact that the PMv is frequently considered to be part of the putative human mirror neuron system (MNS), which might underlie imitative abilities? We suggest that our results do not discount claims that the PMv has a more specific role to play in imitation, but rather that they suggest that these effects may not be derived from inferior regions of the PMv, such as we have stimulated. For example, an article examining neural adaptation for observed and executed actions in the PMv, a proposed marker for mirror neuron processing, reported activity in a ventral premotor area slightly superior and medial to our stimulated location (Dinstein *et al.*, 2007). As in the IPL, there is more work to do to tease apart how different areas of the PMv do or do not support different elements of imitation, and once again the reporting of individual activity maps for neuroimaging experiments is likely to be highly informative regarding the true gross location of contributing premotor regions.

It seems then that our effects observed following stimulation over the left IPL, PMv, and (possibly) MTG are reflective of imitation-general mechanisms, that is, mechanisms that are not specific for any single type of voluntary imitative action. The frequent reporting of these areas in previous neuroimaging experiments suggests a common need for the apprehension of visual kinematic information (MTG), kinematic matching (IPL), and hand shaping (PMv), during imitation of any type of hand action. Only in experiment 4, in which we stimulated the left pMTG, did we observe any dissociation between meaningful and meaningless action imitation following TMS, supporting previous claims that imitation of meaningful and meaningless actions relies on both common and specific routes (Tessari *et al.*, 2007).

Stimulating the left pMTG was found to reduce the wrist velocity of meaningful hand gestures but not meaningless hand gestures. This is strongly supportive of previous research indicating greater left pMTG activity for meaningful (or familiar) versus meaningless (or novel) actions (Decety *et al*., 1997; Peigneux *et al*., 2004), and supports the claims that the pMTG plays a role in storing action representations for action recognition (Kalénine *et al*., 2010), or perhaps calls on these representations for the purpose of imitation (Buxbaum *et al*., 2014). Evidence from healthy individuals and apraxia patients appears to converge in this aspect, but there is still much to do to understand the fine-grained details of the role of occipitotemporal regions in action processing (Lingnau & Downing, 2015).

It is yet unclear whether our results from stimulating the left pMTG reflect influences on the recognition or performance aspects of action imitation, particularly since lateral occipitotemporal regions may be multi-modal, for observation and performance (Oosterhof *et al*., 2010). In addition, the posterior temporal lobe has been associated with analysis of observed gestures, associating action and meaning, and storing action representations for performance (Peigneux *et al*., 2004). Furthermore, the fact that effects were only observed for hand gestures may reflect the fact that the wrist tracker better captured the postural aspects of hand gestures than the postural aspects of finger gestures (in which the wrist generally had to move a shorter distance).

How then might these brain regions interact? We suggest that the left pMTG is involved in the multi-modal (visual and motor) storage of meaningful postural information, which is used for both the recognition of observed meaningful gestures, and possibly calling upon these postural relationships for action execution. Imitating dynamic gestures requires apprehension of their kinematics, which is also subserved by the MTG. This information is further processed in the left IPL in order to generate motor codes that match the observed kinematics in scenarios where it is deemed necessary. Decisions regarding the necessity to match kinematics could be assessed through top-down cognitive measures (Amodio & Frith, 2006; Hamilton, 2014), not examined in this thesis. Finally, the PMv modulates the formation of digit positions in relation to their targets (i.e., other parts of the hand in our intransitive gestures). In support of these claims, there is strong evidence that the MTG is functionally connected to the IPL (Ramayya *et al.*, 2010; Seghier *et al.*, 2013; Xu *et al.*, 2015), and that the IPL is functionally connected to the PMv (Mars *et al.*, 2011; Tomassini *et al.*, 2007; Vingerhoets & Clauwaert *et al.*, 2015).

Our description of suggested functions above implies that distinctions between meaningful and meaningless action imitation arise at both the semantic and kinematic levels. The failure to recognise an observed action is likely to be informative regarding the need to use the kinematic information portrayed in that action. That is, meaningless actions necessitate heavier reliance on the observed kinematics. We must emphasise again, however, that these functions are unlikely to be specific to imitation. The role of the pMTG in action recognition is well established (Kalénine *et al.*, 2010), whilst the IPL is frequently associated with action observation (Caspers *et al.*, 2010). In particular, kinematic analysis in the IPL may also be useful for understanding the actions of others (Becchio *et al.*, 2012), possibly through putative mirror neuron mechanisms.

6.4 Implications for models of imitation

There is some scope for linking the results of this thesis to cognitive models of imitation mentioned in the general introduction. Considering that the dual-route model of imitation provides the most coherent explanation of the way in which we have considered action type (meaningful versus meaningless), it is notable that we have some evidence suggesting both common (IPL, PMv) and distinct (pMTG) brain areas responsible for meaningful and meaningless action imitation. However, we must also consider the fact that other models also suggest distinctions between action types. For example, our results distinctly argue against the MIM hypothesis (Subiaul, 2010), which states that familiar and novel imitation are subserved by dissociable routes. In particular, we found that the processing of kinematics for action in the IPL was common to both meaningful and meaningless action imitation.

Our results do not provide much evidence for or against the GOADI model, which suggests that imitation is achieved by decomposing observed actions into a hierarchy of goals. However, our experiments were not strongly designed to test the difference between goal-directed and non-goal-directed actions. A better approach may be to examine how different brain regions do or do not influence the integration of superfluous goals during object-directed imitation, as Bekkering *et al*., (2005) have done with apraxia patients. However, we are not convinced that any of the brain regions studied in this thesis are suitable targets for such a study. In fact, the failure of apraxia patients to integrate superfluous goals into action imitation may be a more generalised effect of working memory deficits, rather than evidence that imitation is specifically goal-directed (see e.g., Tessari *et al*., 2007).

Since our experiments did not assess the development of imitative capacity, we can comment little on the AIM and ASL models. However, as highlighted above, our results appear to provide support for consistent and dissociable processes underlying the imitation of meaningful and meaningless actions. Can such processes be considered as derivations of a generalised visuomotor stream (Hamilton, 2015), in which action imitation is similar to any other voluntary movement? Our results are broadly supportive of this claim. Our suggestions that the IPL has a role in matching the kinematic task demands of an action, and that the PMv has a general role in hand shaping for gesture, are unlikely to be specific to imitation. Certainly, more work will be needed to better test these hypotheses, in both social and individual scenarios. There is huge scope for further examining the numerous distinctions that can be made between different action types in imitation, and their associated brain regions.

6.5 Why velocity?

Most of our TMS-related effects were observed in velocity, either across the time-series (as in our t-statistic plots) or in peak velocity. We rarely found that TMS influenced acceleration or deceleration. Considering our exploratory approach, it is necessary to consider why this might be the case. Could we make the same conclusions if our TMS-related effects had been observed in peak acceleration or peak deceleration?

To reiterate the meaning of each of these variables, velocity is the first differential of the position data, and acceleration is the second. The peak velocity is the maximum velocity at any point of the movement, the peak acceleration is the greatest increase in velocity at any point of the movement, and the peak deceleration is the greatest decrease in velocity at any point of the movement. The reduction in (absolute or relative) peak velocity reported in our TMS experiments then reflects a reduction in the *maximum velocity* with which participants were performing the action (and possibly a reduction in velocity in general, as reflected over time in our t-statistic plots). What does this actually mean in terms of motor control?

Whilst acceleration is not strongly represented in M1, M1 does seem to be particularly sensitive to target direction, and hand position and velocity for desired actions (Ashe & Georgopoulos, 1994; Paninski *et al.*, 2004). We suggest that a reduction in velocity (which is possibly controlled by M1 prior to action) following stimulation over our target brain regions may reflect poorer apprehension of the desired action demands. That is, by reducing the strength of processing for either kinematic matching (IPL), hand shaping (PMv), or action recognition or recall (pMTG), the intensity of processing for motor output could also be reduced. Further work using paired-pulse or dual-coil TMS would be necessary to confirm the existence of this postulated mechanism.

6.6 Disentangling meaning and effector-specificity

In experiment 2 it appeared that hand gestures were biasing our correlation-based measure of actor-imitator correspondence for the hand, since the wrist and all digits tended to move together for hand gestures (i.e., “salute”). We better accounted for this by using the gesture type as a two-level factor (hand gesture, finger gesture) in our following analyses. This revealed some interesting results in experiments 3 and 4.

Firstly, hand gestures showed significantly better actor-imitator correspondence compared to finger gestures. This is unsurprising, since as mentioned in section 3.4.5, copying the movement of the hand as a whole is possibly easier than distinguishing between each of the digits. In addition, compared to hand gestures, finger gestures have a significantly smaller wrist time to peak acceleration, time to peak velocity, peak velocity, time to peak deceleration, peak deceleration, and movement time. The numerous differences between these two action types confirm that the wrist tracker may be more representative of hand than finger gestures.

Finally, we found that meaningless hand gestures have a significantly greater peak acceleration than meaningful hand gestures, with no significant difference between meaningful and meaningless finger gestures. This possibly indicates that the increase in wrist acceleration associated with meaningless action performance (in experiment 1 and 2) is confined to hand gestures. The increase in acceleration in order to ensure adequate correction time may be more important when the hand has to travel a greater distance. However, it appears that the increased velocity in both meaningless hand and finger gestures is still important for ensuring adequate correction time, since a similar effect was not shown for peak velocity.

6.7 Limitations

As with all new experimental approaches, our work has limitations. Here we provide a brief overview of some of the potential problems in the reported experiments, and what might be done to counteract them.

6.7.1 Action differences and generalisability

One of the main issues with our wrist kinematic approach for preliminary analysis is the fact that the wrist tracker seems to better account for hand gestures than finger gestures. Whilst this is accounted for in our actor-imitator correspondence analysis and t-statistic plotting, it confirms the potential difference in requirements for hand and finger gestures. As noted previously (Goldenberg, 2001), whilst hand gestures are more reliant on spatial positioning of the arm and hand in relation to other parts of the body, finger gestures are more reliant on serial positioning of the digits which are visually similar.

These two types of action are likely to call upon different processing routes. This adds further complexity to the semantic split which we have generally used to consider action types, and our approach in the above experiments seems better for analysing kinematic rather than postural elements of imitation. Perhaps the most obvious example of this is the fact that we observed effects of left pMTG stimulation on wrist velocity in meaningful hand, but not meaningful finger gestures. One possibility is that the postural information potentially represented in the pMTG is more relevant for the broader hand-arm-body spatial relationships present for hand gestures. The other possibility is that the postural aspects of the finger gestures (i.e., their end points) were not adequately accounted for in our other analysis routines, and the association of the left pMTG with postural elements of tool-related gestures (Buxbaum *et al*., 2014) supports this.

The end point positions of the digits for finger gestures are likely to be difficult to quantify, considering that this may encompass at least 15 positional degrees of freedom (5 digits * 3 axes, exclusive of digit joint angles). This may be an advantage of the subjective rating assessments that have been used for previous imitation research (e.g., Buxbaum *et al*., 2014; Tessari & Rumiati, 2004). Whilst our work has been successful in developing more objective measures for assessing action imitation, an experiment to develop objective analyses that can be related to these subjective assessments is likely to be useful for future work.

Another problem touched on briefly in previous discussion chapters is our choice of emblematic gestures rather than action pantomimes (as are frequently used to test for apraxia). The main factor driving this decision was that the dynamic nature of action pantomimes (e.g., pretending to use a hammer) means that they do not conform to a single bell-shaped velocity profile, making it harder to extract the standard peak kinematic parameters. Whilst this may make it more difficult to link our findings to previous work, due to the object-directedness implied by their stimuli, our considerations of action types in terms of meaning remain sound.

One further possible confound, in addition to those discussed above, is that action familiarity may have had an influence on the results of our experiments. For example, actions in our experiments that were designed to be meaningless may nonetheless have *become more familiar* as time went on. It is unclear to what degree this would have influenced participant performance, but it is certainly feasible that performance of these actions would have moved closer to the accuracy expected in meaningful actions over time. Whilst our use (in experiments 2-4) of more meaningless than meaningful gestures was designed to try to avoid this issue, this factor was not accounted for in our analysis. In future work it might be beneficial to examine how imitation kinematics vary as actions become more familiar, and how this may or may not link to the classic dual-route model of imitation.

Each of the above points relate to more general concerns regarding the generalisability of our stimuli. The sheer variety of action types that humans can imitate means that assessing the differences between each of these action types is difficult. However, as emphasised previously, very little work has been done to compare imitative performance for different action types in an objective fashion. It seems then that much more could be done in order to generalise beyond our stimulus set, and testing different types of actions with methods similar to those outlined in this thesis may help in that regard. This may be easier to do with intransitive actions, since they may provide better opportunities for matching (e.g., Bello *et al*., 2013), but the functional nature of object-directed movement may make matching with intransitive gestures more difficult (but see e.g., Bonivento *et al*., 2014 and Carmo & Rumiati, 2009 for examples in the absence of objects).

6.7.2 Sample size, power, and reproducibility

Possible issues that our work shares with many other studies reported in social or cognitive neuroscience are that of sample size, power, and reproducibility. Whilst a number of behavioural effects discovered in experiment 1A are replicated throughout this thesis, more work would be necessary to confirm the neuroscientific claims made regarding our rTMS results. Though our sample size was quite normal for TMS experiments, and necessary considering the relatively long testing time for our two-person paradigm, and the need to minimise the potential risks of TMS, it is worth noting that some experiments had much greater (post-hoc) power than others. For example, the significant difference in wrist velocity for meaningful hand gestures between stimulation over the pMTG and the vertex had an effect size (Hedges' g_{rm}) of 0.497, or a dz of 1.20. For a paired two-tailed t-test at an alpha of .05, the post-hoc power in this instance was .964. By contrast, the significant comparison of mean digit PV between stimulation over the PMv during imitation or observation showed a Hedges' g_{rm} of 0.149, or a dz of 0.666. The post-hoc power in this instance is only 0.557. This suggests that the influence of TMS on movement in imitation may be highly variable, depending on the brain region stimulated or the variable assessed. It also suggests that some results must be more cautiously interpreted than others.

In relation to this, we are strongly supportive of further experiments designed to assess the claims made in this thesis in a more hypothesis-driven fashion. The exploratory nature of these experiments ensured that we could assess imitation in a novel and naturalistic fashion, but exploratory approaches greatly benefit from confirmatory research. This could be done with a less complicated experimental setup, with fewer variables. For example, in order to confirm the claim that the left

PMv has a general role in hand shaping, an experiment focussing on motion-tracking the finger-thumb opposition task in a single participant, following rTMS over this area or an active control site (perhaps in the other hemisphere), would be sufficient.

6.7.3 Analytical and methodological limitations

A key issue in our assessment of imitation kinematics is the number of variables used for analysis, and the possible issues that these many multiple comparisons could cause. For ANOVAs assessing individual trackers we used an alpha value of .05 divided by the number (8) of trackers (0.0063). Despite this more stringent approach, a number of consistent effects were observed with this conservative alpha value. A similar approach for 10 or more kinematic parameters may have been too conservative, however. Instead, we focussed on the consistent effects of action meaning on correction time observed in experiments 1A-C. The kinematic variables reflecting these differences in correction time were then examined for stimulation-related effects in later TMS experiments.

One approach that might have been useful in this case was to use a dimensionality reduction method such as independent component analysis. Dimensionality reduction methods have been highly useful for decomposing hand movements into the minimum number of variable parameters (e.g., Ingram *et al*., 2008). However, such approaches would have drastically increased our analysis time and the computational power required for our analyses. In addition, whilst dimensionality reduction is well suited for stereotyped actions like reaching-to-grasp, the multiple different action types used in our experiments may have made decomposition, and comparison between participants and conditions, much more difficult.

It is also important to emphasise the claims that can and cannot be made with our combined TMS and two-person motion-tracking approach. Whilst we are confident that this approach allows greater association of brain regions with behaviour, there are general concerns regarding the use of TMS that must be considered. Though our neuronavigated approach provides greater certainty regarding the areas stimulated compared to a statistical coordinate-driven or scalp measurement-based approach, stimulation of other areas is still possible. Furthermore, it is unclear to what degree the effects of TMS might represent changes in excitation or inhibition of areas connected to the stimulated region. As such, strong conclusions regarding the exact contribution of the stimulated area *in relation to other areas*, cannot easily be assessed.

6.8 Future directions

Our novel approaches to examining action imitation, along with our interesting findings, have helped develop our understanding of this fascinating and varied social skill. However, we believe that there is still much work to be done to better understand the kinematic and neural aspects of imitation.

6.8.1 Naturalistic neuroscience-driven approaches to imitation

In our neurostimulation experiments we attempted to develop more ecologically valid approaches to action imitation by using two-person motion-tracking designs that allowed participants to use their entire arm and hand to copy a confederate actor. Our experiments confirm the viability of this approach for social interaction research. As we have discussed in previous work (Reader & Holmes, 2016), such approaches are necessary to fully comprehend social interaction as a dynamic phenomenon, and we are pleased to add to the growing number of experiments using naturalistic approaches to examining social interaction.

TMS appears to be a particularly useful tool for examining the brain bases of realistic social interaction, since it allows freedom of movement, which is hard to do in a scanning environment, and can provide a more robust cause-and-effect relationship between brain and behaviour. We strongly support the further use of neuronavigated neurostimulation for the purpose of better linking imitation deficits and imitation in healthy individuals. In particular, paired pulse or dual coil approaches may help develop our understanding of the connectivity between regions in the imitation network.

Beyond this, ecologically valid examinations of social interaction may also need to consider factors beyond the specific phenomena of interest (i.e., imitation). For example, gaze has been found to be an important element of social interaction (Reader & Holmes, 2016), but it is not accounted for in our two-person experiments. In order to better integrate the complexity of realistic social interactions into experimental design, it may be necessary to first develop stronger theoretical models regarding the contribution of different social cognitive elements.

6.8.2 Distinguishing between action types

A consistent theme in this work has been distinguishing actions in semantic terms (meaningful, meaningless). However, this is just one way in which we can consider action. We suggest more frequent attempts to distinguish action types for the purpose of imitation, since in this way we can better understand the relative reliance of imitative performance on different aspects of the observed action.

As an example, a great deal of work has been done regarding the imitation of actions with and without goals (Leighton *et al.*, 2010). Similar to our consideration of action in terms of meaning, goal-directed action imitation may be more reliant on performing the end point of the action, whilst the imitation of actions without goals may be more reliant on kinematic matching (Gowen, 2012). The reliance of imitation on goal-related information is likely to be closely related to action meaning, though emblematic gestures such as ours are likely to transcend this relationship, since emblematic gestures do not necessarily involve objects that can provide contextual information. Similarly, this idea can be linked to discussions of action imitation in terms of transitivity.

Further complexity is introduced if we then begin to consider action in terms of its postural and kinematic features (e.g., Buxbaum *et al*., 2014), or levels of abstraction (e.g., Wurm & Lingau, 2015). As a whole, this suggests that there is still much to be done to understand the commonalities and differences across action types. Our pMTG experiment provides some contribution towards unifying action types, suggesting interactions in this area between action meaning and action effector. Attempts to bridge different theoretical approaches towards action imitation, such as in terms of goals (Bekkering *et al*., 2000), meaning (Rumiati & Tessari, 2002), or effectors (Goldenberg, 2001), are essential. Whilst some have begun to bring these different theoretical frameworks together (e.g., Subiaul, 2010), experiments directly comparing these approaches will be useful.

6.8.3 Methodology

Finally, we hope that the experimental and analytical methods presented here provide a stepping stone for new approaches to imitation. There is much to build on beyond the work we have presented. For example, dimensionality reduction techniques or machine learning may be useful for developing more accurate measures of actor-imitator correspondence. Our correlation-based approach, whilst useful, only provides information regarding single trackers as opposed to the entire action. The variability between different emblematic gestures (and their individual performance) is likely to make dimensionality reduction more difficult than similar analysis in functional actions like reaching and grasping (e.g., Blanchard *et al.*, 2017; Ingram *et al.*, 2008; Naish *et al.*, 2013). However, objective assessments of imitation accuracy will not only improve our understanding of this phenomenon, but may also provide objective assessment tools for neuropsychologists for disorders such as apraxia.

Furthermore, virtual characters may be useful for creating more consistent imitation stimuli whilst maintaining ecological validity. As observed in experiment 2, it is possible for a confederate actor to show biases in their movements. The growing trend to integrate virtual reality into social neuroscience research (Parsons *et al.*, 2017) is a positive one.

6.9 Conclusions

We used motion-tracking and TMS in two-person experiments in order to better understand the kinematics and brain areas associated with meaningful and meaningless action imitation. We found that imitating meaningless actions increased the reaction time for performing a subsequent action, supportive of previous behavioural evidence for dual-route processing of meaningless and meaningful action imitation. In addition, we discovered that the hallmark of meaningless action imitation is a strategy designed to maximise correction time.

Using TMS and two-person motion-tracking experiments, we confirmed the general roles of the left IPL and PMv in imitation, which appear to be involved in kinematic matching and hand shaping respectively. We also found that the left pMTG is specifically involved in meaningful action imitation.

Overall, these findings are suggestive of both action-general and action-specific processes underlying different types of imitation. Importantly, it also indicates that different action-types can overlap on a number of different features, and their reliance on different features of observed action may be contextual.

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8 SUPPLEMENTAL MATERIAL

S3-1: MEAN VALUES, MAIN EFFECTS, AND INTERACTIONS FOR ACTOR-IMITATOR CORRELATIONS (Z-VALUES) IN HAND GESTURES

Significant p-values (<.025) are in bold; SH: shoulder, EL: elbow, WR: wrist, TH: thumb, IN: index finger, MI: middle finger, RI: ring finger, LI: little finger.

Tracker	Mean(±SE) Z-value					Main effect						Site*meaning interaction		
	Site			Meaning										
						Site			Meaning			F (2, 22)	p	η^2
	SMG	AG	no-rTMS	MF	ML	F (2, 22)	p	η^2	F (1, 11)	p	η^2			
SH	0.504 (0.0725)	0.485 (0.0687)	0.525 (0.0534)	0.388 (0.0514)	0.622 (0.0669)	0.243	.787	.022	39.2	**<.001**	.781	2.84	.080	.205
EL	0.906 (0.0930)	0.860 (0.0989)	0.918 (0.0708)	0.753 (0.0862)	1.04 (0.0679)	0.253	.779	.022	28.8	**<.001**	.723	1.48	.250	.118
WR	1.54 (0.0833)	1.57 (0.0740)	1.50 (0.0673)	1.54 (0.0658)	1.53 (0.0822)	1.07	.359	.089	0.051	.826	.005	0.256	.777	.023
TH	1.54 (0.0760)	1.53 (0.0835)	1.52 (0.0646)	1.53 (0.0730)	1.53 (0.0708)	0.076	.927	.007	0.002	.966	<.001	0.905	.419	.076
IN	1.48 (0.0861)	1.50 (0.0772)	1.49 (0.0650)	1.48 (0.0766)	1.50 (0.0686)	0.045	.956	.004	0.263	.618	.023	0.696	.509	.060
MI	1.53 (0.0845)	1.52 (0.0744)	1.52 (0.0615)	1.51 (0.0750)	1.54 (0.0638)	0.004	.997	<.001	0.322	.582	.028	0.698	.508	.060
RI	1.53 (0.0830)	1.52 (0.0738)	1.52 (0.0616)	1.51 (0.0743)	1.53 (0.0621)	0.027	.974	.002	0.173	.685	.015	0.694	.510	.059
LI	1.52 (0.0854)	1.52 (0.0749)	1.52 (0.0624)	1.52 (0.0769)	1.52 (0.0648)	0.011	.989	.001	0.014	.909	.001	0.620	.547	.053

S3-2: MEAN VALUES, MAIN EFFECTS, AND INTERACTIONS FOR ACTOR-IMITATOR CORRELATIONS (Z-VALUES) IN FINGER GESTURES

Significant p-values (<.025) are in bold; SH: shoulder, EL: elbow, WR: wrist, TH: thumb, IN: index finger, MI: middle finger, RI: ring finger, LI: little finger.

Tracker	Mean(±SE) Z-value					Main effect						Site*meaning interaction		
	Site			Meaning		Site			Meaning			F (2, 22)	p	η^2
	SMG	AG	no-rTMS	MF	ML	F (2, 22)	p	η^2	F (1, 11)	p	η^2			
SH	0.122 (0.0328)	0.119 (0.0398)	0.112 (0.0280)	0.0486 (0.0309)	0.187 (0.0277)	0.040	.961	.004	37.1	**<.001**	.771	0.099	.906	.009
EL	0.460 (0.0845)	0.492 (0.112)	0.359 (0.0683)	0.386 (0.0791)	0.488 (0.0710)	1.14	.337	.094	6.54	.027	.373	2.03	.155	.156
WR	1.30 (0.0786)	1.34 (0.0603)	1.21 (0.0633)	1.31 (0.0594)	1.25 (0.0694)	3.19	.061	.225	1.95	.190	.151	1.33	.285	.108
TH	1.27 (0.0538)	1.31 (0.0671)	1.20 (0.0553)	1.30 (0.0614)	1.23 (0.0469)	2.18	.137	.165	2.27	.160	.171	0.045	.956	.004
IN	1.18 (0.0563)	1.24 (0.0701)	1.14 (0.0610)	1.20 (0.0654)	1.17 (0.0495)	1.53	.239	.122	.579	.463	.050	0.739	.489	.063
MI	1.22 (0.0521)	1.31 (0.0516)	1.19 (0.0513)	1.28 (0.0507)	1.20 (0.0403)	2.85	.079	.206	3.43	.091	.238	.088	.916	.008
RI	1.25 (0.0604)	1.31 (0.0511)	1.19 (0.0506)	1.27 (0.0540)	1.23 (0.0414)	2.77	.085	.201	1.17	.303	.096	0.594	.561	.051
LI	1.23 (0.0576)	1.31 (0.0595)	1.18 (0.0487)	1.28 (0.0536)	1.20 (0.0421)	2.90	.076	.208	6.45	.028	.370	0.772	.474	.066

S4-1: TWO-WAY INTERACTIONS FOR WRIST KINEMATIC VARIABLES

Significant p-values are in bold.

Variable	Site*time			Site*meaning				Site*effector				Time*meaning			Time*effector			Meaning* effector		
	F (2, 22)	p	η^2	F	df	p	η^2	F	df	p	η^2	F (1, 11)	p	η^2	F (1, 11)	p	η^2	F (1, 11)	p	η^2
MO	10.3	**.001**	.485	0.710	2, 22	.502	.061	0.134	2, 22	.876	.012	0.171	.687	.015	0.024	.879	.002	1.45	.255	.116
TPA	1.93	.169	.149	2.07	2, 22	.150	.158	0.945	1.3, 14	.404	.079	0.019	.893	.002	0.208	.657	.019	0.024	.880	.002
TPA/ MT	3.63	**.043**	.248	1.24	2, 22	.309	.101	0.500	2, 22	.614	.043	0.109	.747	.010	0.485	.501	.042	2.93	.115	.210
PA	1.69	.207	.133	0.159	1.3, 15	.773	.014	0.353	2, 22	.706	.031	1.17	.302	.096	3.51	.088	.242	11.1	**.007**	.503
TPV	1.07	.361	.088	0.488	2, 22	.621	.042	1.21	2, 22	.319	.099	<.001	.999	<.001	5.40	**.040**	.329	4.10	.068	.272
TPV/ MT	0.217	.807	.019	0.314	2, 22	.734	.028	1.96	2, 22	.164	.151	0.016	.901	.001	0.834	.381	.070	2.14	.172	.163
PV	2.41	.113	.180	0.164	1.3, 15	.763	.015	1.82	2, 22	.186	.142	3.49	.089	.241	0.443	.519	.039	19.1	**.001**	.634
TPD	2.88	.078	.207	0.733	1.3, 14	.440	.062	0.278	2, 22	.760	.025	0.218	.649	.019	0.435	.523	.038	8.49	**.014**	.436
TPD/ MT	0.834	.448	.070	0.956	2, 22	.400	.080	0.046	2, 22	.955	.004	0.277	.609	.025	0.206	.659	.018	0.570	.466	.049
PD	6.49	**.006**	.371	0.018	2, 22	.983	.002	1.46	2. 22	.254	.117	0.092	.768	.008	0.045	.837	.004	10.1	**.009**	.478
MT	1.78	.193	.139	0.126	2, 22	.882	.011	0.476	2, 22	.627	.042	0.071	.795	.006	0.157	.699	.014	16.6	**.002**	.602

S4-2: THREE- AND FOUR-WAY INTERACTIONS FOR WRIST KINEMATIC VARIABLES

Significant p-values are in bold.

Variable	Site*time*meaning				Site*time*effector			Site*meaning*effector			Time*meaning*effector			Site*time*meaning*effector			
	F	df	p	η^2	F (2, 22)	p	η^2	F (2, 22)	p	η^2	F (1, 11)	p	η^2	F	df	p	η^2
MO	0.416	1.28, 14.1	.579	.036	0.82	.452	.070	2.04	.154	.157	0.742	.407	.063	0.037	2, 22	.964	.003
TPA	0.263	2, 22	.771	.023	0.336	.718	.030	1.27	.300	.104	1.25	.287	.102	0.247	2, 22	.784	.022
TPA/MT	0.528	2, 22	.597	.046	0.344	.713	.030	1.63	.220	.129	4.64	.054	.296	0.275	2, 22	.762	.024
PA	1.07	2, 22	.362	.088	2.28	.125	.172	0.264	.771	.023	0.011	.919	.001	1.01	2, 22	.328	.084
TPV	0.530	2, 22	.596	.046	0.089	.916	.008	0.178	.838	.016	1.64	.227	.130	0.249	2, 22	.789	.022
TPV/MT	0.825	2, 22	.451	.070	0.131	.878	.012	2.24	.131	.169	14.20	**.003**	.563	0.326	2, 22	.725	.029
PV	2.26	2, 22	.128	.171	0.539	.591	.047	0.022	.979	.002	0.038	.849	.003	1.46	1.36, 14.9	.255	.117
TPD	2.48	2, 22	.107	.184	0.591	.562	.051	0.110	.896	.010	0.011	.919	.001	0.653	2, 22	.530	.056
TPD/MT	0.487	2, 22	.621	.042	0.266	.769	.024	1.67	.211	.132	1.84	.202	.144	0.359	2, 22	.702	.032
PD	0.242	2, 22	.787	.022	1.46	.253	.117	0.449	.644	.039	4.85	**.050**	.306	0.592	2, 22	.562	.051
MT	1.73	2, 22	.201	.136	0.554	.582	.048	0.850	.441	.072	17.44	**.002**	.613	0.909	2, 22	.417	.076

S4-3: TWO-WAY INTERACTIONS FOR MAX Z-VALUE

SH: shoulder, EL: elbow, WR: wrist, TH: thumb, IN: index finger, MI: middle finger, RI: ring finger, LI: little finger.

Tra-cker	Site* time				Site* meaning				Site* effector			Time* meaning			Time* effector			Meaning* effector		
	F	df	p	η^2	F	df	p	η^2	F (2, 22)	p	η^2	F (1, 11)	p	η^2	F (1, 11)	p	η^2	F (1, 11)	p	η^2
SH	0.179	2, 22	.838	.016	0.016	2, 22	.985	.001	0.072	.931	.006	0.269	.614	.024	1.86	.200	.144	3.56	.086	.244
EL	1.02	2, 22	.377	.085	1.56	2, 22	.232	.124	0.909	.418	.076	1.07	.323	.089	1.35	.270	.109	1.36	.268	.110
WR	0.369	2, 22	.696	.032	1.35	2, 22	.281	.109	1.26	.303	.103	1.71	.218	.134	0.158	.698	.014	0.159	.697	.014
TH	1.41	2, 22	.265	.114	0.011	1.36, 14.9	.962	.001	0.004	.996	<.001	1.02	.335	.085	0.075	.790	.007	1.19	.298	.098
IN	0.296	2, 22	.747	.026	0.072	1.10, 12.1	.817	.006	0.046	.955	.004	0.475	.505	.041	0.124	.732	.011	0.253	.625	.023
MI	0.081	2, 22	.922	.007	0.190	2, 22	.829	.017	0.494	.617	.043	3.09	.107	.219	0.004	.949	<.001	3.91	.073	.262
RI	0.170	1.2, 12.7	.723	.015	0.221	1.19, 13.1	.687	.020	0.047	.954	.004	1.60	.232	.127	0.002	.962	<.001	1.17	.302	.096
LI	1.57	2, 22	.230	.125	0.110	1.17, 12.8	.784	.010	0.071	.932	.006	3.49	.089	.241	2.25	.162	.170	6.85	.024	.384

S4-4: THREE- AND FOUR-WAY INTERACTIONS FOR MAX Z-VALUE

SH: shoulder, EL: elbow, WR: wrist, TH: thumb, IN: index finger, MI: middle finger, RI: ring finger, LI: little finger.

Tracker	Site*time* meaning			Site*time* effector			Site*meaning* effector			Time*meaning* effector			Site*time* meaning*effector		
	F (2, 22)	p	η^2	F (2, 22)	p	η^2	F (2, 22)	p	η^2	F (1, 11)	p	η^2	F (2, 22)	p	η^2
SH	1.03	.375	.085	0.654	.530	.056	0.636	.539	.055	3.06	.108	.218	1.57	.231	.125
EL	0.776	.472	.066	0.481	.624	.042	0.152	.860	.014	4.70	.053	.300	0.878	.430	.074
WR	1.50	.245	.120	0.345	.712	.030	1.30	.293	.106	0.068	.799	.006	0.104	.901	.009
TH	0.681	.516	.058	0.087	.917	.008	0.113	.894	.010	8.51	.014	.436	1.00	.384	.083
IN	0.697	.509	.060	0.251	.780	.022	1.18	.326	.097	4.70	.053	.299	2.90	.076	.209
MI	1.62	.221	.128	0.849	.441	.072	0.605	.555	.052	0.566	.468	.049	0.078	.925	.007
RI	1.15	.334	.095	0.472	.630	.041	0.524	.599	.045	3.18	.102	.224	0.317	.028	.633
LI	0.820	.453	.069	0.068	.934	.006	0.534	.594	.046	0.668	.431	.057	0.463	.635	.040

S4-5: TWO-WAY INTERACTIONS FOR LAG AT MAX Z-VALUE

Significant p-values (<.0063) are in bold; SH: shoulder, EL: elbow, WR: wrist, TH: thumb, IN: index finger, MI: middle finger, RI: ring finger, LI: little finger.

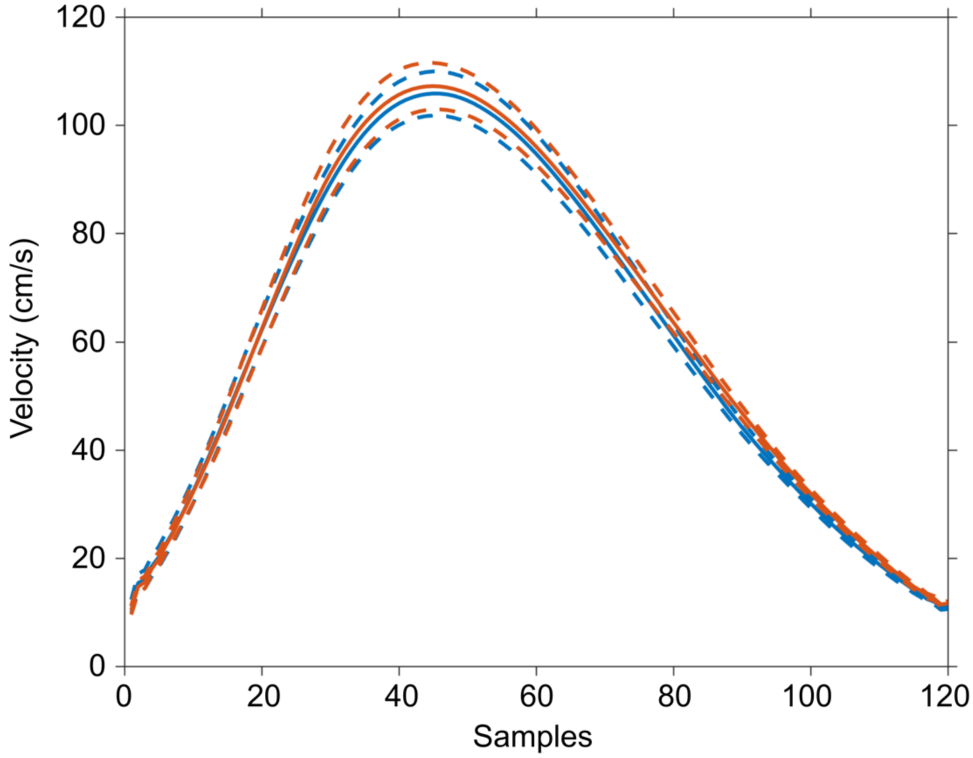
Tracker	Site* time			Site* meaning			Site* effector			Time* meaning			Time* effector			Meaning* effector		
	F (2, 22)	p	η^2	F (2, 22)	p	η^2	F (2, 22)	p	η^2	F (1, 11)	p	η^2	F (1, 11)	p	η^2	F (1, 11)	p	η^2
SH	0.863	.463	.073	0.086	.918	.008	1.89	.175	.146	0.551	.474	.048	0.011	.919	.001	12.1	**.005**	.534
EL	1.89	.175	.146	0.44	.647	.039	1.32	.288	.107	3.15	.104	.223	0.006	.939	.001	0.730	.411	.062
WR	0.335	.719	.030	0.165	.849	.015	0.442	.649	.039	0.235	.638	.021	2.91	.116	.209	0.065	.804	.006
TH	0.286	.754	.025	1.11	.347	.092	1.23	.312	.101	0.515	.488	.045	0.160	.697	.014	1.22	.293	.100
IN	1.97	.163	.152	2.42	.112	.180	0.397	.677	.035	0.138	.717	.012	0.426	.527	.037	1.13	.310	.093
MI	0.291	.751	.026	2.16	.139	.164	0.215	.808	.019	0.048	.830	.004	0.220	.663	.018	0.301	.594	.027
RI	1.83	.184	.142	2.37	.117	.177	0.065	.937	.006	0.028	.871	.003	0.121	.734	.011	0.621	.447	.053
LI	1.19	.322	.098	1.72	.203	.135	0.011	.989	.001	0.684	.426	.059	1.32	.275	.107	0.630	.444	.054

S4-6: THREE- AND FOUR-WAY INTERACTIONS FOR LAG AT MAX Z-VALUE

SH: shoulder, EL: elbow, WR: wrist, TH: thumb, IN: index finger, MI: middle finger, RI: ring finger, LI: little finger.

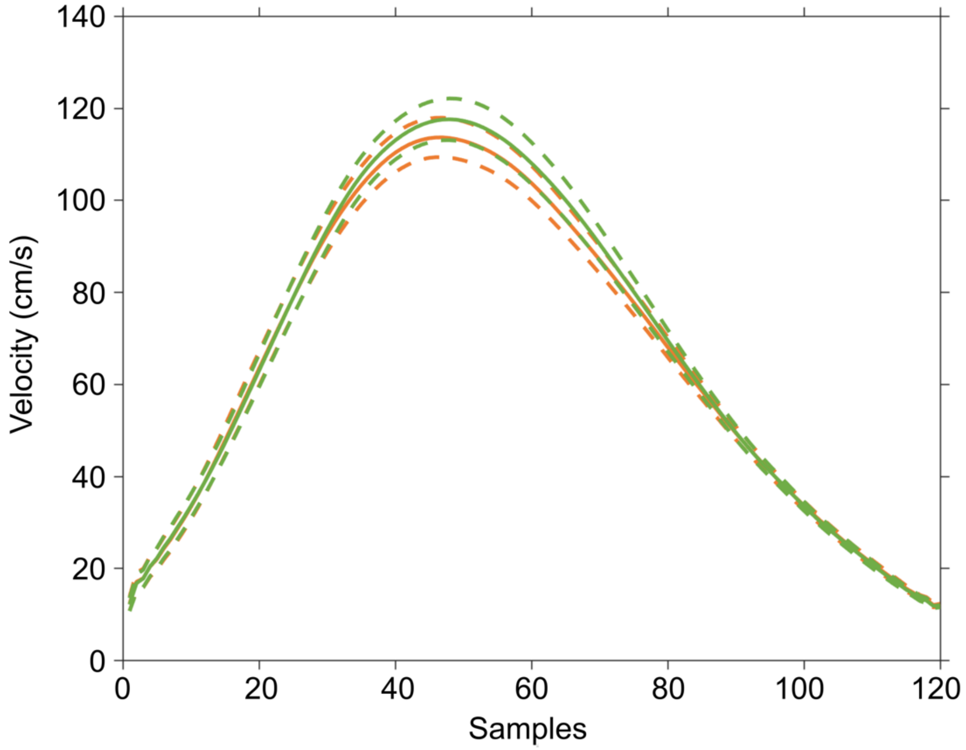
Tracker	Site*time*meaning			Site*time*effector			Site*meaning*effector				Time*meaning*effector			Site*time*meaning*effector		
	F (2, 22)	p	η^2	F (2, 22)	p	η^2	F	df	p	η^2	F (1, 11)	p	η^2	F (2, 22)	p	η^2
SH	1.72	.202	.135	0.182	.835	.016	0.821	1.35, 14.8	.414	.069	4.31	.062	.282	0.551	.584	.048
EL	0.468	.633	.041	4.55	.022	.293	0.621	2, 22	.547	.053	0.179	.680	.016	0.836	.447	.071
WR	2.30	.124	.173	0.800	.462	.068	1.34	2, 22	.283	.109	0.567	.467	.049	1.78	.192	.139
TH	1.97	.164	.152	0.115	.892	.010	0.626	2, 22	.544	.054	0.002	.961	<.001	4.62	.021	.296
IN	0.506	.610	.044	0.277	.761	.025	0.429	2, 22	.656	.038	0.481	.502	.042	3.11	.065	.220
MI	0.312	.735	.028	0.311	.736	.028	0.440	2, 22	.650	.038	0.212	.654	.019	4.32	.026	.282
RI	1.34	.282	.109	0.578	.569	.050	0.471	2, 22	.631	.041	0.028	.870	.003	5.58	.011	.337
LI	2.80	.083	.203	0.131	.878	.012	0.733	2, 22	.492	.062	0.826	.383	.070	3.36	.053	.234

S4-7: RESAMPLED MEAN VELOCITY CURVE FOR THE IMITATOR THUMB COMPARING PMV AND PMD



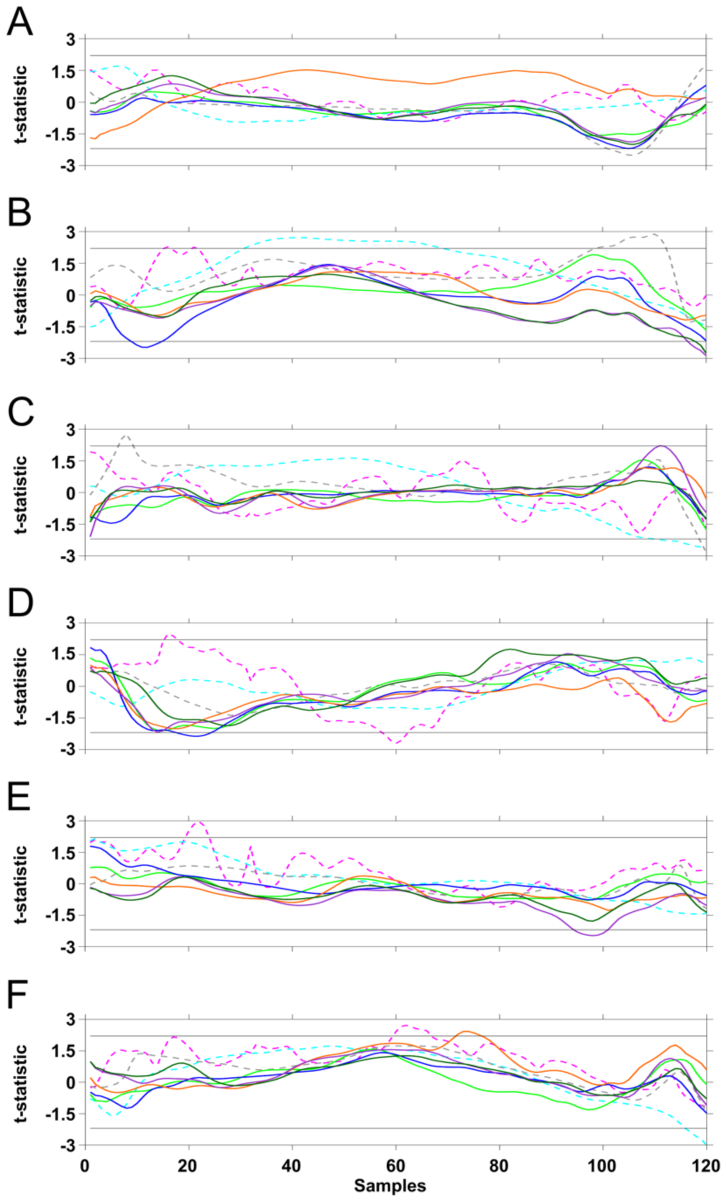
Blue = PMv, red = PMd. Dashed lines = between-subjects SE.

S4-8: RESAMPLED MEAN VELOCITY CURVE FOR THE IMITATOR INDEX FINGER COMPARING OBSERVATION AND IMITATION STIMULATION OVER THE PMV



Orange = observation, green = imitation. Dashed lines = between-subjects SE.

S4-9: T-STATISTIC PLOTS FOR STIMULATION SITE-RELATED INTERACTIONS



A) site*meaning B) site*effector C) site*time*meaning D) site*time*effector E) site*meaning*effector F) site*time*meaning*effector; Horizontal lines indicate positive and negative critical t-values; Dashed magenta = shoulder, dashed cyan = elbow, dashed grey = wrist, light green = thumb, blue = index finger, orange = middle finger, purple = ring finger, dark green = little finger.

S4-10: BONFERRONI-CORRECTED PAIRED T-TESTS FOR ELBOW SITE*EFFECTOR INTERACTION

Bonferroni-corrected alpha cutoff = .025.

Variable	Mean(±SE) values						Paired t-tests											
	Hand			Finger			Hand						Finger					
	PMv	PMd	Vertex	PMv	PMd	Vertex	PMv – Vertex		PMd – Vertex		PMv – PMd		PMv – Vertex		PMd – Vertex		PMv – PMd	
							t (11)	p	t (11)	p	t (11)	p	t (11)	p	t (11)	p	t (11)	p
PA (cm/s^2)	236 (17.4)	229 (11.8)	224 (13.3)	159 (11.6)	167 (7.76)	157 (6.89)	1.0	.324	0.55	.595	0.87	.404	0.19	.853	1.52	.156	-1.1	.295
PV (cm/s)	47.2 (3.23)	44.0 (2.61)	45.4 (2.47)	25.2 (1.63)	26.2 (1.35)	26.0 (1.30)	0.70	.496	-0.85	.416	1.4	.205	-0.67	.516	0.14	.891	-0.72	.486
PD (cm/s^2)	-181 (14.7)	-174 (10.3)	-177 (9.43)	-135 (11.6)	-140 (6.79)	-129 (4.72)	-0.44	.667	0.37	.717	-0.86	.409	-0.71	.492	-2.0	.070	0.63	.539

S5-1: INTERACTIONS FOR MAX Z-VALUE

SH: shoulder, EL: elbow, WR: wrist, TH: thumb, IN: index finger, MI: middle finger, RI: ring finger, LI: little finger.

Tracker	Site*meaning			Site*effector			Meaning*effector			Site*meaning*effector		
	F (1, 11)	p	η^2	F (1, 11)	p	η^2	F (1, 11)	p	η^2	F (1, 11)	p	η^2
SH	0.325	.580	.029	0.011	.919	.001	0.024	.879	.002	1.03	.332	.086
EL	0.324	.580	.029	0.004	.950	<.001	0.160	.697	.014	1.21	.296	.099
WR	1.07	.323	.089	1.21	.295	.099	5.16	.044	.319	0.393	.543	.035
TH	0.174	.685	.016	0.153	.703	.014	0.040	.845	.004	0.016	.900	.001
IN	2.09	.176	.160	0.990	.341	.083	0.399	.541	.035	0.008	.932	.001
MI	1.17	.304	.096	.215	.652	.019	6.00	.032	.353	0.936	.354	.078
RI	1.11	.315	.092	0.059	.812	.005	0.023	.883	.002	0.021	.887	.021
LI	2.96	.114	.212	0.001	.979	<.001	10.8	.007	.496	0.334	.575	.029

S5-2: MEAN VALUES AND MAIN EFFECTS FOR LAG AT MAX Z-VALUE

SH: shoulder, EL: elbow, WR: wrist, TH: thumb, IN: index finger, MI: middle finger, RI: ring finger, LI: little finger.

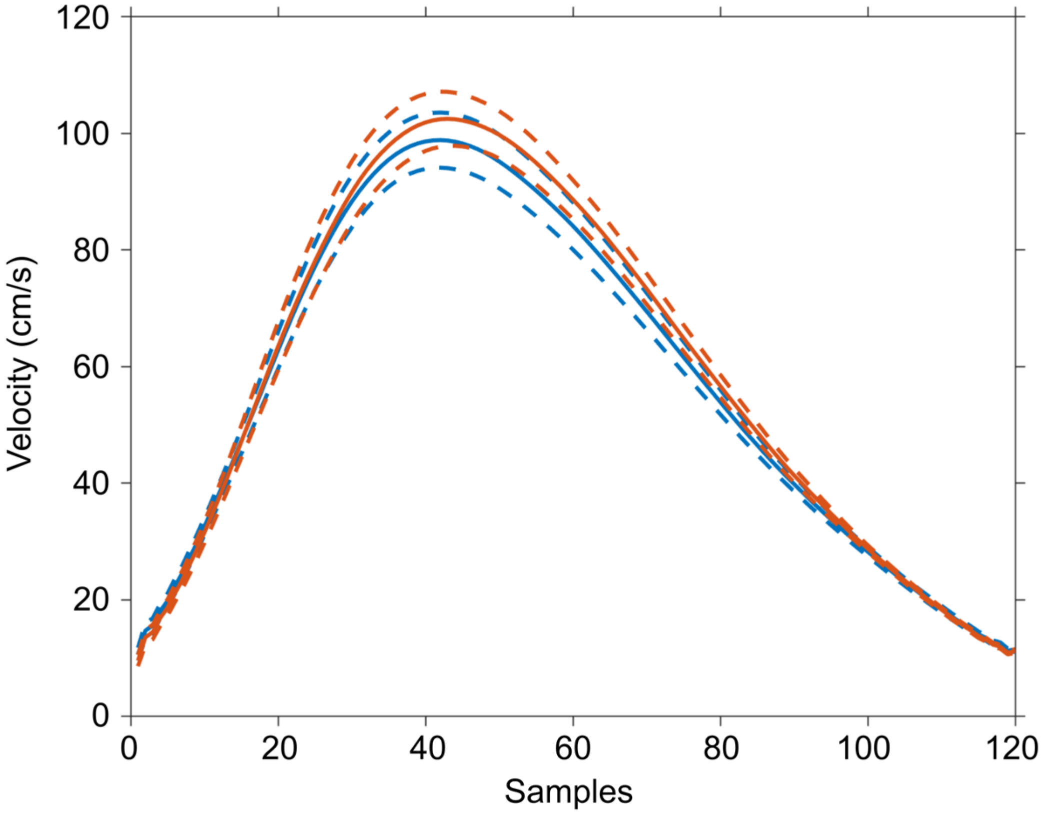
Tracker	Mean(±SE) value						Main effect								
	Site		Meaning		Effector		Site			Meaning			Effector		
	pMTG	Vertex	MF	ML	Hand	Finger	F (1, 11)	p	η²	F (1, 11)	p	η²	F (1, 11)	p	η²
SH	7.08 (1.91)	10.8 (3.14)	8.10 (1.87)	9.79 (2.84)	15.5 (4.41)	2.34 (2.81)	0.887	.366	.075	0.243	.632	.022	6.28	.029	.363
EL	19.1 (5.16)	13.3 (7.01)	17.5 (4.47)	15.0 (7.42)	15.5 (5.49)	16.9 (6.78)	1.49	.248	.119	0.292	.599	.026	0.082	.780	.007
WR	33.2 (7.65)	26.8 (11.2)	34.3 (8.85)	25.7 (10.4)	36.9 (11.4)	23.1 (8.95)	1.08	.321	.089	1.87	.199	.145	2.15	.170	.164
TH	19.7 (7.55)	19.0 (11.1)	22.5 (9.21)	16.2 (9.41)	25.2 (10.8)	13.5 (8.25)	0.012	.915	.001	1.47	.250	.118	2.69	.129	.197
IN	18.9 (7.99)	18.1 (10.6)	22.3 (10.4)	14.6 (8.58)	20.8 (11.1)	16.2 (8.78)	0.022	.886	.002	1.41	.259	.114	0.257	.622	.023
MI	20.1 (7.42)	20.8 (10.9)	23.4 (9.61)	17.5 (9.50)	23.8 (11.5)	17.1 (8.39)	0.021	.886	.002	0.788	.394	.067	0.512	.489	.044
RI	17.6 (8.19)	18.4 (12.1)	20.9 (10.0)	15.2 (10.6)	22.3 (11.6)	13.8 (9.66)	0.015	.906	.001	0.815	.386	.069	1.02	.334	.085
LI	21.8 (8.50)	22.1 (12.8)	24.8 (11.5)	19.1 (10.3)	25.0 (12.0)	18.9 (10.4)	0.002	.969	<.001	0.745	.406	.063	0.509	.490	.044

S5-3: INTERACTIONS FOR LAG AT MAX Z-VALUE

SH: shoulder, EL: elbow, WR: wrist, TH: thumb, IN: index finger, MI: middle finger, RI: ring finger, LI: little finger.

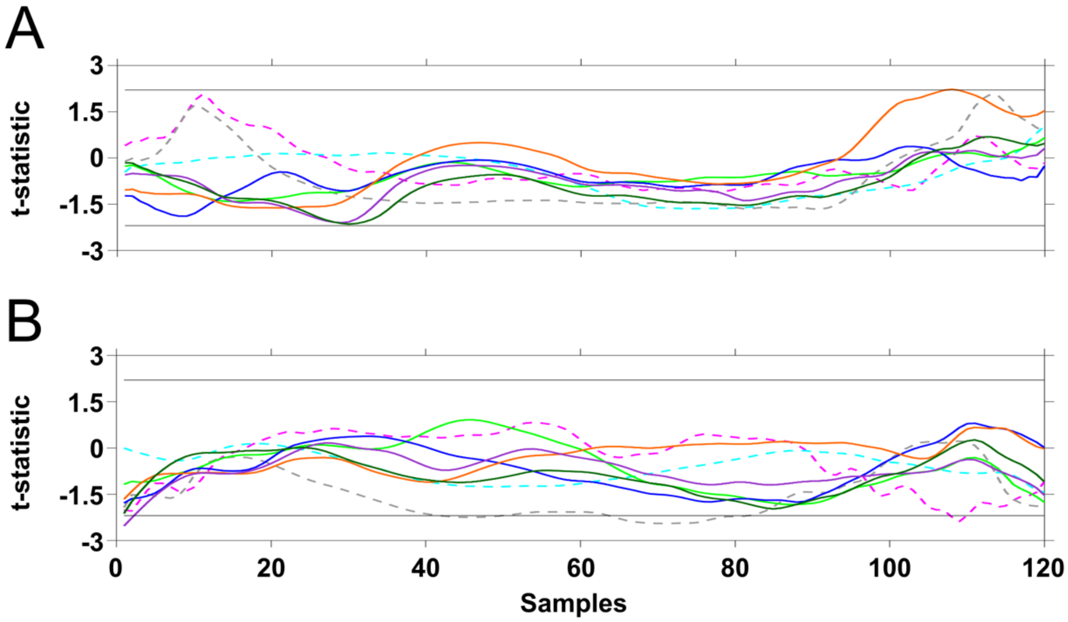
Tracker	Site*meaning			Site*effector			Meaning*effector			Site*meaning*effector		
	F (1, 11)	p	η²	F (1, 11)	p	η²	F (1, 11)	p	η²	F (1, 11)	p	η²
SH	0.104	.753	.009	1.11	.315	.091	0.274	.611	.024	0.196	.667	.017
EL	2.85	.119	.206	0.001	.979	<.001	2.31	.157	.174	0.316	.585	.028
WR	0.999	.339	.083	0.296	.598	.026	3.23	.100	.227	1.96	.189	.151
TH	0.619	.448	.053	0.014	.909	.001	1.36	.268	.110	0.468	.508	.041
IN	0.417	.532	.037	0.133	.722	.012	1.39	263	.112	0.137	.718	.012
MI	6.13	.031	.358	0.028	.870	.003	1.07	.322	.089	0.399	.541	.035
RI	2.60	.135	.191	0.243	.631	.022	2.70	.128	.197	1.07	.324	.088
LI	2.12	.173	.162	0.002	.964	<.001	0.797	.391	.068	0.220	.648	.020

S5-4: RESAMPLED MEAN VELOCITY CURVE FOR THE IMITATOR THUMB COMPARING PMTG AND VERTEX



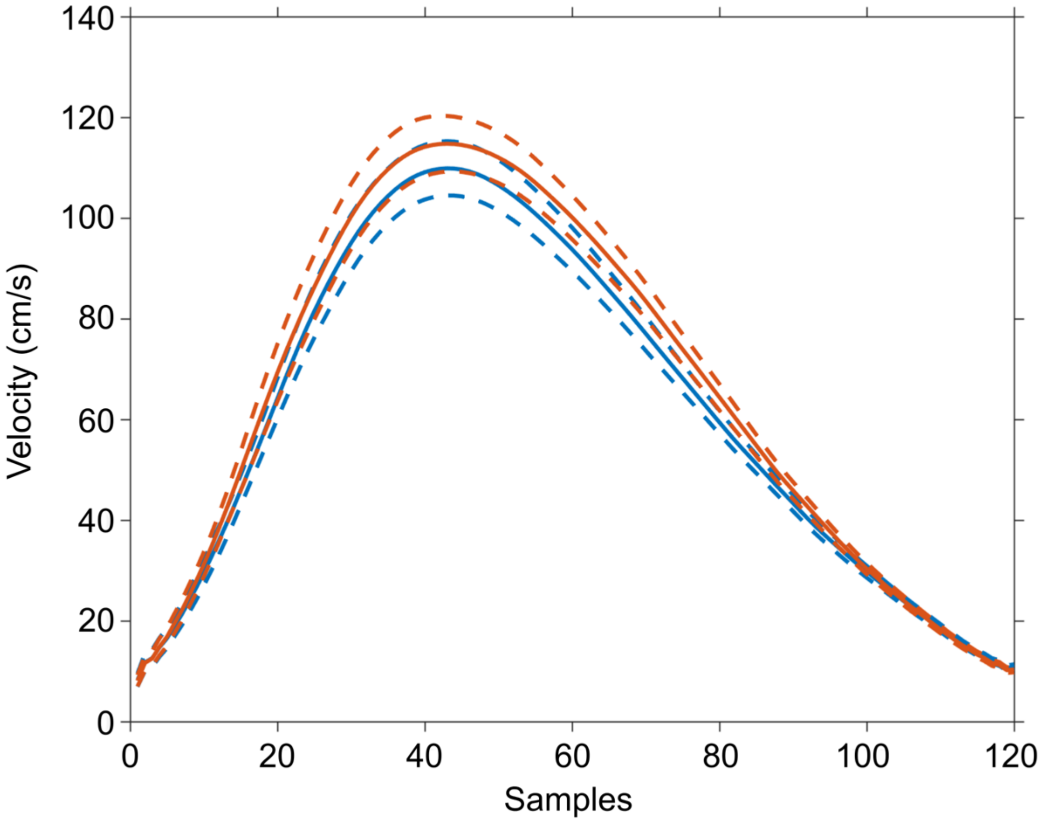
Blue = pMTG, red = vertex. Dashed lines = between-subjects SE.

S5-5: T-STATISTIC PLOTS FOR TWO-WAY STIMULATION SITE-RELATED INTERACTIONS



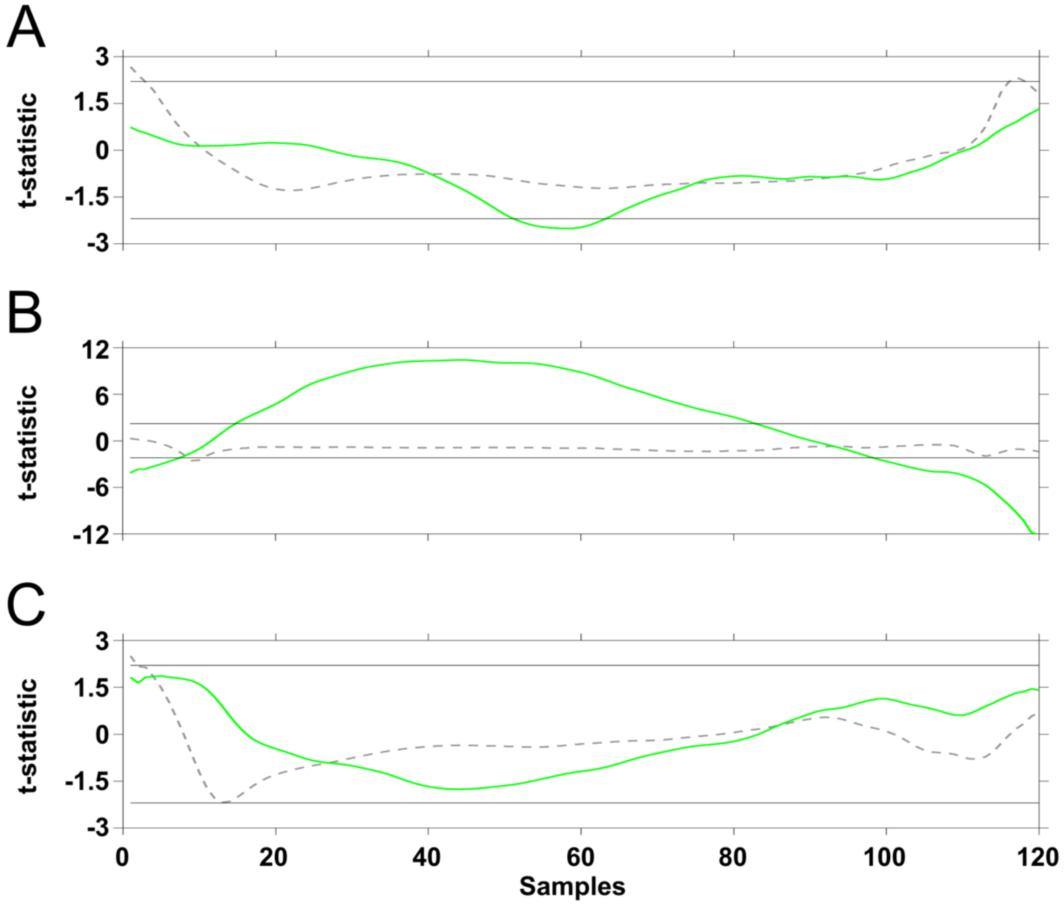
A) site*meaning B) site*effector; Horizontal lines indicate positive and negative critical t-values; Dashed magenta = shoulder, dashed cyan = elbow, dashed grey = wrist, light green = thumb, blue = index finger, orange = middle finger, purple = ring finger, dark green = little finger.

S5-6: RESAMPLED MEAN VELOCITY CURVE FOR THE IMITATOR THUMB COMPARING PMTG AND VERTEX IN MEANINGFUL HAND GESTURES



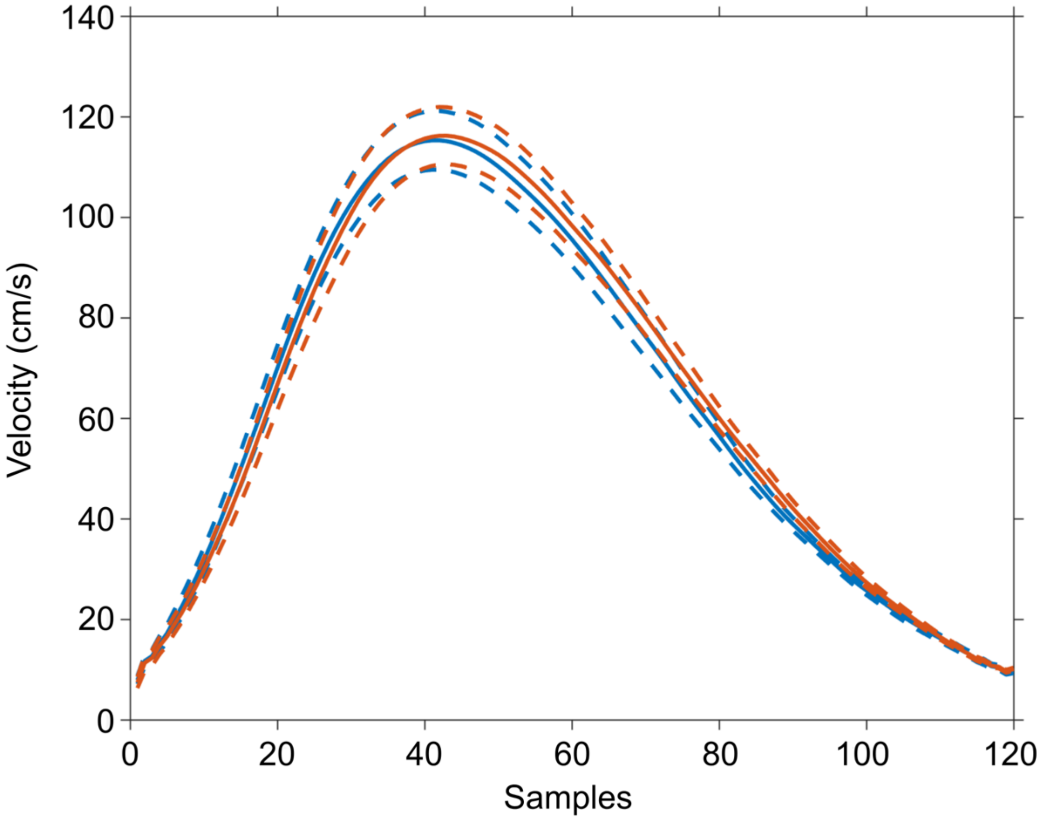
Blue = pMTG, red = vertex. Dashed lines = between-subjects SE.

S5-7: T-STATISTIC PLOTS FOR SITE*MEANING*EFFECTOR PAIRED COMPARISONS



pMTG versus vertex for A) meaningful finger gestures B) meaningless hand gestures C) meaningless finger gestures; Horizontal lines indicate positive and negative critical t-values; Dashed grey = wrist, light green = thumb.

S5-8: RESAMPLED MEAN VELOCITY CURVE FOR THE IMITATOR THUMB COMPARING PMTG AND VERTEX IN MEANINGLESS HAND GESTURES



Blue = pMTG, red = vertex. Dashed lines = between-subjects SE.