Feel the Beat: Heart Rate Variability as a Metric of Adaptive Emotional Responding

Thesis submitted for the degree of Doctor of Philosophy

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Declaration of Original Authorship

I confirm that this is my own work and that the use of all material from other sources has been properly and fully acknowledged. In Chapter 2, William Lloyd assisted with initial pre-processing of the emotion regulation task functional magnetic resonance imaging data. Ifeoma Egbuniwe assisted me with the pre-processing and analysis of the resting-state functional magnetic resonance imaging data and pulse data. Karis Patel and Laura Bucher also helped me with pulse data processing. In Chapter 4, Liz Bushby, Kate Brooker, Doris Lau, and Theresa Wong helped me build the tasks and/or assisted with data collection for either the online or laboratory study.

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The research studies presented in chapters 2-4 have either been published or are currently in preparation for submission.

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Thesis Abstract

The ability to flexibly respond to an ever-changing environment charged with emotional information is essential for effective adaptation and mental health. The Neurovisceral Integration Model (NIM) posits that shared brain areas overlap to support autonomic, emotion, and cognitive regulatory processes, with heart rate variability (HRV) serving as an index of adaptive emotional responding. While prior research has predominantly investigated heart-brain interactions and flexible emotional responses at rest, the principal aim of this thesis was to examine the relationship between HRV and neural and trait affect correlates across both rest and adaptive emotion contexts. In Papers 1 and 2, we demonstrated that task-related and resting HRV exhibited associations with functional coupling of brain areas and dynamic neural networks closely linked to adaptive emotional responding in both younger and older adults. Relatedly, in Paper 3, we found both task-based and resting HRV, but not other emotional disposition variables (i.e., rumination and valence bias), to tentatively predict attentional shifts related to valence aspects of affective flexibility. Collectively, findings from these papers provide some support that HRV reflects adaptive, context-appropriate emotional responding and critically highlight the importance of assessing HRV with associated neural and emotional disposition correlates to elucidate key mechanisms supporting adaptive emotional responding. More broadly, a clearer understanding of HRV and associated flexible emotional responses across contexts has wider implications for HRV as a complementary target for the prevention and/or management of psychological disorders characterised by emotion dysregulation, such as anxiety and depression.

Chapter 1. General Introduction to Thesis

1.1 Adaptive Emotional Responding

In an ever-evolving world, the ability to respond flexibly to dynamic emotional stimuli and events in accordance with contextual demands is essential for adaptive emotional responding (Aldao et al., 2015; Fox, 2022). Due to the multifarious and complex nature of emotion, various definitions of emotional phenomena exist in the literature, however, it is generally acknowledged that emotion involves changes in behaviour and bodily responses, alongside subjective experiences, towards internal and external events (Frijda, 1986). Our daily lives are inherently emotional given the nature of the cues and stressors we encounter, with responses producing a cascade of changes at both subjective (i.e., emotional states/expressions, thoughts) and biological (i.e., changes in heart rate, neural activity) levels. In turn, effective coordination and communication between the brain and body is essential for adaptation and has important implications for both mental and physical health. The current thesis focuses on adaptive emotional responding, which encompasses various processes underlying and supporting flexible emotional responses, including emotion regulation and affective flexibility.

1.2 Emotion Regulation

Emotion regulation is a complex and multifaceted process referring to the modification of the intensity, valence, expression, timing, and/or duration of emotions in a contextually appropriate and goal-directed manner (Gross, 1998, 2015; Thompson, 1994). The inability to effectively regulate emotional responses is associated with psychopathology (Berenbaum et al., 2003; Mennin & Farach, 2007), including anxiety and depression (Cisler et al., 2010; Joormann & Stanton, 2016). Emotion regulation can either be explicit or implicit (Braunstein et al., 2017; Gyurak et al., 2011) and automatic or controlled (Braunstein et al., 2017) depending on the degree of cognitive resources required and the nature of the goal or context. Although earlier research considered certain emotion regulation strategies (i.e., cognitive reappraisal) to be more adaptive and other strategies (i.e., expressive suppression, rumination) more maladaptive, recent work has shifted to endorse a ‘flexibility’ perspective, acknowledging that whether a strategy is considered (mal)adaptive is

highly dependent on the context and goals (Aldao et al., 2015; Kashdan & Rottenberg, 2010; Westphal et al., 2010).

Emotion regulation strategies have typically been assessed via experimental paradigms involving the presentation of an emotion eliciting stimulus and instructions to either increase, decrease, or maintain an emotional response (Johnstone et al., 2007; Ochsner et al., 2002; Urry et al., 2009). One of the most studied emotion regulation strategies is cognitive reappraisal which involves the deliberate modification of an emotional response through reinterpretation of its meaning or relevance (Gross & John, 2003; Gross, 2015). The neural underpinnings of emotion regulation, including specific brain areas and neural networks, have been extensively outlined in prior reviews and meta-analyses (Buhle et al., 2014; Kohn et al., 2014; Morawetz & Basten, 2024; Morawetz et al., 2020; Ochsner et al., 2012). In particular, lateral regions of the prefrontal cortex, such as the ventrolateral prefrontal cortex (vlPFC) and dorsolateral prefrontal cortex (dlPFC) appear to support more cognitively demanding, voluntary emotion regulation, whereas more implicit, automatic emotion regulatory processes appear to recruit the medial prefrontal cortex (mPFC) (Braunstein et al., 2017; Phillips et al., 2008). Moreover, elevated activation in prefrontal areas has been shown to decrease activation in subcortical regions, such as the amygdala (Johnstone et al., 2007; Urry et al., 2006), a key neural region involved in the processing of emotional and salient information (Janak & Tye, 2015). Additionally, research has further suggested that due to strong anatomical connections between the amygdala and mPFC, regulatory processes can be facilitated by higher order neural regions involved in cognitive control (i.e., vlPFC, dlPFC) conveying control messages via the ventromedial prefrontal cortex (vmPFC) to the amygdala (Buhle et al., 2014). Overall, various neural regions and effective coordination of cortical-subcortical circuitry facilitate emotion regulatory processes.

1.3 Affective Flexibility

A process closely coupled to, and underlying, emotion regulation is cognitive flexibility related to the processing of emotional material, ‘affective flexibility’, which is defined as the degree to which an individual can flexibly shift attention both to and from emotional information (Gross & Thompson, 2007; Malooly et al., 2013). For example, in certain situations, such as walking alone in the dark at night, it may be considered adaptive to exhibit heightened attention towards potentially negative or

dangerous information, as this could facilitate effective detection of possible threats to help ensure one reaches their destination safely. Nonetheless, the same level of heightened or sustained attention towards information of this nature may be considered less adaptive, or even maladaptive, in safer contexts and/or if experienced for a prolonged period. Affective flexibility stems from the more general process of cognitive flexibility, with mental set shifting and inhibition of prepotent responses (executive function) underlying both processes. Consequently, research has examined flexibility using experimental paradigms that involve switching between two different task sets or rules for the same type of sequentially presented stimuli (Monsell, 2003). Shifting from one rule to another, in comparison to repeating the same rule, recruits increased cognitive resources due to inhibition of the previous rule and updating to the current rule, producing differences in response times (i.e., a 'switch cost') (Monsell, 2003). A paradigm that has frequently been employed is an affective switching task whereby individuals are instructed to categorise negative and positive emotional images according to either an affective (valence: positive or negative) or non-affective (number of humans: 1 or fewer or 2 or more) rule. A small body of work has investigated the relationship between affective flexibility and various psychological variables related to emotion regulation and mental health using this task, including rumination (Genet et al., 2013), reappraisal (Malooly et al., 2013), resilience (Genet & Siemer, 2011; Grol & De Raedt, 2018), trait anxiety and worry (Twivy et al., 2021), and depressive symptoms (Wen & Yoon, 2019). Ultimately, most of these studies report findings for switch costs pertaining to attentional shifts in the rule type, in turn reflecting cognitive flexibility in the context of emotion. However, there are trials in which the valence of the emotional image changes, but the rule is held constant, which appears to capture attentional shifts related to *affective* information. The degree to which individual differences in pure valence switch costs on this task relate to individual differences is less clear.

1.4 Emotional Disposition Factors and Rigid Emotional Responding

Emotion dysregulation and rigid emotional responding are prominent features across psychological disorders, such as anxiety and depression (Cisler et al., 2010; Joormann & Stanton, 2016). Indeed, both anxiety and depression have been associated with a greater tendency to exhibit heightened attention towards negative emotional information, alongside difficulties disengaging attention from negatively

valenced stimuli (Bar-Haim et al., 2007; Mogg et al., 1995; Koster et al., 2011), and in the case of anxiety, a greater tendency to subsequently avoid negative emotional information (Mogg et al., 2004). Individual differences in emotional disposition can increase the risk of onset or progression of anxiety and/or depression, including trait neuroticism and rumination (Hsu et al., 2015; Kotov et al., 2010; McLaughlin & Nolen-Hoeksema, 2011). Trait neuroticism is a stable disposition characterised by increased negative affect and emotional reactivity (Ormel et al., 2013), while trait rumination is a rigid and maladaptive form of negative thinking that refers to excessive thoughts that are negative, deliberate, and perseverative (Nolen-Hoeksema, 2000; Treynor et al., 2003). Of note, rumination is multifaceted and contains three distinct dimensions: brooding, reflective, and depressive rumination (Treynor et al., 2003). Brooding rumination reflects the tendency to passively compare one's current situation with unachieved standards and is viewed as a more maladaptive form of thinking, whereas reflective rumination is considered more adaptive due to a focus on problem solving (Treynor et al., 2003).

In a similar vein, a growing number of studies have examined associations between an individual's response to emotional ambiguity, or 'valence bias', with various factors relevant to mental health and emotion regulation. One thread of research has operationalised valence bias as the relative dominance of positive versus negative ratings in response to emotionally ambiguous stimuli (i.e., surprise faces) (Neta et al., 2009; 2023; Harp et al., 2021). Specifically, a greater trait-like negativity bias has been associated with anxiety and depressive symptoms (Park et al., 2016; Petro et al., 2021) and stress reactivity in those reporting lower reappraisal use (Raio et al., 2021). Collectively, individual differences in trait rumination, neuroticism, and valence bias have been linked to the onset and maintenance of anxiety and depression. However, emotional experiences are generally accompanied by physiological changes, with effective coordination of the autonomic nervous system facilitating adaptive responses. Therefore, flexible emotional responding can not only be measured at the psychological level, but also on a biological level. Specifically, Heart Rate Variability (HRV), a physiological phenomenon referring to the variation in time intervals (interbeat or 'RR' intervals) between consecutive heartbeats, has increasingly been recognised as a peripheral metric of adaptive autonomic and emotion regulatory ability (Appelhans & Luecken, 2006).

1.5 Heart Rate Variability

The interplay between the heart and the brain can be captured by a physiological phenomenon termed HRV. While the average heart rate for a healthy human adult typically falls within a range of 60-100 beats per minute (BPM) at rest, the time intervals between each heartbeat do not tick at a rigid rate like that of a metronome, but instead vary in a dynamic manner. This variation in the heart period is characterised by the healthy balance and flexible interplay of two branches that comprise the autonomic nervous system (ANS): the excitatory sympathetic nervous system (SNS) and the inhibitory parasympathetic nervous system (PNS). Both sympathetic and parasympathetic divisions directly innervate the heart via the stellate ganglia and vagus nerve respectively, in turn influencing the activity of the sinoatrial node (i.e., the heart's pacemaker) (Berntson et al., 1997). Correspondingly, the SNS and PNS work antagonistically to produce changes in physiological arousal pertaining to the context, such that an elevation in heart rate could reflect either increased sympathetic dominance and/or vagal withdrawal in the form of reduced parasympathetic inhibition (Appelhans & Luecken, 2006; Berntson et al., 1997). Notably, the arms of the ANS differ in their temporal influence on the heart period. Changes in heart rate through the SNS, primarily via norepinephrine neurotransmission, occur more slowly (i.e., peak effect on heart rate after 4 seconds with an associated baseline return of approximately 20 seconds), in comparison to the PNS which produces more efficient changes in heart rate predominantly via acetylcholine (i.e., peak effect on heart rate is approximately 0.5 seconds with a much quicker return to baseline of ~1 second) (Appelhans & Lucken, 2006; Berntson et al., 1997). While both branches influence heart rate, parasympathetic influence is particularly dominant during rest (Berntson et al., 1997) and significantly modulates heart rate (Katona et al., 1982). In turn, the fast, dynamic (dis)engagement of the PNS on cardiac activity helps to facilitate flexible physiological responses to environmental demands (Appelhans & Luecken, 2006). Correspondingly, higher resting levels of HRV therefore reflect an adaptable and highly responsive ANS that is sensitive to contextual demands, whereas lower resting HRV may be indicative of a more rigid and inflexible ANS when confronted with environmental challenges.

Cardiac traces, and consequently HRV, can be captured via various recording techniques, with current empirical research typically using signals acquired from either electrocardiographic (ECG) or photoplethysmography (PPG) recordings (Task Force,

1996; Laborde et al., 2017). An ECG signal reflects electrical activity in the heart and is recorded via leads and electrodes that are typically applied to an individual's chest. HRV derived from an ECG signal provides higher accuracy for beat detection compared to PPG due to measurement of the full QRS complex (i.e., ventricle depolarisation), and the ability to extract RR intervals from the clear, upward spikes of the R wave (Laborde et al., 2017). On the other hand, a PPG signal, usually measured via a pulse oximeter attached to the fingertip or earlobe, is a non-invasive, albeit more distal, technique of obtaining a cardiac trace, that uses both a light source and photo detector to record fluctuations in blood volume at the surface of the skin (Allen, 2007). The pulse signal is divided into two components: AC and DC (Allen, 2007; Korhonen & Yli-Hankala, 2009). The PPG waveform captures beat-to-beat changes in blood volume (AC) which is placed over a slower, more variable (DC) baseline with a range of lower frequency components representing thermoregulation, SNS activity, and respiratory influences (Allen et al., 2007). While PPG is more susceptible to artefacts (e.g., motion), it does not allow for as precise handling of noise in the signal, and curved pulse wave peaks present a greater challenge to extract RR intervals relative to ECG signals (Laborde et al., 2017), HRV recordings from ECG and PPG signals are closely coupled (Lin et al., 2014; Pinheiro et al., 2016; Selvaraj et al., 2008), with one study demonstrating discrepancies between ECG and PPG of below 6% for the majority of HRV measures (Jeyhani et al., 2015). Critically, given practical and current technological constraints of using ECG in a magnetic resonance imaging (MRI) scanning environment, for studies assessing simultaneous MRI data and HRV in the scanner, acquiring a pulse trace via PPG to derive HRV metrics has been a practical approach (Chang et al., 2013; McIntosh et al., 2024).

Currently, there are three major analytical approaches to obtain various HRV parameters: time-domain, frequency-domain, and non-linear measures. Firstly, time-domain HRV metrics directly use the intervals between consecutive heartbeats over the duration of a continuous cardiac trace for calculation (Kleiger et al., 1992). The most frequently adopted time-domain HRV measures across empirical research are the root mean square of successive differences (RMSSD), the standard deviation of all normal-to-normal RR (NN) intervals (SDNN), and the percentage of intervals > 50 milliseconds (ms) different from the preceding interval (PNN50). Of these metrics, the RMSSD (measured in ms) is considered a more robust index of HRV, predominantly reflecting parasympathetic influences on the heart period (Kleiger et al., 2005), and is

a metric that is typically less susceptible to other physiological influences, most notably respiration (Hill et al., 2009). By contrast, frequency-domain HRV measures quantify cyclic fluctuations in the cardiac signal via either Fast Fourier Transform (FFT) or Autoregressive (AR) methods to estimate the absolute or relative power of different frequency bands (Kleiger et al., 2005). Oscillations in the cardiac trace can be segregated into four main frequency bands: ultra-low frequency (ULF), very low frequency (VLF), low frequency (LF) and high frequency (HF) (Shaffer & Ginsberg, 2017; Task Force, 1996). High-Frequency HRV (HF-HRV) primarily captures parasympathetic activity through either the absolute or relative power of the HF band and is heavily influenced by respiration (0.15 - 0.4 Hz; approximately 9 to 24 breaths per minute; Task Force, 1996). The RMSSD and HF-HRV are commonly adopted measures of resting HRV, with both metrics demonstrating a strong positive correlation (r = 0.93; Goedhart et al., 2007; Laborde et al., 2017), alongside reasonable stability over short (Bertsch et al., 2012; Borges et al., 2018; although see: Uhlig et al., 2020) and longer (> 1 year) time periods, including in both adults with and without a history of depression (Seidman et al., 2024). Finally, non-linear HRV indices focus on capturing and quantifying the structure and/or complexity of the RR intervals, with measures including standard deviations in Poincaré plots (Brennan et al., 2001), detrended fluctuation analysis (Peng et al., 1995), and recurrence plot analysis (Webber & Zbliut, 1994). However, the value of non-linear relative to traditional (time- and frequency-domain) HRV techniques in relation to psychophysiological and clinical variables remains unclear, subsequently leading to recommendations that non-linear indices should be adopted as complementary measures with other established HRV metrics (Laborde et al., 2017; Sassi et al., 2015). Taken together, HRV is a physiological phenomenon that reflects the adaptability and flexibility of the ANS. Nevertheless, HRV is a measure that goes beyond ‘just beats’ and has important implications for physical and mental health.

1.6 More Than Just Beats? Heart Rate Variability and Adaptive Emotional Responding

HRV is a psychophysiological marker that reflects adaptability of autonomic activity in the face of environmental challenges, with higher HRV signalling an increased ability to engage in context appropriate, goal-directed and flexible emotional responding (Thayer et al., 2012). As previously outlined, adaptive emotional

responding captures both emotional flexibility, the ability to (dis)engage attention to and from positive and negative emotional information (Gross & Thompson, 2007; Malooly et al., 2013), and emotion regulation, the ability to up- and down-regulate positive and negative affect (Johnstone et al., 2007; Ochsner et al., 2002; Urry et al., 2009). A wealth of psychological research has reported HRV to be linked to adaptive emotional responding. Individuals with higher resting HRV demonstrate both adaptive top-down and bottom-up modulation of attention to emotional stimuli (Park & Thayer, 2014), exhibit effective recognition of threat versus safety as reflected by context appropriate startle reflexes (Ruiz-Padial & Thayer, 2014), alongside successful safety learning and better fear extinction (Pappens et al., 2014). Moreover, individuals with higher HRV self-report fewer emotion regulation difficulties (Visted et al., 2017; Williams et al., 2015) and increases in HRV have been observed during successful emotion regulation (Butler et al., 2006; Ingjaldsson et al., 2003). By contrast, individuals with lower resting HRV have been shown to exhibit reduced adaptive, context-appropriate emotional responding in the form of increased hypervigilance to, and difficulties disengaging from, negative threat stimuli (Park et al., 2013; Park & Thayer, 2014), increased attentional avoidance of negative emotional information (Grol & De Raedt, 2020), and an elevated autonomic stress response in relation to mild fearful stimuli (Gaebler et al., 2013; Park et al., 2014; Park & Thayer, 2014). Furthermore, individuals with lower HRV have also been found to demonstrate deficient safety learning and slower extinction in relation to fear learning (Pappens et al., 2014; Wendt et al., 2015), slower recovery from stress (Weber et al., 2010), and self-report greater emotion regulation difficulties (Visted et al., 2017; Williams et al., 2015). In turn, individuals with lower HRV are also generally at a higher risk of developing and experiencing psychopathology, including anxiety and depression (Beauchaine & Thayer, 2015; Chalmers et al., 2014; Dell-Acqua et al., 2020; Koch et al., 2019). HRV has been found to interact with emotional disposition factors too, with higher resting HRV associated with increased positive valence bias (Madison et al., 2021; Osnes et al., 2023), and lower trait neuroticism (Čukić & Bates, 2015; Shepherd et al., 2015; albeit findings are mixed and not entirely robust, see: Ode et al., 2010; Sloan et al., 2017). Thus, HRV appears to closely reflect processes linked to adaptive emotional responding, with higher HRV promoting more flexible, context-appropriate emotional responding, and lower HRV linked to more rigid, inflexible emotional responding. Accordingly, several psychophysiological frameworks have been

developed to help elucidate the mechanisms by which HRV serves as an index of adaptive emotional responding.

1.7 The Intricate Connection Between the Brain and the Heart: Psychophysiological Frameworks

The interdependence of the brain and the heart has been documented since the 19th century, in which French physiologist Claude Bernard, was one of the first to systematically examine and highlight the intricate connection between both organs (Bernard, 1867). Charles Darwin cited and further highlighted Bernard's pioneering work in '*Expressions of the Emotions in Man and Animals'*, noting bidirectional heart-brain reactivity and their connection via the vagus nerve (Darwin, 1872). The vagus nerve is the 10th cranial nerve in the human body which directly innervates the heart amongst other major organs, including the lungs and the gastrointestinal tract (Kaniusas et al., 2019). Given its widespread influence, the vagus nerve forms a crucial component of the ANS, particularly the parasympathetic arm, supporting vital interactions between the brain and the body (de Lartigue, 2016). Advances have been made in recent years to further expand upon the mechanisms by which the heart and the brain communicate, but more specifically, how coupling between the heart and the brain may facilitate flexible affective, cognitive, and behavioural responses. While the field is still in its infancy, several frameworks have been developed to elucidate the connection between the heart and the brain with HRV as an outcome metric of brain-heart communication (Grossman & Taylor, 2007; Laborde et al., 2018; Porges, 2001, 2003, 2007; Smith et al., 2017; Thayer & Lane, 2000, 2009). The most prominent models informing biopsychosocial and neuroimaging research are the Neurovisceral Integration Model (NIM; Smith et al., 2017; Thayer & Lane, 2000, 2009) and Polyvagal Theory (Porges, 2001, 2003, 2007). Polyvagal theory (Porges, 2001, 2003, 2007) heavily focuses on the evolutionary development of vertebrate neuroanatomy and neurophysiological systems to explain how the ANS and associated neural circuitry evolved to facilitate adaptive behaviours in response to, and in accordance with, dynamic environmental challenges. On the other hand, from a functional neuroanatomy and a computational neuroscience perspective, the NIM (Smith et al., 2017; Thayer & Lane, 2000, 2009) outlines a reciprocal hub of neural regions that overlap to support autonomic, cognitive, and emotional regulatory processes. While both frameworks posit resting HRV to serve as an index of autonomic flexibility, for

conceptual replication purposes and given the greater focus on neural networks, the NIM was the central framework for the research outlined in the present thesis.

1.8 The Neurovisceral Integration Model

The NIM (Smith et al., 2017; Thayer & Lane, 2000, 2009) has served as a prominent and influential framework for a broad range of research examining associations between HRV and adaptive emotional, cognitive, and autonomic responding. At the heart of the model is a complex and reciprocal hub of neural regions that functionally overlap to support autonomic (i.e., heart rate), affective, and cognitive regulatory processes. Many of these shared brain areas form the Central Autonomic Network (CAN; Benarroch, 1993). Specifically, neurovisceral circuitry encompasses higher cortical regions (e.g., (v)mPFC, anterior cingulate cortex, orbitofrontal cortex), subcortical limbic areas (e.g., amygdala, hypothalamus, anterior and posterior insula), and brainstem structures (e.g., periaqueductal gray, the nucleus ambiguus, the locus coeruleus, the rostral and caudal ventrolateral medulla).

A recent extension to the NIM (Figure 1), informed by computational neuroscience and recent findings from functional neuroanatomical research, outlined an eight-level vagal hierarchy of neurovisceral circuitry, detailing relevant neuroanatomical loci and networks that underlie adaptation according to the organism's current and/or future metabolic needs and the environmental context (Smith et al., 2017). The hierarchy spans lower-level regional networks (i.e., nucleus ambiguuus, periaqueductal gray, (hypo)thalamic nuclei) that mainly regulate processes related to an organism's current metabolic needs, such as intra-cardiac control, coordinated cardiovascular control (i.e., baroreceptor reflex), and coordination of brainstem nuclei for cross-organ and coordinated visceromotor and skelemotor control. Higher levels and networks of the vagal hierarchy (i.e., amygdala, insula, posterior and anterior cingulate cortex, medial and dorsal lateral prefrontal cortex) integrate information from lower levels to support awareness of current somatic, visceral, and cognitive or attentional responses, and the recruitment of regulatory processes pertaining to sensory input and past experience, alongside increasing, maintaining, or suppressing internal representations in accordance with an individual's goals (i.e., recruitment of executive control network regions) (Smith et al., 2017). Therefore, higher-order vagal networks not only focus on current metabolic needs, but also involve the control of energy expenditure based on both present and anticipated

future metabolic needs according to an individual's social and emotional goals, supporting context-appropriate responding.

Importantly, the connection between the heart and the brain is bidirectional, such that information can flow top-down from the brain to the heart and vice versa (Smith et al., 2017). In relation to higher-order emotion and self-regulatory processes, the NIM posits that distinct areas of the prefrontal cortex (i.e., mPFC), exert tonic inhibitory control over subcortical cardioacceleratory regions (i.e., amygdala). Coordinated output of the CAN is directed via preganglionic sympathetic and parasympathetic neurons via the stellate ganglia and vagus nerve respectively to the sinoatrial node, influencing variable changes in the time intervals between heart beats, known as HRV (Thayer & Lane, 2000, 2009). Consequently, this cortico-subcortical circuit, alongside other neurovisceral circuitry at lower levels of the vagal hierarchy (as outlined above), facilitates the flexible regulation of autonomic, affective and cognitive processes, with HRV serving as an index of the functioning of this circuitry (Thayer & Lane, 2000, 2009; Smith et al., 2017). Correspondingly, the NIM predicts that higher resting HRV reflects more effective cortical-subcortical control, with the prefrontal cortex exerting inhibitory influence over subcortical regions to support flexible, context-appropriate emotional responding (Thayer & Lane, 2000, 2009; Smith et al., 2017). HRV is therefore considered a metric of adaptive emotional responding, and effective self-regulation more broadly (Appelhans & Luecken, 2006; Balzarotti et al., 2017; Holzman & Bridgett, 2017).

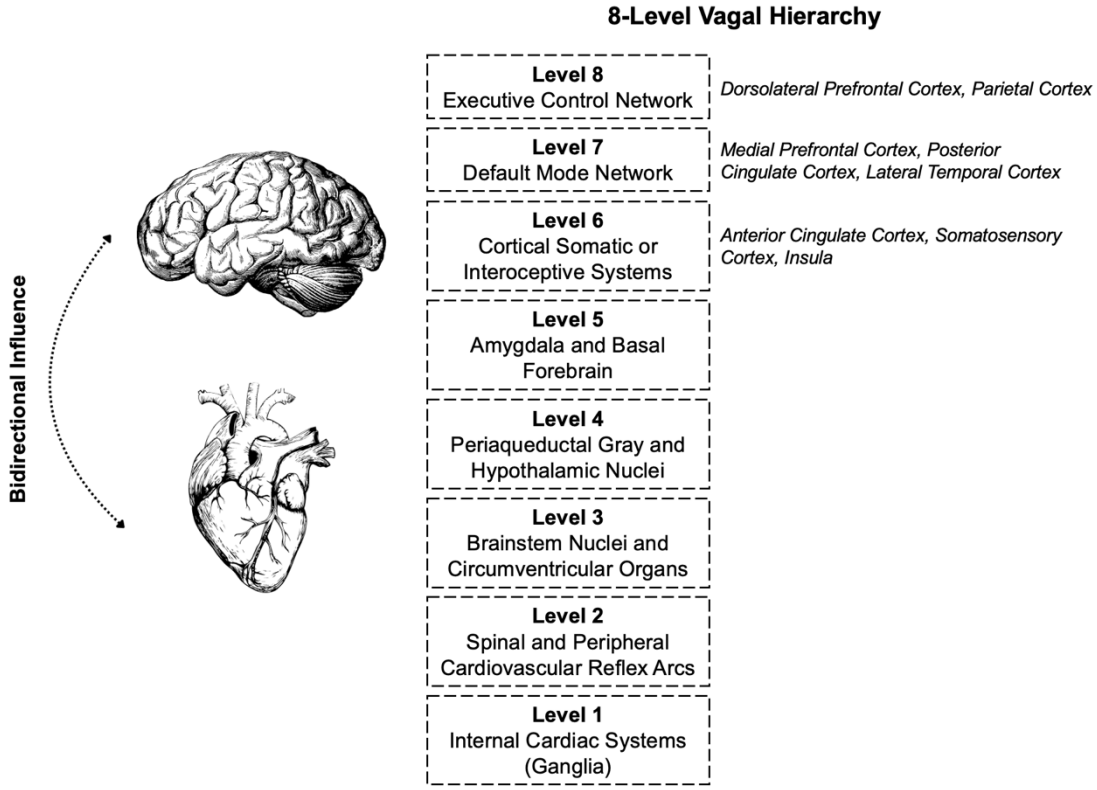

Figure 1. Neurovisceral Integration Model 8-Level Vagal Hierarchy. The connection between the brain and the heart is bidirectional. The brain transmits prediction-error signals to the heart in a top-down fashion and the heart can send information to the brain in a bottom-up manner. The 8-level vagal hierarchy contains cardiac systems and lower-level brainstem nuclei that facilitate coordinated cardiovascular control at subordinate levels of the hierarchy. Higher levels of the hierarchy integrate information from lower-level systems to facilitate awareness of somatic, visceral, cognitive and/or attentional responses. The highest levels of the hierarchy contain higher-order processes associated with greater metabolic demand (i.e., regulatory processes and goal-directed behaviour). *Figure inspired by model presented in Smith et al. (2017)*. *Heart and brain illustrations featured and adapted to create this figure were accessed via Canva with original source contribution via Pixabay.*

1.9 Neurovisceral Integration: Neuroimaging Findings

An ever-expanding body of structural and functional neuroimaging research has found supporting evidence for the NIM with circuitry overlapping brain areas involved in adaptive emotional responding (Maier & Hare, 2017; Sakaki et al., 2016; Schumann et al., 2021; Steinfurth et al., 2018; for meta-analyses and reviews see Holzman & Bridgett, 2017; Thayer et al., 2012). Evidence from structural neuroimaging studies has reported correlations between HRV and cortical thickness of the right anterior midcingulate cortex (Winkelmann et al., 2017), rostral anterior cingulate cortex, and lateral orbitofrontal cortex (Yoo et al., 2018). Furthermore, structural correlations have been reported between the right amygdala with dorsal medial prefrontal cortex (dmPFC) and dorsal anterior cingulate cortex (dACC) into

supplementary motor areas, with those with higher resting HRV exhibiting stronger right amygdala-dmPFC and dACC structural correlations (Wei et al., 2018). Evidence from functional magnetic resonance imaging (fMRI) studies provides further support for the NIM. A meta-analysis by Thayer et al. (2012) reported significant associations between HRV and cerebral blood flow in the amygdala and mPFC (overlapping rostral and subgenual anterior cingulate areas) across studies employing emotional and cognitive tasks. Corroborating this, more recent empirical papers have reported higher resting HRV to be associated with stronger resting mPFC-amygdala functional connectivity, key brain areas facilitating emotion regulation (Nashiro et al., 2023; Sakaki et al., 2016).

While findings have vastly been correlational in nature, a few studies have established more causal links between HRV and neural function underlying flexible emotional responding. Recent studies have examined how increasing baseline levels of HRV via interventions such as HRV biofeedback (Lehrer & Gevirtz, 2014), may alter the activity and interconnectivity of brain areas implicated in the NIM. Both heart rate and breathing tend to resonate or synchronise at around 6 breaths per minute (0.1 Hz) (Steffen et al., 2017), thus breathing at this resonance frequency enhances the amplitude of heart rate oscillations, in turn further elevating HRV (Vaschillo et al., 2006). HRV biofeedback interventions typically involve participants receiving training to breathe slowly at their own resonance frequency (often falling between 4.5 to 6 breath cycles per minute) (Lalanza et al., 2023; Lehrer & Gevirtz, 2014). Findings from biofeedback studies have found that increases in HRV affect brain areas facilitating autonomic and emotion regulatory function (Schumann et al., 2021; Nashiro et al., 2023). Specifically, elevations in HRV strengthened functional connectivity between the left vmPFC and the amygdala, insula, middle cingulate cortex, and lateral prefrontal regions. Moreover, via a 5-week biofeedback paradigm, Nashiro et al. (2023) demonstrated that increases in heart rate oscillations were related to stronger left amygdala-mPFC functional connectivity at rest and enhanced the down-regulation of somatosensory brain areas during an explicit emotion regulation task. Thus, evidence from recent research supports the notion of a causal link between HRV and changes in brain areas underlying adaptive emotional responding.

Critically, many of the brain areas identified in neuroimaging studies overlap with regions that support explicit/voluntary and implicit/automatic emotion regulation (Braunstein et al., 2017; Buhle et al., 2014; Morawetz et al., 2020). Nevertheless,

fewer studies have examined HRV and associated neural activity and/or connectivity concurrently during contexts requiring adaptive emotional responding or self-regulation (Maier & Hare, 2017; Min et al., 2024; Steinfurth et al., 2018) and studies assessing both HRV and neural activity concurrently are even more scarce (Guendelman et al., 2024). Specifically, higher HRV has been correlated with greater (d)mPFC activation during the reappraisal of negative (Steinfurth et al., 2018; Guendelman et al., 2024) and positive (Min et al., 2024) images. Moreover, higher HRV was associated with reductions in activity in areas overlapping the default mode network (DMN), including mPFC, posterior cingulate gyrus, and angular gyrus during repeated and passive viewing of emotional images, possibly reflecting more spontaneous, automatic emotion regulation and/or quicker dissipation of emotional arousal in individuals with higher HRV (Min et al., 2024). Taken together, findings suggest that individuals with higher HRV are better able to recruit brain regions and neural circuitry supporting flexible and context-appropriate emotional responding.

1.10 Rest Versus Task fMRI and the Dynamic Nature of the Brain

As reviewed above, previous studies have predominantly examined HRV and associated neural functional connectivity and/or activity during periods of ‘rest’, that is where the participant lies in the scanner with instructions to stay still and either close their eyes or focus on a fixation crosshair presented on a screen. Resting-state paradigms are often described as capturing ‘intrinsic’ functional connectivity and resting-state connectivity has previously been reported to demonstrate increased heritability relative to connectivity derived from tasks (Ge et al., 2017). However, accumulating evidence suggests that resting-state paradigms may not be optimal for the detection of trait or state individual differences pertaining to emotion or cognition (Finn et al., 2021; Greene et al., 2018). In fact, the state of ‘rest’ could be considered a ‘task’ in and of itself, with various unconstrained internal-state factors contributing to a diverse range of cognitive states (Shah et al., 2016), including mind-wandering and self-generated thoughts (Gorgolewski et al., 2014; Smallwood & Schooler, 2015), and drifts in sleep-wakefulness stages (Tagliazucchi & Laufs, 2014). Therefore, the notion that rest is a passive and/or neutral state that is free from bias is inherently flawed and presents a unique challenge in the form of introducing biases that are difficult to measure and prevent (Finn, 2021). Alternatively, demands imposed by engagement in tasks may help to constrain underlying neural functional connectivity, reducing

variance linked to internal state factors, alongside increasing the relative sensitivity to capture and detect individual differences of interest (Finn, 2021; Finn & Bandettini, 2021). Recent evidence has reported that task-based relative to resting functional connectivity was a stronger predictor of fluid intelligence (Greene et al., 2018) and functional connectivity observed during a naturalistic task paradigm (e.g., movie watching) was reported to effectively predict cognition and emotion (Finn & Bandettini, 2021).

Relatedly, many neuroimaging studies in the literature currently adopt neuroanalytical techniques that assume temporal stationarity of the brain to assess HRV and neural connectivity and/or activity. Nonetheless, evidence from resting and task-based fMRI studies emphasise the inherently dynamic nature of the brain, with functional connectivity between neural regions and networks demonstrating dynamic shifts and temporal variations (Braun et al., 2015; Calhoun et al., 2014; Chang & Glover, 2010; Hutchison et al., 2013; Preti et al., 2017). Research has reported associations with neural network dynamics and cognitive flexibility (Chen et al., 2016; Douw et al., 2016; Kupis et al., 2021), depression and rumination (Kaiser et al., 2016; 2019), and changes following emotional elicitation and affective/cognitive challenges (Gaviria et al., 2021a; 2021b).

A more dynamic approach to examining HRV and associated neural circuitry may promote the identification of transient network states that support and/or potentially alter flexible emotional responses across various contexts that could otherwise be overlooked with the application of conventional, static neuroanalytical techniques. A few empirical studies have investigated both HRV and transient neural connectivity with the sliding window technique (Chand et al., 2020; Chang et al., 2013; Schumann et al., 2021), in which dynamic functional connectivity is measured through application of a sliding time window at a fixed length that correlates changes in functional connectivity between pairs of brain regions (Hindriks et al., 2016; Preti et al., 2017). While this technique is both popular and informative, it is limited by its reliance on arbitrarily fixed time windows (Preti et al., 2017). An alternative approach, Co-Activation Pattern (CAP) analysis (Liu & Duyn, 2013; Liu et al., 2018) overcomes the requirement to select specific time windows and associated parameters, and instead uses a clustering method to separate fMRI data into spatially distinct patterns of co-activation to generate separable brain states throughout the scan. Each brain state or ‘CAP’ is accompanied with temporal metrics, including frequency (i.e., number

of times a brain state is expressed) and average duration (i.e., mean duration or 'dwell time' in which a particular brain state is maintained) which can be used as indicators of neural 'flexibility' in a given context. Overall, while evidence from neuroimaging studies provides support for the NIM, many of these studies have assessed the relationship between HRV and brain activity and/or connectivity using resting-state paradigms and with techniques that assume stationarity of the brain. Therefore, examining HRV and associated neural circuitry during contexts that require flexible emotional responding, alongside the application of dynamic neuroanalytical techniques, may facilitate further, and a more direct, evaluation of the NIM.

1.11 Rest Versus Task-Related HRV and Adaptive Emotional Responding

In a similar vein, HRV research has primarily focused on associations between resting HRV and measures of emotional responding, with less focus on recording HRV during tasks that require adaptive emotional responses and regulation. Indeed, prior studies suggest that resting HRV and phasic HRV changes during tasks are positively coupled (Butler et al., 2006; Park et al., 2014). However, fewer studies have aggregated HRV across the entire duration of the task, herein referred to as 'task-based' or 'task-related' HRV. Strong positive associations have been reported between resting HRV measures and HRV recorded during stress (Wang et al., 2009), a challenging working memory task (Heffner et al., 2022), and active emotion regulation (Guendelman et al., 2024). Taken together, while resting HRV appears to capture an individual's general emotion regulation ability, phasic HRV changes or task-based HRV appear to more directly reflect autonomic flexibility and the ability to adapt or exert regulatory effort. Since the recent extension of the NIM outlines higher-order vagal circuitry that is 'online' during goal-directed behaviour and active regulatory processes (Smith et al., 2017), and considering that HRV is proposed to be an index of adaptive autonomic and self-regulatory function (Appelhans & Luecken, 2006), then measuring both HRV and concomitant neural activity not only at rest, but during contexts that require flexible emotional responding will put higher-order circuitry of the NIM to the test, alongside providing further insight into, and amplifying the ability to detect, neural regions and circuitry that support adaptive emotion (regulatory) processes as a function of HRV.

1.12 Overall Thesis Aim and Overview of Papers

1.12.1 Overall Aim of the Thesis

As reviewed above, the NIM (Smith et al., 2017; Thayer et al., 2000, 2009) is one of the most influential theoretical frameworks informing neuroimaging and psychological research examining HRV and emotion over the last 20 years. At the heart of the NIM framework, resting HRV is posited to serve as a metric of optimal prefrontal functioning and effective heart-brain coupling, such that higher HRV reflects greater adaptability to environmental changes and more effective self-regulation, including emotion regulation (Appelhans & Luecken, 2006; Balzarotti et al., 2017). Nevertheless, most research has focused on the relationship between HRV and neural functional connectivity and/or activity with resting-state paradigms, as opposed to contexts that require the engagement of emotion regulatory processes or flexibility. The recent extension to the NIM outlines an 8-level vagal hierarchy, with higher levels proposed to facilitate coordination of external perception/attention, memory and bodily state, regulatory processes (i.e., enhancement, maintenance, or suppression of representations), and goal-directed behaviour (Smith et al., 2017). While resting-state research has been informative for elucidating key neurovisceral circuitry as a function of HRV, the evaluation and examination of higher vagal control levels requires examination of HRV and neural/behavioural responses in contexts that directly increase metabolic demand and thus recruit proposed neural regions forming part of higher-order vagal control circuitry. Alongside recent criticisms of resting-state paradigms (Finn, 2021), it appears imperative that further neuroscientific and psychological research assesses both HRV and associated adaptive emotional responses at neural, psychological, and behavioural levels, during contexts that require emotion flexibility and regulation. In doing so, this will provide a clearer understanding of the degree to which HRV predicts adaptive emotional responses across contexts with associated findings leading to the development of further, testable predictions that will help to refine the current neurovisceral framework and its proposed mechanisms. This could also potentially inform alternative techniques or treatment options for boosting adaptive emotional responding to prevent the onset or progression of psychopathology, such as anxiety and depression.

The principal aim of this thesis was to examine the degree to which HRV serves as a metric, and facilitates, adaptive emotional responding at the neural and

behavioural level. Three stand-alone papers contributed to this overall aim which are briefly outlined in the following sections.

1.12.2 Chapter 2, Paper 1: Task-Related HRV and Amygdala-mPFC Functional Connectivity During Voluntary Emotion Regulation in Younger and Older Adults

The NIM outlines shared neural regions proposed to support both autonomic and emotion regulatory processes (Thayer et al., 2000, 2009). A growing body of neuroimaging studies provide supporting evidence for the NIM and links between resting HRV and brain areas underlying adaptive emotion regulation, including the mPFC and amygdala (Mather & Thayer, 2018; Nashiro et al., 2023; Sakaki et al., 2016; Schumann et al., 2021; Steinfurth et al., 2018; Thayer et al., 2012). However, the degree to which HRV is associated with neurovisceral circuitry during contexts that require adaptive emotion regulation is comparatively scarce, with fewer studies assessing both HRV and neural functional connectivity or activity in emotional contexts concurrently. Given that the NIM emphasises the role of effective prefrontal functioning and cortical-subcortical coupling as supporting self-regulatory processes reflected by higher HRV, examining HRV and neural circuitry during contexts requiring active engagement of emotion regulatory processes is therefore likely to further current understanding of heart-brain function in supporting adaptive emotion regulation.

Correspondingly, Paper 1 aimed to examine whether task-related HRV was associated with amygdala-mPFC functional connectivity during a voluntary emotion regulation task in a sample of younger and older adults. Furthermore, for conceptual replication and comparative purposes, task-related HRV and corresponding amygdala-mPFC functional connectivity, from resting-state fMRI data acquired 1-2 weeks prior to the session in which the emotion regulation fMRI data and task-based HRV was obtained, was also assessed. Based on prior findings (Sakaki et al., 2016), it was hypothesised that individuals with higher task-related HRV would demonstrate stronger functional coupling between the amygdala and mPFC during emotion and resting-state contexts. Participants engaged in a cognitive reappraisal task, receiving instructions to either enhance (increase), suppress (decrease), or maintain (view), negative affective pictures in the MRI scanner. HRV measures were derived from a finger pulse signal throughout the scan.

1.12.3 Chapter 3, Paper 2: Task-Related and Resting HRV and Associated Dynamic Co-Activation of Neural Networks During Emotion and Resting Contexts

Following on from Paper 1, alongside research primarily focusing on examining HRV and neural connectivity and/or activity during rest, most of these studies have also typically adopted relatively 'static' neural functional connectivity approaches. However, the dynamic and non-stationary nature of the brain and the involvement of wider neural networks has been increasingly recognised (Allen et al., 2014; Chang & Glover, 2010; Liu & Duyn, 2013; Preti et al., 2017). A dynamic approach to examining HRV and associated neural circuitry may promote the identification of transient neural network states that support and/or alter flexible emotional responding across various contexts which could potentially otherwise be overlooked with the application of traditional static neural methods.

Therefore, the primary aim of Paper 2 was to examine the relationship between task-related and resting HRV and co-active neural network states during emotion and resting-state contexts. Two samples of younger adults were derived from the openly available Amsterdam Open MRI Collection (AOMIC) dataset (Snoek et al., 2021). CAP analysis (Liu & Duyn, 2013; Liu et al., 2018) is a clustering method that separates fMRI data into spatially distinct patterns of co-activation to generate different brain states that are each accompanied with temporal metrics. We performed CAP analyses with seed regions of interest in areas closely linked to emotion processing: right and left amygdala and the bed nucleus of the stria terminalis (Baas et al., 2004; Grogans et al., 2024). It was hypothesised that individuals with lower task-based and resting HRV would exhibit increased occurrences and a significantly longer average duration in salience network co-active states. Moreover, trait neuroticism, a stable disposition linked to elevated negative affect and emotional reactivity (Ormel et al., 2013), is associated with a greater risk of onset and progression of anxiety and depression (Kootker et al., 2016; Kotov et al., 2010). Both HRV and neuroticism demonstrate associations with attentional (dis)engagement of negative emotional information, but the relationship between these two trait markers remains unstable (Čukić & Bates, 2015; Ode et al., 2010; Shepherd et al., 2015; Sloan et al., 2017). Thus, a secondary aim of this study was to assess the relationship between HRV and trait neuroticism, alongside their potential interaction, in predicting co-active dynamic networks during emotion and rest. It was hypothesised that younger adults with higher self-reported

trait neuroticism would exhibit a higher average duration and greater occurrences of salience-related and default mode network co-active states during both contexts, but with associations predicted to be weaker in individuals with higher rest and/or task-related HRV. Participants engaged in an emotion processing task which involved matching one of two picture stimuli to a target image, which was either a face depicting a fearful or angry expression (emotion) or a neutral oval shape presented in either a horizontal or vertical position. While the emotion matching task does not directly assess emotion flexibility, effective engagement in the task is facilitated by processes akin to flexibility (i.e., inhibition of processing emotional information when switching to matching neutral stimuli in control blocks). Task-based and resting HRV metrics were derived from pulse signals acquired via a finger pulse oximeter during both the emotion task and resting-state scan.

1.12.4 Chapter 4, Paper 3: Associations Between Individual Differences in Emotional Disposition (Valence Bias and Rumination) and Task-Related and Resting HRV with Affective Flexibility

While the first two papers assessed adaptive emotional responses in the form of emotion regulation (reappraisal of negative emotional information; Paper 1) and adaptive emotional processing (shifting attention to and from negative emotional information; Paper 2), Paper 3 focused on emotion flexibility in the form of attentional switch costs based on adaptive (dis)engagement to and from positive and negative emotional information. Previous studies have examined 'affective flexibility', the degree to which an individual flexibly shifts attention to and from emotional material, using an affective switching task, which involves categorising positive and negative emotional pictures according to either an affective (valence) or non-affective (number of humans) rule (Genet et al., 2013; Malooly et al., 2013). Various studies have focused on the relationship between psychological variables, including rumination and HRV (Genet et al., 2013; Grol & De Raedt, 2020), and switch costs based on the rule (i.e., switching from an affective to a non-affective rule or vice versa when the valence of the image is held constant). However, for the purposes of this paper, we opted to focus more closely on attentional shifts pertaining to the 'affective' aspect of the task, specifically switch costs based on changes in the valence of the emotional image (i.e., where the emotional image changed from a positive valence to a negative valence or vice versa when the trial categorisation rule was held constant). We think that these

switch costs more closely capture *affective* flexibility. We adopted three stable trait-like variables that are posited to reflect (in)flexible emotional responding: valence bias (ratings of emotionally ambiguous stimuli), trait rumination, and HRV. Inclusion of these measures permitted the examination of both psychological (i.e., rumination, affective bias ratings) and physiological (HRV) indices of flexible emotional disposition.

The overall aim of Paper 3 was to examine the degree to which measures of trait affect (valence bias and rumination) and both resting and task-related HRV predicted affective flexibility in both an online (Study 1) and laboratory (Study 2) context. We hypothesised a higher trait-like negativity bias to be correlated with greater switch costs when shifting attention away from images with a negative valence, particularly in an affective context. This hypothesis was based on studies that report individuals with anxiety and depression exhibit difficulties disengaging from negative valenced stimuli (Bar-Haim et al., 2007; Mogg et al., 1995; Koster et al., 2011), and in turn, trait-like negativity biases have been associated with anxiety and depressive symptoms (Park et al., 2016; Petro et al., 2021). Regarding attentional shifts pertaining to rule type, a secondary prediction was that greater negativity bias would significantly predict elevated switch costs when shifting attention from affective towards non-affective aspects of negative information. With relation to trait rumination, it was hypothesised that individuals with higher trait rumination, particularly brooding rumination, would have greater switch costs when the valence of the image switched from negative to positive, especially in an affective rule context. With relation to HRV in Study 2, we anticipated that individuals with higher (resting and task-based) HRV would exhibit reduced switch costs in their response time when shifting attention from negative towards positive valence images (greater affective flexibility), but higher switch costs in response time when shifting attention from positive towards negative valence images (greater affective *in*flexibility). Based on prior work (Genet et al., 2013), we also hypothesised rumination (particularly brooding rumination) to be linked to higher switch costs towards non-affective aspects of negative information, and lower switch costs when shifting attention towards non-affective aspects of positive information. Affective flexibility was measured using an established task paradigm (Genet et al., 2013; Malooly et al., 2013) and both valence and rule switch costs were calculated. Trait-like valence bias was operationalised as the relative dominance of negative versus positive ratings in response to emotionally ambiguous (i.e., surprise

faces) stimuli. A pulse signal was acquired via a finger pulse oximeter throughout the emotion tasks and a rest period in the laboratory (Study 2).

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Chapter 2.

Heart rate variability covaries with amygdala functional connectivity during voluntary emotion regulation

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2.1 Abstract

The Neurovisceral Integration Model posits that shared neural networks support the effective regulation of emotions and heart rate, with heart rate variability (HRV) serving as an objective, peripheral index of prefrontal inhibitory control. Prior neuroimaging studies have predominantly examined both HRV and associated neural functional connectivity at rest, as opposed to contexts that require active emotion regulation. The present study sought to extend upon previous resting-state functional connectivity findings, examining task-related HRV and corresponding amygdala functional connectivity during a cognitive reappraisal task. Seventy adults (52 older and 18 younger adults, 18–84 years, 51% male) received instructions to cognitively reappraise negative affective images during functional MRI scanning. HRV measures were derived from a finger pulse signal throughout the scan. During the task, younger adults exhibited a significant inverse association between HRV and amygdala-medial prefrontal cortex (mPFC) functional connectivity, in which higher task-related HRV was correlated with weaker amygdala-mPFC coupling, whereas older adults displayed a slight positive, albeit non-significant correlation. Furthermore, voxelwise whole-brain functional connectivity analyses showed that higher task-based HRV was linked to weaker right amygdala-posterior cingulate cortex connectivity across older and younger adults, and in older adults, higher task-related HRV correlated positively with stronger right amygdala-right ventrolateral prefrontal cortex connectivity. Collectively, these findings highlight the importance of assessing HRV and neural functional connectivity during active regulatory contexts to further identify neural concomitants of HRV and adaptive emotion regulation.

Keywords: Heart Rate Variability; Neurovisceral Integration Model; Amygdala; Medial Prefrontal Cortex; Functional Connectivity

2.2 Introduction

The ability to flexibly respond to ongoing and complex changes in our environment, in both a timely and contextually appropriate manner, is crucial for successful adaptation to environmental challenges and emotion regulation (Aldao et al., 2015; Thompson, 1994). Responses to such situational demands generates a cascade of changes at both subjective (e.g., emotional states, expressions) and physiological (e.g., elevations or reductions to heart rate, sweating, heightened neural responding) levels. Heart Rate Variability (HRV), physiologically defined as the variation in time intervals between consecutive heart beats, has increasingly been employed as an objective, peripheral measure to capture individual differences in adaptive autonomic responding and self-regulatory capacity, including emotion regulation (Appelhans & Luecken, 2006).

Resting HRV reflects the predominance of the parasympathetic branch of the autonomic nervous system (ANS). Both the sympathetic and parasympathetic branches directly innervate the heart via the stellate ganglia and vagus nerve respectively (Berntson et al., 1997). Dynamic interplay between both branches produces complex variations in the heart rate period that is captured by HRV, but it is the fast, modulatory impact of the parasympathetic nervous system (via the vagus nerve) that reportedly exhibits the strongest influence on the heart's pacemaker (i.e., sinoatrial node) and subsequent variation in heart rate, particularly at rest (Berntson et al., 1997). Greater variation in the time intervals between successive heart beats (Root Mean Square of Successive Differences, RMSSD) and dominance of high frequency (HF) heart rate oscillations (HF-HRV) are HRV parameters that capture the predominance of the parasympathetic branch of the ANS (Shaffer & Ginsberg, 2017). Typically, higher levels of HRV at rest indicate a more adaptive and responsive cardiovascular system, supporting fast and flexible alterations in physiological responses to effectively manage stressors, as well as maintaining homoeostasis (Shaffer & Ginsberg, 2017; but see Kogan et al. (2013) for discussion on the quadratic nature of HRV).

Several models discuss the role of HRV in adaptive psychophysiological responding (Grossman & Taylor, 2007; Laborde et al., 2018; Porges, 2007, 2011; Smith et al., 2017; Thayer & Lane, 2000, 2009). In particular, the Neurovisceral Integration Model (NIM; Smith et al., 2017; Thayer & Lane, 2000, 2009) outlines a complex and reciprocal network of neural regions that overlap to support autonomic,

cognitive and affective regulatory processes. At the heart of the NIM is the 'central autonomic network' (CAN; Benarroch, 1993) which encompasses higher cortical structures (e.g., ventromedial prefrontal cortex, anterior cingulate cortex), subcortical limbic regions (e.g., central nucleus of the amygdala, hypothalamus), and brainstem structures (e.g., periaqueductal gray, parabrachial nucleus), forming a vital, coordinated network that facilitates autonomic function and regulation (Benarroch, 1993; Thayer et al., 2009a). The NIM posits that the prefrontal cortex exerts tonic inhibitory control over subcortical structures, and by extension the vagus nerve. As such, resting HRV is proposed to serve as an index of the effective functioning of inhibitory cortical-subcortical connectivity and Central Nervous System-Autonomic Nervous System integration, in turn promoting adaptive self-regulation (Thayer & Lane, 2000, 2009; Thayer et al., 2009a).

A growing body of neuroimaging research lends support for the NIM and the link between resting HRV and emotion regulation-related brain function (Mather & Thayer, 2018; Sakaki et al., 2016; Schumann et al., 2021a; Steinfurth et al., 2018). A prior meta-analysis highlighted significant and consistent associations between HRV and cerebral blood flow in the mPFC (including rostral and subgenual anterior cingulate regions) and the amygdala across several studies (Thayer et al., 2012). Importantly, despite reported reductions in resting HRV with age (Agelink et al., 2001; Russoniello et al., 2013), both older and younger adults with relatively higher resting HRV exhibited stronger resting medial prefrontal cortex (mPFC)-amygdala functional connectivity (Nashiro et al., 2022; Sakaki et al., 2016). Higher HRV has also been linked to stronger resting amygdala-ventrolateral prefrontal cortex (vlPFC) connectivity in younger adults (Sakaki et al., 2016). Relatedly, a study conducted by Kumral et al. (2019) found that younger adults with higher resting HRV had stronger bilateral ventromedial prefrontal cortex (vmPFC) connectivity, with this vmPFC seed demonstrating further extended functional connectivity with several CAN regions. Increasing resting HRV via biofeedback interventions (e.g., slow breathing, Lehrer & Gevirtz, 2014) has been reported to elevate resting-state functional connectivity of the vmPFC to neural regions implicated in emotional processing and the NIM, including the amygdala, middle cingulate cortex, anterior insula, and lateral PFC (Schumann et al., 2021a). Interestingly, fewer studies have assessed HRV and associated neural activity during tasks that require emotional or self-regulatory processes. Higher resting HRV has previously been linked to increased vmPFC activation during an effortful self-

control dietary task in younger adults (Maier & Hare, 2017). Moreover, while engaging in a voluntary emotion regulation task, younger adults with higher resting HRV more effectively recruited the dorsal medial prefrontal cortex to modulate amygdala responses via reappraisal (Steinfurth et al., 2018).

Collectively, prior research supports the notion that HRV serves as a measure of effective, inhibitory cortical-subcortical connectivity, with the PFC and amygdala showing consistent associations with HRV (Thayer et al., 2012). Relatedly, mPFC-amygdala interconnectivity has been reported to facilitate successful emotion regulation (Etkin et al., 2011). It has been suggested that medial regions of the prefrontal cortex support automatic or implicit forms of emotion regulation, whereas more lateral regions facilitate explicit emotion regulation (Braunstein et al., 2017; Phillips et al., 2008). Others propose that higher order, cognitive control regions (i.e., ventrolateral and dorsolateral prefrontal cortex) impart control messages to the amygdala via the vmPFC given stronger anatomical connections between the amygdala and mPFC (Buhle et al., 2014). Indeed, many of the brain areas identified in HRV neuroimaging studies overlap with regions that support implicit and explicit emotion regulation (Braunstein et al., 2017; Buhle et al., 2014; Morawetz et al., 2020; Wager et al., 2008).

Nonetheless, it is evident that previous research has largely assessed both HRV and neural functional connectivity predominantly at rest. Resting-state paradigms have recently received criticism in the literature, especially in relation to the utility, interpretability, and reliability of neural findings observed under resting-state contexts (Finn, 2021). Indeed, the state of ‘rest’ is increasingly being recognised as a ‘task’ in and of itself, with many unconstrained, internal state factors contributing to diverse cognitive states (Finn, 2021), including mind wandering and self-generated thoughts (Gorgolewski et al., 2014; Smallwood & Schooler, 2015), and drifts in sleep-wakefulness stages (Tagliazucchi & Laufs, 2014). Recent evidence has highlighted the potential advantage of demands imposed by task engagement, and how such demands may constrain underlying neural functional connectivity to reduce variance related to aforementioned internal state factors, in turn increasing sensitivity to detect individual differences of interest (Finn & Bandettini, 2021).

Relatedly, whilst resting HRV has most commonly been assessed in prior work, fewer studies have assessed HRV during tasks. A growing body of research has examined phasic changes in HRV, including phasic HRV changes in reactivity to, and

recovery from, task-related stressors and events relative to baseline HRV levels (Butler et al., 2006; Denson et al., 2011; Park et al., 2014; Segerstrom & Nes, 2007; for a review see: Laborde et al., 2018). Empirical evidence supports the notion that phasic HRV increases are indicative of self-regulatory effort and emotion regulation success (Butler et al., 2006; Denson et al., 2011; Ingjaldsson et al., 2003; Park et al., 2014; Segerstrom & Nes, 2007). Crucially, resting levels of HRV has been found to modulate such phasic HRV increases (Park et al., 2014). For instance, women with higher resting HRV experienced greater phasic HRV increases during successful voluntary emotion regulation via reappraisal and emotional suppression in comparison to those with lower resting HRV (Butler et al., 2006). Phasic HRV increases have also been linked to greater activation in the subgenual anterior cingulate cortex, a region involved in emotion regulation (Lane et al., 2013). In a similar vein, strong positive associations have been reported between resting HRV and HRV assessed during stress (Wang et al., 2009) and a challenging working memory task (Heffner et al., 2022). Collectively, empirical evidence suggests that individuals with higher resting HRV are more likely to demonstrate phasic HRV increases when challenged by stimuli or events that require self-regulatory effort, reflecting more adaptive responding to task demands and successful emotion regulation.

Overall, since the NIM emphasises the role of inhibitory cortical-subcortical circuitry in supporting adaptive self-regulation, examining HRV and associated functional connectivity in contexts that require active engagement of emotion regulatory processes may help to further our understanding of heart-brain function in supporting emotion regulation. The current study sought to extend prior resting-state functional connectivity findings by assessing pulse-derived HRV and neural functional connectivity whilst participants actively engaged in a voluntary emotion regulation task in the scanner. As the pulse signal was acquired during the scan only, we aggregated HRV across the emotion regulatory context to derive task-related HRV. Based on empirical evidence from prior studies linking higher resting HRV to greater phasic HRV during emotion regulation (Butler et al., 2006; Denson et al., 2011), any phasic HRV increases during the reappraisal task in the current study would likely be captured as elevated task-related HRV when aggregated across the entire duration of the task. Also, considering that HRV is positively correlated within individuals across contexts (Heffner et al., 2022; Wang et al., 2009), the relative rank order of task-related HRV metrics across individuals during a reappraisal task should be similar to that observed

during rest (i.e., individuals with lower resting HRV will likely exhibit lower task-based HRV compared to those with higher resting, and thus higher task-based, HRV). Extrapolating from prior resting-state HRV studies, considering the shared role of the mPFC in HRV control and emotion regulation, we hypothesised that task-related HRV would be positively associated with stronger functional connectivity between the amygdala and the mPFC. The mPFC seed region used in the present study was previously adopted as a region of interest in Sakaki et al. (2016) and demonstrated robust associations with resting HRV. Specifically, we predicted that individuals with higher task-related HRV would exhibit stronger positive amygdala-mPFC functional connectivity during a cognitive reappraisal task. Given that pulse recordings were obtained concurrently in the scanning session with the reappraisal task, our primary focus was to examine the relationship between HRV and amygdala connectivity in an emotion regulation context, adopting a functional connectivity analysis similar to that performed on resting-state data (e.g., calculating functional connectivity during the reappraisal task). However, for conceptual replication and comparative purposes, we further assessed task-related HRV and associated resting-state functional connectivity acquired during an initial scanning session that took place 1-2 weeks prior to the session where the task-related HRV measures were obtained. For transparency, further details and results are presented in the Supplementary Material.

2.3 Method

2.3.1 Participants

Participants in the current study were derived from a larger sample of 91 subjects (71 older adults, 20 younger adults) previously recruited as part of an ageing research project (Lloyd et al., 2021; https://openneuro.org/datasets/ds002620)[1]. Participants were recruited via the University of Reading's Older Adult Research Panel and through local poster and newspaper advertisements in Reading. Participants received financial compensation (£7.50 per hour) for their participation. From the overall sample, 74 participants (55 older adults, 19 younger adults) had both emotion regulation task-based functional magnetic resonance imaging (fMRI) and pulse data.

[1] The original research project sought to examine associations between neural function, cognitive function, and emotion regulation within an older adult population. A smaller sample of younger adults matched for gender and education level were recruited as an additional control for age in the original study.

Figure 2 illustrates the participant selection and exclusion process. Following exclusion, 70 participants (52 older and 18 younger adults, aged 18–84 years, *M* age = 58.27 years, SD = 20.33; 51% male) were considered for analyses (see Table 1 for details per age group).

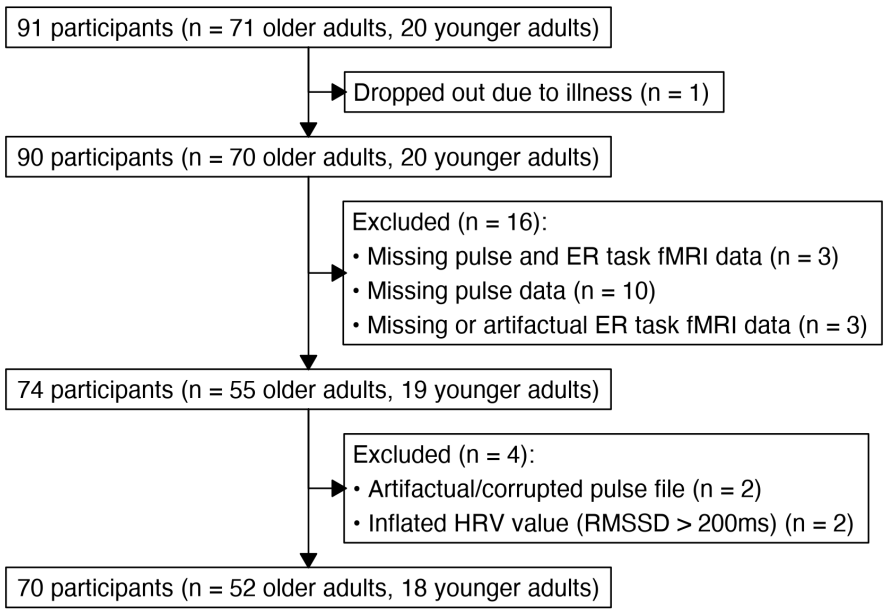

Figure 2. Participant Selection and Exclusion Process. Participants were selected from a larger pool of subjects recruited as part of a wider ageing study.

All participants were right-handed and reported no history of neurological disorder. Medical history and medication details were obtained for the older adults only. Of the older adults included in the study (*N* = 52), 15 disclosed taking regular medication for blood pressure and/or cardiovascular health: statins (*N* = 8), angiotensin-converting enzyme inhibitors (*N* = 2), angiotensin receptor blockers (*N* = 2), calcium channel blockers (*N* = 2) and beta-blockers (*N* = 1). The remaining 37 participants did not report use of medication related to cardiovascular health. Furthermore, 21 participants reported having experienced a cardiovascular health condition: high blood pressure (*N* = 12), high cholesterol (*N* = 6) and mini-stroke (*N* = 3). Given that we did not observe significant differences in task-related HRV between those taking cardiovascular medication ($t(50) = -0.46$, $p = .647$, $d = -0.14$) and those who disclosed a history of cardiovascular disease ($t(50) = -0.70$, $p = .485$, $d = -.20$), with participants who did not report use of

cardiovascular medication and/or a history of cardiovascular disease, we opted to retain these older adults in the analyses.

The research study from which the current sample was derived was carried out in accordance with the Declaration of Helsinki (1991, p.1194). The study's procedures were given a favourable ethical opinion of conduct by the University of Reading's Research Ethics Committee and NHS Research Ethics Service. Participants provided written informed consent prior to their participation.

2.3.2 Materials and Procedure

2.3.2.1 Cognitive Reappraisal Task

Participants engaged in a voluntary emotion regulation task during the scan, which followed an established cognitive reappraisal paradigm employed by previous research (e.g., van Reekum et al., 2007). Cognitive reappraisal is an antecedent-focused strategy that requires an individual to reinterpret or alter the meaning of an emotional event (Gross & John, 2003). A detailed description of the reappraisal task and stimuli can be found in Lloyd et al. (2021).

The cognitive reappraisal task comprised 96 trials in total, in which 72 negative and 24 neutral pictures obtained from the International Affective Picture System (IAPS; Lang et al., 2008) were presented. On a given trial, participants were instructed to either “suppress” (decrease), “enhance” (increase), or “maintain” their emotional response and attend to the image presented (neutral images were always paired with the “maintain” instruction)[2]. The “suppress” instruction in this task involved imagining an outcome less negative than the participant's original thoughts and/or feelings towards the image to reduce the intensity of any emotions experienced, as opposed to (expressive) suppression, a response-focused strategy that involves controlling emotion-expressive behaviours (Gross & John, 2003). The “enhance” instruction required imagining a worse or more negative outcome to increase the intensity of any emotions experienced. In the “maintain” condition, participants were instructed to simply attend to the image and sustain their emotional response. Following the presentation of the picture and engagement in the relevant auditory regulation

[2] Participants received training and practice on the task prior to scanning to ensure that the regulatory strategies were used as intended (see Lloyd et al. (2021) for further details and the full instructions provided during the practice session). Furthermore, the words “suppress” and “enhance” were selected as opposed to “decrease” and “increase” to ensure that the auditory instruction for these conditions was distinctive.

instruction, a rating screen appeared for a fixed duration of three seconds, during which participants were asked to rate the intensity of their emotion in response to each image on a four-point scale (1 = neutral, 2 = somewhat negative, 3 = quite negative, 4 = very negative). Responses were recorded via a 4-button MR-compatible button box held in the participant's right hand and the button order was counterbalanced between subjects (1 = neutral, 4 = very negative or vice versa).

The scanning procedure was distributed across four identical runs, with 24 trials in each run. The duration of each run was approximately seven minutes, with rest breaks offered between runs, leading to an overall task duration of approximately 30 minutes.

2.3.3 Data Reduction and Analysis

2.3.3.1 HRV Processing and Analysis

A pulse signal was continuously recorded via an MRI-compatible pulse oximeter clip attached to the participant's left finger throughout the scanning session, including breaks (sampling rate = 50 Hz). The pulse oximeter was integrated with the Siemens Magnetom Trio MRI scanner, from which the raw pulse signal was subsequently extracted.

The raw pulse files underwent visual inspection for quality and usability prior to pre-processing and were formatted to read into LabChart software (version 8.1.11; AD Instruments, Oxford, UK). Initial manual edits within LabChart involved trimming the beginning and/or end of the file where flatlines and/or obvious calibration and motion-related noise were visually detected. Subsequently, LabChart files were converted and exported into LabChart text files to ensure compatibility with Kubios HRV Analysis software (version 2.2; Biosignal Analysis and Medical Imaging Group, University of Kuopio, Finland; Tarvainen et al., 2014). Further processing of the pulse signal and calculation of HRV measures were performed within Kubios. Taking into consideration variation in breaks between runs and tasks, alongside the quality of the pulse signal, participants had somewhat varying durations of pulse signal for analysis (range 17–76 min, *M* duration = 51 min). Occasionally, the automated peak detection feature either misplaced or missed the pulse peak, thus resulting in manual corrections to either place or (re)move markers to the peak of the pulse waveform. Following manual corrections, data were artefact-corrected using the “low” threshold setting (350 ms)

across all participants to retain as many natural variations between heart beats as possible.

The Root Mean Square of Successive Differences (RMSSD), measured in milliseconds, and High-Frequency HRV (HF-HRV), defined using a frequency band of 0.15–0.40 Hz, measured in absolute power (ms^2, Fast Fourier Transform) were calculated within Kubios. Both measures were natural log transformed (ln) to correct for positive skew within RStudio (version 1.4.1106) using the 'log' command from the *base* package (v3.5.2). Despite variation in pulse duration, this did not demonstrate a significant correlation with either raw RMSSD ($r = -0.04$, $p = .747$) or natural log transformed RMSSD ($r = 0.03$, $p = .839$) values across participants ($N = 70$). Whilst RMSSD and HF-HRV metrics reflect parasympathetic vagal control, the RMSSD is a primary and robust measure of vagal tone (Kleiger et al., 2005), that is generally less susceptible to physiological noise, including respiratory influence (Hill et al., 2009). Also, given that both natural log transformed HRV measures exhibited a strong positive association in the current study ($r = 0.98$, $p < .001$), we proceeded with the (ln)RMSSD as our primary HRV metric for all analyses.

2.3.3.2 MRI Procedure and Image Acquisition

Participants were invited to attend two different sessions within the Centre for Integrative Neuroscience and Neurodynamics (CINN) at the University of Reading. Structural and blood oxygenation level dependent (BOLD) functional imaging data were acquired using a 3T Siemens Magnetom Trio MRI scanner with a 12-channel head coil (Siemens Healthcare, Erlangen, Germany). The first session comprised an initial scanning protocol to obtain anatomical T1-weighted (T1w) structural scans, localisers and a resting-state scan (MRI acquisition details provided in Supplementary Material). Participants also engaged in several cognitive tasks outside of the scanner which are summarised elsewhere (Lloyd et al., 2021). The overall duration of the first session was approximately three hours (one hour scanning time). Participants were invited back for a second session which took place a few days (two weeks maximum) after the first session. For each participant, a 3D structural MRI was obtained via a T1-weighted sequence (Magnetization Prepared Rapid Acquisition Gradient Echo (MPRAGE)), repetition time (TR) = 2020 ms, echo time (TE) = 3.02 ms, inversion time (TI) = 900 ms, flip angle 9°, field of view (FOV) = 250 × 250 × 192 mm, resolution = 1 mm isotropic, acceleration factor = 2, averages = 2, acquisition

time = 9 min, 7 s). Participants also performed two tasks whilst in the scanner: the cognitive reappraisal (emotion regulation) task and an emotional faces processing task. The emotion regulation fMRI data were obtained in four blocks of identical procedure, using an echo planar imaging (EPI) sequence (211 whole-brain volumes, 30 sagittal slices with *P>A* phase encoding, slice thickness = 3.0 mm, slice gap = 33%, TR = 2000 ms, TE = 30 ms, flip angle = 90°, FOV = 192 × 192 mm^2, resolution = 3 mm isotropic, acquisition time = 7 min 10 s per block). The participant's pulse was recorded throughout the scan. The overall duration of the second session was approximately two hours (one hour scanning time). Structural and emotion regulation fMRI task data are publicly available on OpenNeuro: https://openneuro.org/datasets/ds002620/versions/1.0.0.

2.3.3.3 MRI Data Pre-Processing

Functional imaging data were pre-processed and analysed using FMRIB's Software Library (FSL, version 6.0; www.fmrib.ox.ac.uk/fsl; Jenkinson et al., 2012; Woolrich et al., 2009; Smith et al., 2004) and Analysis of Functional NeuroImages (AFNI, version 19.3.03; http://afni.nimh.nih.gov/afni; Cox, 1996). Initial pre-processing steps included: skull stripping (non-brain removal) using FSL's brain extraction tool (BET; Smith, 2002), motion correction using MCFLIRT (Jenkinson et al., 2002), field-map correction to correct for potential magnetic field inhomogeneity distortions, spatial smoothing using a Gaussian kernel with a full-width half maximum (FWHM) of 5 mm and high-pass temporal filtering (Gaussian-weighted least squares straight line fitting with sigma = 50 s). Each subject's functional image was first co-registered to their high resolution T1-weighted image using linear boundary-based registration (BBR) and subsequently normalised to the Montreal Neurological Institute (MNI) 152 T1 2 mm template using a 12 degrees of freedom affine transformation via FMRIB's Linear Image Registration Tool (FLIRT).

Application of individual-level Independent Component Analysis (ICA) via FSL's Multivariate Exploratory Linear Optimized Decomposition into Independent Components (MELODIC; Beckmann & Smith, 2004) separated the fMRI BOLD signal into a set of spatial maps (independent components) representing neural signal and/or noise. Independent components containing structured temporal noise, including scanner and hardware artefacts, physiological artefacts (respiratory and/or cardiac noise), and motion-related noise were identified via visual inspection and removed

using the FSL command line tool '*fslregfilt*' for each emotion regulation task run (Griffanti et al., 2017). An average percentage of 72.07% components were removed across the four runs. This aligns with previous research that has typically identified >70% noise versus signal components in standard sequences at 3T (Griffanti et al., 2017).

Following ICA filtering, low bandpass filtering was applied to the fMRI data using AFNI's '*3dBandpass*' tool (Cox, 1996) to further remove confounding signals below 0.009 Hz and above 0.1 Hz. Prior to analysis, each subject's corresponding mean functional timeseries image was added back to the bandpass filtered data using '*fslmaths*' to ensure compatibility with FSL's FMRI Expert Analysis Tool (FEAT).

Average framewise displacement (FD) for each participant and task run was calculated using the realignment parameters generated after initial motion correction with FSL's MCFLIRT (Power et al., 2012) and after denoising (i.e., following ICA and low bandpass filtering) using FSL's '*fsl_motion_outliers*' to assess changes in motion. Participants or task runs were not initially excluded for exceeding a set mean FD threshold for several reasons. The exclusion of participants with higher motion can introduce selection bias, as greater movement in the scanner may be a marker that correlates with relevant (sociodemographic or clinical) variables of interest, which in turn risks data becoming missing not at random (Nebel et al., 2022). Furthermore, there is still not a universally accepted FD threshold in which volumes or functional data are considered as being contaminated by excess motion, especially as the sensitivity of this threshold is likely to vary as a function of subject and/or acquisition factors (Pham et al., 2023). Importantly, FD is calculated prior to further denoising techniques, which risks the premature removal of functional volumes, task runs, and/or subjects that may exhibit lower motion-related noise following further processing (Pham et al., 2023). Correspondingly, in the current study, average FD across all task runs was minimal following denoising (M = 0.02 mm, SD = 0.01 mm, range = 0.01–0.05 mm), and no single volume across subjects exceeded 0.2 mm, suggesting that motion had been reduced using the outlined techniques.

2.3.3.4 Functional Connectivity Analysis

Regions of interest (ROIs) were separate right and left amygdala seeds, and an area of the mPFC previously found to be correlated with HRV (Sakaki et al., 2016). Separate amygdala ROIs were selected given recent discrepancies in amygdala

lateralisation with the mPFC as a function of HRV (Nashiro et al., 2022; Sakaki et al., 2016), and also observed lateralisation effects highlighted in previous research concerning emotion processing and regulation (Baas et al., 2004; Yang et al., 2020). Amygdala ROI masks were defined using the Harvard-Oxford Subcortical Probability atlas and thresholded at 80% probability (right amygdala: 114 voxels, 912 mm^3, centre of gravity: $x = 24$, $y = -3$, $z = -18$; left amygdala: 95 voxels, 760mm^3, centre of gravity: $x = -23$, $y = -5$, $z = -18$). The mPFC ROI contained voxels from the anterior cingulate cortex (ACC) and paracingulate gyrus thresholded at 25% probability (Harvard-Oxford atlas; 263 voxels, 2104mm^3, centre of gravity: $x = -1$, $y = 47$, $z = 8$). This mPFC area has previously been associated with memory positivity in older adults (Sakaki et al., 2013) but was more recently employed as a seed ROI in Sakaki et al. (2016), in which higher HRV was correlated with stronger amygdala coupling with this mPFC sub-region. Relatedly, both the ACC and mPFC have been shown to facilitate down-regulation of the amygdala (Etkin et al., 2011). All ROI masks (right and left amygdala, mPFC) were first transformed to each participant's native functional space using FSL's Apply FLIRT Transform '*ApplyXFM*' and binarised. Subsequently, the mean time series for each ROI was extracted from the four separate emotion regulation runs for each participant using '*fslmeants*'.

Separate first-level regression analyses were performed for each ROI using FEAT (Woolrich et al., 2001). Similar to a functional connectivity analysis typically performed on resting-state data, individual models included the mean time series extracted from the specific ROI and regressors of no interest, specifically: FSL's six standard head-motion parameters[3], and average white matter and ventricular (CSF) signal. Average signal from white matter and CSF was extracted from masks generated via segmentation of each participant's high resolution T1w image using FMRIB's Automated Segmentation Tool (FAST; Zhang et al., 2001).

Inclusion of global signal regression (GSR) has received scrutiny in the literature and remains a controversial pre-processing technique (Murphy et al., 2009; Murphy & Fox, 2017; Uddin, 2017). Although GSR is effective at removing global sources of noise, including physiological and motion artefacts (Li et al., 2019), the

[3] Note that inclusion of the six rigid-body motion parameters compared to the extended 24 motion parameters (i.e., the six motion parameters, their derivatives, and the squares of these) in the single subject models made a negligible difference to the spatial maps and timecourses at both the lower-level and fixed effects FEAT level.

global signal is not wholly comprised of noise and its topography has been associated with important physiological, cognitive, and age differences (Bolt et al., 2022; Li et al., 2019; Nomi et al., 2022). Importantly, in task-based contexts, global signal is highly correlated with the task paradigm (Mayer et al., 2019). Given the controversy and lack of consensus surrounding GSR, we did not include GSR as a regressor in the model.

Furthermore, the task design was not included as a regressor in the model. It is recognised that not including the task design as a regressor in task-based functional connectivity analyses can result in spurious correlations and systematic inflation of functional connectivity estimates due to task-induced coactivations (Cole et al., 2019). Whilst techniques such as finite impulse response (FIR) task regression have been recommended to reduce the influence of spurious or inflated results corresponding to task-evoked activations (Cole et al., 2019), this approach may not be as effective when applied to relatively fast event-related fMRI designs. Crucially, the overarching aim of the present study was to examine HRV and associated neural functional connectivity in a voluntary emotion regulation context. Since the visual presentation of the images and emotion regulatory processes were designed to be perfectly confounded in the reappraisal task, and HRV is also closely related to, and considered a metric of, regulatory ability, if task activation events that mainly reflect variation in emotion regulatory processes were to be regressed from the data, any brain coactivation with HRV would then be derived from residualised data, without the emotion regulatory context. Moreover, not regressing the task design has been reported to increase the reliability of functional connectivity measures (Cho et al., 2021). For these reasons, task design was not included as a regressor in the models.

Prior to group-level analyses, a second-level fixed effects analysis using FSL's FEAT was applied to the emotion regulation task-based fMRI data to collapse the ROI connectivity maps across the four task runs[4]. This generated mean positive and negative functional connectivity maps for input to higher-level analyses.

2.3.3.5 Amygdala-mPFC Functional Connectivity Analyses

Beta values (mean positive parameter estimates) from right and left amygdala connectivity maps were extracted using FSL's Featquery, with the mPFC seed as the

[4] Two participants were missing the final run of the emotion regulation task (run 4), so ROI connectivity maps were averaged across the three available task runs (runs 1-3) for these participants.

reference mask. The corresponding beta values served as an index of amygdala-mPFC connectivity strength.

Multiple regression analyses were employed to examine associations between task-related HRV and amygdala-mPFC functional connectivity strength in the whole sample. Separate multiple regression models were tested with (i) right amygdala-mPFC connectivity and (ii) left amygdala-mPFC connectivity values as dependent variables. A segregation in age (years) was observed between the older and younger adults, leading to a natural formation of two separate age groups (see Fig. S2 in the Supplementary Material). We therefore entered age as a categorical predictor in the regression models. The following predictors were entered into the regression model: age group (1 = older adults, 0 = younger adults), (ln)RMSSD (centered), and a HRV x age interaction term[5]. In each model, age group and HRV were entered first (step 1), followed by the HRV x age interaction predictor (step 2). Standardised beta coefficients are reported for all predictors in the Results.

2.3.3.6 Whole-Brain Functional Connectivity Analyses

Given the heterogeneous neurological profiles often observed in ageing brains (Chen et al., 2016), and the larger sample of older adults in the current study, we performed whole-brain functional connectivity analyses for all ROIs across the whole sample, including age as a blocking factor in the analyses, and further performed separate whole-brain analyses restricted to the older adult sample only. This allowed us to be more inclusive in our search for functionally-relevant regions associated with HRV that may have been excluded or otherwise missed using a ROI approach. Furthermore, the decision to run separate whole-brain connectivity analyses restricted to adults in the older age group was primarily driven by the unequal number of older relative to younger adults (and the comparative small sample size of the younger adult group), along with the strong effect of biological age on HRV (Agelink et al., 2001; Russoniello et al., 2013).

Whole-brain group analyses for each seed region were performed using FMRIB's Local Analysis of Mixed Effects (FLAME; Woolrich et al., 2004). The general linear model (GLM) included four explanatory variables: group mean and three

[5] To reduce the influence of multicollinearity that can occur between the original variables and the subsequent interaction that is comprised of those variables, the HRV x age interaction term was calculated by multiplying the centered (ln)RMSSD scores by the dummy coded age group.

predictors, HRV (lnRMSSD, centred), age (effect coded using +1 and −1 to define older and younger adult groups respectively) and a HRV by age interaction term (lnRMSSD centred x age group). Seven contrasts were entered into the model: group mean, HRV, age and the HRV by age interaction term (positive and negative contrasts for each EV). Clusters surviving a threshold of $Z > 3.1$ and correction for multiple comparisons with Gaussian random field theory (cluster significance: $p = 0.05$-corrected) were identified (Worsley, 2001). The locations of significant clusters that survived correction were labelled using the Harvard Oxford Cortical Structural and Subcortical atlases in MNI space within FSL. Mean beta values from significant clusters that emerged as a main effect of HRV were extracted for visualisation purposes.

2.4 Results

2.4.1 Descriptive Statistics

Table 1 summarises general descriptives for the whole sample and for older and younger adult age groups separately. HRV significantly differed by age group, such that older adults demonstrated significantly reduced HRV as indexed by lower (ln)RMSSD values ($M = 3.92$, $SD = 0.55$), in comparison to younger adults ($M = 4.29$, $SD = 0.44$), $F(1,66) = 6.06$, $p = .016$, $\eta_p^2 = 0.08$. However, there was no significant difference in (ln)RMSSD values between females ($M = 4.07$, $SD = 0.52$) and males ($M = 3.96$, $SD = 0.57$) across the whole sample, $F(1,66) = 0.09$, $p = .764$, $\eta_p^2 = 0.00$, nor was there a significant interaction between age group and sex on (ln)RMSSD values, $F(1,66) = 0.15$, $p = .698$, $\eta_p^2 = 0.00$. Thus, no significant differences in HRV related to sex were observed in the present study (see Fig. S1 in the Supplementary Material). Additionally, there was a significant difference in the mean RR interval ($t(68) = 2.06$, $p = .044$, $d = 0.56$), but no significant difference in mean heart rate ($t(18) = -1.64$, $p = .117$, $d = -0.68$) between older and younger adults.

Moreover, in relation to self-reported ratings of negative emotional intensity, older and younger adults reported significantly greater negative emotional intensity after the enhance (increase) regulatory instruction ($M = 2.78$, $SD = 0.39$) relative to the maintain (attend) instruction ($M = 2.60$, $SD = 0.33$) in response to negative images ($t(69) = 4.76$, $p < .001$, $d = 0.57$). Counterintuitively, negative emotional intensity ratings were slightly higher for the suppress (decrease) regulatory instruction

(*M* = 2.62, *SD* = 0.35) in comparison to the maintain instruction in response to negative pictures, but there was no significant difference in the ratings between these conditions ($t(69) = -0.52$, $p = .602$, $d = -0.06$). Overall, findings suggest that participants actively engaged in the reappraisal task and followed instructions to regulate, but reappraisal did not appear to significantly reduce negative affect beyond the control (maintain) condition[6].

[6] To target a more implicit metric of emotional reactivity, we examined differences in amygdala activation between the main regulatory conditions. Given that task events were not modelled in the present study, the findings reported here have been derived from analyses on the full dataset that formed part of a previous study (Lloyd et al., 2021). Using FSL's FeatQuery, the average % change in amygdala signal between the different regulatory conditions was extracted for left and right amygdala respectively (amygdala seed regions were the same as those adopted in the functional connectivity analyses in the present study). One-sample t-tests were conducted on the amygdala reactivity difference scores between regulatory conditions against zero. Following a similar pattern to self-reported negative emotional intensity, there was a significant change in amygdala reactivity between enhance (increase) and maintain (attend) conditions while responding to negative images across older and younger adults (for right amygdala: $t(69) = 3.67$, $p < .001$, $d = 0.44$; for left amygdala: $t(69) = 2.50$, $p = .015$, $d = 0.30$), in which right and left amygdala activation was greater after enhance relative to maintain, thus suggesting effective up-regulation, particularly of the right amygdala. No significant difference in amygdala activation emerged for suppress (decrease) relative to maintain in response to negative images (right amygdala: $t(69) = 0.60$, $p = .548$, $d = 0.07$; left amygdala: $t(69) = -0.12$, $p = .904$, $d = -0.01$), therefore no significant down-regulation of right or left amygdala reactivity was observed following the suppress regulatory instruction. For enhance relative to suppress in response to negative images, there was a significant difference in amygdala reactivity in which amygdala activation was significantly greater after enhance versus suppress across older and younger adults (right amygdala: $t(69) = 3.58$, $p < .001$, $d = 0.43$; left amygdala: $t(69) = 2.72$, $p = .008$, $d = 0.33$).

Table 1.
Participant characteristics (age, sex, HRV-related metrics, amygdala-mPFC connectivity and self-reported negative emotional intensity ratings for each task condition) across the whole sample and each age group. Data is provided in means and standard deviations (in parenthesis).

	Whole Sample (18-84 years) (N = 70)	Older Adults (55-84 years) (N = 52)	Younger Adults (18-35 years) (N = 18)
Demographics			
Age (years)	58.27 (20.33)	69.34 (8.08)	26.28 (4.75)
Sex (%)	49% F/51% M	44% F/56% M	61% F/39% M
lnRMSSD (ms)	4.01 (0.54)	3.92 (0.55)	4.29 (0.44)
Heart Rate (BPM)	67.60 (17.64)	64.61 (9.78)	76.24 (29.48)
RR Interval (ms)	937.73 (156.19)	959.80 (141.43)	873.97 (182.24)
fMRI Variables			
Right Amygdala-mPFC Connectivity (PE)	0.03 (0.13)	0.02 (0.11)	0.05 (0.16)
Left Amygdala-mPFC Connectivity (PE)	0.03 (0.11)	0.02 (0.10)	0.05 (0.11)
Emotion Intensity Ratings			
Enhance	2.78 (0.39)	2.75 (0.41)	2.88 (0.31)
Suppress	2.62 (0.35)	2.58 (0.37)	2.73 (0.28)
Attend (Negative)	2.60 (0.33)	2.56 (0.33)	2.73 (0.30)
Attend (Neutral)	1.26 (0.41)	1.26 (0.30)	1.28 (0.63)

2.4.2 HRV and Amygdala-mPFC Functional Connectivity Analysis

2.4.2.1 HRV and Right Amygdala-mPFC Functional Connectivity

Neither age (β = −0.12, t = −0.94, p = .350) nor task-related HRV (β = −0.02, t = −0.14, p = .886) contributed significantly to the overall regression model, $F(2,67) = 0.45$, p = .637, explaining only 1.3% of the variance in right amygdala-mPFC functional connectivity. Entering the HRV x age interaction term into the model improved the proportion of variance explained in right amygdala-mPFC connectivity (ΔR^2 = 0.13, $F(3,66) = 3.62$, p = .018). The interaction between task-related HRV and age significantly predicted right amygdala-mPFC functional connectivity strength (β = 0.86, t = 3.14, p = .003). Follow-up regression models indicated that the younger adults appeared to drive this interaction, such that younger adults with higher task-based HRV exhibited significantly weaker right amygdala-mPFC functional connectivity (β = −0.54, t = −2.54, p = .022), whereas older adults

demonstrated a slight positive, albeit non-significant, association between HRV and right amygdala-mPFC connectivity during the task (β = 0.17, t = 1.24, p = .222) (Figure 3a).

2.4.2.2 HRV and Left Amygdala-mPFC Functional Connectivity

Similar to the right amygdala-mPFC functional connectivity findings, task-related HRV (β = −0.03, t = −0.26, p = .797) and age (β = −0.09, t = −0.73, p = .466) did not contribute significantly to the overall model, $F(2,67) = 0.27$, p = .764, and explained very minimal variance (0.8%) in left amygdala-mPFC functional connectivity strength. However, when the HRV x age interaction term was entered into the model, this slightly improved the proportion of variance explained in left amygdala-mPFC connectivity (ΔR^2 = 0.08), although the overall model remained non-significant, $F(3,66) = 2.07$, p = .112. The HRV x age interaction was found to predict left amygdala-mPFC connectivity strength (β = 0.67, t = 2.38, p = .020). Follow-up regression models per age group revealed younger adults to drive this significant interaction, whereby greater task-based HRV significantly predicted weaker left amygdala-mPFC functional connectivity in younger adults (β = −0.51, t = −2.37, p = .031). Conversely, a non-significant, weak positive association between task-related HRV and left amygdala-mPFC connectivity strength was observed in older adults (β = 0.10, t = 0.74, p = .461) (Figure 3b)[7].

[7] Average FD values (across the four task runs) derived from the realignment parameters following MCFLIRT (natural log-transformed to correct for non-normal distribution, Shapiro-Wilk $p < .001$) and a FD by age interaction were not found to significantly predict either right or left amygdala-mPFC functional connectivity strength and therefore do not change the nature of the findings reported here (data not shown).

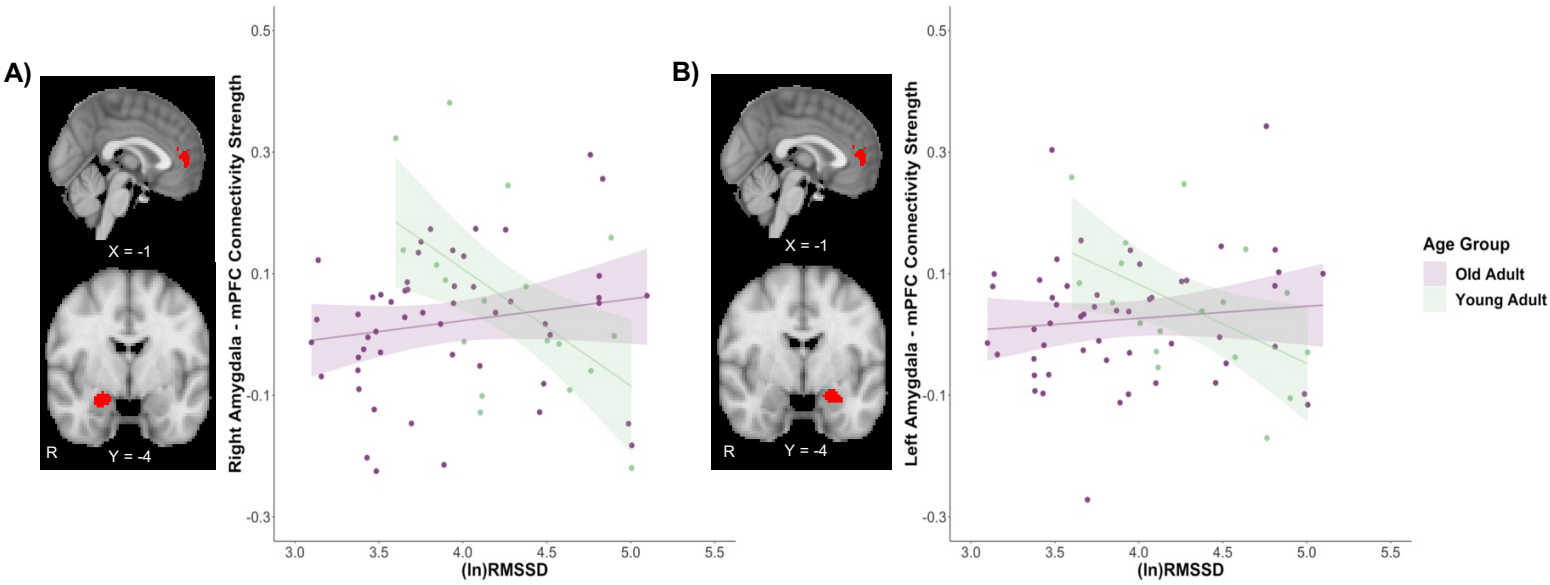

Figure 3. HRV and Amygdala-mPFC Functional Connectivity During the Reappraisal Task. **A)** mPFC seed (top) and right amygdala seed (bottom). Significant HRV x age interaction for right amygdala-mPFC connectivity strength. In younger adults (light green), higher task-based HRV significantly predicted weaker connectivity between the right amygdala and mPFC, whereas a slight positive, albeit non-significant, association between task-related HRV and right amygdala-mPFC connectivity was observed in the older adults (purple). **B)** mPFC seed (top) and left amygdala seed (bottom). Significant HRV x age interaction for left amygdala-mPFC connectivity strength. Similar to the right amygdala connectivity findings, in younger adults, greater task-related HRV significantly predicted weaker left amygdala-mPFC connectivity, whereas a non-significant, weak positive association between HRV and left amygdala-mPFC connectivity was observed in the older adults during the reappraisal task. *HRV*, *heart rate variability*; *mPFC*, *medial prefrontal cortex*; *(ln)RMSSD*, *natural log transformed root mean square of successive differences*.

2.4.3 Whole-Brain Functional Connectivity Analyses

2.4.3.1 Right Amygdala Whole-Brain Functional Connectivity

Significant clusters surviving correction as a main effect of HRV for the right amygdala whole-brain functional connectivity analyses are displayed in Table 2. Across adults in both the older and younger age groups, higher task-related HRV was associated with weaker right amygdala connectivity between the right angular gyrus (extending into right superior lateral occipital cortex), and bilateral posterior cingulate gyrus ($Z > 3.1$, $p = 0.05$-corrected). A scatterplot displaying beta values extracted from the bilateral posterior cingulate gyrus cluster with task-based HRV are displayed in Figure 4. No other clusters survived correction for the positive HRV contrast, nor for positive or negative HRV by age interaction contrasts across the whole sample.

Repeating this analysis in the older adult sample only, a significant main effect of HRV emerged, such that higher task-related HRV was positively correlated with stronger functional connectivity between the right amygdala and the right inferior frontal gyrus, a cluster forming part of the right ventrolateral prefrontal cortex (vlPFC).

A scatterplot displaying beta values extracted from this right vlPFC cluster with task-based HRV are displayed in Figure 4. Moreover, for the HRV negative contrast, higher task-related HRV was associated with weaker right amygdala connectivity with several regions, including bilateral superior lateral occipital cortex extending into left angular and supramarginal gyrus, and bilateral precuneus.

2.4.3.2 Left Amygdala Whole-Brain Functional Connectivity

No significant clusters survived correction as a function of HRV for left amygdala functional connectivity in the whole sample ($Z > 3.1$, $p = 0.05$-corrected), suggesting that task-based HRV did not covary with left amygdala whole-brain functional connectivity across older and younger adults throughout the reappraisal task.

When the left amygdala voxelwise whole-brain search was restricted to adults in the older age sample, a significant positive main effect of HRV was observed, in which higher task-related HRV was correlated with stronger left amygdala connectivity with the right inferior frontal gyrus (vlPFC) and more extensively with the right precentral gyrus ($Z > 3.1$, $p = 0.05$-corrected). Furthermore, significant clusters also survived correction for the negative HRV contrast, such that higher task-based HRV correlated with reduced left amygdala – left lateral occipital cortex connectivity. Other brain regions that survived correction as a main effect of HRV for the left amygdala whole-brain functional connectivity analyses in the older adults are displayed in Table 3.

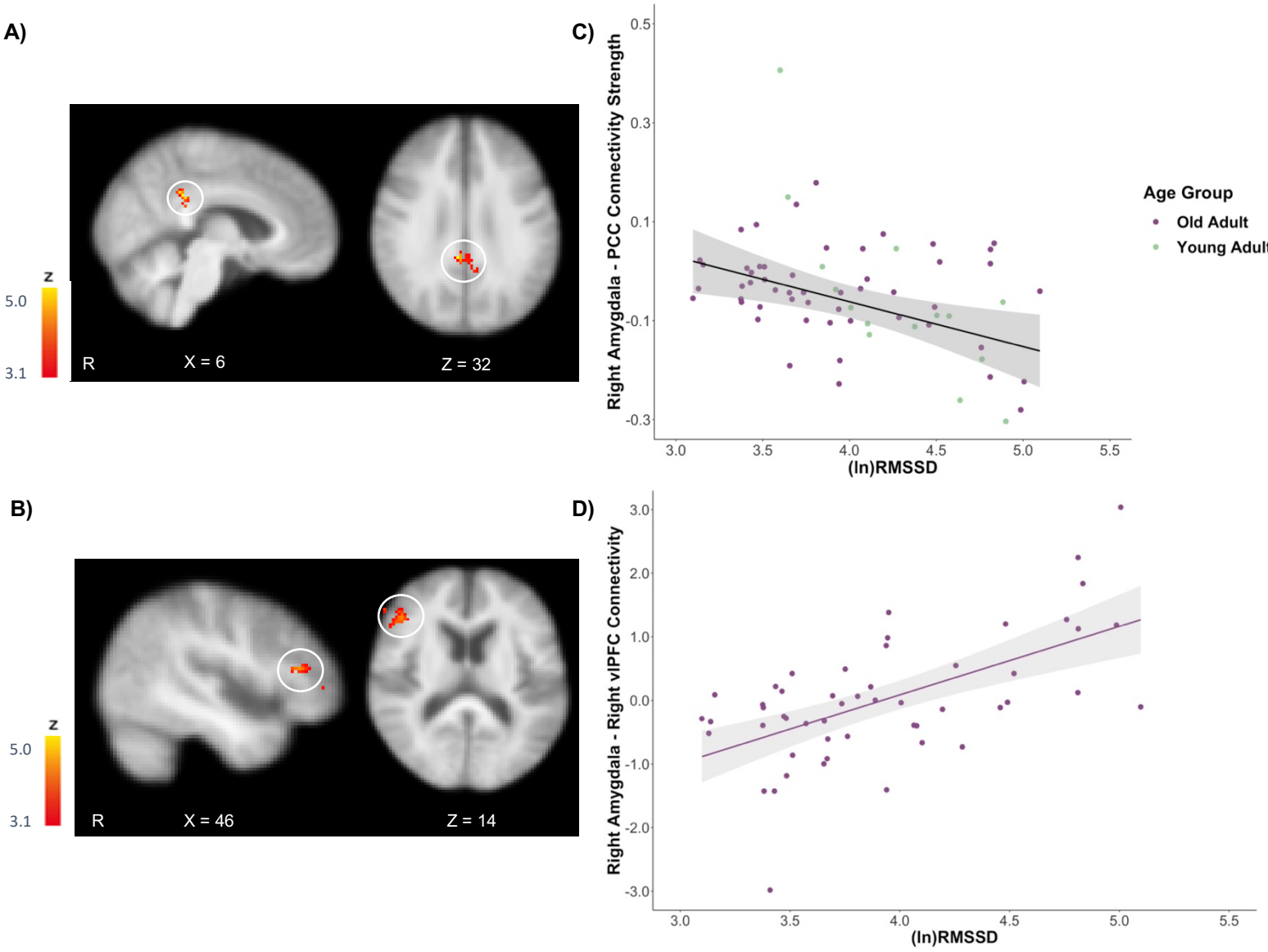

Figure 4. Significant Voxelwise Whole-Brain Functional Connectivity Clusters as a Function of HRV During the Reappraisal Task. **A)** Significant bilateral PCC cluster that survived correction as a main effect for the negative HRV contrast in the right amygdala whole-brain analysis (Z > 3.1, *p* = 0.05-corrected). **B)** Significant right inferior frontal gyrus (vlPFC) cluster that survived correction as a main effect for the positive HRV contrast in the right amygdala whole-brain analysis restricted to the older adult sample (Z > 3.1, *p* = 0.05-corrected). **C)** Scatterplot displays the inverse association between task-based HRV ((ln)RMSSD) values and standardised beta values depicting right amygdala-bilateral PCC connectivity strength in the whole sample during the reappraisal task in older and younger adults (N = 70). Note that the different colours assigned to older (purple) versus younger (light green) adult age groups are depicted for display purposes only. **D)** Scatterplot displays the positive association between task-related HRV ((ln) RMSSD) values and standardised beta values depicting right amygdala-right vlPFC connectivity strength in the older adult sample (controlling for age). *PCC*, *posterior cingulate cortex*; *HRV*, *heart rate variability*; *vlPFC*, *ventrolateral prefrontal cortex*; *(ln)RMSSD*, *natural log transformed root mean square of successive differences.*

Table 2.
Neural Regions and Local Maxima for Right Amygdala Whole-Brain Connectivity

Region	H	Cluster Size	BA	MNI Coordinates x	y	z	Z
HRV + (older and younger adults)							
No significant results							
HRV - (older and younger adults)							
Angular Gyrus extending into Superior Lateral Occipital Cortex	**R**	**103**	**39**	**40**	**-58**	**16**	**5.89**
White Matter	R			36	-52	10	4.27
Superior Lateral Occipital Cortex	R			56	-66	24	3.30
Posterior Cingulate Gyrus	**R**	**87**	**23**	**6**	**-40**	**32**	**5.12**
	R			2	-42	34	4.59
	L			0	-38	26	4.29
	R/L			0	-40	30	4.06
	L			-4	-48	34	3.59
HRV x Age Interaction + (older and younger adults)							
No significant results							
HRV x Age Interaction – (older and younger adults)							
No significant results							
HRV + (older adults)							
Inferior Frontal Gyrus	**R**	**111**	**46**	**46**	**32**	**14**	**4.16**
	R			52	34	10	3.82
Frontal Pole	R			48	44	2	3.76
	R			58	38	12	3.76
Inferior Frontal Gyrus	R		45	54	24	12	3.49
	R		44	52	20	12	3.25
HRV - (older adults)							
Superior Lateral Occipital Cortex extending into Angular Gyrus	**L**	**359**	**39**	**-38**	**-62**	**46**	**4.86**
	L			-36	-76	36	4.43
	L			-36	-70	34	4.35
Supramarginal Gyrus	L			-50	-46	46	4.33
Angular Gyrus extending into Supramarginal Gyrus	L			-44	-48	38	4.26

	L			-44	-54	44	4.24
Precuneus	**R/L**	**159**	**7**	**2**	**-74**	**60**	**5.41**
	R/L			0	-64	48	3.90
Superior Lateral Occipital Cortex	R			10	-78	54	3.33

Neural regions that demonstrated associations with right amygdala as a function of task-related HRV (Z = 3.1; cluster significance: $p < 0.05$, corrected). Local maxima are listed for clusters containing more than one peak. Cluster size refers to the number of voxels contained within a specific cluster. Coordinates (MNI space) represent location of clusters and their maximum Z-scores (bold) and the location of local maxima within significant clusters and their associated Z-statistic. The Harvard Oxford Structural Cortical and Subcortical atlases within FSL were used to label significant clusters. BA refers to the Brodmann Area for each cluster. The 'R' package *label4MRI* (v1.2) was used to generate the BA label based on the MNI coordinates. H = hemisphere (L = left, R = right).

2.4.3.3 MPFC Whole-Brain Functional Connectivity

No clusters survived correction as a main effect of HRV for the mPFC seed in a voxelwise whole-brain search in the whole sample, nor when the analysis was restricted to adults in the older age group ($Z > 3.1$, $p = 0.05$-corrected). Therefore, task-related HRV did not significantly predict functional connectivity of this particular area of the mPFC during reappraisal.

Table 3.
Neural Regions and Local Maxima for Left Amygdala Whole-Brain Connectivity

Region	H	Cluster Size	BA	MNI Coordinates x	y	z	Z
HRV + (older and younger adults)							
No significant results							
HRV - (older and younger adults)							
No significant results							
HRV x Age Interaction + (older and younger adults)							
No significant results							
HRV x Age Interaction – (older and younger adults)							
No significant results							
HRV + (older adults)							
Inferior Frontal Gyrus	**R**	**78**	**44**	**48**	**12**	**30**	**4.10**
Precentral Gyrus	R		6	38	0	32	3.99
Precentral Gyrus extending into Middle Frontal Gyrus	R		8	44	8	34	3.71
Precentral Gyrus	R		6	46	4	28	3.65
	R			48	6	32	3.39
	R		8	32	0	34	3.28
HRV - (older adults)							
Superior Lateral Occipital Cortex	**L**	**156**	**39**	**-42**	**-68**	**44**	**4.25**
	L			-48	-78	36	4.14
	L			-38	-68	40	3.87
	L			-40	-70	36	3.83
Angular Gyrus	L			-44	-56	46	3.66
Angular Gyrus extending into Posterior Supramarginal Gyrus	L			-48	-52	42	3.59

Neural regions that demonstrated associations with left amygdala as a function of task-related HRV (Z = 3.1; cluster significance: $p < 0.05$, corrected). Local maxima are listed for clusters containing more than one peak. Cluster size refers to the number of voxels contained within a specific cluster. Coordinates (MNI space) represent location of clusters and their maximum Z-scores (bold) and the location of local maxima within significant clusters and their associated Z-statistic. The Harvard Oxford Structural Cortical and Subcortical atlases within FSL were used to label significant clusters. BA refers to the Brodmann Area for each cluster. The 'R' package *label4MRI* (v1.2) was used to generate the BA label based on the MNI coordinates. H = hemisphere (L = left, R = right).

2.5 Discussion

The principal aim of the present study was to examine the relationship between HRV and neural functional connectivity whilst older and younger adults engaged in a voluntary emotion regulation task. Based on the NIM (Smith et al., 2017; Thayer & Lane, 2000, 2009), we hypothesised that higher task-related HRV would be positively associated with stronger functional coupling between the amygdala and mPFC in an active regulatory context. In older adults, we observed a slight positive, but non-significant, association between HRV and amygdala-mPFC connectivity. Conversely, and inconsistent with the NIM framework, younger adults displayed a stronger, inverse association, whereby higher task-related HRV was linked to reduced functional connectivity between the amygdala and mPFC. Furthermore, in a voxelwise whole-brain search, we discovered that older and younger adults with higher task-based HRV exhibited weaker right amygdala-PCC connectivity. Interestingly, in older adults, higher HRV during reappraisal was associated with stronger coupling between the right amygdala and right vlPFC. Our findings indicate that task-related HRV covaries with amygdala functional connectivity during emotion regulation, and more crucially highlight the importance of assessing both HRV and brain function during an active emotion regulatory context.

Functional connectivity between the amygdala and mPFC is proposed to support adaptive emotion regulation, with resting HRV posited to serve as a peripheral index of prefrontal inhibitory control (Thayer & Lane, 2000, 2009; Thayer et al., 2009a). In line with this proposition, prior studies have reported positive associations between resting HRV and amygdala-mPFC connectivity strength irrespective of age (Nashiro et al., 2022; Sakaki et al., 2016). However, within the context of the emotion regulation task, we found significant interactions between age and task-related HRV to predict both right and left amygdala coupling with the mPFC. The direction of the effect was unexpected, with the younger adults driving the interaction, but in whom higher task-based HRV was linked to weaker, rather than a strong positive, coupling between the amygdala and mPFC. Medial prefrontal areas have been suggested to support automatic/implicit emotion regulation, while lateral regions of the prefrontal cortex have been implicated in explicit or voluntary emotion regulatory processes requiring greater cognitive control (Braunstein et al., 2017; Phillips et al., 2008). Moreover, the mPFC has been classified as one of the main nodes of the default mode network

(DMN), a neural hub underlying introspective-related mental processes during rest, including emotional and self-referential processing (Andrews-Hanna et al., 2010; Buckner & Carroll, 2007; Raichle et al., 2001). Regions comprising the DMN are generally suppressed while actively engaging in cognitive tasks (Raichle et al., 2001). It is therefore likely that this particular region of the mPFC is more heavily recruited during rest compared to an active task context that requires individuals to reappraise. Thus, prior findings indicating stronger resting amygdala-mPFC connectivity as a function of higher resting HRV may reflect more implicit/automatic emotion regulation in the absence of an emotion regulation task that targets more explicit/controlled regulatory processes (Braunstein et al., 2017; Sakaki et al., 2016). Indeed, during rest, we found a sub-threshold cluster within the mPFC close to our ROI that demonstrated increased functional connectivity with the left amygdala as a function of higher task-related HRV across older and younger adults (see Figure S3 in the Supplementary Material). Recently, Nashiro et al. (2022) also found that increases in resting HRV via biofeedback were correlated with stronger left, but not right, amygdala coupling with the mPFC at rest. Furthermore, prior work has found inverse amygdala-mPFC coupling when using reappraisal to decrease negative affect in a student-aged population (Lee et al., 2012). Hence, the inverse association reported here in younger adults may be driven by the decrease conditions throughout the task. However, given the short trial durations in the current study, an event-related connectivity analysis would be susceptible to fit too much noise and thus render any findings unreliable. Whilst our findings potentially suggest that the regulatory context can affect both the laterality and directionality of amygdala-mPFC functional connectivity associations with task-based HRV, future work should aim to replicate these findings using a task paradigm with longer trial durations to allow for a more targeted event-related connectivity analysis.

Moreover, higher task-related HRV was significantly associated with weaker right amygdala connectivity between the right angular gyrus and bilateral PCC across the emotion regulation task in both age groups. The angular gyrus and PCC also form major nodes of the DMN (Raichle et al., 2001). Weaker resting-state functional connectivity between the right amygdala and PCC has previously been linked to greater reappraisal success (i.e., effective down-regulation of negative emotion) in younger adults (Uchida et al., 2015), whereas increased amygdala-PCC resting-state functional connectivity has been observed following exposure to an acute stressor

(Veer et al., 2011). More recently, Baez-Lugo et al. (2021) reported that greater right amygdala-PCC functional connectivity following exposure to videos containing highly negative emotional content (i.e., people suffering) was significantly correlated with higher rumination, anxiety, and stress in elderly individuals (Baez-Lugo et al., 2021). Critically, those older adults who self-reported more frequent negative thoughts after watching the negative emotional videos were those who also exhibited stronger right amygdala-PCC connectivity. At a trait level, lower resting HRV has been linked to both increased rumination and emotion dysregulation (Visted et al., 2017; Williams et al., 2017). Relatedly, individuals with lower resting HRV have been reported to exhibit phasic HRV suppression in response to fearful distractor stimuli under conditions of both low and high cognitive load, thus displaying an autonomic stress response to relatively trivial threat cues (Park et al., 2014). Conversely, individuals with higher resting HRV appear to exert greater self-regulatory effort as indicated by phasic HRV enhancement in the face of fearful distractors under conditions of low cognitive load, and no presence of phasic HRV suppression under conditions of high cognitive load (Park et al., 2014). Therefore, even under relatively stressful conditions of the task, individuals with higher HRV did not demonstrate an autonomic stress response, whereas those with lower HRV experienced difficulties with engaging self-regulatory processes to effectively cope with task demands. Collectively, the observation of weaker right amygdala-PCC connectivity in older and younger adults with overall elevated task-related HRV in our study may therefore reflect an increased ability to effectively engage with the emotion regulation task at hand.

Finally, consistent with the NIM's proposal that higher HRV reflects more effective cortical-subcortical functioning, we found that older adults with greater task-related HRV exhibited stronger functional connectivity between the amygdala and right vlPFC in a reappraisal context. This finding is particularly interesting since Sakaki et al. (2016) reported a similar association between resting HRV and resting amygdala-vlPFC connectivity in younger, but not older adults, suggesting that younger adults with relatively higher resting HRV were more likely to spontaneously recruit neural regions involved in explicit emotion regulation. Considering empirical evidence that has reported phasic HRV increases to reflect greater self-regulatory effort and emotion regulatory success (Butler et al., 2006; Denson et al., 2011; Segerstrom & Nes, 2007), overall elevated task-related HRV when directly challenged by stimuli designed to elicit negative emotions may also indicate a greater ability to actively engage brain regions

underlying successful voluntary emotion regulation. The vlPFC has increasingly been identified as a pivotal neural region involved in emotion regulatory processes (Wager et al., 2008; Zhao et al., 2021), and is an area in which age-related differences have been reported during reappraisal (Opitz et al., 2012; Winecoff et al., 2011). The vlPFC, and lateral prefrontal cortex more broadly, is particularly vulnerable to structural and functional atrophy in healthy ageing (Fjell et al., 2009; Raz et al., 2004). The present finding suggests that higher task-related HRV in older age, at least in a voluntary emotion regulation context, may support increased engagement, and possibly functional preservation, of lateral prefrontal cortex, specifically the right vlPFC, facilitating effective reappraisal of negative emotions. Although the left vlPFC has been more frequently reported in reappraisal studies (Berboth & Morawetz, 2021; Buhle et al., 2014), involvement of the right vlPFC here may be characterised by dominance of the right hemisphere in supporting inhibitory-related processes for affective, cognitive, and physiological regulation more broadly (Lane et al., 2009; Thayer et al., 2009b; 2012). Irrespective of any laterality, our findings build on the extant literature on prefrontal mechanisms in reappraisal by highlighting that elevated task-related HRV is associated with positive coupling between the amygdala and vlPFC, which may have implications for psychological wellbeing and resilience in later life.

A few important limitations should be considered when interpreting our findings. Our sample comprised a larger pool of adults in the older age relative to the younger age group, leading to an unequal age distribution. Although age was included as a predictor in our regression models, the small sample of younger adults rendered any findings specific to the younger group as possibly spurious and requiring replication in a larger sample. Moreover, as previously outlined, the reappraisal task contained trials of a relatively short duration which does not lend itself as an optimal design for a more targeted, event-related connectivity analysis. While non-regression of the task design has previously been shown to increase reliability of functional connectivity measures (Cho et al., 2021), in the absence of including the task design to explicitly model regulatory events, and without direct comparison with a non-emotional task, the current findings may not specifically reflect emotion regulation or emotional processing. Similarly, while the resting-state connectivity findings produced a cluster, albeit sub-threshold, in the mPFC that was close to our seed region of interest and not observed during the emotion regulation task, this is based on visual inspection of the data. Indeed, without directly comparing HRV associations with functional connectivity

during the emotion regulation task and at rest, it remains unclear whether connectivity patterns as a function of task-related HRV are significantly different between these two contexts.

Furthermore, HRV was derived from a finger pulse oximeter whilst participants were lying down in the scanner and whilst engaging in emotion-related tasks, predominantly reappraisal. Both factors have previously been shown to elevate heart rate and HRV (Butler et al., 2006; Cacioppo et al., 1994), and the use of photoplethysmography to derive HRV metrics, especially RMSSD (Schumann et al., 2021b), could have further resulted in an elevated HRV estimate. However, given that HRV metrics tend to demonstrate strong positive correlations across contexts (Heffner et al., 2022; Wang et al., 2009) and resting HRV modulates phasic HRV changes during emotion regulation (Butler et al., 2006; Segerstrom & Nes, 2007), the relative rank order of task-related HRV across subjects in the present study are likely to be similar to those observed outside of the scanner at rest. Additionally, other lifestyle factors known to influence HRV measures, including smoking status, general fitness/activity level, caffeine intake, and body mass index (Hayano et al., 1990; Karason et al., 1999; Sammito & Böckelmann, 2016) were not obtained, therefore we cannot rule out the influence of these factors on the current findings. Future research should aim to acquire reliable heart rate recordings to derive HRV metrics both inside and outside of the scanner (Schumann et al., 2021b) and during rest and whilst performing tasks for calculation of phasic HRV changes (reactivity and recovery measures relative to baseline). Relatedly, aggregation of HRV measures across contexts to capture variance that more strongly represents ‘trait-like’ HRV may also be insightful (see Bertsch et al., 2012).

Whilst our study augments prior findings which have heavily relied on associations between HRV and functional connectivity during rest by assessing heart-brain function in an active emotion regulatory context, the current study and the majority of prior work have typically relied on relatively static functional connectivity techniques. Although a few studies have examined transient HRV changes and functional connectivity using dynamic functional connectivity (dFC) techniques such as the sliding window approach (Chand et al., 2020; Chang et al., 2013; Schumann et al., 2021a), this method is limited by its reliance on arbitrary selection of truncated time windows to assess both functional connectivity and HRV, with the latter particularly affected by the shorter duration of the measurement period (Shaffer & Ginsberg, 2017;

Task Force, 1996). It would therefore be fruitful for future research to employ novel and alternative dFC methods that overcome existing constraints (e.g., co-activation pattern analysis; Liu et al., 2013; 2018) to determine associations between HRV and dynamic neural networks underlying adaptive and flexible regulation across the lifespan.

In conclusion, the current study extends prior resting-state findings by highlighting that task-related HRV covaries with amygdala-cortical functional connectivity in the context of a voluntary emotion regulation task. While the amygdala-mPFC findings did not align with the NIM, task-based covariation between functional connectivity of amygdala-vlPFC and task-based HRV provide some support for the notion that higher HRV reflects stronger cortical-subcortical integrity. This circuitry may facilitate adaptive emotion regulation which could have implications for wellbeing and resilience in later life. Collectively, our findings accentuate the importance of assessing neurovisceral circuitry during active regulatory contexts to further elucidate core neural mechanisms involved in supporting adaptive self-regulation as a function of HRV more broadly.

CRediT Authorship Contribution Statement

Emma Tupitsa: Conceptualization, Formal analysis, Writing – original draft. **Ifeoma Egbuniwe:** Conceptualization, Formal analysis. **William K. Lloyd:** Methodology, Software, Formal analysis, Writing – review & editing. **Marta Puertollano:** Formal analysis, Writing – review & editing. **Birthe Macdonald:** Investigation, Writing – review & editing. **Karin Joanknecht:** Investigation. **Michiko Sakaki:** Conceptualization, Writing – review & editing. **Carien M. van Reekum:** Conceptualization, Methodology, Writing – original draft, Supervision, Funding acquisition.

Declaration of Competing Interest

Declarations of interest: none. The authors declare no conflict of interest.

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Data Availability

The MRI data that support the findings of this study are openly available on OpenNeuro: 10.18112/openneuro.ds002620.v1.0.0. The pulse data, processing and analysis scripts that support this study are openly available on the Open Science Framework (OSF): https://osf.io/6zdph/.

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Supplementary Material

S1. Resting-state fMRI Details

S1.1 Resting-state fMRI Data Acquisition

Resting-state fMRI data were acquired using an echo planar imaging (EPI) sequence (200 whole-brain volumes, 56 sagittal slices, with P>A phase encoding, slice thickness = 3.0mm, slice gap = 0%, TR = 3000 ms, TE = 30 ms, flip angle = 90°, FOV = 192 x 192 mm^2, resolution = 3 mm isotropic, acquisition time = 10 minutes, 11 seconds).

S1.2 Resting-state Scan Procedure

Participants were asked to maintain their gaze on a fixation cross in the middle of screen presented on a white background. The total duration of the resting-state scan was 10 minutes and 11 seconds.

S1.3 Resting-state fMRI Pre-processing

Resting-state functional imaging data were preprocessed and analysed using FMRIB's Software Library (FSL, version 6.0; Jenkinson et al., 2012; Woolrich et al., 2009; Smith et al., 2004) and Analysis of Functional NeuroImages (AFNI, version 19.3.03; http://afni.nimh.nih.gov/afni; Cox, 1996), akin to the preprocessing and analytical procedure applied to the emotion regulation fMRI task-based data. These initial pre-processing steps included: skull stripping (non-brain removal) using FSL's brain extraction tool (BET; Smith, 2002), motion correction using MCFLIRT (Jenkinson et al., 2002), spatial smoothing using a Gaussian kernel with a full-width half maximum (FWHM) of 5 mm and high-pass temporal filtering (Gaussian-weighted least squares straight line fitting with sigma = 50 s). Each subject's native image was normalised to the standard Montreal Neurological Institute (MNI) space via co-registration to their high resolution T1-weighted image. Application of FSL's MELODIC Independent Components Analysis (ICA; Beckmann & Smith, 2004) separated the fMRI BOLD signal into a set of spatial maps (independent components) representing neural signal and/or noise. An average of 53.17% components were removed across participants' resting-state fMRI data. Following ICA filtering, low bandpass filtering was applied using AFNI's '*3dBandpass*' tool (Cox, 1996) to further remove confounding signals below 0.009 Hz and above 0.1 Hz. Prior to analysis, each subject's corresponding

mean functional timeseries image was added back to the bandpass filtered data using *fslmaths* to ensure compatibility with FSL's FMRI Expert Analysis Tool (FEAT).

S1.4 Participants, rsfMRI Pre-Processing and Analytical Pipeline

Of the original sample of 96 participants, a total of 77 participants (58 old and 19 young adults) had resting-state fMRI and pulse data. Following quality checks of the rsfMRI and task-related HRV data (including: scanner interference, registration issues, RMSSD values > 200ms), a total of 55 participants (41 old and 14 young adults) were included in the final analyses. The same analytical steps applied to the emotion regulation task-based fMRI data were also performed on the resting-state fMRI data. We conducted both a region of interest functional connectivity analysis to assess the extent to which task-based HRV (obtained during the second session scan) predicted amygdala-mPFC functional connectivity during rest (acquired in the first session). We also examined resting-state whole-brain functional connectivity in the right and left amygdala and the mPFC seeds using FEAT (Woolrich et al., 2004). Clusters surviving a threshold of $Z > 3.1$ and correction for multiple comparisons with Gaussian random field theory (cluster significance: $p = 0.05$-corrected) were identified (Worsley, 2001).

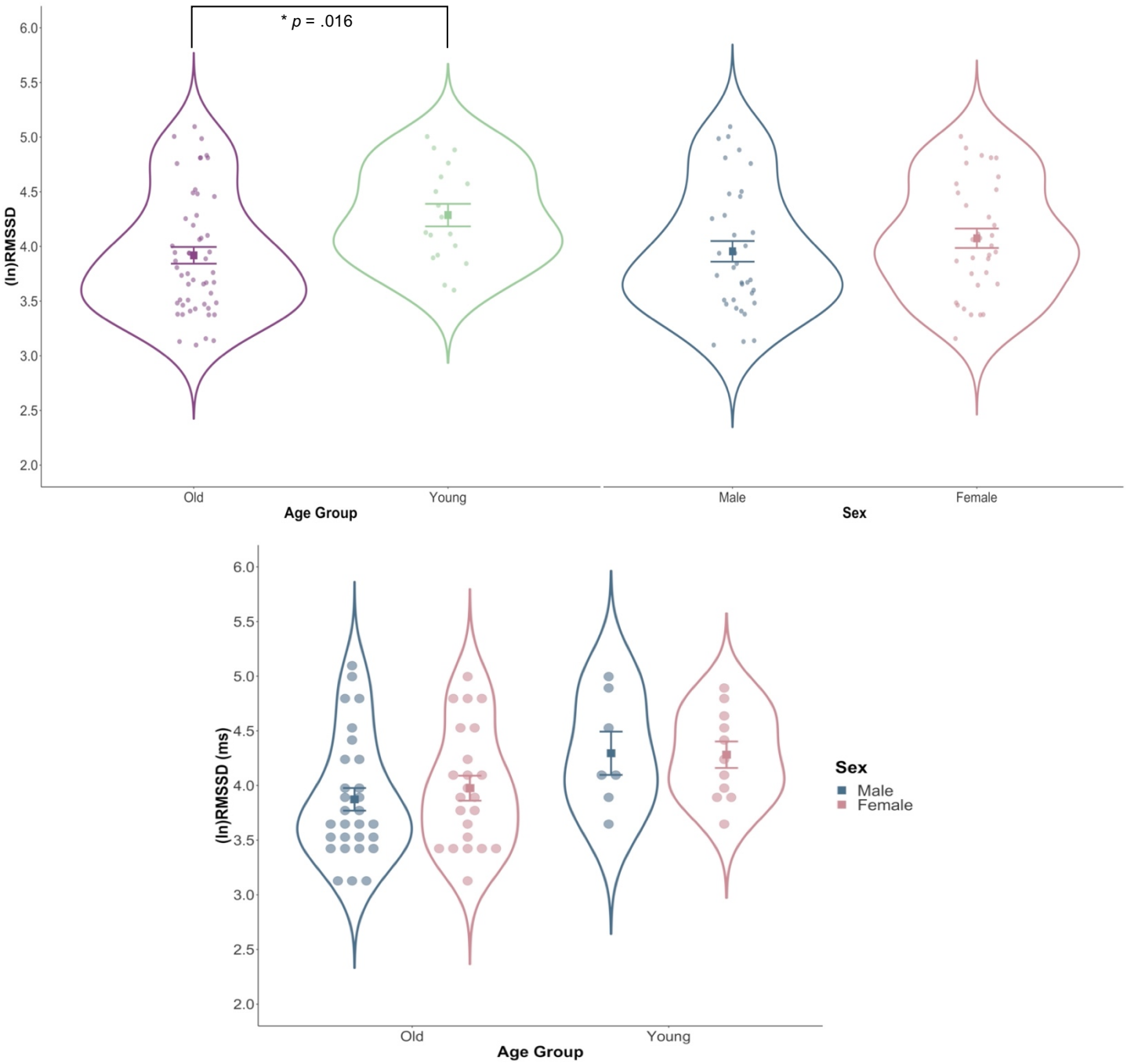

Figure S1. A series of violin plots to display task-related HRV as indexed by (ln)RMSSD values for age group, sex and age group by sex (whole sample, N = 70). **A)** Violin plot displays the significant difference between older (purple, N = 52) and younger (light green, N = 18) adults' HRV as indexed by (ln)RMSSD values ($F(1,66) = 6.06$, $p = .016$, $\eta_p^2 = 0.08$). Older adults were observed to have significantly lower task-related HRV compared to younger adults. **B)** Violin plot displays the (ln)RMSSD values for males (blue) and females (pink) across the whole sample. There was no significant difference in task-based HRV between males and females ($F(1,66) = 0.09$, $p = .764$, $\eta_p^2 = 0.00$). **C)** Violin plot displays the (ln)RMSSD values for males (blue) and females (pink) per age group. No significant age group by sex interaction for (ln)RMSSD values was found ($F(1,66) = 0.15$, $p = .698$, $\eta_p^2 = 0.00$). The square represents the mean (ln)RMSSD value and the whiskers represent ± 1 standard error around the mean. *(ln)RMSSD*; natural log transformed root mean square of successive differences.

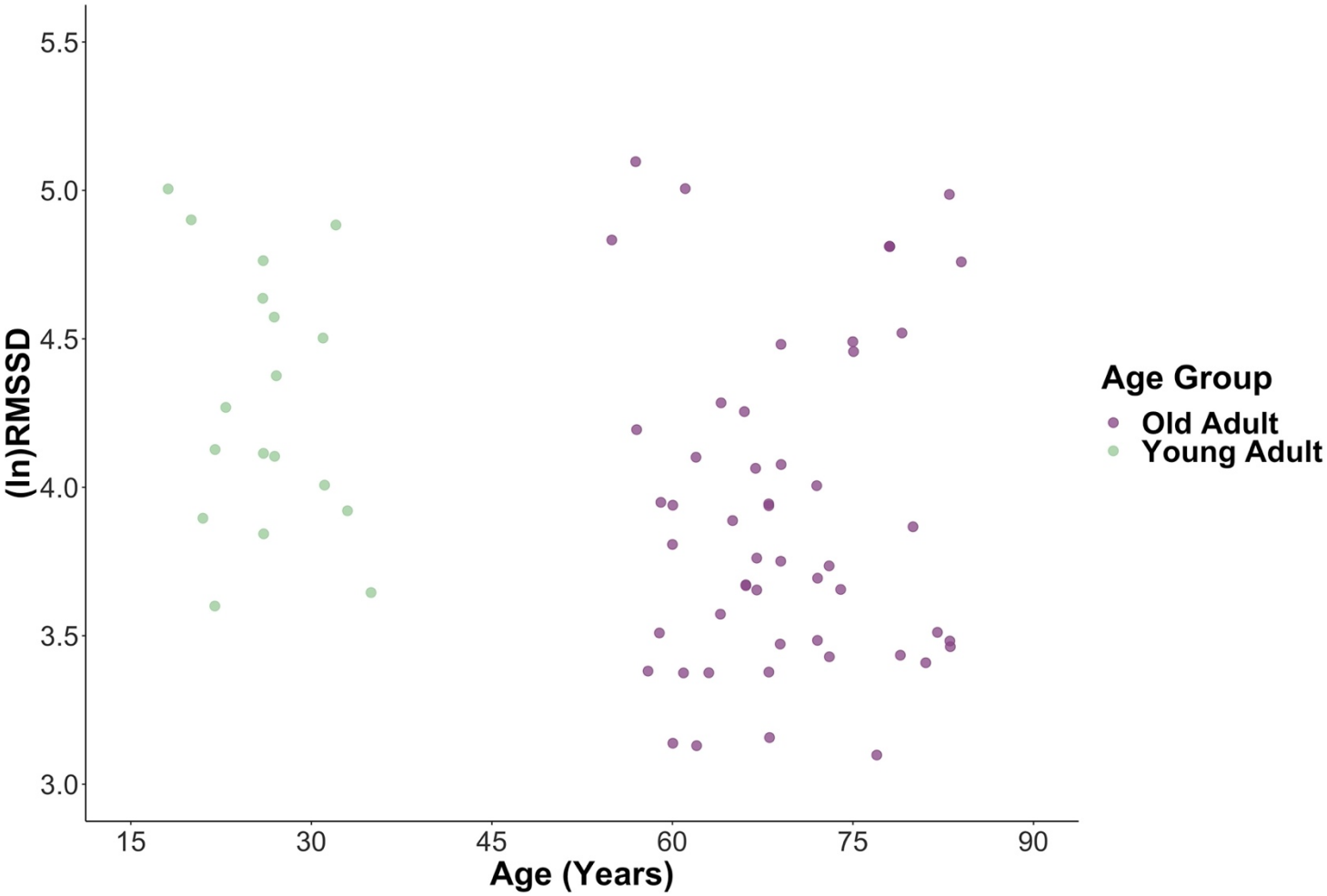

Figure S2. The scatterplot displays the natural gap in age (years) between older (purple) and younger (light green) adults with natural log transformed RMSSD values ((ln)RMSSD) presented on the y axis.

S2. HRV and Resting-state Amygdala-mPFC Functional Connectivity Analyses

Multiple regression analyses were employed to examine associations between HRV and resting-state amygdala-mPFC functional connectivity strength in the whole sample (N = 55). Separate multiple regression models were tested with (i) right amygdala-mPFC connectivity and (ii) left amygdala-mPFC connectivity values as dependent variables. The following predictors were entered into the regression model: age group (1 = older adults, 0 = younger adults), (ln)RMSSD (centered), and a HRV x age interaction term. In each hierarchical regression model, age group and HRV were entered first (step 1), followed by the HRV x age interaction predictor (step 2) using the enter method. Standardised beta coefficients are reported for all predictors.

HRV and Resting-state Right Amygdala-mPFC Functional Connectivity

At step 1, neither the main effect of age (β = 0.19, t = 1.30, p = .198) or task-based HRV (β = 0.08, t = 0.53, p = .596) were found to be significant predictors of the

regression model, explaining only 3.20% of the variance in resting-state right amygdala-mPFC functional connectivity ($F(2,52) = 0.85$, $p = .431$). Entering the HRV x age interaction term did not significantly improve the proportion of variance explained in right amygdala-mPFC functional connectivity ($\Delta R^2 = 0.01$) and the overall regression model remained non-significant ($F(3,51) = 0.80$, $p = .498$). Thus, the interaction between task-related HRV and age ($\beta = 0.26$, $t = 0.84$, $p = .404$) was not found to significantly predict right amygdala-mPFC resting-state functional connectivity.

HRV and Resting-state Left Amygdala-mPFC Functional Connectivity

Similar to the right amygdala-mPFC resting-state functional connectivity findings, neither the main effect of age ($\beta = -0.11$, $t = -0.74$, $p = .463$) or task-based HRV ($\beta = 0.10$, $t = 0.69$, $p = .491$) were found to be significant predictors of the overall regression model and only explained 2.90% of the variance in resting-state left amygdala-mPFC functional connectivity ($F(2,52) = 0.78$, $p = .462$). When the HRV x age interaction term was subsequently entered into the model, this did not significantly improve the proportion of variance explained in left amygdala-mPFC resting-state connectivity ($\Delta R^2 = .001$) and the overall regression model remained non-significant ($F(3,51) = 0.52$, $p = .668$). Therefore, the interaction between HRV and age ($\beta = 0.06$, $t = 0.18$, $p = .855$) was not found to significantly predict left amygdala-mPFC resting-state functional connectivity.

Table S1
Neural Regions and Local Maxima for Right Amygdala Whole-Brain Resting-state Functional Connectivity as a Function of Task-Related HRV

Region	H	Cluster Size	BA	MNI Coordinates x	y	z	Z
HRV + *(older and younger adults)*							
No significant results							
HRV - (*old and young adults*)							
Precentral Gyrus extending into Postcentral Gyrus	**R**	**83**	**4**	**8**	**-26**	**66**	**4.19**
	R		4	12	-28	68	4.13
	R		6	8	-22	64	3.96
	R		4	14	-34	64	3.52
HRV x Age Interaction + (older and younger adults)							
No significant results							
HRV x Age Interaction - (older and younger adults)							
No significant results							
HRV + *(older adults)*							
No significant results							
HRV - *(older adults)*							
No significant results							

Neural regions that demonstrated associations with right amygdala during rest as a function of task-related HRV across the whole sample (N = 55) and old adult sample only (N = 41), Z = 3.1; cluster significance: $p < 0.05$, corrected). Local maxima are listed for clusters containing more than one peak. Cluster size refers to the number of voxels contained within a specific cluster. Coordinates (MNI space) represent location of clusters and their maximum Z-scores (bold) and the location of local maxima within significant clusters and their associated Z-statistic. The Harvard Oxford Structural Cortical and Subcortical atlases within FSL were used to label significant clusters. BA refers to the Brodmann Area for each cluster. The 'R' package *label4MRI* (v1.2) was used to generate the BA label based on the MNI coordinates. H = hemisphere (L = left, R = right).

Table S2
Neural Regions and Local Maxima for Left Amygdala Whole-Brain Resting-state Functional Connectivity as a Function of Task-Related HRV

Region	H	Cluster Size	BA	MNI Coordinates x	y	z	Z
HRV + *(older and younger adults)*							
No significant results							
HRV - (*older and younger adults*)							
No significant results							
HRV x Age Interaction + (older and younger adults)							
No significant results							
HRV x Age Interaction - (older and younger adults)							
No significant results							
HRV + *(older adults)*							
Lingual Gyrus	**R**	**80**	**19**	**12**	**-42**	**-10**	**4.17**
	R		19	10	-50	-4	3.97
	R		19	12	-52	-8	3.68
	R		19	20	-46	-8	3.43
HRV - *(older adults)*							
No significant results							

Neural regions that demonstrated associations with left amygdala during rest as a function of task-related HRV across the whole sample (N = 55) and old adult sample only (N = 41), Z = 3.1; cluster significance: $p < 0.05$, corrected). Local maxima are listed for clusters containing more than one peak. Cluster size refers to the number of voxels contained within a specific cluster. Coordinates (MNI space) represent location of clusters and their maximum Z-scores (bold) and the location of local maxima within significant clusters and their associated Z-statistic. The Harvard Oxford Structural Cortical and Subcortical atlases within FSL were used to label significant clusters. BA refers to the Brodmann Area for each cluster. The 'R' package *label4MRI* (v1.2) was used to generate the BA label based on the MNI coordinates. H = hemisphere (L = left, R = right).

Table S3
Neural Regions and Local Maxima for MPFC Whole-Brain Resting-state Functional Connectivity as a Function of Task-Related HRV

Region	H	Cluster Size	BA	MNI Coordinates x	y	z	Z
HRV + *(older and younger adults)*							
No significant results							
HRV - (*older and younger adults*)							
No significant results							
HRV x Age Interaction + (older and younger adults)							
No significant results							
HRV x Age Interaction - (older and younger adults)							
White matter extending into Superior Lateral Occipital Cortex	**L**	**79**		**-32**	**-64**	**20**	**4.43**
	L		39	-30	-74	26	4.20
	L		39	-34	-70	28	3.90
HRV + (older adults)							
No significant results							
HRV - (older adults)							
No significant results							

Neural regions that demonstrated associations with the mPFC during rest as a function of task-related HRV across the whole sample (N = 55) and old adult sample only (N = 41), Z = 3.1; cluster significance: $p < 0.05$, corrected). Local maxima are listed for clusters containing more than one peak. Cluster size refers to the number of voxels contained within a specific cluster. Coordinates (MNI space) represent location of clusters and their maximum Z-scores (bold) and the location of local maxima within significant clusters and their associated Z-statistic. The Harvard Oxford Structural Cortical and Subcortical atlases within FSL were used to label significant clusters. BA refers to the Brodmann Area for each cluster. The 'R' package *label4MRI* (v1.2) was used to generate the BA label based on the MNI coordinates. H = hemisphere (L = left, R = right).

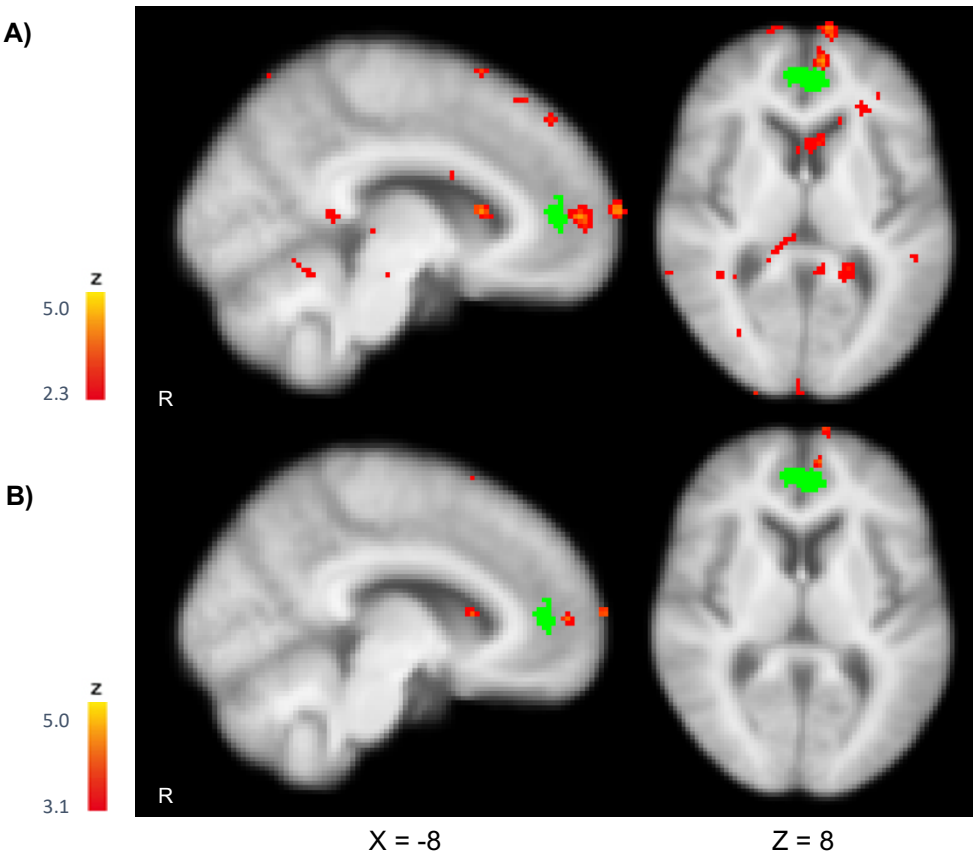

Figure S3. Sub-threshold frontal medial cluster which was positively coupled with the left amygdala as a function of higher task-related HRV during rest, but did not survive correction for multiple comparisons (Z = 3.95). The solid green cluster represents the mPFC seed region of interest used in all analyses (Sakaki et al., 2013, 2016). **A)** Frontal medial cluster displayed when Z thresholded at > 2.3. **B)** Frontal medial cluster displayed when Z thresholded at > 3.1.

Chapter 3.

Heart rate variability and neural co-activation patterns during emotion processing and at rest

Tupitsa, E., & Van Reekum, C. M. (In Preparation). Heart rate variability and neural co-activation patterns during emotion processing and at rest.

3.1 Abstract

The Neurovisceral Integration Model (NIM) posits that heart rate variability (HRV) is a metric of adaptive emotional responding and mental health. Shared neural networks support autonomic, affective, and cognitive function. However, most studies have examined the heart-brain relationship during rest in comparison to contexts requiring active engagement. The present study sought to examine HRV, trait neuroticism, and co-active brain networks during an active emotion processing context and at rest. Two samples (sample 1 emotion task N = 92, rest N = 87; replication sample 2 emotion task N = 93, rest N = 90) were derived from a wider pool of younger adults from the Amsterdam Open Magnetic Resonance Imaging Collection (AOMIC). Participants engaged in an emotion matching task and a resting-state scan during which a finger pulse signal was recorded to derive task-related and resting HRV measures. Co-Activation Pattern (CAP) analyses with right and left amygdala and bed nucleus of the stria terminalis (BNST) seeds were conducted for the emotion matching task and resting-state data across both samples. In sample 2, a higher average duration of co-activation between left amygdala and BNST with CAPs reflecting visual attention network states was positively correlated with task-related and resting HRV across both the emotion task and at rest, reflecting a potential link between elevated HRV and enhanced exteroceptive visual attention across contexts. Moreover, during emotion processing, higher HRV predicted increased occurrences of a core DMN CAP at low, but not high, neuroticism levels as a function of left amygdala/BNST in sample 2, possibly indicating more flexible (dis)engagement of the DMN in accordance with task/contextual demands. Higher occurrences of a CAP reflecting co-activation between the salience network and right amygdala/BNST was associated with higher resting HRV in sample 1, which may suggest a greater propensity to dynamically switch between interoceptive and exteroceptive states during rest. Collectively, these findings highlight low replicability of CAP temporal metrics during emotion and rest contexts across two samples and critically accentuate the significance of assessing HRV and associated neural function across contexts to identify key neural vagal control circuitry underlying adaptive emotional responding.

Keywords: Heart Rate Variability; Neurovisceral Integration Model; Amygdala; BNST; Co-Activation Pattern Analysis

3.2 Introduction

The ability to rapidly and flexibly respond to ongoing environmental changes in a contextually appropriate manner is critical for self-regulation and effective adaptation (Aldao et al., 2015). Environmental challenges produce changes at both a subjective (i.e., emotional state) and physiological (i.e., heart rate) level, thus requiring effective coordination of the mind and body to facilitate contextually appropriate responses. More specifically, advances have been made in recent years to understand the mechanisms by which two major human organs, the heart and the brain, communicate and coordinate with one another to promote such flexibility. In particular, the Neurovisceral Integration Model (NIM; Smith et al., 2017; Thayer & Lane, 2000, 2009) is a prominent and influential theoretical framework which delineates a neural network that comprises the brainstem, subcortical, and cortical structures, originating from the Central Autonomic Network (CAN; Benarroch, 1993), that partially overlap with areas involved in autonomic, affective, and cognitive responding. Specifically, this model outlines mechanisms by which the brain influences the rhythm of the heart, proposing that effective top-down inhibition via prefrontal-subcortical pathways, particularly the medial prefrontal cortex (mPFC) and amygdala, facilitate successful adaption and emotional flexibility in response to challenges (Smith et al., 2017). In turn, heart rate variability (HRV), a physiological phenomenon capturing time intervals between consecutive beats, is posited to serve as an objective and peripheral metric of this effective cortical inhibition (Thayer & Lane, 2000, 2009). Optimal and efficient functioning of this network reflected by higher resting HRV promotes more effective assessment of, and responses to, environmental challenges, adept discrimination of threat versus safety, and flexible autonomic, emotional, and cognitive responses in accordance with environmental demands.

Accumulating research evidence supports the NIM and HRV as an index of adaptive emotional responding. Evidence from neuroimaging studies has consistently found HRV to be linked to effective prefrontal functioning and strength of prefrontal-subcortical circuitry (Koenig et al., 2021; Kumral et al., 2019; Sakaki et al., 2016; Schumann et al., 2021; Thayer et al., 2012; Tupitsa et al., 2023). Individuals with higher resting HRV have been found to demonstrate better top-down and bottom-up modulation of responses towards emotional stimuli (Park & Thayer, 2014) and successful self- and emotion regulation (Appelhans & Luecken, 2006; Balzarotti et al., 2017). Conversely, individuals with lower resting HRV have been reported to exhibit

increased hypervigilance to, and difficulties engaging from, negative or threatening information (Park et al., 2013; Park & Thayer, 2014), self-report increased emotion dysregulation (Visted et al., 2017; Williams et al., 2015), and are at an increased risk of developing and experiencing psychological disorders, including anxiety and depression (Beauchaine & Thayer, 2015; Chalmers et al., 2014; Dell'Acqua et al., 2020; Koch et al., 2019).

Individuals with anxiety disorders have been reported to have lower resting HRV, reflecting an impaired central autonomic network that manifests as ineffective inhibition of the sympathetic nervous system, excessive and uncontrollable worrying, and an inability to discriminate threat from safety (Chalmers et al., 2014; Cheng et al., 2022; Tomasi et al., 2023). Similarly, neuroticism, a stable disposition characterised by elevated negative affect and emotional reactivity (Ormel et al., 2013) is also considered to be a risk factor for the onset and progression of psychopathology, including anxiety and depression (Kootker et al., 2016; Kotov et al., 2010). Greater emotional reactivity in high trait neurotic individuals has previously been linked to altered fronto-limbic activity and/or connectivity, and differences in structural integrity of areas underlying emotion processing and regulation (Bjørnebekk et al., 2013; Cremers et al., 2010; Silverman et al., 2019). Furthermore, individuals with high trait neuroticism exhibited increased dominance of salience and emotion-processing neural hubs in functional network organisation (Servaas et al., 2015) and demonstrated slower amygdala recovery following negative emotional images (Schuyler et al., 2014). Many of the neural regions outlined as being altered as a function of trait neuroticism overlap with those outlined in the NIM and relate to changes in attentional (dis)engagement.

Taken together, HRV and anxiety/neuroticism appear to be linked to attentional (dis)engagement of negative or threatening information. However, the interconnection between HRV and neuroticism is less clear. A few studies have reported direct inverse associations between HRV and trait neuroticism (Čukić & Bates., 2015; Shepherd et al., 2015), whereas other studies have reported less consistent or no direct correlations (Ode et al., 2010; Sloan et al., 2017), suggesting that potential links may be more nuanced. Indeed, Ode et al. (2010) found that elevated resting HRV significantly predicted higher reported negative emotions and stress in daily life at low levels of trait neuroticism, but predicted fewer negative outcomes when trait neuroticism was high (Ode et al., 2010). Relatedly, trait anxiety was discovered to

moderate associations between HRV and threat bias (Miller et al., 2023). The extent to which trait neuroticism serves as a moderator of potential associations between HRV and co-active brain states across different contexts is currently unknown.

Relatedly, fewer neuroimaging studies have examined HRV and associated neural networks during emotional contexts and/or transient changes via application of dynamic functional connectivity (dFC) approaches (Chang et al., 2013, Chand et al., 2020; Schumann et al., 2021). During rest, transient increases in HRV were linked to dFC changes in the ventromedial prefrontal cortex (vmPFC) (Schumann et al., 2021), and the dorsal anterior cingulate cortex (dACC) and amygdala (Chang et al., 2013) with all regions exhibiting stronger connectivity with key areas involved in emotional and cognitive processing. Nevertheless, prior studies have typically used a sliding window approach to assess transient functional connectivity changes (Allen et al., 2014; Lurie et al., 2020), a technique that is limited to the selection of a small number of regions of interest and their pairwise associations over time (Liu et al., 2013). Alternative neuroanalytical methods such as 'Co-Activation Pattern' (CAP) analysis (Liu & Duyn, 2013; Liu et al., 2018) overcome some of these limitations while providing the opportunity to examine the flexible nature of the heart-brain relationship.

The CAP technique diverges from other functional and effective connectivity methods, such as psychophysiological interactions (PPI; Friston et al., 1997) and dynamic causal modelling (DCM; Friston et al., 2003) which utilise fMRI timecourses across the duration of the scan to estimate connectivity between brain regions, by focusing on single fMRI volumes at individual time points as the basic unit of analysis (Liu et al., 2018). Assuming non-stationarity of the brain, CAP is based on the notion that co-activation of functionally related neural regions and networks are unlikely to exhibit stationary activity and are instead characterised by brief and transient moments of co-(de)activation (Liu & Duyn, 2013). Therefore, adopting a data-driven and frame-wise approach, CAP relies on the selection of the strongest, or 'peak', amplitudes of activation across the whole brain (seed-free approach) or in particular seed regions (seed-based approach) to examine which other voxels/brain regions demonstrate synchronous co-activation (Tagliazucchi et al., 2016). CAP analysis comprises three main steps: (1) standardise each voxel's time course to generate Z scores; (2) cluster all time points or time points belonging to a specific seed exceeding a set high signal activation threshold; (3) voxel-wise average spatial maps of selected time points to generate CAPs or brain states (Liu & Duyn, 2013; Liu et al., 2018). Computational

studies have reported that voxel-wise averaging spatial maps only in the fMRI volumes exhibiting peak BOLD activity produces networks with spatial similarity to those obtained by conventional temporal correlation-based functional connectivity (Cifre et al., 2020; Tagliazucchi et al., 2012). Critically, alongside spatial information, CAP produces temporal metrics regarding each CAP or brain state, including temporal information such as dwell time (i.e., the duration in which a certain brain state is sustained) and frequency (i.e., the number of occurrences of a particular brain state across the functional scan). While techniques such as DCM have the ability to establish more causal interpretations related to the direction of connectivity patterns, CAP relies on few assumptions and produces more stable brain states in contrast to those acquired via sliding window analyses (Chen et al., 2015). Moreover, by focusing on only the most salient time points of activity, CAP further reduces the requirement for widespread comparisons which may in turn increase statistical power, especially in small samples (Georgiopoulos et al., 2024).

Importantly, prior research has typically utilised resting-state fMRI paradigms and relied on resting HRV measures to assess brain-heart interactions. However, if neurovisceral circuitry and HRV do indeed reflect adaptive emotional responding, then examining HRV and concomitant neural activity during contexts or situations that require flexible emotional responses will potentially provide further insight into, and increase the ability to detect, neural regions and networks that facilitate adaptive emotional responding as a function of HRV.

The aim of the current study was to examine resting and task-based HRV with associated co-active brain states during rest and an emotion processing task in a large sample of younger adults from the Amsterdam Open MRI (Magnetic Resonance Imaging) Collection (AOMIC; Snoek et al., 2021). While the emotion matching task is not specifically designed to assess emotion flexibility, effective engagement in this task still requires a certain degree of flexibility, particularly the ability to shift from processing emotional stimuli (i.e., matching angry/fearful faces) to processing neutral stimuli (i.e., matching oval shapes). Correspondingly, flexibility in the current context was reflected by an individual's ability to inhibit the processing of emotional information when switching to matching neutral stimuli in the control blocks, that is, the individual should no longer be actively searching for emotional stimuli during these blocks. Since HRV is considered to be a metric of adaptive emotional responding (Appelhans & Luecken, 2006), HRV and associated co-active brain states were expected to be expressed in

this attentional 'goal' shift between conditions. Therefore, it was predicted that individuals with lower task-based HRV would exhibit an increased duration (dwell time) and greater occurrences of salience-related co-active brain states throughout the emotion processing task, reflecting sustained vigilance towards negative emotional faces throughout the duration of the task. Relatedly, the same relationship was predicted for lower resting HRV with dwell time and occurrences of salience-network states, albeit with the expectation that associations would be weaker than that observed during the emotion processing task (given the absence of external emotional stimuli).

A secondary aim of the current study was to further examine the relationship between HRV and trait neuroticism, a disposition linked to increased risk of developing anxiety, alongside their potential interaction as predictors of co-active brain states during rest and emotion contexts. Given the complex and inconsistent relationship between HRV and trait neuroticism, the hypotheses outlined were more exploratory in nature. Specifically, we predicted that higher trait neuroticism would demonstrate significant associations with increased dwell time and greater occurrences (counts) of salience-related and self-referential default mode network (DMN) co-active brain states during rest or the emotion matching task (e.g., Hamilton et al., 2011; Qiao et al., 2020; Servaas et al., 2015), with such an association expected to be weaker in individuals with higher rest and task-based HRV.

3.3 Method

3.3.1 Pre-Registration

This project was pre-registered via the Open Science Framework (OSF) prior to formal data analysis. The research aims, predictions, methods, data processing and analysis scripts can be accessed via the associated OSF project: https://osf.io/xph3y.

3.3.2 Participants

Participants were derived from the wider AOMIC Population of Imaging Psychology 2 (PIOP2) dataset containing 242 younger adult subjects (Snoek et al., 2021). All participants were University students from either the Amsterdam University of Applied Sciences or the University of Amsterdam, recruited via university websites, Facebook, and poster advertisements placed around the University grounds. The authors of the original dataset initially excluded participants according to several

criteria, including: scanner-related artefacts and corruption where relevant correction could not be applied, insufficient data quality resulting in pre-processing failures, absence of a structural scan, and/or incidental findings, leaving a total sample of 226 subjects (for full details of the exclusion criteria, see Snoek et al., 2021). From the overall sample, 216 participants had either task or resting-state fMRI data and accompanying physiology (pulse trace) data. Figure 5 illustrates the participant selection and exclusion process for both task and rest analyses.

As outlined in the pre-registration, the original analytical plan was to perform CAP analyses across the full sample of participants with clean (emotional processing task and resting-state) fMRI and pulse data. However, as highlighted in the pre-registration, a few of the steps applied using the TbCAPs toolbox (Bolton et al., 2020) can impose high computational demands (i.e., consensus clustering step). Thus, it was noted in the pre-registration that analytical decisions may be altered to accommodate this. Indeed, technical errors were encountered at the consensus clustering step due to insufficient cluster capacity and exceeding memory limits enabled within MATLAB when running analyses across the full sample. With accommodations to memory and capacity that was obtainable, we opted to run a split-sample to circumvent technical issues pertaining to cluster capacity. Crucially, the split sample also provided a unique opportunity to observe whether spatial clusters and corresponding temporal metrics for each CAP replicated across two samples from the same dataset.

Following exclusion, participants with emotion matching task fMRI and pulse data (N = 185) were split into two separate samples via stratified sampling which considered balanced groups by sex. Consequently, the split sample resulted in 92 participants in sample 1 and 93 participants in sample 2 for the emotion matching task analyses, and following further exclusion of participants without resting-state fMRI/pulse data, 87 participants in sample 1 and 90 participants in sample 2. The original study procedures were given a favourable ethical opinion of conduct by the corresponding faculty's ethics committee (PIOP2 EC number: 2017-ECT-7568) and all participants gave informed consent prior to their participation.

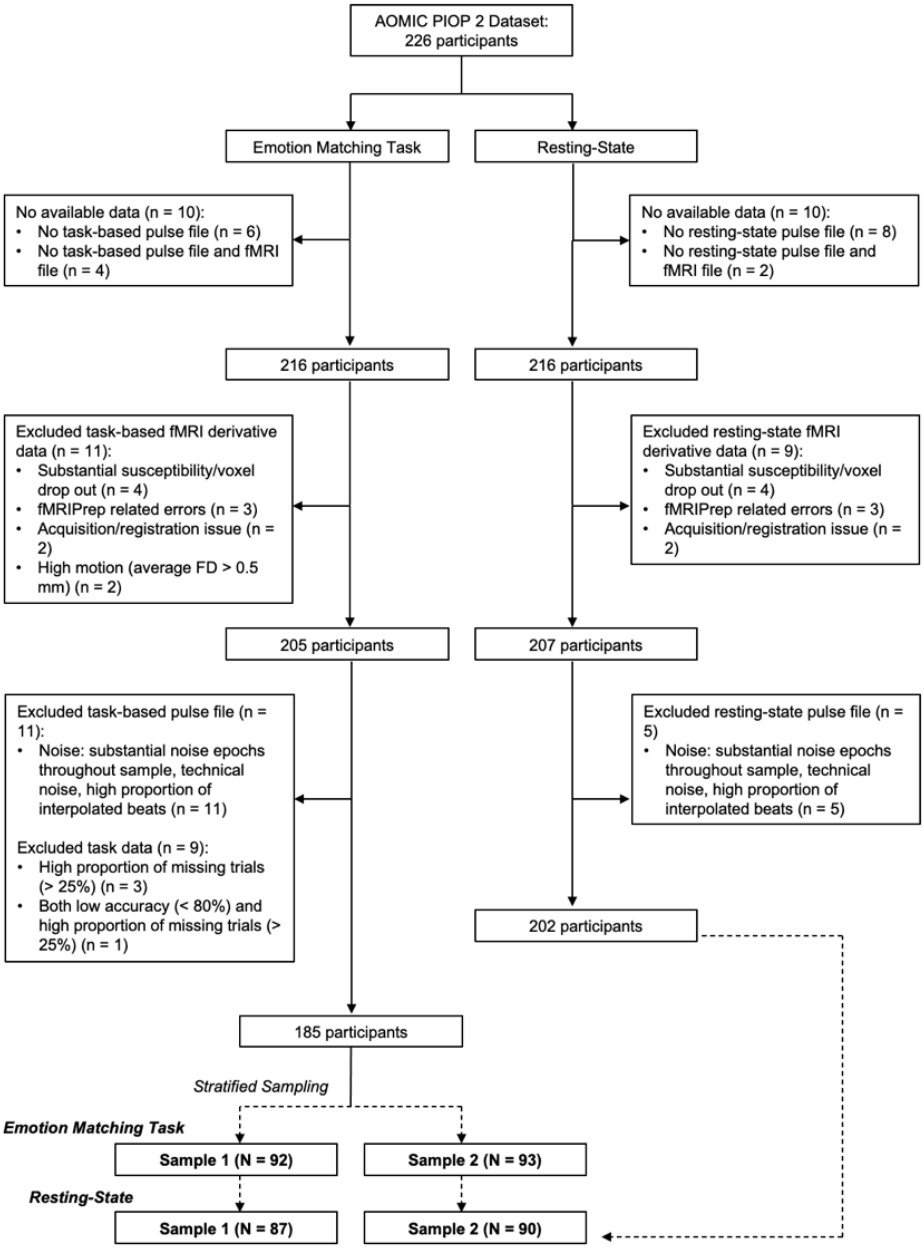

Figure 5. Participant Selection and Exclusion Process for the Emotion Matching Task and Resting-State fMRI Data. Following visual inspection and relevant data processing, 185 participants were found to have clean pulse and fMRI emotion matching task data. Stratified sampling was performed on the sample of 185 participants with the *sample_frac* function from the *dplyr* package in R, resulting in N = 92 participants in Sample 1 and N = 93 participants in Sample 2 for the emotion matching task CAP analyses. Per separate sample, participants with missing or noisy resting-state pulse and/or fMRI data (based on exclusion criteria outlined in the flow chart) were excluded, resulting in N = 87 participants in Sample 1 and N = 90 participants in Sample 2 for the resting-state CAP analyses.

3.3.3 Materials and Procedure

3.3.3.1 Neuroticism

The NEO Five-Factory Inventory (NEO-FFI; McCrae & Costa, 1987) measured five core personality traits (agreeableness, conscientiousness, extraversion, neuroticism, openness to experience, and openness to experience). The total sum score on the neuroticism subscale was used as a metric of trait neuroticism. Individual questionnaire items were not openly accessible; therefore Cronbach's alpha scores are not reported here (refer to Snoek et al., 2021 for information regarding cross-correlations between the different NEO-FFI subscales).

3.3.3.2 Emotion Matching Task

The emotion matching task adopted an established paradigm developed by Hariri et al. (2000). On a given trial, participants were instructed to match one of two stimuli (positioned in the bottom right- and left-hand sides of the screen) to a target stimulus (always presented in the top centre of the screen). Specifically, during the 'emotion' condition, participants saw three images on the screen: an emotional target face centred above two emotional probe faces situated in the bottom right- and left-hand sides of the screen respectively. The 'control' condition followed the same format, but with neutral oval shapes. Participants were asked to match the emotional expression depicted by the target face (anger or fear), or the orientation of the target oval (horizontal or vertical) by selecting one of the two probe stimuli that was congruent with the target stimulus as quickly as possible. Responses were recorded via a button press with the index finger of the participant's left or right hand using an MRI-compatible, four button fibre optic response pad. Response times were measured in seconds. Both the target and probe stimuli disappeared following a response or after a duration of 4.8 seconds if no response was given. The following trial always appeared five seconds after the onset of the present trial, with a blank screen presented between the trials. The emotion matching task followed a block design, with control and emotion blocks consistently presented in alternating order (i.e., control, emotion, control...). Each block contained the presentation of six stimuli with a total duration of five seconds (approximately 30 seconds per block). Four blocks of each emotion type were presented, resulting in eight blocks and 48 stimuli in total. The same stimuli always belonged to each block, but the order of presentation within each block

was randomised across participants. The task had an approximate duration of 4 minutes and 30 seconds (Snoek et al., 2021).

The images of facial expressions presented during the emotion blocks were derived from the NimStim Face stimulus set (Tottenham et al., 2009) which depicted either stereotypical ‘anger’ or ‘fear’ expressions. The target face and one of the two probe options portrayed the same facial expression on a given trial. The stimuli presented contained both male and female faces, alongside faces from different ethnic categories (Asian, Black, and White). However, within a single trial, faces were matched such that they always belonged to the same sex (male or female) and ethnic category (Asian/Black or White). For the control blocks, oval shape stimuli were generated by pixelating the face stimuli used in the emotion condition and matched for colour and size accordingly. The orientation was displayed as horizontal (long side horizontally aligned) or vertical (long side vertically aligned) and within a single trial, two ovals (the target oval and one of the probe options) were aligned in the same position. All stimuli were presented on a grey background (RGB: [248, 248, 248]) on a Cambridge Electronics BOLDscreen 32 IPS LCD screen (120 Hz refresh rate) that was positioned at 113 cm distance from the mirror mounted on top of the head coil (Snoek et al., 2021).

3.3.3.3 Resting-State

Participants were instructed to allow their thoughts to run freely while maintaining their gaze on a fixation cross positioned in the middle of the screen on a grey background (RGB: [150, 150, 150]). Eye tracking was also measured during the scan, but this was not a key measure of interest in the current study. The scan had an approximate duration of eight minutes.

3.3.3.4 Data Acquisition

Relevant acquisition and scanning procedures are outlined below (refer to Snoek et al., 2021 for more details). MRI data were acquired using a Philips Achieva dStream 3T MRI scanner and a 32-channel SENSE head coil. A 3D-structural image using a T1-weighted (T1w) sequence was obtained for each participant (Magnetization-Prepared Rapid Acquisition with Gradient Echo (MPRAGE)), repetition time (TR) = 8.5 ms, echo time (TE) = 3.9 ms, flip angle = 8°, field of view (FOV) = 188 x 240 x 220 mm, resolution = 1 mm isotropic, acceleration factor = 2.5 (right to left), 2

(feet to head), number of signals (repetitions) = 2, acquisition direction = axial, acquisition time = 6 minutes, 3 seconds. Functional MRI data were acquired using a gradient echo-based echo planar imaging (GE-EPI) sequence (135 whole-brain volumes for emotion task scan, 240 whole-brain volumes for resting-state scan), 37 slices, slice gap = 0.3 mm, TR = 2000 ms, TE = 28 ms, flip angle = 76.1°, FOV = 240 x 240 x 122 mm, resolution = 3 mm isotropic. Acquisition time for the emotion-matching scan varied slightly across participants, with an approximate duration of 4 minutes 30 seconds, whereas acquisition time for the resting-state scan was more consistent with an approximate duration of 8 minutes.

3.3.3.5 General Procedure

Prior to participation in the study, all participants were informed of the research aims, the standard MRI procedures and associated safety protocols, the general experimental procedure, and relevant privacy and data sharing policies. All participants provided informed consent and underwent an MRI screening checklist prior to any formal testing. A maximum of four participants were tested on a given day, with the testing session typically taking place between 8:30am-1pm. Whilst two participants began with the MRI protocol, the other two completed self-report questionnaires concerning demographic (age, biological sex, height, weight, handedness, and place of education) and psychometric information (including the NEO-FFI). The MRI procedure included an initial survey scan, a T1w anatomical scan, and engagement in several functional scans: a working memory task, resting-state scan, diffusion weighted imaging scan, a stop-signal task, and the emotion matching task (in this order). The MRI session had a duration of approximately 1 hour.

3.3.4 Data Processing and Analysis

3.3.4.1 Pulse Processing

Raw physiology files downloaded from OpenNeuro were exported to RStudio (v1.4.1006) to isolate the cardiac trace and to calculate the time of the signal (seconds) based on the sampling rate (496 Hz). Files were trimmed to reflect the start of the resting-state or emotion matching task scan using the task onset time stamp provided in the appropriate corresponding event (.json) file. Subsequently, data files were exported into Kubios HRV Premium software (version 3.5.0; Biosignal Analysis and

Medical Imaging Group, University of Kuopio, Finland; Tarvainen et al., 2014) for further processing and HRV analysis.

Separate samples of the pulse signal from the emotion matching task and resting-state scan were processed and analysed for each participant. The PPG setting within Kubios was applied to the data wherein the pulse peak detection feature appends beat markers to the pulse waveform using a matched filtering approach. Where the beat detection feature either misplaced or missed placing beat markers, manual corrections were applied to the signal to either place or (re)move markers to a suitable location on the pulse waveform. Automatic noise correction (alongside manual corrections) was primarily used across participants' data to reduce the influence of noise and artefacts in the signal (i.e., ectopic, extra or missed beats, motion, and technical noise/interference). In cases where automatic noise correction was too stringent (i.e., unnecessary over-interpolation of beats) or did not adequately account for noise in the signal, threshold and/or manual correction was applied. In order to retain as much natural variation in the signal as possible, and in light of recent recommendations for the application of lower threshold settings for correcting noise in cardiac traces in younger adult populations, threshold correction settings between 'very low' - 'medium' (0.45 - 0.25 seconds) were applied in accordance with noise severity and artefacts observed in the participant's data (Alcantara et al., 2020). Moreover, in cases where the automatic noise detection feature identified particularly noisy epochs within the signal that could not be cleaned using available correction methods, the longest duration of clear pulse signal either preceding or following the noise epoch(s) was retained for analysis. Adhering to Kubios guidelines, pulse signal requiring 5% or more of the beats to be interpolated were excluded from further analysis. Several measures, including the Root Mean Square of Successive Differences (RMSSD; measured in milliseconds) were derived. In this study, we opted to proceed with the RMSSD as the HRV metric since it is a robust measure of parasympathetically mediated HRV that has also been reported to be less influenced by other physiological factors, importantly respiration (Hill et al., 2009; Kleiger et al., 2005). A natural log transformation was applied to the RMSSD (herein referred to as (ln)RMSSD) to correct for positive skew using the *log* command from the *base* package (v3.5.2) in RStudio (version 1.4.1106).

3.3.4.2 fMRIPrep Processing

The task and rest fMRIPrep derivative files were downloaded from OpenNeuro (dataset: ds002790, https://openneuro.org/datasets/ds002790). Snoek et al. (2021) performed initial pre-processing of the anatomic and functional data using fMRIPrep version 1.4.1 (RRID:SCR_016216) (Esteban et al., 2019; 2020), a Nipype based tool (RRID:SCR_002502) (Gorgolewski et al., 2011). T1w volumes were corrected for intensity non-uniformity via N4BiasFieldCorrection v2.1.0 (Tustison et al., 2010) and skull-stripped using antsBrainExtraction.sh v2.1.0 (OASIS template). The tool recon-all from FreeSurfer v6.0.1 (RRID:SCR_001847) (Dale et al., 1999) was used to reconstruct brain surfaces, and refinement of the estimated brain mask was performed using a custom variation of the method to reconcile ANTs-derived and FreeSurfer-derived segmentations of the cortical gray-matter of Mindboggle (RRID:SCR_002438) (Klein et al., 2017; Snoek et al., 2021). Data were normalised to the ICBM 152 Nonlinear Asymmetrical template version 2009c (MNI152NLin2009cAsym; RRID:SCR_008796; Fonov et al., 2009) through nonlinear registration via the antsRegistration tool of ANTs v2.1.0 (RRID:SCR_004757; Avants et al., 2008) using the brain-extracted versions of the T1w volume and the template. T1w segmentation of cerebrospinal fluid (CSF), white matter (WM) and gray matter (GM) was performed using '*fast'* (FSL v5.0.9; RRID:SCR_002823; Zhang et al., 2001).

Slice-time correction was not applied to the functional data. Both task and resting-state functional images underwent motion correction via '*mcflirt'* (FSL v5.0.9; Jenkinson et al., 2002) using the average volume after an initial first-pass motion correction procedure as the reference volume and normalised correlation as the image similarity cost function. The authors also opted to use 'fieldmap-less' distortion correction via antsRegistration (ANTs) which involved co-registering the functional image to the subject's corresponding T1w image with intensity inverted (Huntenburg, 2014; Wang et al., 2017) constrained with an average fieldmap template (Treiber et al., 2016). Following distortion-correction, co-registration to the subject's corresponding T1w image was performed using boundary-based registration (BBR; Greve & Fischl, 2009) with 6 degrees of freedom via '*bbregister'* (FreeSurfer v6.0.1). The motion correction transformations, field distortion to correct for warp, BOLD-to-T1w transformation and T1w-to-MNI-template warp were all concatenated and applied in a single step through antsApplyTransforms (ANTs v2.1.0) using Lanczos interpolation.

The CompCor (Behzadi et al., 2007) method was used to extract physiological noise regressors, with principal components estimated for both temporal (tCompCor) and anatomical (aCompCor) variants. The brain mask was eroded to create a mask that only captured subcortical structures, excluding signal related to cortical areas. Subsequently, six tCompCor components were calculated by including the top 5% variable voxels within the subcortical mask. With relation to aCompCor, six components were calculated within both the intersection of the subcortical mask and the union of WM and CSF masks in the subject's T1w space following their projection to the native space per functional run. A measure of framewise displacement (FD; Power et al., 2014) per functional run was also calculated using the implementation of Nipype.

Many internal operations of fMRIPrep use Nilearn (RRID:SCR_001362; REF), principally within the BOLD-processing workflow. For more details of the pipeline see: https://fmriprep.org/en/1.4.1/workflows.html.

3.3.4.3 Post-fMRIPrep Processing

The fMRIPrep functional images were downloaded and visually inspected for quality prior to any further processing carried out in the current study. Correspondingly, functional images were skull-stripped using the subject's corresponding brain mask per each functional run (via *'fslmaths'* command). Following this, nuisance regression was performed via FSL's '*fsl_regfilt'* tool, with the following regressors included in the model: 24 motion parameters (three translational and three rotational parameters, their temporal derivatives, and the quadratic terms of both (Satterthwaite et al., 2013)), top five WM and top five CSF components identified via aCompCor (Behzadi et al., 2007; Muschelli et al., 2014), and three discrete cosine regressors. The top 5 WM and CSF components via the aCompCor method were regressed from the data instead of the global signal regression approach since the former technique does not depend upon regressing gray matter from gray matter signals, reducing the risk of false or increased negative correlations (Murphy et al., 2009). Functional data were smoothed with a Gaussian kernel (full width at half maximum of 4 mm) and split into individual 3D NIFTI volume files for input to the TbCAPs toolbox (Bolton et al., 2020).

3.3.4.4 Co-Activation Pattern (CAP) Analysis

Seed-based CAP analyses were conducted to derive brain states and spatiotemporal dynamics of amygdala- and bed nucleus of the stria terminalis (BNST)-related networks. CAP analysis is a data-driven neuroanalytical technique that relies on fewer statistical assumptions than other techniques (e.g., sliding window analysis) and is potentially more effective in its assessment of transient changes in co-activation patterns due to higher temporal resolution (i.e., at the level of individual fMRI volumes; Liu et al., 2018). CAP analyses were conducted using the 'TbCAPs' toolbox (Bolton et al., 2020) for i) right versus left amygdala and BNST seed regions and ii) emotion task versus resting-state scan for both samples. Separate right and left central extended amygdala seeds (amygdala and BNST) were selected due to reported amygdala lateralisation effects in both prior HRV and emotion literature (Baas et al., 2004; Sakaki et al., 2016; Tupitsa et al., 2023), alongside observed reactivity differences in the amygdala relative to the BNST as a function of neuroticism (Grogans et al., 2024). Both central extended amygdala and BNST seed region masks were derived from Tillman et al. (2018) and subsequently normalised and resampled to the MNI 2009c Non-Linear Asymmetric template. A union seed-based approach was implemented across analyses to identify volumes that exceeded an activation threshold of $Z > 0.8$ for either the (R/L) central extended amygdala, (R/L) BNST, or a combination of both, ensuring only volumes pertaining to these specific salience regions were selected for further analysis. Volumes with a framewise displacement threshold of higher than 0.5 mm were scrubbed.

Retained volumes of co-active areas were clustered into spatially distinct brain states across time and participants by K-means clustering. Specifically, consensus clustering (Monti et al., 2003) was performed for K values 2-11, over 20 folds with each fold using 80% of the data per individual K value to determine the optimal number of brain states. The optimal number of brain states was determined by the proportion of ambiguously clustered pairs (PAC; Şenbabaoğlu et al., 2014). Given two data points, a robust cluster number should reflect these data points either consistently being clustered together or clustered separately across the specified number of folds, with lower PAC values indicating a more consistent and robust cluster number (Bolton et al., 2020). A stability value is derived via 1-PAC, in which higher values indicate more consistent and robust clusters (Bolton et al., 2020). Correspondingly, an optimum cluster value of 4 was identified based on visual inspection of the PAC values for the

right amygdala and BNST CAP analysis on sample 1's emotion matching task data. Notably, while K-means clustering is commonly adopted in fMRI research, there is controversy in relation to the optimal criteria for selecting the appropriate cluster number. As prior research has outlined, while the extraction of two clusters provides a limited representation of neural network patterns that can be generated (Chen et al., 2015; Liu & Duyn, 2013), a higher cluster number is often linked to fewer data time points (e.g., fMRI volumes) contributing to the brain states which can negatively impact the stability of the findings (Li et al., 2024). The PAC values varied across the different CAP analyses and samples, however, to aid interpretation of results and replicability, we opted to retain the same optimal, trade-off cluster value (K = 4) for extracting CAPs across all analyses.

The key temporal measures of interest per CAP calculated within each participant were: (1) *occurrences* which reflected the total number (N) of volumes exceeding the set threshold per brain state across the duration of the scan and (2) *average duration* which represented the mean time duration a given brain state was sustained in seconds ($Occurrences_{CAP}$ / $Number\ of\ Entries_{CAP}$ * TR).

3.3.4.5 Statistical Analysis

Multiple hierarchical regression analyses were conducted to examine associations between HRV and temporal metrics of each CAP for both samples. Separate multiple regression models were conducted for right versus left amygdala and BNST seed regions and emotion versus rest. The following predictors were entered into the model: age, body mass index (BMI), number of frames retained, (ln)RMSSD, total neuroticism score, and a HRV x neuroticism interaction term. Predictors were entered in the following order: age, BMI, frames retained (step 1), HRV (step 2), neuroticism score (step 3), and HRV x neuroticism interaction predictor (step 4). Standardised beta coefficients of the predictors and uncorrected *p*-values are reported in the Results.

While the pre-registration originally outlined frequentist analyses with traditional null hypothesis significance testing, supplementary Bayesian linear regressions were performed as complementary analyses to determine the relative magnitude of support for the alternative versus null hypothesis. Bayesian regressions were conducted using JASP (version 0.19.3; JASP Team, 2025). JASP's default priors were used: Beta-Binomial model prior (a = 1, b = 1) and the default Jeffreys-Zellner-Siow prior with an

r scale of 0.354 (Love et al., 2019; Rouder & Morey, 2012). While the frequentist regressions rely on the *p*-value falling below the 0.05 threshold to reject the null hypothesis, we also report the Bayes Factor (BF) which serves as a metric of the strength of evidence for either the null or alternative hypothesis. BF values can be reported as either increased support for the alternative hypothesis (BF_{10}) or increased support for the null hypothesis (BF_{01}). To enhance interpretability of the findings, we reported BF_{10} in the case of a significant finding as indicated by the frequentist regression analyses with evidence suggesting greater support for the alternative hypothesis, and BF_{01} where a non-significant finding was observed with evidence suggesting increased support for the null hypothesis. The following labels were used to interpret the magnitude of support: 1-3 as anecdotal, 3-10 as moderate, 10-30 as strong, 30-100 as very strong, and > 100 as decisive evidence (Jeffreys, 1961; van Doorn et al., 2021).

3.4 Results

3.4.1 Descriptive Statistics

Table 4 summarises the key descriptives for each sample. There were no significant differences between the samples on any of the main predictors or key variables of interest.

3.4.2 Associations Between HRV and Trait Neuroticism

Pearson correlations revealed that there was no significant association between either task-based HRV (Sample 1, $r = 0.02$, $p = .858$; Sample 2, $r = -0.10$, $p = .352$) or resting HRV (Sample 1, $r = -0.02$, $p = .856$; Sample 2, $r = -0.08$, $p = .429$) and trait neuroticism.

Table 4.
Descriptive Statistics Per Sample for the Emotion Matching Task and Resting-State Analyses

	Sample 1 (Emotion Matching Task; N = 92)	Sample 2 (Emotion Matching Task; N = 93)	Sample 1 (Resting-State; N = 87)	Sample 2 (Resting-State; N = 90)
Demographics				
Age (years)	21.72 (1.66)	21.94 (1.81)	21.76 (1.68)	21.91 (1.79)
Sex (%)	51% F/ 48% M/ 1% Unknown	57% F/ 43% M	51% F / 48% M/ 1% Unknown	58% F/ 42% M
BMI	22.65 (2.65)	22.59 (2.85)	22.63 (2.67)	22.52 (2.86)
Neuroticism	31.12 (8.01)	31.06 (8.10)	31.07 (7.98)	31.33 (8.01)
lnRMSSD(ms)	4.13 (0.51)	4.04 (0.53)	4.10 (0.53)	4.00 (0.51)
Heart Rate (BPM)	64.06 (10.14)	64.15 (9.11)	63.48 (10.80)	63.48 (9.41)
RR Interval (ms)	958.78 (146.97)	954.30 (136.74)	970.00 (153.55)	966.08 (144.46)
fMRI Variables*				
Right Amygdala Right BNST Total Volumes (N)	49.82 (3.68)	49.14 (3.71)	89.48 (4.98)[a]	88.53 (5.59)
Right Amygdala Right BNST CAP 1 Volumes (N)	14.02 (3.51)	13.87 (3.26)	23.22 (4.49)	25.41 (5.48)
Right Amygdala Right BNST CAP 2 Volumes (N)	12.39 (3.29)	13.73 (3.51)	23.07 (4.74)	24.48 (5.15)
Right Amygdala Right BNST CAP 3 Volumes (N)	11.82 (2.76)	10.84 (3.63)	22.69 (5.37)	19.94 (4.86)
Right Amygdala Right BNST CAP 4 Volumes (N)	11.59 (3.32)	10.70 (3.43)	20.51 (4.33)	18.70 (4.42)
Left Amygdala Left BNST Total Volumes (N)	48.96 (4.61)	49.22 (3.28)	89.17 (5.03)	88.61 (4.83)
Left Amygdala Left BNST CAP 1 Volumes (N)	13.10 (3.01)	13.15 (3.46)	25.61 (5.74)	23.72 (4.97)
Left Amygdala Left BNST CAP 2 Volumes (N)	12.67 (3.32)	12.61 (3.34)	21.92 (4.81)	23.70 (4.62)
Left Amygdala Left BNST CAP 3 Volumes (N)	11.97 (3.82)	12.40 (3.41)	21.72 (4.46)	21.42 (5.10)
Left Amygdala & BNST CAP 4 Volumes (N)	11.22 (3.29)	11.05 (3.07)	19.92 (3.97)	19.77 (4.93)

[a] Note that the number of volumes refers to the average number of volumes/frames retained for the CAP analyses (i.e., volumes exceeding set threshold of amygdala and BNST seed activation). The volumes are greater for the resting-state versus emotion matching task fMRI data due to a longer resting-state scan duration (i.e., 240 versus 135 total fMRI volumes to sample from for the resting-state versus emotion matching task data).

3.4.3 CAP Characteristics

Four distinct brain states were identified for each seed-based CAP analysis and per sample. The CAP number indicates the order of the CAPs in relation to the total variance explained per each CAP analysis (right and left amygdala/BNST) and sample, with CAP 1 reflecting the brain state with the most variance explained. However, for ease of visual interpretation, individual CAPs generated per analysis and per sample were clustered together into more general brain states and labelled according to relevant prior literature.

With relation to the emotion matching task (Figure 6), CAPs comprising state 1 were characterized by heightened activation in the lateral occipital cortex (superior and inferior divisions), bilateral superior parietal lobe, temporal occipital fusiform cortex, bilateral middle and inferior frontal gyri, and precentral gyri, with co-deactivation mainly in anterior medial prefrontal cortex (more consistent in sample 2) and precuneus. This brain state was consistent with a visual attention/task engagement network (Uddin et al., 2019). Furthermore, CAPs contributing to state 2 followed neural co-activation patterns reflecting the ‘core’ DMN, marked by greater activation in the paracingulate gyrus and frontal pole, with more extended anterior cingulate and posterior cingulate cortex co-activation in sample 1 as a function of left amygdala and BNST, paired with deactivation in occipital cortex regions (Andrews-Hanna et al., 2010). State 3 CAPs appeared to predominantly reflect a mixture of salience-related and somatosensory network regions, with co-activation in the juxtapositional lobe (formerly known as the supplementary motor area), frontal and opercular cortex, and insula, alongside co-deactivation in occipital cortex areas and the superior frontal gyrus (Uddin et al., 2019). However, the most similar network state in sample 1 was CAP 4 for left amygdala and BNST which appeared to involve more salience-related states over somatosensory regions, including co-activation of the anterior cingulate and posterior cingulate cortex, and precuneus. Finally, the CAPs under state 4 appeared to reflect a similar pattern to that of the extended face processing network (Haist & Anzures, 2017; Haxby et al., 2000; Ishai, 2008; Jamieson et al., 2024), with co-activation of bilateral amygdala, the temporal occipital fusiform cortex (encompassing the fusiform gyrus, and lateral occipital cortex (inferior and superior divisions) and deactivation in the superior frontal gyrus, paracingulate gyrus, angular gyrus and posterior and anterior cingulate cortex (default mode and salience network nodes).

For the resting-state CAP analyses (Figure 7), state 1 involved co-activation of the occipital cortex and superior parietal lobe with co-deactivation in the posterior cingulate cortex, precuneus and superior frontal gyrus, reflecting a visual attention CAP (Uddin et al., 2019). State 2 was characterised by co-activation in the superior frontal and paracingulate gyrus (dorsal medial prefrontal cortex) and frontal pole with simultaneous co-deactivation in the cuneal cortex extending into precuneus (with the latter region more prominent in sample 2 as a function of left amygdala and BNST), reflecting the dorsal medial DMN (Andrews-Hanna et al., 2010). Furthermore, state 3 was marked by increased co-activation of the posterior cingulate cortex, precuneus and frontal medial cortex and co-deactivation of supramarginal gyrus, insula and inferior frontal gyrus, a pattern consistent with the core DMN (Andrews-Hanna et al., 2010). Finally, in state 4, co-activation of the anterior cingulate cortex, insula, and juxtapositional lobe was paired with co-deactivation mainly in occipital regions, reflecting a salience network (Uddin et al., 2019).

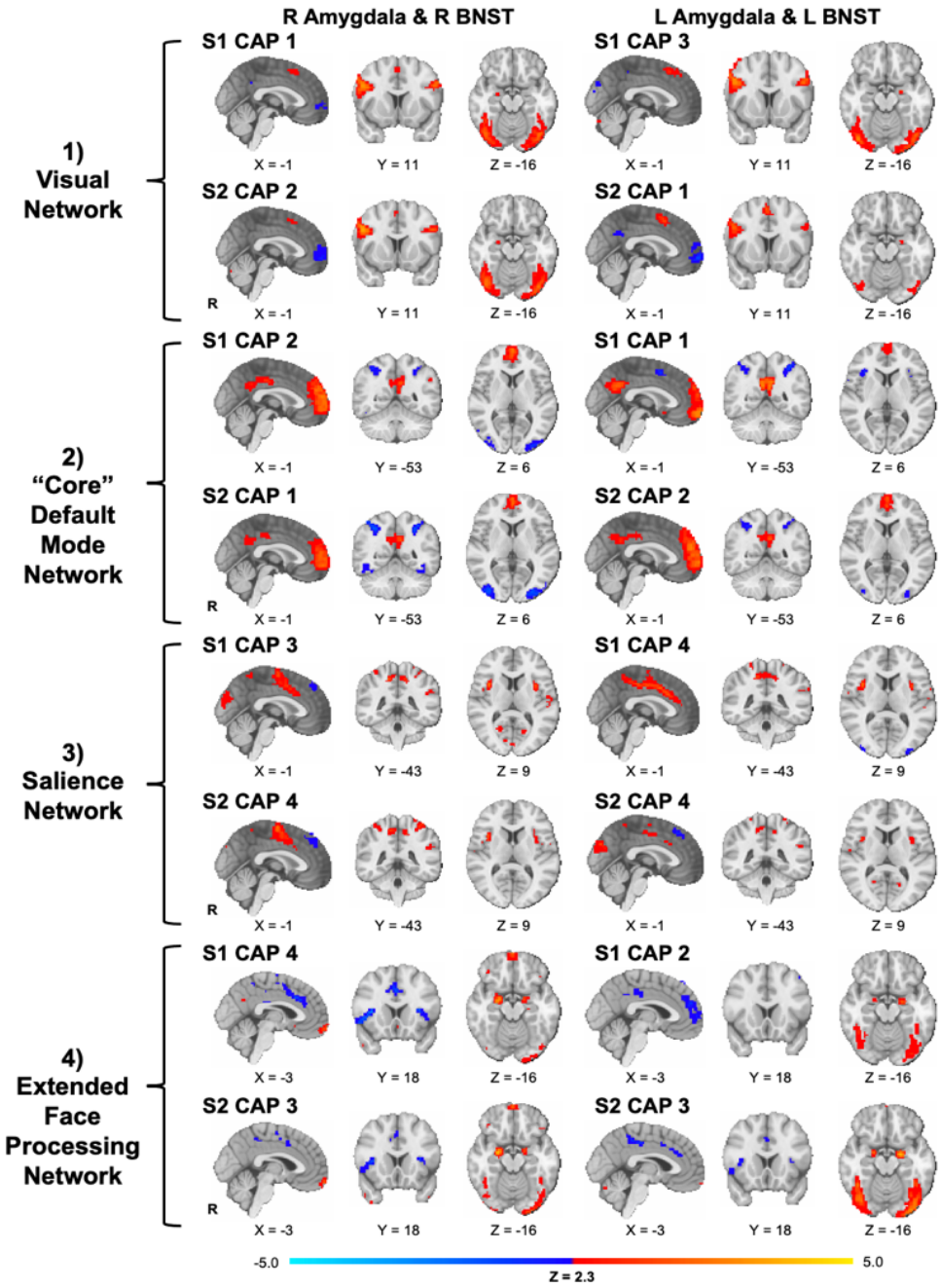

Figure 6. Emotion Matching Task Co-Activation Patterns (CAPs). Four CAPs displayed per sample 1 (S1) and sample 2 (S2) and categorised into general brain states. Activations (warm colours) and deactivations (cool colours) for each Z-scored CAP are thresholded at 2.3 and displayed in MNI 2009c non-linear asymmetric space. The four brain states were identified as the following: **1)** Visual Attention Network with heightened activation in the occipital cortex, lateral occipital cortex (superior and lateral divisions), precentral, middle frontal and inferior frontal gyri, and de-activation in the precuneus and paracingulate gyrus; **2)** "Core" Default Mode Network with co-activation in paracingulate gyrus, frontal pole, anterior cingulate and posterior cingulate regions and co-deactivation in occipital regions; **3)** Salience Network with increased activation in the juxtapositional lobe, insula, and frontal and opercular cortex alongside deactivation in the superior frontal gyrus and occipital regions; **4)** Extended Face Processing Network with co-activation of bilateral amygdala, temporal occipital fusiform cortex (fusiform gyrus), and lateral occipital cortex (inferior and superior), alongside co-deactivation in superior frontal gyrus, angular gyrus, and posterior and anterior cingulate cortex.

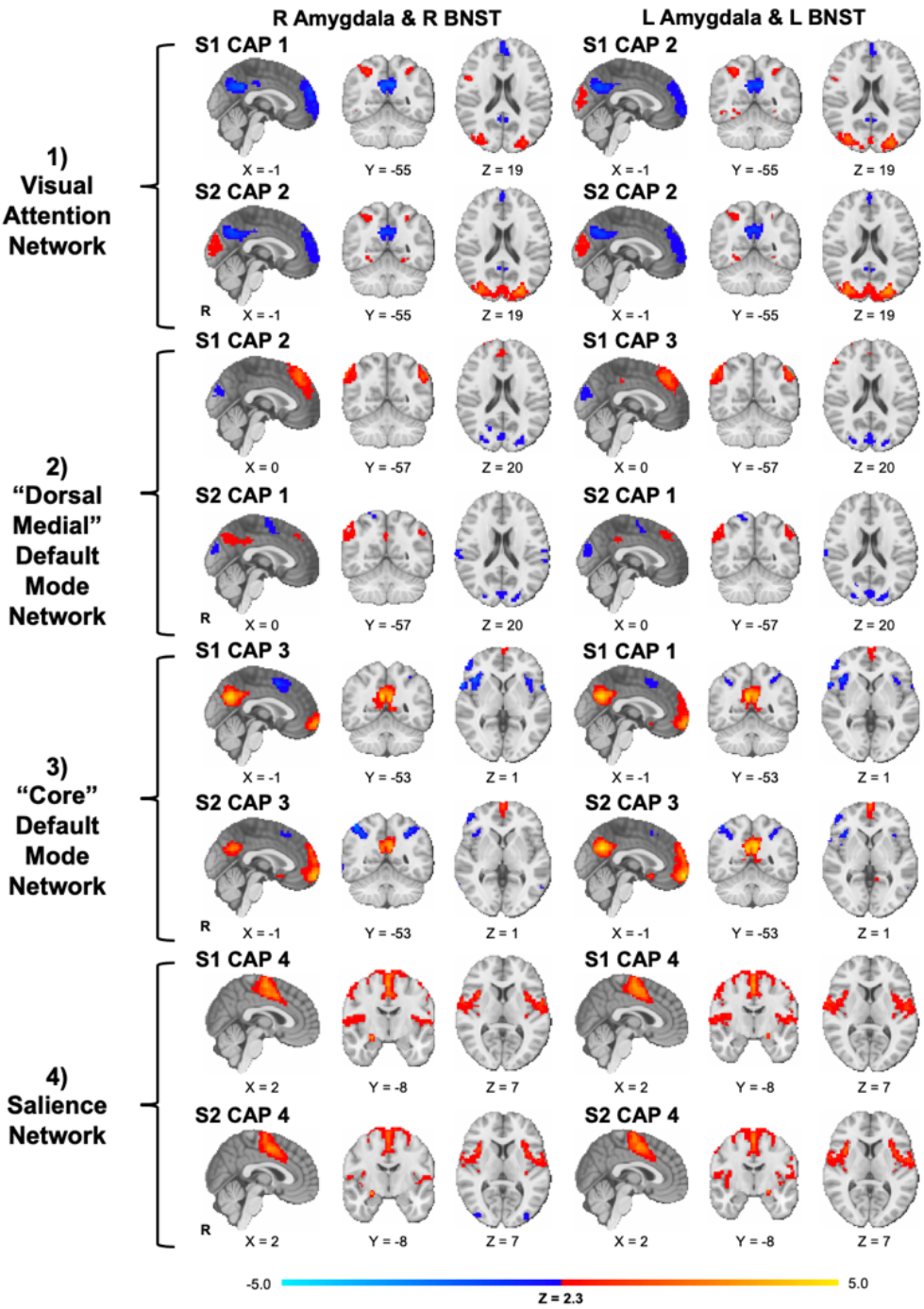

Figure 7. Resting-State Co-Activation Patterns (CAPs)**.** Four CAPs displayed per sample 1 (S1) and sample 2 (S2) and categorised into general brain states. Activations (warm colours) and deactivations (cool colours) for each Z-scored CAP thresholded at 2.3 are displayed in MNI 2009c non-linear asymmetric space. The four brain states included: **1)** Visual Attention Network with co-activation of the occipital cortex and superior parietal lobe alongside co-deactivation in the posterior cingulate cortex, precuneus, and superior frontal gyrus; **2)** Dorsal Medial Default Mode Network involving co-activation of dorsomedial prefrontal cortex, superior frontal gyrus, paracingulate gyrus, angular gyrus, and frontal pole, with further co-activation in precuneus and posterior cingulate in sample 2 and co-deactivation in the cuneus, with further co-deactivation in the juxtapositional lobe in sample 2; **3)** Core Default Mode Network with co-activation in the posterior cingulate cortex, precuneus, and frontal medial cortex and co-deactivation of supramarginal gyrus, insula, and inferior frontal gyrus; **4)** Salience Network including co-activation of the anterior cingulate cortex, insula, and juxtapositional lobe with co-deactivation in occipital cortex regions.

3.4.4 Emotion Matching Co-Activation Patterns

3.4.4.1 Right Amygdala and Right BNST

Neither task-based HRV nor self-reported trait neuroticism significantly predicted the occurrences or average duration of any of the CAPs derived from the right amygdala and BNST CAP seed region analyses in either of the samples during the emotion processing task.

3.4.4.2 Left Amygdala and Left BNST

In sample 1, although the overall regression model was not significant (R^2 change = 0.05, $F(5, 90) = 1.75$, $p = .132$ Model 3), after entering trait neuroticism into the model, frequentist regression analyses showed that trait neuroticism predicted the average duration of CAP 3, a visual network state, such that individuals with higher trait neuroticism appeared to spend a lower average duration of time in this visual network state co-active with the left amygdala and left BNST throughout the task (β = -0.22, t = -2.09, p = .039). However, neither the model with control variables (age, BMI, total volumes retained in CAP analysis per participant) and the addition of task-related HRV (R^2 change = 0, $F(4, 90) = 1.05$, $p = .386$ Model 2) nor the full model including control variables, task-related HRV, trait neuroticism and the interaction between HRV and neuroticism (R^2 change = 0.01, $F(6, 90) = 1.59$, $p = .161$ Model 4) showed HRV (β = 0.01, t = 0.05, p = .957), or the interaction term (β = -0.09, t = -0.89, p = .374), to predict the average duration of CAP 3. Akin to the frequentist model, Bayesian analyses indicated moderate evidence in support of the null for the model including control variables, HRV and trait neuroticism ($BF_{01} = 6.33$), whereas anecdotal support emerged for trait neuroticism as a sole predictor of the average duration of this visual CAP ($BF_{10} = 1.97$). Moderate to strong support for the null hypothesis emerged for task-related HRV ($BF_{01} = 4.44$) as a sole predictor and the other models including control variables with task-related HRV and the interaction between HRV and neuroticism ($BF_{01} = 15.73$ Model 2; $BF_{01} = 10.18$ Model 4).

Comparatively, in sample 2, for the equivalent visual network brain state (CAP 1), the frequentist regression model indicated that task-related HRV predicted the average duration of co-activation between this visual network CAP and left amygdala and left BNST. Specifically, while adding task-based HRV to the model did not result in a significant change in the variance explained for the average duration of CAP 1 (R^2 change = 0.04, $F(4, 92) = 2.08$, $p = .090$ Model 2), higher task-based HRV was associated

with a greater average duration of this visual network state (β = 0.21, t = 2.00, p = .049). Nevertheless, unlike in sample 1, trait neuroticism (R^2 change = 0.01, F(5, 92) = 1.87, p = .107 Model 3) did not significantly predict the average duration of this visual network that was co-active with left amygdala and left BNST trait (β = 0.11, t = 1.02, p = .313). Akin to sample 1, the interaction between HRV and neuroticism (R^2 change = 0.02, F(6, 92) = 1.89, p = .093 Model 4) did not predict the average duration of CAP 1 (β = 0.14, t = 1.36, p = .177). Bayesian analyses revealed unconvincing support for task-based HRV as a sole predictor of the average duration of CAP 1 (BF_{10} = 0.74) and moderate evidence for the null for trait neuroticism as a sole predictor (BF_{10} = 4.26) and across models (BF01 = 3.31 Model 2; BF01 = 5.18 Model 3; BF01 = 5.56 Model 4). Therefore, while there was some weak evidence that trait neuroticism (sample 1), and to a lesser extent, task-based HRV (sample 2) predicted the average duration of a visual network that was co-active with left amygdala and left BNST, the main predictor results were not replicated across each sample respectively.

Finally, within sample 2, entering trait neuroticism into the frequentist regression model contributed to a significant change in the variance explained for CAP 2 occurrences, a brain state reflecting a core DMN pattern (R^2 change = 0.05, F(5, 92) = 2.49, p = .037 Model 3). Higher trait neuroticism was linked to fewer occurrences of this core default mode state throughout the emotion matching task (β = -0.23, t = -2.18, p = .032). While the model including task-related HRV (R^2 change = 0, F(4, 92) = 1.86, p = .125 Model 2) did not find HRV to predict the occurrences of this core DMN state (β = 0.05, t = 0.46, p = .649), the interaction between HRV and neuroticism interaction significantly explained the variance in the occurrences of this CAP (R^2 change = 0.05, F(6, 92) = 3.04, p = .010 Model 4; β = -0.23, t = -2.27, p = .026). Specifically, the simple slope of HRV on CAP 2 occurrences appeared to be approaching significance at low levels of neuroticism (β = 0.24, t = 1.74, p = .085), such that higher HRV predicted increased occurrences in this core DMN CAP at low, but not high levels of neuroticism (β = -0.26, t = -1.52, p = .132). Bayesian analyses indicated anecdotal support for trait neuroticism as a sole predictor of DMN occurrences (BF_{10} = 2.09) and the full model including control variables, HRV, trait neuroticism and their interaction term (BF_{10} = 2.00). Support for the model including control variables, task-related HRV and trait neuroticism was unclear (BF_{10} = 0.60) and moderate support for the null was found for the model with only control variables and task-related HRV (BF_{01} = 9.33 Model 2).

On the other hand, this pattern of findings was not replicated in sample 1 for the equivalent core DMN brain state (CAP 1). Frequentist regression models containing control variables and where task-based HRV (R^2 change = 0, $F(4, 90) = 0.30$, $p = .876$ $_{\text{Model 2}}$), trait neuroticism (R^2 change = 0.02, $F(5, 90) = 0.50$, $p = .733$ $_{\text{Model 3}}$), and their interaction term (R^2 change = 0, $F(6, 90) = 0.43$, $p = .857$ $_{\text{Model 4}}$) were added, showed none of the predictors of interest to demonstrate associations with the occurrences of CAP 1 in this sample. Bayesian regressions indicated moderate support for task-related HRV ($BF_{01} = 3.98$) and anecdotal support for trait neuroticism ($BF_{01} = 2.55$) with relation to the null. Strong to extreme support ($BF_{01} = 50.68$ $_{\text{Model 2}}$; $BF_{01} = 65.25$ $_{\text{Model 3}}$; $BF_{01} = 128.08$ $_{\text{Model 4}}$) was found for the null across the models.

See Figure 8 for a visual depiction of these results.

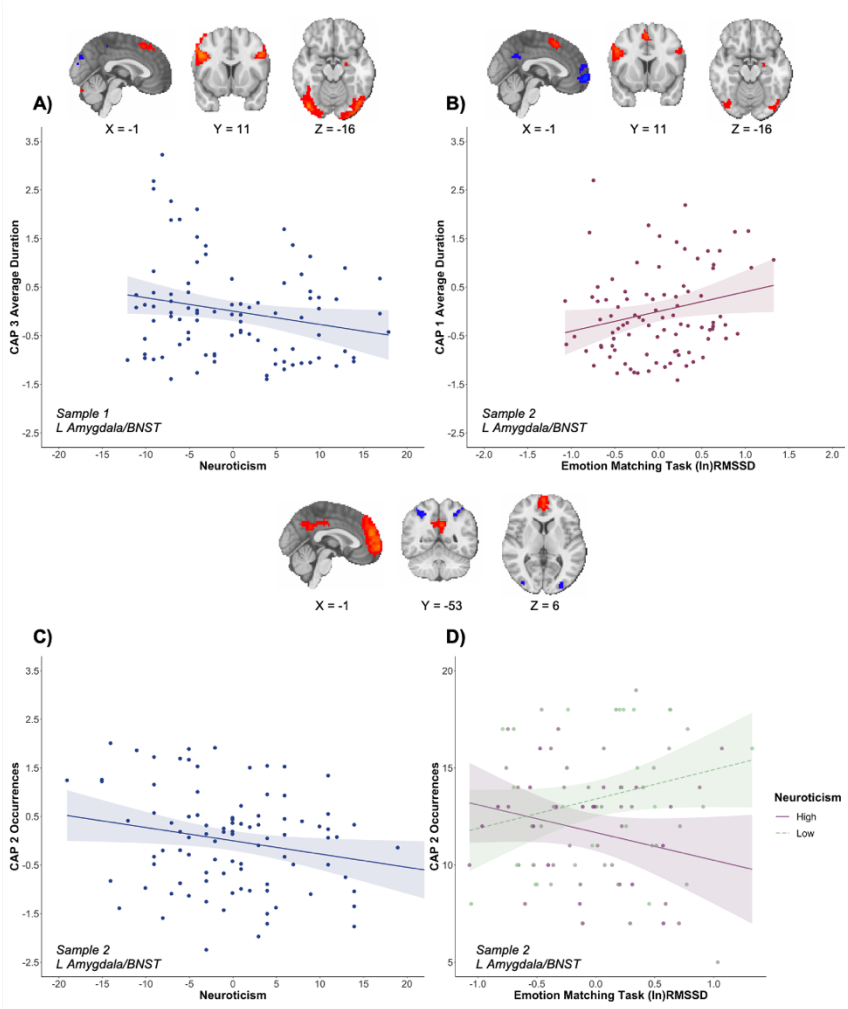

Figure 8. HRV and Trait Neuroticism Findings from the Emotion Matching Task CAP Analyses. **A)** In sample 1, higher trait neuroticism was associated with a lower average duration of CAP 3, a visual attention brain state, as a function of the left amygdala/BNST. **B)** In sample 2, higher task-related HRV correlated with a higher average duration of CAP 1 as a function of the left amygdala/BNST, a brain state overlapping the spatial pattern of the visual attention CAP observed in sample 1. **C)** Higher trait neuroticism predicted fewer occurrences of CAP 2, a brain state reflecting a core DMN state that was found to be co-active with the left amygdala/BNST in sample 2. **D)** An interaction between task-related HRV and trait neuroticism predicted the occurrences of this core DMN state in sample 2, such that higher task-based HRV was linked to fewer occurrences of this CAP for individuals with lower, but not higher, trait neuroticism. Original units for temporal CAP metrics were number of volumes ('Occurrences') and average duration in seconds ('Average Duration'). Standardised residuals (controlling for mean centered age, BMI, total number of retained fMRI volumes in the CAP analysis, and either task-related HRV or trait neuroticism depending on the relevant predictor) are displayed for visualisation purposes in A-C. The HRV by trait neuroticism interaction plot was created using the *interactions* package in R with high and low neuroticism groups reflecting a ± 1SD split.

3.4.5 Resting-State Co-Activation Patterns

3.4.5.1 Right Amygdala and Right BNST

In sample 1, while adding resting HRV to the frequentist regression model with control variables did not produce a significant change in variance explained (R^2 change = 0.08, $F(4, 85) = 2.38$, $p = .058$ Model 2), resting HRV emerged as a significant predictor of the average duration of CAP 2, a neural pattern reflecting the dorsal medial DMN. Higher resting HRV was linked to a lower average duration of this default subsystem brain state during rest ($\beta = -0.28$, $t = -2.64$, $p = .010$). Neither the models that included trait neuroticism (R^2 change = 0.02, $F(5, 85) = 2.31$, $p = .052$ Model 3) nor the HRV by trait neuroticism interaction term (R^2 change = 0.01, $F(6, 85) = 2.00$, $p = .076$ Model 4) showed trait neuroticism ($\beta = -0.15$, $t = -1.38$, $p = .172$) or the interaction term ($\beta = 0.08$, $t = 0.71$, $p = .478$) to predict the average duration of medial DMN co-activation with right amygdala and right BNST. Bayesian analyses mirrored the frequentist models, showing moderate evidence for HRV as a sole predictor ($BF_{10} = 4.90$) of the average duration of CAP 2, but anecdotal evidence for a null effect in the model including control predictors and resting HRV ($BF_{01} = 1.96$ Model 2). Anecdotal to moderate evidence emerged for the null for trait neuroticism as a sole predictor ($BF_{01} = 2.13$) and the other models ($BF_{01} = 2.17$ Model 3 ; $BF_{01} = 3.99$ Model 4).

Comparatively, in sample 2, frequentist models that included HRV (R^2 change = 0.01, $F(4, 89) = 2.75$, $p = .033$ Model 2), followed by trait neuroticism (R^2 change = 0, $F(5, 89) = 2.18$, $p = .065$ Model 3) and their interaction (R^2 change = 0.01, $F(6, 89) = 1.88$, $p = .095$ Model 4) did not indicate any of the predictors of interest to demonstrate an association with the average duration of the equivalent dorsal medial DMN state (CAP 1) (resting HRV: $\beta = 0.08$, $t = 0.78$, $p = .437$; trait neuroticism: $\beta = 0.01$, $t = 0.08$, $p = .941$; resting HRV x trait neuroticism interaction: $\beta = 0.07$, $t = 0.67$, $p = .506$). Bayesian analyses suggested moderate support for the null in the case of resting HRV ($BF_{01} = 3.78$) and trait neuroticism ($BF_{01} = 4.53$) as sole predictors and the model including control variables and resting HRV ($BF_{01} = 8.93$ Model 2). Strong support for the null emerged in the case of the other models that included trait neuroticism and the HRV by neuroticism interaction term ($BF_{01} = 21.76$ Model 3; $BF_{01} = 41.16$ Model 4). Thus, while there was some evidence to suggest HRV predicted the average duration of dorsal medial DMN in sample 1, this finding was not replicated in sample 2.

Contrary to our hypothesis that resting HRV would predict reduced salience network occurrences, in sample 1, while adding resting HRV to the frequentist

regression model containing control variables did not result in a significant change in the variance explained (R^2 change = 0.05, $F(4, 85) = 2.41$, $p = .056$ Model 2), HRV was found to significantly predict the occurrences of CAP 4, a salience network state. Higher resting HRV was significantly associated with increased occurrences of this salience network state that was co-active with right amygdala and right BNST (β = 0.22, $t = 2.08$, $p = .041$). When adding trait neuroticism (R^2 change = 0, $F(5, 85)$ = 1.94, $p = .097$ Model 3) and the HRV by trait neuroticism interaction term (R^2 change = 0.03, $F(6, 85) = 2.05$, $p = .068$ Model 4) to the model, neither trait neuroticism ($\beta = 0.04$, $t = 0.38$, $p = .704$) nor the interaction between HRV and neuroticism ($\beta = -0.17$, $t = -1.57$, $p = .121$) were found to significantly predict CAP 4 occurrences. The Bayesian regression for the model including control variables and resting HRV indicated moderate evidence for a null effect ($BF_{01} = 3.54$), but some weak, anecdotal support for resting HRV as a sole predictor of CAP 4 occurrences ($BF_{10} = 1.20$). Also, mirroring the frequentist regression models, moderate evidence was found for the null for trait neuroticism as a sole predictor ($BF_{01} = 4.43$) and the other models including trait neuroticism and the interaction between HRV and neuroticism ($BF_{01} = 4.22$ Model 3; $BF_{01} = 3.54$ Model 4). Thus, while resting HRV appeared to predict the occurrences of co-activation between the salience network and right amygdala and right BNST, this association is fairly tentative and unlikely to be robust.

This finding was not replicated in sample 2 for the equivalent salience network state (CAP 4). In the frequentist regression model combining control variables and resting HRV (R^2 change = 0, $F(4, 89) = 1.60$, $p = .183$ Model 2), HRV was not found to significantly predict CAP 4 occurrences ($\beta = 0.06$, $t = 0.60$, $p = .549$). The subsequent models that included trait neuroticism (R^2 change = 0.02, $F(5, 89) = 1.57$, $p = .176$ Model 3) and the HRV by neuroticism interaction term (R^2 change = 0.02, $F(6, 89) = 1.63$, $p = .149$ Model 4) did not indicate either of these predictors to demonstrate associations with CAP 4 occurrences (trait neuroticism: $\beta = -0.13$, $t = -1.21$, $p = .232$; HRV x trait neuroticism interaction: $\beta = 0.15$, $t = 1.35$, $p = .180$). Bayesian analyses revealed moderate evidence for resting HRV ($BF_{01} = 3.58$) and anecdotal evidence for trait neuroticism ($BF_{01} = 1.34$) in support of the null, reinforcing the frequentist regression models that neither of these variables solely predicted CAP 4 occurrences. Moderate evidence for a null association was found for all other models, failing to replicate the resting HRV pattern of findings observed in sample 1, however, replicating the lack of associations between trait neuroticism and the interaction between HRV and trait

neuroticism in relation to CAP 4 occurrences (BF_{01} = 6.71 $_{\text{Model 2}}$; BF_{01} = 8.62 $_{\text{Model 3}}$; BF_{01} = 9.17 $_{\text{Model 4}}$).

Finally, in sample 1, while the overall frequentist regression model was not significant (R^2 change = 0.06, $F(5, 85) = 1.46$, $p = .212$ $_{\text{Model 3}}$), trait neuroticism significantly predicted the average duration of CAP 3, a core DMN state. Contrary to our hypothesis, elevated trait neuroticism predicted a lower average duration of this default mode brain state ($\beta = -0.24$, $t = -2.24$, $p = .028$). The linear models combining control predictors with resting HRV (R^2 change = 0.02, $F(4, 85) = 0.55$, $p = .700$ $_{\text{Model 2}}$) and the HRV by trait neuroticism interaction term (R^2 change = 0.02, $F(6, 85) = 1.48$, $p = .195$ $_{\text{Model 4}}$) did not find either resting HRV ($\beta = -0.14$, $t = -1.28$, $p = .205$ $_{\text{Model 3}}$) or the HRV by neuroticism interaction term ($\beta = 0.14$, $t = 1.24$, $p = .220$ $_{\text{Model 4}}$) to significantly predict the average duration of CAP 3. Akin to the frequentist regression approach, Bayesian analyses generated moderate evidence in favour of the null for the model including control variables and trait neuroticism (BF_{01} = 10.00), but anecdotal evidence for trait neuroticism as a sole predictor of the average duration of the core DMN state (BF_{10} = 1.88). Anecdotal support for the null emerged for resting HRV (BF_{01} = 2.27) as a sole predictor and the other models indicated moderate to strong evidence for the null, suggesting that neither resting HRV or an interaction between HRV and trait neuroticism predicted the average duration of CAP 3 (BF_{01} = 31.81 $_{\text{Model 2}}$; BF_{01} = 11.78 $_{\text{Model 4}}$).

In sample 2, the equivalent brain state depicting the core DMN pattern was CAP 3. None of the models containing control variables with the addition of resting HRV (R^2 change = 0, $F(4, 89) = 0.43$, $p = .788$ $_{\text{Model 2}}$), trait neuroticism (R^2 change = 0, $F(5, 89) = 0.39$, $p = .855$ $_{\text{Model 3}}$), and their interaction term (R^2 change = 0.01, $F(6, 89) = 0.44$, $p = .850$ $_{\text{Model 4}}$), indicated any of the key variables of interest to significantly predict the average duration of the core DMN co-active with right amygdala and right BNST (resting HRV: $\beta = -0.02$, $t = -0.20$, $p = .840$; trait neuroticism: $\beta = 0.06$, $t = 0.50$, $p = .620$; HRV x trait neuroticism interaction: $\beta = 0.10$, $t = 0.84$, $p = .403$). Bayesian analyses suggested moderate evidence for the null with respect to resting HRV (BF_{01} = 4.51) and trait neuroticism (BF_{01} = 4.43) as sole predictors of the average duration of CAP 3. Strong to extreme evidence for the null hypothesis was observed across models (BF_{01} = 40.91 $_{\text{Model 2}}$; BF_{01} = 79.53 $_{\text{Model 3}}$; BF_{01} = 122.51 $_{\text{Model 4}}$), suggesting a non-replication of the trait neuroticism finding in sample 1, while replicating null

findings for resting HRV and the HRV by neuroticism interaction as predictors of the average duration of this core DMN CAP.

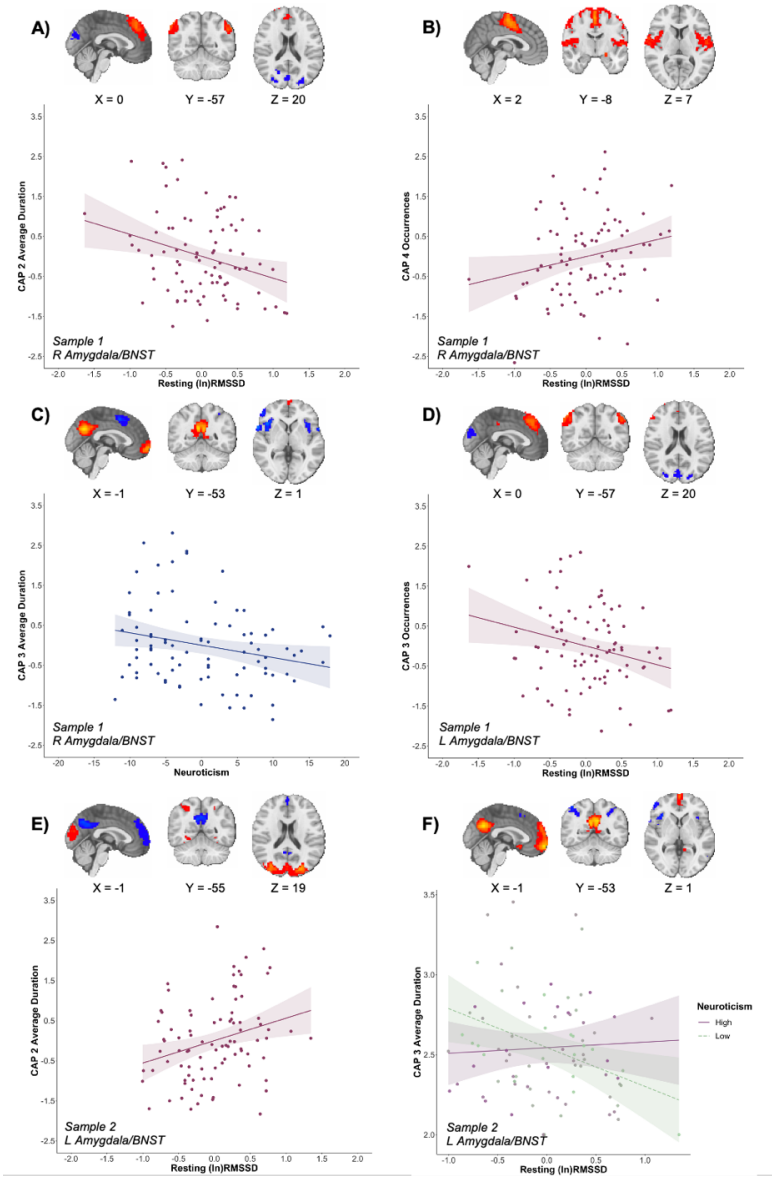

Figure 9. HRV and Trait Neuroticism Findings from the Resting-State CAP Analyses. **A)** The right amygdala and BNST seed region CAP analyses in sample 1 revealed higher resting HRV to be associated with a reduction in the average duration of CAP 2, a neural pattern reflecting the dorsal medial prefrontal cortex default mode subsystem network. **B)** Greater resting HRV was found to predict increased occurrences of CAP 4, a salience network state, as a function of right amygdala/BNST co-activation in sample 1. **C)** Higher trait neuroticism was linked to a lower average duration of CAP 3, a core DMN brain state as a function of right amygdala/BNST in sample 1. **D)** As a function of left amygdala/BNST seeds, elevated resting HRV was associated with fewer occurrences of a dorsal medial DMN CAP in sample 1. **E)** In sample 2, higher resting HRV predicted a greater average duration of CAP 2, a visual attention network state, as a function of the left amygdala and BNST. **F)** An interaction between resting HRV and trait neuroticism predicted the average duration of CAP 3, such that individuals with lower trait neuroticism and decreased resting HRV spent a longer time in this core DMN brain state as a function of the left amygdala and BNST. Original units for temporal metrics were number of volumes ('Occurrences') and average duration in seconds ('Average Duration'). Standardised residuals (controlling for mean centered age, BMI, number of volumes, and either resting HRV or trait neuroticism depending on the relevant predictor) are displayed for visualisation purposes. The HRV by trait neuroticism interaction plot was created using the *interactions* package in R with high and low neuroticism groups reflecting a ± 1SD split.

3.4.5.2 Left Amygdala and Left BNST

In sample 1, the frequentist linear regression model (R^2 change = 0.06, F(4, 85) = 3.09, p = .020 $_{\text{Model 2}}$) indicated that adding resting HRV to the model resulted in a significant change in the variance explained in CAP 3 occurrences, a dorsal medial DMN brain state that was co-active with left amygdala and left BNST. Specifically, higher resting HRV predicted fewer occurrences of this dorsal medial default state (β = -0.25, t = -2.38, p = .020). This followed the same pattern observed in this sample for the average duration of the equivalent CAP derived from the right amygdala and right BNST seed region CAP analyses. However, adding trait neuroticism to the model resulted in a change in variance explained that was close to 0 (R^2 change = 0, F(5, 85) = 2.46, p = .040 $_{\text{Model 3}}$), with trait neuroticism not found to significantly predict CAP 3 occurrences (β = 0.03, t = 0.25, p = .805. The full model including the HRV by trait neuroticism interaction (R^2 change = 0.01, F(6, 85) = 2.14, p = .058 $_{\text{Model 4}}$) did not significantly predict CAP 3 occurrences either (β = 0.08, t = 0.79, p = .430). Bayesian analyses indicated anecdotal evidence in favour of the model including control variables and resting HRV (BF_{10} = 1.44) and resting HRV as a sole predictor (BF_{10} = 1.39) of CAP 3 occurrences. However, moderate evidence in support of the null emerged for trait neuroticism as a sole predictor (BF01 = 4.10) and anecdotal evidence for the null for the models where trait neuroticism was added (BF_{01} = 1.67 $_{\text{Model 3}}$) and the HRV and neuroticism interaction term (BF_{01} = 2.95 $_{\text{Model 4}}$).

Compared to sample 1, in sample 2, the frequentist regression models indicated none of the predictors to explain variance in the occurrences of the equivalent dorsal medial DMN state (CAP 1). Models including control variables where resting HRV was added (R^2 change = 0, F(4, 89) = 0.72, p = .580 $_{\text{Model 2}}$), followed by inclusion of trait neuroticism (R^2 change = 0, F(5, 89) = 0.58, p = .714 $_{\text{Model 3}}$), and the full model with the addition of the HRV and neuroticism interaction term (R^2 change = 0.01, F(6, 89) = 0.61, p = .723 $_{\text{Model 4}}$) suggested that resting HRV (β = 0.01, t = 0.11, p = .916), trait neuroticism (β = 0.03, t = 0.24, p = .814) and their interaction (β = -0.01, t = -0.87, p = .387) did not significantly predict CAP 1 occurrences. Bayesian analyses further reinforced moderate evidence for a null association for resting HRV (BF_{01} = 4.53) and trait neuroticism (BF_{01} = 4.43) as sole predictors and strong to very strong support for the null hypothesis across models (BF_{01} = 25.90 $_{\text{Model 2}}$; BF_{01} = 55.20 $_{\text{Model 3}}$; BF_{01} = 84.35 $_{\text{Model 4}}$).

In sample 2, the frequentist linear regression model (R^2 change = 0.08, $F(4, 89) = 2.20$, $p = .076$ Model 2) showed resting HRV to significantly predict the average duration of CAP 2, a visual network brain state that was co-active with left amygdala and left BNST. Higher resting HRV predicted a longer average duration of this visual network state during rest ($\beta = 0.29$, $t = 2.76$, $p = .007$). Including trait neuroticism in the model did not significantly improve the variance explained (R^2 change = 0, $F(5, 89) = 1.75$, $p = .133$ Model 3) nor was trait neuroticism a significant predictor of the average duration of CAP 2 ($\beta = 0.02$, $t = 0.18$, $p = .855$). Additionally, including the HRV and neuroticism interaction term in the model (R^2 change = 0, $F(6, 89) = 1.44$, $p = .209$ Model 4) did not significantly predict average duration of this visual network state either ($\beta = 0.01$, $t = 0.08$, $p = .938$). Bayesian regressions showed moderate evidence for resting HRV as a sole predictor of CAP 2 duration ($BF_{10} = 6.32$), but anecdotal evidence for the null hypothesis in the model combining control variables and resting HRV ($BF_{01} = 2.68$ Model 2). Moderate evidence in support of the null was observed for trait neuroticism as a sole predictor ($BF_{01} = 4.50$) and moderate to strong evidence emerged in support of a null effect for the model that included trait neuroticism as a predictor ($BF_{01} = 6.27$ Model 3) and following inclusion of the HRV and neuroticism interaction term ($BF_{01} = 13.75$ Model 4).

However, in sample 1, the frequentist linear model (R^2 change = 0, $F(4, 85) = 2.11$, $p = .087$ Model 2) did not find resting HRV ($\beta = -0.03$, $t = -0.26$, $p = .794$) to significantly predict the average duration of the equivalent brain state reflecting a visual network pattern (CAP 2). Moreover, models adding trait neuroticism (R^2 change = 0.01, $F(5, 85) = 1.83$, $p = .116$ Model 3) and the HRV by neuroticism interaction (R^2 change = 0.01, $F(6, 85) = 1.59$, $p = .162$ Model 4) did not find either of these predictors (trait neuroticism: $\beta = -0.10$, $t = -0.87$, $p = .389$; HRV x trait neuroticism: $\beta = -0.07$, $t = -0.66$, $p = .510$) to be linked to the average duration of this visual network that was co-active with left amygdala and left BNST. Bayesian analyses reinforced anecdotal to moderate support for the null for resting HRV ($BF_{01} = 4.45$) and trait neuroticism ($BF_{01} = 2.74$) as sole predictors and across models ($BF_{01} = 2.96$ Model 2; $BF_{01} = 5.11$ Model 3; $BF_{01} = 9.40$ Model 4).

In sample 2, the frequentist regression model in which resting HRV was added (R^2 change = 0.03, $F(4, 89) = 0.75$, $p = .561$ Model 2) and subsequently where trait neuroticism was included (R^2 change = 0, $F(5, 89) = 0.61$, $p = .696$ Model 3) revealed neither resting HRV ($\beta = -0.17$, $t = -1.56$, $p = .123$) or trait neuroticism ($\beta = -0.03$, $t =$ -

0.25, p = .807) to significantly predict the average duration of CAP 3, a core DMN state co-active with left amygdala and left BNST. However, while the overall model was not significant (R^2 change = 0.05, F(6, 89) = 1.26, p = .285 $_{\text{Model 3}}$), the HRV by neuroticism interaction term predicted the average duration of core DMN co-activation in sample 2 (β = 0.24, t = 2.10, p = .039). Specifically, the interaction showed that at low levels of trait neuroticism, lower HRV resulted in a greater average duration of CAP 3 (β = -0.39, t = -2.61, p = .011) but not at higher trait neuroticism (β = 0.06, t = 0.37, p = .711). Indeed, the Bayesian regression model revealed strong support for the null when considering the full model including control variables, resting HRV, trait neuroticism, and the HRV by neuroticism interaction term (BF_{01} = 20.28), but the interaction term as a sole predictor indicated anecdotal support as a predictor of the average duration of CAP 3 (BF_{10} = 1.29). Anecdotal to moderate evidence for the null was observed for resting HRV (BF_{01} = 1.37) and trait neuroticism (BF_{01} = 4.53) as sole predictors, and strong to very strong evidence for the full models (BF_{01} = 24.75 $_{\text{Model 2}}$; BF_{01} = 52.73 $_{\text{Model 3}}$). Thus, while there does seem to be some support for an interaction between resting HRV and trait neuroticism for predicting the average duration of the core DMN state, this finding is unlikely to be robust.

Comparatively, in sample 1, for the equivalent core DMN state (CAP 1), the frequentist linear model (R^2 change = 0, F(6, 85) = 0.73, p = .626 $_{\text{Model 4}}$) did not show the interaction between resting HRV and trait neuroticism to predict the average duration of this brain state (β =0.02, t = 0.14, p = .888). Moreover, the models in which resting HRV (R^2 change = 0.04, F(4, 85) = 1.07, p = .379 $_{\text{Model 2}}$) and trait neuroticism (R^2 change = 0, F(5, 85) = 0.89, p = .495 $_{\text{Model 3}}$) were added did not suggest either resting HRV or trait neuroticism to predict the average duration of this core DMN state that was co-active with left amygdala and left BNST (resting HRV: β =0.19, t = 1.74, p = .085; trait neuroticism: β = 0.05, t = 0.45, p = .655). Bayesian analyses reinforced anecdotal to moderate evidence for the null when considering resting HRV (BF_{01} = 1.49) and trait neuroticism (BF_{01} = 3.87) as sole predictors, and strong to very strong support for the null hypothesis across full models (BF_{01} = 14.33 $_{\text{Model 2}}$; BF_{01} = 29.04 $_{\text{Model 3}}$; BF_{01} = 59.23 $_{\text{Model 4}}$).

Refer to Figure 9 for a visual depiction of these findings.

3.5 Discussion

Most research has focused on interactions between the heart and the brain at rest, with fewer studies assessing transient temporal connectivity changes of neurovisceral circuitry and HRV during contexts that require flexible emotional responding. The present study used CAP analyses to examine HRV, self-reported trait neuroticism, and associated co-active neural networks in two samples of younger adults derived from the AOMIC PIOP 2 dataset. Crucially, since HRV has been considered to reflect adaptive emotional responding (Appelhans & Luecken, 2006; Thayer & Lane, 2000, 2009), this study examined the degree to which both task-related and resting HRV predicted temporal metrics (i.e., occurrences and average duration) of neural networks that were co-active with the amygdala and BNST during an emotion processing task and at rest.

During the emotion processing task, a network encompassing neural regions related to visual attention, including bilateral lateral occipital cortex (superior and inferior divisions), middle and inferior frontal gyri (more extensive bilateral co-activation in sample 1 with slightly higher threshold in right middle frontal gyri), and superior parietal lobe (SPL), emerged in both samples. Prior research has found areas of the ventral visual system, such as the lateral occipital cortex and inferior frontal gyrus (IFG), to exhibit stronger functional connectivity with the amygdala in response to emotional (angry and fearful) faces versus control (shape) stimuli, highlighting the involvement of these regions in facilitating emotion processing (Labuschagne et al., 2024). The IFG is involved in emotion processing (Adolphs, 2002) and emotion regulation (Kohn et al., 2014; Messina et al., 2015; Wager et al., 2008), with left IFG/ventrolateral prefrontal cortex (vlPFC) commonly observed in emotion regulation studies (Berboth & Morawetz, 2021; Buhle et al., 2014), and right IFG/vlPFC linked to (emotional) inhibitory control (Aron et al., 2004; Lieberman et al., 2007) and task-related HRV (Tupitsa et al., 2023). This CAP also contained the SPL, which forms part of the dorsal attention network and facilitates the orientation of attention (Corbetta & Shulman, 2002). Considering the neural regions found to be co-active with moments in which amygdala/BNST were particularly active during the task, it could be that this CAP reflected increased visual attention and engagement while performing the task across samples. In sample 1, although anecdotal evidence emerged for trait neuroticism as a sole predictor of the average duration of this CAP, the model including control variables, HRV and trait neuroticism indicated moderate support for no overall

association. Moreover, moderate support for no association was found in sample 2, highlighting that trait neuroticism did not appear to predict the average duration of this visual CAP in this sample. Additionally, in sample 2, while there was an indication that higher task-related HRV as a sole predictor was linked to a lower average duration of this CAP, the support for this association was weak.

A similar brain state emerged in sample 2 during rest, characterised by co-activation of bilateral ventral visual areas and SPL (with slightly more extensive right-lateralised co-activation), with simultaneous co-deactivation of bilateral PCC, precuneus and mPFC (core DMN areas). According to prior research, visual/oculomotor and salience network activation during rest may constitute an increased 'exteroceptive' state, reflecting greater attention and vigilance in an eyes open resting-state paradigm, in contrast to eyes closed paradigms, in which neural activation and connectivity of areas such as the mPFC promote an 'interoceptive' state (Costumero et al., 2020; Riedl et al., 2014; Zhang et al., 2015). Higher resting HRV has been linked to more effective attentional maintenance in younger adults (Siennicka et al., 2019) and this pattern of findings may suggest individuals with higher HRV demonstrated more sustained engagement of exteroceptive visual attention during rest. Evidence revealed moderate support for HRV as a sole predictor of this co-activation duration in sample 2, however, such an association between HRV and this visual network was not supported in sample 1. Thus, while there might be some indication that higher trait neuroticism predicted less sustained engagement of visual attention in an emotional processing context (sample 1), and elevated HRV predicted more sustained engagement of visual attention across emotional and rest contexts (sample 2), the pattern of these findings is supported by fairly weak and inconsistent evidence.

Furthermore, in sample 2, tentative evidence emerged for a potential interaction between trait neuroticism and HRV during the emotion task in relation to occurrences of CAP 2, a neural network pattern consistent with the core DMN (Andrews-Hanna et al., 2010). The DMN is a neural hub underlying various processes, including self-reflection and self-generated thoughts, autobiographical memory, and mind-wandering (Andrews-Hanna et al., 2010; Buckner & Caroll, 2007; Raichle, 2015). While the DMN can be considered a single neural hub, it has been parcellated into three underlying sub-networks: the 'core' DMN (PCC and anterior mPFC), the dorsomedial prefrontal cortex (dmPFC, the temporoparietal junction, temporal pole,

and lateral temporal cortex), and the medial temporal lobe system (vmPFC, posterior inferior parietal lobe, parahippocampal cortex, and hippocampal formation) (Andrews-Hanna et al., 2010). In both samples, the 'core' DMN CAP during the task contained extensive clusters in bilateral PCC and anterior mPFC that were co-active with left amygdala and BNST. It was expected that higher trait neuroticism and lower task-related HRV would be linked to increased occurrences and/or a higher average duration of the DMN, given its involvement in self-referential processing and prior evidence suggesting persistent dominance (i.e., increased average dwell time) and activation of the DMN linked to increased anxiety (Qiao et al., 2020; Zeidan et al., 2014). Unexpectedly, higher task-related HRV predicted increased occurrences of this core DMN CAP in individuals with low, but not high, trait neuroticism during the task. Increased DMN activation has been shown to support cognitive transitions that are dependent on the prominence of context representations (Crittenden et al., 2015; Smith et al., 2018). Specifically, increased activation in core and medial temporal lobe subsystems of the DMN has been observed during cognitively demanding switches on task trials and switches between rest and task engagement (Crittenden et al., 2015; Smith et al., 2018). Therefore, it is possible that individuals with lower trait neuroticism and elevated task-related HRV more effectively switched and disengaged during the task, potentially throughout the less emotionally salient control blocks and/or brief periods of rest, as reflected by more frequent occurrences of the core DMN. However, this would require a targeted analysis examining CAP occurrences for emotion versus control blocks to establish whether this particular brain state was expressed more frequently during control trials or brief rest periods. Crucially, this finding is also highly speculative considering that Bayesian analyses provided anecdotal support for the interaction between HRV and trait neuroticism as a sole predictor in sample 2, and strong evidence to support no association in sample 1.

Resting-state CAP analyses revealed that, in sample 1, higher resting HRV predicted increased occurrences of a neural pattern comprised of bilateral ACC, insula, and juxtapositional lobe co-active with the right amygdala and right BNST. Both the ACC and anterior insula are considered central nodes of the salience network (Seeley et al., 2007; Uddin et al., 2019), a neural hub facilitating integration and identification of autonomic and interoceptive signals, alongside adjusting arousal and directing attention to salient information (Uddin, 2015). The salience network, primarily via the dorsal anterior insula, also facilitates dynamic and automatic shifts between

the DMN and central executive network, flexibly directing attention to and from internal and external environmental cues (Uddin, 2015). On the basis that lower resting HRV is often observed in individuals with anxiety (Chalmers et al., 2014; Cheng et al., 2022; Tomasi et al., 2023), and both anxiety and neuroticism have been linked to greater dominance of salience/emotion processing neural hubs, including overactivation in salience-related areas (Massullo et al., 2020), it was hypothesised that lower resting HRV would predict greater occurrences or a higher average duration of the salience network. Thus, the pattern of findings observed in sample 1 is in an opposite direction to that of our original hypothesis. However, as confirmed by Bayesian analyses, there was anecdotal evidence to support resting HRV as a sole predictor of the occurrences of this salience network CAP, and in sample 1, moderate evidence for no association was uncovered for HRV as a predictor, reinforcing a lack of robust findings observed across the samples. That said, while this is likely a spurious finding, it is interesting that an association between HRV and the salience network was observed during rest, as opposed to an emotion processing context in which salient emotional information (angry and fearful face stimuli) was presented. Nevertheless, transient HRV changes have previously been linked to altered functional connectivity in salience network nodes at rest (Chang et al., 2013). Increased occurrences of the salience network during rest may also reflect the eyes open nature of the resting-state paradigm, with previous research reporting the primary visual cortex to be strongly coupled with the salience network during an eyes open paradigm, suggesting greater engagement of external attention systems (Costumero et al., 2020).

Moreover, during rest, a neural network pattern consistent with the dmPFC subsystem of the DMN (Andrews-Hanna et al., 2010) emerged in both samples, comprising bilateral dmPFC, SFG, angular gyrus, and frontal pole. The dmPFC DMN subsystem is typically engaged in relation to self-referential judgements and inferring the mental states of others (Andrews-Hanna et al., 2010). A meta-analysis found core DMN regions and the dmPFC subsystem to exhibit increased activation during rumination (Zhou et al., 2020). In particular, the dmPFC has been reported to activate in response to induced anxiety in healthy individuals (Mechias et al., 2010) and has exhibited positive coupling with the amygdala as a function of heightened anxiety (Robinson et al., 2012; Vytal et al., 2014). The current study findings revealed higher resting HRV to predict a lower average duration of co-activation of this CAP with right amygdala and right BNST and fewer occurrences of co-activation of the equivalent

CAP with left amygdala and left BNST in sample 1. Indeed, lower resting HRV has been linked to increased hypervigilance and difficulties disengaging from negative or threatening information (Park et al., 2013; Park & Thayer, 2014) and anxiety (Chalmers et al., 2014; Cheng et al., 2022; Tomasi et al., 2023), whereas higher resting HRV reflects more adaptive emotional responding and regulation (Appelhans & Luecken, 2006; Balzarotti et al., 2017). Taken together, a lower average duration and reduced occurrences of amygdala co-activation with this network featuring a large dorsal medial cluster in the frontal cortex could potentially reflect a lower state of anxiety, an increased ability to regulate anxious feelings, and/or reduced introspection and inference about mental states in the absence of a task. Nevertheless, as indicated by complementary Bayesian analyses, these findings are highly speculative and greater evidence to support a null association was observed in sample 2. Also, given the lack of a concurrent measure of self-reported state anxiety, there is not adequate supporting evidence in this study to indicate whether the current findings align with prior literature linking enhanced amygdala and dorsal medial prefrontal coupling with heightened anxiety.

Finally, neuroticism is a shared risk factor for developing anxiety and depression (Kootker et al., 2016; Kotov et al., 2010). Higher average DMN dwell time has been associated with increased self-reported anxiety (Qiao et al., 2020), and DMN dominance (relative to a task-positive network) with elevated maladaptive depressive rumination (Hamilton et al., 2011). An interaction emerged between resting HRV and trait neuroticism in sample 2, whereby individuals with reduced resting HRV and lower trait neuroticism exhibited an increased average duration of the core DMN state co-active with left amygdala and left BNST. Increased amygdala-PCC (Veer et al., 2011; Wang et al., 2018) and amygdala-precuneus (Maron-Katz et al., 2016) resting-state functional connectivity has been observed following acute stress. Additionally, higher task-related HRV has been linked to weaker right amygdala functional coupling with the PCC during reappraisal in older and younger adults (Tupitsa et al., 2023). Therefore, it could be that individuals with lower neuroticism and *higher* HRV are experiencing less stress and/or sustaining other brain states linked to exteroceptive attention, whereas individuals with reduced resting HRV and lower trait neuroticism may have a greater propensity to focus their attention inwardly to internal milieu. While anecdotal support was found for the interaction term as a sole predictor, the full model was not supported and no support for an association was observed in sample 1 either,

so again, this finding should be interpreted with caution. Also, in the absence of eye tracking measures to assess the degree of visual scanning or exploration and/or participant thoughts (i.e., via explicit thought sampling), it remains unclear as to whether internal versus external focus facilitated this pattern of findings.

Collectively, the current findings do not provide clear or consistent support for our original hypotheses in accordance with the NIM framework and prior literature. The weak and inconsistent nature of the findings is likely to be closely linked to the temporal metrics (i.e., occurrences and average duration) derived from the CAPs, as opposed to the spatial clusters that comprise each CAP state. Clusters forming the key neural networks that emerged across emotion processing and resting-state contexts appeared to demonstrate strong overlap between the samples, suggesting a fairly robust spatial similarity of the CAPs. Indeed, a notable feature of the CAP technique is its ability to derive stable, co-active neural networks using only the time points (fMRI volumes) exhibiting the highest threshold of activation, with CAP states displaying equivalently high spatial similarity and stability as networks obtained from conventional, temporal correlation-based connectivity approaches (Cifre et al., 2020; Tagliazucchi et al., 2012). By comparison, while the spatial maps were fairly robust, where tentative associations were observed for either HRV or trait neuroticism with temporal metrics, such correlations were weak, with complementary Bayesian analyses mainly indicating anecdotal support for sole predictors, and inconsistent, wherein if HRV or neuroticism predicted the occurrences or average duration of a particular CAP, this same pattern was not supported or was in the opposite direction, in the other sample. Therefore, it is highly probable that the key findings raised in this study are spurious and should be interpreted with caution.

Wider literature has highlighted inconsistencies in temporal metrics (i.e., dwell time, frequency and persistence) of the DMN in CAP studies examining major depressive disorder, suggesting that differences may emerge due to heterogeneity in sample characteristics, data processing methods, and limitations pertaining to statistical power (An et al., 2024). In this study, the samples did not appear to show differences in key variables of interest and both physiology and fMRI data adhered to the same processing protocols. However, limited statistical power may be a contributing factor when considering the weak and inconsistent associations between HRV and trait neuroticism with the CAP temporal metrics. While a decision to split the sample into two groups was implemented for replication purposes and to account for

practical and technical constraints that were encountered, this resulted in a relatively small number of participants being assigned to each sample. It has been acknowledged that many neuroimaging studies are underpowered and that substantially larger sample sizes are required to reliably examine inter-individual differences in mental health and cognitive phenotypes (Button et al., 2013; Marek et al., 2022). Small sample size is likely a contributing factor to the instability of findings reported here. With respect to the observed robustness of the spatial maps, by selecting only the time points with the most salient activity, the CAP clustering procedure reduces the requirements for widespread comparisons, which can consequently increase statistical power in small samples (Georgiopoulos et al., 2024). Thus, this may also partly explain the difference observed in the robustness of the spatial maps in contrast to the temporal metrics. It will be imperative for future research to examine relationships between HRV and/or emotional disposition with co-active neural networks in larger, representative samples.

A few other limitations should be considered when interpreting the current findings. A temporal fMRI resolution of two seconds is likely to be inadequate for assessing indirect transient changes in neuronal activity and therefore may also have impacted the relative measurement sensitivity of the CAP temporal metrics. Relatedly, while the emotion processing task reliably activates the amygdala (key seed region of interest in the current study) and still requires a degree of flexible emotional responding (i.e., the ability to shift from processing emotional to neutral stimuli and vice versa), the task followed a block design which more reliably assesses emotional processing as opposed to flexibility. An event-related design with more frequent shifts in response to emotion versus neutral information would have required more flexibility in the form of switching and thus would potentially increase the sensitivity of the temporal metrics of the various brain states too. Beyond block versus event-related designs, it would be fruitful for future research to utilise tasks specifically designed to assess affective flexibility (i.e., the affective flexibility task; Genet et al., 2013; Malooly et al., 2013) to further elucidate dynamic brain states underlying adaptive emotional responding and potential associations with HRV and anxiety/depression in non-clinical and/or clinical populations. Finally, while BMI was included as a relevant control variable in the present study, information on other lifestyle/health factors such as caffeine intake, smoking status, physical fitness/activity, and medications including beta-blockers and anti-depressants reported to influence HRV were not available and

consequently not controlled for (Hayano et al., 1990; Sammito & Böckelmann, 2016). Therefore, we cannot rule out the potential influence some of these factors may have had on the HRV findings in the current study.

In conclusion, the present study investigated and uncovered neural networks that were co-active with the amygdala and BNST during emotion processing and rest in younger adults. While the spatial maps of the brain states across contexts were fairly robust for both samples, associations between HRV and trait neuroticism and the occurrences and average duration of neural networks co-active with the amygdala and BNST produced anecdotal and inconsistent findings. There was tentative evidence to suggest that task-related and resting HRV predicted the average duration of visual attention network states co-active with amygdala and BNST in one sample, potentially reflecting a greater ability to engage with, and monitor, external visual information across contexts. Relatedly, higher resting HRV and occurrences of co-a salience network CAP at rest, and interactions between HRV and trait neuroticism in predicting occurrences of core DMN states during emotion processing, albeit weak and inconsistent findings, possibly indicate flexible regulation of attention processes, especially in individuals with higher HRV and low trait neuroticism. This study reinforces the importance of assessing heart-brain interactions across contexts, and more critically, highlights the need for replication in larger, representative samples to elucidate key vagal control circuitry that facilitates flexible and context-appropriate emotional responding.

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Supplementary Material

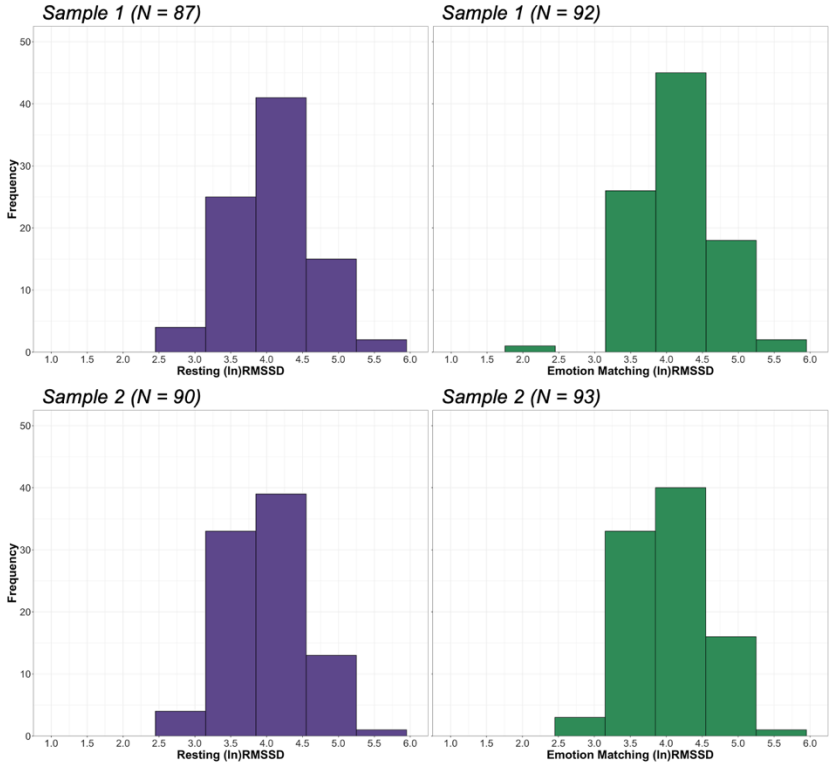

Figure S4. Histograms displaying the distributions for resting (left, purple) and emotion matching (right, green) HRV in Sample 1 (top row) and Sample 2 (bottom row). *(ln)RMSSD*, natural log transformed root mean square of successive differences.

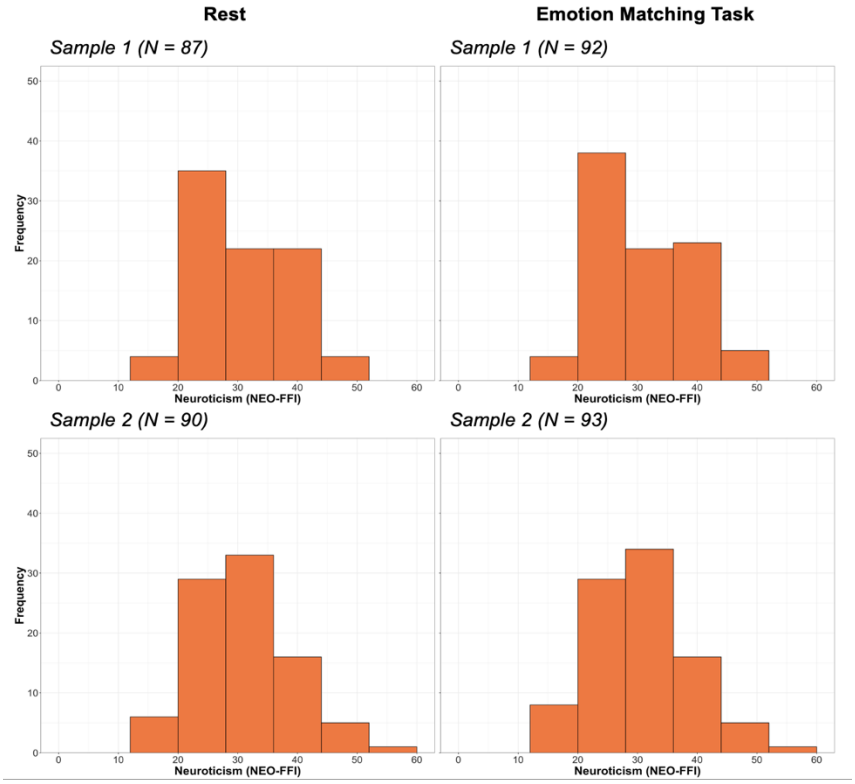

Figure S5. Histograms displaying the distributions for neuroticism scores for the resting (left) and emotion matching task (right) data in Sample 1 (top row) and Sample 2 (bottom row). *NEO-FFI*, NEO-Five Factory Inventory.

Chapter 4.

Heart rate variability, but not trait rumination or valence bias, predicts valence related attentional shifts during an affective switching task

Tupitsa, E., & Van Reekum, C. M. (In Preparation). Heart rate variability, but not trait rumination or valence bias, predicts valence related attentional shifts during an affective switching task

4.1 Abstract

The ability to flexibly engage with, and disengage from, emotional information in our environment, termed 'affective flexibility', facilitates adaptive emotional responding and effective emotion regulation. Individual differences in trait affect have been shown to impact affective flexibility, which in turn has implications for mental health and overall wellbeing. Trait rumination, valence bias, and heart rate variability (HRV), a non-invasive and objective index reflecting emotion regulatory ability, all tap into, and potentially reflect, dispositional levels of (in)flexible emotional responding. The present research sought to examine associations between trait-like affect and HRV with affective flexibility performance in both an online (N = 72; Study 1) and laboratory (N = 73; Study 2) context. Affective flexibility was assessed using an established task switching paradigm in which participants categorised emotional pictures according to either an affective (valence) or non-affective (number of humans) rule. Trait-like valence bias was operationalised as the relative dominance of positive versus negative ratings of emotionally ambiguous stimuli (surprise faces). In Study 2, a pulse signal was recorded during a rest period and throughout the affective flexibility and valence bias tasks to derive resting and task-based HRV metrics. Across studies, neither trait-like valence bias or brooding and reflective trait rumination significantly predicted affective flexibility. In Study 2, higher task-related HRV was tentatively associated with slower response times when shifting attention towards positive valence images on trials where the non-affective rule repeated, whereas greater resting HRV showed some indication of being linked to slower response times when shifting attention from positive towards negative valence images, specifically in the presence of an affective trial rule. This research reinforces the notion that inflexibility may not always be maladaptive and extends prior work by highlighting potential associations between rest and task-related HRV to specific attentional shifts pertaining to valence (emotion) as opposed to more cognitive aspects of affective flexibility.

Keywords: Affective flexibility, heart rate variability, neurovisceral integration model, rumination, valence bias

4.2 Introduction

The ability to flexibly engage and disengage with complex stimuli and events in an environment characterised by rapid and dynamic change is essential for adaptive self-regulation (Aldao et al., 2015). A limited set of cognitive control processes (executive function) facilitate adaptive responses in accordance with an individual's goals and contextual demands. These processes include inhibition of prepotent responses, mental set shifting, and the active updating and monitoring of information in working memory (Miyake et al., 2000). Both mental set shifting and inhibition underlie cognitive flexibility, the ability to alter goals and shift both thoughts and behaviour in a contextually appropriate manner (Lezak, 2004). Research has typically assessed cognitive flexibility using experimental paradigms that involve switching between two different task sets or rules on the same type of sequentially presented stimuli (Monsell, 2003). The switch from one rule to another (versus repeating the same rule) requires increased cognitive resources due to inhibition of the previous rule and updating to the current rule, typically resulting in slower response times and an increased susceptibility to make errors on switch trials relative to trials in which the rule is repeated, recorded as a 'switch cost' (Monsell, 2003). While general cognitive flexibility has clinical relevance and implications for mental health and emotion regulation (Eysenck et al., 2007; Grant & Chamberlain, 2023), it is the flexible control of emotional information, that is the degree to which an individual can flexibly shift attention to and from, emotional material, a phenomenon termed 'affective flexibility', that has been posited to be more closely coupled to emotion regulation (Gross & Thompson, 2007; Malooly et al., 2013).

A small body of research has examined associations between affective flexibility and various psychological variables related to emotion regulation and mental health, including rumination (Genet et al., 2013), depressive symptoms (Wen & Yoon, 2019), worry and anxiety (Twivy et al., 2021), reappraisal ability following stress (Malooly et al., 2013), and resilience (Genet & Siemer, 2011; Grol & De Raedt, 2018). An early study by Genet and Siemer (2011) assessed affective flexibility with a paradigm whereby participants were instructed to categorise word stimuli in relation to an affective rule (i.e., positive or negative valence) or a non-affective, emotionally neutral rule (i.e., adjective or noun). Lower switch costs, reflected by faster response times and thus more efficient switching between the emotional and non-emotional rule instruction, was associated with greater trait resilience. The affective task switching

paradigm was subsequently adapted and modified to incorporate emotional picture stimuli, with participants instructed to categorise emotional images of a positive or negative valence according to an affective rule (i.e., positive versus negative valence) or a non-affective rule (i.e., one or fewer versus two or more humans) (Genet et al., 2013; Malooly et al., 2013). Using this task, Genet et al. (2013) reported that greater switch costs (i.e., lower flexibility) when shifting attention away from affective aspects of negative emotional material was linked to higher reported rumination in daily life, whereas greater switch costs (lower flexibility) when switching from affective aspects of positive emotional material predicted less reported rumination use. Similarly, more efficient switching (greater flexibility) from affective to non-affective aspects of positive emotional material, and slower switching (lower flexibility) from non-affective to affective aspects of negative emotional material was associated with greater use of maladaptive emotion regulation strategies, such as rumination and catastrophising (Grol & De Raedt, 2021). Furthermore, Twivy et al. (2021) reported that slower shifts of attention (lower affective flexibility) from non-affective towards affective aspects of positive emotional stimuli correlated with higher levels of trait anxiety, and faster attentional shifts (greater affective flexibility) from affective to non-affective aspects of negative emotional material was associated with increases in both trait anxiety and worry over a 7-week period. Importantly, of the studies directly comparing general cognitive flexibility with affective flexibility switch costs, either no correlations or correlations with a small effect size were observed (Genet et al., 2013; Genet & Siemer, 2011; Malooly et al., 2013), suggesting that affective flexibility explains unique variance (Twivy et al., 2021) and may reflect a distinct process above and beyond general cognitive flexibility (Grol & De Raedt, 2021). In addition, these findings demonstrate that higher or lower affective flexibility may not always be (mal)adaptive per se. For example, more efficient attentional shifts towards non-affective aspects of negative emotional material may reflect attentional avoidance of emotional aspects of negative emotional information (Twivy et al., 2021). Thus, context appears to play an important role when considering whether affective flexibility is (mal)adaptive (Genet et al., 2013; Godara et al., 2023). Relatedly, while the addition of valence adds a contextual and emotional component to the paradigm in comparison to pure cognitive flexibility measures, the focus of prior studies using this task has also mainly been based on switch costs pertaining to the rule (i.e., shifts in attention based on the relative focus of an affective versus non-affective rule instruction in the presence of

positive or negative emotional material). However, this task contains trials in which the valence shifts but the rule is held constant, alongside trials characterised by a shift in both the valence and the rule. The degree to which individual differences interact with attentional shifts pertaining to valence, regardless of the rule on this task, is less clear.

Adaptive responses to dynamic events and stimuli in the environment rely on the flexible shift of attention to and from both positive and negative emotional information. For example, in certain situations, such as walking alone late at night, heightened attention to potentially dangerous or threatening information may be adaptive, such that it could promote the effective detection of potential threats to ensure one reaches their destination safely. However, the same level of heightened or sustained attention towards negative emotional information may become less adaptive or even maladaptive in safer contexts and if experienced for a prolonged period. Indeed, a static attentional bias to either negative or positive stimuli may prevent an individual from being able to flexibly respond to dynamic changes in the environment and adapt to different goals accordingly (Godara et al., 2023), resulting in a more rigid and inflexible profile of emotional responding (i.e., affective *in*flexibility). Psychological disorders such as depression and anxiety have been linked to a greater tendency to attend to negative emotional information and difficulties disengaging attention from negatively valenced stimuli (Bar-Haim et al., 2007; Mogg et al., 1995; Koster et al., 2011). In a similar vein, an evolving body of research has examined how an individual's response to emotionally ambiguous information, or 'valence bias', is linked to mental health and wellbeing (Neta et al., 2009; 2023; Neta & Brock, 2021; Park et al., 2016; Petro et al., 2021; Raio et al., 2021). A greater trait-like negativity bias towards emotionally ambiguous information has been associated with anxiety (Neta et al., 2017; Park et al., 2016), depressive symptoms (Petro et al., 2021), negative affect (Neta & Brock, 2011) and stress reactivity (Raio et al., 2021).

Relatedly, rumination, a rigid and maladaptive form of negative thinking, is also considered a transdiagnostic factor underlying both anxiety and depression (Hsu et al., 2015; McLaughlin & Nolen-Hoeksema, 2011). Rumination is defined as the experience of excessive thoughts that are negative, deliberate, and perseverative (Nolen-Hoeksema, 2000; Treynor et al., 2003). While prior research has examined the relationship between rumination and affective flexibility (Genet et al., 2013), rumination is considered a multifaceted form of perseverative cognition, comprised of at least three distinct dimensions: brooding, reflective, and depressive rumination (Treynor et

al., 2003). Whereas brooding rumination reflects the tendency to passively compare one's current situation with unachieved standards and is viewed as a more maladaptive form of repetitive thinking, reflective rumination is the tendency to purposefully engage in cognitive problem solving and is regarded a more adaptive form of thinking that may help to alleviate depressive symptoms (Treynor et al., 2003). Brooding rumination has previously been associated with attention towards negative information (Duque et al., 2014; Joorman et al., 2006; Owens & Gibb, 2017) and may therefore be a stronger predictor of affective inflexibility in comparison to reflective rumination, which is considered a more adaptive form of rumination. The extent to which different facets of rumination may uniquely predict affective (in)flexibility is yet to be examined.

Overall, it appears that a disposition to more rigid responding, such as ruminative thinking and/or a negativity bias towards emotionally ambiguous information, have implications for overall health and wellbeing. Importantly, flexible emotional responding can also be observed at the biological level. Considering the intricate connection between the heart and the brain, the Neurovisceral Integration Model (NIM; Smith et al., 2017; Thayer & Lane, 2000, 2009) proposes that shared neural regions functionally overlap to support autonomic, affective, and cognitive regulatory processes. Specifically, effective, top-down, inhibitory function of prefrontal areas (i.e., medial prefrontal cortex) over subcortical structures (i.e., amygdala) can be indexed by an objective, non-invasive metric known as heart rate variability (Thayer et al., 2012). HRV refers to the physiological phenomenon in which the time intervals between consecutive heartbeats vary. Given the involvement of prefrontal structures in supporting emotion regulation/flexibility and executive function, the NIM proposes that resting HRV serves as an index of prefrontal functioning and can thus be considered an indicator of adaptive self-regulation and cognitive control (Thayer & Lane, 2000, 2009; Thayer et al., 2009). Prior empirical research and meta-analyses support associations between HRV and top-down self-regulation, emotion regulation, executive function, and affective flexibility (Appelhans & Luecken, 2006; Grol & De Raedt, 2020; Holzman & Bridgett, 2017; Mather & Thayer, 2018; Thayer et al., 2009), with higher resting HRV facilitating effective adaptation to environmental demands.

Prior studies have shown that individuals with greater resting HRV tend to have higher wellbeing and exhibit more flexible emotional responses, including more effective top-down and bottom-up modulation of responses in relation to emotional

stimuli (Park & Thayer, 2014) and greater emotion regulation ability (Thayer & Lane, 2000; Appelhans & Luecken, 2006). On the other hand, individuals with lower resting HRV self-report higher emotion regulation difficulties (Visted et al., 2017; Williams et al., 2015) and have also been found to demonstrate increased hypervigilance to, alongside difficulties disengaging from, negative threat stimuli (Park et al., 2013; Park & Thayer, 2014). Other research focusing on affective flexibility found lower resting HRV to be correlated with more efficient shifting of attention to non-affective aspects of negative emotional material, reflecting increased avoidance of negative emotional information (Grol & De Raedt, 2020). Furthermore, evidence from a few studies suggests a potential interconnection between HRV and valence bias (Madison et al., 2021; Osnes et al., 2023). Higher resting and task-based HRV have previously been found to predict a greater positivity bias, whereby women with higher HRV interpreted both neutral and ambiguous vocal stimuli as positive (Madison et al., 2021). More recently, a study employing the Reading the Mind in the Eyes test reported that individuals with greater resting HRV demonstrated an increased preference for selecting positive items on the test, in turn reflecting a higher tendency of interpreting negative visual stimuli as positive, regardless of the correct response (Osnes et al., 2023). However, while some studies have examined both resting HRV and phasic HRV changes (Butler et al., 2006; Denson et al., 2011; Park et al., 2014), fewer studies have examined both rest and task-related measures of HRV in relation to adaptive emotional responding (Guendelman et al., 2024; Tupitsa et al., 2023). Indeed, phasic HRV increases have been linked to higher self-regulatory effort and successful emotion regulation (Butler et al., 2006; Denson et al., 2011; Park et al., 2014). Since HRV is considered a metric of adaptive emotional responding, it therefore seems imperative to not only assess HRV during periods of rest, but to critically examine HRV during contexts that actively require flexible emotional responding.

Taken together, rumination, valence bias, and HRV all tap into, and have implications for (in)flexible responding and psychopathology. While various measures of emotional disposition and flexibility exist, we opted to focus on the outlined measures for several reasons. Firstly, prior research highlights and provides supporting evidence for a close link between rumination and flexible emotional responding (Genet et al., 2013; Grol & De Raedt, 2021) and trait rumination has been reported to demonstrate strong associations with psychopathology relative to other cognitive styles/emotion regulation strategies (Aldao et al., 2010). Nonetheless, the

degree to which different facets of rumination may differentially predict the ability to flexibly engage with and disengage from emotional information is less known. Moreover, valence bias, operationalised as interpretations of emotionally ambiguous (dual-valence) stimuli, is a fairly stable individual difference measure exhibiting high test-retest reliability (Neta et al., 2009) which has been linked to mental health (Harp et al., 2024) and has implications for adaptive emotional responding (Neta et al., 2023). In comparison to the other two measures, HRV is a biological, non-invasive, and more objective measure of flexibility that has also previously been linked to affective flexibility (Grol & De Raedt, 2020) and is considered a biomarker of mental illness (Beauchaine & Thayer, 2015). Critically, adopting all three measures in the present research permitted examination of psychological (rumination, valence bias) and physiological (HRV) indexes of flexible emotional responding. The overall aim of the present studies was to examine whether the aforementioned individual difference factors could predict affective flexibility performance on an established affective switching task. Study 1 was conducted using an online sample with the aim to assess the degree to which valence bias and self-reported trait rumination could predict affective flexibility switch costs in relation to changes in the trial valence and rule. Study 2 sought to further examine the relationship between these individual differences and affective flexibility, with an additional and primary focus on the extent to which resting and task-related HRV measures could predict affective flexibility performance in a laboratory setting.

4.3 Study 1

4.3.1 Aims and Hypotheses

The primary aim of Study 1 was to examine whether valence bias, that is trait-like biases in the ratings of emotionally ambiguous information (surprise facial expressions), could predict affective flexibility performance (Genet et al., 2013; Malooly et al., 2013). Since prior research has mainly focused on attentional shifts pertaining to rule type when the valence of the image is held constant, the current study sought to focus more closely on the ‘affective’ aspect of the task, specifically when the valence of the emotional images switch (i.e., when the image valence shifted from positive to negative, regardless of a shift or repetition in the rule type). Difficulties disengaging attention from negatively valenced stimuli is a key characteristic of anxiety and depression (Bar-Haim et al., 2007; Mogg et al., 1995; Koster et al., 2011),

and in turn, an increased trait-like negativity bias has been linked to both anxiety and depressive symptoms (Park et al., 2016; Petro et al., 2021). Therefore, it was predicted that a higher negativity bias would be positively associated with greater switch costs (lower flexibility) when shifting attention away from images with a negative valence towards those with a positive valence, particularly in an affective rule context. With relation to attentional shifts based on rule type, a secondary prediction was that greater negativity bias would be correlated with greater switch costs (lower flexibility) when shifting attention from affective towards non-affective aspects of negative information. Moreover, the current study aimed to assess and conceptually replicate associations between rumination and affective flexibility. Previous research has reported associations between affective flexibility and rumination levels in daily life (Genet et al., 2013). However, it is unclear whether certain facets of *trait* rumination, such as brooding and reflective rumination, differentially predict affective flexibility, especially when the valence of information switches. Correspondingly, it was hypothesised that individuals with higher trait rumination, particularly higher brooding rumination, would exhibit greater switch costs when the valence of the image switched from negative to positive, especially in an affective rule context. In line with prior research (Genet et al., 2013), it was anticipated that individuals with higher trait rumination, particularly brooding rumination, would exhibit greater switch costs (lower flexibility) when shifting attention from affective towards non-affective aspects of negative information, and lower switch costs (greater flexibility) when shifting attention from affective towards non-affective aspects of positive information.

4.3.2 Method

4.3.2.1 Participants

A total of 120 participants[8] initially accessed the online experiment and were recruited using convenience sampling through three online recruitment platforms: Prolific (https://prolific.co), the SONA Systems recruitment platform (https://sona-systems.com) at the University of Reading, or via various social media platforms (i.e.,

[8] An a-priori power analysis for a hierarchical multiple linear regression based on R2 increase with 3 predictors (negativity bias and brooding and reflective facets of trait rumination, with 4 predictors in total) assuming a medium effect size (f2 = 0.15) and power of 0.80, indicated a necessary sample size of 77 participants. Accounting for 10% attrition, we aimed to recruit 85 participants. The effect size was determined based on a similar design and power analyses carried out by Grol and De Raedt (2018) and Twivy et al. (2021). Power analyses were calculated using G*Power (v3.1).

Twitter/X, Facebook, and Instagram). Of these participants, 85 completed the online experiment. Participants were excluded for falling below 60% accuracy on clear valence negative trials (n = 4) and for missing or losing more than 50% of trials on the affective flexibility task (n = 9). The final sample contained 72 participants (*M* age = 29.51 years, SD = 13.87, range = 18-75 years; gender identity: 47 female, 25 male; ethnicity: 41 White, 15 Latinx, 10 Asian, 3 Black/African/Caribbean, 1 Middle Eastern, 1 Multi-ethnic, 1 Unknown; Nationality: 42 European, 12 North American, 7 Asian, 4 African, 4 Australasian, 3 South American; Handedness: 65 right-handed, 7 left-handed). Any individual over the age of 18 years was eligible to participate in the online study. Participants recruited from Prolific received £7.50 for their participation and those recruited from SONA received course credit. Other participants were volunteers recruited by word of mouth with no form of compensation. All participants provided virtual informed consent prior to accessing the online experiment. Information concerning past or present experience of mental health conditions (anxiety and depression) was not obtained, or controlled for, in the current sample. This study was given a favourable ethical opinion of conduct by the University of Reading's Research Ethics Committee (reference: 2021-028-CvR).

4.3.2.2 Materials and Procedure

4.3.2.2.1 Trait Rumination

Trait rumination was assessed using the Ruminative Response Scale Short-Form (RRS; Treynor et al., 2003), a self-report scale containing 10 items assessing two facets of rumination: brooding and reflective, alongside total rumination. Each item is rated on a 4-point Likert scale from 1 ("Almost never") to 4 ("Almost always"). Scores range from 10 to 40, with higher scores indicating higher self-reported rumination. Internal consistency for the whole scale (Cronbach's α = 0.80) and brooding (α = 0.74) and reflective (α = 0.70) subscales was acceptable or good.

4.3.2.2.2 Valence Bias Task

The valence bias task (Harp et al., 2021; Neta et al., 2009; Neta et al., 2013; Neta et al., 2023) involved participants viewing images of human faces that either signalled an expression of a clear positive (happy), clear negative (angry), or an ambiguous (surprise) valence and rating each expression as either positive or

negative. A total of 48 faces (24 ambiguous and 24 clear valence) were presented across main trials, with 14 discrete identities (7 females, ages 21-30 years) from the NimStim database (Tottenham et al., 2009) and 20 discrete identities (10 females, 20-30 years) from the Karolinska Directed Emotional Faces database (KDEF; Goeleven et al., 2008). The practice block contained 12 faces (4 faces per discrete (angry, happy, ambiguous) valence category) with a further 6 identities from the NimStim (3 females) and 6 identities from the KDEF (3 females) that were different to those presented in the main trials (see Table S8 for further information about the stimuli in the Supplementary Material).

On a given trial, a black central fixation cross on a white background was presented for 1,500 ms, followed by an image of a face for 500 ms. The image of the face remained on the screen until either a response had been recorded or a response limit of 2000 ms elapsed. Participants recorded their response by pressing either the 'A' or 'L' key on their keyboard to indicate whether the image was positive or negative. The task instructions encouraged participants to respond as quickly as possible and to go with their gut feeling.

Participants engaged in a practice block that comprised 12 trials prior to proceeding to the main task. There were 48 main trials in total, split across two task blocks with each block containing 24 trials. Per block, 12 ambiguous (surprise) and 12 clear valence (six positive (happy) and six negative (angry) faces) images were presented. Participants were randomly assigned to a pseudorandom (counterbalanced) presentation order across the two blocks of faces and the cue-response key mapping was counterbalanced across participants (e.g., A = negative, L = positive, or vice versa). Valence bias was calculated as the percentage of trials in which a negative response was recorded across all ambiguous trials within each subject. For example, if a participant provided negative ratings for all images displaying a surprise facial expression, then their negative valence bias score would be 100%.

4.3.2.2.3 Affective Flexibility Task

Affective flexibility was assessed using a previously established affective task switching paradigm (Genet et al., 2013; Malooly et al., 2013) which involved sorting emotional images according to either an 'affective' (i.e., indicating whether the image was positive or negative) or a 'non-affective' (i.e., indicating whether there were ≤ 1

or ≥ 2 people depicted in the image) category rule (see Figure 10). Importantly, across some of the trials the emotional valence of the image repeated (i.e., remained positive or negative across consecutive trials) or switched (i.e., changed from a negative to a positive valence image, or vice versa). The category rule also either repeated or switched. Across the main trials, a total of 160 emotional images from the International Affective Picture System (IAPS; Lang et al., 2008) were presented, with 40 images selected per main category: negative valence with one or fewer people, positive valence with one or fewer people, negative valence with two or more people, and positive valence with two or more people. Images were balanced in terms of normative ratings for arousal, such that there was no significant difference in self-reported arousal for negative (M = 5.20, SD = 0.78) compared to positive (M = 5.20, SD = 0.68) IAPS images (t(158) = 0, p = .999)). An additional 20 IAPS images, representative of those shown in the experimental blocks, were selected and presented during the practice blocks (see Supplementary Material for IAPS codes).

On a given trial, a blank, black screen (250 ms) followed by the appearance of a white central fixation cross (250 ms) always preceded the presentation of the emotional image. The emotional picture appeared in the centre of the screen with visual cues situated on the left- and right-hand side of the image which represented the relevant task rule. Specifically, the symbols '+' and '-' represented the affective categorisation rule whereas '≤ 1' and '≥ 2' represented the non-affective categorisation rule. Both the emotional image and respective cues remained on the screen until either a response was made or if the maximum response limit of 5000 ms elapsed. The background colour of the screen (grey or white frame) further reflected the categorisation rule (i.e., affective rule = white frame, non-affective rule = grey frame, or vice versa). Participants recorded their response by pressing either the 'A' or 'L' key with their index finger, in which the 'A' key always represented the left-hand cue and the 'L' key the right-hand cue. Participants were instructed to respond quickly but to also be as accurate as possible.

Participants engaged in four guided practice blocks. The first two practice blocks comprised four separate affective and non-affective sort rule trials respectively. The remaining practice blocks consisted of six mixed affective and non-affective sort rule practice trials that were pseudorandomised. Following the practice trials, participants engaged in two blocks of main trials that consisted of 160 trials each (320 trials in total) with a self-paced break offered in between blocks. Across trials, there

were 16 different trial conditions in total: trials in which the emotional valence of the image and task rule both repeated (e.g., a negative affective trial preceded by a negative affective trial), trials in which the valence of the image changed but the task rule repeated (e.g., a negative affective trial preceded by a positive affective trial), trials in which the valence of the image remained the same but the task rule switched (e.g., a negative affective trial preceded by a negative non-affective trial), and trials where both the valence of the image and task rule switched (e.g., a negative affective trial preceded by a positive non-affective trial). The total number of trials for each of the 16 trial conditions ranged between 13-30 trials. The main trials were presented in a pseudorandom order (Malooly et al., 2013). Participants were assigned to one of eight different versions of the task, in which the different combination of cue to key mappings and rule (affective/non-affective) to background frame colour (grey/white) mappings were counterbalanced. Within a specific version of the task, the response key mapping and task rule to background frame colour mapping were held constant throughout the duration of the task.

Affective flexibility was assessed using switch costs, calculated as the difference in mean reaction time (RT) between repetition and switch trials. Separate main switch costs were calculated based on repetitions and switches in emotional valence and rule type respectively. For emotional valence, four main RT-based switch costs were calculated in relation to a shift in the valence of the image: positive to negative with an affective category rule, positive to negative with a non-affective category rule, negative to positive with an affective category rule, and negative to positive with a non-affective category rule. For example, a positive switch cost in an affective rule context was calculated by subtracting the mean RT on trials where a positive image repeated in the presence of an affective rule from the mean RT where the emotional valence of the image shifted from negative to positive in the presence of an affective rule. Furthermore, in line with prior research (Malooly et al., 2013), four RT-based switch costs were calculated in relation to a switch in task rule: affective positive, affective negative, non-affective positive, and non-affective negative switch costs. For example, negative non-affective switch costs were calculated by subtracting the mean RT on trials where the non-affective rule repeated in the presence of negative emotional images from the mean RT on trials where the task rule switched from affective to non-affective when the image was negative. Generally, greater switch

costs indicate less efficient/slower shifting of attention and thus reflect lower overall flexibility.

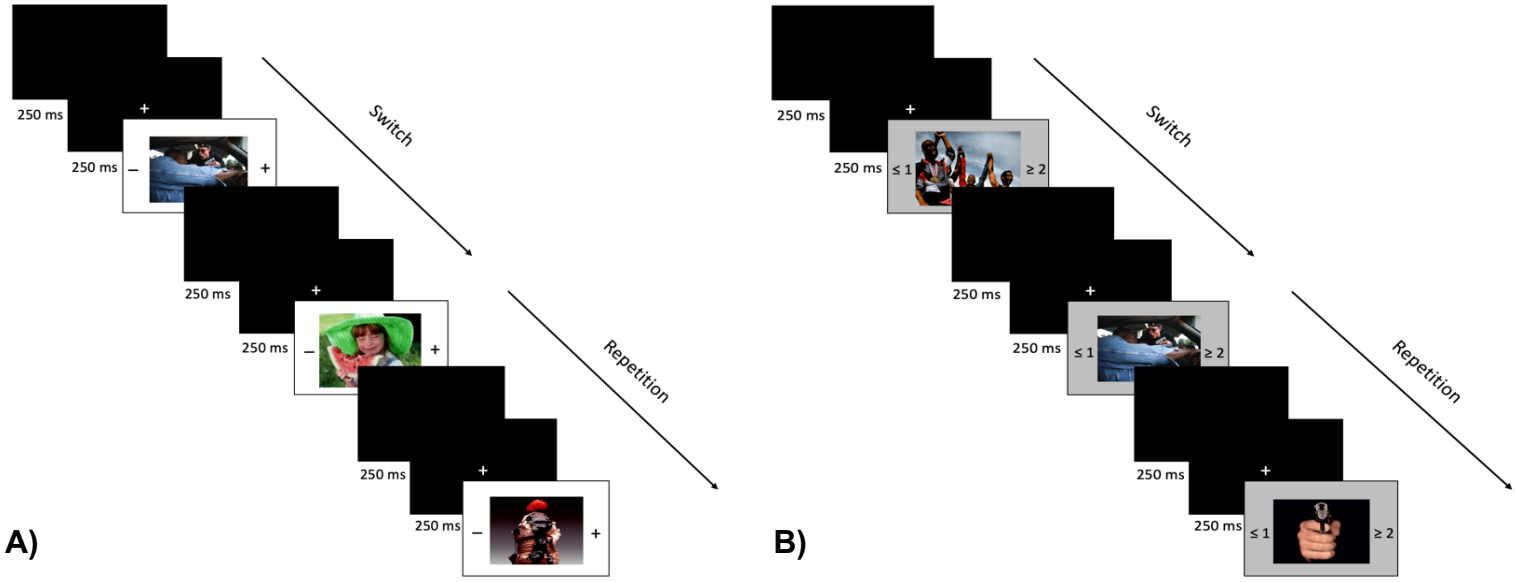

Figure 10. Affective Flexibility Task. **A)** A positive valence switch trial (affective context). The first trial contains a negative valence image which then switches to a positive valence image in the subsequent trial ('SWITCH' from negative to positive in an affective rule context). A positive valence image is then presented in the next trial ('REPETITION' of a positive valence image in an affective rule context). **B)** A negative valence switch trial (non-affective context). A positive valence picture is displayed with the non-affective rule, which switches to a negative valence image with the non-affective rule in the subsequent trial ('SWITCH' from positive towards negative image in a non-affective rule context). The following trial displays a negative valence image with a non-affective rule ('REPETITION' of negative valence image in a non-affective rule context). Images displayed in this Figure are from the International Affective Picture System (IAPS).

4.3.2.2.4 Attentional ('Bot') Check

Given the prevalence of 'bots' in online research, we incorporated a simple visual search task in the experimental procedure to verify participant responses and to serve as an additional attentional and validity check. The task was directly cloned from Gorilla's openly available 'bot check' tasks (www.gorilla.sc; Anwyl-Irvine et al., 2020). Participants were instructed to find and select an image of a cat amongst images of dogs. The task involved two trials, and on each trial, four images were presented at a random position on the screen. Images on both trials were the same, with one image of a cat (target image) three images of dogs (non-target images).

Accuracy was assessed. The majority of participants (97.22) achieved 100% accuracy and passed the check (i.e., correct responses registered on both trials).[9]

4.3.2.2.5 Procedure

Participants responded to online study advertisements via Prolific, Sona, and various social media platforms (Twitter/X, Instagram, and Facebook). The online experiment was accessed through a secure link that directed participants to the experiment page built with Gorilla Experiment Builder (Anwyl-Irvine et al., 2020). The study could only be accessed using a desktop computer or laptop (phone and tablet devices were restricted). Consenting participants first responded to several demographic questions (including age, gender identity, ethnicity, nationality, education level, and handedness) and completed questionnaires that assessed general mood and stress exposure over the last two weeks (self-report measures not described here). Following this, participants engaged in the valence bias task and responded to further questionnaires that measured resilience and use of different emotion regulation strategies. Subsequently, participants performed a quick visual attention (visual search) task, completed the RRS questionnaire, and engaged in the affective flexibility task. At the end of the study, participants engaged in a five-minute recovery period to alleviate potential negative mood or feelings of distress that could have been evoked by the affective flexibility task. Participants were presented with a variety of positively valenced soothing images from the Project Soothe database (Wilson et al., 2018; www.projectsoothe.com) and rated their mood prior to, and after, exposure to the images via the Positive and Negative Affect Schedule-NOW (PANAS-NOW; data are not reported here). Upon completion of the study, participants were fully debriefed on the purpose of the research study. Overall, the experiment took one hour to complete.

[9] One participant provided incorrect responses on both trials but indicated in the debrief feedback that they encountered technical difficulties during this task whereby the images failed to load. This was reflected in their responses which indicated they had clicked on a blank image to proceed. Another participant encountered similar loading delays, but only on one trial. Given that both participants encountered technical difficulties as opposed to selecting the wrong image, these participants were retained for further analyses.

4.3.2.3 Data Processing and Preliminary Data Analysis

4.3.2.3.1 Valence Bias

Only the first response on a given trial was retained for analysis. Missing/timed-out trials (n = 117) and trials with a RT less than 250 ms (n = 8) were removed prior to analysis. Trials with a RT greater than three standard deviations from the mean RT within each subject and within each trial category (i.e., positive clear valence, negative clear valence, and ambiguous valence) were also calculated and removed (n = 19 trials across the sample). Following initial task processing, accuracy of responses to the clearly valenced stimuli (i.e., trials with angry and happy face stimuli) was assessed. We opted to exclude participants with an accuracy falling below 50% on either positive or negative clear valence trials (n = 4 participants falling below 50% accuracy on positive clear valence trials). All participants in the final sample (N = 72) had an overall clear valence accuracy over 60% which follows accuracy cut-offs adopted in prior studies (Harp et al., 2021; Neta et al., 2013; Petro et al., 2018).

4.3.2.3.2 Affective Flexibility

Practice trials (n = 20) and the first trial from each block (n = 2) were removed prior to processing and analysis (total n = 318 main trials for each participant). Subsequently, trials that were missing/timed out (n = 212 across the sample), had an average image load lag exceeding 2000 ms (n = 87), and with RTs below 250 ms (n = 168) were removed. Only trials that were preceded by a correct trial were retained for main analyses as an incorrect response on a previous trial is likely to cause post-error slowing and, from the participant's point of view, may lead to ambiguity regarding whether the current trial is a repetition or switch (Grol & De Raedt, 2020). Nine participants were excluded for losing over 50% of their trials on the affective flexibility task. The average percentage of trials lost in the final sample (N = 72) was 13.28% (SD = 8.60, range = 0.63% - 48.74%), with an average of 273.82 (SD = 31.68, range = 140-316) main trials retained for analyses. Furthermore, in line with previous studies (Genet et al., 2013; Grol & De Raedt, 2020; Malooly et al., 2013; Twivy et al., 2021), RTs that were 2.5 standard deviations above or below the mean RT within each participant and the specific trial condition were identified and replaced with the upper and lower cutoff values respectively (*M* trials = 6.35, SD = 2.39, range = 2-12).

Non-parametric Wilcoxon signed-rank tests were conducted due to skewed variables across all global switch and repetition trials for valence and rule category.

Accuracy for trials where valence repeated (*M* = 93.93, SD = 5.10) was slightly higher than trials where valence switched from positive to negative or vice versa (*M* = 93.38, SD = 4.64), but this difference was non-significant, *Z* = -1.89, *p* = .059. Furthermore, accuracy was significantly higher on trials where the rule repeated (*M* = 94.42, SD = 3.81) compared to when the rule switched (*M* = 92.82, SD = 5.99), *Z* = -3.46, *p* < .001. With relation to response times, there was a significant difference in RT for global repetition and switches in valence, such that RTs on switch trials were significantly longer in duration (*M* = 1527.67, SD = 219.22) compared to repetition trials (*M* = 1489.46, SD = 311.76), *Z* = -4.73, *p* < .001. However, unexpectedly, for global repetitions and switches based on the rule category, RTs were of a longer duration for repetition (*M* = 1641.76, SD = 346.43) versus switch (*M* = 1580.59, SD = 332.46) trials, *Z* = -4.48, *p* <.001. Therefore, we cannot rule out the possibility of a speed-accuracy trade-off for rule category, in which participants were faster to respond to trials where the rule switched from affective to non-affective (or vice versa) alongside lower accuracy for these trials.

4.3.3 Results

Multiple hierarchical regression models were used to examine whether trait-like negativity bias and self-reported brooding and reflective facets of trait rumination predicted key affective flexibility switch costs based on shifts in valence and in rule instruction. The following predictors were entered into the model in a stepwise order: age (years; step 1), negativity bias (step 2), and brooding and reflective rumination subscale scores (step 3). All predictors were mean centered. Standardised beta coefficients are reported in the Results. Bonferroni corrections were performed to account for multiple tests (*p* = 0.00625 (0.05/8)).

4.3.3.1 Descriptive Statistics

Table 5 displays the descriptives for negativity bias, self-reported brooding and reflective rumination, and key valence and rule switch costs of interest from the affective flexibility task.

One-way ANOVAs and, in the case of violence of homogeneity (based on Levene's median test), Welch's ANOVA tests were conducted to assess whether there were any systematic differences for key variables based on recruitment platform (Social Media N = 29, Sona N = 13, Prolific N = 30). No significant differences were

observed for negative valence bias, brooding and reflective rumination subscales, or for the key affective flexibility switch costs based on recruitment method. Age was the only variable to demonstrate a significant difference based on recruitment platform $F_{Welch}(2, 25.78) = 8.92$, $p = .001$). Games-Howell post-hoc tests were performed to account for unequal variances, which revealed the average age of participants recruited via social media ($M = 38$, $SD = 17.17$) to be significantly higher in comparison to both Sona ($M = 23.31$, $SD = 10.35$, $p = .004$) and Prolific ($M = 24$, $SD = 4.63$, $p < .001$). Thus, participants recruited from social media were slightly older on average in comparison to the other recruitment platforms. However, since age was not a variable of interest in the present study and included in the linear models as a relevant control variable, and no other systematic differences were detected as a function of recruitment method across the other key variables, recruitment platform was not considered in further analyses.

Table 5.
Descriptive Statistics for Key Sample Characteristics (Study 1). Data is provided in means and standard deviations (in parenthesis).

	Data (N = 72)
Negativity Bias (%)	72.54 (18.82)
Brooding Rumination[a]	12.32 (3.36)
Reflective Rumination[a]	12.32 (3.21)
Total Rumination[b]	24.64 (5.75)
Accuracy Global Valence Repeat (%)	93.93 (5.10)
Accuracy Global Valence Switch (%)	93.38 (4.64)
Accuracy Global Rule Switch (%)	94.42 (3.81)
Accuracy Global Rule Repeat (%)	92.82 (5.99)
RT Global Valence Repeat (ms)	1489.46 (311.76)
RT Global Valence Switch (ms)	1527.67 (319.22)
RT Global Rule Repeat (ms)	1641.76 (346.43)
RT Global Rule Switch (ms)	1580.59 (332.46)
Positive Valence Switch Cost (Non-Affective Context; ms)	142.47 (162.45)
Positive Valence Switch Cost (Affective Context; ms)	45.87 (165.65)
Negative Valence Switch Cost (Non-Affective Context; ms)	5.05 (170.15)
Negative Valence Switch Cost (Affective Context; ms)	-80.57 (199.29)
Non-Affective Switch Cost (Negative Valence; ms)	73.02 (204.62)
Affective Switch Cost (Negative Valence; ms)	159.32 (226.27)
Non-Affective Switch Cost (Positive Valence; ms)	164.58 (188.82)
Affective Switch Cost (Positive Valence; ms)	139.23 (202.18)

[a] Score range for RRS brooding and reflective rumination subscales = 5-20 ; [b] Score range for RRS total rumination scale = 10-40

4.3.3.2 Affective Flexibility Switch Costs: Valence

In general, the average RT on trials where the valence of the image switched was slightly slower in comparison to trials where the valence of the image repeated, apart from conditions contributing to the negative valence affective switch cost, in which the average RT for when negative images repeated was slower (M = 1390.88, SD = 362.05) in comparison to trials in which the image switched from a positive to a negative valence (M = 1310.31, SD = 314.81) when the affective rule repeated, (t(71) = -3.43, p = .001, survived Bonferroni-correction). The only other significant valence cost surviving correction for multiple comparisons was the positive valence non-affective switch cost. Pairwise comparisons between main switch and repeat trial conditions used for the calculation of key valence switch costs with associated

uncorrected *p*-values are presented in Table S6 in the Supplementary Material. See Figures 11a-d for mean RTs per repeat and switch condition used to calculate switch costs based on valence.

4.3.3.3 Affective Flexibility Switch Costs: Rule

The average RT on trials where the trial rule switched was consistently slower than when the trial rule repeated for all of the main rule switch costs of interest. The only switch cost that did not survive correction for multiple comparisons was the non-affective rule negative switch cost ($t(71) = 3.03$, $p = .003$). Pairwise comparisons between main switch and repeat trial conditions used for the calculation of key rule switch costs with associated uncorrected *p*-values are presented in Table S6 in the Supplementary Material. See Figures 11e-h for mean RTs per repeat and switch condition used to calculate switch costs based on valence.

4.3.3.4 Affective Flexibility Valence Switch Cost Regression Analyses

Table 6 displays the hierarchical regression results for age, negativity bias, and rumination on the various affective flexibility switch costs based on valence. Neither negativity bias or self-reported rumination, were found to significantly predict affective flexibility based on the key switch costs of interest. Age (control variable) was found to significantly predict negative valence switch costs in an affective context, such that older participants appeared to demonstrate less efficient shifts from positive to negative emotional information (when the categorisation rule was affective) in comparison to those of a younger age ($\beta = -0.26$, $t = -2.22$, $p = .030$). However, this finding did not survive correction for multiple comparisons. Furthermore, adding negativity bias did not result in a significant change in $R^2 = 0.01$, $F(2, 69) = 2.63$, $p = .079$, nor did inclusion of the two rumination subscales in a subsequent step, R^2 change = 0.01, $F(4, 67) = 1.54$, $p = .202$.

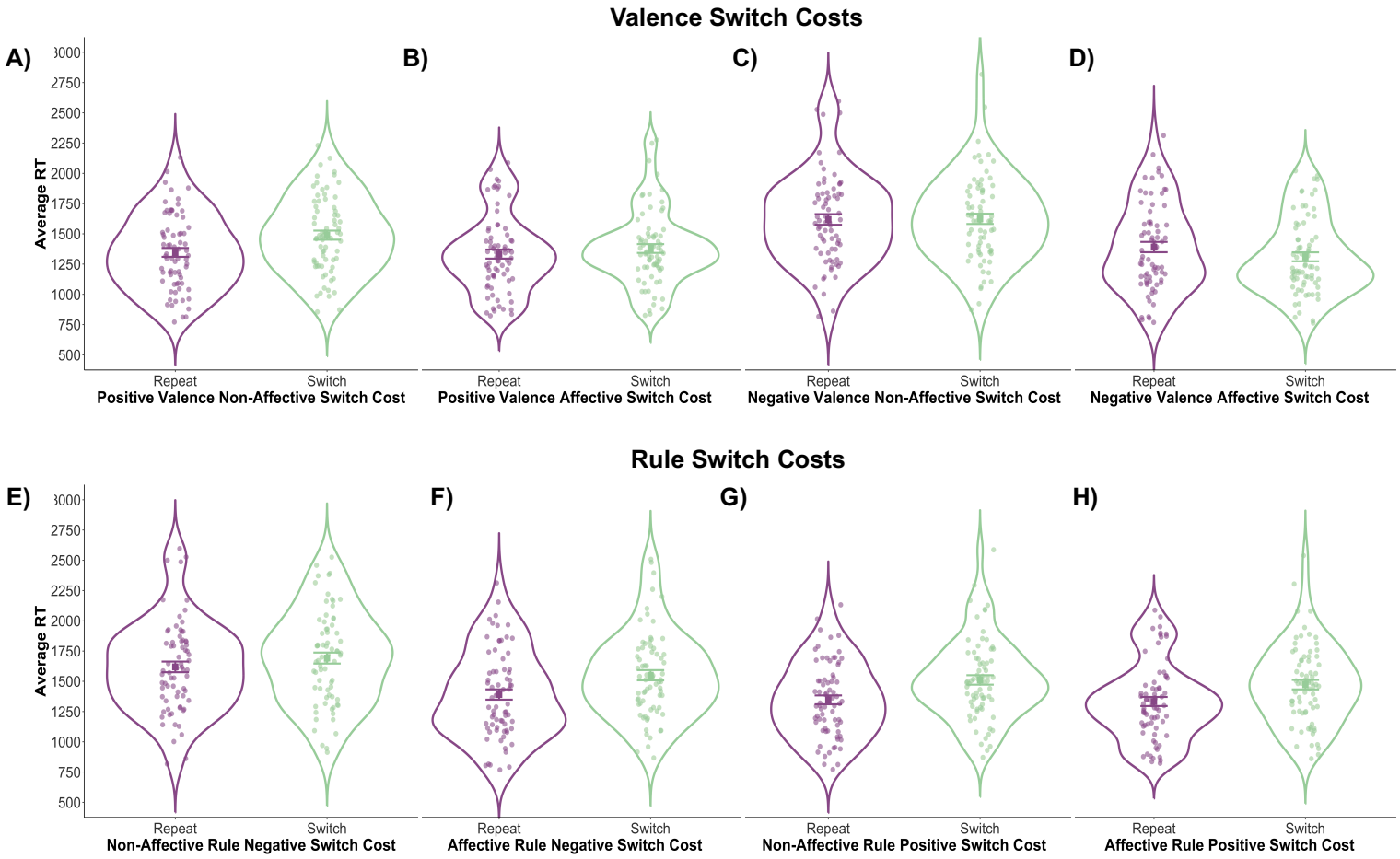

Figure 11. Mean Reaction Times for Key Valence and Rule Repeat Versus Switch Conditions (Study 1). **A)** Mean RT for trials where there was a repetition of a positive valence image on consecutive trials (repeat) and trials where there was a switch from a negative valence to a positive valence picture (switch) when the trial rule was non-affective. **B)** Mean RT for trials where there was a repetition of a positive valence image on consecutive trials (repeat) and trials where there was a switch from a negative valence to a positive valence picture (switch) when the trial rule was affective. **C)** Mean RT for trials where there was a repetition of a negative valence image on consecutive trials (repeat) and trials where there was a switch from a positive valence to a negative valence picture (switch) when the trial rule was non-affective. **D)** Mean RT for trials where there was a repetition of a negative valence image on consecutive trials (repeat) and trials where there was a switch from a positive valence to a negative valence image (switch) when the trial rule was affective. **E)** Mean RT for trials where there was a repetition of a non-affective rule (repeat) and trials where there was a switch from an affective rule to a non-affective rule (switch) with images of a negative valence. **F)** Mean RT for trials where there was a repetition of an affective rule (repeat) and trials where there was a switch from a non-affective to an affective rule (switch) with images of a negative valence. **G)** Mean RT for trials where there was a repetition of a non-affective rule (repeat) and trials where there was a switch from an affective rule to a non-affective rule (switch) with images of a positive valence. **H)** Mean RT for trials where there was a repetition of an affective rule (repeat) and trials where there was a switch from a non-affective to an affective rule (switch) with images of a positive valence. Error bars reflect ± 1 standard error around the mean.

Table 6.
Hierarchical Regression Analyses for Age, Negativity Bias, and Trait Rumination on Affective Flexibility Valence Switch Costs (Study 1)

Model	Predictor	*b*	95% CI	*β*	*t*	*p*	R^2	R^2 Change	*F*	*p*
Positive Valence Switch Cost (Non-Affective Context)										
Step 1	Age	0.05	-2.74, 2.84	0	0.04	.970	0	0	0.01	.970
Step 2	Age	0	-2.80, 2.80	0	0	1	0.01	0.01	0.28	.756
	Negativity Bias	-0.78	-2.80, 1.29	-0.09	-0.75	.457				
Step 3	Age	-0.30	-3.31, 2.70	-0.03	-0.20	.841	0.04	0.04	0.75	.563
	Negativity Bias	-0.49	-2.59, 1.61	-0.06	-0.46	.645				
	Brooding Rumination	1.33	-13.09, 15.75	0.03	0.18	.854				
	Reflective Rumination	-10.34	-24.84, 4.17	-0.20	-1.42	.160				
Positive Valence Switch Cost (Affective Context)										
Step 1	Age	-0.08	-2.93, 2.77	-0.01	-0.05	.956	0	0	0	.956
Step 2	Age	0.01	-2.83, 2.85	0	0.01	.993	0.02	0.02	0.82	.443
	Negativity Bias	1.34	-0.75, 3.44	0.15	1.28	.204				
Step 3	Age	-0.69	-3.69, 2.32	-0.06	-0.46	.650	0.08	0.06	1.48	.218
	Negativity Bias	1.66	-0.44, 3.76	0.19	1.58	.119				
	Brooding Rumination	-2.72	-17.12, 11.68	-0.06	-0.38	.708				
	Reflective Rumination	-11.20	-25.69, 3.29	-0.22	-1.54	.128				
Negative Valence Switch Cost (Non-Affective Context)										
Step 1	Age	-0.49	-3.41, 2.43	-0.04	-0.33	.740	0	0	0.11	.740
Step 2	Age	-0.51	-3.46, 2.43	-0.04	-0.35	.729	0	0	0.12	.888
	Negativity Bias	-0.39	-2.56, 1.78	-0.04	-0.36	.721				
Step 3	Age	-0.45	-3.66, 2.77	-0.04	-0.28	.783	0	0	0.07	.992
	Negativity Bias	-0.36	-2.61, 1.88	-0.04	-0.32	.748				
	Brooding Rumination	1.24	-14.16, 16.64	0.03	0.16	.873				
	Reflective Rumination	-1.02	-16.52, 14.48	-0.02	-0.13	.896				
Negative Valence Switch Cost (Affective Context)										
Step 1	Age	-3.68	-6.99, -0.37	-0.26	-2.22	.030	0.67	0.07	4.92	.030
Step 2	Age	-3.63	-6.96, -0.30	-0.25	-2.18	.033	0.07	0.01	2.63	.079
	Negativity Bias	0.76	-1.70, 3.21	0.07	0.62	.541				
Step 3	Age	-3.36	-6.97, 0.25	-0.23	-1.86	.068	0.08	0.01	1.54	.202
	Negativity Bias	0.97	-1.55, 3.49	0.09	0.77	.444				
	Brooding Rumination	6.73	-10.57, 24.03	0.11	0.78	.440				
	Reflective Rumination	-7.96	-25.37, 9.45	-0.13	-0.91	.365				

4.3.3.5 Affective Flexibility Rule Switch Cost Regression Analyses

Table 7 shows the hierarchical regression findings for age, negativity bias, and rumination on the key affective flexibility switch costs based on rule type. None of the overall models were significant, nor did the negativity bias or the two self-reported facets of rumination significantly predict any of the affective flexibility switch costs of interest.

Table 7.
Hierarchical Regression Analyses for Age, Negativity Bias, and Trait Rumination on Affective Flexibility Rule Switch Costs (Study 1)

Model	Predictor	*b*	95% CI	*β*	*t*	*p*	R^2	R^2 Change	*F*	*p*
Non-Affective Switch Cost (Negative Valence)										
Step 1	Age	-1.43	-4.93, 2.07	-0.10	-0.81	.418	0.10	0.01	0.66	.418
Step 2	Age	-1.30	-4.78, 2.18	-0.09	-0.75	.458	0.20	0.03	1.39	.255
	Negativity Bias	1.87	-0.70, 4.43	0.17	1.45	.150				
Step 3	Age	-1.53	-5.30, 2.25	-0.10	-0.81	.422	0.22	0.01	0.87	.487
	Negativity Bias	1.67	-0.97, 4.30	0.15	1.26	.212				
	Brooding Rumination	-5.95	-24.05, 12.14	-0.10	-0.66	.514				
	Reflective Rumination	7.42	-10.79, 25.63	0.12	0.81	.419				
Affective Switch Cost (Negative Valence)										
Step 1	Age	-1.22	-5.10, 2.66	-0.08	-0.63	.533	0.08	0.01	0.39	.533
Step 2	Age	-1.22	-5.13, 2.70	-0.07	-0.62	.538	0.08	0	0.20	.824
	Negativity Bias	0.06	-2.82, 2.95	0.01	0.04	.966				
Step 3	Age	-0.10	-4.29, 4.09	-0.01	-0.05	.962	0.21	0.04	0.76	.555
	Negativity Bias	0.28	-2.65, 3.20	0.02	0.19	.850				
	Brooding Rumination	16.36	-3.71, 36.43	0.24	1.63	.108				
	Reflective Rumination	-8.27	-28.46, 11.94	-0.12	-0.82	.417				
Non-Affective Switch Cost (Positive Valence)										
Step 1	Age	2.08	-1.12, 5.29	0.15	1.30	.200	0.02	0.02	1.68	.200
Step 2	Age	2.15	-1.08, 5.37	0.16	1.33	.188	0.03	0.01	1.14	.324
	Negativity Bias	0.94	-1.44, 3.31	0.09	0.79	.434				
Step 3	Age	2.12	-1.39, 5.64	0.16	1.21	.232	0.03	0	0.56	.695
	Negativity Bias	0.95	-1.50, 3.41	0.10	0.77	.442				
	Brooding Rumination	-0.03	-16.87, 16.82	0	-0	.997				
	Reflective Rumination	-0.49	-17.44, 16.47	-0.01	-0.06	.954				
Affective Switch Cost (Positive Valence)										
Step 1	Age	-0.29	-3.76, 3.19	-0.02	-0.17	.869	0	0	0.03	.869
Step 2	Age	-0.16	-3.60, 3.29	-0.01	-0.09	.928	0.03	0.03	1.18	.314
	Negativity Bias	1.94	-0.60, 4.48	0.18	1.53	.132				
Step 3	Age	-0.40	-4.14, 3.33	-0.03	-0.22	.830	0.05	0.01	0.83	.511
	Negativity Bias	2.17	-0.44, 4.78	0.20	1.66	.101				
	Brooding Rumination	0.98	-16.92, 18.88	0.02	0.11	.913				
	Reflective Rumination	-8.20	-26.22, 9.81	-0.13	-0.91	.367				

4.3.4 Study 1 Discussion

The main aim of Study 1 was to examine the extent to which affect bias and facets of trait rumination could predict key valence and rule switch costs on an affective switching task in an online sample. In relation to main effects of valence, RTs were generally of a longer duration on trials in which the valence of the image switched versus a repetition of valence, however, the only switch costs surviving correction for multiple comparisons were positive valence (non-affective) and negative valence (affective). Interestingly, there was also an exception to the latter valence switch cost, in which the average RT for trials in which the image switched from a positive to a negative valence was faster in comparison to the average RT when negative images repeated. This suggests that individuals were generally quicker to disengage from

images of a positive valence in order to orient attention towards images of a negative valence when the trial rule instructed focus on emotional aspects of the images. All rule switch costs indicated a higher overall RT on switch versus repeat trials, with non-affective negative rule switch costs being the only switch cost to not survive correction for multiple comparisons. Critically, in relation to our hypotheses, neither brooding or reflective facets of self-reported trait rumination, nor negative valence bias, were found to predict key affective flexibility switch costs of interest based on shifts in either valence or rule. These findings do not provide supporting evidence for the current study hypotheses, in which a higher negativity bias was predicted to be positively associated with greater switch costs when shifting attention from negative towards positive valence images (especially in an affective context). Critically, the lack of associations between trait rumination and rule-based switch costs do not replicate prior findings, in which higher rumination use has been linked to lower flexibility when shifting attention from affective towards non-affective aspects of negative information and greater flexibility for attentional shifts from affective towards non-affective aspects of positive emotional material (Genet et al., 2013).

While valence bias and trait rumination are important and reliable measures of emotional disposition, neither of these metrics capture physiological underpinnings of flexibility. Responses to emotional cues and stressors not only generate a cascade of changes at a subjective, cognitive, psychological level (i.e., emotional states, appraisals) but also at a physiological level (i.e., elevated or reduced heart rate) (Urry & Gross, 2010). Effective communication between the brain and body is critical for facilitating emotion flexibility. HRV is a biological, non-invasive measure of adaptive emotional responding (Appelhans & Luecken, 2006) that has previously been linked to affective flexibility (Grol & De Raedt, 2020) and has also been regarded as a biomarker of mental illness (Beauchaine & Thayer, 2015). Prior research has examined associations between resting HRV (Grol & De Raedt, 2020) and phasic HRV changes in response to a stressor (Grol & De Raedt, 2021) in relation to affective flexibility rule switch costs, however, less is known about potential links between HRV and attentional shifts dependent on valence.

4.4 Study 2

4.4.1 Aims and Hypotheses

Akin to the primary aims of Study 1, Study 2 examined individual differences in trait affect (trait rumination and valence bias) in relation to affective flexibility, but in a more controlled laboratory environment and with the addition of HRV, a non-invasive, biological marker of adaptive emotional responding and mental health (Appelhans & Luecken, 2006; Beauchaine & Thayer, 2015). Critically, this second study in the laboratory sought to examine individual differences in both resting and task-related HRV measures in relation to valence and rule switch costs on the affective flexibility task. It was hypothesised that individuals with higher resting and task-based HRV would exhibit reduced switch costs in their RT (higher flexibility) when shifting their attention from emotional images with a negative valence towards those with a positive valence (i.e., more efficient attentional disengagement from negative information). In a similar vein, it was also predicted that individuals with higher HRV may exhibit greater switch costs (lower flexibility) when switching attention from images with a positive valence towards those with a negative valence (e.g., more likely to have their attention held by positive emotional information). Furthermore, on the basis that HRV has previously demonstrated closer associations with positivity biases (Madison et al., 2021; Osnes et al., 2023), this second study focused on trait-like positivity (relative to negativity) biases. It was hypothesised that there would be an association between resting and task-related measures of HRV and trait-like valence bias, such that individuals with elevated levels of resting and task-based HRV would demonstrate a greater positivity bias in the face of emotionally ambiguous information. The measure of valence bias captured using the valence bias task is operationalised as the proportion of positive versus negative ratings towards emotionally ambiguous stimuli. On this basis, the positivity bias metric is the inverse of the negativity bias metric and vice versa. Therefore, in relation to affective flexibility, the same hypotheses were made as in study 1, but in the inverse direction. On this basis, it was predicted that a higher positivity bias would be associated with lower switch costs (greater flexibility) when shifting attention away from images with a negative valence towards those with a positive valence, particularly in an affective rule context. Furthermore, for attentional shifts based on rule type, a secondary prediction was that a greater positivity bias would be correlated with lower switch costs when shifting attention from affective towards non-affective aspects of negative information. Finally, it was hypothesised that

individuals with higher trait rumination, particularly elevated brooding rumination, would exhibit greater switch costs when the valence of the image switched from negative to positive, especially in an affective rule context. In line with prior research (Genet et al., 2013), it was anticipated that individuals with higher trait rumination, particularly higher brooding rumination, would exhibit greater switch costs (i.e., lower flexibility) when shifting attention from affective towards non-affective aspects of negative information, and lower switch costs (i.e., greater flexibility) when shifting attention from affective towards non-affective aspects of positive information.

4.4.2 Method

4.4.2.1 Participants

A total of 87 participants were recruited using convenience sampling[10]. Participants were excluded due to data loss relating to technical issues (n = 2), poor quality or noisy pulse signal (n = 8), pressing inaccurate keys during the valence bias task (n = 2), and missing more than 50% of trials on the affective flexibility task (n = 2). The final sample comprised 73 participants (*M* age = 21.78 years, SD = 5.40, range = 18-48 years; sex at birth: 60 female, 13 male; gender identity: 59 female, 13 male, 1 non-binary; ethnicity: 33 White, 21 Asian, 11 Multi-ethnic, 5 Black/African/Caribbean, 3 not specified; nationality: 57 European, 12 Asian, 1 African, 3 Dual-nationality; handedness: 65 right-handed, 8 left-handed). Most participants in the sample were Psychology students recruited from the university SONA recruitment system in exchange for course credits. A few participants were volunteers recruited by word of mouth with no form of compensation. All participants provided written informed consent prior to participation. This research study was carried out in accordance with the Declaration of Helsinki (1991, p. 1194). This study was given a favourable ethical opinion of conduct by the University of Reading's Research Ethics Committee (reference: 2023-178-CvR).

[10] An a-priori power analysis for a hierarchical multiple linear regression based on R2 increase with 3 predictors (rest and task-based HRV, and positivity bias, with 5 predictors in total) assuming a medium effect size (f2 = 0.15) and power of 0.80, indicated a necessary sample size of 77 participants. Accounting for 10% attrition, we aimed to recruit 85 participants. The effect size was determined based on a similar design and power analyses carried out by Grol and De Raedt (2018) and Twivy et al. (2021). Power analyses were calculated using G*Power (v3.1).

4.4.2.2 Materials and Procedure

Methods employed in this study were similar to Study 1 with a few changes to accommodate the laboratory setting. Both the valence bias and affective flexibility tasks were built and presented with E-Prime version 3.0 software (Psychology Software Tools, Inc., Sharpsburg, Pennsylvania, USA). Due to the finger pulse sensor attached to the index finger of the participant's non-dominant hand to record cardiac signals, different letter keys were assigned as response buttons for both tasks. Specifically, 'A' (right) and 'L' (left) keys were switched to 'B' (right) and 'M' (left) keys to accommodate a one-handed response. Furthermore, given potential ambiguity in relation to valence and/or number of humans present in some of the IAPS images presented in the AF task, 6 practice pictures and 17 main trial pictures were changed in the laboratory version of this task (see Table S9 in the Supplementary Material for further details). As in Study 1, selected main trial images were balanced in terms of normative ratings for arousal, such that there was no significant difference in self-reported arousal for negative (M = 5.24, SD = 0.78) compared to positive (M = 5.19, SD = 0.69) IAPS images ($t(158) = 0.41$, $p = .685$)). An optional mood recovery period was also offered in this study which involved watching a compilation of funny, viral internet videos of cats and dogs. Videos of this nature have previously been found to elicit both amusement and happiness in adults (Gilman et al., 2017). A few different questionnaires were also assessed in this study but are not reported here.

4.4.2.2.1 Trait Rumination

Trait rumination was assessed using the Ruminative Response Scale Short-Form (RRS; Treynor et al., 2003). Internal consistency for the whole scale (Cronbach's α = 0.77) and brooding (α = 0.66) and reflection (α = 0.71) subscales was acceptable or good in the current study.

4.4.2.2.2 Procedure

Informed consent was obtained at the start of the experiment prior to participation. Participants completed a few initial questionnaires regarding demographic information (age, sex at birth, gender identity, ethnicity, nationality, education, handedness, physical and mental health conditions and medication), their general mood, and symptoms of anxiety and depression. Subsequently, participants

completed an 8-minute resting baseline period where they watched a video of nature scenes and were instructed to breathe naturally and to stay as still as possible with both of their feet on the ground and the palms of their hands facing upwards. A finger pulse sensor was secured to the participant's index finger with a Velcro band to record a resting baseline of the heart rate period. Participants then completed a few more questionnaires regarding their emotional flexibility and ruminative thoughts prior to the emotion tasks. All participants completed the valence bias task followed by the affective flexibility task. Following completion of the tasks, participants were given the opportunity to engage in an optional mood recovery period, of which 30.10% of participants in the included sample chose to engage with this. Finally, participants completed a final questionnaire to assess their current mood and were debriefed on the purpose of the research study. The study took approximately 1 hour and 15 minutes to complete (not including the 5–10-minute recovery period).

4.4.2.3 Data Processing and Preliminary Data Analysis

4.4.2.3.1 HRV Processing and Analysis

A pulse signal was recorded using a finger pulse oximeter secured with a velcro band to the index finger of the participant's non-dominant hand via the PowerLab 26T data acquisition system (AD Instruments, Oxford, UK) connected to a Dell computer running LabChart (version 8; AD Instruments, Oxford, UK) software (sampling rate = 1000 Hz). The pulse trace was measured continuously throughout a resting baseline period, during a short break in which participants completed a few questionnaires prior to the emotion tasks (not signal of interest), and during both emotion tasks. LabChart files containing the time (seconds), pulse trace, and events were exported to text files and imported into Kubios HRV Premium Software (version 3.5.0; Biosignal Analysis and Medical Imaging Group, University of Kuopio, Finland; Tarvainen et al., 2014) for further processing and HRV analysis.

Separate samples of the pulse signal from the resting baseline period, valence bias, and affective flexibility tasks were processed and analysed for each participant. Kubios' PPG setting was selected whereby the pulse peak detection feature applies beat markers to the pulse waveform via a matched filtering approach. In cases where the beat detection feature misplaced or missed beats, manual corrections were applied to either place or (re)move markers to the appropriate location on the pulse waveform. The automatic correction noise feature (alongside manual correction) was

primarily used across subjects to reduce the influence of noise and artefacts in the signal, including ectopic, extra or missed beats, arrhythmias, motion, and technical noise/interference. In the instance where automatic correction did not adequately adjust for noise or was too stringent (i.e., unnecessary interpolation of beats), threshold and/or manual correction was implemented. Considering recent evidence recommending the application of less stringent settings for correcting noise in cardiac traces, especially in younger adult populations, and to preserve as much natural variation in the signal as possible, threshold correction settings between 'very low' - 'medium (0.45 - 0.25 seconds) were typically selected in accordance with the severity of the artefacts observed in the participant's data (Alcantara et al., 2020). Furthermore, where automatic noise detection identified noise epochs within the signal and these could not be corrected using manual or automatic/threshold correction settings, then the longest, continuous duration of clear pulse signal either preceding or following the noise epoch(s) was retained for analysis. In line with Kubios guidelines, pulse signals requiring 5% or more of the beats to be interpolated, alongside those with poor quality pulse signal that could not be adequately corrected, were excluded from further analysis (n = 8 participants). Several metrics, including the Root Mean Square of Successive Differences (RMSSD), measured in milliseconds, were calculated within Kubios. We opted to use the RMSSD as our main HRV variable given that it is a robust measure of parasympathetic vagal control that is less influenced by physiological noise, such as respiration (Hill et al., 2009; Kleiger et al., 2005) The RMSSD was natural log transformed (ln) to correct for positive skew within RStudio (version 1.4.1106) using the '*log'* command from the *base* package (v3.5.2).

4.4.2.3.2 Valence Bias

Missing/timed-out trials (n = 65) and trials with a RT less than 250 ms (n = 2) were removed prior to analysis. Trials with a RT greater than three standard deviations from the participants' mean RT per trial category (i.e., positive clear valence, negative clear valence, and ambiguous valence) were also calculated and removed (n = 17). Following initial task processing, accuracy of responses to the clearly valenced stimuli (i.e., trials with angry and happy face stimuli) was assessed. Participants with an accuracy falling below 50% on either positive or negative clear valence trials were excluded (n = 2 participants excluded due to 0% accuracy as a result of mixing up button responses). All participants in the final sample (N = 73) had an overall clear

valence accuracy over 60% which aligns with accuracy cut-offs adopted in prior studies (Harp et al., 2021; Neta et al., 2013; Petro et al., 2018).

4.4.2.3.3 Affective Flexibility

Practice trials (n = 20) and the first trial from each block (n = 2) were removed prior to processing and analysis (total n = 318 main trials). Subsequently, trials that were missing/timed out (n = 113) or with RTs below 250 ms (n = 8) were also removed. Importantly, only trials that were preceded by a correct response on the previous trial were included in analyses. The reasons for doing so aligned with previous studies (Grol & De Raedt, 2020), such that an incorrect response on a previous trial is likely to cause post-error slowing and, from the participant's point of view, may lead to ambiguity regarding whether the current trial is a repetition or switch. Two participants were excluded for losing over 50% of their trials on the affective flexibility task. The average percentage of trials lost in the final sample (N = 73) was 14.16% (SD = 10.21, range = 2.5%-48.74%), with an average of 272.99 (SD = 32.47, range = 163-310) main trials retained for analyses. Furthermore, also in line with previous studies (Genet et al., 2013; Grol & De Raedt, 2020; Malooly et al., 2013; Twivy et al., 2021), RTs that were 2.5 standard deviations above or below the mean RT within each participant and the specific trial condition were identified and replaced with the upper and lower cutoff values respectively (*M* trials = 6.53, SD = 2.69, range = 0-12).

Non-parametric Wilcoxon signed-rank tests were employed (due to non-normal distribution) across global switch and repetition trials for valence and rule category. Slightly higher accuracy was observed for trials where valence repeated (*M* = 93.40%, SD = 5.35) in comparison to when valence switched (*M* = 92.46%, SD = 5.64), Z = -2.27, p = .023. Moreover, accuracy was significantly higher for trials where the category rule repeated (*M* = 93.91%, SD = 4.84) in comparison to trials where the rule switched (*M* = 91.84%, SD = 6.39), Z = -4.84, p < .001. For valence, RTs were significantly longer in duration when the valence switched (*M* = 1407.25, SD = 283.01) compared to when valence repeated across trials (*M* = 1356.12, SD = 269.90), Z = -5.42, p < .001. However, RTs were slightly and unexpectedly slower for repetition (*M* = 1497.59, SD = 303.36) versus switch (*M* = 1452.98, SD = 290.93) trials) rule category trials, Z = -3.96, p < .001. Therefore, while participants had greater accuracy on trials where the valence or rule category switched, the RT when the trial rule category switched was significantly, albeit slightly, shorter in duration compared to a

repetition of the rule category. This is not in line with prior studies that typically report the opposite pattern (Grol & De Raedt, 2020; Twivy et al., 2021), but does however replicate the same pattern of findings observed in Study 1. While we cannot rule out potential speed-accuracy trade-off from influencing switch costs pertaining to shifts in category rule, the overall global difference in RT is fairly small.

4.4.2.3.4 Regression Models

Multiple hierarchical regression analyses assessed whether resting and task-related HRV, trait-like positivity bias, and brooding and reflective facets of self-reported trait rumination predicted key affective flexibility switch costs based on a shift in valence and in rule. Given the greater risk of multicollinearity with three separate HRV measures recorded across three contexts: rest, valence bias, and affective flexibility, the two emotion task HRV variables were aggregated to form a single 'task-based' HRV variable based on the average of the two task measures (for a discussion on aggregating HRV measures, see: Bertsch et al., 2012). The following predictors were entered into the model in a stepwise order: age (years; step 1), resting and task-based HRV (step 2), positivity bias (step 3), and brooding and reflective rumination (step 4). All predictors were mean centered. Standardised beta coefficients are reported in the Results. Bonferroni corrections were performed to account for multiple tests (p = 0.00625 (0.05/8)).

4.4.3 Results

4.4.3.1 Descriptive Statistics

Table 8 summarises descriptives for resting and task-based HRV, rest and task-based heart rate, rest and task-based RR interval, positivity bias, trait rumination, and key valence and rule switch costs of interest from the affective flexibility task.

Table 8.
Descriptive Statistics for Key Sample Characteristics (Study 2). Data is provided in means and standard deviations (in parenthesis).

	Data (N = 73)
Resting lnRMSSD (ms)	3.41 (0.64)
Resting HR (BPM)	82.30 (10.47)
Resting RR Interval (ms)	741.22 (97.84)
Task-based lnRMSSD (ms)	3.53 (0.61)
Task-based HR (BPM)	80.48 (9.25)
Task-based RR Interval (ms)	755.99 (90.01)
Positivity Bias (%)	29.87 (19.61)
Brooding Rumination[a]	12.04 (3.03)
Reflective Rumination[a]	11.64 (3.44)
Total Rumination[b]	23.68 (5.52)
Accuracy Global Valence Repeat (%)	93.40 (5.35)
Accuracy Global Valence Switch (%)	92.46 (5.64)
Accuracy Global Rule Repeat (%)	93.91 (4.84)
Accuracy Global Rule Switch (%)	91.84 (6.39)
RT Global Valence Repeat (ms)	1356.12 (269.90)
RT Global Valence Switch (ms)	1407.25 (283.01)
RT Global Rule Repeat (ms)	1497.59 (303.36)
RT Global Rule Switch (ms)	1452.98 (290.93)
Positive Valence Switch Cost (Non-Affective Context; ms)	168.04 (220.92)
Positive Valence Switch Cost (Affective Context; ms)	78.51 (197.60)
Negative Valence Switch Cost (Non-Affective Context; ms)	30.14 (180.90)
Negative Valence Switch Cost (Affective Context; ms)	-54.19 (196.53)
Non-Affective Switch Cost (Negative Valence; ms)	22.27 (195.59)
Affective Switch Cost (Negative Valence; ms)	244.45 (233.49)
Non-Affective Switch Cost (Positive Valence; ms)	205.55 (208.21)
Affective Switch Cost (Positive Valence; ms)	116.00 (243.19)

[a] Score range for RRS brooding and reflective rumination subscales = 5-20 ; [b] Score range for RRS total rumination scale = 10-40

4.4.3.2 HRV and Positivity Bias

Pearson correlations revealed that while there was a strong positive correlation between rest and task-related measures of HRV (r = .92, p < .001), there was no significant association between either rest (r = -.04, p = .717) or task-related (r = -.015, p = .897) HRV and trait-like positivity bias.

4.4.3.3 Affective Flexibility Switch Costs: Valence

In general, the average RT on trials where the valence of the image switched was slightly slower in comparison to trials where the valence of the image repeated. However, as observed in Study 1, the exception to this general pattern was found in the conditions contributing to the negative valence affective switch cost, in which the average RT for when negative images repeated was slower (M = 1232.52, SD = 329.45) in comparison to trials in which the image switched from a positive to a negative valence (M = 1178.33, SD = 254.48) when the affective rule repeated across trials, although this difference in RT does not survive correction for multiple comparisons ($t(72) = -2.36$, $p = .021$). The only switch cost surviving correction for multiple comparisons was the positive valence non-affective switch cost. Pairwise comparisons between main switch and repeat trial conditions used for the calculation of key valence switch costs with associated uncorrected p-values are presented in Table S7 in the Supplementary Material. See Figures 12a-d for mean RTs per repeat and switch condition used to calculate switch costs based on valence.

4.4.3.4 Affective Flexibility Switch Costs: Rule

The average RT on trials where the trial rule switched was consistently slower than when the trial rule repeated for all of the main rule switch costs of interest. Again, akin to the main effect observed in Study 1, the only switch cost not surviving correction for multiple comparisons was the non-affective rule negative switch cost ($t(72) = 0.97$, $p = .334$. Pairwise comparisons between main switch and repeat trial conditions used for the calculation of key rule switch costs with associated uncorrected p-values are presented in Table S7 in the Supplementary Material. See Figures 12e-h for mean RTs per repeat and switch condition used to calculate switch costs based on valence.

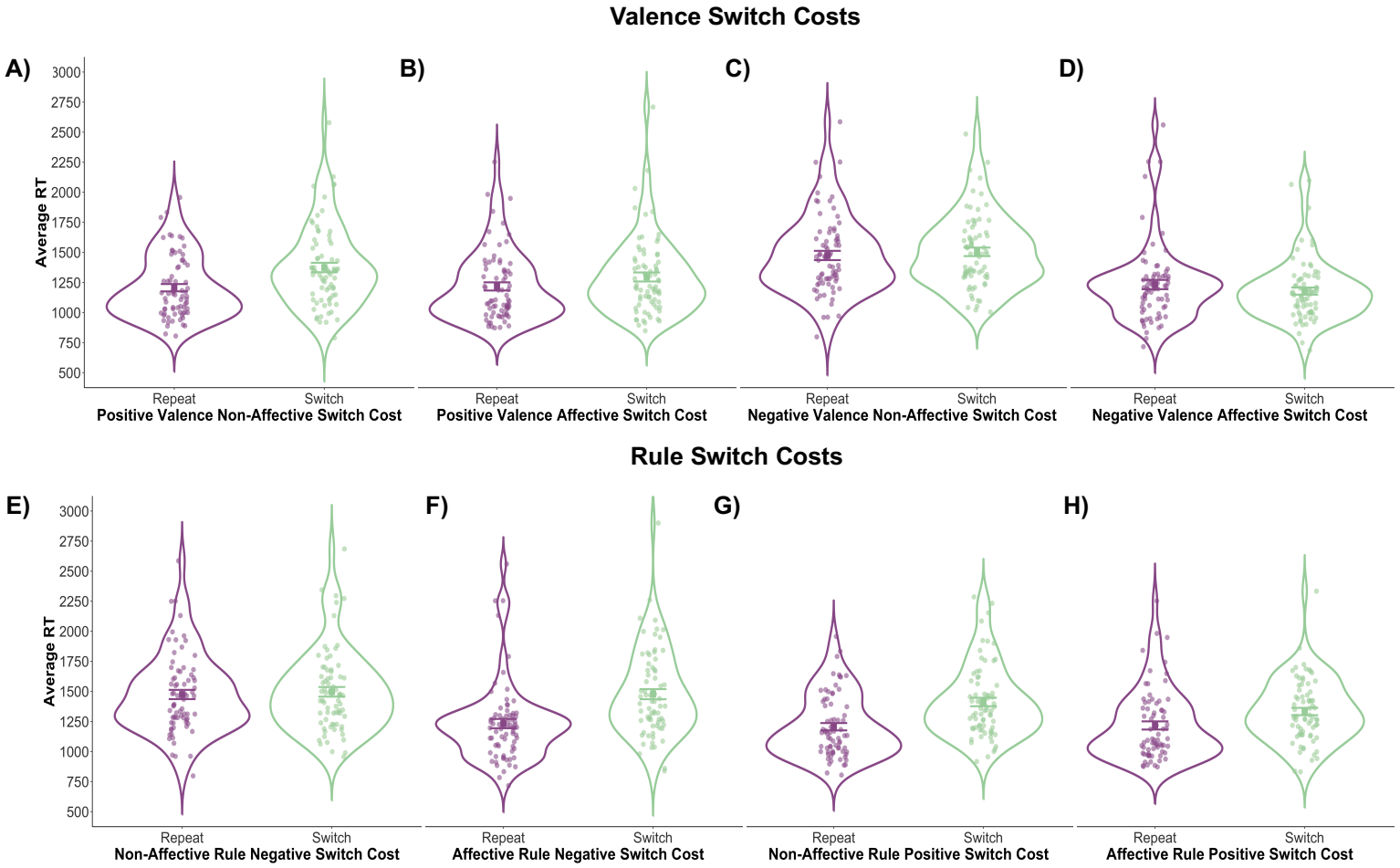

Figure 12. Mean Reaction Times for Key Valence and Rule Repeat Versus Switch Conditions (Study 2). **A)** Mean RT for trials where there was a repetition of a positive valence image on consecutive trials (repeat) and trials where there was a switch from a negative valence to a positive valence picture (switch) when the trial rule was non-affective. **B)** Mean RT for trials where there was a repetition of a positive valence image on consecutive trials (repeat) and trials where there was a switch from a negative valence to a positive valence picture (switch) when the trial rule was affective. **C)** Mean RT for trials where there was a repetition of a negative valence image on consecutive trials (repeat) and trials where there was a switch from a positive valence to a negative valence picture (switch) when the trial rule was non-affective. **D)** Mean RT for trials where there was a repetition of a negative valence image on consecutive trials (repeat) and trials where there was a switch from a positive valence to a negative valence image (switch) when the trial rule was affective. **E)** Mean RT for trials where there was a repetition of a non-affective rule (repeat) and trials where there was a switch from an affective rule to a non-affective rule (switch) with images of a negative valence. **F)** Mean RT for trials where there was a repetition of an affective rule (repeat) and trials where there was a switch from a non-affective to an affective rule (switch) with images of a negative valence. **G)** Mean RT for trials where there was a repetition of a non-affective rule (repeat) and trials where there was a switch from an affective rule to a non-affective rule (switch) with images of a positive valence. **H)** Mean RT for trials where there was a repetition of an affective rule (repeat) and trials where there was a switch from a non-affective to an affective rule (switch) with images of a positive valence. Error bars reflect ± 1 standard error around the mean.

4.4.3.5 Affective Flexibility Valence Switch Cost Regression Analyses

Table 9 summarises the hierarchical regression analyses for age, HRV, and positivity bias on affective flexibility performance for switch costs based on valence. Key predictors of interest (resting and task-related HRV, positivity bias, and brooding and reflective rumination) were not found to significantly predict positive valence switch costs in the presence of an affective rule nor negative valence switch costs in the presence of a non-affective rule. While the overall model was not significant (R^2 = 0.06, F(3, 72) = 1.48, p = .228 Model 2), task-related HRV was found to predict unique variance in positive valence switch costs in a non-affective context (β = 0.64, t = 2.07, p = .042 Model 2), in which individuals with higher task-based HRV were slower to switch from negative to positive valence images when the instruction was non-affective. This finding was specific to task-related HRV and not found for resting HRV (β = -0.57, t = -1.86, p = .068 Model 2). Task-related HRV remained the only predictor of positive valence switch costs when positivity bias (β = -0.02, t = -0.19, p = .852 Model 3) and brooding (β = 0.21, t = 1.60, p = .115 Model 4) and reflective rumination (β = -0.02, t = -0.18, p = .859 Model 4) facets were added as predictors, albeit this did not survive correction for multiple comparisons. Given insignificance of the overall model and the high multicollinearity between the HRV predictors (with resting HRV in the opposite direction), this finding is likely spurious and should be interpreted with caution. With relation to negative valence switch costs in the presence of an affective rule, entering rest and task-based HRV into the model significantly contributed to the overall variance explained (R^2 = 0.12, F(3, 72) = 3.03, p = .035 Model 2). Specifically, albeit not surviving correction for multiple comparisons, resting HRV predicted negative valence switch costs in an affective context, with higher resting HRV associated with slower switching from positive towards negative valence images in the presence of an affective rule instruction (β = 0.65, t = 2.17, p = .033 Model 2) but task-related HRV did not (β = -0.48, t = -1.60, p = .115). The inclusion of positivity bias resulted in the overall model becoming insignificant and therefore did not contribute a significant change in the variance explained (R^2 = 0.12, F(4, 72) = 2.34, p = .063 Model 3). Positivity bias was not a significant predictor of negative valence switch costs in the presence of an affective rule (β = -0.07, t = -0.60, p = .548 Model 3). Resting HRV remained the only significant predictor (β = 0.63, t = 2.12, p = .038 Model 3). Finally, while resting HRV remained a predictor (β = 0.65, t = 2.12, p = .038 Model 4), neither brooding (β = -0.10, t = -0.77, p = .445 Model 4) or reflective (β = 0.07, t = 0.49, p = .624 Model 4) rumination

significantly predicted negative valence switch costs in the presence of an affective rule instruction, and thus did not significantly contribute to a change in the variance explained (R^2 = 0.13, F(6, 72) = 1.63, p = .152 Model 4). See Figure 13 for a visual depiction of these findings.

Table 9.
Hierarchical Regression Analyses for Age, HRV, Positivity Bias, and Trait Rumination on Affective Flexibility Valence Switch Costs (Study 2)

Model	Predictor	*b*	95% CI	*β*	*t*	*p*	R^2	R^2 Change	*F*	*p*
Positive Valence Switch Cost (Non-Affective Context)										
Step 1	Age	1.58	-8.10, 11.26	0.04	0.33	.745	0	0	0.11	.745
Step 2	Age	3.33	-6.45, 13.10	0.08	0.68	.499	0.06	0.06	1.48	.228
	Resting HRV	-195.45	-405.38, 14.48	-0.57	-1.86	.068				
	Task-based HRV	231.87	8.79, 454.95	0.64	2.07	.042				
Step 3	Age	3.22	-6.69, 13.13	0.08	0.65	.519	0.06	0	1.10	.363
	Resting HRV	-196.76	-408.68, 15.17	-0.57	-1.85	.068				
	Task-based HRV	232.82	7.87, 457.76	0.64	2.07	.043				
	Positivity Bias	-0.25	-2.92, 2.42	-0.02	-0.19	.852				
Step 4	Age	1.87	-8.11, 11.85	0.05	0.37	.709	0.10	0.04	1.23	.300
	Resting HRV	-192.12	-406.45, 22.22	-0.56	-1.79	.078				
	Task-based HRV	230.44	4.86, 456.02	0.64	2.04	.045				
	Positivity Bias	-0.11	-2.78, 2.56	-0.01	-0.08	.935				
	Brooding Rumination	15.60	-3.87, 35.07	0.21	1.60	.115				
	Reflective Rumination	-1.55	-18.85, 15.75	-0.02	-0.18	.859				
Positive Valence Switch Cost (Affective Context)										
Step 1	Age	0.84	-7.83, 9.50	0.02	0.19	.848	0	0	0.04	.848
Step 2	Age	-1.60	-10.14, 6.94	-0.04	-0.37	.710	0.10	0.10	2.66	.055
	Resting HRV	-2.71	-186.10, 180.64	-0.01	-0.03	.977				
	Task-based HRV	-103.39	-298.27, 91.49	-0.32	-1.06	.294				
Step 3	Age	-1.66	-10.32, 7.01	-0.05	-0.38	.704	0.10	0	1.97	.109
	Resting HRV	-3.42	-188.58, 181.75	-0.01	-0.04	.971				
	Task-based HRV	-102.88	-299.42, 93.66	-0.32	-1.05	.300				
	Positivity Bias	-0.14	-2.47, 2.20	-0.01	-0.12	.908				
Step 4	Age	-1.26	-10.13, 7.62	-0.03	-0.28	.778	0.11	0.01	1.37	.239
	Resting HRV	-14.29	-204.93, 176.36	-0.05	-0.15	.882				
	Task-based HRV	-94.83	-295.48, 105.81	-0.29	-0.94	.349				
	Positivity Bias	-0.12	-2.49, 2.26	-0.01	-0.10	.923				
	Brooding Rumination	-1.99	-19.31, 15.33	-0.03	-0.23	.819				
	Reflective Rumination	-3.88	-19.27, 11.50	-0.07	-0.50	.616				
Negative Valence Switch Cost (Non-Affective Context)										
Step 1	Age	-7.77	-15.49, -0.05	-0.23	-2.01	.049	0.05	0.05	4.03	.049
Step 2	Age	-8.59	-16.57, -0.61	-0.26	-2.15	.035	0.07	0.01	1.61	.195
	Resting HRV	37.94	-133.50, 209.39	0.14	0.44	.660				
	Task-based HRV	-65.93	-248.11, 116.26	-0.22	-0.72	.473				
Step 3	Age	-8.62	-16.71, -0.52	-0.26	-2.12	.037	0.07	0	1.19	.323
	Resting HRV	37.62	-135.50, 210.73	0.13	0.43	.666				
	Task-based HRV	-65.69	-249.44, 118.06	-0.22	-0.71	.478				
	Positivity Bias	-0.06	-2.24, 2.12	-0.01	-0.06	.954				

Step 4	Age	-8.90	-17.22, -0.59	-0.27	-2.14	.036	0.07	0	0.82	.560
	Resting HRV	44.58	-133.99, 223.15	0.16	0.50	.620				
	Task-based HRV	-70.82	-258.76, 117.12	-0.24	-0.75	.455				
	Positivity Bias	-0.07	-2.29, 2.15	-0.01	-0.07	.948				
	Brooding Rumination	1.65	-14.57, 17.87	0.03	0.20	.840				
	Reflective Rumination	2.41	-12.00, 16.82	0.05	0.33	.740				
Negative Valence Switch Cost (Affective Context)										
Step 1	Age	-7.42	-15.86, 1.02	-0.20	-1.75	.084	0.04	0.03	3.07	.084
Step 2	Age	-7.33	-15.77, 1.10	-0.20	-1.75	.087	0.12	0.08	3.03	.035
	Resting HRV	197.19	16.09, 378.29	0.65	2.17	.033				
	Task-based HRV	-153.84	-346.28, 38.61	-0.48	-1.60	.115				
Step 3	Age	-7.63	-16.17, 0.90	-0.21	-1.79	.079	0.12	0.01	2.34	.063
	Resting HRV	193.58	11.20, 375.95	0.63	2.12	.038				
	Task-based HRV	-151.20	-344.77, 42.39	-0.47	-1.56	.124				
	Positivity Bias	-0.70	-2.99, 1.60	-0.07	-0.60	.548				
Step 4	Age	-7.24	-15.97, 1.50	-0.20	-1.65	.103	0.13	0.01	1.63	.152
	Resting HRV	199.38	11.74, 387.01	0.65	2.12	.038				
	Task-based HRV	-156.03	-353.52, 41.45	0.49	-1.58	.119				
	Positivity Bias	-0.78	-3.12, 1.55	-0.08	-0.67	.505				
	Brooding Rumination	-6.57	-23.61, 10.48	-0.10	-0.77	.445				
	Reflective Rumination	3.73	-11.41, 18.87	0.07	0.49	.624				

4.4.3.6 Affective Flexibility Rule Switch Cost Regression Analyses

Table 10 shows the hierarchical regression analyses for age, HRV, positivity bias, and rumination on affective flexibility when considering switch costs based on the rule (affective versus non-affective) type. None of the overall models were significant and none of the key predictors of interest (age, resting and task-related HRV, positivity bias, and brooding and reflective trait rumination) were significantly associated with the key affective flexibility switch costs of interest based on trial rule instruction.

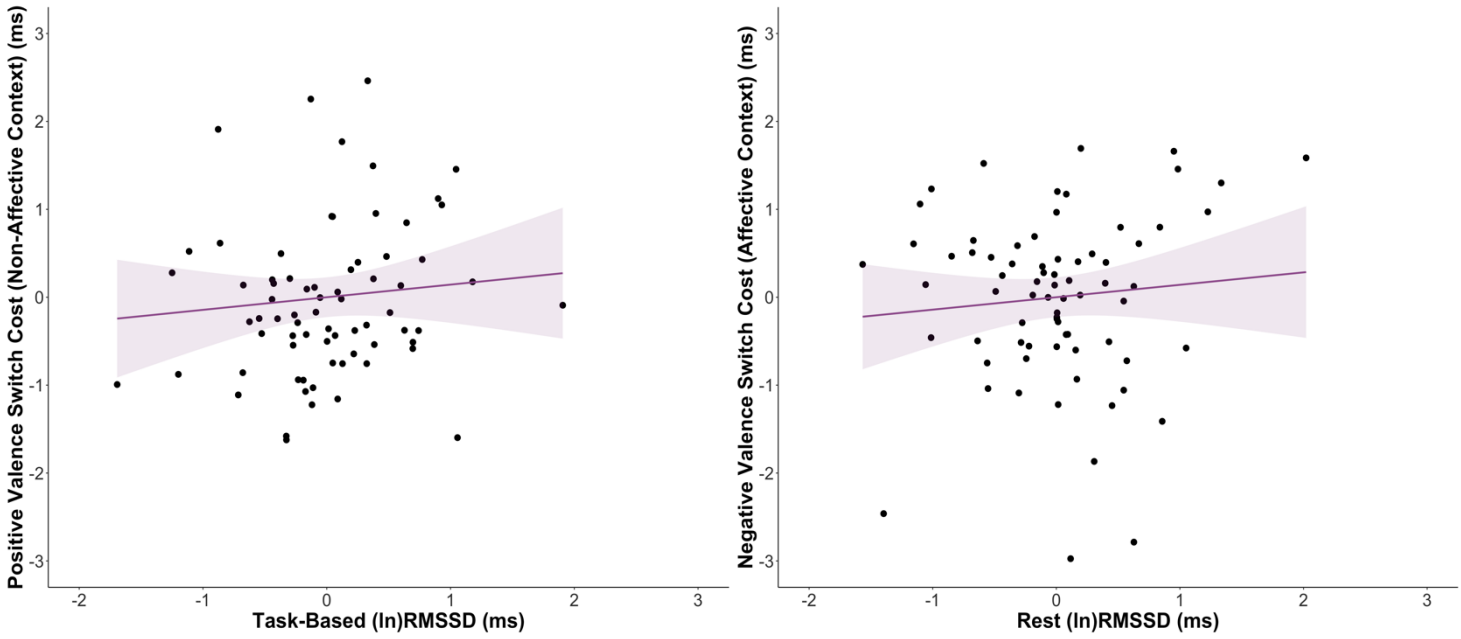

Figure 13. Scatterplots of Valence Switch Costs Demonstrating Associations with HRV. **A)** Scatterplot displaying task-based HRV and positive valence switch costs in a non-affective context where values have been adjusted for mean centred age, resting HRV, positivity bias, and brooding and reflective rumination scores (Model 4). **B)** Scatterplot displaying resting HRV and negative valence switch costs in an affective context where values have been adjusted for mean centered age, task-based HRV, positivity bias, and brooding and reflective rumination scores (Model 4). Standardised residuals are plotted for visual display purposes. *HRV*, *heart rate variability; (ln)RMSSD, natural log transformed root mean square of successive differences.*

Table 10.
Hierarchical Regression Analyses for Age, HRV, Positivity Bias, and Trait Rumination on Affective Flexibility Rule Switch Costs (Study 2)

Model	Predictor	*b*	95% CI	*β*	*t*	*p*	R^2	R^2 Change	*F*	*p*
Non-Affective Switch Cost (Negative Valence)										
Step 1	Age	-2.34	-10.89, 6.22	-0.06	-0.54	.588	0	0	0.30	.588
Step 2	Age	-1.64	-10.51, 7.23	-0.05	-0.37	.713	0.01	0.01	0.29	.835
	Resting HRV	-50.99	-241.53, 139.56	-0.17	-0.53	.595				
	Task-Based HRV	70.83	-131.65, 273.32	0.22	0.70	.488				
Step 3	Age	-1.94	-10.92, 7.04	-0.05	-0.43	.667	0.02	0.01	0.30	.880
	Resting HRV	-54.61	-246.55, 137.33	-0.18	-0.57	.572				
	Task-based HRV	73.48	-130.25, 277.21	0.23	0.72	.474				
	Positivity Bias	-0.70	-3.11, 1.72	-0.07	-0.58	.567				
Step 4	Age	-2.62	-11.78, 6.55	-0.07	-0.57	.571	0.03	0.02	0.37	.894
	Resting HRV	-57.48	-254.29, 139.34	-0.19	-0.58	.562				
	Task-based HRV	76.29	-130.85, 283.44	0.24	0.74	.465				
	Positivity Bias	-0.59	-3.04, 1.86	-0.06	-0.48	.630				
	Brooding Rumination	9.21	-8.67, 27.09	0.14	1.03	.307				
	Reflective Rumination	-3.14	-19.02, 12.75	-0.06	-0.40	.694				
Affective Switch Cost (Negative Valence)										
Step 1	Age	3.96	-6.24, 14.16	0.09	0.78	.441	0.01	0.01	0.60	.441
Step 2	Age	2.80	-7.69, 13.29	0.07	0.53	.596	0.03	0.02	0.75	.525

	Resting HRV	130.00	-95.24, 355.23	0.36	1.15	.254				
	Task-based HRV	-154.18	-393.52, 85.16	-0.40	-1.29	.203				
Step 3	Age	2.31	-8.28, 12.90	0.05	0.44	.665	0.04	0.01	0.72	.581
	Resting HRV	124.05	-102.32, 350.42	0.34	1.09	.278				
	Task-based HRV	-149.85	-390.12, 90.43	-0.39	-1.24	.218				
	Positivity Bias	-1.14	-3.99, 1.71	-0.10	-0.80	.427				
Step 4	Age	3.76	-6.91, 14.42	0.09	0.70	.485	0.08	0.04	0.96	.458
	Resting HRV	112.11	-116.98, 341.19	0.31	0.98	.332				
	Task-based HRV	-141.91	-383.02, 99.21	-0.37	-1.18	.244				
	Positivity Bias	-1.25	-4.10, 1.60	-0.11	-0.87	.385				
	Brooding Rumination	-14.81	-35.62, 6.00	-0.19	-1.42	.160				
	Reflective Rumination	-1.53	-20.01, 16.96	-0.02	-0.17	.870				
Non-Affective Switch Cost (Positive Valence)										
Step 1	Age	0.43	-4.74, 13.41	0.11	0.95	.344	0.01	0.01	0.91	.344
Step 2	Age	5.67	-3.65, 14.98	0.15	1.21	.229	0.04	0.03	0.95	.422
	Resting HRV	-3.38	-203.40, 196.64	-0.01	-0.03	.973				
	Task-based HRV	60.52	-152.03, 273.06	0.18	0.57	.572				
Step 3	Age	5.51	-3.94, 14.95	0.14	1.16	.249	0.04	0	0.72	.578
	Resting HRV	-5.31	-207.16, 196.54	-0.02	-0.05	.958				
	Task-based HRV	61.93	-152.32, 276.17	0.18	0.58	.566				
	Positivity Bias	-0.37	-2.91, 2.17	-0.04	-0.29	.772				
Step 4	Age	4.39	-5.17, 13.95	0.11	0.92	.363	0.07	0.03	0.84	.543
	Resting HRV	6.11	-199.22, 211.44	0.02	0.06	.953				
	Task-based HRV	54.10	-162.01, 270.20	0.16	0.50	.619				
	Positivity Bias	-0.30	-2.86, 2.25	-0.03	-0.24	.813				
	Brooding Rumination	10.86	-7.79, 29.52	0.16	1.16	.249				
	Reflective Rumination	2.18	-14.40, 18.75	0.04	0.26	.794				
Affective Switch Cost (Positive Valence)										
Step 1	Age	-0.94	-11.60, 9.72	-0.02	-0.18	.861	0	0	0.03	.861
Step 2	Age	-3.16	-13.86, 7.54	-0.07	0.59	.558	0.07	0.07	1.75	.166
	Resting HRV	-50.54	-280.38, 179.30	-0.13	-0.44	.662				
	Task-based HRV	-56.01	-300.25, 188.22	-0.14	-0.46	.649				
Step 3	Age	-2.62	-13.42, 8.18	-0.06	-0.49	.629	0.08	0.01	1.49	.216
	Resting HRV	-44.05	-274.87, 186.79	-0.12	-0.38	.705				
	Task-based HRV	-60.75	-305.77, 184.27	-0.15	-0.50	.622				
	Positivity Bias	1.25	-1.66, 4.15	0.10	0.86	.394				
Step 4	Age	-1.94	-12.97, 9.09	-0.04	-0.35	.727	0.09	0.01	0.13	.354
	Resting HRV	-61.66	-298.59, 175.28	-0.16	-0.52	.605				
	Task-based HRV	-47.75	-297.12, 201.62	-0.12	-0.38	.703				
	Positivity Bias	1.28	-1.67, 4.22	-0.10	-0.87	.390				
	Brooding Rumination	-3.71	-25.23, 17.82	-0.05	-0.34	.732				
	Reflective Rumination	-6.19	-25.31, 12.93	-0.09	-0.65	.520				

4.4.4 Study 2 Discussion

In accordance with our findings in Study 1, neither brooding or reflective facets of trait rumination or valence bias significantly predicted key affective flexibility switch costs pertaining to shifts in valence or rule type. Interestingly, while not surviving

correction for multiple comparisons, findings from Study 2 suggest that both task-related and resting HRV appear to be associated with affective flexibility, specifically attentional shifts pertaining to valence. Contrary to our hypothesis, higher task-related HRV was tentatively associated with greater switch costs (i.e., lower affective flexibility) when shifting attention from negative towards positive valence images when a non-affective rule instruction (number of humans present in the image) repeated across trials. However, this finding should be interpreted with caution given non-significance of the overall model and the risk of high multicollinearity between task-related and resting HRV producing spurious (and opposing) effects for these predictors. Nevertheless, some evidence, albeit not surviving correction for multiple comparisons, was found for our hypothesis concerning higher HRV being linked to greater attentional capture relating to positive emotional information, in which individuals with elevated resting HRV were demonstrated greater switch costs (i.e., lower affective flexibility) when shifting attention from positive to negative valence images when the affective task rule instruction repeated across trials (i.e., heightened focus on the emotional aspects of the image). Contrary to previous findings that have reported a link between lower resting HRV and more efficient switching (greater flexibility) from affective to non-affective aspects of negative emotional images (Grol & De Raedt, 2020), Study 2 did not uncover significant findings for either resting or task-related HRV metrics and affective flexibility switch costs pertaining to shifts in the affective or non-affective rule instruction. Findings from Study 2 also replicated main effects observed for the affective flexibility task in Study 1. Specifically, RTs were generally of a longer duration on trials in which the valence of the image switched in comparison to when the valence repeated, however, the only switch cost surviving correction for multiple comparisons was the positive valence non-affective switch cost. Furthermore, akin to Study 1, the only main effect diverging from this overall RT pattern was the negative valence affective switch cost, in which the average RT for trials where images switched from a positive to a negative valence was faster in comparison to the average RT when negative images repeated. This highlights that across two separate samples, individuals were generally quicker to disengage from positive valence images when the trial rule focused on emotional (affective) aspects of the images. All rule-related switch costs indicated a higher overall RT on switch versus repeat trials, although as observed in Study 1, non-affective negative rule switch costs did not survive correction for multiple comparisons.

Taken together, findings from Study 2 replicate the lack of associations between trait rumination and valence bias found in Study 1, and more critically, provide some indication that individual differences in HRV appear to be more closely coupled with attentional flexibility pertaining to shifts in valence. These findings contribute to, and complement, a wider research concept which outlines that affective (in)flexibility may not always be (mal)adaptive, with context (in this case valence) playing an important role (Parsons et al., 2016).

4.5 General Discussion

The present research sought to conceptually replicate and extend prior findings in the literature by examining associations between valence bias, facets of trait rumination, and HRV with performance on an established affective switching task in online (Study 1) and laboratory-based (Study 2) studies. While previous research employing the affective flexibility task paradigm has primarily focused on attentional shifts pertaining to changes in the trial rule (i.e., categorising images according to affective versus non-affective rules), which assesses cognitive flexibility in the context of emotion (i.e., the valence of the image), the present studies further examined attentional shifts relating to valence on trials where the trial rule was held constant, which, we argue, captures *affective* flexibility. Across both studies, neither brooding or reflective facets of trait rumination, nor trait-like negative or positive valence biases significantly predicted affective flexibility switch costs based on either shifts in valence or trial rule. In Study 2, while no associations emerged between resting and task-related HRV and trait-like positivity bias, HRV appeared to predict switch costs on the affective flexibility task that were specific to attentional shifts based on changes in valence, although these associations did not survive correction for multiple comparisons.

HRV is a psychophysiological phenomenon that is proposed to serve as an objective, non-invasive metric of adaptive emotional responding (Appelhans & Luecken, 2006) and is also considered to be a transdiagnostic biomarker of mental health (Beauchaine & Thayer, 2015). Higher levels of resting HRV have been found to facilitate flexible top-down and bottom-up attentional modulation (Park & Thayer, 2014), effective self and emotion regulation (Butler et al., 2006; Denson et al., 2011; Ingjaldsson et al., 2003), and positivity biases (Madison et al., 2021; Osnes et al., 2023). While most research has typically focused on assessing HRV at rest, other

studies have also assessed changes in phasic HRV, reporting increases in phasic HRV in the context of high self-regulatory effort or emotion regulation (Butler et al., 2006; Denson et al., 2011; Park et al., 2014). Furthermore, higher resting HRV is linked to greater phasic/task-related HRV (Guendelman et al., 2024; Park et al., 2014). Since higher resting HRV has previously been associated with biases towards positive information (Osnes et al., 2023), in the context of the affective flexibility task, it was expected that individuals with higher rest and task-related HRV would demonstrate greater affective flexibility in the form of more efficient switching from negative towards positive valence information, as well as higher *in*flexibility when shifting attention from images with a positive to a negative valence (e.g., greater attentional capture of positive emotional information).

Contrary to our first hypothesis, higher task-related HRV appeared to be linked to greater switch costs (i.e., lower flexibility) when shifting attention away from negative and towards positively valenced images. While this finding did not survive correction, is likely spurious and should be interpreted with caution, this would suggest that individuals with higher HRV during emotional contexts (across both the affective flexibility and valence bias tasks) were slower to disengage their attention from images of a negative valence when the non-affective rule (i.e., identifying the number of humans in the image) repeated across trials. This finding may be explained in the context of negative attentional avoidance, in which individuals with elevated task-related HRV appeared to spend a longer time on trials with negative valenced images when instructed to focus on the non-emotional aspects of the images, whereas those with lower task-related HRV were quicker to disengage and proceed to the next trial, possibly reflecting underlying attentional avoidance towards negative emotional information. Indeed, Grol & De Raedt (2020) reported that individuals with lower resting HRV exhibited greater affective flexibility in the form of faster attentional shifts towards non-affective aspects of negative pictures, a pattern that has also been linked to higher worry and anxiety over a 7-week period (Twivy et al., 2021). Moreover, during a decision-making task that involved the presentation of IAPS images, it was documented that individuals with reduced resting HRV demonstrated a tendency to avoid negative emotional pictures compared to those with higher HRV (Katahira et al., 2014). Collectively, these findings could be contextualised through the vigilance-avoidance model of anxiety (Mogg et al., 2004) and links between elevated anxiety and a higher tendency to avoid negative emotional information (Cisler & Koster, 2010).

The vigilance-avoidance model proposes that individuals with higher anxiety more quickly orient their attention to potentially threatening stimuli initially, but this is subsequently followed by later avoidance in comparison to those with lower anxiety (Mogg et al., 2004). Interestingly, the current finding emerged on trials in the context of the non-emotional rule. This would suggest that even when instructed to focus on non-emotional aspects of negative valence images, individuals with lower task-related HRV were quicker to disengage from these trials. It could be that individuals with lower task-based HRV found the negative IAPS images more aversive and were therefore motivated to respond more quickly, even when instructed to focus on non-affective elements. This explanation would somewhat align with research that has found individuals with lower HRV to exhibit an elevated autonomic stress response to relatively trivial threat cues under both low and high load cognitive conditions (Park et al., 2014). Nevertheless, without accompanying self-reported ratings of the images, it is difficult to confirm whether this was the case in the present research. Taken together, while the current finding potentially aligns with previous research linking low HRV to negative attentional avoidance, this finding is not likely to be robust (i.e., did not survive correction for multiple comparisons) and is likely spurious (i.e., given opposing strong directions of task-related versus resting HRV predictors), thus this warrants further replication and validation.

Moreover, individuals with higher resting HRV exhibited slower attentional shifts (i.e., lower affective flexibility) from positive towards negative valence images on trials where the affective (emotion) trial rule repeated, although this finding also did not survive correction for multiple comparisons. Individuals with higher resting HRV potentially had their attention held to a greater extent by the positive valence images, resulting in slower attentional disengagement when instructed to focus on emotional aspects of negative valence images. Interestingly, as a main effect, for trials in which the image switched from a positive to a negative valence image, RTs were slightly faster across the sample on average in comparison to when a negative affective valence image repeated, suggesting a slightly quicker engagement on trials where the image shifted from a positive to a negative valence. Considering this, it is interesting that this switch cost is greater (and in the expected direction) for those with higher HRV and reduced in those with lower HRV. This finding, albeit tentative, complements a small body of literature that has reported coupling between higher HRV and biased processing of positive emotional information (Madison et al., 2021; Osnes et al., 2023).

Indeed, higher resting HRV has been linked to positive appraisals of neutral and ambiguous vocal stimuli in women (Madison et al., 2021) and an increased tendency to interpret negatively valenced facial expressions more positively (Osnes et al., 2023). While the current finding may suggest individuals with higher resting HRV are slower, and those with lower resting HRV are quicker, to disengage from positive emotional images on the affective flexibility task, in Study 2, we found no supporting evidence for associations between either resting or task-related HRV and trait-like positivity bias in the current study. Unfortunately research examining HRV and valence bias is still fairly limited, with current and previous research relying on student populations and different measures of positivity bias (i.e., ambiguous auditory stimuli, Madison et al., 2021; RMET, Osnes et al., 2023). Thus, examining HRV, affective flexibility, and measures of trait affect that control for different stimulus modalities (i.e., visual, auditory) could be an interesting avenue for future research.

Finally, in both the online (Study 1) and laboratory-based (Study 2) studies, no associations were uncovered for either depressive or reflective trait rumination, nor for total rumination score, and key valence or rule switch costs on the affective switching task. Rumination is a form of perseverative cognition, characterised by negative, repetitive, and recurrent thoughts relating to oneself, feelings, and upsetting events or experiences (Treynor et al., 2003). Regarding specific facets of trait rumination, it was anticipated that brooding rumination would exhibit closer coupling with affective (in)flexibility given its correspondence with negative attentional biases and since it is a more maladaptive form of ruminative thinking which lacks the more intentional pondering and problem-solving elements that capture reflective rumination (Duque et al., 2014; Joorman et al., 2006; Owens & Gibb, 2017). Rumination has previously been linked to affective flexibility and attentional shifts based on the rule (Genet et al., 2013; Grol & De Raedt, 2021). Specifically, slower attentional shifts when shifting attention away from emotional elements of negative images was linked to greater self-reported daily rumination use, whereas slower attentional shifts from focusing on emotional aspects of positive images was correlated with reduced rumination (Genet et al., 2013). Similarly, Grol & De Raedt (2021) found that faster attentional switches towards non-emotional aspects of positive images was correlated with elevated use of maladaptive emotion regulation strategies (including rumination). Nevertheless, both studies assessed rumination tendencies in response to specific unpleasant events on a given day (RRS; Genet et al., 2013) or in response to a specific same day stressor

(i.e., rumination subscale of the Cognitive Emotion Regulation Questionnaire; Garnefski & Kraaij, 2006; Grol & De Raedt, 2021), whereas the present study assessed more general, trait rumination with no reference to a specific event or stressor. Therefore, it could be that state-like ruminative tendencies may be more closely related to the dynamic nature of affective flexibility in comparison to more generic, trait-level measures of rumination. Indeed, similar observations have been found for state and trait anxiety. While both trait anxiety and daily worry have previously been linked to affective flexibility (Twivy et al., 2021), more recently, trait anxiety was not found to be associated with affective task switching across two studies (Van Bockstaele et al., 2024). Given potential discrepancies in sensitivity of state-like and trait-like measures of emotional disposition, future studies should consider potential state versus trait differences in emotional disposition measures in relation to affective flexibility.

There are a few limitations of the current studies. Firstly, both studies did not include measures of either cognitive flexibility (i.e., general mental set shifting in the absence of emotional information) or working memory, thus we cannot rule out the influence of general cognitive ability on the current study findings. However, of the findings demonstrating significance, these appeared to be specific to switch costs pertaining to attentional shifts in the valence of the images, as opposed to more cognitively demanding attentional shifts based on the rule type.

Furthermore, although switch costs are commonly calculated to index affective flexibility (Genet et al., 2013; Grol & De Raedt, 2020, 2021; Malooly et al., 2013; Twivy et al., 2020), difference scores have been reported to be inherently unreliable (Draheim et al., 2016; Hughes et al., 2014). Also, switch costs do not adequately capture or control for individual differences in speed versus accuracy (Barulli et al., 2023; Hughes et al., 2014). Indeed, across both of our studies, valence and rule switch costs typically demonstrated a higher standard deviation than the average RT, a pattern that has also been recorded in prior studies adopting the same affective flexibility task (Grol & De Raedt, 2020, 2021; Twivy et al., 2020). Moreover, associations found between HRV and valence switch costs did not survive correction for multiple comparisons, and the multicollinearity between rest and task-based HRV measures likely produced spurious findings in relation to task-related HRV and positive valence switch costs in a non-affective rule context. Therefore, considering the unreliability of switch costs measures and the lack of robust associations observed,

the current study findings should be interpreted with caution and require further replication and validation with more reliable measures to index flexibility, such as rate residual or bin scores (Hughes et al., 2014). Relatedly, considering the correlational nature of these findings, it would be fruitful for future research to assess whether altering HRV, either via transcutaneous vagus nerve stimulation (Machetanz et al., 2021) or HRV biofeedback (Lehrer & Gevirtz, 2014), impacts affective flexibility, and whether such changes contribute to unique variance explained by valence or rule switch costs in the affective flexibility task. Finally, other lifestyle factors known to have an impact HRV, including exercise, body mass index, and smoking status (Hayano et al., 1990; Karason et al., 1999; Sammito et al., 2024; Sammito & Böckelmann, 2016) were not obtained or controlled for, thus we cannot rule out aforementioned factors as not having influenced the present study findings.

To conclude, the current findings highlight tentative associations between resting and task-related measures of HRV and closer coupling with affective flexibility in relation to shifts in valence, as opposed to more cognitively demanding shifts pertaining to changes in trial rule. Moreover, the present studies further extend prior literature by demonstrating that neither brooding or reflective facets of trait rumination or trait-like valence bias appear to predict affective flexibility in respect to either attentional shifts in valence or rule. This research critically reinforces the importance of considering the emotional context, and offers further evidence to support the notion that affective *in*flexibility may not always be maladaptive.

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Supplementary Material

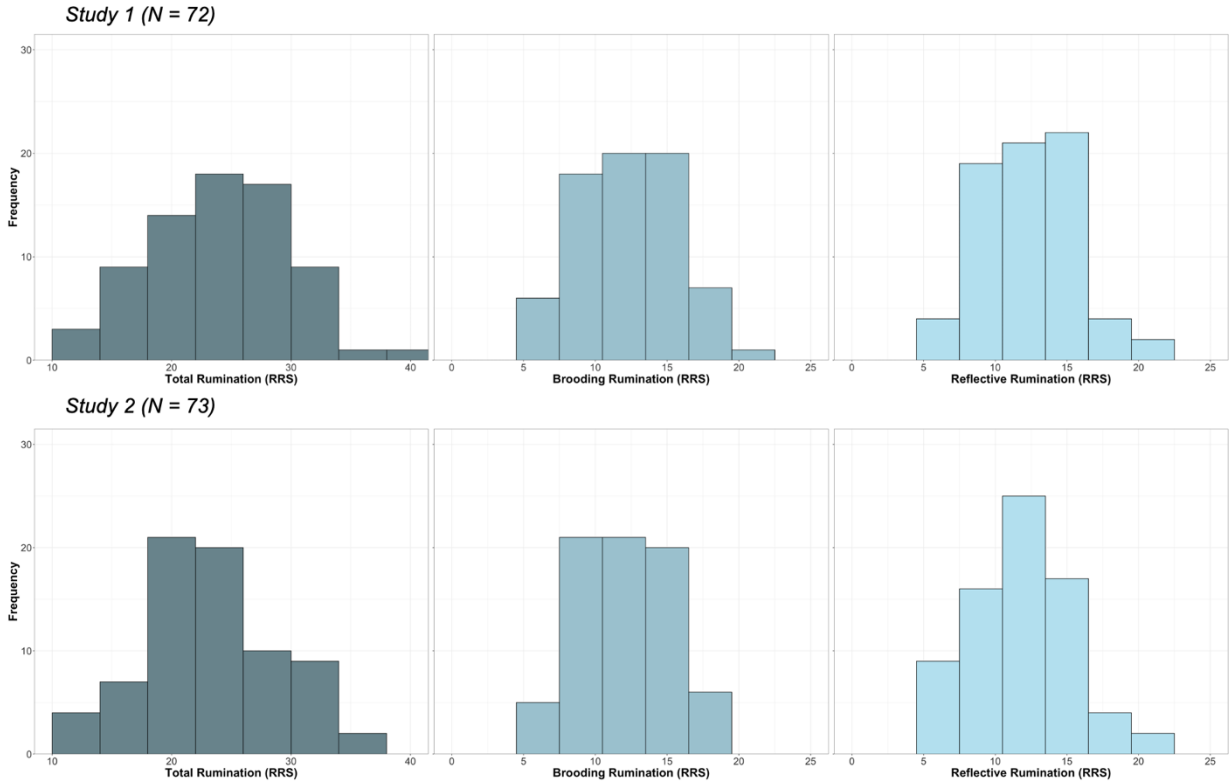

Figure S6. Histograms displaying the distributions for total rumination and brooding and reflective subscale scores. Study 1 (top panel). Study 2 (bottom panel). *RRS*; Ruminative Response Scale.

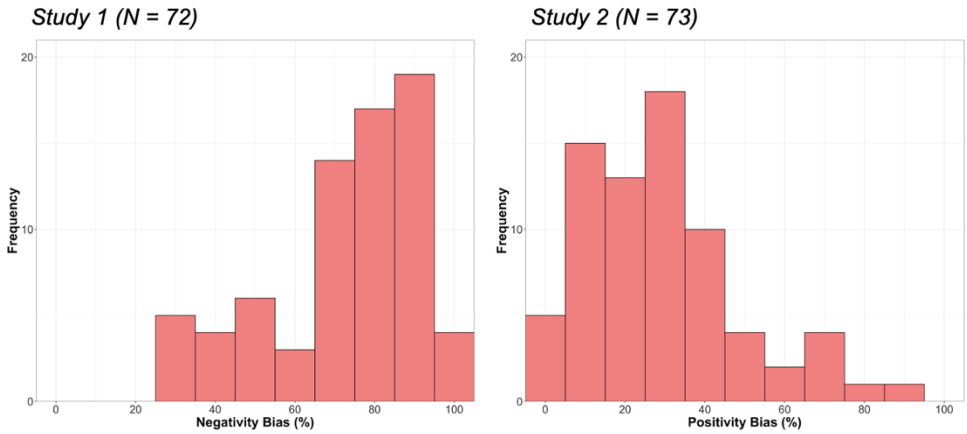

Figure S7. Histograms displaying the distributions for negative valence bias (left, Study 1) and positive valence bias (right, Study 2). Valence bias is operationalised as the percentage of negative or positive ratings towards emotionally ambiguous stimuli respectively.

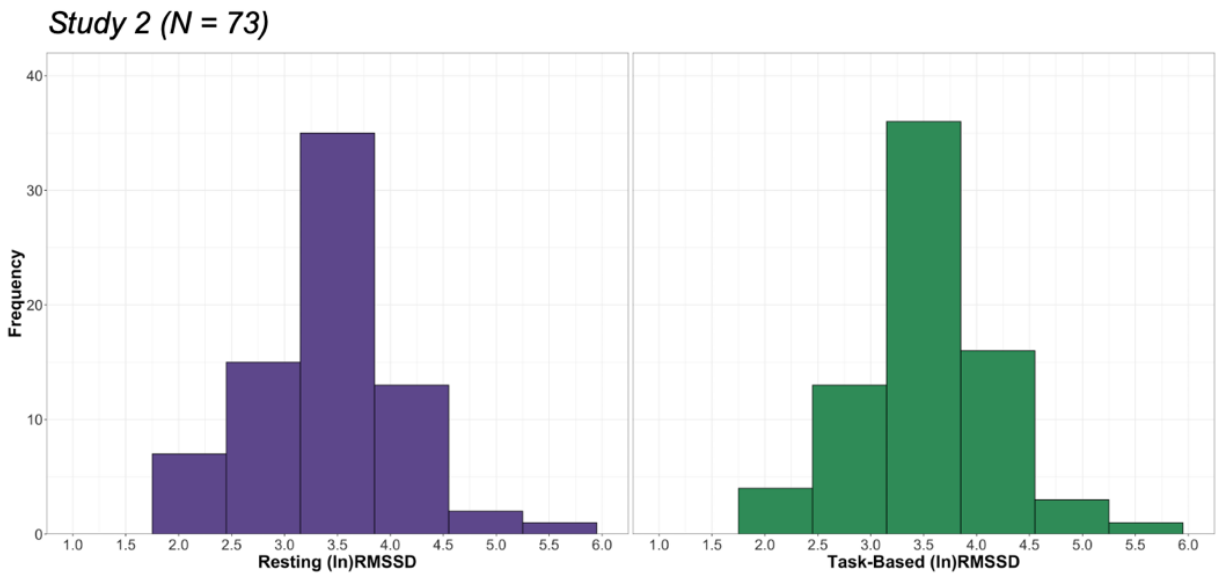

Figure S8. Histograms displaying the distributions for resting (left) and task-based (right) HRV in Study 2. *(ln)RMSSD*, natural log transformed root mean square of successive differences.

Table S4
Correlation Matrix Showing Associations Between Rumination (Total, Brooding, and Reflective) and Negativity Bias (Study 1)

		Total Rumination	Brooding Rumination	Reflective Rumination	Negativity Bias
Total Rumination	*r*	-			
	p				
Brooding Rumination	*r*	.881	-		
	p	<.001			
Reflective Rumination	*r*	.868	.530	-	
	p	<.001	<.001		
Negativity Bias	*r*	.111	.024	.173	-
	p	.355	.842	.146	

Table S5
Correlation Matrix Showing Associations Between HRV (Resting and Task-Based), Rumination (Total, Brooding, and Reflective) and Positivity Bias (Study 2)

		Resting HRV	Task-Based HRV	Total Rumination	Brooding Rumination	Reflective Rumination	Positivity Bias
Resting HRV	*r*	-					
	p						
Task-Based HRV	*r*	.924	-				
	p	<.001					
Total Rumination	*r*	-.151	-.112	-			
	p	.203	.346				
Brooding Rumination	*r*	-.076	-.071	.833	-		
	p	.524	.549	<.001			
Reflective Rumination	*r*	-.176	-.117	.873	.458	-	
	p	.137	.324	<.001	<.001		
Positivity Bias	*r*	-.043	-.015	0	-.068	.059	-
	p	.717	.897	.997	.568	.620	

Table S6
Pairwise Comparisons for Main Switch and Repeat Trial Conditions Used for Calculation of Key Valence and Rule Switch Costs (Study 1)

Switch Cost	**Pairwise Comparison**	***M* RT**	***SD* RT**	***M* Difference**	***t*(71)**	***p***	***d***
Positive Valence Switch Cost (Non-Affective Context)	NegNonAff_PosNonAff	1489.21	318.62	142.47	7.44	<.001	0.88
	PosNonAff_PosNonAff	1346.74	311.27				
Positive Valence Switch Cost (Affective Context)	NegAff_PosAff	1378.944	308.49	45.87	2.35	.022	0.23
	PosAff_PosAff	1333.07	319.20				
Negative Valence Switch Cost (Non-Affective Context)	PosNonAff_NegNonAff	1624.11	360.66	5.05	0.25	.802	0.03
	NegNonAff_NegNonAff	1619.07	374.04				
Negative Valence Switch Cost (Affective Context)	PosAff_NegAff	1310.31	314.81	-80.57	-3.43	.001	-0.40
	NegAff_NegAff	1390.88	362.05				
Non-Affective Switch Cost (Negative Valence)	NegAff_NegNonAff	1692.09	385.87	73.02	3.03	.003	0.36
	NegNonAff_NegNonAff	1619.07	374.04				
	NegNonAff_NegAff	1550.20	357.69	159.32	5.98	<.001	0.70

Affective Switch Cost (Negative Valence)	NegAff_NegAff	1390.88	362.05				
Non-Affective Switch Cost (Positive Valence)	PosAff_PosNonAff PosNonAff_PosNonAff	1511.32 1346.74	332.24 311.27	164.58	7.40	<.001	0.87
Affective Switch Cost (Positive Valence)	PosNonAff_PosAff PosAff_PosAff	1472.30 1333.07	331.64 319.20	139.23	5.84	<.001	0.69

Trial condition names are formatted as 'PreviousTrial_CurrentTrial'; *Pos*, Positive Valence Image; *Neg,* Negative Valence Image; *Aff*, Affective Rule Instruction; *NonAff*, Non-Affective Rule Instruction

Table S7
Pairwise Comparisons for Main Switch and Repeat Trial Conditions Used for Calculation of Key Valence and Rule Switch Costs (Study 2)

Switch Cost	**Pairwise Comparison**	***M* RT**	***SD* RT**	***M* Difference**	***t*(72)**	***p***	***d***
Positive Valence Switch Cost (Non-Affective Context)	NegNonAff_PosNonAff PosNonAff_PosNonAff	1374.44 1206.41	335.40 260.77	168.04	6.50	<.001	0.76
Positive Valence Switch Cost (Affective Context)	NegAff_PosAff PosAff_PosAff	1295.48 1216.98	321.70 290.48	78.51	3.39	.001	0.40
Negative Valence Switch Cost (Non-Affective Context)	PosNonAff_NegNonAff NegNonAff_NegNonAff	1504.57 1474.43	303.58 329.44	30.14	1.42	.159	0.17
Negative Valence Switch Cost (Affective Context)	PosAff_NegAff NegAff_NegAff	1178.33 1232.52	254.48 329.45	-54.19	-2.36	.021	-0.28
Non-Affective Switch Cost (Negative Valence)	NegAff_NegNonAff NegNonAff_NegNonAff	1496.70 1474.43	342.57 329.44	22.27	0.97	.334	0.11
	NegNonAff_NegAff	1476.97	358.87	244.45	8.95	<.001	1.05

Affective Switch Cost (Negative Valence)	NegAff_NegAff	1232.52	329.45				
Non-Affective Switch Cost (Positive Valence)	PosAff_PosNonAff PosNonAff_PosNonAff	1411.96 1206.41	302.24 260.77	205.55	8.44	<.001	0.99
Affective Switch Cost (Positive Valence)	PosNonAff_PosAff PosAff_PosAff	1332.98 1216.98	260.96 290.48	116	4.08	<.001	0.48

Trial condition names are formatted as 'PreviousTrial_CurrentTrial'; *Pos*, Positive Valence Image; *Neg,* Negative Valence Image; *Aff*, Affective Rule Instruction; *NonAff*, Non-Affective Rule Instruction

Table S8

Picture Stimuli Used in the Valence Bias and Affective Flexibility Tasks (Study 1)

VALENCE BIAS TASK (Example Trials)	Positive	11F_HA_O	26M_HA_O	AM20HAS	AF24HAS
	Negative	10F_AN_C	39M_AN_C	AF15ANS	AM02ANS
	Ambiguous	13F_SP_O	25M_SP_O	AF29SUS	AM11SUS
VALENCE BIAS TASK (Main Trials)	Positive	01F_HA_O	03F_HA_O	07F_HA_O	08F_HA_O
		24M_HA_O	28M_HA_O	36M_HA_O	37M_HA_O
		AF06HAS	AF08HAS	AM01HAS	AM14HAS
	Negative	01F_AN_C	03F_AN_C	08F_AN_C	09F_AN_C
		20M_AN_C	28M_AN_C	36M_AN_C	37M_AN_C
		AF07ANS	AF14ANS	AM10ANS	AM28ANS
	Ambiguous	01F_SP_O	02F_SP_O	06F_SP_O	07F_SP_O
		08F_SP_O	09F_SP_O	20M_SP_O	23M_SP_O
		24M_SP_O	27M_SP_O	28M_SP_O	36M_SP_O
		AF01SUS	AF02SUS	AF03SUS	AF13SUS
		AF30SUS	AF34SUS	AM06SUS	AM12SUS
		AM13SUS	AM18SUS	AM34SUS	AM35SUS
AFFECTIVE FLEXIBILITY TASK (Practice Trials)	Positive (one or fewer people)	1540	2050	5760	7250
		8330			
	Positive (two or more people)	1340	2057	4603	8371
		8461			
	Negative (one or fewer people)	2717	3181	3225	9571
		9911			
	Negative (two or more people)	3350	6415	6540	9250
		9433			
AFFECTIVE FLEXIBILITY (Main Trials)	Positive (one or fewer people)	1440	1463	1500	1510
		1710	1722	2055.2	2071
		2650	4250	4574	5260
		5450	5460	5470	5480
		5600	5628	5700	5814
		5849	5910	7260	7270
		7289	7330	7350	7400

	7430	7470	7480	8034
	8120	8170	8300	8350
	8500	8501	8510	8531
Positive (two or more people)	2080	2091	2150	2154
	2160	2170	2208	2209
	2216	2224	2310	2331
	2340	2345	2391	2398
	2540	2550	4542	4599
	4609	4610	4614	4622
	4623	4626	4641	5621
	5830	5833	7502	8341
	8370	8380	8420	8490
	8496	8497	8540	8600
Negative (one or fewer people)	1275	2095	2276	2375.1
	2399	2710	2722	2750
	2800	2981	3180	3220
	3230	3300	3550	6200
	6260	6300	6570.1	9000
	9001	9007	9008	9040
	9041	9140	9180	9265
	9280	9290	9320	9331
	9340	9342	9470	9471
	9561	9570	9630	9830
Negative (two or more people)	2053	2141	2205	2278
	2312	2352.2	2455	2590
	2694	2700	2703	2718
	2799	2900.1	3301	4621
	6211	6212	6213	6242
	6315	6360	6555	6560
	6571	6821	6838	9220
	9253	9341	9400	9415
	9420	9421	9435	9495
	9592	9910	9920	9921

Table S9

Picture Stimuli Used in the Valence Bias and Affective Flexibility Tasks (Study 2)

VALENCE BIAS TASK (Example Trials)	Positive	11F_HA_O	26M_HA_O	AM20HAS	AF24HAS
	Negative	10F_AN_C	39M_AN_C	AF15ANS	AM02ANS
	Ambiguous	13F_SP_O	25M_SP_O	AF29SUS	AM11SUS
VALENCE BIAS TASK (Main Trials)	Positive	01F_HA_O	03F_HA_O	07F_HA_O	08F_HA_O
		24M_HA_O	28M_HA_O	36M_HA_O	37M_HA_O
		AF06HAS	AF08HAS	AM01HAS	AM14HAS
	Negative	01F_AN_C	03F_AN_C	08F_AN_C	09F_AN_C
		20M_AN_C	28M_AN_C	36M_AN_C	37M_AN_C
		AF07ANS	AF14ANS	AM10ANS	AM28ANS
	Ambiguous	01F_SP_O	02F_SP_O	06F_SP_O	07F_SP_O
		08F_SP_O	09F_SP_O	20M_SP_O	23M_SP_O
		24M_SP_O	27M_SP_O	28M_SP_O	36M_SP_O
		AF01SUS	AF02SUS	AF03SUS	AF13SUS
		AF30SUS	AF34SUS	AM06SUS	AM12SUS
		AM13SUS	AM18SUS	AM34SUS	AM35SUS
AFFECTIVE FLEXIBILITY TASK (Practice Trials)	Positive (one or fewer people)	2050	2306	7250	7325
		8330			
	Positive (two or more people)	1340	2057	2352	4603
		8371			
	Negative (one or fewer people)	3181	3017	3225	9571
		9911			
	Negative (two or more people)	6415	6540	9045	9428
		9433			
AFFECTIVE FLEXIBILITY (Main Trials)	Positive (one or fewer people)	1463	1500	1510	1710
		1722	1811	2040	2055.2
		2070	2071	2650	2660
		4250	4574	5260	5450
		5460	5470	5600	5628
		5629	5700	5814	5849
		5910	7270	7289	7330
		7350	7400	7430	7508
		8034	8120	8200	8300
		8350	8500	8510	8531
	Positive (two or more people)	2080	2091	2150	2154
		2160	2170	2208	2209
		2216	2224	2310	2331
		2340	2345	2391	2398
		2540	2550	4542	4599
		4609	4610	4622	4623
		4626	4641	5621	5830
		5833	7502	8341	8370
		8380	8420	8461	8490
		8496	8497	8540	8600
	Negative (one or fewer people)	1275	2276	2375.1	2399
		2710	2722	2750	2981
		3180	3230	3300	3550

	6020	6200	6260	6300
	6570.1	9000	9007	9008
	9040	9090	9140	9180
	9181	9265	9280	9290
	9320	9331	9340	9342
	9470	9471	9560	9561
	9570	9630	9830	9912
Negative (two or more people)	2141	2205	2278	2312
	2352.2	2455	2694	2700
	2703	2718	2799	2900.1
	3301	4621	6211	6212
	6213	6242	6315	6360
	6555	6560	6571	6821
	6838	9220	9250	9253
	9400	9404	9415	9420
	9421	9435	9495	9520
	9592	9910	9920	9921

Codes highlighted in yellow highlight differences in the picture stimuli used in the valence bias and affective flexibility tasks in comparison to Study 1

Chapter 5. Thesis General Discussion

The overarching aim of the current thesis was to examine associations between HRV and emotional disposition factors with neural and performance-based indices of adaptive emotional responding. The NIM posits that HRV serves as an index of effective prefrontal inhibitory control and central nervous system-autonomic nervous system coordination (Thayer & Lane, 2000, 2009). More recently, an extension to the NIM outlined an 8-level vagal hierarchy, in which higher levels of neurovisceral circuitry involving the prefrontal cortex are proposed to support more complex coordination of attentional, regulatory, and goal-directed processes (Smith et al., 2017). However, research has predominantly focused on resting HRV and neural functioning at rest, that is, in the absence of contexts requiring adaptive emotional responding. To address this, the current body of research examined the relationship between HRV and emotional disposition factors with concurrent neural and performance-based indices of adaptive emotional responding across emotion and resting contexts.

5.1 Review of the Studies

5.1.1 Paper 1

While neuroimaging studies have previously examined associations between resting HRV and neurovisceral circuitry at rest (Kumral et al., 2019; Sakaki et al., 2016; Schumann et al., 2021), fewer studies have investigated HRV and associated neural functional connectivity concomitantly during contexts that require adaptive emotional responding. Consequently, the main aim of Paper 1 was to examine the association between task-related HRV and amygdala-mPFC functional connectivity strength during a reappraisal task in younger and older adults from a wider ageing dataset. A secondary aim of the paper was to conceptually replicate prior resting-state findings (Sakaki et al., 2016), assessing the link between task-related HRV and resting amygdala-mPFC functional coupling. Participants engaged in a reappraisal paradigm which involved reinterpreting negative (and neutral) emotional pictures to either increase, decrease, or maintain their emotional response. Task-based HRV was derived from a finger pulse signal acquired during the scan.

Partial support was found for the NIM and our first hypothesis, such that a slight positive, albeit non-significant, association between HRV and amygdala-mPFC connectivity emerged in older adults. However, younger adults exhibited a stronger, inverse association, in which higher task-related HRV was associated with reduced

amygdala-mPFC functional connectivity strength during the reappraisal task. Moreover, in relation to resting-state functional connectivity, we uncovered a sub-threshold cluster within the mPFC that was spatially close to, but did not overlap with, our mPFC seed which demonstrated increased coupling with the left amygdala as a function of higher task-related HRV across the whole sample, however, this finding did not survive correction for multiple comparisons. Wider voxelwise whole-brain analyses of the task-related fMRI revealed that elevated task-based HRV was correlated with weaker right amygdala-PCC connectivity across both age groups and stronger right amygdala-right vlPFC connectivity in older adults, reflecting higher task engagement and effective recruitment of neural circuitry underlying emotion regulation. Taken together, findings from Paper 1 extend prior work, and more critically, reinforce the importance of testing neurovisceral circuitry in active emotion contexts to further identify neural concomitants of HRV and adaptive emotional responding.

5.1.2 Paper 2

Alongside studies predominantly focusing on resting HRV and neural functional connectivity/activity at rest, with the exception of a few studies (Chand et al., 2020; Chang et al., 2013; Schumann et al., 2021), most research has further assumed stationarity of the brain, adopting relatively static neuroanalytical techniques to examine heart-brain interactions. Consequently, the primary aim of Paper 2 was to apply co-activation pattern analysis to examine both task-related and resting HRV with associated transient temporal changes in co-active neural networks during an emotion processing task and at rest to identify shared versus context-specific neural networks. Furthermore, trait neuroticism is a stable emotional disposition metric that closely reflects emotion (in)flexibility, however, the relationship between HRV and trait neuroticism remains unclear and inconsistent, as is the extent to which both individual difference measures potentially interact to predict temporal dynamics of co-active neural networks across contexts. Correspondingly, a secondary aim of Paper 2 was to examine associations between HRV and trait neuroticism alongside potential interactions in relation to temporal dynamics derived from co-active neural patterns during emotion processing and rest. Two samples of younger adults were derived from the open access AOMIC neuroimaging dataset. The emotional matching task involved matching one of two stimuli to a target stimulus (emotion condition: angry or fear facial expressions, control condition: horizontal or vertical orientation of oval shapes). Both

task-based and resting HRV measures were extracted from a pulse signal that was acquired during the emotion processing and resting-state fMRI scans respectively.

During the emotion matching task, higher trait neuroticism (sample 1) predicted a lower average duration, whereas elevated task-related HRV (sample 2) predicted a higher average duration, of a brain state involving co-activation between left amygdala and BNST with a visual attention network. Relatedly, elevated resting HRV was linked to a greater average duration of a similar ventral visual dominant brain state with left amygdala and BNST during rest in sample 2. These findings potentially indicate that individuals with higher HRV are engaging in more exteroceptive visual attentional processes across contexts. An interaction emerged between task-related HRV and trait neuroticism during the emotional processing task, such that higher task-related HRV predicted increased occurrences of a core DMN state co-active with left amygdala and BNST in individuals with lower, but not higher trait neuroticism (sample 2). This was in the opposite direction to our hypothesis, whereby we anticipated high trait neuroticism to be linked to more self-referential DMN processing (i.e., increased occurrences and average duration). That being said, this finding conceptually aligns with prior work reporting increased activation in core DMN areas during cognitive switches within tasks and from breaks to task engagement (Crittenden et al., 2015; Smith et al., 2018), suggesting that individuals with lower trait neuroticism and higher task-based HRV were possibly more able to flexibly (dis)engage throughout the task.

During rest, individuals with higher resting HRV more frequently entered a state of co-activation between right amygdala and BNST with regions consistent with the salience network (sample 1). While we had hypothesised that lower HRV would be linked to increased occurrences or a higher average duration of salience network co-activation reflecting sustained vigilance, this finding corroborates a prior research study reporting salience-related regions to be linked to transient HRV changes (Chang et al., 2013), and, in this context, may in fact reflect a greater preparedness to dynamically switch between interoceptive and exteroceptive states during an eyes-open resting-state paradigm (Costumero et al., 2020). In the same sample, higher resting HRV correlated with a lower average duration of right amygdala and BNST, and lower occurrences of left amygdala and BNST, co-activation with a dmPFC DMN state. Finally, higher trait neuroticism predicted a lower average duration of co-activation between right amygdala and BNST with a core DMN state (sample 1), and a significant HRV by neuroticism interaction emerged in sample 2, such that

individuals with lower neuroticism and higher resting HRV demonstrated a lower average duration of a similar core DMN state with left amygdala and BNST (sample 2).

Overall, while findings concerning the transient temporal metrics exhibited low replicability across both samples and Bayesian analyses indicated anecdotal and fairly weak support for such associations, in line with Paper 1, this paper further reinforces the importance of examining task-related and resting HRV across contexts to elucidate shared, and disparate, neurovisceral regions supporting adaptive emotional responding according to the context and associated demands.

5.1.3 Paper 3

Whereas the first two papers investigated adaptive emotional responses in the form of emotion regulation (reappraisal of negative emotional information; Paper 1) and adaptive emotional processing (attentional shifting to and from negative and neutral emotional information; Paper 2), Paper 3 focused on affective flexibility in the form of flexible attentional (dis)engagement to and from positive and negative emotional information. The primary aim of Paper 3 was to examine the degree to which psychological (valence bias and trait rumination) and physiological (HRV) metrics of emotional disposition predicted affective flexibility in both an online (Study 1) and laboratory (Study 2) context. In both studies, participants engaged in an affective switching task and a valence bias task. The affective flexibility task involved categorising positive and negative emotional images according to either an emotional (valence) or non-emotional (number of humans) rule. Switch costs were calculated based on shifts in valence (i.e., trials where the valence of the image changed from positive to negative or vice versa accompanied by a repetition in the trial rule) and rule (i.e., trials where the rule changed from affective to non-affective or vice versa accompanied by a repetition in the valence of the image). The valence bias task involved providing positive or negative ratings in response to facial expressions of a clear or emotionally ambiguous valence. Task-based and resting HRV measures were derived from a pulse signal acquired during the emotion tasks and a rest period (Study 2).

We hypothesised that higher negativity biases and trait rumination would significantly predict greater affective inflexibility when shifting attention away from images with a negative valence towards those with a positive valence, especially when

the affective trial rule repeated (valence prediction). Based on prior findings (Genet et al., 2013), it was anticipated that higher trait rumination, especially brooding rumination, would predict greater switch costs (lower flexibility) when shifting attention from affective aspects of negative emotional information, and lower switch costs (greater flexibility) when shifting attention from affective towards non-affective aspects of positive information. No significant associations emerged between either valence bias or trait (brooding or reflective) rumination with affective flexibility switch costs based on shifts in valence or trial rule. providing no supporting evidence for our hypotheses or prior findings (Genet et al., 2013). The lack of replication, at least in the case of rumination, may be explained by state versus trait differences in measures of emotional disposition, with state-like variables perhaps more closely capturing variance associated with the dynamic nature of affective flexibility. Moreover, in Study 2, contrary to our hypothesis, higher task-related HRV was tentatively associated with a greater switch cost (i.e., affective *in*flexibility) when shifting attention towards positive valence images on trials where the non-affective rule repeated. We also found some support for our hypothesis that individuals with elevated resting HRV would exhibit greater switch costs (i.e., affective *in*flexibility) when shifting attention from positive towards negative valenced images when the affective rule repeated, although neither of these findings survived correction for multiple comparisons. While it is important to consider the potential spurious nature of these findings, HRV appeared to be more closely coupled to switch costs based on shifts in emotion (valence) as opposed to attentional shifts pertaining to greater cognitive demand (trial rule). Collectively, these findings reinforce the notion that context matters, and critically highlight that affective (in)flexibility may not always be (mal)adaptive.

5.2 Comparison of Findings to the Wider Literature

5.2.1 Comparison with Prior HRV, Neuroimaging, and Adaptive Emotional Responding Studies

The NIM proposes that higher-order prefrontal cortical structures exert control over subcortical cardioacceleratory regions (i.e., amygdala) at rest, with stronger integrity of the prefrontal cortex and cortical-subcortical circuitry indexed by greater resting HRV (Thayer & Lane, 2000, 2009). Prior work has supported this notion, with higher HRV linked to cerebral blood flow in the amygdala and mPFC (Thayer et al., 2012), stronger resting-state amygdala-mPFC functional connectivity (Nashiro et al.,

2023a; Sakaki et al., 2016), and greater structural covariance in dmPFC (Wei et al., 2018). In Paper 1, there was a slight positive, albeit non-significant, association between higher task-based HRV and amygdala-mPFC functional connectivity strength in older adults during the reappraisal task. Moreover, a sub-threshold cluster in mPFC was observed at rest that demonstrated increased functional connectivity with the left amygdala as a function of higher task-related HRV across the whole sample. In Paper 2, we reported clusters in mPFC to form part of core DMN brain states, with these mPFC areas demonstrating partial spatial overlap with the mPFC seed region of interest in Paper 1. Interestingly, no main effects of HRV were found for DMN core state, but significant interactions between HRV and neuroticism emerged. Higher task-related HRV predicted increased occurrences during emotional processing, and a reduced average duration at rest, of co-activation between the left amygdala and BNST with core DMN states in individuals with lower but not higher trait neuroticism. Collectively, these findings tentatively support the notion that HRV can serve as an index of prefrontal functioning and corroborates links between HRV and amygdala-PFC circuitry in supporting adaptive emotional responding across emotional and resting contexts.

The extension to the NIM outlined an 8-level vagal hierarchy in which brain regions forming the DMN (i.e., mPFC, PCC) and executive control network (i.e., dorsolateral prefrontal cortex, parietal cortex) regions are proposed to facilitate processes associated with greater metabolic demand, such as regulation and goal-directed behaviour (Smith et al., 2017). Consequently, through application of both static and dynamic neuroanalytical techniques, the current research extends prior findings, highlighting the pivotal role emotional context plays in shaping associations between HRV and neural circuitry reflecting adaptive emotional responding. For example, while we found partial support for an association between task-related HRV and amygdala-mPFC connectivity strength, in younger adults, the inverse effect was observed, such that higher task-based HRV correlated with weaker amygdala-mPFC functional connectivity during reappraisal. While prior research has found higher HRV to be associated with greater (d)mPFC during reappraisal of negative and positive images (Guendelman et al., 2024; Min et al., 2024; Steinfurth et al., 2018), reappraisal has been reported to not require engagement of (v)mPFC in order to control amygdala activity (Berboth & Morawetz, 2021; Buhle et al., 2014). It is likely that other areas, such as lateral prefrontal cortex, become more relevant to HRV and adaptive

emotional responding in contexts requiring higher cognitive (metabolic) demands and goal-directed behaviour. We found higher task-related HRV to be positively coupled with stronger right amygdala-right vlPFC connectivity in older adults during an active emotion regulatory context, highlighting that when more explicit emotion regulation is required, older adults with higher HRV were able to recruit emotion regulation related circuitry to support engagement in the task. Additionally, in Paper 2, the IFG/vlPFC was co-active with other brain areas linked to visual attention (i.e., occipital cortex and SPL) as a function of left amygdala and BNST in which higher task-related HRV was linked to a longer average duration of this brain state throughout the emotional processing task in younger adults. Indeed, the IFG has not only been reported to be involved in emotion processing (Adolphs, 2002), but also in emotion regulation (Kohn et al., 2014; Messina et al., 2015; Wager et al., 2008), with left IFG/vlPFC consistently identified as supporting reappraisal (Berboth & Morawetz, 2021; Buhle et al., 2014).

The current research also contributes further insight into HRV and associations with flexible emotional processing and affective flexibility. Findings from both Papers 2 and 3 show some initial patterns that indicate HRV may potentially be more closely coupled with flexible allocation of attention in emotional contexts. In particular, Paper 2 applied a novel neuroanalytical technique to derive transient temporal metrics from data-driven brain states such as occurrences (i.e., number of times a brain state was expressed throughout the duration of the scan) and average duration (i.e., mean duration a brain state was sustained for). Correspondingly, these metrics appear more relevant to the concept of flexibility compared with relatively static functional connectivity metrics that assess average connectivity strength over the scan. For instance, in individuals with lower, but not higher trait neuroticism, greater task-related HRV predicted increased occurrences of a core DMN state co-active with left amygdala and BNST. If adopting a static connectivity approach, this brain state may have been expressed as having overall higher connectivity strength or increased activation, but the associated temporal dynamic metric provides crucial context for interpreting how fluctuations in this brain state may constitute adaptive responding throughout the scan. Indeed, higher frequency of co-activation between the amygdala and DMN appears to align with research that has reported increased activation in core DMN areas during cognitive switches between tasks and between engaging in tasks and breaks (Crittenden et al., 2015; Smith et al., 2018). Moreover, during rest, individuals with elevated resting HRV more frequently entered salience network

states, which may reflect a greater preparedness to dynamically switch between interoceptive and exteroceptive states (Costumero et al., 2020). While fairly weak evidence was uncovered to support these associations and results were not replicated across both samples, they provide some indication that HRV influences flexibility of neural states overlapping neurovisceral circuitry, with higher HRV underlying more frequent occurrences of DMN and salience network during emotional processing and rest respectively.

Critically, the NIM posits that shared neural regions overlap to support autonomic, emotional, and cognitive regulatory processes (Thayer & Lane, 2000, 2009). Indeed, previous studies have found higher HRV to be associated with greater executive functioning and cognitive performance (Magnon et al., 2022; Thayer et al., 2009). HRV has also previously been associated with affective flexibility, such that lower switch costs (higher flexibility) when shifting attention from affective to non-affective aspects of negative emotional information was associated with reduced resting HRV (Grol & De Raedt, 2020). In Paper 3, we did not find associations between HRV and switch costs pertaining to more cognitively demanding attentional shifts based on the trial rule, but instead found associations with attentional shifts related to the valence of the emotional images. Interestingly, higher task-related HRV was associated with less efficient shifting of attention from images with a negative valence in the presence of a non-affective rule, and higher resting HRV correlated with less efficient shifting of attention from positive valence images on trials when the affective rule repeated, although these findings did not survive correction for multiple comparisons. On the surface, these findings do not support the overlap between emotion and cognition as proposed by the NIM and could be considered somewhat contradictory given that higher HRV is related to lower affective flexibility in the case of both findings. However, in this context, higher attentional capture towards negative images during the task (i.e., potentially reflecting a lower tendency to avoid negative emotional information in those with lower HRV which has relevance to the vigilance-avoidance model of anxiety; Mogg et al., 2004), and positive images during rest (i.e., potentially reflecting a positivity bias as observed in prior work in individuals with higher HRV; Madison et al., 2021; Osnes et al., 2023), may actually be considered adaptive emotional responding. These findings contribute to the wider literature which emphasises the importance of context (i.e., valence, current goals) to establish whether (in)flexibility is considered (mal)adaptive (Parsons et al., 2016).

5.2.2 Comparison with Prior Emotional Disposition Studies

The NIM, amongst other psychophysiological frameworks, posit that HRV is an index of adaptive self-regulatory ability (Appelhans & Luecken, 2006; Thayer & Lane, 2000, 2009), and, in turn, (HF-)HRV has been proposed to be transdiagnostic marker of psychopathology (Beauchaine & Thayer, 2015). Trait neuroticism and rumination are both emotional disposition factors that have been linked to increased risk of onset of anxiety and depression (Hsu et al., 2015; Kootker et al., 2016; Kotov et al., 2010; McLaughlin & Nolen-Hoeksema, 2011). Moreover, anxiety and depressive symptoms have been linked to negativity biases in response to emotional ambiguity, and reductions in HRV have been reported in anxious and depressed individuals (Beauchaine & Thayer, 2015; Chalmers et al., 2014; Dell-Acqua et al., 2020; Koch et al., 2019). Interestingly, results from the current work indicated neither resting or task-based HRV during emotional contexts to be associated with a range of trait-like emotional dispositional factors linked to the risk of onset of anxiety and depression, including self-reported trait neuroticism in two samples of younger adults (Paper 2), nor trait rumination or valence bias in a sample containing predominantly younger adults (Paper 3, Study 2). These findings diverge from prior work reporting direct associations between HRV and trait neuroticism (Čukić & Bates, 2015; Shepherd et al., 2015) and rumination (Carnevali et al., 2018). Nonetheless, there have been mixed and inconsistent findings between HRV and both neuroticism and rumination in previous studies (Aldao et al., 2010; Ode et al., 2010; Sloan et al., 2017), which suggests that the relationship between HRV and other emotional disposition factors is likely more nuanced. Indeed, Ode et al. (2010) reported a significant interaction between HRV and trait neuroticism, such that greater HRV was beneficial in individuals with higher neuroticism, predicting less problematic daily outcomes, however, at lower levels of neuroticism, higher HRV was not necessarily beneficial and somewhat problematic. In the current work, significant interactions emerged between HRV and neuroticism to predict temporal metrics of co-activation states linked to the DMN across emotion and resting contexts. Specifically, we observed higher HRV at lower trait neuroticism levels to predict increased occurrences of a brain state reflecting the DMN, whereas in those with higher trait neuroticism, higher HRV predicted fewer occurrences of this network during the emotion processing task. Given prior work reporting increased DMN activation in supporting cognitive transitions (Crittenden et al., 2015; Smith et al., 2018), this could reflect an increased ability to

(dis)engage the DMN during an emotion processing task in individuals with lower trait neuroticism and higher HRV, reflecting adaptive emotional responding. With relation to resting-state, the HRV by neuroticism interaction appeared to be driven by low trait neuroticism, such that lower HRV predicted a higher average duration of the DMN, whereas higher HRV predicted a lower average duration of this state during rest. In this context, individuals with lower trait neuroticism and higher HRV may have been experiencing less stress and/or sustaining other brain states linked to exteroceptive attentional engagement as opposed to focusing their attention internally. On the other hand, for higher trait neuroticism, resting HRV did not appear to have much of an influence on average duration of the DMN. Overall, this work and previous studies suggest more nuanced and complex interactions between HRV and trait emotional disposition variables which warrant further investigation.

Notably, while the current research did not find direct associations between HRV and other emotional disposition factors, across all papers, we found resting and task-based HRV measures to predict concomitant functional connectivity strength of brain areas and temporal dynamics of co-active neural states underlying adaptive emotional responses (Papers 1-2), alongside the observation of HRV being the only individual difference metric to tentatively predict attentional shifts in response to emotional material relative to other trait-like markers of emotional disposition (Paper 3). This provides some support for the NIM's assertion of HRV being a measure of adaptive autonomic and emotion regulatory responding (Appelhans & Luecken, 2006; Thayer & Lane, 2000, 2009), although in the case of the latter paper, findings reinforce the notion that *in*flexibility may indeed constitute an adaptive attentional response depending on the context. Taken together, HRV may capture unique and/or additional variance underlying adaptive emotional responses over and above other measures of emotional disposition.

5.3 Limitations of the Research

5.3.1 Correlational Nature of the Findings

While the papers forming this thesis make valuable contributions to the literature by assessing HRV in contexts requiring various degrees of adaptive emotional responding, the findings between HRV and other emotional disposition variables (i.e., trait neuroticism, rumination, and valence bias) with neural (i.e., functional connectivity and temporal metrics of co-active brain states) and

performance-based (affective flexibility) measures of adaptive emotional responding are correlational in nature. Thus, while we have identified associations between HRV and adaptive emotional responding across different contexts, the direction of such findings is unclear. For example, in Paper 1, does higher HRV strengthen and reinforce functional connectivity between the amygdala and vlPFC in older age in a reappraisal context, or is it the preservation of amygdala-vlPFC connectivity in the first instance that promotes more effective emotional responding during the task, which in turn elevates task-related HRV? HRV is a non-invasive and malleable metric that can be altered either via HRV biofeedback (Lehrer & Gevirtz, 2014; Lehrer et al., 2020) or transcutaneous vagus nerve stimulation (Machetanz et al., 2021). Indeed, research has already taken initial steps to investigate similar research questions in a more causal manner via implementation of HRV biofeedback interventions to change resting HRV levels. These studies have shown that altering HRV results in changes in neural circuitry at rest (Nashiro et al., 2023a; Schumann et al., 2021) and during emotion regulation (Nashiro et al., 2023a), alongside improvements in cognitive performance (Nashiro et al., 2023b). Correspondingly, it would be interesting to examine HRV changes and the impact this has on affective flexibility, especially given observed specificity of valence relative to rule switch costs in Study 2 of Paper 3. Relatedly, the direct manipulation of HRV may facilitate identification of an 'optimum' level of HRV (for a discussion on the quadratic nature of HRV, see Kogan et al., 2013) and how this may change, or be influenced by, either individual differences in emotional disposition and/or contexts with varying emotional/cognitive demands. Consequently, such evidence may support the use of HRV as a complementary intervention to target emotion dysregulation, a feature underlying various psychopathology, including anxiety and depression (Cisler et al., 2010; Joormann & Stanton, 2016). Overall, the adoption of biofeedback and/or vagus nerve stimulation interventions to further test the NIM and investigate HRV as an index of adaptive emotional responding will be a continued and fruitful avenue for future research.

5.3.2 Sample Characteristics

The papers comprising this thesis primarily sampled younger (healthy) adults who were predominantly White and European. HRV has been found to differ based on ethnicity (Hill et al., 2015) and ethnic differences have also been reported to influence findings between resting cerebral blood flow and HRV in relation to affect (Thayer &

Koenig, 2019). Moreover, sex has been reported to influence HRV (Koenig & Thayer, 2016). While the presented papers were relatively balanced in terms of biological sex (Papers 1 and 2), the studies forming Paper 3 contained a higher proportion of participants who identified as female (Study 1 and 2) and who were assigned female sex at birth (Study 2). Most of the participants recruited across the presented papers were also healthy younger adults, therefore our findings likely capture 'normal' or average variation in HRV and metrics of adaptive emotional responding.

5.3.3 Single Time-Domain HRV Measure and Confounding Factors

Across all papers, the root mean square of successive differences (RMSSD) served as a metric of both resting and task-based HRV. The RMSSD is a frequently used time-domain HRV measure in wider neuroimaging and psychological research and has been described as a robust measure of parasympathetic tone (Kleiger et al., 2005) which is generally less susceptible to physiological sources of noise, especially respiration (Hill et al., 2009). For these reasons and conceptual replication purposes, we proceeded with RMSSD as a single measure of HRV throughout the current body of research. However, it is unclear whether findings in the current work would be replicated using other frequency-domain (i.e., High-Frequency HRV) and non-linear indices of HRV. It is acknowledged that there are dynamic, non-linear processes within the ANS that influence both heart rate and HRV, with the inherent variation of such non-linear systems facilitating quick and flexible autonomic responses to environmental challenges (Beckers et al., 2006; Shaffer & Ginsberg, 2017). Thus, non-linear HRV methods may provide further insight into adaptive emotional responding beyond traditional time-or frequency-domain HRV measures (de la Torre-Luque et al., 2017). However, given caution in the literature regarding non-linear metrics (Sassi et al., 2015) there have been recommendations to adopt such measures as complementary indicators of HRV, along with more traditional, established HRV metrics (Laborde et al., 2017). Furthermore, many confounding stable and transient factors have been found to influence HRV parameters, including, but not limited to, smoking status, general fitness/activity level, caffeine intake, and BMI (Hayano et al., 1990; Karason et al., 1999; Sammito & Böckelmann, 2016; Zimmermann-Viehoff et al., 2016; for a full list see: Laborde et al., 2017). Given that Papers 1 and 2 used existing datasets to perform secondary data analyses, these studies were not specifically designed to measure HRV and by extension, did not consider assessing

confounding factors that influence HRV. Moreover, in the case of Study 2 in Paper 3, we did not collect information pertaining to a wide range of physical health factors such as height, weight, exercise, smoking status, and sleep given time constraints with data collection and to reduce risk of participant burden or fatigue when accounting for the other tasks and questionnaires already included in the protocol. Therefore, it will be important for future studies assessing HRV and adaptive emotional responding to control for both stable and transient factors influencing HRV.

5.3.4 Statistical Power and Reliability

A final limitation to consider when interpreting the findings across studies in this thesis is low statistical power. All studies comprised of relatively small sample sizes and in the case of the final empirical chapter, despite attempting to account for 10% participant attrition, the sample size for both studies fell below the recommended sample N to detect effects of a medium size as indicated by corresponding power analyses. It is acknowledged that neuroimaging studies examining associations between neural functioning and inter-individual differences in mental health or cognitive phenotypes typically involve small sample sizes (Button et al., 2013; Marek et al., 2022). In turn, smaller sample sizes have been reported to increase sampling variability and are linked to a heightened risk of detecting unstable or inflated associations/effects (Marek et al., 2022). Larger sample sizes reduce both sampling variability and facilitate the ability to detect small to large effect sizes (e.g., Pearson correlation r = 0.2-0.8; Marek et al., 2022; Schönbrodt & Perugini, 2013; Varoquaux, 2018). Therefore, given that the studies in this thesis were generally underpowered and considering the potential for increased instability of effects in small sample sizes and cross-sectional research, it will be important for future research to replicate current findings and examine relationships between HRV, neural functioning and affective flexibility in larger, representative samples.

Nonetheless, although increasing sample size is important, research quality and the reliability of key measures has been considered to be even more crucial for statistical power (Makowski et al., 2025). Measurements with poorer test-retest reliability require greater sample sizes to reach adequate statistical power (Hedge et al., 2018; Parsons et al., 2019). The studies in this thesis utilised both resting and task-related measures of HRV that were acquired while participants were in the MRI scanner (Papers 1 and 2) or in the laboratory (Paper 3, Study 2). An early review by

Sandercock et al. (2005) documented temporal instability of HRV measures in the form of significant variability in test-retest reliability, leading to HRV being reported as a time unstable measure. On the other hand, recent research has reported HRV metrics, especially time-domain measures such as the RMSSD, to be robust across laboratory and home settings and sitting versus standing positions (intra-class correlations (ICC) often higher than 0.75) (Besson et al., 2025). Furthermore, Schumann et al. (2021) reported no systematic difference in HRV based on laboratory versus MRI settings and HRV measures exhibited good stability across conditions and signals (ECG, PPG) as indicated by high ICC values (above 0.80). Relatedly, HRV has been reported to exhibit good reliability across task conditions (reaction time task, spontaneous breathing and controlled breathing), however, trait variance was found to increase from 49% to 75% when aggregating across measurement occasions (Bertsch et al., 2012). Given that the studies in this thesis did not obtain HRV measures in the same individuals across multiple time points, it is unclear whether the HRV metrics exhibit both good stability over time and whether test-retest reliability differs based on condition (rest versus task). Future studies should aim to assess and report the reliability of HRV metrics across multiple time points and conditions alongside considering aggregating HRV across measurement periods to increase trait variance (Bertsch et al., 2012).

Alongside HRV, the current research employed a mixture of self-reported measures of trait neuroticism and rumination, and assessed behavioural measures of affective flexibility in the form of switch costs. Self-report measures have been found to demonstrate increased stability in the form of test-retest reliability in comparison to experimental/task metrics (Enkavi et al., 2019; Pennington et al., 2025). Interestingly, while test-retest reliability is typically considered when creating self-report questionnaires, the stability of individual difference variables obtained via experimental tasks has generally been neglected (Parsons et al., 2019). Wider research has reported that behavioural tasks are typically characterised by high within-subject variability with robust main effects of task at the group level, but low between-subject variability (Hedge et al., 2018). This low between-subject variability produces low reliability for individual differences (Enkavi et al., 2019; Hedge et al., 2018; Pennington et al., 2025). Similarly, behavioural measures that rely on difference scores have been reported to be inherently unreliable (Draheim et al., 2016; Hughes et al., 2014) given associations between the conditions used to calculate the difference

score and generally high within-subject versus low between-subject variability (Enkavi et al., 2019; Caruso, 2004). A combination of these factors likely underlies the inability to replicate prior findings in Paper 3 and also the lack of associations observed between self-reported individual differences in trait rumination with behavioural switch costs on the affective flexibility task. Future research should assess test-retest reliabilities of experimental tasks, especially when utilising dependent variables as an index of individual differences (Pennington et al., 2025) and also consider alternative flexibility measures, such as rate residual or bin scores (Hughes et al., 2014), to increase the reliability of flexibility measures, in turn enhancing statistical power.

5.4 Implications of the Research and Future Directions

The work of this thesis complements prior research and provides further insight into HRV as a predictor of adaptive emotional responding at the neural and psychological level. Collectively, these studies reinforce the importance of investigating heart-brain interactions in emotional contexts to elucidate key neurovisceral circuitry and mechanisms that support adaptive emotional responding at higher levels of the vagal hierarchy. This research further supports the utility of task fMRI data more generally for highlighting shared and state-specific connectivity and brain states. Since recent research has advocated for the use of more naturalistic paradigms (i.e., movie watching) to constrain the variance in a manner that increases sensitivity to capture and detect individual differences over pure resting-state paradigms (Finn, 2021; Finn & Bandettini, 2021), it may be beneficial for future work to employ naturalistic paradigms to study HRV and neurovisceral circuitry.

Critically, the current research has broader implications for the potential utility of HRV as a non-invasive and objective psychophysiological marker for promoting more effective and appropriate emotional responding across contexts. In all three papers, HRV was consistently linked to neural and performance-based indices of adaptive emotional responding, and in the case of Paper 3, was found to be the sole predictor of attentional shifts pertaining to the valence of emotional material. HRV provides insight into the neurobiological underpinnings of adaptive emotional responding while also overcoming limitations linked to self-reported emotion regulation or flexibility, such as social desirability bias or misunderstanding of questionnaire items (Seeley et al., 2015; Visted et al., 2017). Relatedly, HRV is a malleable metric that can be altered using biofeedback or vagus nerve stimulation methods. Therefore, since

HRV appears to reflect adaptive emotional responding, it could potentially be used as a complementary target for the prevention or management of emotion dysregulation which is usually a feature of psychological disorders, such as anxiety and depression (Cisler et al., 2010; Joormann & Stanton, 2016). Notably, HRV also has implications for physical health and has been found to predict cardiovascular disease markers (Thayer et al., 2010). Thus, HRV could serve as a potential complementary treatment target for physical and mental health comorbidities, (e.g., links between cardiovascular disease risk and depression; Hare et al., 2014).

Despite important contributions and implications of the current work, research examining concurrent heart-brain associations across contexts requiring adaptive emotional responding remain relatively scarce. While the present findings provide some supporting evidence for the NIM during active emotion regulation and flexible emotional processing, findings were fairly weak and not as robust as anticipated and the directionality of these findings remains unclear. Therefore, a clear and critical avenue for future research will be the adoption of causal experimental designs, via HRV biofeedback or transcutaneous vagal nerve stimulation, to assess the degree to which individual differences in HRV predict emotion flexibility across various contexts. Existing studies have started to implement HRV biofeedback interventions to observe how HRV changes impact neural circuitry during rest and emotion contexts (Nashiro et al., 2023a; Schumann et al., 2021), however, the biofeedback intervention periods have been relatively short (i.e., 5 to 8 weeks). Future work should assess the longer-term impact of HRV changes and the subsequent influence this has on relevant indices of adaptive emotional responding, alongside interaction effects with other emotional disposition variables. Relatedly, (HF-)HRV is proposed to be a transdiagnostic biomarker of psychopathology, however, if HRV is to be considered a potential complementary target for emotion dysregulation underlying psychological disorders, it will be critical to assess the impact of biofeedback interventions in relevant clinical samples across tasks with varying contextual demands (i.e., emotion regulation, affective switching). Additionally, the consideration of various sample characteristics, including but not limited to, age, biological sex, gender identity, and ethnicity, alongside other confounding factors that have been reported to influence HRV metrics, will be important to determine how these factors influence observed associations between HRV and adaptive emotional responding.

5.5 Conclusion

The principal aim of this thesis was to examine the degree to which individual differences in HRV could predict both neural and performance-based indices of adaptive emotional responding. Collectively, the research studies lend some support for the notion that HRV reflects adaptive emotional responding, demonstrating that resting and task-related HRV show tentative associations with both neural and attention-related measures of emotion flexibility. The current work contributes to an evolving body of neuropsychological research examining heart-brain interactions, critically highlighting the importance of assessing such associations during contexts that actively require adaptive emotional responding to elucidate key neurovisceral circuitry and attentional processes that support flexible emotional responses. Critically, this research reinforces the importance of context and associated demands, showing that *in*flexibility may not always be maladaptive. This work enhances our understanding of HRV interactions with neural and performance-based measures of adaptive emotion across contexts and has potential implications for the consideration of HRV as a complementary target for managing psychological disorders characterised by emotion dysregulation, such as anxiety and depression. It will be crucial for future work to implement causal and longitudinal experimental designs, alongside the recruitment of clinical populations, to further assess HRV, trait emotional disposition, and adaptive emotional responding across various contexts.

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