SHIFTING ACROSS INTERNALLY AND EXTERNALLY ORIENTED COGNITION: BEHAVIOURAL AND NEURAL EXPLORATIONS USING TASK-SWITCHING AND RESTING-STATE PARADIGMS

By

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ABSTRACT

The human brain frequently shifts between internal and external monitoring, and these changes in cognitive content can occur spontaneously or intentionally both at rest as well as during task performance. Specific frontoparietal networks have been associated with internal and external cognition and were shown to often display anticorrelated activation. Despite this being a persistent feature of human cognition, the neuroscientific study of cognitive flexibility lacks proper investigation of the exchange between internal and external processes. Cognitive flexibility research commonly employs task-switching paradigms, which often demonstrated the presence of switch costs (decreased performance) and increased lateral frontoparietal activation in conditions where people switched between tasks as compared to repeating the same task. However, all these studies mainly focused on switching between tasks requiring attention to external stimulus features, and have not investigated switching across internal and external cognition. Specifically, no studies have ever explored task-switching involving self-referential processes. Therefore, it is of interest to the scientific community to expand our understanding of cognitive flexibility in relation to these prominent aspects of cognition. In addition to this, despite the great deal of attention towards the correlation patterns between frontoparietal networks, there is little neuroscientific research focusing on identifying specific points of change within and across these networks.

Therefore, this thesis investigates the behavioural and neural correlates of cognitive shifts across self-referential and externally oriented processes using novel task-switching paradigms, and explores the changes in brain networks subserving internal and external cognition at rest using change-point detection.

Chapter 3 finds significant behavioural switch costs both in the external and internal domain, as well as additional costs in switching between domains as compared to within each domain. Chapter 4 partly replicates these behavioural findings and finds domain-specific activation of dorsal attention and default mode network when preparing externally and internally oriented tasks, respectively, as well as domain-general preparatory control in lateral parietal regions and dorsal precuneus. Chapter 5 investigates the same task-switching dynamics with another paradigm using different tasks and stimuli, confirming the presence of switch costs in both domains, but not the presence of additional costs to between-domain switching.

Finally, Chapter 6 investigates the brain activity around change points as found through change-point detection and reveals small clusters in mediodorsal thalamus and regions of salience and default mode networks. It also explores dynamic functional connectivity and graph measures after segmentation based on this novel approach. Moreover, it examines the differences in the above measures across chronotypes, probing the effects of arousal fluctuations on brain dynamics, as induced by circadian preferences.

Together, these empirical chapters provide novel information regarding the cognitive control of domain switching when involving internally oriented versus externally oriented tasks, and regarding the resting-state dynamics of the networks underlying these processes.

Due to COVID-19, the entire trajectory of the thesis was adapted to allow the conduction of online behavioural studies (Chapters 3 and 5) and the analysis of existing datasets (Chapter 6), while waiting for in-person testing to resume (Chapter 4).

This thesis is dedicated to
my late Dad and Grandmas
Roberto (Billy), Bruna and Sira

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KEY ABBREVIATIONS

BMA	Bayesian Model Averaging
BMR	Bayesian Model Reduction
BOLD	Blood Oxygenation Level-Dependent
CCID	Cross-Covariance Isolate Detect
CTI	Cue-to-Target Interval
DAN	Dorsal Attention Network
DCM	Dynamic Causal Modelling
dlPFC	Dorsolateral Prefrontal Cortex
DMN	Default Mode Network
ECN	Executive Control Network
EEG	Electroencephalography
FC	Functional Connectivity
fMRI	Functional Magnetic Resonance Imaging
FWE	Family Wise Error
GLM	General Linear Model
IPL	Inferior Parietal Lobule
IPS	Inferior Parietal Sulcus
ITI	Inter Trial Interval
MD	Mediodorsal nucleus of thalamus
mPFC	Medial Prefrontal Cortex
PCC	Posterior Cingulate Cortex
PEB	Parametric Empirical Bayes
PPC	Posterior Parietal Cortex
ROI	Region Of Interest
rs-fMRI	Resting State Functional Magnetic Resonance Imaging
SN	Salience Network
SPL	Superior Parietal Lobule
SPM	Statistical Parametric Mapping
tDCS	Transcranial Direct Current Stimulation

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Paper 1

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Paper 2

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Chapter 1

CHAPTER 1 : GENERAL INTRODUCTION

1.1 Frontoparietal brain networks

The human brain is constantly active and engaged in mental processes, whether these are elicited by external stimulation from the environment, or whether they arise internally from our own mind.

One technique used to study brain activity is functional Magnetic Resonance Imaging (fMRI), which measures changes in blood flow as an indirect measure of changes in neural activation in a non-invasive manner (Logothetis & Wandell, 2004). Using fMRI, brain activity is typically investigated by comparing the blood oxygenation level-dependent (BOLD) signal elicited by the response to an experimental task with a control or baseline condition. Studying these signal changes allowed researchers to relate activity in specific brain regions with a vast number of cognitive, perceptual, affective and behavioural processes (Damoiseaux et al., 2006). However, in the absence of external stimulation or tasks, the resting brain is characterised by spontaneous low-frequency fluctuations in BOLD signal, that can also be measured by fMRI (Demertzi & Whitfield-Gabrieli, 2016). These endogenous fluctuations, which typically range between 0.01 - 0.1 Hz, are not random, but appear synchronised across different brain regions forming spatially and temporally organised patterns of activation (Leopold & Maier, 2012). In 1995, Biswal and colleagues found that some of these slow resting-state activation patterns (in sensorimotor areas) closely resembled those elicited by behavioural tasks (Biswal et al., 1995). Since then, a multitude of studies further revealed that the resting-state hemodynamic activity correlates with the underlying neuronal activation and reflects the intrinsic functional organisation of the brain (Leopold & Maier, 2012; Thompson et al., 2013). In fact, the fMRI activity at rest appears defined by large-scale (spatially distributed) groups of cortical and subcortical regions that exhibit temporal correlation, the so-called ‘intrinsic connectivity networks’ (Damoiseaux et al., 2006; Laird et al., 2011; Seeley et al., 2007). These functional networks show a strong (but not complete) resemblance with structural connections (Damoiseaux & Greicius, 2009) and with task-related activation patterns (Gonzalez-Castillo et al., 2015; Laird et al., 2011; Smith et al., 2009). This

suggests that functional networks are based on structural constraints, but flexibly reconfigure between (and within) rest and task to allow changes in cognitive content and behaviour based on contextual needs (Cohen & D'Esposito, 2016).

Some of the key intrinsic resting-state networks more frequently identified - often using independent component analysis (ICA) - are: the default mode (DMN), visual, auditory and sensorimotor networks, the executive control (CEN) and salience networks (SN), ventral and dorsal attention networks (VAN and DAN), a basal ganglia/limbic network and a cerebellar network (Damoiseaux et al., 2006; Moussa et al., 2012). In the next paragraphs, I will focus on those networks that have been more tightly linked with higher-order cognitive processing rather than first-order sensory and perceptual processing, as the focus of this thesis is mainly on the goal-directed preparation of working-memory and semantic categorisation tasks and self-referential tasks (Chapters 3-5), and on the resting-state dynamics of the networks underlying such processes (Chapter 6).

1.1.1. Default Mode network

The Default Mode network (DMN) has received a great deal of attention due to its multifaceted cognitive and physiological properties and its wide range of functions. The main core of the DMN encompasses the medial prefrontal cortex (mPFC), the posterior cingulate cortex/precuneus complex (PCC), and inferior parietal lobule/angular gyrus (Raichle, 2015). According to seminal studies, the DMN is more active at rest and during passive tasks (Greicius et al., 2003; Shulman et al., 1997), while it appears deactivated during attentional tasks (Buckner et al., 2008). These initial findings contributed to the definition of DMN as a "task-negative" network, associated with spontaneous, stimulus-unrelated thoughts, and mind-wandering (Christoff et al., 2009). This definition has since been disputed, given the emerging evidence of a much wider engagement of DMN in a number of cognitive domains. In fact, the DMN has been found active during tasks that elicit self-related processing, affective and social decision-making, theory of mind, internal mentation, autobiographical memory and future planning (Andrews-Hanna et al., 2010; Spreng & Grady, 2010). Given this variety of findings, some researchers hypothesised that DMN

might not be linked to self-related thoughts specifically, but is rather responsible for scene reconstruction, mental generation and maintenance of scenarios and events more broadly. This provides a different perspective to explain its involvement in episodic memory and future planning alike, as well as theory of mind, day-dreaming and imagination (Hassabis & Maguire, 2007). Instead, Andrews-Hannah and colleagues (2010) were able to distinguish three DMN subcomponents from resting-state and from tasks requiring self-related decision-making in present and future scenarios, potentially explaining the variety of functions associated with this network. In particular, they found that, while both self-referential conditions activated midline core regions of DMN (anterior mPFC and posterior cingulate), a dorsal medial prefrontal subsystem (comprising dorsal mPFC, temporoparietal junction, lateral temporal cortex, and temporal pole) was activated in response to self-referential judgments about present situation or mental states, while a medial temporal lobe (MTL) subsystem (ventral mPFC, posterior IPL, retrosplenial cortex, hippocampal and parahippocampal cortex) was activated by decisions about personal future (both components were first identified in resting-state). This DMN subdivision was subsequently corroborated by a number of resting-state (DiNicola et al., 2020; S. Lee et al., 2021; Shirer et al., 2012), although others found further distinctions in its activation patterns (Laird et al., 2011; Smith et al., 2009), delineating the DMN as a complex and flexible system of multiple interacting hubs (Buckner et al., 2008). Given its engagement at rest and in a wide variety of high-order processes, it is not surprising to note that the DMN connectivity was found to be disrupted in a high number of neurological and psychiatric conditions, highlighting its importance for the general health of brain organisation. DMN dysregulations and/or structural impairments are in fact associated with attention deficit hyperactivity disorder (ADHD), autism, schizophrenia, depression, Alzheimer's disease and disorders of consciousness (Broyd et al., 2009; Buckner et al., 2008; Fernández-Espejo et al., 2012).

1.1.2. Dorsal Attention network

The dorsal attention network (DAN) comprises the Intraparietal Sulcus (IPS) and Frontal Eye Fields (FEF), and has been associated with external visuospatial attention

(Corbetta & Shulman, 2002). In particular, it was shown to engage in the top-down selection of stimuli and responses based on cognitive factors, acting in cooperation with the ventral attention network (right temporoparietal junction and ventral frontal cortex) which instead reorients attention to salient unexpected stimuli in a bottom-up manner (Corbetta et al., 2000; Vossel et al., 2014). Sustained activation in the DAN was initially observed in studies that cued participants about where to covertly pay attention in order to detect visual stimuli (e.g., in Posner's location-cueing paradigm; Posner et al., 1980), whereby DAN regions activated in the cueing period. This first suggested that such pre-stimulus activation was related to the anticipatory control processes needed to redirect the focus of attention to a specific spatial location (Corbetta & Shulman, 2002). Subsequently, more evidence identified a similar involvement of DAN in different types of attentive processes beyond spatial attention, such as attention to motion and other stimulus features (shape, colours, objects; Greenberg et al., 2010; Liu et al., 2003; Shulman et al., 2002) as well as auditory stimuli (Cowan et al., 2011; Majerus et al., 2016). For instance, studies that used coloured and moving dots found transient activation of DAN areas both when participants shifted their attention to the motion direction and when they shifted attention to the colour of the dots, working in concert with feature-specific areas that consistently responded only to motion or colour (T. Liu et al., 2003). Crucially, DAN regions appear to be engaged not only in the anticipatory cognitive representations needed to allocate attention, but also in the maintenance of such representations in working memory (Awh & Jonides, 2001; Jerde et al., 2012) and in the selection of appropriate responses related to the attended stimuli (stimulus-response association mapping; Rushworth et al., 2001). For instance, in typical working memory paradigms called delayed match-to-sample tasks, a test stimulus is presented a few seconds after a sample stimulus. Participants need to indicate if test and sample stimuli matched, which requires them to keep information regarding the sample stimulus in short-term memory, use that information at a later stage without the stimulus being present, and empty their memory store after each trial (Habeck et al., 2005; Pessoa et al., 2002). Sustained signals during the delay period were found in the FEF, dorsolateral PFC, pre-SMA and parietal cortices (superior parietal lobule and IPS) for successful trials as compared to incorrect ones (Habeck et al., 2005; Pessoa et al., 2002). Moreover, the strength of activity in those regions during the delay period reliably predicted subsequent behavioural performance (Pessoa et al., 2002). All in all, the broad nature

of DAN activation patterns corroborates the idea of a high-order role of this network in directing the attentional focus in a top-down manner, and manipulating related information in working memory (Cowan et al., 2011; T. Liu et al., 2003).

1.1.3. Anticorrelation between DMN and DAN

Resting-state fMRI studies often reported the DMN and DAN to be anticorrelated, i.e., to display strong negative correlations with one another during resting periods (Fox et al., 2005). Similarly, the activity within DMN was found to decrease (although not extinguished) during attentional and cognitive tasks which, as described above, induce increased DAN activity (Greicius & Menon, 2004; Raichle et al., 2001). This DMN attenuation was found to be stronger with more cognitively demanding tasks, and almost absent with extremely simple tasks that require minimal attentional resources (Singh & Fawcett, 2008). Previous research suggested that this task-related DMN deactivation was linked with optimal behavioural performance and activation of sensory areas while, vice versa, a failure in disengaging this network correlated with attentional lapses and inaccurate performance (Greicius & Menon, 2004; Kelly et al., 2008a; Weissman et al., 2006). This anticorrelation thus suggests a potential conflict between internal and externally oriented cognitive processes, which might have to compete for resources (Buckner et al., 2008), and was shown to relate to the anticorrelation observed in spontaneous cognitive contents (Vanhaudenhuyse et al., 2011). Specifically, this study showed that when participants were allowed to freely mind-wander, they reported to switch between spontaneous thoughts that were directed internally or externally every ~20 seconds, on average. Interestingly, this spontaneous switch in awareness was correlated with changes in BOLD activation in DMN and DAN areas (Vanhaudenhuyse et al., 2011). It is however important to note that, in this study, the sampling frequency of awareness content might have biased the estimation of cognitive switching, and that nonetheless participants displayed substantial variability in the anticorrelation of their awareness scores. In either case, this contributed to the notion that, even when unconstrained by tasks, the brain might cyclically undergo different cognitive states, one associated with attention to the external world and sensory processing (engaging the DAN) and one involving introspective and autobiographical exploration (engaging the DMN) (Fransson, 2005).

Studies that correlated resting-state neural activity with metanalytical findings from task-fMRI supported this view (Laird et al., 2011; Smith et al., 2009).

Such distinction between self and external environment, supposedly maintained by the anticorrelated pattern of these networks, is thought to contribute towards conscious cognition and broadly reflect a neurologically healthy brain. DMN and DAN in fact appear to be functionally disconnected in patients with disorders of consciousness (Demertzi et al., 2013), their metabolic activity being correlated with clinical scores of consciousness and with the patients' diagnosis (vegetative state, minimally conscious and emerging from minimally conscious state) (Thibaut et al., 2012).

Relatedly, research on other clinical disorders highlighted the importance of transitioning between DMN and DAN functions. For instance, altered patterns of network antagonism in schizophrenia and autism (increased and decreased anticorrelation, respectively) were linked to attentional and emotional control deficits in these conditions (Broyd et al., 2009). Further, reduced anticorrelation was associated with the increased attentional lapses in ADHD (Broyd et al., 2009; Hoekzema et al., 2014).

In contrast with the view of a central role of the DMN-DAN anticorrelation in healthy cognition, there have been other accounts that regarded this as over-simplistic and/or spurious. Notably, seminal studies (Fox et al., 2005) relied on global signal regression during preprocessing, in order to remove artefact from motion, respiration and cardiac activity. However, this technique might artificially induce negative signals, possibly leading to artefactual anticorrelations or inflating existing ones (J. Li et al., 2019). This sparked a debate and further research on the matter, since weaker anticorrelations or even independence between DMN and DAN were reported among studies that did not apply global signal regression (Dixon et al., 2017; Hampson et al., 2010; Murphy et al., 2009; Weissenbacher et al., 2009). On the other hand, valid negative correlations were demonstrated after alternative preprocessing steps, reinforcing the biological plausibility of the original findings (Chai et al., 2012; Chang & Glover, 2009; Fox et al., 2009).

Beyond this methodological issue, the view of a purely competitive relation between DMN and DAN was undermined by findings of a DMN involvement in a number of external cognitive tasks (Elton & Gao, 2015). For instance, increased DMN activation correlated with fast performance in low-demand target-detection tasks (Gilbert et al.,

2006; Hahn et al., 2007). This led researchers to hypothesise a role of DMN regions in supporting a type of broad, general attention ('watchfulness') in place during a state of relaxed exploration of the environment that does not require focused attention (Buckner et al., 2008; Gilbert et al., 2006).

Another hypothesis which recently emerged from studies of dynamic functional connectivity (FC) is that the correlation patterns across networks are transient rather than a ubiquitous and constant property, and may vary across time depending on cognitive states and context (Dixon et al., 2017; Douw et al., 2016). Dixon and colleagues indeed performed a dynamic resting-state FC analysis using 60 s sliding windows, and found alternating periods of negative and positive DMN-DAN correlations, with a percentage of anticorrelation in around 67% of time-windows (Dixon et al., 2017). Moreover, the authors tested the DMN-DAN interaction across a number of different cognitive contexts (rest, movie watching, artwork analysis, shopping task, evaluation-based introspection and acceptance-based introspection), and found the network interaction to be highly variable across states. In addition, DAN had variable interactions with different DMN subsystems, whereby negative correlations were mainly observed with core DMN regions only. Other studies also found different anticorrelations patterns in different DMN subcomponents (Fornito et al., 2012; Uddin et al., 2009). Interestingly, a support vector machine classifier was able to reliably discriminate across cognitive states based on such interaction patterns (Dixon et al., 2017). These and other similar findings suggest more complex dynamics are at play, in which current environmental demands and mental context dynamically interact to give rise to flexible connectivity patterns (Dixon et al., 2017; Douw et al., 2016; Fornito et al., 2012; Spreng et al., 2010).

1.1.4. Frontoparietal Control networks

An important question in the study of the aforementioned dynamics is how frontoparietal networks are recruited and what mechanisms mediate between them. In this context, two other intrinsic networks have been extensively studied for their potential role in supporting large-scale neural changes during cognition.

The Executive Control network (ECN; also known as Central Executive network) mainly comprises bilateral dorsolateral prefrontal cortex (dlPFC) and posterior parietal

cortex (PPC). ECN is engaged by cognitively demanding tasks that involve voluntary decision-making and executive control. It was in fact implicated in various stages of goal-directed cognition, such as learning and rule encoding (Hampshire et al., 2019), inhibition of irrelevant stimuli (Bunge et al., 2001) and decision-making (Koechlin & Hyafil, 2007).

The Salience network (SN), which encompasses bilateral anterior insula and anterior cingulate cortex (ACC), instead responds to various kinds of salient and events both in cognitive and interoceptive settings, i.e., stimuli that are relevant from a cognitive, emotional or homeostatic perspective (A. D. Craig, 2002; Critchley et al., 2004; Seeley et al., 2007). The right anterior insula is activated by a plethora of interoceptive processes such as awareness of visceral sensations, heartbeat detection, emotional processing of pain and much more (Menon & Uddin, 2010). The dorsal ACC instead appears to be recruited during error and conflict detection (Botvinick et al., 2004). Together, these regions are thought to detect salient information across external (environmental) and internal (personal and bodily) signals (Menon & Uddin, 2010). The SN also includes limbic and subcortical areas such as amygdala, mediodorsal thalamus, hypothalamus and other regions related to homeostatic regulation, which are often disregarded in cognitive studies (Seeley et al., 2007).

The involvement of these networks in regulating internal and external cognition (and related networks) is widely accepted nowadays. Still, the exact mechanisms behind such regulation are still debated. Some studies investigated ECN and SN as a single 'frontoparietal control network' (FPC). This research suggested that FPC is anatomically interposed between DMN and DAN, and demonstrated that it can coordinate the activation of these two networks (Dixon et al., 2017; Gao & Lin, 2012; Spreng et al., 2013; Vincent et al., 2008). For instance, Gao & Lin investigated functional and effective connectivity during a resting-state, a finger tapping and a movie watching condition (Gao & Lin, 2012). They found a positive FPC-DAN correlation and a negative FPC-DMN correlation during finger-tapping, but the opposite correlation pattern (positive FPC-DMN and negative FPC-DAN) during movie watching (both as compared to rest). Granger causality revealed directional connectivity from FPC to both DMN and DAN, highlighting its causal role in regulating those networks. Similarly, Spreng and colleagues found that autobiographical and visuospatial planning engaged DMN and DAN, respectively, while both activating the FPC (Spreng et al., 2010).

Still, a number of studies also demonstrated ECN and SN display differential activation patterns (Petersen & Posner, 2012). This was demonstrated during a number of cognitive tasks (Crittenden et al., 2016; Dosenbach et al., 2006; Hampshire et al., 2012), but also emerged from intrinsic resting-state correlation patterns, where correlation within these two networks was stronger than the correlation between them (Dosenbach et al., 2007).

Seminal studies even pointed at a role of the SN in recruiting DMN or ECN based on salient stimuli (Goulden et al., 2014; Menon & Uddin, 2010; Seeley et al., 2007; Sridharan et al., 2008). For instance, the right anterior insula displayed a high degree of causal outflow towards both ECN and DMN regions when investigated with Granger Causality (Sridharan et al., 2008). This was true during resting-state as well as during visual odd-ball and music listening paradigms (Sridharan et al., 2008).

Overall, SN and ECN were shown to support reallocation of cognitive resources in response to current environmental demands, including the reorganisation of other frontoparietal networks (Menon & Uddin, 2010). Nonetheless, while it is possible to delineate broad functional characteristics of each network, the literature still presents mixed results regarding the specific dynamics subserving their interaction.

1.1.5. Thalamus and thalamocortical connections

The thalamus is a complex and multifaceted structure that comprises a number of specialised subnuclei, each receiving inputs from a different sensory modality and projecting to different cortical areas. The thalamus is in fact traditionally known as a relay station that conveys relevant sensory, motor and autonomic information to the cortex (Sherman & Guillery, 1996). Another major thalamic function (midline and reticular nuclei in particular) is the control of arousal and sleep-wake cycles (Gent, Bassetti, et al., 2018; Llinás & Steriade, 2006), particularly the generation of sleep spindles during sleep onset as well as of slow-waves in later sleep stages (Gent, Bandarabadi, et al., 2018; Steriade et al., 1993). Moreover, higher-order thalamic nuclei that connect to multiple sensory and associative areas were shown to serve an integrative and modulatory function in attention, perception, and arousal processes (Sherman, 2016).

Recent accounts suggest that the thalamus is well positioned to serve as a major hub for large-scale brain connectivity, given its widespread connections with a high number of cortical and subcortical regions (Hwang et al., 2017; Nakajima & Halassa, 2017). Of particular importance in the context of cognition and large-scale cortical networks is the mediodorsal thalamus (MD). Several studies on humans have indicated strong functional and structural connectivity between MD and core DMN regions, especially precuneus and mPFC (Cunningham et al., 2017; Fransson, 2005; Greicius et al., 2007; Tomasi & Volkow, 2011). Others have also demonstrated connections with the anterior insula and SN regions (Eckert et al., 2012; Menon, 2015), suggesting that the thalamus may serve as a hub that binds the rest of the SN components together (Seeley et al., 2007). Crucially, recent high-resolution parcellation studies found that each thalamic nucleus (Hwang et al., 2017), and even each fine-grained subregion of MD (Li et al., 2022), have specific preferential patterns of functional connectivity with multiple cortical intrinsic networks, including DMN, DAN, ECN and SN. This suggests that the thalamus plays a fundamental role in the organisation of cortical dynamics more broadly, and in the integration of multimodal information (Hwang et al., 2017). Disrupted communication between thalamus and frontoparietal networks was in fact found in patients with disorders of consciousness (DOC), suggesting a fundamental role of these projections in the maintenance of healthy brain functioning (J. S. Crone et al., 2014; Fernández-Espejo et al., 2012; Monti et al., 2015; Weng et al., 2017). DOC patients showed bilateral MD atrophy specifically (Fernández-Espejo et al., 2010), as well as significantly decreased functional and structural connectivity from MD to mPFC and precuneus as compared to healthy controls (Fernández-Espejo et al., 2012; J. H. He et al., 2015; Lant et al., 2016).

Despite this region being equipped with such widespread and diverse connectivity patterns to high-order cortical networks, little attention has been directed to the potential contribution of the thalamus to human cognition. In particular, its role in cognitive functions during task-based paradigms is still largely unexplored and/or overlooked in humans, as research focused almost exclusively on cortical areas. This can be mostly attributed to the inherent technical difficulties associated with non-invasive functional imaging of subcortical structures in general (e.g., lower sensitivity and spatial resolution at low field strengths due to greater distance to the head coils, small size of the nuclei and more artefacts due to motion and physiological noise; iron-rich nuclei requiring different acquisition parameters and contrasts) (Forstmann et al.,

2017; Isherwood et al., 2021; Johansen-Berg, 2013; O'Callaghan et al., 2013). Nonetheless, the available evidence calls for a more explicit effort to focus on thalamic functions in cognition.

Recent investigations on rodents and non-human primates implicated MD-mPFC connections in the regulation of cognitive processes such as memory, learning and processing of newly acquired information, reward associations, working memory and decision-making (Baxter, 2013; Bolkan et al., 2017; Browning et al., 2015; Mitchell, 2015; Parnaudeau et al., 2018). In humans, this has been acknowledged in clinical settings, mostly by observing the effects of thalamic lesions or dysfunctions in neurological and psychiatric disorders (Pergola et al., 2018). Notably, one study on epileptic human patients undergoing deep brain stimulation found evidence of a causal role of MD in working memory, inhibition and set-shifting, as measured by a modified go/no-go task (Peräkylä et al., 2017).

Ground-breaking optogenetic studies on mice also revealed a causal role of MD thalamus in cognitive flexibility, providing evidence of the specific role of its connections with the mPFC (Rikhye et al., 2018; Schmitt et al., 2017). Mice were trained to perform a cued attentional control task: they had to pay attention to a sensory cue in order to make a selection among two competing targets and receive milk as reward. In each trial, a cue signalled the mice to either focus on a flash of light or a sound, which were simultaneously presented either to the left or to the right of their enclosure. A subset of PFC neurons responded to initial cues, while another PFC assembly responded to the task rule (i.e. attend to light or sound), showing a clear hierarchical cue-to-rule transformation. However, while task performance was initialised and supported in the PFC, MD neurons were found to be recruited to sustain the appropriate task-relevant cortical representations (excitatory MD neurons), and suppress irrelevant representations (inhibitory MD neurons) based on contextual cues. In other words, MD neurons allowed mice to flexibly switch between different rule contexts, providing fundamental support for the dynamic creation of cortical patterns during contextual changes (Rikhye et al., 2018; Schmitt et al., 2017). This shows that the thalamus (MD in particular) supports abstract cognitive representations regardless of sensory modality, and does so in a highly flexible manner to allow adaptive cognitive changes. This recent evidence, along with the known role in arousal regulation, raised a novel interpretation of MD engagement as a process of "directed arousal" that stands between general arousal and the processing of specific cognitive content (Nakajima &

Halassa, 2017). It is thus plausible to hypothesise that this widely connected and adaptable region is an integral part of cortical network organisation and of cognitive control. As such, more research should focus on formally assessing its place in current frameworks of neural and cognitive regulation (Hwang et al., 2017; Nakajima & Halassa, 2017; Pergola et al., 2018).

1.2 Internally oriented cognition, self-referential processing and interoception

In addition to scanning the environment for potentially relevant stimuli such as food or hazards, our minds also turn inwards to generate thoughts and scenes that are unrelated to the external world, such as when recollecting past memories and planning the future. These two different phenomena have been referred to as externally oriented and internally oriented cognition, respectively (Dixon et al., 2014). Both are thought to reflect fundamental and recurring signatures of human cognition, and are often regarded as opposed or complementary to each other.

Internally oriented cognition is generally thought to direct attention to internal stimuli inside our head or body, usually thoughts, experiences or feelings (Dixon et al., 2014; Lieberman, 2007). A number of cognitive processes are included in this definition, such as autobiographical memory and the related re-enactment of past experiences, mental imagery, simulation of future events, theory of mind, and stimulus-unrelated thoughts such as mind-wandering - especially when including self-referential elements (Andrews-Hanna, 2012; Buckner et al., 2008; Dixon et al., 2014).

Some researchers distinguished between internal and external attention purely based on the presence or absence of perceptual targets, thus labelling processes like working memory and response selection as internal, given that they operate in the absence of immediate external stimulation (Chun et al., 2011; Gilbert et al., 2005; Verschooren, Schindler, et al., 2019). Other traditional accounts have instead regarded internal cognition as mostly spontaneous (as well as independent from external inputs), due to the initial discovery of mind-wandering during resting-state and related attentional lapses during tasks (Kelly et al., 2008a; Mason et al., 2007; Weissman et al., 2006). In fact, mind-wandering (often described as an internal flow of thoughts that is unconstrained by external stimuli) has been one of the most studied

internal processes in recent years (Christoff et al., 2009). However, it is important to note that internally oriented cognition can take place both in the presence or absence of external stimuli (e.g. task-free mind-wandering or attentional fluctuations during a repetitive task) (Schooler et al., 2011). Moreover, despite being generally decoupled from perceptual elements, internally oriented cognition can be also initiated by external stimulation (e.g., memory recall sparked by a visual stimulus) (Schooler et al., 2011). Dixon and colleagues make a further distinction between spontaneous and intentional cognition, with the idea that intentionality is a continuous dimension that applies to both external and internal processes (Dixon et al., 2014). Examples of intentional, goal-directed and externally triggered internal processes are widely available: e.g., voluntarily planning and simulating future scenarios based on current goals and requirements (such as bills to pay, school exams, etc…).

In this thesis I will mainly focus on self-referential, autobiographical and interoceptive processes, i.e., on processes that relate to the inner mental and physical life of individuals, regardless of their level of intentionality and the presence of external stimuli, as proposed by (Dixon et al., 2014). Working memory is instead defined as the short-term maintenance and manipulation of information and has been often involved in executive functions and in modulating attention (Baddeley, 2003). As such, it displays features of externally oriented cognition too (Chun et al., 2011), and thus I will not discuss it as an internal process henceforth in this thesis.

1.2.1 Self-referential processes

The internally oriented processes defined above are all inherently based upon personal and subjective experiences or thoughts, even if blended with other aspects of cognition to various degrees. For instance, various forms of social reasoning such as theory of mind or empathy are based on a first observation of 'external stimuli' (i.e., other people and their behaviour). However, people need to be able to distinguish between themselves and others while carrying out embodied simulations of their experiences (Lieberman, 2007). Similarly, thinking about the future requires the ability to construct mental images and simulate scenarios, and has an important role in goal-directed planning and decision-making (D'Argembeau, 2020). Still, this first and foremost necessitates retrieval of autobiographical knowledge about one's self, in

order to create meaningful scenarios that can be integrated with personal goals and expectations (D'Argembeau, 2020). Therefore, all these processes require an underlying knowledge of the concept of "self" and the ability to manipulate that information. But what do we mean with "self" and how can we scientifically define such an abstract concept? Approaching the self from a neuroscientific point of view led some researchers to distinguish between different cognitive phenomena related to it. For instance, the ability to visually recognise oneself (e.g., one's own face in a mirror or in photographs) as well as to experience a bodily sense of ownership associated with sensorimotor and proprioceptive elements has been defined as self-recognition or "proto-self" (Lieberman, 2007; Northoff et al., 2011). Instead, self-reflection relates to the ability to consciously reflect upon one's own current and/or past experiences and gain explicit insight into one's own situation (Lieberman, 2007). This also includes the ability to make judgements upon one's own self-concept in terms of trait and personality (Christoff et al., 2011). This concept implies a mixture of core and autobiographical self, as it includes access to self-knowledge, i.e., fixed self-schemas or representations, as well as the notion of self within time (past, present and future events) (Lieberman et al., 2004; Northoff et al., 2011). The cognitive processes involved with evaluating, judging and manipulating these mental self representations are generally known as 'self-referential' processing (Christoff et al., 2011; Northoff et al., 2011).

Other forms of self-referential processing, as proposed by Lieberman and colleagues, involve self-regulation and control such as intentional impulse control and reappraisal of emotional events, or even more automatic processes like affective labelling (Lieberman, 2007). However, the empirical chapters of this thesis will focus on cognitive aspects such as those defined by Christoff and Northoff above, since they rely more heavily on internal inputs and internally-generated thoughts as compared to self-control and recognition which were shown to rely on largely different neural mechanisms involved with either processing of external stimuli or executive functions (Christoff et al., 2011; Lieberman, 2007).

In order to isolate the neural correlates of these self-referential processes, fMRI studies mainly employed event-related or block paradigms that contrast "self" versus "non-self" conditions and/or tasks (Christoff et al., 2011). Participants are often presented with stimuli such as words, pictures or faces. In the "self" conditions they usually have to judge the degree of self-relatedness, meaning if they feel that they

personally relate to the stimuli because they become aware of themselves once they see those stimuli (Northoff et al., 2011). In control conditions, they either have to judge if the stimuli relate to someone else (e.g., a close friend, a family member, a famous public figure) or perform control tasks with a more external focus (e.g., count the number of vowels in words, discriminate between male and female faces, discriminate between indoor and outdoor pictures,...) (Lieberman, 2007; Northoff et al., 2011). For instance, Davey and colleagues used a block design in which they asked participants to either judge whether written trait adjectives described their personality or count the number of vowels in the written traits (Davey et al., 2016). Similarly, other studies compared self-referential judgement of written traits with case (lowercase vs uppercase of trait adjectives; Kelley et al., 2002) or valence judgement of written traits (positive vs negative; Whitfield-Gabrieli et al., 2011). These studies found that mPFC and PCC were activated by self-related judgments as compared to externally oriented tasks. Importantly, these regions were found to overlap with core DMN regions activated at rest, although comparing self-referential judgements with resting-state also resulted in differential DMN activation. Specifically, while self-referential judgements engaged more left-lateralised prefrontal regions of DMN, posterior and parietal DMN regions activated more during rest (Davey et al., 2016; Whitfield-Gabrieli et al., 2011). Instead, studies that compared self-referential judgements with judgements about familiar others found a specific engagement of the mPFC (D'Argembeau et al., 2007; Fossati et al., 2003; Johnson et al., 2002; Kelley et al., 2002). Similar findings came from studies employing different stimuli (e.g., affectively normed pictures) as well as from studies on memory, suggesting results are not tied to one specific stimulus or task type. In fact, in a seminal study, Gusnard and colleagues asked participants to judge the pleasantness of pictures or to discriminate whether they depicted an indoor or outdoor scene, finding increased mPFC activation associated to self-reflection as compared to the externally oriented control task (Gusnard et al., 2001). This was also found when making decisions about colours based on self preference versus external features such as hue or luminance (Johnson et al., 2005). On a different note, memory studies found mPFC activation during autobiographical memory (re-living of personal events from the past) but not during episodic memory of non-personal items (retrieval of previously encoded lists of stimuli), which instead activated more dorsolateral portions of PFC (Gilboa, 2004). Finally, DMN core regions (mPFC and PCC) were engaged by self-reflection across

different times (past, present and future), showing modulations related to different temporal perspectives (i.e., increased mPFC activity for present self-reflection in D'Argembeau et al., 2008, 2010; engagement of medial temporal DMN subcomponent during judgement about future self in Andrews-Hanna et al., 2010).

As can be noticed from the above description, most studies used fMRI measures and differentiated self-referential vs non-self conditions based on neural activity. This is due to the subjective and personal nature of the topic under investigation, which makes the use of purely behavioural or cognitive measures non-trivial. Nonetheless, sparse behavioural evidence exists which suggests that self-relevant information might be qualitatively different from other non-self information and promote further elaboration and encoding (Fossati et al., 2004). For instance, self-referential decisions in present and future situations were associated with higher mental imagery and vividness scores as rated by participants, as compared to semantic tasks that were not self-related (Andrews-Hanna et al., 2010). Furthermore, self-relevance was also associated with better memory performance: traits that were judged as self-referential were associated with increased subsequent recollection and/or recognition as compared to non-self-referential ones, showing that the memory system is biased towards self-related information (Fossati et al., 2004; Kelley et al., 2002; Macrae, 2004). Crucially, these effects were not only related to the level of stimulus encoding in the self-referential condition, since they were also present when comparing self-referential judgement versus judgements towards familiar others, both requiring semantic processing (Kelley et al., 2002). Finally, self-evaluation was also shown to modulate cognitive control during a N-back task (Bengtsson et al., 2011). Adaptive performance monitoring was in fact increased after participants were primed to think positively about themselves ('clever') as compared to thinking negatively. All in all, this evidence proved the uniqueness of self-processing, its importance for every-day cognitive activities and its interaction with a wide variety of brain functions.

1.2.2 Interoception

The term interoception refers to the perception of visceral sensations from various organs as well as internal bodily states, as opposed to exteroception (perception of stimuli outside the body) (A. D. Craig, 2002). One of the most commonly studied

phenomena is brain-heart interaction, although neural responses to respiration, gastric and intestinal sensations (e.g., thirst, hunger) and more (e.g., genitourinary, nociceptive, thermal sensations, …) have also been investigated (Prentice & Murphy, 2022).

Researchers have subdivided interoception in three main components: interoceptive accuracy, interoceptive sensibility and interoceptive awareness (Garfinkel et al., 2015). Interoceptive accuracy is the most studied component of interoception in neuroscience. For instance, the vast majority of studies investigated heartbeat evoked responses via heartbeat counting or discrimination tasks, while less studies also looked at respiration via load or resistance detection tasks, or at gastric interoception via distension detection tasks (Prentice & Murphy, 2022). More variations exist, all aimed at measuring an objective ability to detect or discriminate interoceptive signals. Interoceptive sensibility instead refers to the subjective evaluation of one's own ability to detect and perceive interoceptive sensations (Garfinkel et al., 2015). This component is traditionally assessed with self-report questionnaires (e.g. the Body Perception Questionnaire by Porges and colleagues; Cabrera et al., 2018) or confidence ratings. Finally, interoceptive awareness measures the correspondence between objective and subjective dimensions (accuracy and sensibility), thus providing information on the metacognitive abilities of participants (Garfinkel et al., 2015). These different dimensions of interoception are partially independent and weigh differently on cognitive and perceptual processes, which can provide complementary viewpoints for the characterisation of brain-body interactions (Forkmann et al., 2016; Garfinkel et al., 2015).

Beyond its important role in homeostatic regulation, interoception was proven to be an integral part of a number of internally-oriented cognitive processes such as subjectivity, sense of agency, body ownership, selfhood and emotional processing (Christoff et al., 2011; Garfinkel et al., 2014; Northoff, 2011; Seth & Tsakiris, 2018), but also for perceptual processes and decision-making (Salvato et al., 2020; Tallon-Baudry et al., 2018; Werner et al., 2009). In fact, neural responses to interoceptive signals were shown to aid performance in perceptual tasks, such that a higher amplitude in heart-evoked responses predicted correct perception of visual stimuli (Park et al., 2014). This appears to relate to the presence of fluctuations in the subject-centred perspective (i.e., experiencing things in first-person), which can enhance or diminish conscious perception (Tallon-Baudry et al., 2018). Moreover, neural

responses to heartbeat were shown to correlate with highly self-relevant spontaneous thoughts during task-free mind-wandering (Babo-Rebelo, Richter, et al., 2016; Babo-Rebelo, Wolpert, et al., 2016). Interestingly, in these studies, changes in heart-evoked responses depending on the intensity and level of self-relevance activated DMN regions (ventral precuneus and mPFC) along with the anterior insula (Babo-Rebelo, Richter, et al., 2016; Babo-Rebelo, Wolpert, et al., 2016). These results are fascinating because the majority of literature instead points at a major role of insula and anterior cingulate cortices in processing interoceptive signals (A. D. B. Craig, 2009; Critchley et al., 2004). This is likely due to the fact that the neuroscientific investigation of interoception has been mainly conducted with paradigms measuring objective interoceptive accuracy. Very little is known regarding the neural correlates of self-reported interoceptive sensibility per se, or the interaction between interoceptive accuracy and self-referential measures. The need for further investigation in this regard is supported by findings indicating that thinking about one's own emotional state and directly experiencing emotions are not completely analogous from a functional perspective (Lieberman, 2007; S. F. Taylor et al., 2003).

1.3 Externally oriented cognition and cognitive control

In psychology and neuroscience, the majority of research in the last few decades has mainly focused on externally oriented cognition, as it allows humans and other animals to navigate the environment (e.g., to search for food) and keep away from threats. Moreover, it is more easily assessed with objective measures and behaviour as compared to internally oriented processing, since it does not rely on subjective reports (Buckner et al., 2008; Gonzalez-Castillo et al., 2021). Externally oriented cognition is a broad term that refers to a variety of cognitive processes that require attention directed to elements of our surroundings outside of our body and mind, but also the subsequent manipulation, processing and encoding of those stimuli, along with the actions made in response to them (Chun et al., 2011; Dixon et al., 2014). A basic requirement of this type of cognition is that it involves the presence of a physical external stimulus (as opposed to internal cognition as reviewed in section 1.2), whether because it is perceptually salient or because it is required or sought in order

to fulfil a goal. In particular, external stimuli can be perceived via all sensory modalities, although more likely through “distal” senses such as vision and audition, as opposed to bodily and interoceptive signals (Dixon et al., 2014).

Both low-level and higher-order attentional processes belong to this category. For instance, the alerting and orienting components of attention allow to prepare for incoming stimuli and to direct our focus upon stimulus presentation, respectively (Petersen & Posner, 2012). Attentional reorienting can happen spontaneously via the exogenous or bottom-up detection of perceptually salient stimuli (supported by ventral frontoparietal regions), or voluntarily via endogenous or top-down selection of relevant information based on current goals and needs (supported by DAN) (Corbetta & Shulman, 2002). Prominent studies in the field suggest that elements in a scene all compete to access cortical responses, and that top-down signals (e.g., from long-term memory) interact with perceptual information to bias selection towards behaviourally relevant elements (Corbetta et al., 2008). These processes have been primarily investigated in the visual domain, although there is evidence linking similar mechanisms to other sensory modalities such as touch and audition (Downar et al., 2000).

Beyond selective attention, humans rely on further executive control processes that support goal-directed adaptive behaviour, flexible adaptation to novel circumstances, and abstract reasoning e.g., problem-solving (Diamond, 2013; Gilbert & Burgess, 2008). More specifically, executive functions include a range of cognitive processes such as working memory, stimulus and response inhibition, conflict monitoring, and cognitive flexibility (Diamond, 2013). Frequently used paradigms for the study of executive control include the Wisconsin Card Sorting Test, the Tower of London test and the Trail-Making Test (Gilbert & Burgess, 2008). During executive control tasks, the brain needs to encode and maintain relevant stimuli, select and activate the rules needed to respond appropriately (stimulus-response mappings), and initiate the response (Corbetta et al., 2008; Gratton et al., 2018). In doing so, working memory allows to temporarily hold and manipulate a limited amount of information during a (short) delay period (Baddeley, 2003). Moreover, we monitor performance and engage conflict monitoring processes to detect the presence of contrasting information (e.g., during Stroop or Simon tasks where the same target stimuli can afford correct or incorrect responses), in order to compensate with attentional adjustments (conflict adaptation) (Enriquez-Geppert et al., 2010). Relatedly, we require inhibitory

mechanisms to stop task-irrelevant information from entering working-memory (in situations where there are target and distractor stimuli), and/or suppress competing inappropriate responses and actions (Schmidt et al., 2007). Response inhibition was found to activate regions of ECN and SN such as inferior frontal gyrus, anterior insula, anterior cingulate, pre-SMA and subthalamic nucleus in stop signal and go/no-go tasks (Aron et al., 2014), while conflict monitoring was shown to engage partially overlapping areas such as inferior frontal gyrus, dorsal anterior cingulate/midcingulate regions in those same paradigms (Botvinick et al., 2004; Enriquez-Geppert et al., 2010).

1.4 Cognitive flexibility and task-switching paradigms

Cognitive flexibility is a fundamental component of adaptive behaviour, as it allows us to promptly reconfigure our cognitive systems to meet changing environmental demands (Badre & Wagner, 2006; Dosenbach et al., 2007). Cognitive flexibility is a broad term that refers to the ability to mentally shift across different concepts or representations based on context ('set-shifting'), and is tightly linked to behavioural flexibility, i.e., the ability to adaptively adjust behaviour in response to new environmental changes (Kiesel et al., 2010; Uddin, 2021). This type of flexible control was shown to be compromised in a number of clinical conditions such as ADHD, autism and schizophrenia, and is often impaired in dementia (Uddin, 2021). Cognitive flexibility has been mostly studied with the use of task-switching paradigms (Dosenbach et al., 2006), which I will discuss in detail in this section.

1.4.1. Main characteristics and findings

Task-switching paradigms are widely used to study the processes underlying human cognitive flexibility, and have received a great deal of interest in the last 2 decades (Kiesel et al., 2010). In these experiments, participants perform one out of two (or more) possible tasks in each trial. In the following trial, they either repeat the same task as the trial before, or switch to a different one. These conditions are referred to

as ‘repetition’ and ‘switch’ trials, respectively. Traditional task-switching paradigms often compare behavioural performances (RTs and error rates) in switch versus repetition trials, generally demonstrating that flexible cognitive changes have limitations and come with a cost (Vandierendonck et al., 2010). In fact, switching across tasks usually results in slower RTs and higher error rates as compared to task repetitions (Monsell, 2003). This effect is called “switch cost” (Monsell, 2003), and it has been consistently observed across a number of paradigm variations.

There are indeed many versions of task-switching experiments, where different types of stimuli and tasks are used, different sequences give rise to repetitions and switches, and participants are instructed in various ways as to what task to perform in each trial. First, a task can be defined as any specific mental operation or measurable action in response to a stimulus, such that each task involves the use of a specific ‘task-set’ (Kiesel et al., 2010; Vandierendonck et al., 2010). Specifically, a task-set is a configuration of cognitive processes that usually includes the representation and classification of specific stimulus features and responses that are relevant to the task, as well as the correct stimulus-response (S-R) mapping (Kiesel et al., 2010; Monsell, 2003).

Crucially, the currently available literature mainly includes tasks that would fall within the definition of externally oriented processing as described in section 1.3, such as: categorisation of digits in relation to magnitude or parity, categorisation of letters as vowel or consonant, semantic categorisation of words or pictures (e.g., as living or nonliving), word reading, colour or object naming, or spatial localisation of a stimulus (Kiesel et al., 2010). Relatedly, stimuli can be shapes, digits, words, pictures - mostly presented visually, although there are studies presenting stimuli in the auditory domain (Koch & Lawo, 2014; Strobach et al., 2012). Stimuli are usually bivalent, meaning they are suitable for all tasks in the paradigm, and the same type of response is requested for all tasks, in order to keep confounding factors related to perceptual input and motor output to a minimum (Kiesel et al., 2010). For instance, a traditional paradigm involves presenting digits from 1 to 9 (except 5), and requires participants to switch between categorising the digits based on parity (odd/even) or magnitude (smaller or greater than 5) (Koch & Allport, 2006). Another prototypical paradigm is the Wisconsin Card Sorting Test, where participants need to select one of four cards to match it with a target card, based on rules that vary along the experiment (e.g., colour, shape or number) (Kim et al., 2012).

Researchers initially adopted a type of paradigm where blocks of fixed alternating sequences of tasks (ABAB) were compared to single-task blocks (AAA or BBB) (Allport et al., 1994). However, these paradigms are rarely used nowadays, given the clear imbalance in working-memory load across blocks (Kiesel et al., 2010). Other studies employed predictable task sequences where switches occurred after a fixed number of repetition trials (Rogers & Monsell, 1995). For instance, in a seminal study, Roger and Monsell showed pairs of one letter and one number to participants, and asked them to either categorise the letters as vowel or consonant, or the numbers as odd or even, using the stimulus location (position into upper or lower quadrants of the screen) as a signal for which task to perform (Rogers & Monsell, 1995). A different version of the paradigm involves letting participants voluntarily decide when to switch between tasks, employing bivalent stimuli but different sets of response keys to disentangle across the two tasks. While a detailed explanation of each version of this paradigm is beyond the scope of this thesis, it is interesting to notice that smaller but consistent switch costs were found in the case of voluntary switching as well (K. Arrington & Logan, 2005).

Finally, a widely used approach is the cued task-switching paradigm. In this version, an explicit cue is presented either in advance or concurrently with the stimulus, to signal which task to be performed in that trial (Kiesel et al., 2010). Cues can be explicit task names or initials ('transparent' cues) or arbitrary symbols (Vandierendonck et al., 2010). This allows for random sequences of switches/repetitions, and consequently the possibility to introduce a specific proportion of switch trials (e.g., 30%, 40% or 50%) (De Baene & Brass, 2013). Importantly, it also enables the manipulation of anticipatory preparation to study its impact on adaptive performance (Karayanidis et al., 2010). This is achieved by varying the interval length between cue and stimulus (cue-to-target interval or CTI), in addition to the period between response and the next trial (intertrial interval or ITI) (Kiesel et al., 2010). The majority of studies found that increasing the CTI reduced (but not eliminated) the switch costs, demonstrating that advanced preparation (partly) accounts for the costs (Monsell, 2003). Nonetheless, residual costs are often found, as tested with varying CTIs between 100-2500ms, as well as after long preparation times (e.g., 5 s) (Koch & Allport, 2006; Meiran, 2000; Monsell, 2003; Qiao et al., 2017).

1.4.2. Theories of task-switching

Based on seminal behavioural studies on task-switching, three main theoretical frameworks have been developed to explain the presence of switch costs. A first prominent theory by Rogers and Monsell suggests that performance decreases originate from an effortful and time-consuming process of task-set configuration during task switches (Rogers & Monsell, 1995). This active reconfiguration process involves the controlled (endogenous) retrieval and activation of the currently relevant task-set, which does not occur in task repetitions since the relevant task-set is already active (Monsell, 2003). In this view, increased RTs in switch trials reflect the time needed to perform this active reconfiguration, which is drastically reduced by advanced preparation as it can take place even before the stimulus is presented (Monsell & Mizon, 2006). However, residual switch costs after long preparation times are explained with the presence of an additional exogenous component (possibly the recruitment of the correct S-R mapping into working memory) that can only be triggered by stimulus presentation (Monsell, 2003; Rubinstein et al., 2001). This two-stage theory of reconfiguration assumes that there is a qualitative difference between task-reconfiguration and task-execution processes, as supported by findings on the additive effects of switch costs and task-execution modulations (e.g., task difficulty and stimulus discriminability) (Rubinstein et al., 2001).

An alternative theory suggests that residual switch costs result from the average of trials with successful advanced preparation (which would yield no costs) and trials where participants failed to engage in preparation (De Jong, 2000). This failure-to-engage hypothesis was derived from observing the distribution of RTs and switch costs, and makes strong assumptions about the presence of an all-or-none preparation process (De Jong, 2000). However, a more relaxed version of this hypothesis states that task preparation could happen any time after cue presentation, and thus that residual costs might be due to a mixture of fully advanced, unfinished, or delayed reconfiguration (after stimulus onset) (S. Brown et al., 2006).

A different perspective was adopted in a seminal paper by Allport and colleagues, which instead proposed that switch costs are induced by the persisting interference from previously required task-sets over the current one (Allport et al., 1994). Under this approach, switch costs are thought to reflect the time required for the passive

decay of irrelevant information and context (Allport et al., 1994). This passive interference has been referred to as task-set inertia or proactive interference, emphasising the role of involuntary residual activations, rather than the active engagement of new task-sets (Bratzke et al., 2009). In support of this account, larger switch costs were found when switching from a non-dominant to a dominant (easier and automatic) task as compared to the opposite transition, e.g., in the Stroop task where word-reading is more automatic than colour-naming, or in bilingualism when switching between native and second language (Meuter & Allport, 1999; Yeung & Monsell, 2003). This was interpreted in terms of carry-over effect from the more difficult and unfamiliar task, which requires additional effort to inhibit its strong task-set (Allport et al., 1994).

Nonetheless, some authors proposed that the inhibition of irrelevant task-sets might be part of the active process of reconfiguration, or that both active reconfiguration and passive decay coexist and contribute to switch costs (Goschke, 2000). In fact, more recent hybrid accounts of task switching support this view of a combined contribution from active and passive processes (Bratzke et al., 2009; Vandierendonck et al., 2010). The asymmetric costs due to task difficulty in the Stroop paradigm (discussed above) have been reviewed as likely reflecting a combination of carry-over effect and endogenous top-down control by many (Wu et al., 2015; Yeung & Monsell, 2003). Specifically, Wu and colleagues found event-related potentials (ERPs) associated with inhibition (N2 component) for switches to word-reading, but found components related to endogenous control (P3 and P3b) for switches to colour-naming (Wu et al., 2015). Overall, there is evidence in favour of both reconfiguration (in particular two-stage hypothesis) and interference accounts, and no findings are strong enough to completely reject either of these hypotheses, but rather they depict these as two complementary aspects of the same control process. In fact, after reviewing the available literature, Vandierendonk and colleagues suggested that the two-stage reconfiguration hypothesis could be extended to include not only a delayed endogenous reconfiguration, but also a component of interference from previous irrelevant associations at the level of stimulus presentation (second stage) (Vandierendonck et al., 2010).

1.4.3. Neuroimaging findings associated with task-switching

Beyond behavioural performance, task-switching paradigms have been adopted by a large body of neuroimaging studies, which allowed to further characterise and disentangle the processes involved in cognitive flexibility. Although extremely useful, behavioural indices such as RTs and accuracy are by definition measured at the end of the decision-making process. They thus have limitations in the amount of information they can convey, especially in the case of advance preparation (Karayanidis et al., 2010). On the other hand, neuroimaging studies have proven useful in the investigation of preparatory activation as well as in the nuanced characterisation of general control processes versus domain- and task-specific control.

A number of fMRI studies found that frontoparietal brain regions are more active during switch trials as compared to repetitions, including mPFC, lateral PFC (lPFC) / inferior frontal junction (IFJ), and PPC (often involved in S-R associations). According to a seminal meta-analysis, IFJ and PPC in particular were found to activate in a variety of task-switching paradigms (Kim et al., 2012). Nonetheless, while many studies frequently mention the involvement of a generic frontoparietal control network (supposedly the ECN, as reviewed in section 1.1.4), findings are actually quite heterogeneous, particularly regarding frontal activations (Brass & Cramon, 2004). In fact, in the same meta-analysis cited above, Kim and colleagues found that perceptual (i.e., attentional shifts across stimulus features) and contextual switches (e.g., shifts in abstract categorisation rules) also engaged pre-SMA, ACC, temporal and visual areas, in addition to IFJ and PPC (Kim et al., 2012). Further, only perceptual switches also engaged portions of the DAN such as FEF, while only contextual switching also activated mPFC, lPFC, inferior and middle frontal gyri, cuneus and precuneus (Crone et al., 2006; Kim et al., 2012). This variability very likely depends on specific task parameters and demands, and is also accompanied by the presence of multiple types of preparatory pre-stimulus processing distributed across frontoparietal areas, when cued paradigms are employed (Ruge et al., 2013). In fact, task-switching preparation (i.e., cue-related activations before stimulus presentation) was shown to consistently activate the left PPC (Karayanidis et al., 2010; Ruge et al., 2013), but with modulations depending on the types of switching. For example, Chiu and Yantis found that preparing to switch attention between spatial locations engaged a number of DAN

regions such as the superior parietal lobule (SPL), FEF, middle and inferior frontal gyrus and supramarginal gyrus, while preparing to switch across categorisation rules (magnitude/parity judgements of digits) only activated SPL and IPS (Chiu & Yantis, 2009). It is important to note that most areas that appear engaged in preparation of task switches only exhibit a stronger activation relative to task repetitions, but they do not seem to constitute a switch-specific preparatory circuit. In other words, the proactive control that allows people to switch tasks relies on the same control processes that allow task repetition, but to a greater extent (Ruge et al., 2013). Further, in addition to the variability among high-order areas, preparatory control processes were also shown to interact with task-specific lower-level areas (Capizzi et al., 2015; Shi et al., 2014; Wylie et al., 2006). For instance, studies that induced switches across colour and motion or location processing found that preparing for and performing the colour task both engaged the same inferior temporal and fusiform areas (traditionally associated with colour processing) (Slagter et al., 2007; Wylie et al., 2006).

This evidence reflects the presence of both generalised and domain- and/or task-specific preparatory processes that likely interact to allow successful switching.

Finally, it is important to mention that a number of studies also found thalamic activation associated with switching, although most do not explicitly comment or interpret this (Jamadar et al., 2010; Karayanidis et al., 2010; Monchi et al., 2001; Nakashima et al., 2018).

1.4.4. Experimental factors influencing task-switching results

There are a number of parameter choices that can influence the outcomes of task-switching paradigms. As explained in section 1.4.1, the time allowed for preparation in the case of cued paradigms influences the magnitude of switch costs, whereby longer anticipatory preparation reduces the switch cost effects (Monsell, 2003). Such preparation effect appears to depend on the specific experimental design. For instance, the reduced switch costs were found only when CTI variations were implemented within-subjects, but not between subjects (i.e., when each subject only experienced one fixed CTI length). This suggests that participants might strategically adapt the reconfiguration process in a flexible manner based on context, and that these strategic choices can influence behavioural outcomes (De Baene & Brass, 2014;

Vandierendonck et al., 2010). It is worth mentioning that, in this context, strategy can encompass both implicit and voluntary processes (De Baene & Brass, 2014). Nonetheless, neuroimaging studies found that similar brain regions were activated by fixed and variable CTIs (with slightly different sensitivities in certain regions), suggesting that different designs did not detect qualitatively different preparatory processes (Ruge et al., 2013). Further to this, the number of switch trials in proportion to repetitions was shown to affect both behavioural outcomes and neural underpinnings of switch preparation. For instance, Duthoo and colleagues compared behavioural performances at 30%, 50% or 70% of switch probability, and found that switch costs were reduced as the switch rate increased, which was associated with a diminished expectation for task repetition when participants' predictions were taken into account (Duthoo et al., 2012). Likewise, in a cued task-switching study on motion vs colour discrimination, De Baene and Brass examined the effect of low (30%) and high (50%) switch rates on switch-specific anticipatory activation, using a within-subject block design (De Baene & Brass, 2013). They found that a low switch probability induced activation in lPFC, pre-SMA, IPL, SPL and MTG, while the high switch probability only engaged some of those areas (pre-SMA, dorsal ACC and SPL), with the activation in the remaining areas being quite stable across switch and repeat trials. lPFC and IPL were previously associated with task goal update and activation, while pre-SMA and SPL are thought to subserve task rule activation (De Baene & Brass, 2013). Therefore, the authors suggested that, when the switch probability is low, participants were more likely to maintain the previous task-set active and inhibit it in the case of switches (requiring additional effort in switch trials as compared to repetitions), while at a high switch probability, participants kept a more neutral preparatory state which required reconfiguring the current task-set in both switch and repetition trials alike. On a similar note, other studies found that lower switch rates (and thus increased repetitions) resulted in decreased preparatory activation in pre-SMA, FEF and SPL in repetition trials (Slagter et al., 2006).

This evidence thus reflects the adjustment of control strategies based on task expectancy and experimental context, but where only certain components of anticipatory control appear to be strategically adapted (such as task set updating), while other components such as task rule activation are likely invariant to switch probability changes. Such perspective of an adaptive adjustment of preparatory

processes conveniently connects and links together the seemingly opposed theoretical accounts (task set reconfiguration and inhibition) defined in section 1.4.2.

On a different note, as also stated in section 1.4.2, the dominance or familiarity of the tasks can induce asymmetries in the switch costs. These effects have been related to the influence of task difficulty and complexity. However, it is important to note that, while asymmetric switch costs have been often found, the direction of such asymmetry is still debated, as studies present mixed results. For instance, by testing multiple types of tasks and rule complexity, Rubinstein and colleagues consistently found greater costs when participants switched from a familiar to an unfamiliar task (Rubinstein et al., 2001). These incongruencies can be perhaps explained by the fact that not all components of control are affected by task complexity. In fact, a very recent review of 29 task-switching studies suggested that an imbalanced task complexity (e.g. semantic judgements as compared to visual discrimination) only influences exogenous components such as task-rule activation (occurring at stimulus presentation) rather than changing the endogenous, preparatory process of task-goal activation, as indexed by a general increase in RTs during task repetitions as well (Gamble & May, 2022). These effects might therefore interact with the time allowed for preparation, as explained above.

In addition to this, and perhaps more importantly, the similarity of the tasks employed in the experiment was also shown to modulate behavioural switch costs, such that tasks that share more processing components facilitate switching as compared to more dissimilar tasks (Arrington et al., 2003). Arrington and colleagues performed a cued task-switching experiment in which they separately manipulated the level of task similarity in terms of perceptual encoding of stimulus features. They used 4 tasks that were paired for similarity, i.e., height and width judgements, both focused on spatial characteristics (form) of the stimulus, and hue and brightness judgements, both focused on surface properties (colour). They found that switch costs were smaller when switching between similar tasks as compared to switching across dissimilar tasks, suggesting a less effortful reconfiguration across similar task-sets.

Together, these effects suggest that an adaptive high-order process such as cognitive flexibility is a highly complex and multifaceted phenomenon in which different cognitive features react to different parameter changes (Ruge et al., 2013). These ad-hoc adjustments are likely required to ensure system adaptability (Vandierendonck et al.,

2010).

1.4.5. Gaps in the research of task-switching across external and internal domains

The importance of internal processes has not been acknowledged in the cognitive flexibility literature yet, and so how we adjust control towards internal processes is not yet understood. Consequently, the literature also lacks suitable experimental paradigms to explore these aspects specifically (Verschooren, Schindler, et al., 2019). To the best of my knowledge, only a small number of studies have started to investigate this from a task-switching perspective. The definition of internal processing in these studies (which includes working memory as a stimulus-independent process) differs from the categorisation I explained in section 1.3 based on content and neural correlates associated with self-referential processing. I will discuss them here nonetheless, as they share a similar rationale to my work, unlike more traditional task-switching paradigms.

Verschooren and colleagues investigated the behavioural outcomes of switching between perceptual attention and working memory processes, under the assumption that these would reflect instances of external and internal attention, respectively. In a series of studies, these authors employed cued task-switching paradigm involving probe-target matching tasks with abstract figures or numbers as stimuli (Verschooren, Liefooghe, et al., 2019; Verschooren, Schindler, et al., 2019). In one study (Verschooren, Liefooghe, et al., 2019), participants had to either judge if a target abstract figure matched a subsequently presented probe (external trials), or, in the absence of such figure, they had to retrieve abstract figures presented to them at the beginning of the block, and remember if the figure in the target position matched the probe (internal trials). They found that switch costs were asymmetric, in that they were greater in the case of switches from perceptual to working memory processing as compared to the opposite switch (Verschooren, Liefooghe, et al., 2019). However, this study only included switches across domains, but not switches within each domain. In another, perhaps more complex, study (Verschooren, Schindler, et al., 2019), they employed a baseline task requiring external attention (i.e., visual discrimination on geometric shapes), and randomly alternated that either with another external task (find

digits with a certain perceptual features such as bold or italic font) or an internal one (judge if digits were in the same position as the digits presented before the block). They compared the behavioural performances to the baseline task after a switch from either the external or the internal tasks, or after a repetition of the same baseline task. They found that switch costs were also present when switching from the internal to the baseline task, although the costs did not significantly differ in magnitude as compared to switches from the external task to baseline (Verschooren, Schindler, et al., 2019). They interpreted these switch costs as reflecting the time needed to redirect attentional resources (which have limited capacity) to the new task set, and that perceptual and working memory processes share and compete for such limited resources. This view, termed 'resource sharing account', was previously proposed by Gilbert and Burgess in a series of conceptually similar experiments (Burgess et al., 2007; Gilbert et al., 2005). However, these authors categorised working memory as an internal process in that it does not require the concurrent presence of an external stimulus, as opposed to the immediate encoding of perceptual stimuli in the field of attention.

Another body of research adopted a different approach, aimed at studying the effects of emotional regulation on working memory (Chambers et al., 2008; Z. Chen et al., 2016; De Lissnyder et al., 2012; Moreno et al., 2015). These studies employed a paradigm called Internal Shifting Task (IST), which involves neutral and emotional faces or neutral and affective words (although neutral and emotional conditions are administered in separate blocks). In each block, participants perform two concurrent mental counting tasks based on non-emotional features such as gender or object category (neutral blocks), or based on emotional features such as neutral vs angry or sad faces, or positive vs negative words (emotional blocks). These studies found that larger switch costs in the emotional conditions as compared to the neutral ones were associated with increased self-reported depressive brooding and rumination (Chen et al., 2016; De Lissnyder et al., 2012) and mindfulness (Chambers et al., 2008). Whilst important to characterise the effect of emotional valence on working memory and its consequences on switch costs, these studies also lacked a specific focus on self-referential processing and conscious control of self-related thoughts. Specifically, they focused on the effect of different stimulus features on the same type of working-memory task, rather than on exploring the shift across different (external and internal) cognitive domains. Moreover, they do not allow a direct investigation of the switch within and between domains.

All in all, these experiments were useful to reveal that switch costs are also present in the case of shifts between perceptual and working memory processing, and in the case of shifts in the covert focus of attention between mental objects. More research and novel paradigms are still needed to instead explore the shifts across external monitoring and self-referential judgements.

1.5 Influences of arousal and chronotype on cognition and frontoparietal networks

1.5.1. Arousal

Arousal is defined as a general contentless activation state which defines wakefulness in healthy humans (Oken et al., 2006). In humans, sleep-wake cycles are regulated by a number of interconnected but antagonist components, including sleep-promoting and wakefulness-promoting systems. Briefly, the ventrolateral preoptic nucleus of hypothalamus sends inhibitory GABAergic connections to the wakefulness-promoting system when initiating sleep. The wakefulness system instead includes noradrenergic inputs from locus coeruleus (LC), as well as serotonergic, histaminergic and cholinergic neurons in raphe, tuberomammillary and brainstem nuclei, respectively. These nuclei innervate thalamus, lateral hypothalamus and basal forebrain, and then project to the entire cortex (Saper & Fuller, 2017). In particular, thalamocortical projections and firing patterns in the reticular nucleus were shown to modulate responsiveness towards the external environment during transitions to sleep (Oken et al., 2006). Moreover, the noradrenergic projections from LC were shown to project to parietal areas important for attentional control and to modulate both tonic (sustained) and phasic alertness to sensory processing (Alnæs et al., 2014; Oken et al., 2006; Petersen & Posner, 2012).

The arousal system is thus thought to modulate vigilance (a state of sustained attention or alertness; Oken et al., 2006) and subsequently influence a number of cognitive processes, as highlighted by the effects of sleep deprivation. Studies found that sleep deprivation decreases performance in attentional tasks, language, working memory and decision making (M. W. Chee & Chuah, 2008; M. Thomas et al., 2000).

Crucially, sleep loss was shown to affect performance in cognitive flexibility and attentional shifting too, leading to increased RTs and error rates during task switching (Bratzke et al., 2009; Couyoumdjian et al., 2010; Heuer et al., 2004; Slama et al., 2018; Whitney et al., 2017).

From a neural perspective, some fMRI studies revealed adaptive compensatory changes in prefrontal and parietal regions after sleep deprivation (M. W. L. Chee & Choo, 2004), while others found decreased activation (M. W. L. Chee et al., 2006; Habeck et al., 2005). Effects were contingent to the specific cognitive demands under investigation, e.g., verbal learning, divided attention, arithmetic (M. W. Chee & Chuah, 2008; Drummond & Brown, 2001). In the context of cognitive flexibility, Nakashima and colleagues observed increased frontoparietal activation after sleep deprivation which was not accompanied by increased switch costs, suggesting neural compensatory mechanisms that adaptively respond to maintain intact behavioural performance (Nakashima et al., 2018). Studies also found decreased resting-state thalamocortical activation after sleep deprivation, as well as increased thalamic and decreased DAN activation in working memory and attentional tasks (M. W. L. Chee & Choo, 2004; Habeck et al., 2004; Shao et al., 2013; Tomasi et al., 2009). To explain this, Tomasi and colleagues hypothesised that, in order to maintain vigilance in conditions of depleted arousal, thalamic resources are redeployed away from task performance. This could potentially cause the decreased frontoparietal activation observed in many studies (which may vary depending on task demands), and particularly the deactivation in PFC which appears to be particularly vulnerable to sleep loss (M. L. Thomas et al., 2003; Tomasi et al., 2009). The observed changes in mPFC suggest that internally oriented processes might also be affected by sleep deprivation. In fact, sleep deprivation and related modulations in mPFC were associated with alterations in social behaviour such as lower self-control, social monitoring and emotional disinhibition (Dorrian et al., 2019; Kamphuis et al., 2012; Vohs et al., 2011). Moreover, sleep loss was shown to alter interoceptive feelings too, leading to increased pain sensitivity, negative mood, and a general feeling of unwellness (Wei & Van Someren, 2020). Interestingly, sleep deprivation was also found to change the connectivity within DMN regions as well as between DMN and DAN regions in attentional tasks and at rest (De Havas et al., 2012; Gujar et al., 2009; Sämann et al., 2010; Xu et al., 2018).

Together, evidence suggests that the level of arousal can significantly influence different cognitive processes and induce neural modulations in frontoparietal regions, although with variability across paradigms. Nonetheless, to the best of my knowledge, no study has ever explored the effects of arousal in the coordination of externally and internally oriented processes. Importantly, the joint investigation of cognition and arousal has also proven helpful to unveil the role of thalamocortical connections in cognitive changes.

1.5.2. Chronotype

The regulation of arousal in humans and other mammals is thought to involve a homeostatic process, which increases sleep pressure throughout the day, and a circadian pacemaker for which sleep propensity oscillates at a nearly-24h period (Borbély, 1982; Schmidt et al., 2007). The natural propensity to sleep and wake up at a particular time is termed chronotype, and it is determined by interindividual differences in the biological regulation of sleep/wake cycles, at least partly due to genetic factors (Roenneberg et al., 2007; Schmidt et al., 2015). Individuals display variability in their preference for sleep and wake times: at one end of the spectrum, extreme morning types ('early' chronotypes) prefer to wake up at very early hours and struggle to stay awake past a certain time; at the other end, extreme evening types ('late' chronotypes) prefer to go to bed very late at night and struggle with waking up in the morning (Schmidt et al., 2007). Beyond the natural entrainment of our circadian clocks to solar time, our decisions regarding sleep and wake times are also influenced by a number of more artificial factors such as social and professional constraints (e.g. waking up early to go to school or work) (Roenneberg et al., 2007; Schmidt et al., 2015). While neutral chronotypes tend to be aligned with light-dark cycles and social constraints, extreme chronotypes are often phase shifted with regards to those factors. This aspect is important because chronotype can influence alertness levels, as moments of high and low alertness are partly contingent upon the preferred timing for daily activities (Schmidt et al., 2007). In other words, people may experience peaks in vigilance and performance in morning or evening times, depending on chronotype (early preferring mornings, late preferring evenings) (Facer-Childs et al., 2018). In addition, extreme late chronotypes are highly impacted by the need for early

awakening times dictated by society, which usually leads them to compensate during free days (e.g., the weekend) – a phenomenon termed ‘social jetlag’ (Wittmann et al., 2006). For late chronotypes, this constant mismatch between endogenous clock and social times results in a number of adverse effects due to sleep restriction and poor sleep quality, such as increased health risks and cognitive impairments (Banks & Dinges, 2007; Zelinski et al., 2014). Nonetheless, the neuroscientific literature has given little attention to the effects of chronotype on cognitive and neural activity, and results are still unclear (Taillard et al., 2021). In a working-memory study (N-back task), Schmidt and colleagues found modulations in thalamus and middle frontal gyrus depending on time-of-day, chronotype and cognitive load (Schmidt et al., 2015). Specifically, when the cognitive load was high (N3-back), higher thalamic activation was found in the evening for late chronotypes compared to early, while early chronotypes exhibited higher frontal activation in the morning as compared to late chronotypes (Schmidt et al., 2015). Only recently, a few neuroimaging studies started to investigate the differences in resting-state connectivity due to chronotype. One study found a positive correlation between resting-state DMN connectivity and MEQ scores, showing that late chronotypes were associated with decreased activation in precuneus and posterior cingulate cortex (Horne & Norbury, 2018). Similarly, another study found increased connectivity within DMN and between DMN and SN regions in early chronotypes as compared to late chronotypes (Facer-Childs et al., 2019). However, another study found late chronotypes and poor sleep quality to be associated with higher resting-state FC between mPFC and precuneus, with the strength of FC between those regions mediating between chronotype and sleep quality (Tian et al., 2020).

This suggests that further research is still needed to fully appreciate the effects of chronotype on large-scale networks and related cognitive processes.

Chapter 2

CHAPTER 2 : GENERAL METHODS

2.1 Overview

This thesis consists of 4 empirical chapters. Chapters 3 to 5 focus on investigating switches within and across the internal and external domains using a task-switching approach. Specifically, Chapter 3 presents the behavioural correlates (RTs) of a novel task-switching paradigm where I used written word stimuli and cued participants to alternate between 4 possible tasks (two internally oriented tasks involving self-referential cognition and subjective assessment of bodily sensations, and two externally oriented tasks involving letter categorisation). Chapter 4 investigates the brain activity (BOLD signal and effective connectivity) associated with these within and between domain switches, using the task in Chapter 3 in a separate cohort (thus also providing a replication to the behavioural effects in Chapter 3). I specifically focus on the anticipatory neural activation between cue and stimulus presentation, in order to investigate network reconfiguration during switch planning, before the tasks are actually performed. Finally, Chapter 5 reports behavioural performance (RTs) on a different cued task-switching paradigm using pictorial stimuli and different sub-tasks (pleasantness and self-relatedness judgements as internal tasks, semantic categorisation of scenes based on their external features as external ones). The structure and aims remain the same as those in Chapter 3, providing a generalisation of the behavioural findings in previous chapters beyond specific task demands.

Chapter 6 focuses on the analysis of resting-state fMRI data. I employed a recently developed change-point detection algorithm on regions of the functional networks involved in internal and external processing, task-switching and cognitive control (DMN, DAN, ECN, SN), with the aim of detecting spontaneous “switches” at rest, in a data-driven manner.

A summary of the task designs and analysis methods is provided in sections 2.2 - 2.7 below, highlighting similarities and differences across chapters.

The original plan for this project before the COVID-19 pandemic was to develop and test the task-switching paradigm both behaviourally and with fMRI, and then test potential modulations induced by different arousal levels using sleep deprivation. Further to this, we planned a final experiment that would use non-invasive brain stimulation (NIBS) to perturb key brain networks identified during previous steps and assess their causal role in cognitive switching. Due to the lack of access to participant testing during the multiple COVID-19 lockdowns, the trajectory of the thesis was adapted to use online behavioural paradigms (Chapter 3 and 5) and the analysis of existing datasets (Chapter 6), prioritising the core fMRI experiment as planned (Chapter 4) once lockdowns were lifted, but removing additional measurements and manipulations (i.e., sleep deprivation and NIBS). While I was not able to study the effects of sleep deprivation on cognitive flexibility, in Chapter 6 I investigated resting-state data at different times of day and in early and late chronotypes, still shedding some light onto the unexplored differences in intrinsic dynamics due to the arousal fluctuations induced by circadian preferences.

2.2 Experimental procedure and design

This section describes the development of the experimental paradigms used in Chapters 3-5. Similarities and differences across studies are summarised in **Table 2.1**. In all three studies (Chapters 3-5) I adopted within-subject designs in which participants completed all conditions of the experiments in one session. I pre-registered the two behavioural studies (Chapters 3 and 5) before data collection under the Open Science Framework (OSF) (Chapter 3: https://osf.io/p7xrq; Chapter 5: https://osf.io/3vx6g).

2.2.1. Pilots

Our task design drew upon a previous task-switching study which found DMN activation during switches from task to rest (Sidlauskaite et al., 2014), and block-design studies which explored the neural bases of self-referential processing with word stimuli (Davey et al., 2016) and pictures (Gusnard et al., 2001). Thus, elements

of those studies were taken and adapted to develop the two behavioural paradigms used in this thesis.

To this end, I piloted various versions online behaviourally, while keeping the parameters suitable for the future implementation in the fMRI scanner. The first version of the paradigm used written word stimuli and included two externally oriented tasks (counting vowels in the word to judge if there are more than 3 vowels, or judging if the letter 'T' is present in the word), one internally oriented task (judging if the trait applies to one's own personality) and a resting condition. The first pilot (n = 28) returned significant switch costs overall (BF10 = 3194.25; $t(27) = 5.23$, $p < 0.001$, d = 1.001), but highlighted issues with the task design such as the limited use of resting-state in a purely behavioural paradigm (which became a greater focus on this thesis due to COVID-19 restrictions to in person testing), and a clear difficulty imbalance between the two externally oriented tasks when comparing task repetitions only (BF10 = 384230.35; $t(27) = 8.68$, $p < 0.001$, d = 1.62). In a subsequent pilot, I removed the rest condition and included a second internally oriented task (judging the presence of current interoceptive sensations) to enable the investigation of switches within the internal domain as well. I also changed the externally oriented condition to aim for more similar and balanced tasks: judging if the second letter of the word was a vowel, or judging if the second letter from the end of the word (penultimate) was a consonant. This pilot (n = 38) also revealed significant switch costs overall (BF10 = 7.563e+8; $F(1,37) = 124.52$, $p < 0.001$, $\eta^2_p = 0.77$) and in both external (BF10 = 3.008e+8; $t = 8.14$, $p < 0.001$, d = 0.63) and internal (BF10 = 4.651e+6; $t = 8.65$, $p < 0.001$, d = 0.67) domains. Moreover, it showed an additional cost in switching between domains as compared to within each domain (BF10 = 16885.9; $F(1,37) = 49.96$, $p < 0.001$, $\eta^2_p = 0.57$). However, it still showed an imbalance in task difficulty (BF10 = 7.885e+13; $F(1.668,61.723) = 37.96$, $p < 0.001$, $\eta^2_p = 0.51$), which led me to further modify the external tasks as per the final design employed in Chapter 3 and 4 and briefly explained in this section. I also developed a version of the paradigm that employed pictorial stimuli, with the aim to provide an alternative paradigm where both external and internal tasks required semantic categorisation, in order to have a more similar level of stimulus processing across domains and provide a generalisation of the novel effects I had found. In this pilot it used the same task conditions that I then employed in Chapter 5, which are also summarised below. This pilot (n = 44) returned partially similar results to the other study version, i.e., switch costs present in both external

(BF10 = 10572.19; t = 8.14, p < 0.001, d = 0.63) and internal (BF10 = 4.21; t = 4.64, p =0.015, d = 0.25) domains, but no additional costs in between-domain switching (BF01 = 4.90; F(1,43) = 0.728, p = 0.398, η^2_p = 0.017). This paradigm also presented differences in task difficulty (BF10 = 1.313e+14; F(2.287,98.32) = 36.61, p < 0.001, η^2_p = 0.46). The decision to proceed with the main behavioural studies with larger sample size using both task versions was made based on the fact that the main findings of switch costs in both domains appeared reliable despite the unresolved task difficulty balance.

2.2.2. Task design

In each trial, participants had to perform one of four possible tasks, as instructed by a geometric cue before each stimulus. I designed the tasks to induce attention towards external stimuli (2 'external' tasks) or towards self-related processes (2 'internal' tasks). Within each study, I employed the same stimuli and response format for all experimental conditions: written words (Chapters 3 and 4) or greyscale pictures (Chapter 5) presented at the centre of the screen. Tasks required binary 'yes' or 'no' responses in all studies. More details regarding the stimuli are given in the empirical chapters.

In Chapters 3 and 4, the two externally oriented tasks asked to either assess if the third letter of the written word stimulus was a consonant (consonant finding task), or if the second to last letter was a vowel (vowel finding task). The two internally oriented tasks were to either judge if the written word described one's own personality (personality judgement task), or if it described a present bodily sensation (interoceptive judgement task). In Chapter 5, the two externally oriented tasks were to assess if the picture represented an outdoor scene rather than indoor (indoor/outdoor discrimination task), or if the picture represented a natural scene as opposed to something man-made (natural/man-made discrimination task). The two internally oriented tasks were to judge if the picture was subjectively pleasant (pleasantness task), or if the picture was related or associated with one's own experience (self-relatedness task).

Studies in Chapter 3 and 4 included 380 trials each (95 for each task), while the study in Chapter 5 included 400 trials each, 100 for each of the four tasks. The study in

Chapter 3 included less trials than its alternative version (Chapter 5) and previous pilot studies because I wanted to test whether a slightly shorter version of the task could still provide the same results, in preparation of the fMRI task (Chapter 4) for which I wanted to reduce the time participants needed to spend inside the MRI scanner. In all studies, trials were pseudo-randomly shuffled for each participant to obtain 60% repetition trials (i.e., trials with the same task as in the previous trial) and 40% switch trials (i.e., trials where the task was different from the previous trial). This specific switch probability was taken from a previous study with the aim to achieve a trade-off between too much predictability of switching and thus a lack of strategy (with 50% switches) and having a too low number of trials of interest (with 30% of switches) (De Baene & Brass, 2011, 2014). Repetitions were evenly distributed between repetitions of internal tasks and repetitions of external tasks. Among the switch trials, 1/4 were switches between the two internal tasks, 1/4 between the two external tasks, 1/4 went from an external to an internal task, and 1/4 from an internal to an external task. Participants had a self-paced break at every quarter of task (every 12-13 minutes).

The initial training phase consisted of 60 trials divided in 5 blocks: the first four (6 trials each) ensured participants became familiar with each task separately; the last block included 36 switch trials with all four tasks.

In each trial, a string of fixation crosses (Chapters 3-4) or a single fixation cross (Chapter 5) first appeared for 500 ms, followed by a string of black geometrical shapes (Chapters 3-4) or a single one (Chapter 5) for 500 ms that instructed participants about which task to perform. Cues were a circle, square, triangle or diamond, and the assignment of each shape to a specific task instruction was randomised across participants, drawing from 4 possible cue-task pairing combinations. The choice of using strings of symbols for fixation and cues in Chapters 3 and 4 was made to provide similar low-level visual stimulation throughout each trial. This set up was established due to the original pre-COVID plans which included collecting pupillometric measurements along with behavioural ones, thus requiring minimisation of possibly confounding visual changes across elements of the task. Stimuli appeared on the screen after a pseudorandom cue-to-target interval (CTI) and stayed on-screen until participants made a response, up to a maximum of 3 seconds. During the CTI and inter-trial intervals (ITI) participants saw a grey screen with a string of black dots (a single one in Chapter 5) in the centre. CTI and ITI were pseudo-logarithmically jittered with intervals ranging from 200 ms to 6150 ms in steps of 350 ms. Specifically, 50%

of the trials ranged between 200-1950 ms, 1/3 of the trials between 2300-4050 ms, and the remaining 1/6 of trials between 4400-6150 ms. This jittering method was taken from previous studies (De Baene & Brass, 2011). The time available for task preparation (i.e., the CTI) was shown to influence the costs of task-switching (Kiesel et al., 2010), so I kept the same jittering method across all studies for consistency. For Chapters 3 and 5, I prepared the stimuli lists, CTI and trial order using MATLAB (R2018b), coded the experiment using PsychoPy and delivered it to participants online via Pavlovia (https://pavlovia.org/). For Chapter 4, I used MATLAB and Psychtoolbox.

2.2.3. Data preprocessing

In all three studies (Chapters 3-5), I calculated the mean percentage of correct yes/no responses overall and for each task. I inferred the correctness (accuracy) of the internal tasks by comparing responses in the main experiments with the responses to the post-task questionnaires (considered the ground truth). I excluded participants from the analyses if they failed to respond to 10% or more of the trials or if their accuracy for any of the 4 task conditions dropped below 60%, as this would indicate they were not following the task instructions. For each participant we also removed outlier trials, defined by the Tukey's method (Tukey, 1977) as RTs more than 1.5 interquartile ranges above the upper quartile (75%) or below the lower quartile (25%) for each condition (repetitions, within- and between-domain switches for each task) within each subject, as done in previous studies (Schmitz & Voss, 2014; Verschooren, Schindler, et al., 2019). We also removed trials with RT below 200 ms as previously done (Arrington et al., 2003). I then measured the mean reaction times (RTs) for each trial type: repetitions (trials where participants performed the same task as in the previous trial) and switches (trials where participants performed a different task compared to the previous trial). I further categorised switch trials as within- (internal-to-internal and external-to-external) or between-domain switches (from internal to external and vice versa).

2.3 Bayesian statistics and task analysis

2.3.1. Theory of Bayesian statistics

Frequentist and Bayesian statistics are the two main approaches to statistical inference. Frequentist statistics is based on null hypothesis significance testing, which provides a test-statistic (measuring the distance between data and model predictions) and an associated probability (p-value) of obtaining that test-statistics or a larger one under the assumption that the null hypothesis is true, and that all model assumptions were met (Greenland et al., 2016; Quintana & Williams, 2018). If this probability is small enough (according to a cutoff or alpha level aimed at reducing false alarms), then the null hypothesis can be rejected. In other words, it starts by assuming the null hypothesis is true and that the treatment has no effect, and then focuses on quantifying how likely the collected data are under the null hypothesis (Fornacon-Wood et al., 2022). While frequentist statistics are the most popular method for quantitative research, this approach suffers from several limitations and is often misused by researchers. First, it does not allow to test if the data favour the null hypothesis as compared to the alternative (since we can only disprove the null hypothesis) (Altman & Bland, 1995). Second, it does not inform regarding the sensitivity of a dataset if not with an a priori power analysis (Goodman, 2008; Greenland et al., 2016).

The Bayesian framework conceptually and formally differs from the frequentist in a number of fundamental ways, and provides a valid alternative to overcome the above issues. Briefly, the Bayesian approach treats hypotheses and parameters as probabilistic distributions while the data are fixed, which is already more intuitive given that we can only deal with the data at hand (Fornacon-Wood et al., 2022). The Bayes' theorem underlies the update of probability distributions based on prior and current knowledge, as follows:

$$P(\theta|data) = \frac{p(data|\theta) \cdot p(\theta)}{p(data)}$$

where p(θ) is the prior distribution, or prior information about the model parameters or hypothesis before seeing the data; p(data) is the model evidence, and p(data|θ) is the likelihood or probability of observing the data given a certain hypothesis or parameters. p(θ|data) is the posterior distribution, i.e., the updated probability of observing a certain effect after the data have been taken into consideration. From this, we can thus

quantify the probability associated with different hypotheses (e.g. null and alternative), and compare them by computing the ratio between them, i.e., the Bayes factor (Quintana & Williams, 2018). The Bayes factor thus constitutes a continuous and relative measure of evidence, meaning it does not impose a cut-off for significance and it provides the relative proportion of one model performance against another (van den Bergh et al., 2020).

2.3.2. Statistical analysis of behavioural data

In this thesis, I used JASP (Team, 2018) to perform both frequentist and Bayesian analyses with the behavioural data in Chapters 3-5. When performing frequentist tests, I set the criterion for significance at $p<.05$. For Bayesian tests, I considered a Bayes factor (BF10) equal or over 3 as substantial evidence for the alternate hypothesis (with BF10 >= 10 being strong evidence and BF10 >= 100 being very strong evidence), and a BF10 equal or under 0.3 as substantial support for the null hypothesis. In cases of BF10 < 0.3 we report the BF01 instead, which quantifies the evidence in favour of the null hypothesis. As mentioned above, the Bayes factor does not provide categorical cutoffs, but the above interpretations originated from standard guidelines aimed at providing an approximate classification to facilitate the communication of results (M. D. Lee & Wagenmakers, 2014; Schönbrodt & Wagenmakers, 2018). JASP implements the Cauchy distribution as default model priors, which introduces the assumption that effect sizes are likely to be small (Love et al., 2019). While the adoption of appropriately informed priors is often advised to avoid overly conservative constraints (Vanpaemel, 2010), varying the prior distribution requires strong justifications to avoid arbitrary results (Lindley, 2004). Furthermore, the use of default priors is unlikely to mislead a Bayes factor analysis unless with very small sample sizes, small true effect size and a prior for large effect size (Wagenmakers et al., 2018). Even then, distortions will likely be modest (Wagenmakers et al., 2018). Therefore, throughout the thesis (Chapters 3-5), I used the JASP default priors.

Finally, posterior probabilities can be continuously monitored and updated as more data are gathered, which makes it useful to determine when to stop data collection based on the amount of accumulated evidence, referred to as Bayesian stopping rule (Steel, 2003; van den Bergh et al., 2020). I applied this procedure in Chapters 3 and

5, while for Chapter 4 I selected a smaller and fixed sample size due to resource and time restrictions related to the costs of MRI scanning and the low availability of the MRI scanner during a period in which many labs resumed in-person testing.

I performed all behavioural analyses (Chapters 3-5) on mean RTs from accurate trials only, excluding incorrect trials and the trials from the training phase. I followed any significant main effect or interaction in an ANOVA with post-hoc pairwise t-tests using Bonferroni correction for multiple comparisons. Using Tukey's method, I detected outlier participants and performed the pre-registered analyses both including and excluding them. I always report results that include data from all participants in the main text of each chapter, but report results after exclusion of outlier participants in the relative appendices.

In Chapters 3-5, I performed repeated measures ANOVAs (rANOVA) and T-tests to investigate the presence of switch costs in the two cognitive domains and to explore the presence of an additional cost in switching across domains as compared to within each domain. I also checked for task difficulty irrespective of switch costs and further looked at the effect of each task on switch costs. These last analyses on task difficulty and task effects were not performed in Chapter 4, since previous studies suggested that preparatory processes are likely unaffected by task complexity (Gamble & May, 2022; Rubinstein et al., 2001).

Finally, I checked for the effect of varied preparation times (cue-to-target interval or CTI) on switch costs, and whether switch costs were present across all CTI durations.

See **Table 2.1** for an overview of the first three empirical chapters, including a detailed list of statistical analyses performed in each chapter.

		Chapter 3	**Chapter 4**	**Chapter 5**
Procedure	**Delivery**	online	in-person	online
	Software	Pavlovia/PsychoPy	MATLAB/Psychtoolbox	Pavlovia/PsychoPy
Design	**Measures**	Behavioural (RTs, accuracy)	fMRI and behavioural (RTs, accuracy)	Behavioural (RTs, accuracy)
	Stimuli	written words	written words	pictures

		Chapter 3	Chapter 4	Chapter 5
	External tasks	vowel/consonant	vowel/consonant	outdoor/natural
	Internal tasks	personality/interoception	personality/interoception	pleasantness/relatedness
Analysis	**rANOVA**	2x2 domain x trial type 2x2 domain x sw. type 4x2 task x sw. type 1x4 task difficulty 2x3 domain x CTI 1x3 switch costs by difficulty	2x2 domain x trial type 2x2 domain x switch type	2x2 domain x trial type 2x2 domain x switch type 4x2 task x switch type 1x4 task difficulty 2x3 domain x CTI
	T-tests	One-sample on switch costs from 2x2, 4x2 and 2x3 ANOVAs	One-sample on switch costs from 2x2 ANOVA	One-sample on switch costs from 2x2, 4x2 and 2x3 ANOVAs; Switch costs by difficulty

Table 2.1. Similarities and differences across studies in Chapter 3, 4 and 5.

2.4 functional Magnetic Resonance Imaging

Magnetic resonance Imaging (MRI) is a non-invasive medical imaging technique that is widely adopted for the imaging of soft tissues such as the brain (Soares et al., 2016). Functional MRI uses a specific type of contrasts (T2* weighted imaging) which is sensitive to the magnetic properties of haemoglobin. Specifically, changes in the blood oxygenation level dependent (BOLD) signal are thought to originate from changes in the brain's metabolic demands (e.g., during cognitive performance) (Soares et al., 2016). When the oxygen consumption increases, the regional cerebral blood flow increases as well to compensate for the energy needs, which in turn decreases the concentration of deoxygenated haemoglobin (dHb) in the area (Ogawa et al., 1990). This dynamic is reflected by the haemodynamic response function (HRF), characterised by an initial dip (when the dHb, which is paramagnetic, increases), a high peak (when the the dHB decreases and the oxygenated haemoglobin increases), and a subsequent undershoot (return to baseline after a surplus in oxygenated haemoglobin) (Soares et al., 2016). This method thus provides an indirect (but spatially accurate) measure of brain function, and is characterised by markedly slower

fluctuations (i.e., in the order of seconds) as compared to the underlying neuronal activity (Buckner, 1998).

2.5 General Linear Model

A major portion of neuroimaging research has focused on studying the brain's response to stimuli or tasks. This has been widely done via Statistical Parametric Mapping (SPM) in which, after preparation and preprocessing, data are analysed with a general linear model (GLM) (Poline & Brett, 2012; Soares et al., 2016). The GLM is simply formed by conventional multiple linear regression models with the possibility to incorporate analysis of variance, covariance and other statistical models via coding of dummy variables (regressors) (Friston et al., 1994; Poline & Brett, 2012). Under this framework, stimulus onsets and durations of each condition of interest are convolved with the canonical HRF to estimate the BOLD signal. Conditions are then entered in the GLM as independent variables (with the time-series from each voxel as dependent), along with any nuisance regressor such as head motion parameters (Pernet, 2014; Poline & Brett, 2012). This results in a statistical map reporting the test statistics for each voxel in the brain (Soares et al., 2016). At the first level, this is done for each subject and run, while group average across participants and/or group comparisons are done at the second level. While providing information regarding statistically significant changes in BOLD activation, this procedure also constitutes the basis of other connectivity measures such as dynamic causal modelling (DCM, see section 2.8) (Soares et al., 2016).

In this thesis, I performed GLM analyses of fMRI data in Chapters 4 and 6. In Chapter 4, a GLM was performed on task data both as a standalone analysis of whole-brain activation as well as a foundation for DCM analysis. In Chapter 6, I used a GLM to analyse specific events in resting-state data. These events were first detected with a change-point detection method, as described in the next section 2.7 and in the Methods section of Chapter 6. More details regarding the respective GLM analyses will be in Chapters 4 and 6.

2.6 Functional connectivity measures and change-point detection

Functional connectivity (FC) is widely adopted in the analysis of resting-state fMRI and allows to measure statistical dependencies (such as correlation) among the BOLD activity of brain regions. Historically, many studies selected a ROI a priori and explored which voxels in the brain were correlated with it (seed-based correlation) (Soares et al., 2016). Others instead expanded on the use of a single predefined ROI and employed data-driven approaches to separate fMRI time-series into spatially independent components (as in the case of Independent Component Analysis or ICA) or into clusters of voxels with similar connectivity parameters (clustering methods such as K-means) that reflect functionally distinct regions or networks (Soares et al., 2016). A powerful alternative for FC analysis is graph theory, where the brain is modelled as a graph network with nodes (regions) and edges (FC measures e.g., correlation among regions). This allows to explore all possible connections across regions of interest and to obtain various measures of network topology depending on the properties of interest, e.g. local (nodal) characteristics or global (network) behaviour such as small-worldness, integration, segregation, resilience, modularity, etc. (Sporns, 2018).

All these approaches have been typically used after fMRI activity was averaged across the entire scan duration (stationary FC), under assumptions of spatial and temporal stationarity (i.e., assuming the strength of relationships across regions was constant over time) (Hutchison et al., 2013). While this enables a convenient simplification for results analysis and interpretation, it has been consistently proven that brain activity is not stationary and that spontaneous fluctuations reflect meaningful changes in the underlying neuronal patterns in response to mental and cognitive changes (Bassett et al., 2011; Kopell et al., 2014). Thus, the more recent dynamic FC (dFC) approach involves the exploration of such time-varying fluctuations, which were shown to be reproducible and highly informative, especially in resting-state (Hutchison et al., 2013). The most commonly adopted strategy for dynamic FC is the sliding windows approach, which consists of segmenting data into time windows of a predefined length and overlap, and calculating a chosen FC metric (e.g., correlation or partial correlation) for each pairwise connection in each window (Allen et al., 2012). This is often followed by clustering (usually K-means), so that windows with similar FC patterns get clustered together forming FC states, which represent recurrent connectivity patterns throughout

the scans (Allen et al., 2012). From this, researchers can explore the frequency of occurrence and stability ('dwell time') of such states, as well as the proportion of switches across them (transition probability) (Allen et al., 2012; Denkova et al., 2019; Kopell et al., 2014). However, this method suffers from a number of well-known limitations, including the need for an arbitrary a priori choice of window length, shape and overlap, which can greatly influence dFC results (Preti et al., 2017). Moreover, by definition, this technique requires a fixed window length, which limits the FC analysis in a specific frequency range, independently of the true frequency of fluctuations in the data (Preti et al., 2017).

Other alternative methods for dFC are still being explored to this date. Among them, change-point detection algorithms represent a promising option. Change-point detection is a broad term that refers to a number of statistical analysis methods that aim at finding abrupt changes in time-series (Aminikhanghahi & Cook, 2017). These methods generally aim at understanding whether a change has occurred in a given property of the data and where it occurred, and there exist a multitude of different approaches applicable to various signals and scenarios, e.g., for medical diagnosis, speech analysis, meteorology, and more (Aminikhanghahi & Cook, 2017). Some of these methods have been developed specifically for human neuroimaging data (Cribben et al., 2012; Cribben & Yu, 2017), where the focus is on detecting when a change in brain activity occurred, or when the relationship between different brain regions changed. Still, these methods are not widely used in the field of human neuroscience yet due to the complexity of brain data (multidimensional time-series with multiple changes occurring simultaneously). Nonetheless, after recent improvements they can be highly advantageous as compared to traditional analysis approaches. One of the main advantages is the fact that information from this analysis is extracted in a data-driven manner, i.e., obtained from the data without the need to have a priori assumptions. Because of this, it has been suggested as an alternative to the sliding-windows approach (Anastasiou et al., 2022; Hutchison et al., 2013). Moreover, given that resting-state activity was shown to be characterised by transient, temporally sparse coactivation events, change-point detection can be a more suitable approach to the study of intrinsic dynamics rather than averaging across entire runs or large segments of data (Gonzalez-Castillo et al., 2021; X. Liu & Duyn, 2013; Mancho-Fora, Montalà-Flaquer, Farràs-Permanyer, Bartrés-Faz, et al., 2020; Petridou et al., 2013). In Chapter 6, I used a recently developed change-point detection

algorithm called cross-covariance isolate detect (CCID) (Anastasiou et al., 2022), which I fully explain in the Methods section of the chapter. I used this to spot transient changes in pairwise connections in intrinsic networks of interest (DMN, DAN, ECN, SN, as recurrently cited in this thesis), and used those changes as events in a GLM analysis and to segment data for dFC analysis using K-means clustering and graph theory metrics.

2.7 Dynamic Causal Modelling

Dynamic Causal Modelling (DCM) is a generative modelling approach that allows to estimate the effective connectivity among a set of pre-defined brain regions, i.e., the directed causal influence across regions, as opposed to functional connectivity which reflects undirected statistical dependencies such as correlation (Soares et al., 2016). DCM relies on Bayesian inference to infer hidden neuronal states from the BOLD signal.

Specifically, neural dynamics (which are not directly observed in fMRI data) are mapped using a cascade of biologically plausible models of neuronal and neurovascular coupling, hemodynamic and BOLD signal (plus observation noise) using linear or nonlinear differential equations (Stephan et al., 2010). Once a forward model is specified, fMRI time-series can be simulated for different model parameters (connections and external inputs) until the model that most closely resembles the observed fMRI data is found (Zeidman, Jafarian, Corbin, et al., 2019). More specifically, the parameters estimated by DCM encode the strength (or rate of change) of connections, as a result of incoming signals from other brain regions and/or by the experimental manipulation. At a first within-subject level Bayesian inversion is used to find the parameters with the best trade-off between accuracy and complexity, as quantified by the model evidence (also called marginal likelihood) (Zeidman, Jafarian, Corbin, et al., 2019). In other words, the best model needs to be plausible, but also parsimonious (Kahan & Foltynie, 2013). At a second level (usually between subjects), the Parametric Empirical Bayes (PEB) framework can be adopted for finding commonalities and/or differences at the group level, and for hypothesis testing

(Zeidman, Jafarian, Seghier, et al., 2019). PEB applies another Bayesian inversion scheme over the first-level DCM parameters in order to enhance estimation precision using group-level constraints (K. Friston et al., 2015). Within PEB, Bayesian Model Comparison is applied to compare the evidence across reduced models, i.e., models where some connections are switched off. Comparing these reduced models with the full models (Bayesian Model Reduction) allows to iteratively prune away connections that do not contribute to model evidence (Zeidman, Jafarian, Seghier, et al., 2019). Then, Bayesian Model Averaging is used to perform a weighted average on the parameters from all reduced models, taking into account the models' posterior probability. Only the results that surpass a certain posterior probability threshold (95% as commonly used) are retained for interpretation (Zeidman, Jafarian, Seghier, et al., 2019).

In Chapter 4, I used a bilinear, one-state, deterministic DCM model (and subsequent group PEB) to investigate the effective connectivity of task-fMRI data. This version was chosen in order to allow a more straightforward interpretation of the estimated parameters, in absence of strong motivations to use a more complex model. More specifically, the deterministic version of DCM only allows external inputs (experimental stimuli and afferent connections from other regions) to drive neural changes, as compared to the stochastic version where intrinsic time-varying neural fluctuations are also taken into account (Kahan & Foltynie, 2013). Moreover, if set as bilinear, the model allows only experimental modulatory inputs to interact with the connectivity across regions, whereas the nonlinear version allows the connectivity in one region to influence that of other regions (Zeidman, Jafarian, Corbin, et al., 2019). Finally, the choice of a one-state model (instead of a two-state one) reflects an approximation where each connection is associated with one neuronal population only, instead of two (excitatory and inhibitory populations). Under these conditions, each extrinsic connection (i.e., across different regions) is considered excitatory or inhibitory based on the sign of the estimated parameter (i.e., connectivity strength). Moreover, each region is equipped with a self-connection that can only be inhibitory, biologically explained as the presence of inhibitory interneurons that can interact with pyramidal neurons (Bastos et al., 2012; Zeidman, Jafarian, Corbin, et al., 2019).

Chapter 3

CHAPTER 3 : INVESTIGATING THE SHIFT BETWEEN EXTERNALLY AND INTERNALLY ORIENTED COGNITION; A NOVEL TASK-SWITCHING PARADIGM[1]

3.1 Abstract

Despite our constant need to flexibly balance internal and external information, research on cognitive flexibility has focused solely on shifts between externally oriented tasks. In contrast, switches across internally oriented processes (and self-referential cognition specifically), and between internal and external domains have never been investigated. Here, we report a novel task-switching paradigm developed to explore the behavioural signatures associated with cognitive flexibility when self-referential, as well as more traditional external processes, are involved. 200 healthy volunteers completed an online task. In each trial, participants performed one of four possible tasks on written words, as instructed by a pre-stimulus cue. These included two externally and two internally oriented tasks: assessing whether the third letter was a consonant, or the penultimate letter was a vowel vs. assessing whether the adjective applied to their personality, or if it described a bodily sensation they were currently experiencing. 40% of trials involved switches to another task and these were equally distributed across within-external, within-internal, internal-to-external and external-to-internal switches. We found higher response times (RT) for switches compared to repetitions both in the external and internal domain, thus demonstrating the presence of switch costs in self-referential tasks for the first time. We also found higher RTs for between-domain switches compared to switches within each domain. We propose that these effects originate from the goal-directed engagement of different domain-specific cognitive systems that flexibly communicate and share domain-general control features.

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3.2. Introduction

Human beings deal with a continuous flow of sensory stimuli coming from our environment, as well as interoceptive sensations and spontaneous thoughts. Our brain is thus constantly integrating and coordinating external and internal inputs in a dynamic manner. The field of cognitive psychology has widely used task-switching paradigms to investigate our ability to flexibly shift between different cognitive and attentional processes (Kim et al., 2012). In these paradigms, two or more tasks are performed sequentially, either with a predictable sequence or in random alternation. Participants typically show worse performance in trials with different task demands to the previous trial (switch) compared to trials preceded by the same type of task (repetition) – a phenomenon termed "switch cost" (Koch et al., 2018). Switch costs represent the cognitive costs associated with task set changes in a context where other active competing task sets are interfering (Dove et al., 2000), and usually translate into higher response times (RT) and / or error rates in switch trials compared to repetitions.

Despite the shift between external and internal worlds being a ubiquitous and fundamental feature of our brain and cognition, research on cognitive flexibility to date has almost exclusively focused on switches between externally oriented tasks (e.g., categorising digits based on parity or magnitude, stimuli based on colour or shape, etc.; Koch, 2003; Schneider & Logan, 2010). An exception to this is a series of recent studies by Verschooren and colleagues that aimed to understand how the attentional switches between traditionally used external tasks (in this case perceptual attention) and those requiring working memory processes (i.e., when no external stimulus is present during the task) occur (Verschooren, Liefooghe, et al., 2019; Verschooren, Schindler, et al., 2019). They found that costs are also present when switching between these two type of tasks, although of similar magnitude compared to switches within the perceptual domain (Verschooren, Schindler, et al., 2019), and that such costs are asymmetric (i.e., greater when switching towards their working memory task compared to switching to the perceptual attention task; Verschooren, Liefooghe, et al.,

2019). While Verschooren work elegantly demonstrates the existence of costs between domains, their internal attention/working memory task required the internal manipulation of previously presented digits (see also Gilbert et al., 2005 for a similar line of research). Instead, we here focus on self-referential cognition, encompassing physical and psychological aspects such as representation and awareness of one's own body and bodily actions, autobiographical and semantic memory, personal traits and subjective perspective (Christoff et al., 2011; D'Argembeau, 2020; Gillihan & Farah, 2005). There is vast literature investigating self-referential processes (Gillihan & Farah, 2005; Knyazev, 2013; Northoff et al., 2006) but, to our knowledge, the switch between different types of self-referential tasks or between these tasks and externally oriented tasks is yet to be explored. Neuroimaging research has demonstrated that internal and external processes are subserved by different brain networks (Benoit et al., 2010; Mäki-Marttunen et al., 2016; Northoff & Bermpohl, 2004). The relationship between these networks is characterised by complex dynamics (Davey et al., 2016; Fox & Raichle, 2007; Kelley et al., 2002; Vanhaudenhuyse et al., 2010; Weissman et al., 2006; Whitfield-Gabrieli et al., 2011), suggesting that switching across the two domains might be more costly than the traditionally reported switches between external tasks.

The study of self-reference often entails the comparison between stimuli that participants recognise as referring to themselves and stimuli attributed to others or simply not recognised as one's own (Brédart et al., 2006; Devue & Brédart, 2008; Kawahara & Yamada, 2004). A common experimental paradigm requires participants to judge whether a series of traits apply to them or not. This is usually accompanied by control conditions such as judging if the trait applies to someone else (e.g., a famous public figure or a friend) and/or focusing on purely linguistic or stylistic attributes of the words such as counting letters or discriminating case or font (Davey et al., 2016; Kelley et al., 2002; Liu et al., 2017).

Here we report a novel task-switching paradigm that requires either attention towards external stimulus features or an internal, self-related focus.

Based on the above literature and our own (unpublished) pilot data, we hypothesized that:

1. We will find evidence of an overall switch cost: i.e., switching from one task to another will result in higher RT compared to repeating the same task, irrespective of task type.
2. Internally oriented tasks will also exhibit switch costs: i.e., switching between self-referential tasks will result in higher RT as compared to repetitions.
3. Switch costs involving self-referential tasks will be similar to those involving externally oriented tasks.
4. Switching between similar tasks (i.e., within the internal or the external domains) will be associated with faster RTs than switching between more distant cognitive processes or domains i.e., from externally to internally oriented tasks and vice-versa.

Finally, we explored whether the difference in within- versus between-domain switches changes as a function of the direction of the switch (i.e., when the switch goes towards an internal versus an external task).

3.3. Methods

We pre-registered our methods, research hypotheses, and planned analyses prior to data collection on the Open Science Framework (https://osf.io/p7xrq). Any deviations from the pre-registration are noted.

3.3.1. Participants

We recruited a total of 230 participants (mean age = 28.29 ± 4.5; 144 women, 85 men, 1 non-binary). To be eligible, participants had to be aged 18-35, right-handed, native English speakers, with no history of neurological or psychiatric conditions nor sleep problems (insomnia/hypersomnia), and a normal sleep schedule (e.g., no night-shift jobs). Participants enrolled in the study via Prolific (www.prolific.co) and received compensation upon completion of the study at a rate of £5 per hour. They received written information and provided written informed consent before participating. This study was approved by the University of Birmingham STEM Ethics committee.

We discarded 5 participants based on not actually meeting eligibility criteria (4 were not monolingual British English speakers and 1 had a diagnosis of dyslexia), 1 for having more than 10% of missing trials, and 24 due to low accuracy (< 60%) in one or more task conditions. This resulted in a total of 200 participants (mean age = 28.49 ± 4.4; 126 women, 73 men, 1 non-binary) included in the analysis.

As per our pre-registration, after obtaining 200 valid datasets, we applied a Bayesian stopping rule (see below) to decide whether to continue data collection. Specifically, a Bayes factor of 3 or more (either in support of the alternative or the null hypothesis) in the t-test comparing RTs during repetition trials versus all types of switch trials (i.e., evidence of overall switch costs, *Hypothesis 1*) would mean data collection could be stopped. As we obtained very strong evidence in support of the presence of a switch cost (see Results) we did not require any further participants.

3.3.2. Experimental design and procedure

We adopted a within-subjects design. Participants completed all conditions of the behavioural experiment online in one session lasting approximately 1 hour and 20 minutes (**Figure 3.1**), and could only participate using a PC or laptop (no phones or tablets). From Prolific, participants directly accessed an online form on Qualtrics (Qualtrics, Provo, UT), where they received written information regarding the study, gave informed consent and provided demographic data, and carefully read the task instructions. They were then automatically redirected to Pavlovia (www.pavlovia.org), where they performed an initial training session and the task-switching paradigm for approximately 1 hour (10 minutes for training and 50 minutes for the main experiment, see the next subsection for details). After completion, they were redirected to Qualtrics for a final questionnaire aimed at verifying the correct responses for the two internal task conditions. This lasted approximately 10 minutes. Specifically, participants were asked to perform the same two internal tasks again (‘personality’ and ‘current sensations’ tasks, as described in the next subsection) in a self-paced questionnaire that displayed all stimuli at once in a list. We used this as a proxy to calculate participants’ accuracy in these tasks on the main paradigm: i.e., we considered correct only those responses that matched the ones given on the questionnaire.

3.3.3. Task

On each trial, participants had to complete one of four possible tasks on a written word presented on the screen, with a geometric cue appearing before each stimulus to indicate which task to perform. We designed the tasks to induce attention towards external stimuli (2 ‘external’ tasks) or towards self-related characteristics (2 ‘internal’ tasks). We used the same stimuli and response format throughout the paradigm: personality traits and bodily adjectives presented in written form on the screen that required binary yes / no responses. The four tasks were:

- Consonant finding (external task 1): participants had to assess whether the third letter of the written form of the word was a consonant.
- Vowel finding (external task 2): participants had to assess whether the penultimate (second to last) letter of the written form of the word was a vowel.
- Personality (internal task 1): participants had to report whether the adjective described their own personality, focusing on how their character is in everyday life.
- Current physical sensations (internal task 2): participants had to report whether the adjective described their present sensations, with a focus on current feelings from their body.

We designed our tasks to be as balanced as possible and not have intrinsic differences in difficulty (based on pilot data). Therefore, we expected the performance in task repetition trials to be similar across tasks.
The experiment included 381 trials in total (95 for each task except the consonant task which had 96) to ensure an even number of switches and repetitions, since the first trial did not belong to either category and was therefore not considered for the analysis. Trials were pseudo-randomly shuffled for each participant in order to obtain 60% repetition trials (i.e., trials where participants repeated the same task done in the previous trial) and 40% switch trials (i.e., trials where the task was different than the previous trial). Repetition trials were evenly distributed to obtain 50% of internal task repetitions and 50% of external task repetitions. Among the switch trials, 1/4 were switches between the two internal tasks, 1/4 between the two external tasks, 1/4 went from an external to an internal task, and 1/4 from an internal to an external task.

Participants had the chance to have a self-paced break every 95 trials (once every ~12 minutes).

The initial training phase consisted of 60 trials divided in 5 blocks: the first four allowed participants to become familiar with each task separately and included 6 trials each; the last block included 36 switch trials with all four tasks.

All stimuli appeared in black at the centre of a grey screen. In each trial, a string of black fixation crosses ('+++++') first appeared for 500 ms, followed by a string of 5 black geometrical shapes (500 ms) that instructed participants about which task to perform (see **Figure 3.1**). Specifically, cues were circles, squares, triangles or diamonds, and the assignment of each shape to a specific task instruction was randomised across participants, drawing from 4 possible cue-task pairing combinations. The presence of anticipatory cues allows for the engagement of preparatory processes in advance of the upcoming task, as compared to reactive processes only (Koch & Allport, 2006). It also allowed us to use the identical stimuli across tasks. Target stimuli (words) appeared on the screen after a pseudorandom cue-to-target interval (CTI) and stayed on-screen until participants made a response, up to a maximum of 3 seconds. All trial elements were scaled based on the screen: fixation crosses maintained a height equal to 8% of screen size, stimuli of 4.5%, and cues were approximately 5.5% of screen size (with slight variations to level off the different shapes). During the CTI and inter-trial intervals (ITI) participants saw a grey screen with five black dots in the centre. CTI and ITI were pseudo-logarithmically jittered according to previous task-switching paradigms (De Baene & Brass, 2011), with intervals ranging from 200 ms to 6150 ms in steps of 350 ms. Specifically, 50% of the trials ranged between 200-1950 ms, 1/3 of the trials between 2300-4050 ms, and the remaining 1/6 of trials between 4400-6150 ms. Since the time available for task preparation (i.e., the CTI) was shown to influence the costs of task-switching (Kiesel et al., 2010), we decided to employ such jittering method in this behavioural study as well, to maintain consistency with future fMRI studies.

We prepared the stimuli lists, CTI and trial order using MATLAB (R2018b), coded the experiment using PsychoPy (Peirce et al., 2019) and delivered it to participants via Pavlovia (https://pavlovia.org/).

3.3.4. Stimuli

Stimuli were all English adjectives pooled from Anderson's list of 555 personality-trait words (Anderson, 1968) and from a recently published list of concepts rated for interoceptive strength (Connell et al., 2018). We gathered a series of psycholinguistic variables and ratings for the selected words, which we used for the creation of well-balanced individual lists. These included number of syllables, letters, and phonemes from the MRC psycholinguistics database (Coltheart, 1981) and the N-Watch software (Davis, 2005); valence and arousal ratings from an extended version of the ANEW database (Warriner et al., 2013); interoception ratings from Connell et al. (2018); frequency ratings from the SUBTLEX-UK database (Heuven et al., 2014); and mean age of acquisition ratings from Catling & Johnston (Catling & Johnston, 2009). We also labelled each word as congruent or incongruent depending on whether it was associated with the same yes/no response to the vowel and the consonant finding tasks (to control for possible congruency effects on response times).

With a custom MATLAB script, we first randomly sorted the words into four lists (one per task). Then, we performed a 1x4 ANOVA on each of the above-mentioned variables to check that these four lists were not significantly different from each other in any of the above variables. Interoception ratings were the only exception: by necessity, the lists for the current sensation task had higher interoceptive ratings than the personality task, to encourage more embodied feelings in one task versus more abstract characteristics in the other. In addition to controlling for confounding variables, the lists assigned to the consonant finding task had approximately half of the words with a consonant in the third position while the lists for the vowel finding task had approximately half of the words containing a vowel in the penultimate position (to ensure balanced responses throughout the experiment). In doing this, we allowed for a small difference of ± 3 words to ensure that reaching a solution was computationally feasible. Importantly, the lists for the two external tasks each consisted of half trait and half bodily adjectives, while the personality and current sensations tasks were entirely composed of trait and bodily adjectives, respectively. This full procedure was iteratively repeated until 70 suitable lists were obtained. From these, the platform sequentially assigned a list for each participant. As there were more participants than available lists, some participants received the same list. However, as the lists

contained unique words (i.e., no words were repeated within or across lists), for each participant each word only appeared once.

For the training phase trials (before the main task), we only controlled stimuli for number of letters, frequency, valence, and responses to external tasks, using the same procedure described above. In the case of valence, when ratings were missing, we used ratings from the most similar words available e.g., 'relieved' from 'relieve'. Note that this only applied to the training list and for the main experiment we only used words for which we could identify and control for all the variables of interest described in the above paragraph.

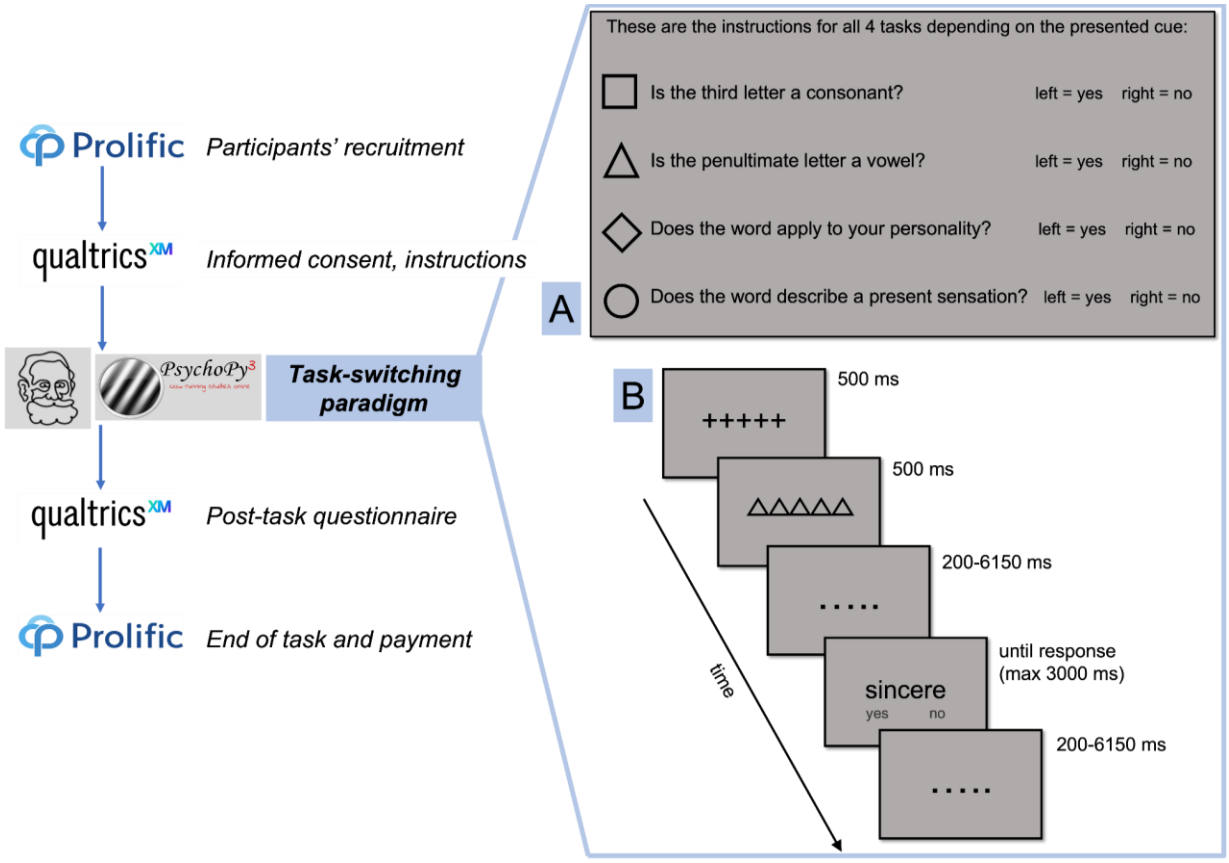

Figure 3.1. Online study pipeline (left) and details of main paradigm (right) including an instruction screen showing one of the 4 possible cue-task mappings (A) and the structure of a single trial (B).

3.3.5. Statistical Analysis

We analysed data using JASP 0.16.1 (JASP Team 2020). First, we calculated the overall mean percentage of accuracy (percentage of correct yes/no responses) across the full experiment as well as the mean percentage of accuracy for each task individually, to check that participants paid attention throughout. We obtained accuracy for the two internally oriented tasks by comparing responses during the main experiment with the responses to the post-task questionnaire. The answers to the questionnaire were the reference to which task responses had to coincide in order to be considered correct. We then used accuracy to decide what participants needed to be excluded for further analysis: i.e., we removed participant data if they failed to respond to 10% or more of the trials (cut-off based on pilot data from our lab) or if their accuracy levels for any of the 4 task conditions were below 60%, as this would indicate they were not following the task instructions. As described in the participant section, this resulted in the exclusion of 25 participants (final n = 200). Moreover, for each participant we removed outlier trials, defined by the Tukey's method (Tukey, 1977) as RTs more than 1.5 interquartile ranges above the upper quartile (75 percent) or below the lower quartile (25 percent) for each of the 12 conditions (repetitions, within- and between-domain switches for each task) within each subject, as done in previous studies (Schmitz & Voss, 2014; Verschooren, Schindler, et al., 2019). This resulted in an average of 3.42% (± 1.38) discarded trials per participant, in addition to the trials discarded due to incorrect responses (7.75% ± 4.76). We also removed trials with RT below 200 ms (this occurred in 6 participants only; 2.31% ± 4.65 trials), as per previous studies (Arrington et al., 2003). This last step (removal of trials < 200ms) was not specified in the pre-registration but was necessary to ensure that very fast (and likely meaningless) responses were excluded.

We then measured reaction times (RTs) for each trial type: repetitions and switches. We defined a 'repetition' trial as a trial in which participants performed the same task as in the previous trial. 'Switch' trials were trials in which participants performed a different task compared to the previous one. We further categorised switch trials as within- (internal-to-internal and external-to-external) or between-domain switches (from internal to external and vice versa).

We performed both frequentist and Bayesian statistics. We set the criterion for significance at $p<.05$ for frequentist statistics. For Bayesian tests, we always used

default model priors (Cauchy distribution) and we considered a Bayes factor (BF_{10}) equal or over 3 as substantial evidence for the alternate hypothesis (with BF_{10} >= 10 being strong evidence and BF_{10} >= 100 being very strong evidence), and a BF_{10} equal or under 0.3 as substantial support for the null hypothesis, as per standard guidelines (Schönbrodt & Wagenmakers, 2018). In cases of BF_{10} < 0.3 we report the BF_{01} instead, which quantifies the evidence in favour of the null hypothesis.

We performed all analyses on mean RTs for accurate trials only and excluded the data from the training phase. We followed any significant main effect or interaction in an ANOVA with post-hoc pairwise t-tests using Bonferroni correction for multiple comparisons.
We tested for normality but used ANOVAs even in cases where some violated these tests, since ANOVAs are robust enough even when assumptions of normality are not met (Schmider et al., 2010). Using Tukey's method, we detected outlier participants and performed our pre-registered analyses both including and excluding these. In the next section we report results that include data from all participants. Results after the removal of outlier participants are available in Appendix A.

3.3.5.1. Pre-registered analyses

We performed a 2x2 repeated measures ANOVA (rANOVA) with domain (internal tasks, external tasks) and trial type (repetitions, switches) as factors, to assess the presence and nature of switch costs in the two cognitive domains. Specifically, a main effect of trial type (followed by post hoc confirmation of higher RTs for switches compared to repetitions) would provide support for *Hypothesis 1*; a significant post-hoc t-test revealing lower RTs for repetitions versus switches to an internal task would provide support for *Hypothesis 2*; an absence of interaction between domain and trial type would provide support for *Hypothesis 3*. Switches included all switch types (both within-domain and between-domains).
We then performed a 2x2 rANOVA with factors domain (internal tasks, external tasks) and switch type (within-domain, between-domains) on the switch costs. Switch costs were calculated by subtracting the average RTs during each switch type minus the average RTs during repetitions in the equivalent domains for each subject: e.g.,

switches from external to internal domain minus repetitions of internal tasks, or switches within external domain minus repetitions of external tasks. This tested for *Hypothesis 4* (main effect of switch type with post hoc confirmation of higher RTs for between- vs within-domain switches) and our exploratory question about the direction of the between-domain switches.

A 1x4 rANOVA on RTs of repetition trials only (factor task repetition: external task 1, external task 2, internal task 1, internal task 2) allowed us to check for the overall level of difficulty for each task (we expected to find no main effect), irrespective of switch costs.

Finally, we carried out a 4x2 rANOVA with factors task (external task 1, external task 2, internal task 1, internal task 2) and switch type (within-domain, between-domains) on switch costs. For this we calculated switch costs as the average RTs during switches minus the average RTs during repetitions for each task independently. For example, switches from both external tasks to internal task 1 (i.e., between-domain switches towards internal task 1) minus repetitions of internal task 1. This further investigated the potential effects of task difficulty when addressing *Hypothesis 4*, and the exploratory question about the direction of the between domain switches (NB. the above-mentioned 1x4 rANOVA highlighted an imbalance in task difficulty, as described in the Results section).

3.3.5.2. Exploratory analyses

In addition to the pre-registered analyses, to complement the 2x2 rANOVA on switch costs with factor domain and switch type, we performed one sample t-tests comparing each switch type (switches within external and within internal domains, switches from internal to external and from external to internal) to 0. We performed this to make sure that the switch cost effects detected in our main analyses were not solely driven by between-domain switches (i.e., the most effortful ones). Therefore, this complements our main test for *Hypothesis 2*, in the case of switches within the internal domain.

Similarly, to complement the 4x2 rANOVA on switch costs with factors task and switch type, we also performed one sample t-tests comparing each switch type (within- and between-domain switches for each task) to 0, to check if they all significantly differed from repetitions (same rationale as above).

In addition to this, to account for the effect of task difficulty revealed in our pre-registered analyses, we grouped specific switch subtypes into 3 categories (hard-to-easy, neutral, easy-to-hard) based on results from the 1x4 ANOVA on task repetitions (see **Figure 3.4A**). We then carried out a 1x3 repeated measures ANOVA (frequentist and Bayesian) on switch costs with factor difficulty in the full sample, to explore the possible influence of task difficulty irrespective of domain and task. In grouping the switch subtypes (averaging across switch costs per participant), we interpreted switches from the consonant finding task (which had slower reaction times than the rest) to all other tasks as switches from a hard to an easy task. This was also the case for the switches from personality to current sensations tasks. In contrast, we interpreted switches from the vowel finding task to either internal task and vice versa as switches to tasks of similar difficulty ("neutral" switches). We considered all other switches (i.e., from all tasks towards consonant finding and from current sensations to personality) as switches from an easy to a hard task.

Moreover, to further assess whether our reported effects were influenced by differences in difficulty across tasks, we performed all our pre-registered analyses, as described above, also on a subset of 70 participants (mean age = 28.09 ± 4.02; 50 women, 20 men) that did not display a significant difference in difficulty between tasks (as indicated by the 1x4 rANOVA on task repetitions). With this approach we aimed to completely exclude the influence of task difficulty on our effects of interest while still performing the specific analyses that we pre-registered. Specifically, this allowed us to confirm whether any differences (or similarities) between internal and external tasks were driven by differences in the difficulty of the tasks we used, or were inherent to the cognitive processes of interest, and thus aid the interpretation of our main results. We selected this subset of participants by randomly drawing 70 participants and performing the frequentist 1x4 rANOVA on task repetitions in an iterative fashion until non-significance was achieved.

Finally, at a Reviewer's suggestion, we performed an additional analysis to account for the effect of varied durations for task preparation. As explained in section 2.3, our CTIs ranged between 200 ms and 6150 ms. In traditional task-switching paradigms (using externally oriented tasks) it is well established that the time allowed for preparation of the upcoming task (i.e., CTI) can greatly influence the magnitude of switch costs, with shorter CTIs leading to larger costs (Kiesel et al., 2010; Koch, 2003; Kray, 2006; Meiran, 2000; Monsell & Mizon, 2006). In order to establish whether this

effect is also present in the internal domain, and whether its influence is similar for internal than for external tasks, we divided our CTI distribution into 3 bins: short (200 – 1250 ms), medium (1600 – 3000 ms) and long (3350 – 6150 ms) CTI length. Note that each bin had a similar number of trials, although not identical due to the randomisation. We then performed a 2x3 rANOVA with factors domain (internal, external) and CTI (short, medium, long) on switch costs. We also performed one-sample t-tests for each of the 6 switch cost conditions of this ANOVA to check whether switch costs were present across all CTI durations.

3.4. Results

As mentioned in the Methods section, here we report results from all 200 participants, including outliers. Please refer to Appendix A for the equivalent tests without outliers.

3.4.1. Accuracy

Overall, participants completed the experiment with high accuracy (92.04% ± 5.19). The mean accuracy for the external tasks (consonant and vowel finding) was 94.39% (± 5.46) and 94.92% (± 5.66) respectively. Internal tasks (personality and current sensations) had a mean accuracy of 89.49% (± 7.20) and 89.41% (± 7.08) respectively.

3.4.2. Switch costs

The Bayesian t-test comparing repetition and switch trials - performed as part of the Bayesian stopping rule - revealed very strong evidence for the presence of overall switch costs (BF_{10}=5.763e+52; frequentist $t(199)=22.27$, $p<.001$, $d=-1.57$). This provided support for *Hypothesis 1*. See **Figure 3.2A**.

As can be expected, the 2x2 repeated measures ANOVA with factors domain and trial type on RTs (**Figure 3.2B**) also resulted in a significant main effect of trial type (BF_{10}=4.337e+34, $F(1,199)=494.18$, $p<.001$, $\eta_p^2=0.71$), with repetitions significantly faster than switches (*Hypothesis 1*). In addition, we found a significant main effect of

domain indicating that, overall, external tasks led to slower RTs than internal tasks (BF_{10}=8.061e+9, F(1,199)=32.27, p<.001, η_p^2=0.14). Finally, we found a significant interaction between domain and trial type (BF_{10}=11.90, F(1,199)=37.13, p<.001, η_p^2=0.16), against our *Hypothesis 3*. As predicted, post-hoc t-tests confirmed the presence of switch costs in both the external (BF_{10}=1.836e+46, t=21.33, p_{bonf}<.001) and the internal domain (BF_{10}=9.456e+30, t=13.91, p_{bonf}<.001), in support of *Hypothesis 2*. However, the difference between repetitions and switches was significantly greater in the external domain, as captured by the above interaction. **Table 3.1**. displays means and standard deviations of all conditions.

3.4.3. Additional costs in between-domain switches

The 2x2 ANOVA with factors domain and switch type (**Figure 3.2C**) on switch costs (i.e., RT for switch trials minus repetition trials) resulted in a significant main effect of domain (indicating greater costs for switches to external than to internal tasks; BF_{10}=3.595e+8, F(1,199)=37.03, p<.001, η_p^2=0.16), and switch type (BF_{10}=4.761e+6, F(1,199)=49.76, p<.001, η_p^2=0.20). The latter supported *Hypothesis 4*, in showing additional costs when switching domains compared to staying within domain. However, we also found a significant interaction between domain and switch type (BF_{10}=12.01, and F(1,199)=10.81, p=.001, η_p^2=0.05). Post-hoc t-tests confirmed additional costs to switching from external to internal domain compared to staying within the internal domain (BF_{10}=1.457e+9, t=7.31, p_{bonf}<.001). The extra costs in switches from internal to external domain compared to those within the external domain were significant in our frequentist tests but showed only anecdotal Bayesian evidence (BF_{10}=2.39, t=2.67, p_{bonf}=.048).

Switching within the external domain resulted in higher costs compared to switching within the internal domain (BF_{10}=4.560e+8, t=6.82, p_{bonf}<.001). Moreover, switching from the internal to the external domain led to higher RTs compared to switching in the opposite direction, although with anecdotal Bayesian evidence (BF_{10}=2.53, t=2.79, p_{bonf}=.033). All 4 switch types exhibited a switch cost (i.e., switch cost different from 0; all one sample t-tests: p<.001; see Table A1a in Appendix A), including the switches within the internal domain (BF_{10}=2.141e+11, t=8.20, p<.001, d=0.58), further

supporting *Hypothesis 2*.

Similarly, our 4x2 ANOVA comparing switch costs for each task individually revealed a significant main effect of task (BF_{10}=1.207e+7, $F(3,597)=13.03$, $p<.001$, $\eta_p^2=0.06$) and switch type (BF_{10}=1.483e+6 and $F(1,199)=44.18$, $p<.001$, $\eta_p^2=0.18$), as well as a significant interaction (BF_{10}=34.05 and $F(3,597)=8.03$, $p<.001$, $\eta_p^2=0.04$) (**Figure 3.2D**). Post-hoc t-tests confirmed significantly greater costs in between-domain switches compared to within-domain ones for all tasks except vowel finding (Table A2), explaining the significant interaction. All 4 tasks showed a switch cost (see Table A1b in Appendix A).

Table 3.1. Mean and SD for all conditions in the pre-registered analyses. Includes all participants. All units are seconds. E1: external task 1 (consonant finding); E2: external task 2 (vowel finding); I1: internal task 1 (personality task); I2: internal task 2displays means and standard deviations for all conditions.

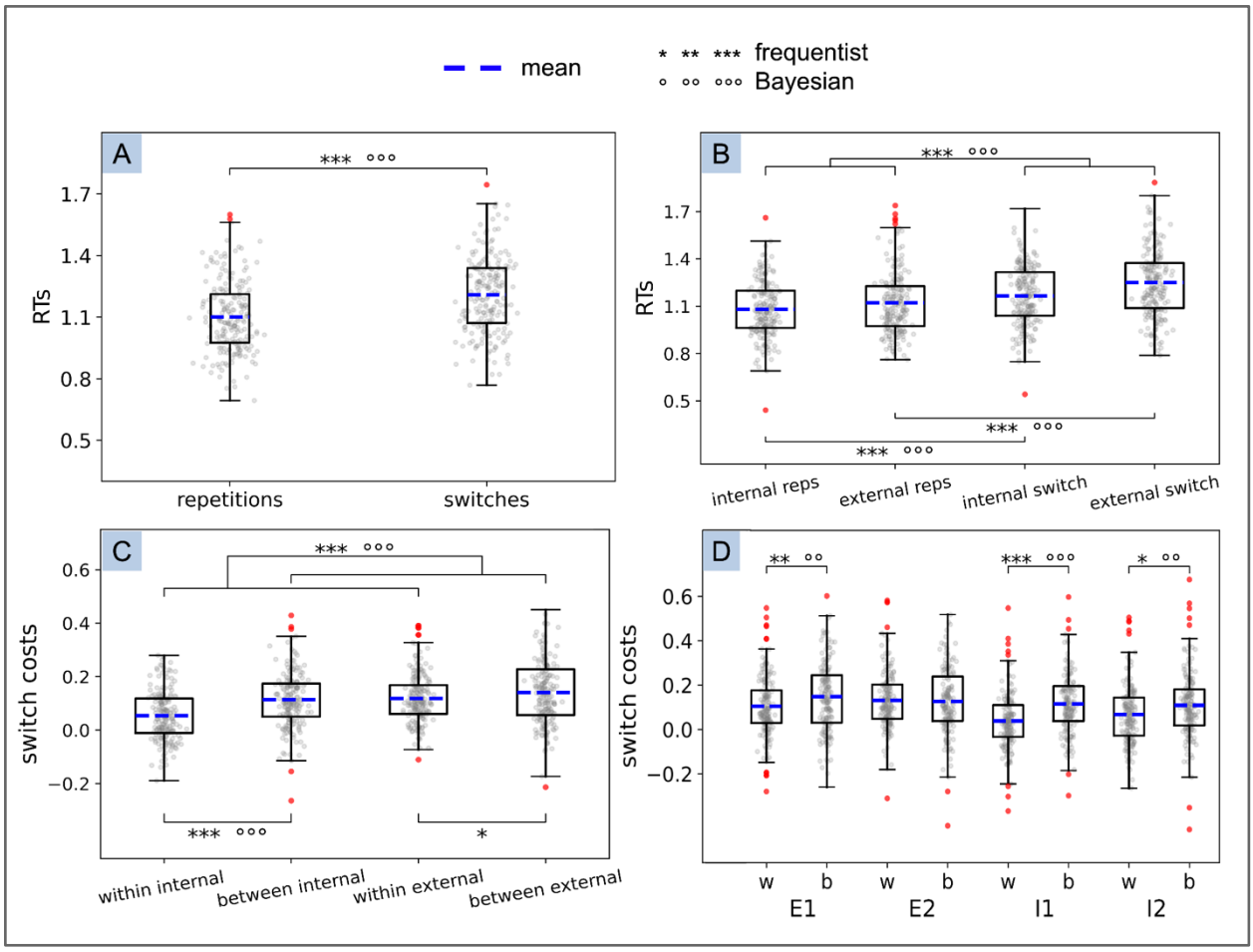

Figure 3.2. Boxplots representing data from all pre-registered statistical analyses. (A) Comparison of all repetitions versus all switches (overall switch costs); (B) main effect of trial type and post-hoc t-tests from the 2x2 rANOVA with factors domain (internal, external) and trial type (switches, repetitions) that measures the switch costs in each domain; (C) main effect of switch type and post-hoc t-tests from the 2x2 rANOVA on switch costs with factors domain and switch type (within, between domain) that measures the extra costs due to switching between domains; (D) post-hoc t-tests from the 4x2 rANOVA on switch costs with factors task and switch type, aimed at further exploring the additional costs when switching across domains.
Outlier participants appear as red dots. These were included in all results reported in the main text (see Supplementary materials for results excluding outliers). The mean is represented as a blue dashed line. The whiskers represent the range between minimum and maximum i.e., the variability outside the upper and lower quartiles. * p<.05; ** p<.01, *** p<.001, ° BF10>=3 (substantial evidence), °° BF10 >=10 (strong evidence), °°° BF10 >=100 (very strong evidence).

3.4.4. Difficulty of task repetitions

We found a significant main effect in the 1x4 ANOVA (**Figure 3.3**; Table A3 in Appendix A) comparing RT for repetitions in each task (BF_{10}=4.791e+15, F(1.9,378.19)=31.18, p<.001, η_p^2=0.135; Greenhouse-Geisser sphericity correction was needed). This suggests possible intrinsic differences in difficulty between task conditions, against our predictions. Post-hoc t-tests indeed revealed that external task 1 (consonant finding) resulted in higher RTs than all other tasks and that the personality task had higher RTs than the current sensations task (Table A3). **Table 3.1** includes the descriptive statistics of all conditions in the pre-registered analyses (RTs after subtraction of task repetitions are reported, where relevant. See Table A4 for the raw RTs).

	Repetitions	**Combined switches**	**Within domain**	**Between domains**
All	1.102 (0.172)	1.209 (0.187)		

Internal	1.081 (0.178)	1.165 (0.187)	0.055 (0.094)	0.114 (0.103)
External	1.121 (0.200)	1.251 (0.219)	0.119 (0.094)	0.140 (0.121)
E1	1.165 (0.221)		0.106 (0.135)	0.150 (0.155)
E2	1.076 (0.197)		0.132 (0.132)	0.128 (0.153)
I1	1.097 (0.189)		0.041 (0.124)	0.116 (0.137)
I2	1.065 (0.181)		0.069 (0.133)	0.111 (0.147)

Table 3.1. Mean and SD for all conditions in the pre-registered analyses. Includes all participants. All units are seconds. E1: external task 1 (consonant finding); E2: external task 2 (vowel finding); I1: internal task 1 (personality task); I2: internal task 2 (current sensations).

3.4.5. Switch costs grouped by difficulty

We found no effect of difficulty in the 1x3 ANOVA on switch costs grouped according to the differences in task difficulty (i.e., from hard to easy, neutral, and from easy to hard). However, there was a tendency towards significance with frequentist statistics only (hard-to-easy, 0.108 ± 0.094 s; neutral, 0.122 ± 0.109 s; easy-to-hard, 0.101 ± 0.100 s; BF_{10}=0.329, F(1.879,373.874)=3.03, p=0.053, η_p^2=0.015; Greenhouse-Geisser sphericity correction was needed). This trend towards significance was likely led by the (weak) difference between neutral and easy-to-hard switches (neutral switches having larger switch costs; BF_{10}=1.16, t=2.42, p_{bonf}=0.047), since no other post-hoc comparison resulted significant (with hard-to-easy vs neutral having inconclusive evidence in either direction: BF_{10}=0.404, t=1.588, p_{bonf}=0.339; and hard-to-easy vs easy-to-hard having evidence in support of the lack of an effect: BF_{01}=9.43, t=0.84, p_{bonf}=1.000). See **Figure 3.3** for a representation of the results.

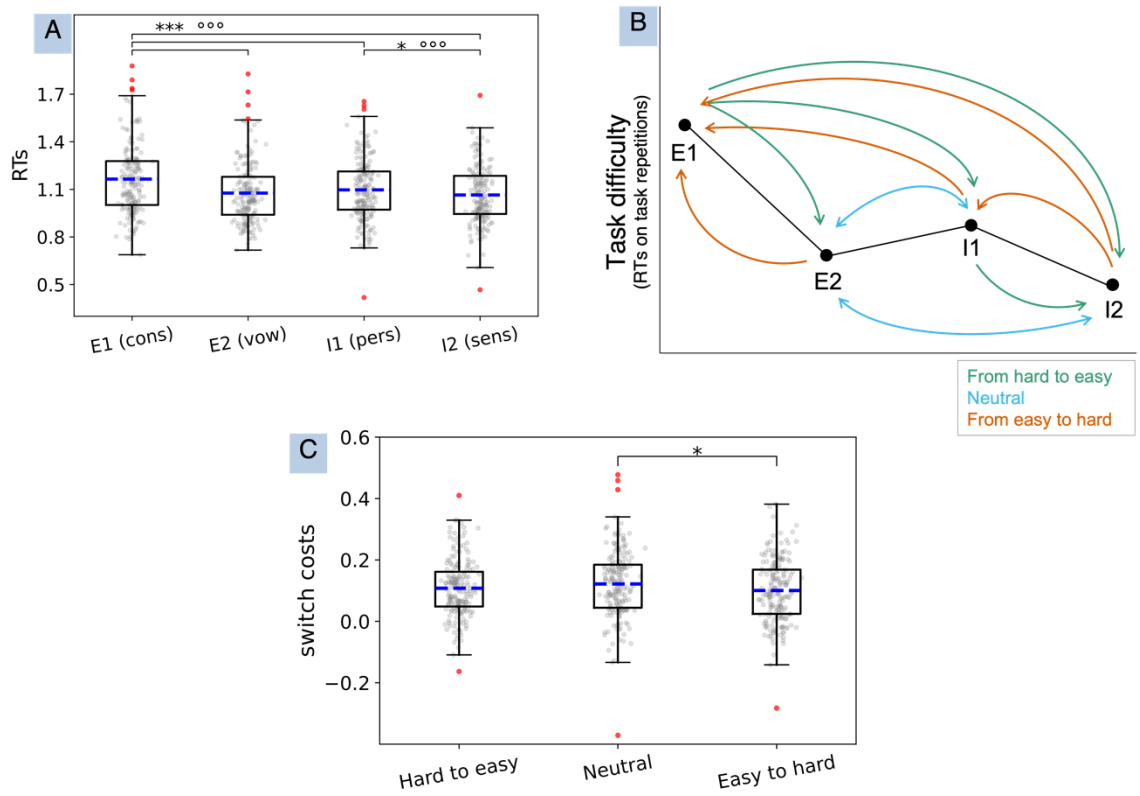

Figure 3.3. (A) 1x4 ANOVA with task repetitions, to measure task difficulty irrespective of switch costs. (B) Categorisation of each switch subtype in light of the level of difficulty of each task, as found in A. (C) Boxplots showing the results from the 1x3 rANOVA (additional, non pre-registered analysis) comparing switch costs grouped as hard-to-easy, neutral, or easy-to-hard on the basis of differences in task difficulty. Outlier participants appear as red dots (these were not removed from analyses). The mean is represented as a blue dashed line. The whiskers represent the range between minimum and maximum i.e., the variability outside the upper and lower quartiles. * p<.05; ** p<.01, *** p<.001, ° BF10>=3 (substantial evidence), °° BF10>=10 (strong evidence), °°° BF10>=100 (very strong evidence).

3.4.6. Subset of participants with no difference in task difficulty

We analysed a subset of 70 participants that showed no significant difference in intrinsic task difficulty i.e., no differences in RTs for repetitions across the four tasks (F(1.902,131.257)=2.32, p=.105, η_p^2=0.03; with Greenhouse-Geisser sphericity correction, **Figure 3.4D**), along with strong Bayesian evidence supporting the absence

of such difference (BF_{01}=3.18). This replicated the majority of the effects described above for the main analyses, with a few differences.

Specifically, the 2x2 ANOVA on RTs with factors domain and trial type (**Figure 3.4A**) resulted in a significant main effect of trial type which was consistent with our previous analyses (BF_{10}=1.757e+11 and $F(1,69)=124.89$, $p<.001$, $\eta_p^2=0.64$), However, contrary to our above results, we found no effect of domain (BF_{01}=4.85 and $F(1,69)=0.63$, $p=.43$, $\eta_p^2=0.009$). As above, the interaction was significant, but now showed only inconclusive Bayesian evidence (BF_{10}=0.48 and $F(1,69)=7.49$, $p=.008$, $\eta_p^2=0.098$). As above, post-hoc tests confirmed the presence of switch costs in both domains (external: BF_{10}=1.723e+13, $t=10.52$, $p_{bonf}<.001$; internal: BF_{10}=1.326e+7, $t=7.18$, $p_{bonf}<.001$).

Similarly, as above, the 2x2 ANOVA on switch costs with factors domain and switch type (**Figure 3.4B**) returned a significant main effect of domain (BF_{10}=10.60 and $F(1,69)=7.33$, $p=.009$, $\eta_p^2=0.096$) and switch type (BF_{10}=607.25 and $F(1,69)=23.72$, $p<.001$, $\eta_p^2=0.25$) but no interaction (BF_{10}=0.57 and $F(1,69)=3.11$, $p=.082$, $\eta_p^2=0.04$). Post-hoc t-tests revealed a significantly greater cost in switching from external to internal domain versus switching within the internal domain, in accordance with the results in the full sample (BF_{10}=2255.89, $t=4.68$, $p_{bonf}<.001$), but there was no significant increase in switches from internal to external domain compared to switches within the external domain (BF_{10}=1.06, $t=2.18$, $p_{bonf}=.185$). The difference between switches within internal and external domain remained significant (BF_{10}=19.14, $t=3.22$, $p_{bonf}=.01$), while the two types of between-domain switches were not significantly different anymore (BF_{01}=4.53, $t=1.07$, $p_{bonf}=1.00$).

As above, the 4x2 ANOVA with factors task and switch type (**Figure 3.4C**) revealed a main effect of task (with Greenhouse-Geisser correction: $F(2.688,185.489)=3.172$, $p=.030$, $\eta_p^2=0.044$) albeit with inconclusive Bayesian evidence (BF_{10}= 0.93), and a main effect of switch type (BF_{10}=375.14 and $F(1,69)=19.01$, $p<.001$, $\eta_p^2=0.22$). Similarly, the interaction was significant as before ($F(2.923,201.661)=3.23$, $p=.024$, $\eta_p^2=0.045$), although accompanied by inconclusive Bayesian evidence (BF_{10}=0.58).

Table 3.2 includes the descriptive statistics of all conditions in these additional analyses (RTs after subtraction of task repetitions are reported, where relevant. See Table A5 for the raw RTs).

	Repetitions	Combined switches	Within domain	Between domains
All	1.074 (0.164)	1.169 (0.181)		
Internal	1.075 (0.155)	1.153 (0.173)	0.044 (0.102)	0.110 (0.112)
External	1.071 (0.199)	1.184 (0.217)	0.097 (0.088)	0.128 (0.125)
E1	1.092 (0.195)		0.093 (0.109)	0.145 (0.160)
E2	1.050 (0.216)		0.101 (0.119)	0.105 (0.166)
I1	1.084 (0.169)		0.031 (0.131)	0.121 (0.131)
I2	1.067 (0.154)		0.059 (0.142)	0.095 (0.150)

Table 3.2. Descriptive statistics of all conditions in the analyses of a balanced subset of 70 participants. E1: external task 1 (consonant finding); E2: external task 2 (vowel finding); I1: internal task 1 (personality task); I2: internal task 2 (current sensations).

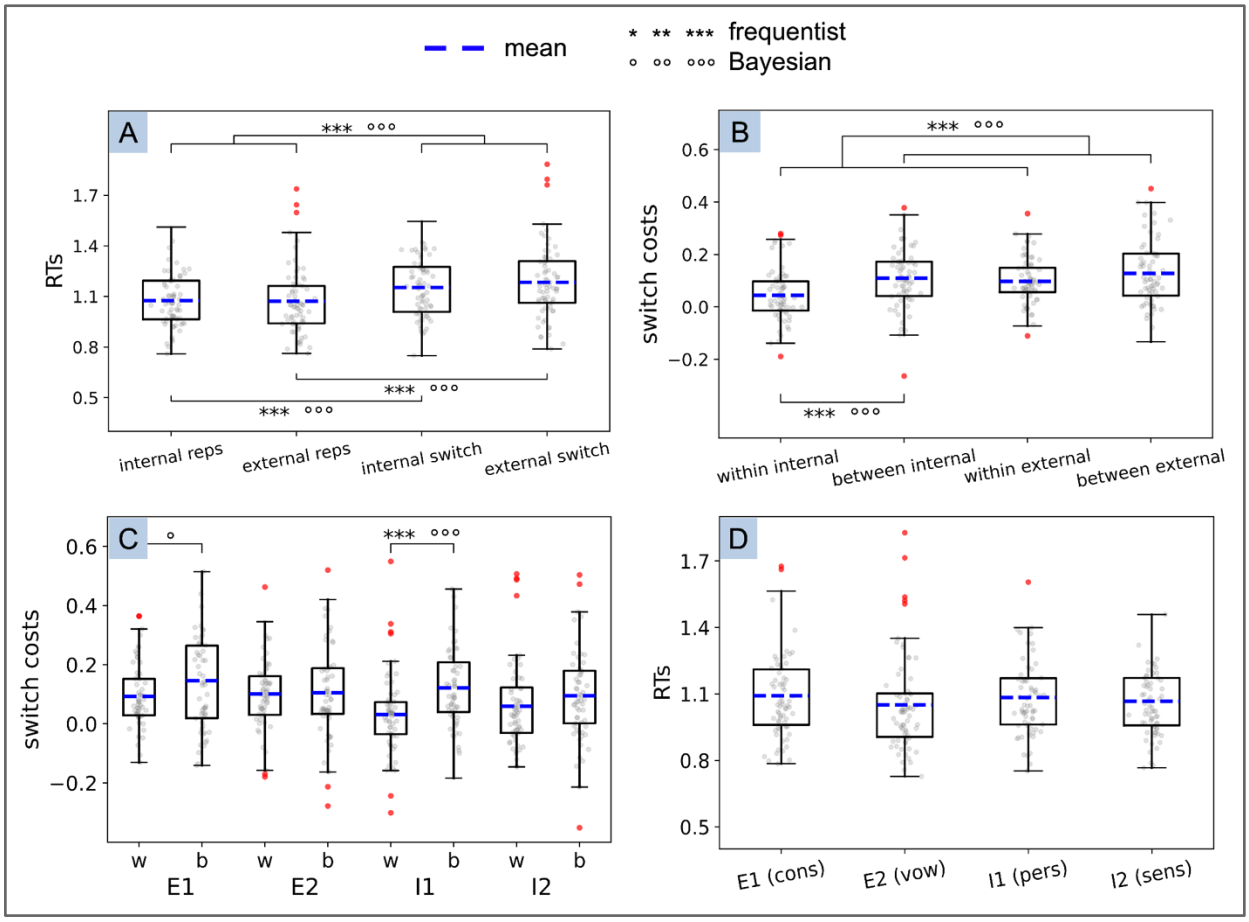

Figure 3.4. Boxplots showing data from a subset of 70 participants who did not show differences in task difficulty across the 4 tasks. (A) main effect of switch type and post-hoc t-tests from the 2x2 rANOVA with factors domain and trial type (switch costs in each domain); (B) main effect of switch type and post-hoc t-tests from the 2x2 rANOVA with factors domain and switch type (extra costs due to switching between domains); (C) 4x2 rANOVA with factors task and switch type (further exploration of additional costs when switching across domains); (D) 1x4 ANOVA with task repetitions (measure of task difficulty irrespective of switch costs). Outlier participants appear as red dots (these were not removed from analyses). The mean is represented as a blue dashed line. The whiskers represent the range between minimum and maximum i.e., the variability outside the upper and lower quartiles. * p<.05; ** p<.01, *** p<.001, ° BF10>=3 (substantial evidence), °° BF10>=10 (strong evidence), °°° BF10>=100 (very strong evidence).

3.4.7. Effects of CTI duration

The 2x3 rANOVA on switch costs with factors domain and CTI (**Figure 3.5**) showed a significant main effect of CTI (BF_{10}=6.912e+17, F(1.908,379.715)=59.01, p<.001, η_p^2=0.23; with Greenhouse-Geisser sphericity correction) and domain (with greater switch costs in the external as compared to internal domain; BF_{10}=3.010e+10, F(1,199)=39.93, p<.001, η_p^2=0.17), but strong evidence for the lack of an interaction (BF_{01}=38.07, F(1.913,380.732)=0.44, p=.634, η_p^2=0.002; with Greenhouse-Geisser sphericity correction). Post-hoc t-tests revealed greater switch costs in short CTIs compared to both medium (BF_{10}=4.193e+12, t=8.16, p_{bonf}<.001) and long CTIs (BF_{10}=3.739e+18, t=10.29, p_{bonf}<.001), but no difference between medium and long CTIs (BF_{10}=0.53, t=2.14, p_{bonf}=.10). This pattern was present both in the internal (short vs medium: BF_{10}=6975.18, t=5.16, p_{bonf}<.001; short vs long: BF_{10}=2.187e+8, t=7.16, p_{bonf}<.001; medium vs long: BF_{10}=0.48, t=2.01, p_{bonf}=.67) and external domain (short vs medium: BF_{10}=2.273e+8, t=6.42, p_{bonf}<.001; short vs long: BF_{10}=1.306e+9, t=7.44, p_{bonf}<.001; medium vs long: BF_{01}=7.25, t=1.02, p_{bonf}=1). Importantly, despite the difference between short and medium/long CTIs, switch costs were significantly greater than 0 in all CTI durations, as measured by the one-sample t-tests (all p<.001).

Table 3.3. Mean and SD for all conditions in the 2x3 rANOVA. Includes all participants. All units are seconds includes the descriptive statistics of all conditions in this analysis (RTs after subtraction of task repetitions are reported; see Table A6 for the raw RTs).

	Internal	**External**
Short CTIs	0.125 (0.125)	0.177 (0.132)
Medium CTIs	0.075 (0.107)	0.114 (0.111)
Long CTIs	0.055 (0.112)	0.104 (0.112)

Table 3.3. Mean and SD for all conditions in the 2x3 rANOVA. Includes all participants. All units are seconds**.**

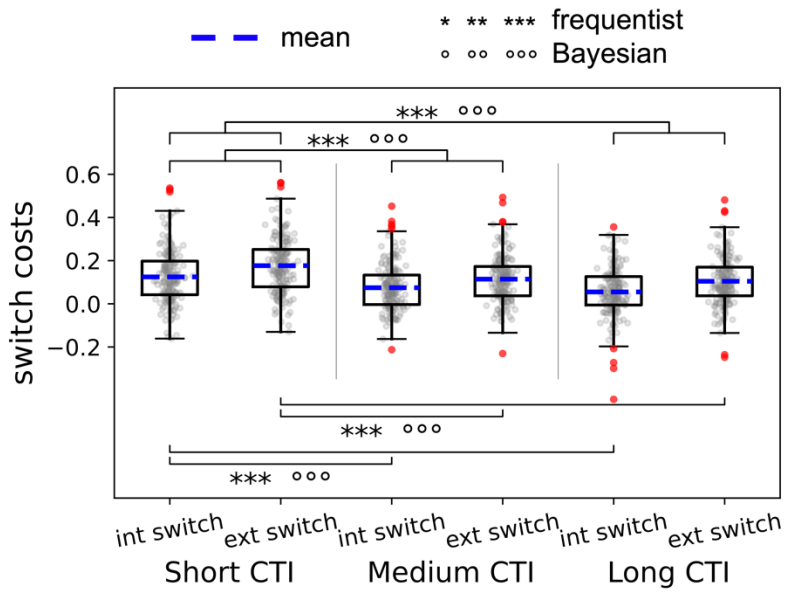

Figure 3.5. Boxplots representing the data from the analysis on the effects of CTI duration. The figure shows the post-hoc t-tests from the 2x3 rANOVA on switch costs with factors domain (internal, external) and CTI (short, medium, long). Outlier participants appear as red dots. These were included in all results reported in the main text (see Supplementary materials for results excluding outliers). The mean is represented as a blue dashed line. The whiskers represent the range between minimum and maximum i.e., the variability outside the upper and lower quartiles. * p<.05; ** p<.01, *** p<.001, ° BF10>=3 (substantial evidence), °° BF10>=10 (strong evidence), °°° BF10>=100 (very strong evidence).

3.5. Discussion

In this study we tested a novel paradigm for the investigation of task switches within and between external and internally oriented (specifically self-referential) cognitive domains. We provide the first evidence of switch costs towards self-referential tasks, confirming our main hypothesis. Interestingly, and contrary to what we expected, internal switch costs were smaller than those between our external tasks (which we designed to be similar to the tasks more typically studied in the task switching literature). Crucially, we also observed an additional cost for switches across the two domains (internal to external and vice versa) compared to within-domain switches, confirming our fourth hypothesis.

There is vast literature reporting costs associated with switching between externally oriented tasks (see Kiesel et al., 2010; Monsell, 2003; Vandierendonck et al., 2010 for reviews). Here, we found evidence of similar switch costs in the internal, self-referential domain as well. Importantly, these costs were present when taking into account all types of switches towards internal tasks (i.e., both those coming from an internal or from an external task), but also when focusing only on switches within the internal domain. To our knowledge, this is the first study to report switch cost effects involving self-referential processes. In an earlier study aimed at assessing the impact of mindfulness meditation over cognitive control, Chambers and colleagues (Chambers et al., 2008) used an attention-switching task that included blocks of neutral (food/household objects) versus affective (positive/negative) words with the aim of measuring “internal switching” on affective stimuli. However, their paradigm instructed participants to mentally count the appearance of each word category across the task and, therefore, while the nature of the stimuli (neutral vs affective) could be described as external vs internal (respectively), the task itself involved mental counting for both types of words, rather than an actual affective or, in our case, self-referential judgement. In that sense, the underlying processes in their study are similar to those captured by traditional task-switching studies employing working memory tasks.

The presence of switch costs both in the internal and external domains in our data could be explained by either the presence of one domain-general mechanism for task-switching that controls both domains (as suggested by some; see e.g., (Chiu & Yantis, 2009), or the existence of distinct domain-specific mechanisms that operate in a similar fashion. Importantly, and contrary to what we expected (see *Hypothesis 3*), we

found a significant interaction between domain and trial type, whereby switch costs were greater for external than for internal tasks. While, in our main analyses, this interaction could have been partially due to a difficulty imbalance across the tasks, the same analysis over a subset of participants that showed no significant differences in the RTs of task repetitions still returned a significant effect (albeit with much weaker Bayesian evidence). This might suggest the presence of two distinct (domain-specific) mechanisms for the flexible control of internal and external processes, whereby the difference in the magnitude of switch costs would reflect differences in the underlying cognitive processes (i.e., in the way goal-shifting and rule retrieval and activation are implemented). In line with this view, a number of studies point towards switch costs capturing an increased preparatory control effort (during switches compared to repetitions) in the system responsible for the task, instead of a dedicated process in place for task-switching specifically (Kiesel et al., 2010; Ruge et al., 2013). For instance, studies that systematically varied the cue-to-target interval showed benefits of longer preparation time (leading to faster responses) not only on switch trials, but on repetition trials as well (Altmann, 2004). Similarly, the predictability of the upcoming task appears to benefit the preparation of both switches and repetitions, indicating that task-specific control processes are engaged both when switching and repeating tasks (Dreisbach et al., 2002; Koch, 2005). Furthermore, neuroimaging research has identified a set of lateral frontoparietal regions (i.e., inferior frontal gyrus, inferior frontal junction, pre-SMA, intraparietal sulcus and posterior parietal cortex) that appear more active during switches between similar (external) tasks compared to repetitions (Brass & Cramon, 2004; Braver et al., 2003). Interestingly, however, most of these regions also appeared to activate during task repetitions (Dove et al., 2000), providing evidence against a specific network dedicated to task-set reconfiguration during switches only, and in support of an effect of an adaptation or facilitation process during task repetitions instead (i.e., leading to less activation in the network during repetitions; De Baene et al., 2012). Similarly, studies employing tasks that rely on different processes (e.g., colour vs motion discrimination, semantic vs spatial tasks, etc.) showed activation of lower-level areas (e.g., fusiform gyrus for colour encoding) and differential ERP signatures that depend on the specific task features during the post-cue preparatory period of switch trials versus repetitions (Capizzi et al., 2015; Wylie et al., 2006). These results possibly suggest the presence of varied subtypes of preparatory control (or at least a dynamic interaction between general control areas

and other more specialised areas) that can be engaged depending on the specific task demands (Ruge et al., 2013). While behavioural evidence cannot directly speak about underlying networks, our results seem to agree with this view of two local, specific systems that aid the flexible control of self-referential and external processes respectively.

Crucially, we also found additional costs associated with switches across the two domains compared to those that stayed within-domain, although this effect was weaker in switches towards the external domain (i.e., we only obtained anecdotal Bayesian evidence when comparing internal-to-external switches vs within-external switches). Our results are in apparent contrast to Verschooren and colleagues (Verschooren, Schindler, et al., 2019) who found switch costs between perceptual and working memory tasks were similar to those within the perceptual domain. The authors proposed that their results support the presence of one limited shared resource that the two domains (perception and memory) have to compete for (termed 'resource sharing account'; Burgess et al., 2007; Gilbert et al., 2005). As discussed earlier on, they considered working memory as a separate domain in that (unlike perception and other classically used tasks in the task-switching literature) it entails a focus on information that is not perceptually available (versus stimulus-dependent information). However, the inherent differences with self-referential processes preclude direct comparisons between our results. Self-referential cognition is defined by a focus over information about the self as opposed to information about the external world (i.e., a distinction in the content of information regardless of perceptual input). In contrast, working memory would be considered part of our definition of the external domain, due to its focus on non-self stimuli and its engagement of lateral frontoparietal regions (Awh & Jonides, 2001; Pollmann & von Cramon, 2000). The resource sharing account thus may provide an explanation for the control of externally oriented (perceptual or working-memory) processes, but is not exhaustive for the interpretation of our findings that include the self-referential domain.

Instead, we believe the additional cost between domains in our study might reflect a more effortful control needed to switch between different domains, as the tasks are subserved by different (domain-specific) cognitive systems, compared to the effort and resources needed to switch within the same system configuration. In other words, the necessary steps of deactivating the currently irrelevant system and activating the relevant one would take more time compared to more "local" within-domain

adjustments. To allow an effective communication between domain-specific systems, one possibility is that these systems are directly linked with each other. As discussed above, regions of the DAN show increased activation during task switches. In contrast, the default mode network (DMN) has been involved in the performance of self-referential tasks similar to the ones we used in our study (see Davey et al., 2016; Kelley et al., 2002) but is also recruited by large shifts in cognitive context (Crittenden et al., 2015; Smith et al., 2019), as well as in preparation of rest trials (Sidlauskaite et al., 2014) in other task-switching paradigms. It is thus possible that the DMN would link with the DAN, possibly via a functional segregation of the precuneus (Leech et al., 2011). Indeed, these two networks are known to anti-correlate both at rest (Fox et al., 2005) and during cognitive tasks (Kelly et al., 2008; Weissman et al., 2006). Another possibility is that switching across domains engages a higher level domain-general control system, which couples with both specific subsystems when a domain shifting is needed. In the task-switching literature, there is evidence for the concurrent engagement of a small number of DAN areas (including the superior parietal cortex, and ACC/pre-SMA) during switching irrespective of specific task features and switch types. In contrast, other regions in this network show task-specific modulations (Esterman et al., 2009; Kim et al., 2012; Tamber-Rosenau et al., 2011; Yeung et al., 2006). This could suggest a higher-order control system that can coordinate the implementation of task-relevant rules during cognitive shifts (Yeung et al., 2006). Importantly, however, this was found through studies that employed externally oriented tasks only. In contrast, a vast literature on the dynamics of large-scale intrinsic networks points towards a role of the salience network in the flexible coupling of DMN and DAN to support adaptive changes between external and internal processes (Shaw et al., 2021; Spreng et al., 2010; Sridharan et al., 2008), suggesting this may be a potential candidate to regulate between domain (internal/external) switches. Future neuroimaging studies may clarify whether this is the case.

Importantly, we found that the magnitude of the switch costs in our paradigm was influenced by the length of preparation time (CTI duration) in a similar way for internal and external tasks. Specifically, short CTIs induced greater switch costs than medium and long ones on both domains. This is consistent with the vast literature demonstrating that longer preparation times have a facilitatory effect on task-switching for externally oriented tasks (Kiesel et al., 2010; Koch, 2003; Monsell & Mizon, 2006), and expands those findings to the internal domain for the first time. Crucially, the lack

of interaction between CTI duration and domain suggests that the internal and external cognitive systems might share common features of cognitive control, further supporting the above discussed presence of domain-general processes, affecting the preparatory phase in this case. It is important to also note that both domains retained a switch-cost effect even after long preparatory times, consistently with previous studies using our CTI jittering (De Baene & Brass, 2011, 2013; Sidlauskaite et al., 2014), and further supporting the suitability of our design for the study of task-switching.

In a similar line, we found an interaction between domain and switch type, further suggesting that the extra costs associated with between-domain switching differed depending on which domain participants switched from and to. Post-hoc comparisons revealed that this interaction was mainly led by a marked difference among the within-domain switches. Specifically, switching within the external domain induced slower RTs compared to switching within the internal domain. Furthermore, while this difference persisted in the subsample of participants with a balanced difficulty across tasks, the between-domain asymmetry did not. It is possible that the slower RTs in external within-domain switches in the full group were (at least partially) induced by the large difference in difficulty between task E1 and E2. Previous studies showed that an imbalanced dominance and/or familiarity between tasks can influence the magnitude of switch costs, with higher costs related to switching to the more dominant task compared to switching to the less dominant one. For instance, word reading was associated with greater costs compared to colour naming in the Stroop task (Wu et al., 2015; Yeung & Monsell, 2003). However, while according to this logic, switching from task E1 (harder) to E2 (easier) should result in slower RTs compared to the opposite switch, such difference was not present in our data. However, the wide difference between switches within the internal and external domain was only reduced (not abolished) in the balanced sample of participants, indicating that task difficulty was not the (only) cause for the interaction between domain and switch type in our data. This further supports the idea that the magnitude of the switch costs within each domain might reflect the employment of domain-specific cognitive processes (as stated above). It is also possible that our experimental design induced a stronger task set interference between external tasks (sharing similar instructions and stimuli lists) compared to between internal tasks (where tasks require larger shifts in focus and have homogeneous lists of either trait or bodily adjectives), due to a higher level of

competition between the stimuli features (Sdoia & Ferlazzo, 2008). However, it is worth noting that, because the bodily adjectives did not all relate to purely physical sensations (e.g., 'hungry') but also included emotional states that are accompanied by bodily sensations (e.g., 'anxious'), the difference between these words and those used for the personality task might not have been obvious to participants and thus should have minimised this issue. In either case, studies that systematically varied the number of stimuli and response modalities (Dykstra et al., 2022), or included switching between similar or dissimilar tasks (Arrington et al., 2003; Crittenden et al., 2015) and domains (Foti et al., 2015) highlighted that, in agreement with our results, the specific task demands and characteristics do influence switch costs.

There are a number of further considerations to be acknowledged when interpreting our data. First, we had to rely on a proxy measure for the accuracy of the internal conditions (via a post-task questionnaire), as the required judgments inherently lack a 'ground truth' that can be directly accessed by other than the participants' themselves. This is naturally a less objective and reliable measure as compared to our external tasks. Without a ground truth measure it is not possible to establish whether our participants were truly able to accurately assess information about themselves. However, while we used self-referential tasks in a task-switching paradigm for the first time, personality judgment tasks have been extensively used in previous studies on the sense of self and its neural bases in similarly fast-paced experiments (D'Argembeau et al., 2007; Davey et al., 2016; Kelley et al., 2002). Moreover, where accuracy was lower for internal than for external tasks, it remained very high (and with low variance) across them (>89%), with internal tasks displaying faster or similar response times to the external ones. Overall, this suggests that our participants were indeed able to successfully perform the self-referential tasks. Moreover, we focused our analysis on RTs only, and only included trials with correct responses. Therefore, any potential influence of the discrepancy between internal and external tasks should be limited. In either case, we used accuracy to make sure that participants were following instructions and engaging in the processes of interest, and in this case, attempting to access internal information. Understanding whether they were reliable and truthful in their personality assessment or measuring their interoceptive sensibility was beyond the scope of our study, and remains an interesting question to be addressed in future research.

Second, our externally oriented tasks required detection and categorisation of specific letters in a written word, thus calling for a shift in spatial attention (to locate the third or penultimate letter) and orthographic classification (to recognise consonants or vowels). In contrast, the internally oriented tasks both required a more conceptual (semantic) encoding of the words, as well as autobiographical knowledge (personality task) and interoceptive sensibility (current sensations task). Therefore, the level of stimulus processing required by each domain is different. Previous studies reported greater switch costs for switches between dissimilar tasks compared to switches between tasks that share the same cognitive operations (Arrington et al., 2003). For instance, switching within two similar language tasks, within two semantic categorisation tasks or within visual perception tasks was found to be easier (faster RTs) than switching across them (Crittenden et al., 2015). Similarly, the switch costs associated with switching within attention to the form of visual stimuli (width and height) or within attention to their colour (hue and brightness) were smaller compared to the costs of switching between those perceptual features (Arrington et al., 2003). Importantly, this similarity effect was not related or attributable to differences in the difficulty of specific tasks. While this did not affect the presence of reliable switch costs in our paradigm (which we found in both domains even when only taking within-domain switches into account), it might have influenced over the magnitude of the additional costs we found in between-domain vs within-domain switches. It is however important to note that these differences are intrinsic to the specific processes we aimed to investigate and thus were not avoidable. As stated elsewhere in this paper, we designed our external tasks to bridge with the vast task-switching literature employing digit and letter categorisation (Rogers & Monsell, 1995; Schneider & Logan, 2010), while keeping the same stimuli for both domains. Future studies might focus on testing this paradigm with other (more semantic) externally oriented tasks.

3.6. Conclusions

We identified switch costs in both external and internal (self-referential) domains and an additional cost for between-domain versus within-domain switches. This may suggest the goal-directed engagement of two domain-specific cognitive systems (for the control of external and internal processes) that communicate and share domain-general control features for their flexible management.

Chapter 4

CHAPTER 4 : NEURAL CORRELATES OF GOAL-DIRECTED PREPARATION TO SWITCHING ACROSS EXTERNAL AND INTERNAL DOMAINS

4.1. Introduction

Our brain constantly encodes and coordinates information from the external environment, internal signals from our body, and inner thoughts. Seminal research has identified distinct functional brain networks specifically linked to external or internal processing (Fox & Raichle, 2007). In particular, the default mode network (DMN) is associated with self-related thoughts, spontaneous cognition and mind-wandering, autobiographical memory and simulation of events (Andrews-Hanna, 2012; Buckner et al., 2008; Raichle, 2015). On the other hand, the dorsal attention network (DAN) is associated with externally oriented attention and working memory (Corbetta & Shulman, 2002; Miller & Buschman, 2013). These networks are traditionally thought to be anticorrelated, as they show opposite patterns of activation during rest (Vanhaudenhuyse et al., 2010), attentional (Weissman et al., 2006) and self-referential tasks (Davey et al., 2016; Kelley et al., 2002; Whitfield-Gabrieli et al., 2011). However, in occasions, the DMN is also involved in task preparation (Hampshire et al., 2019; Koshino et al., 2014), and demanding cognitive shifts between tasks (Crittenden et al., 2015), suggesting a DMN contribution to goal-directed cognition as well. Recent accounts in fact highlight the highly variable nature of DMN-DAN interactions depending on the cognitive context, (e.g. rest, movie viewing, introspection,…) (Dixon et al., 2017). The organisation between these two networks is thought to be coordinated by executive control and/or salience networks (ECN and SN, sometimes collectively referred to frontoparietal control network) (Gao & Lin, 2012; Menon & Uddin, 2010; Seeley et al., 2007; Spreng et al., 2010). In addition, recent animal studies revealed a fundamental contribution of the mediodorsal (MD) thalamus (which displays wide functional connections with all the above-mentioned networks) in supporting and boosting cortical representations during cognitive switching (Rikhye et al., 2018; Schmitt et al., 2017). However, there is a lack of research that specifically

focuses on understanding the relationship across these networks during acts of controlled, adaptable cognitive changes that specifically include internally oriented tasks, so how all these networks interact to allow goal-directed cognitive shifts across external and internal processes is still poorly understood. These dynamics have been often investigated with task-switching paradigms. In these paradigms, preparing to switch to a different task elicits activation in a set of lateral frontoparietal regions generally overlapping with the ECN (i.e., inferior frontal gyrus, inferior frontal junction, pre-SMA, intraparietal sulcus and posterior parietal cortex), along with task-specific areas (e.g., fusiform gyrus for colour encoding) (Brass & Cramon, 2004; Wylie et al., 2006). However, previous studies only included externally oriented tasks (e.g., parity and magnitude judgment tasks, letter identification, colour or object naming, etc…; Kiesel et al., 2010), and the switches between the external and internal (self-referential) domain (as well as within the internal domain) were never investigated with neuroimaging.

In an earlier study, we developed a novel task-switching paradigm (Chapter 3; Calzolari et al., 2022) to characterise behavioural switches between external and internal (self-referential) processing. We provided the first evidence of switch costs (higher RTs for switches compared to repetitions) in internal tasks, and of additional costs associated with between-domain (i.e., from internal to external and vice versa) compared to within-domain switches (Calzolari et al., 2022). This suggested the presence of two domain-specific control subsystems that communicate and share common features of cognitive control (possibly via a higher-order domain-general system). Here, we built upon our behavioural findings to address the neural correlates of task-switch preparation when externally oriented and internally oriented tasks are involved using fMRI. We expected to replicate our behavioural results, and importantly to see DMN and DAN activation in preparation of internal and external tasks respectively. We also hypothesised to find activation in areas associated with cognitive control and working memory (i.e., ECN/DAN regions) in preparation of switches compared to task repetitions, and to see common neural activation associated with switching in both domains (i.e., an overarching control system), including the MD thalamus. We also explored whether such hypothesised activation patterns would differ when looking at between-domain and within-domain switches, expecting differential activation between switch types (thus mirroring the behavioural results from our previous study) possibly located in domain-general control areas. Finally, we

explored modulations in effective connectivity in response to different type of switches to shed light on the causal directed relationships between regions during network reorganisation.

4.2. Methods

4.2.1. Participants

We recruited a total of 33 participants (mean age = 22.61 ± 2.83; 22 women, 11 men) via the University of Birmingham Research Participation Scheme and advertisements across campus. Participants were aged 18-35, right-handed, native English speakers, and reported no history of neurological or psychiatric conditions. They also met the eligibility criteria to enter the MRI environment. Participants had the chance to read the information sheet and ask questions before starting the experiment. They filled in the MRI screening form and gave written informed consent prior to MRI scanning. They received compensation in the form of cash or research credits. The University of Birmingham's Science, Technology, Engineering and Mathematics Ethical Review Committee provided approval for our study.

We discarded 2 participants due to low accuracy (< 60% of correct responses) in one or more task conditions, and 1 participant due to technical issues in the post-scan questionnaire. This resulted in a total of 30 participants (mean age = 21.50 ± 2.90; 21 women, 9 men) included in the analysis.

4.2.2. Experimental design and procedure

The main experiment consisted of one single session (**Figure 4.1A**) lasting approximately 2 hours and 30 minutes. At the beginning of the session, participants read the study information and filled in MRI screening form and informed consent. They were provided with both written and oral task instructions and had the chance to ask questions to the experimenter. They performed an initial training session of 10 minutes outside the scanner. Once inside the scanner, they first underwent a structural

T1 scan (approximately 7 minutes), then performed the main task (approximately 50 minutes divided into 4 runs, see the next subsection for details), and underwent a final anatomical scan (3 minutes, not reported in this paper). After the scanning session, participants completed a questionnaire (10 minutes) aimed at verifying the correct responses for the two internal task conditions to use for further analyses. This instructed them to perform the 'personality' and 'current sensations' judgements again (as described in Chapter 3) but in a self-paced way and using a list that displayed all stimuli.

4.2.3. Task and stimuli

We used the same task than in our previous study (Chapter 3; Calzolari et al., 2022), but presented in person inside the MRI scanner via custom MATLAB scripts (version R2018b) and Psychtoolbox-3 (Kleiner et al., 2007) instead of PsychoPy. In brief, the experiment was a cued task-switching paradigm with written English words (personality trait and bodily adjectives) as stimuli. Based on a geometric cue appearing in advance (with pseudologarithmically jittered intervals), participants had to either direct their attention towards specific stimulus features in 'external' tasks (i.e., to assess if the third letter of the stimulus was a consonant or if the penultimate letter was a vowel), or they needed to access self-related characteristics in 'internal' tasks (i.e., judge if the stimulus described their own personality, or if it described a present bodily sensation). In this study, participants responded using index and middle fingers of their right hand and by pressing either the left (for 'yes') or right (for 'no') buttons of a NAtA Technologies Inc. response box. The jittered cue-to-target and intertrial intervals allowed for an optimal separation between cue-related and target-related activity as well as between trials (De Baene & Brass, 2011).

The main experimental phase inside the scanner (380 trials) was divided in 4 runs (95 trials each, lasting 13 minutes and 12 seconds). Participants saw the task instructions at the beginning of each run and had the chance to rest for a few minutes between runs. See Chapter 3 (sections 3.3.3 and 3.3.4) for a full description of the task paradigm, parameters, and stimuli. **Figure 4.1B** offers a representation of the trial structure.

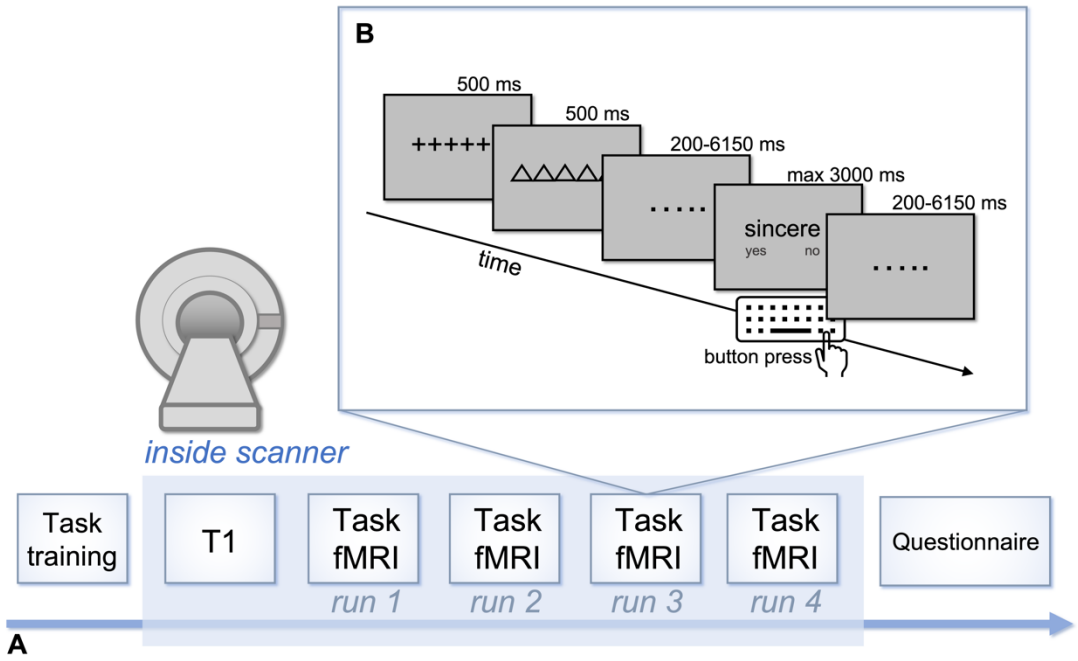

Figure 4.1. (A) Structure of the main experimental session including an initial task training phase outside the MRI scanner, a structural T1 scan and 4 runs of task-fMRI. A post-task questionnaire immediately after scanning allowed us to obtain accuracy for the internally oriented tasks. (B) Structure of a single trial: after a 500 ms fixation screen, a geometrical cue (500 ms) signalled participants which of the four tasks to perform on the following word stimulus. After a jittered interval (pseudologarithmic jittering), a written adjective appeared and stayed at the centre of the screen until button press, for a maximum of 3 s. Participants had to respond yes (left arrow key) or no (right arrow key) using index and middle finger of their right hand, respectively. After response, another jittered interval separated the trial from the following one.

4.2.4. Behavioural analysis

We analysed the behavioural data using JASP 0.16.3 (JASP Team 2020). The analytical steps for the analysis of these behavioural data are the same as those in our previous study (Chapter 3; Calzolari et al., 2022). We did not have to discard any participant based on the number of missing trials (no one missed 10% of trials or more; mean percentage of missing trials = 0.49% ± 0.80), but discarded 2 participants with less than 60% accuracy in any of the 4 tasks. We removed outlier trials (Tukey's

method; Tukey, 1977) and trials with RTs below 200 ms, resulting in an average of 3.44% (± 1.33) discarded trials per participant, in addition to the trials discarded due to incorrect responses (7.30% ± 4.22).

We performed the two main analyses from Chapter 3: a 2x2 rANOVA (frequentist and Bayesian) with domain (internal, external) and trial type (repetitions, all switches) as factors on mean RTs, and another 2x2 rANOVA with factors domain (internal, external) and switch type (within-domain, between-domains) on switch costs. We also performed one sample t-tests comparing each type of switch costs in this last ANOVA to 0. We included accurate trials only and excluded the data from the training phase.

4.2.5. MRI acquisition

We acquired the data on a Siemens MAGNETOM Prisma 3T system at the Centre for Human Brain Health (CHBH, University of Birmingham) using a 64-channel head coil. We collected the task fMRI data in 4 separate runs, all with an EPI sequence and the following parameters: 528 volumes per run, 57 slices, TR = 1500 ms, TE = 35 ms, voxel size = 2.5x2.5x2.5 mm, flip angle = 71°, matrix size = 84x84x57, field of view = 210x210 mm, iPAT acceleration factor = 3. We also obtained T1-weighted images for anatomical co-registration with parameters TR = 2400 ms, TE = 2.22 ms, flip angle = 8°, matrix size = 208x300x320, field of view = 256x256, voxel size = 0.8x0.8x0.8 mm. In addition, we collected susceptibility weighted images, but we did not analyse them within the current study.

4.2.6. fMRI preprocessing

We preprocessed and analysed the fMRI data using SPM12 version v7771 (Ashburner et al., 2016) on MATLAB R2019b. The pipeline (**Figure 4.2**) followed standard preprocessing steps (realignment, slice timing correction, coregistration between anatomical and functional images, spatial normalisation, and smoothing with an $5mm^3$ Gaussian kernel), plus the modelling and removal of physiological noise using the TAPAS PhysIO Toolbox (Kasper et al., 2017), a denoising procedure that resembles the aCompCor method (Behzadi et al., 2007). Specifically, the procedure involved a principal component analysis (PCA) on the segmented white matter and cerebrospinal

fluid (CSF) masks, based on the assumption that the temporal fluctuations in those regions are related to respiratory and cardiac artifacts (Behzadi et al., 2007). White matter and CSF ROIs were extracted using a 99% and 85% threshold for voxel inclusion, respectively, and cropping 1 voxel (mask erosion). We computed the first 5 PCs and added them as noise regressors (along with movement) in our subsequent general linear model (GLM). Within the PhysIO toolbox, we also performed motion censoring on volumes with more than 2 mm translation and/or 2 degrees rotation.

4.2.7. GLM Analysis

We based the fMRI analysis on the 6 task conditions of interest in this design: repetitions of internal tasks, repetitions of external tasks, switches within internal tasks, switches within external tasks, switches from external to internal (i.e., between-domain switches towards internal tasks) and, vice versa, from internal to external (i.e., between-domain switches towards external tasks). Importantly, for these analyses we focused on the cue-to-target period only, to investigate preparatory activation and not task performance itself. We always included correct trials only.

We conducted a whole-brain analysis using the general linear statistical model (GLM; Friston et al., 1994) on SPM12. At the first-level (single-subject), the GLM model included the 6 task conditions mentioned above as regressors of interest. All pairwise contrasts are provided in **Table 4.1.**

GLM contrasts					
		Condition A > Condition B			Conjunction
Effect of Domain	**1**	Internal (all trial types)	>	External (all trial types)	
	2	External (all trial types)	>	Internal (all trial types)	
Effect of Switching	**3**	Switches (both domains)	>	Repetitions (both domains)	
	4	Switches to internal	>	Repetitions of internal	X
	5	Switches to external	>	Repetitions of external	
	6	Switches within internal	>	Repetitions of internal	X
	7	Switches within external	>	Repetitions of external	
	8	External-to-internal switches	>	Repetitions of internal	X
	9	Internal-to-external switches	>	Repetitions of external	
Comparison across switch types	**10**	All between-domain switches	>	All within-domain switches	
	11	External-to-internal switches	>	Switches within internal	X
	12	Internal-to-external switches	>	Switches within external	

Table 4.1. List of all GLM pairwise contrasts.

Contrasts 1 and 2 assessed the difference between domains regardless of trial types. See Appendix B for additional contrasts between domains (internal > external and external > internal on repetitions only and on switches only). Contrast 3 investigated the activity in preparation of all switches as compared to repetitions, while contrasts 4 and 5 looked at domain-specific effects on switching. Moreover, we performed more nuanced comparisons to explore the effect of each specific switch type as compared to repetitions (contrasts 6, 7, 8, 9). Finally, contrasts 10, 11, 12 explored the differences across switch types. All contrasts were replicated across runs so that the effects were averaged across the 4 experimental blocks. All the GLMs also included a regressor of no interest with the onsets of the button presses (duration of zero) to regress out the motor activity associated with responding, as well as the realignment parameters, censored volumes and physiological noise regressors from the PhysIO

toolbox as effects of non-interest. We used the default SPM high-pass filter with a cut-off period of 128 s to remove slow-signal drifts. We then performed second-level GLMs with a one-sample t-test design in order to test the group effects for each of our contrasts of interest. In addition, we performed a conjunction analysis for each of the 4 pairs of first-level contrasts indicated in **Table 4.1**. We carried out these conjunction analyses in separate second-level GLMs by selecting a one-way ANOVA design with 2 groups (one for each first-level pairwise contrast) and contrasts that separately computed the average of each group. These contrasts were then selected for conjunction analysis in SPM, for which we chose the conjunction null option to only retain the activation common to both contrasts (Nichols et al., 2005).
We report voxels that survived family-wise error (FWE) correction with $p<0.05$ at the voxel level as statistically significant. We do not report clusters with only two significant voxels or less.

4.2.8. DCM Analysis

4.2.8.1. Region selection and timeseries extraction

First, we performed another first-level GLM where we concatenated the 4 runs for each subject. Given the results from the main GLM (see Results section 4.3.2), we decided to collapse across within- and between-domain switches to obtain a simpler design that included 4 conditions (internal repetitions, external repetitions, all switches to internal, all switches to external). We then extracted 8 regions of interest (ROI) corresponding to the main activation clusters from the main GLM. In particular, since our goal was to investigate the connectivity between DMN and DAN and potentially spot the influence of domain-general control regions, we used the T-contrast 'internal > external' to extract left-lateralised mPFC, ventral precuneus, and inferior orbitofrontal cortex, while we used the T-contrast 'external > internal' to extract left superior parietal, right supramarginal and left superior frontal cortex (frontal eye fields, FEF). We also used the T-contrast 'switches > repetitions' to extract the activity of left IPL and dorsal precuneus regions. Since we could not find thalamic activation in these GLM contrasts, the MD thalamus was not included as ROI despite the hypotheses and expectations related to it. To derive the ROI coordinates, we identified the cluster peaks in the

activation maps obtained from the above-mentioned contrasts in the previous GLM. These group coordinates served as a starting point to search for the individual peaks in the activation maps of the new GLM. Individual peaks were constrained to be within a 10 mm radius (twice the FWHM smoothing kernel) from the group coordinate and exceed the statistical threshold of p<.001 uncorrected. When no peak was found with this threshold, we reduced it by 0.05 until a minimum threshold of 0.15 was reached, as suggested by (Zeidman et al., 2019a). We then extracted the timeseries in a sphere of 6 mm radius from the individual coordinates. We adjusted the timeseries using an F-contrast that identified the effects of interest (i.e., the 4 task conditions), regressing out any other nuisance factor i.e., head motion, physiological noise, button presses.

4.2.8.2. Individual level DCM specification and estimation

For each participant, we specified an individual bilinear, one-state, deterministic DCM model. We included the 8 ROIs and specified 4 conditions of interest (internal repetitions, external repetitions, all switches to internal, all switches to external), mean-centring the inputs. We specified a fully connected model where all extrinsic and intrinsic connectivity parameters were switched on (“matrix A”), and we set each condition as driving input to all regions (“matrix C”). Each condition was also set as modulatory input on the entire fully connected network (“matrix B”). The choice of specifying a fully connected B matrix is not standard (commonly, the task is set to modulate self-connections only), but justified by the nature of our paradigm and research questions, as it allowed us to investigate whether the preparation of switches towards the internal or the external domain can modulate the connectivity from domain-general regions towards domain-specific regions. We also included button presses in the model, which were however not set as a driving nor modulatory inputs. This model yielded the most positive free energy among the models we designed (strong Bayesian evidence given by a difference in free energy greater than 3).

4.2.8.3. Group level Parametrical Empirical Bayes

Within the PEB framework (explained in General Methods, section 2.7), we computed the average of individual DCM models across participants and computed an automatic

search procedure across reduced models (Zeidman et al., 2019b). We then filtered the resulting parameters by retaining those that exceed 95% of posterior probability (equivalent to a Bayes factor of 3 and considered as strong evidence). See **Figure 4.2. fMRI preprocessing and analysis pipeline.** for a summary of the analysis pipeline including preprocessing, GLM and DCM procedures.

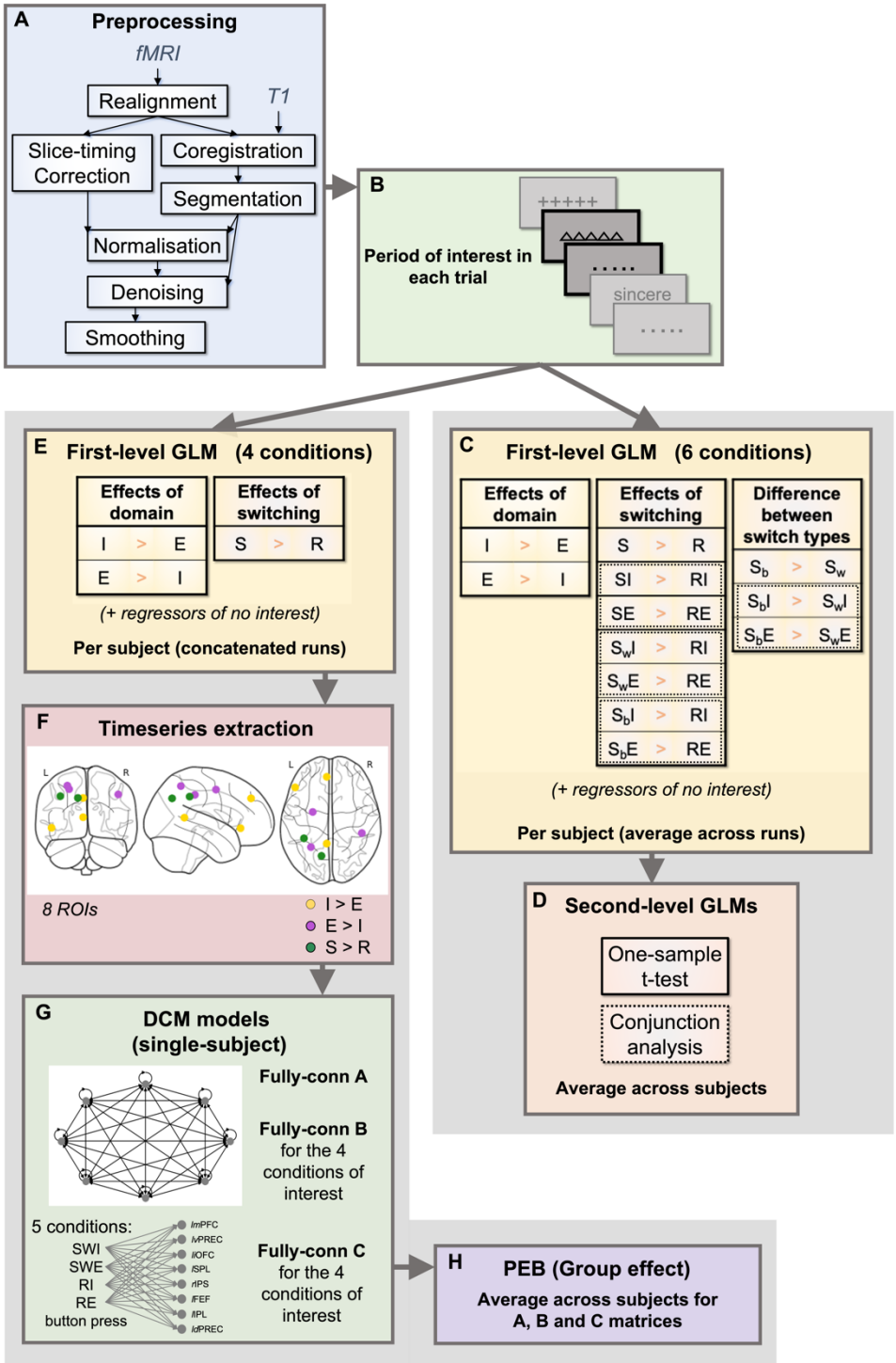

Figure 4.2. fMRI preprocessing and analysis pipeline. (A) A standard preprocessing pipeline was implemented on SPM12, with the addition of a denoising step (TAPAS PhysIO toolbox) which modelled physiological noise such as cardiac and respiratory activity. This was regressed out in the first-level GLM along with movement regressors. (B) The analysis focused on the cue-to-target interval (correct trials only) to capture the anticipatory activation in preparation of task performance. (C) The tables show the pairwise contrasts performed in the first-level GLMs (per subject, averaging across runs): I = all trials with internal tasks; E = all trials with external tasks; R = all repetitions; RI = repetition of internal tasks; RE = repetition of external tasks; S = all switches; SI = all switches towards internal tasks; SE = all switches towards external tasks; S_wI = switches within internal tasks; S_wE = switches within external tasks; S_bI = switches from external to internal tasks (between-domain); S_bE = switches from internal to external tasks (between-domain). (D) A one-sample t-test at the second level then computed the group average effect of each contrast. We also performed conjunction analyses (contrasts marked with a dotted line) to highlight patterns of activation common to both the internal and external domain. (E) Tables show the pairwise contrasts performed in the new GLM (4 conditions only: internal repetitions, external repetitions, switches to internal, switches to external) which was used to concatenate the runs within each subject and obtain activation maps for timeseries extraction (F) Timeseries extraction from 8 ROIs (G) Individual DCM models including 4 conditions + button press, fully connected A, B and C matrices (B and C matrices were specified for each of the 4 conditions of interest). Abbreviations: *lm*PFC = left middle prefrontal cortex; *lv*PREC = left ventral precuneus; *li*OFC = left inferior orbitofrontal cortex; *l*SPL = left superior parietal lobule; rIPS = right intraparietal sulcus; *l*FEF = left frontal eye fields; *l*IPL = left inferior parietal lobule; *ld*PREC = left dorsal precuneus. (H) Individual models were averaged across participants under the Parametric Empirical Bayes framework to obtain effective connectivity at the group level.

4.3. Results

4.3.1. Behavioural results

Participants performed the experiment with high accuracy (overall mean score of 92.90% ± 4.47). The mean accuracy for the external tasks (consonant and vowel finding) was 94.90% (± 4.71) and 96.77% (± 2.98) respectively, while internal tasks (personality and current sensations) resulted in 91.35% (± 8.61) and 88.74% (± 7.23) of mean accuracy, respectively.

The first 2x2 rANOVA on RTs (factors domain and trial type**; Figure 4.3A**) resulted in a significant main effect of trial type (BF_{10}=5.581e+7, F(1,29)=108.21, p<.001, η_p^2=0.79) whereby switches were significantly slower than repetitions, as per our *Hypothesis 1* and in line with our previous behavioural study (Chapter 3; Calzolari et al., 2022). There was no main effect of domain (BF_{10}=0.56, F(1,29)=0.85, p=0.36, η_p^2=0.029). The interaction between domain and trial type was significant, again in line with our previous results (BF_{10}=7.945, F(1,29)=7.57, p=.01, η_p^2=0.21). Post-hoc t-tests confirmed the presence of switch costs in both the external (BF_{10}=1.195e+7, t=9.47, p_{bonf}<.001) and the internal domain (BF_{10}=16658.084, t=5.70, p_{bonf}<.001), supporting *Hypothesis 2*.

The 2x2 rANOVA on switch costs (factors domain and switch type; **Figure 4.3B**) resulted in a significant main effect of domain (greater costs for switches to external than to internal tasks; BF_{10}=4.02, F(1,29)=7.09, p=.013, η_p^2=0.20) and switch type (BF_{10}=2.92, F(1,29)=9.44, p=.005, η_p^2=0.25). There was no significant interaction between domain and switch type (BF_{10}=0.33, F(1,29)=0.02, p=.894, η_p^2=6.217e-4). The main effect of switch type would support *Hypothesis 4* in showing additional costs when switching domains compared to staying within domain. However, post-hoc t-tests did not show such additional costs in neither of the two domains: switching from external to internal domain was not slower than staying within the internal domain, although the Bayesian t-test shows anecdotal evidence in favour of a difference (BF_{10}=2.07, t=1.83, p_{bonf}=.434) and switching from internal to external domain was not slower than staying within the external domain (BF_{10}=0.73, t=2.04, p_{bonf}=.276). This was against our predictions as well as our previous behavioural study (Chapter 3; Calzolari et al., 2022). Nonetheless, it is important to notice that all 4 switch types were

significantly different from repetitions (i.e., different from 0 in the one-sample t-tests: all p<.001), including the switches within the internal domain (BF_{10}=396.80, t=4.67, p<.001, d=0.85) and the between-domain switches from external to internal tasks (BF_{10}=6035.42, t=5.75, p<.001, d=1.05), further supporting *Hypothesis 2*. **Table 4.2** displays mean and standard deviation of all conditions (RTs after subtraction of task repetitions are reported, where relevant).

	Repetitions	Combined switches	Within domain	Between domains
All	1.129 (0.165)	1.251 (0.197)		
Internal	1.161 (0.220)	1.252 (0.235)	0.070 (0.081)	0.112 (0.107)
External	1.099 (0.168)	1.250 (0.205)	0.125 (0.099)	0.173 (0.137)

Table 4.2. Mean and SD of RTs for all conditions. In the case of within- and between-domain switches, we report the mean difference between their RTs and those of task repetitions, since that is what we used to perform that analysis. Raw RTs for those conditions can be found in Appendix B (Table B2). All units are seconds.

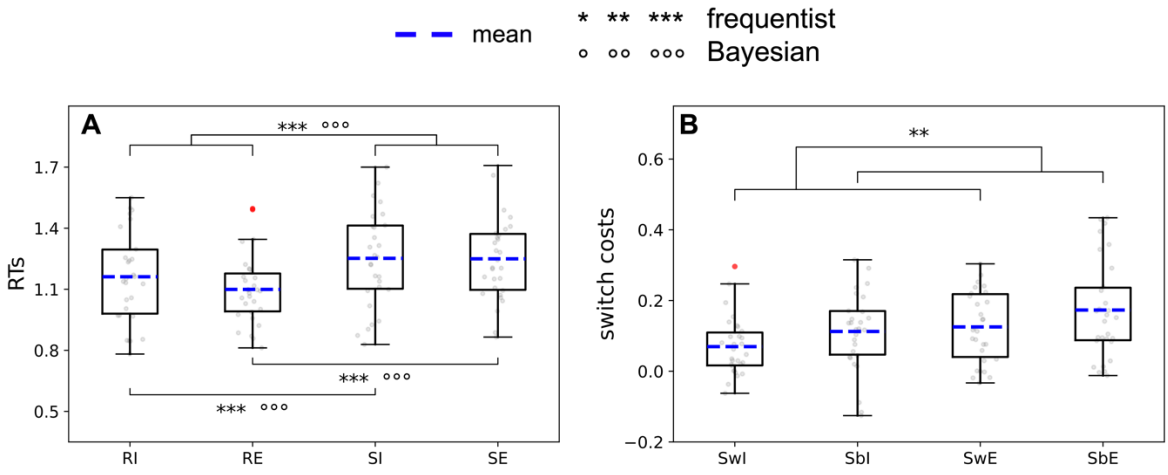

Figure 4.3. Boxplots showing the results from the analyses on RTs. (A) main effect of trial type and post-hoc t-tests from the 2x2 rANOVA with factors domain (internal, external) and trial type (switches, repetitions); (B) main effect of switch type from the 2x2 rANOVA on switch costs with factors domain and switch type (within, between domain). Outlier participants are represented as red dots, but were not excluded from the analyses. The mean is represented as a blue dashed line. The whiskers represent

the range between minimum and maximum i.e., the variability outside the upper and lower quartiles. * p<.05; ** p<.01, *** p<.001, ° BF10>3 (substantial evidence), °° BF10 >10 (strong evidence), °°° BF10 > (very strong evidence). Abbreviations: RI = repetition of internal tasks; RE = repetition of external tasks; SI = all switches towards internal tasks; SE = all switches towards external tasks; S_wI = switches within internal tasks; S_wE = switches within external tasks; S_bI = switches from external to internal tasks (between-domain); S_bE = switches from internal to external tasks (between-domain).

4.3.2. fMRI results

Here we report all the statistically significant clusters (FWE-corrected p<0.05) with a size of at least 10 voxels. Full results including smaller clusters (minimum 3 voxels size) are reported in the tables. The anatomical labels corresponding to peak activation were taken from the third version of the automated anatomical labelling atlas (AAL3; Rolls et al., 2020).

Starting from the effects of domain (**Figure 4.4**), the comparison of all internal task trials versus all external task trials revealed activation mostly in DMN regions (various portions of left medial prefrontal cortex, precuneus, angular gyrus, bilateral middle temporal gyrus), as well as left inferior orbitofrontal cortex (OFC) and right cerebellum. See **Table 4.3A** for a full list of results. The opposite comparison (external > internal trials) instead resulted in the activation of DAN regions such as bilateral superior frontal lobes (FEF), left superior and inferior parietal lobules (SPL and IPL), right angular and supramarginal gyri (**Table 4.3B**). See Appendix B (Figure B1 and Table B3) for the results to these contrasts separately for repetition and switch trials.

Regarding the effects of switching (**Figure 4.5**), when comparing all switches versus all repetitions we found left-lateralised activity in DAN regions (IPL, IPS, precentral gyrus) as well as precuneus, supplementary motor cortex (SMA), inferior frontal lobe, inferior temporal lobe and right cerebellum (**Table 4.4A**).

When focusing on each domain specifically, we found that switching towards internal tasks (both from the other internal task and from external tasks) elicited greater activation in the above-mentioned DAN/ECN regions (e.g., left IPL, precuneus, SPL,

…) as compared to repeating internal tasks (**Table 4.4B**). Switching towards external tasks (both from the other external task and from internal tasks) instead resulted in a greater activation in small clusters (<10 voxels) of the DAN but also SN network (left middle frontal and precentral gyrus, left insula, precuneus and IPL) as compared to external task repetitions (**Table 4.4C**). The conjunction analysis of these two contrasts (all switches towards internal > repetitions of internal + all switches towards external > repetitions of external) showed a joint activation of left IPL, middle occipital cortex and precuneus (**Table 4.4D**).

We performed a more detailed exploration of switch costs by focusing on each switch type as well as each domain. Switches within the internal domain elicited greater activation in the left inferior frontal lobe (pars triangularis) and DMN precuneus, as compared to repetitions of internal tasks (**Table 4.4E**). Switches within the external domain elicited greater activation in DAN regions (left IPL and middle frontal lobe), bilateral precuneus and right cerebellum when compared to repetitions of external tasks (**Table 4.4F**). Interestingly, the conjunction analysis showed a joint activation of the left precuneus by these two contrasts (switches within internal > repetitions of internal + switches within external > repetitions of external) (**Table 4.4G**). Instead, the switches from external to internal tasks resulted in greater activation of some DAN regions (left IPL), bilateral precuneus, and cerebellum as compared to repetitions of internal tasks (**Table 4.4H**). In turn, switches from internal to external tasks induced activation in right cerebellum and left precentral gyrus as compared to repetitions of external tasks (**Table 4.4I**). The conjunction analysis of these two contrasts (external-internal switches > repetitions of internal + internal-external switches > repetitions of external) showed a joint activation of a different portion of the left precuneus (although only a small cluster of 3 voxels) with respect to that activated by within-domain switches (**Table 4.4J**).

Finally, we investigated the differences between switch types (**Figure 4.6**). No voxels survived the multiple comparisons correction when comparing all between-domain switches versus all within-domain switches. Looking at the two domains separately, we found that switching from external to internal tasks elicited greater activation in DAN (left IPL and right SPL) compared to switching within internal tasks (small clusters of 4 and 3 voxels only, respectively; **Table 4.5A**). Instead, switches from internal to external tasks induced greater activation mostly in the right cerebellum, as compared

to switches within external tasks (**Table 4.5B**). No voxels survived correction in the conjunction analysis between the two latter contrasts.

Table 4.3. Comparisons across domains

Contrast	Region (AAL3)	Peak Coordinates			Voxels per cluster	z-score	Peak $p_{FWE\text{-}corr}$	Cluster $p_{FWE\text{-}corr}$
A) I > E	L Inferior Orbitofrontal	-49.5	30.5	-5	563	7.066	<.001	.000
	R Crus I	30.5	-84.5	-32.5	396	6.835	<.001	.000
	L Precuneus	-4.5	-49.5	10	427	6.675	<.001	.000
	L Rectus (Medial Frontal)	-2	33	-17.5	87	6.606	<.001	<.001
	L Medial Superior Frontal	-4.5	45.5	37.5	505	6.503	<.001	.000
	L Middle Temporal	-57	-34.5	0	73	6.457	<.001	<.001
	L Angular	-49.5	-57	25	167	6.410	<.001	.000
	R Middle Temporal Pole	45.5	18	-27.5	42	6.340	<.001	<.001
	L Inferior Temporal	-47	5.5	-35	370	6.247	<.001	.000
	R Cerebellar Tonsil	5.5	-52	-45	17	6.224	<.001	<.001
	R Middle Temporal	53	-9.5	-17.5	19	5.787	<.001	<.001
	L Mid Frontal	-34.5	18	52.5	4	5.652	<.001	.001
	L Inf Frontal, pars triangularis	53	28	12.5	18	5.445	.002	<.001
	L Crus II	-24.5	-79.5	-35	5	5.384	.003	<.001
	L Superior Occipital	-14.5	-99.5	15	5	5.376	.003	<.001
	L Cuneus	-9.5	-92	27.5	12	5.270	.006	<.001
	L Superior Frontal	-22	55.5	12.5	4	5.262	.007	.001
	R Crus II	43	-59.5	-45	3	5.255	.007	.002
	R Inf Frontal, pars triangularis	58	25.5	0	7	5.171	.011	<.001
	L Lingual	-17	-82	-7.5	3	5.157	.012	.002
	L Middle Cingulate	-4.5	-14.5	37.5	5	5.144	.013	<.001
	L Superior Temporal	-62	-44.5	20	3	5.005	.027	.002

B) E > I	L Superior Frontal (FEF)	-24.5	-4.5	50	69	6.153	<.001	<.001
	L Superior Parietal	-27	-54.5	55	602	6.476	<.001	.000
	R Supramarginal	45.5	-34.5	42.5	88	6.400	<.001	<.001
	R Angular	23	-62	47.5	216	6.220	<.001	.000
	R Superior Frontal (FEF)	28	-2	55	50	5.648	<.001	<.001
	L Culmen	-24.5	-59.5	-32.5	6	5.430	.003	<.001
	L Vermis	-2	-74.5	-22.5	4	5.372	.004	.001
	L Superior Parietal	-29.5	-47	65	3	5.227	.008	.002
	R Superior Frontal	28	3	65	3	5.209	.009	.002
	R Culmen	35.5	-42	-35	4	4.961	.033	.001

Table 4.3. Results from the second-level GLM analyses (one-sample t-test) testing for the group effects of domain on brain activation. Specific contrasts include: internal vs external domain (all trial types included), external vs internal domain (all trial types included). Results survived a threshold of $p < 0.05$ with family wise error (FWE) correction. Abbreviations: I = internal tasks; E = external tasks.

Table 4.4. Effect of switching

Contrast	Region (AAL3)	Peak Coordinates			Voxels per cluster	z-score	Peak $p_{FWE\text{-}corr}$	Cluster $p_{FWE\text{-}corr}$
A) S > R	R Culmen	28	-57	-30	133	6.898	<.001	.000
	L Precuneus	-9.5	-69.5	47.5	167	6.590	<.001	.000
	L Inferior Parietal Lobule	-37	-42	40	313	6.573	<.001	.000
	R Vermis	8	-72	-27.5	30	6.287	<.001	<.001
	R Inferior Semi-Lunar Lobule	33	-67	-52.5	60	6.044	<.001	<.001

	L Parahippocampal	-19.5	-39.5	2.5	3	5.810	<.001	.002
	L Precentral	-39.5	8	-39.5	84	5.726	<.001	<.001
	L Cingulate	-2	-27	27.5	20	5.647	<.001	<.001
	L Inferior Temporal	-52	-52	-10	21	5.592	.001	<.001
	L SMA	-9.5	3	62.5	10	5.576	.001	<.001
	L Inf Frontal, pars Triangularis	-42	25.5	25	27	5.562	.001	<.001
	L Cingulate	-4.5	-17	27.5	8	5.424	.003	<.001
	L Middle Frontal	-24.5	3	50	17	5.407	.003	<.001
	L Inf Frontal, pars Triangularis	-42	33	17.5	10	5.326	.005	<.001
	R Sup Parietal/Precuneus	13	-67	50	7	5.188	.010	<.001
	R Cingulate	8	-19.5	27.5	3	5.143	.013	.002
	L SMA	-4.5	10.5	57.5	6	5.025	.024	<.001
B) SI > RI	R Culmen	28	-57	-32.5	22	6.394	<.001	<.001
	L Inferior Parietal Lobule	-37	-42	40	294	6.333	<.001	.000
	L Precuneus	-7	-69.5	50	75	5.948	<.001	<.001
	L Inferior Temporal	-52	-54.5	-7.5	18	5.722	<.001	<.001
	R Parietal	30.5	-52	40	26	5.669	<.001	<.001
	R Inferior Semi-Lunar Lobule	33	-64.5	-52.5	19	5.502	.002	<.001
	L Cingulate	-4.5	-12	27.5	3	5.324	.005	.002
	R Sup Parietal / Precuneus	13	-67	50	16	5.261	.007	<.001
	R Parietal	33	-62	32.5	3	5.076	.018	.002
	R Superior Parietal Lobule	30.5	-57	60	3	5.057	.020	.002
	L Inferior Semi-Lunar Lobule	-32	-69.5	-52.5	3	4.985	.029	.002
C) SE > RE	L Middle Frontal / Precentral	-39.5	10.5	30	5	5.393	.003	<.001
	L Insula	-29.5	28	0	5	5.318	.005	<.001
	L Ventrolateral Thalamus	-9.5	-12	2.5	3	5.275	.006	.002

	L Precuneus / Cuneus	-14.5	-64.5	27.5	5	5.203	.009	<.001
	L Inferior Parietal	-32	-44.5	40	5	5.197	.010	<.001
	L Superior Frontal	-24.5	-4.5	50	5	5.184	.010	<.001
	L Precuneus	-12	-64.5	35	7	5.145	.013	<.001
	R Tuber	28	-84.5	-40	5	5.111	.015	<.001
	L Mid Occipital	-27	-67	32.5	3	4.907	.044	.002
D) ***Conjunction***	L Inf Parietal Lobule	-37	-42	40	10	5.568	.001	<.001
SI > RI +	L Mid Occipital	-27	-64.5	32.5	14	5.460	.002	<.001
SE > RE	L Precuneus	-12	-67	37.5	12	5.271	.006	<.001
	R Culmen	28	-57	-32.5	5	5.216	.009	.001
	R Inf Parietal Lobule	-44.5	-32	42.5	5	5.155	.012	.001
E) **$S_wI > RI$**	L Inf Frontal, pars Triangularis	-47	28	20	44	5.911	<.001	<.001
	L Precuneus	-9.5	-67	30	31	5.688	<.001	<.001
	L Cingulate	-4.5	-17	27.5	3	5.584	.001	.002
	L Middle Frontal	-39.5	3	42.5	5	5.341	.004	<.001
	L Middle Frontal	-37	10.5	35	8	5.245	.007	<.001
	L Inf Frontal, pars Triangularis	-37	20.5	22.5	3	5.099	.016	.002
	L Inferior Parietal Lobule	-37	-49.5	40	3	5.013	.026	.002
F) **$S_wE > RE$**	L IPL / Precuneus	-39.5	-37	42.5	341	6.311	<.001	.000
	L Middle Frontal	-24.5	-2	50	21	6.127	<.001	<.001
	R Precuneus	15.5	-69.5	52.5	24	5.932	<.001	<.001
	R Inferior Semi-Lunar Lobule	33	-67	-52.5	13	5.461	.002	<.001
	R Angular	28	-62	45	5	5.443	.002	<.001
	R Declive	25.5	-59.5	-30	6	5.211	.009	<.001
G) ***Conjunction***	R Inferior Semi-Lunar Lobule	33	-67	-52.5	8	5.539	.001	<.001
$S_wI > RI$ +	L Inferior Parietal	-27	-59.5	42.5	7	5.323	.005	<.001

	S_wE > RE	L Precuneus	-12	-67	42.5	11	5.320	.005	<.001
		L Inferior Parietal Lobule	-34.5	-49.5	40	9	5.053	.021	<.001
H)	**S_bI > RI**	L Inferior Parietal	-27	-57	42.5	332	6.236	<.001	.000
		L Precuneus	-7	-67	50	64	6.110	<.001	<.001
		R Culmen	28	-57	-30	16	5.969	<.001	<.001
		R Superior Parietal	18	-64.5	55	53	5.699	<.001	<.001
		R Angular / SPL	30.5	-59.5	47.5	87	5.487	.002	<.001
		R Inferior Semi-Lunar Lobule	-29.5	-67	-52.5	4	5.457	.002	.001
		L Superior Frontal	-22	3	50	3	5.070	.019	.002
I)	**S_bE > RE**	R Crus II	28	-84.5	-37.5	115	6.012	<.001	.000
		Undefined	-24.5	28	-5	6	5.759	<.001	<.001
		L Precentral / Frontal Inf Opercular	-39.5	10.5	30	11	5.613	<.001	<.001
		R Crus II	10.5	-87	-40	4	5.520	.002	.001
		R Crus II	13	-92	-32.5	5	5.263	.007	<.001
		Undefined	25.5	-92	-25	5	5.038	.022	<.001
J)	***Conjunction*** **S_bI > RI + S_bE > RE**	L Precuneus	-12	-67	37.5	3	4.994	.028	.004

Table 4.4. Results from the second-level GLM analyses (one-sample t-test) testing for the group effects of switching on brain activation. Contrasts include: all switches vs all repetitions; switches to internal vs internal repetitions and switches to external vs external repetitions (plus conjunction analysis); switches within internal vs internal repetitions and switches within external vs external repetitions (plus conjunction analysis); external to internal switches vs internal repetitions and internal-external switches vs external repetitions (plus conjunction analysis). Results survived a threshold of $p < 0.05$ with family wise error (FWE) correction. Abbreviations:

R = all repetitions; RI = repetition of internal tasks; RE = repetition of external tasks; S = all switches; SI = all switches towards internal tasks; SE = all switches towards external tasks; S_wI = switches within internal tasks; S_wE = switches within external tasks; S_bI = switches from external to internal tasks (between-domain); S_bE = switches from internal to external tasks (between-domain).

Table 4.5. Comparison across switch types

Contrast	Region (AAL3)	Peak Coordinates			Voxels per cluster	z-score	Peak $p_{FWE\text{-}corr}$	Cluster $p_{FWE\text{-}corr}$
A) S_bI > S_wI	L Inf Parietal Lobule / Postcentral	-39.5	-39.5	60	4	5.628	.001	.001
	R Superior Parietal Lobule	18	-67	57.5	3	5.233	.008	.002
B) S_bE > S_wE	R Crus I (Uvula)	30.5	-84.5	-32.5	91	6.019	<.001	<.001
	L Inferior Temporal	-42	5.5	-35	8	5.191	.010	<.001
	L Posterior Cingulate	-7	-37	5	4	5.188	.010	.001

Table 4.5. Results from the second-level GLM analyses (one-sample t-test) testing for the group differences between switch types. Contrasts include: switches from external to internal vs. switches within the internal domain; switches from internal to external vs. switches within the external domain. Results survived a threshold of $p < 0.05$ with family wise error (FWE) correction. Abbreviations: S_wI = switches within internal tasks; S_wE = switches within external tasks; S_bI = switches from external to internal tasks (between-domain); S_bE = switches from internal to external tasks (between-domain).

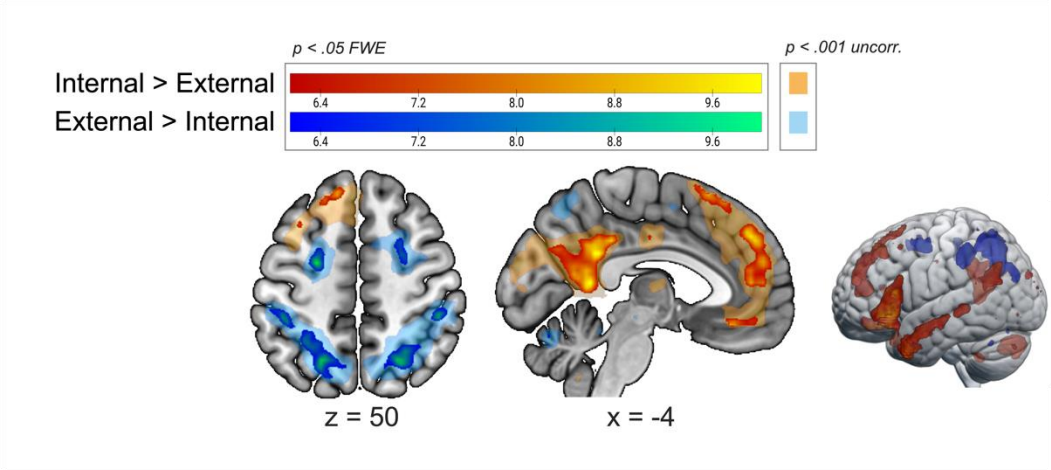

Figure 4.4. Brain activation at the group level (one-sample t-test) for the whole-brain comparisons between domains, regardless of trial type. Specifically, the first-level GLMs compared 'internal > external' and 'external > internal' on a multi-run model for each subject (4 runs of task per participant). The activation maps are shown at p<0.05 FWE-corrected (bright colours; warm scale = internal > external; cold scale = external > internal) and rendered on a standard template (mni152 template in MRIcroGL). Uncorrected activation maps at *p*<.001 are also shown for representational purposes with faint, transparent colours. For each slice, the relative MNI coordinate is reported.

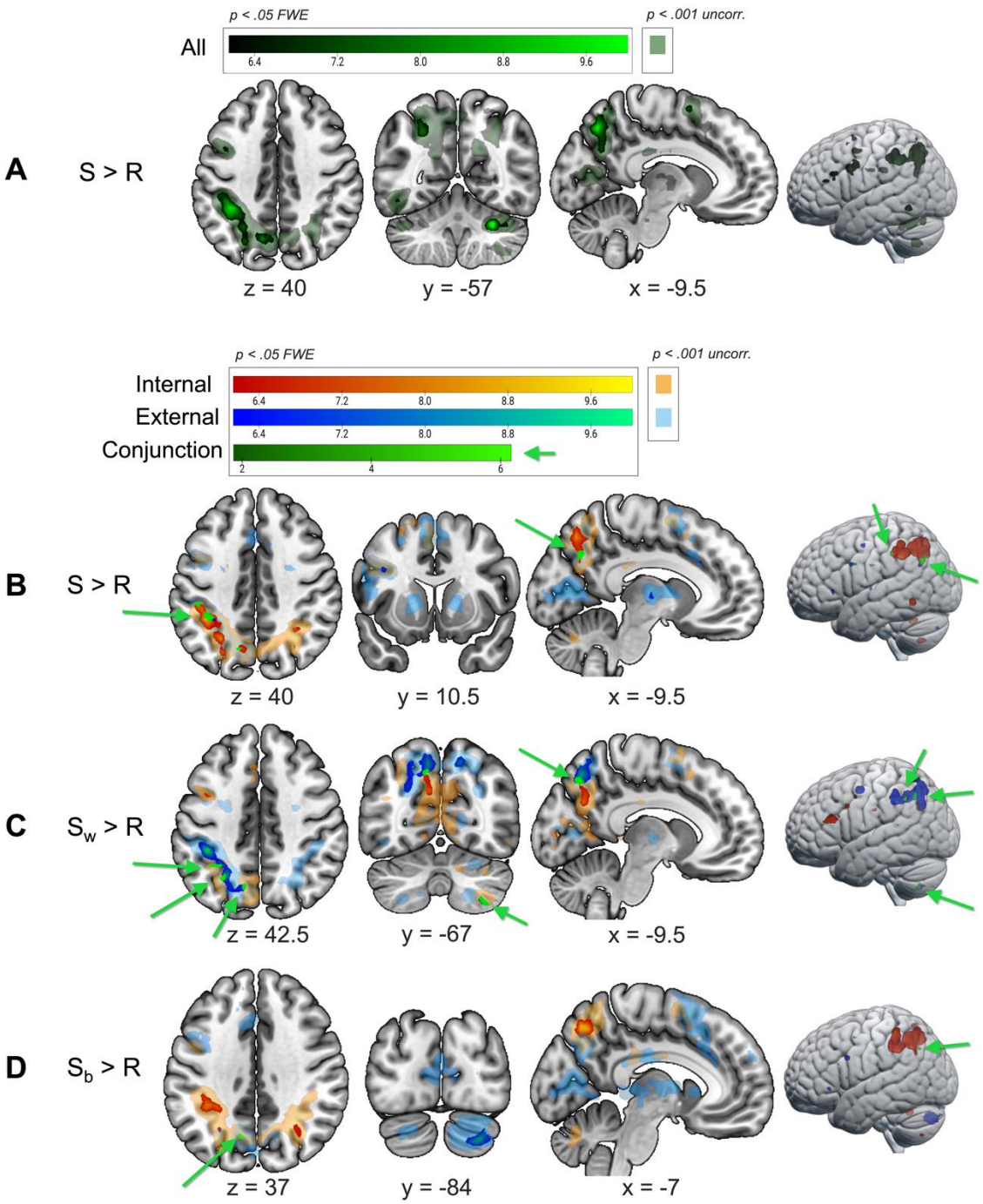

Figure 4.5. Brain activation at the group level (one-sample t-test) for the whole-brain comparisons between switches and repetitions. Specifically, the first-level GLMs compared 'all switches > all repetitions'(A), 'internal switches > internal repetitions' and 'external switches > external repetitions' (their conjunction performed at the second level is shown in green) (B), 'switches within internal > internal repetitions' and 'switches within external > external repetitions' (their conjunction performed at the second level is shown in green) (C), 'switches from external to internal > internal repetitions' and 'switches from internal to external > external repetitions' (their

conjunction performed at the second level is shown in green) (D) on a multi-run model for each subject (4 runs of task per participant). The activation maps are shown at p<0.05 FWE-corrected (bright colours; warm scale = internal; cold scale = external; green scale = both domains together (A) or conjunctions (C, D) and rendered on a standard template (mni152 template in MRIcroGL). Uncorrected activation maps at p<.001 are also shown for representational purposes with faint, transparent colours. For each slice, the relative MNI coordinate is reported.

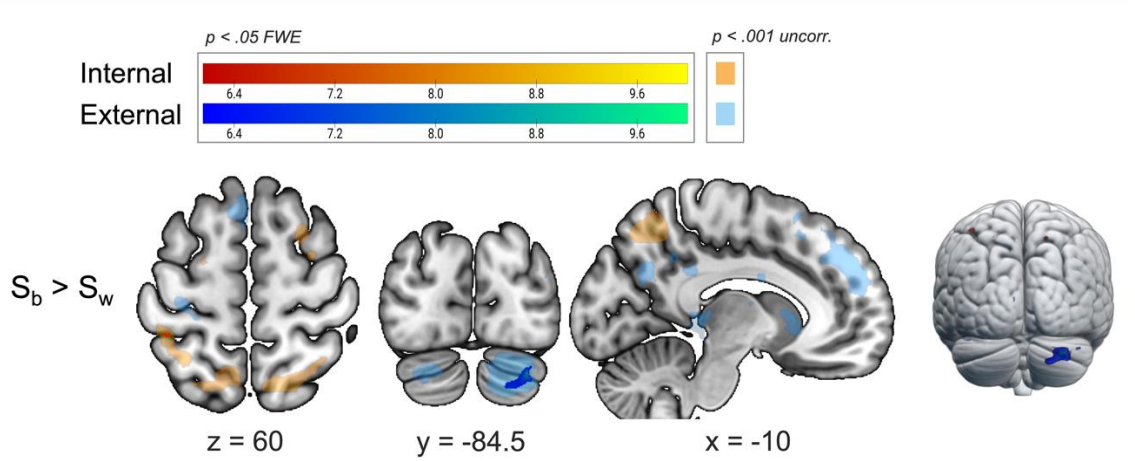

Figure 4.6. Brain activation at the group level (one-sample t-test) for the whole-brain comparisons between switch types. Specifically, the first-level GLMs compared 'switches from external to internal > switches within internal' and 'switches from internal to external > switches within external' on a multi-run model for each subject (4 runs of task per participant). The activation maps are shown at p<0.05 FWE-corrected (bright colours; warm scale = internal; cold scale = external) and rendered on a standard template (mni152 template in MRIcroGL). Uncorrected activation maps at p<.001 are also shown for representational purposes with faint, transparent colours. For each slice, the relative MNI coordinate is reported.

4.3.3. DCM results

On average, individual DCM models explained 19.23% of variance (SD = ± 9.37). This is unsurprising and acceptable in the case of task designs in which baseline periods (e.g., ITIs) are not modelled (Zeidman, Jafarian, Corbin, et al., 2019a).

At the group level, the estimation of average effective connectivity across conditions (A matrix) highlighted an overall prevalence of excitatory connections and a reduced inhibition in 7 out of 8 self-connections. This is not surprising given that we selected regions that were engaged by the task, according to our GLM results. Notably, we notice a pattern of excitation between regions of the DAN, such as between SPL, IPS and FEF bidirectionally as well as from those regions to dorsal precuneus and IPL, accompanied by inhibition from DAN towards DMN regions (**Figure 4.7**). Interestingly, we also found that IPL and dorsal precuneus showed excitatory connectivity towards DMN regions and inhibitory connectivity towards the other DAN regions.

The estimation of driving inputs (C matrix; dotted lines in **Figure 4.8**) indicated that the preparation of internal repetitions perturbed the network via a negative drive into two DAN regions (right IPS and left SPL). Similarly, the preparation of switches towards internal tasks negatively perturbed the right IPS. On the contrary, preparing for switches towards external tasks negatively perturbed the inferior OFC and positively affected left SPL and FEF. No driving inputs surpassed the 95% posterior probability threshold in the external repetitions condition.

The estimation of modulatory inputs (B matrix; solid lines in **Figure 4.8**) showed that the preparation of internal task repetitions, modulated the connectivity from both precuneal subregions towards the left SPL (inhibition by dorsal and excitation by ventral precuneus), which in turn inhibited the connectivity towards left FEF and right IPS and excited the left iOFC. The right IPS also reduced its inhibition towards iOFC, excited mPFC (which showed increased sensitivity to inputs), and inhibited the left FEF. Instead, the preparation of external task repetitions induced inhibition from dorsal to ventral precuneus, which in turn excited the right IPS (displaying increased sensitivity to inputs). The dorsal precuneus also excited the left FEF. Most of the modulations were however located in the connectivity from left SPL towards iOFC, mPFC (both excited), FEF and IPS (inhibited). The preparation of switches to the internal domain instead induced inhibition from the dorsal precuneus towards left IPL, which then excited iOFC. Both left ventral precuneus and right IPS displayed increased sensitivity to inputs, the right IPS receiving inhibition from the left SPL and in turn exciting the ventral precuneus. Finally, the preparation of switches to the external domain elicited widespread excitatory modulations from iOFC to all DAN regions (except FEF). In addition, inhibitory modulations were found from dorsal

precuneus to left SPL, IPL and FEF. The left SPL in turn inhibited the right IPS, while the left IPL inhibited the ventral precuneus.

Table 4.6 shows the group coordinates of the 8 ROIs included in the DCM analysis. The values of all estimated parameters are reported in Figure B2, B3, B4 (for A, B and C matrices, respectively) in Appendix B.

Table 4.6. Group coordinates for DCM

Region (AAL3)	Peak Coordinates		
L Inferior Orbitofrontal	-49.5	30.5	-5
L ventral Precuneus	-4.5	-49.5	10
L Medial Superior Frontal	-4.5	45.5	37.5
L Superior Parietal	-27	-54.5	55
R Supramarginal	45.5	-34.5	42.5
L Superior Frontal	-24.5	-4.5	50
L Inferior Parietal Lobule	-37	-42	40
L dorsal Precuneus	-9.5	-69.5	47.5

Table 4.6. Group coordinates of the 8 ROIs included in the DCM analysis. These coordinates were extracted from GLM T-contrasts and formed the starting point for the search of individual coordinates in the GLM activation maps. Orbitofrontal, ventral precuneus and medial superior frontal cortex were extracted from the contrast 'internal > external'; superior parietal, supramarginal and lateral superior frontal were extracted from 'external > internal'; finally, IPL and dorsal precuneus were extracted from 'switches > repetitions' (all spheres of 6 mm radius).

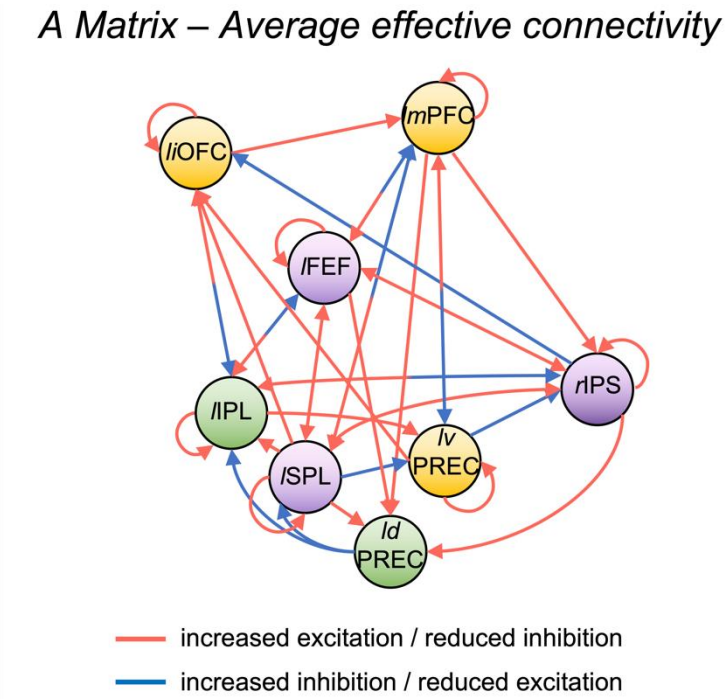

Figure 4.7. Estimated average effective connectivity across experimental conditions (A matrix). We report the connections that exceeded the 95% posterior probability threshold in the PEB analysis. Red arrows indicate more excitation / less inhibition as compared to baseline (i.e., rest), while blue arrows signal connections with more inhibition / less excitation compared to baseline. Note that self-connections are always inhibitory so red indicates a reduction in inhibition while blue indicates increased inhibition. The coordinates of yellow regions were extracted from the GLM contrast 'internal > external', those of purple regions were extracted from 'external > internal', and those of green regions were extracted from 'all switches > all repetitions'. Abbreviations: *lm*PFC = left middle prefrontal cortex; *lv*PREC = left ventral precuneus; *li*OFC = left inferior orbitofrontal cortex; *l*SPL = left superior parietal lobule; rIPS = right intraparietal sulcus; *l*FEF = left frontal eye fields; *l*IPL = left inferior parietal lobule; *ld*PREC = left dorsal precuneus.

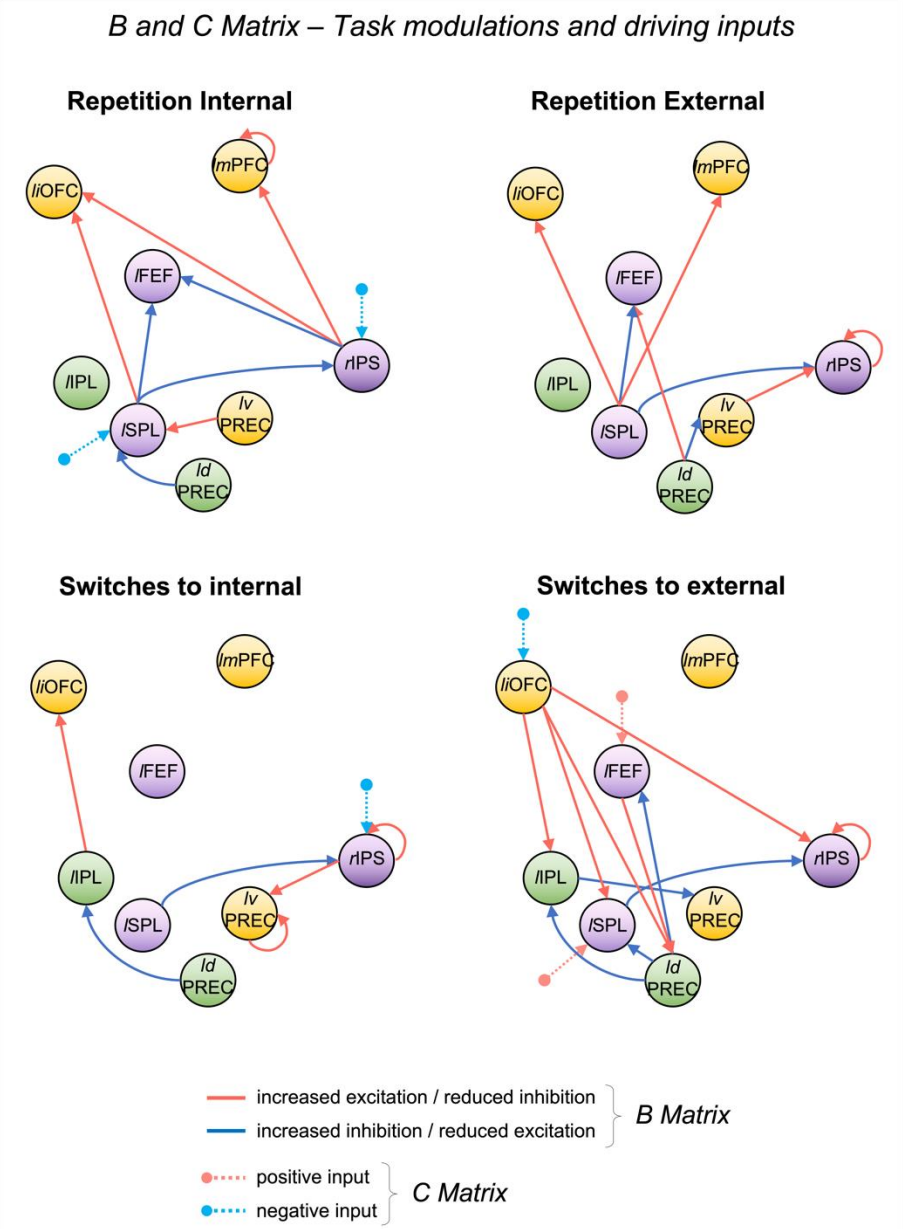

Figure 4.8. Effects of task conditions on the network. We report the connections that exceeded the 95% posterior probability threshold in the PEB analysis. Solid lines represent the modulatory effect of each task condition (B matrix) while dotted lines indicate the driving inputs from the task (C matrix) – i.e., where each task condition enters the network. Red solid lines indicate an excitatory modulation (up-regulation) by a specific task condition, while blue lines indicate inhibitory modulation (down-regulation). In the case of self-connections, the modulation is interpreted as decreased (red) or increased (blue) inhibition, which means self-connections become more or less sensitive (respectively) to inputs from the rest of the network as a result of task influence. Light red dotted lines indicate a positive drive from task condition while light blue dotted lines indicate a negative drive. The coordinates of yellow regions were

extracted from the GLM contrast ‘internal > external’, those of purple regions were extracted from ‘external > internal’, and those of green regions were extracted from ‘all switches > all repetitions’. Abbreviations: RI = internal repetitions; RE = external repetitions; SWI = switches to internal; SWE = switches to external; *lm*PFC = left middle prefrontal cortex; *lv*PREC = left ventral precuneus; *li*OFC = left inferior orbitofrontal cortex; *l*SPL = left superior parietal lobule; rIPS = right intraparietal sulcus; *l*FEF = left frontal eye fields; *l*IPL = left inferior parietal lobule; *ld*PREC = left dorsal precuneus.

4.4. Discussion

In this study, we collected fMRI data while participants performed a cued task-switching paradigm with two internally oriented and two externally oriented tasks, and investigated the neural activity associated with anticipatory preparation of switches within and between the internal and external domain. We found that switching is accompanied by slower RTs and the anticipatory activation of lateral frontoparietal regions in both the internal and external domain, as compared to repetitions. In addition, we observed DMN activation in preparation of internal tasks.

First, we replicated the main behavioural results from our previous study (Chapter 3; Calzolari et al., 2022). In particular, we observed again a switch cost effect which was present both in the external and internal domain, as well as an interaction between domain and trial type. We also replicated the main effect of switch type which would signal additional costs for switching between domains compared to within domain. However, this effect was not present in the post-hoc tests that measured it for the external and internal domains separately. Since the Bayesian evidence did not confirm the absence of a behavioural effect, we believe this lack of significance might be due to the smaller sample size in the current fMRI study. In accordance with this, and against our predictions, the only noticeable difference between switch types was a greater activation in the right cerebellum when comparing internal-to-external switches with switches within external tasks. This also suggests that the number of trials might

have been insufficient to fully capture the differences across switch types. We tried to balance between having a suitable number of trials and a reasonable duration for the overall experiment, but it might have not been enough to spot nuanced differences between different types of switches.

We previously interpreted these results as evidence for the presence of two domain-specific cognitive systems that communicate with each other and share domain-general features to allow the flexible shift to a different task and/or domain (Calzolari et al., 2022). Our fMRI results confirm this view.

When comparing the preparation of internal versus external tasks regardless of trial type, we found activation in regions of the core DMN system (left medial prefrontal cortex, precuneus and middle cingulate cortex) associated with self-reflection and autobiographical memory, as well as regions of the extended dorsal medial PFC subsystem (left inferior and middle temporal lobe, left inferior OFC, superior frontal lobe) associated with social reasoning and mentalizing (Andrews-Hanna et al., 2010). Some of these areas, such as the OFC and temporal lobe, are also associated with language comprehension, and in particular with controlled semantic retrieval and semantic judgement (Abutalebi et al., 2008; Sabb et al., 2007), which fits with the kind of internal tasks we used in our paradigm. On the contrary, when comparing external versus internal trials, we found activation in areas of the DAN bilaterally (right supramarginal gyrus, left inferior parietal lobe, left and right superior frontal lobes in correspondence of the frontal eye fields) (Szczepanski et al., 2013). In accordance with this, our DCM results show an overall pattern of excitatory effective connectivity within DAN areas and within DMN areas, but an inhibitory connectivity from DAN areas towards DMN. Taken together, these results are in line with previous research suggesting a role of DMN areas in the processing of various self-referential information and implicating the DAN in visuospatial attention (Braga et al., 2013; Corbetta & Shulman, 2002; Miller & Buschman, 2013). However, it is important to note that our results demonstrate the involvement of these networks in the preparatory phase of internally and externally oriented tasks, prior to the actual task execution and prior to viewing the stimulus. While previous studies already showed the presence of a rapid, preparatory engagement of task-specific areas during switch cueing (Murray et al., 2009; Wylie et al., 2006), the fact that the DMN also displays such task-driven activation, in particular, is noteworthy. In one occasion, a previous study on state-

switching (from task to rest and vice versa) found rapid modulation of DMN regions during the cue-to-target intervals (Sidlauskaite et al., 2014). Specifically, DMN activation increased after cues signalling upcoming rest, and decreased after rest-to-task cues. Conversely, the anterior insula activated in anticipation of task performance when switching from rest to task. This supports the idea that anticipatory preparation might be flexibly assigned to different networks depending on the required brain state, and specifically demonstrates an early engagement of DMN in preparation of a task-related instruction change (Sidlauskaite et al., 2014). Nonetheless, whether a similar activation pattern could also be present during the preparation of self-referential tasks in a cognitive switching context was not explored. Here we expand these results to a purely cognitive scenario involving the preparation of self-referential tasks. Indeed, we demonstrate that the DMN is actively involved in the goal-directed control of (internally oriented) cognition, and that its connectivity pattern with DAN can flexibly adjust based on task requirements. In fact, while, as stated above, the majority of DAN regions presented excitatory connections within the network and inhibitory connectivity towards DMN, the left IPL and dorsal precuneus (which we found engaged during task switching) instead displayed inhibitory connectivity towards other DAN regions and excitatory connectivity towards DMN. Moreover, the effective connectivity modulations induced by the task revealed that DMN regions upregulated regions of the DAN in preparation of switching towards the external domain. These results discredit the idea of DMN as a purely 'task-negative' or even 'stimulus-independent' network (Anticevic et al., 2012). The growing number of studies finding an active role of DMN in cognition suggest that this network is involved in the representation of context and situations (both current and internally generated or retrieved from memory), a view that could merge and explain the manifold range of DMN functions (Smith et al., 2018; Spreng, 2012).

Interestingly, our data show that the DMN is also active in preparation of subjective reports of interoceptive sensations (interoceptive sensibility), an aspect of interoception that is often only explored through questionnaires (e.g., Body Perception Questionnaire; Cabrera et al., 2018) and rarely investigated with neuroimaging. In fact, the majority of EEG and MRI studies focus on objective and physiological measures of interoception (e.g., heartbeat detection tasks), and highlight the importance of the insular cortex in interoceptive performance (Craig, 2009). However, a recent study by Araujo and colleagues investigated the neural bases of different self-related states

including interoceptive sensibility, and found that core DMN regions such as mPFC, precuneus and angular gyrus were active during the judgment of interoceptive sensations (e.g., 'do you feel hungry?') both as compared to a baseline N-back task and as compared to the judgment of exteroceptive sensations (i.e., proprioceptive or sensory features related to skin and limbs; Araujo et al., 2015). The results from our study confirm this and provide further evidence of a role of DMN in multiple aspects of self-awareness. In particular, the fact that DMN is active in preparation of the bodily sensations judgment aligns with previous accounts proposing a role of DMN regions in visceromotor predictions and anticipatory control of homeostatic states (Barrett & Simmons, 2015).

During the preparation of switch trials, we observed a pattern of activation that partially overlapped with the set of areas we found active in preparation of external (vs internal) tasks (DAN network), although peaking in more ventral and lateral portions. More specifically, a wide cluster in the left IPL/IPS as well as superior frontal / precentral gyrus (including the inferior frontal junction, IFJ) were more active in preparation of switches as compared to repetitions, although this time mainly localised in the left hemisphere. This is in line with previous studies demonstrating left lateralisation of brain activity associated with task-switching (Badre & Wagner, 2006; Kim et al., 2011; Vallesi et al., 2015) as well as with semantic and lexical processing in general (Braver et al., 2003). Further, these results are mostly consistent with previous task-switching studies showing greater activity in lateral frontoparietal regions during switches as compared to repetitions (E. A. Crone et al., 2006; Jamadar et al., 2010; Vallesi et al., 2015; Witt & Stevens, 2013), although the current patterns show a larger involvement of parietal DAN regions as compared to frontal ECN/SN regions (e.g. dorsolateral PFC, dorsal ACC) (Brass & Cramon, 2004). The activation of IPL and IPS has been implicated in visuospatial reorientation and working memory, but also with task-rule representation and mapping of relevant responses during cued task-switching (De Baene & Brass, 2014; Fox et al., 2005; Natale et al., 2008). This difference with previous literature might be thus due to the adoption of long preparation intervals (CTI), which naturally favour the implementation of working memory processing to aid task-switching (Brass & Cramon, 2004) and likely attenuates the activity in conflict monitoring/detection areas (e.g. ACC and pre-SMA, showing small activation clusters when correcting for multiple comparisons, as per **Figure 4.5A**) (Walsh et al., 2011). However, although smaller than parietal clusters, we still observed clusters of

activation in portions of the inferior frontal gyrus, which have been consistently linked with general goal-shifting and general task representations (Brass & Cramon, 2004). Importantly, we also found a marked activation of the left precuneus during switch preparation, specifically in a section of the precuneus located more dorsally as compared to the precuneus/posterior cingulate cluster that activated in preparation of internal tasks. This portion of the precuneus is thought to be part of a domain-general frontoparietal control network implicated in a range of executive functions (Niendam et al., 2012), and is generally associated with working memory/category encoding (Braunlich et al., 2015) and visuospatial reorienting (Indovina & Macaluso, 2007). In agreement with our results, a number of task-switching studies also found activation in this dorsal portion of precuneus extending towards the SPL, as well as in the IFJ, during task switches (vs repetitions) regardless of task rule and/or domain, confirming the important role of these areas in a superordinate, general type of cognitive control (Chiu & Yantis, 2009; Stelzel et al., 2011; Yeung et al., 2006). The precuneus is a highly heterogeneous region and its subregions are characterised by different functional connectivity (FC) patterns at rest, both in humans and macaque monkeys (Margulies et al., 2009). In particular, our findings agree with a study by Margulies and colleagues, which identified a 'central' precuneal region (similar to the one we found during switching preparation) connected to IPL and dorsal PFC and thus associated to high-order executive processing and working memory. In the same study, another more ventral subregions was instead ascribed to limbic functions and connected to DMN regions (medial PFC, medial temporal cortex) and hippocampal/parahippocampal cortices (Margulies et al., 2009). Similarly, others also found differential resting-state FC patterns for dorsal and ventral precuneus, which were functionally connected to the parietal cortex and posterior cingulate/mPFC, respectively (Zhang & Li, 2012). Due to these heterogeneous patterns, some researchers suggested a pivotal role of the precuneus in connecting and interfacing distinct frontoparietal networks that subserve internal and external processing (Leech et al., 2011; Lyu et al., 2021). We support this view by observing a strong involvement of the dorsal precuneus in task switching and an engagement of ventral precuneus in preparation of internal tasks. Importantly, in our study, the precuneus is the only region that displays conjoint activation across all types of switches (within and between domains), further confirming its role in domain-general cognitive control.

However, contrary to what we expected, we did not observe thalamic activation during switching, except for a small cluster in the ventrolateral thalamus only for switches in the external domain. Activation in this specific nucleus has been linked to attentional biases towards contents in working memory (de Bourbon-Teles et al., 2014). Therefore, this partially hints at the presence of thalamic involvement in switching, although it does not show a domain-general involvement of the MD. Further research is needed to specifically test the role of MD thalamus in cognitive switching.

Overall, we show the anticipatory engagement of DMN and DAN in the context of cognitive control of internal and external tasks respectively, along with domain-general frontoparietal regions (e.g., left IPL and precuneus) that are involved in switching regardless of specific task demands. An additional evaluation of the activity in specific switch types can be found in Appendix B.

4.5. Conclusions

We employed a task-switching paradigm to directly investigate network reconfiguration during changes in internally and externally oriented cognition for the first time to our knowledge. Our findings support the idea that the adaptive communication between DMN and DAN can guide task performance in the context of a goal-directed control of self-referential and external processing. These dynamics appear supported by the domain-general activation of dorsal precuneus and IPL.

Chapter 5

CHAPTER 5 : BEHAVIOURAL SIGNATURES OF SWITCHING BETWEEN EXTERNALLY AND INTERNALLY ORIENTED COGNITION; AN ALTERNATIVE STUDY DESIGN

5.1. Introduction

In a previous study (Chapter 3; Calzolari et al., 2022) I built a novel cued task-switching paradigm which induced participants to switch across externally and internally oriented tasks. I employed word stimuli and asked participants to either pay attention to specific features of the words (i.e., vowel and consonant finding tasks) or to use the words as prompts to access information about themselves (personality and bodily sensations judgement). I found switch costs in both the external and internal domain as well as an additional costs to between-domain switching as compared to within-domain switching. This constituted the first research – to the best of my knowledge – to ever bridge the study of cognitive control with the study of self-referential cognition. Whilst exciting, these findings required further validation in order to generalise conclusions beyond the specific task design that I adopted. In fact, previous research showed that the nature of the specific tasks and the type of processing they engage can affect the magnitude of switch costs. In particular, participants' behaviour can be affected by the level of task similarity or dissimilarity (where switching between more dissimilar tasks induces greater costs), by the level of familiarity with each task (where disengaging from familiar tasks results in slower responses), and even the specific stimulus attributes, even in cases where the attributes are task-irrelevant (C. M. Arrington et al., 2003; Rubin & Koch, 2006; Yeung & Monsell, 2003). Given the evidence for an influence of task similarity on switch costs, and given the marked difference in terms of stimulus processing between external and internal tasks in my previous paradigm (Chapter 3), I deemed necessary to conduct additional research using tasks with more balanced processing requirements across domains. While words and letters constitute the most common stimuli in task-switching, images and pictures have been previously used in other research fields to successfully investigate self-referential cognition,

employing externally oriented semantic categorisation tasks as control conditions (Gusnard et al., 2001; R. Smith et al., 2016). Therefore, I designed another experiment with the same structure as the previous study (Chapter 3; Calzolari et al., 2022), but employing picture stimuli and semantic categorisation tasks, along with self-referential judgements. I aimed at ensuring I could replicate the previous results regardless of task- and stimulus-specific qualities. I hypothesized that:

1. I would find evidence of an overall switch cost i.e., switching from one task to another leads to higher RT compared to repeating the same task, irrespective of task type.
2. Internally oriented tasks would also exhibit switch costs i.e., switching to self-referential tasks as well as switching from a self-referential task to the other results in higher RT as compared to repetitions.
3. There would be an interaction between domain and trial type whereby internal and external domains would result in switch costs of different magnitude. This is different from the preregistered hypothesis, which entailed an absence of interaction and similar switch cost effects across domains.
4. There would be additional costs for switching between domains compared to within domain, i.e., switching between domains (from externally to internally oriented tasks and vice-versa) is associated with slower RTs than switching across tasks of the same domain.
5. There will be an interaction between domain and switch type, i.e., the magnitude of the additional cost of switching between domains is different between external and internal domain (this was exploratory in the preregistration).

5.2. Methods

The experimental design and statistical analyses for this study are the same as those in Chapter 3, as also described in the General Methods. Therefore, in this section I will provide details only on the aspects that differ from the previous chapter, i.e., participants' information, task instructions and stimuli.

I pre-registered methods, research hypotheses, and analyses prior to data collection on the Open Science Framework (https://osf.io/3vx6g). I explicitly report any deviation

from the pre-registration. Importantly, this preregistration was created during the analysis of Chapter 3, and did not fully benefit from my previous findings (e.g., *Hypothesis 3* was the same as in Chapter 3, and not updated based on those findings).

5.2.1. Participants

I recruited a total of 223 participants (mean age = 26.20 ± 4.5; 107 women, 116 men). To be eligible, participants had to be aged 18-35, right-handed, with no history of neurological or psychiatric conditions nor sleep problems (insomnia/hypersomnia), and a normal sleep schedule (e.g., no night-shift jobs). Participants enrolled in the study via Prolific (www.prolific.co) and received compensation upon completion of the study at a rate of £5 per hour. They received written information and provided written informed consent before participating. This study was approved by the University of Birmingham STEM Ethics committee.

I discarded 6 participants based on not actually meeting eligibility criteria, 1 due to technical issues that brought to a partial loss of data, and 15 due to low accuracy (< 60% correct responses) in one or more task conditions. This resulted in a total of 201 participants (mean age = 26.22 ± 4.46; 98 women, 103 men) included in the analysis. Once I obtained 200 valid datasets, we applied a Bayesian stopping rule to decide whether to continue data collection, as stated in our preregistration. Specifically, I could stop data collection after reaching a Bayes factor >= 3 (either in support of the alternative or the null hypothesis) in the t-test comparing RTs during repetition trials versus all types of switch trials (i.e., evidence of overall switch costs, *Hypothesis 1*). Since I obtained very strong evidence for the presence of a switch cost (see Results), I did not acquire further data (sample size is 201 because at first I wrongfully discarded one more participant).

5.2.2. Experimental design and procedure

The experimental procedure was the same as Chapter 3 (see section 3.3.2).

5.2.3. Task

The general structure of the task and initial training phase, as well as the flow structure of each trial (including cue and stimulus duration, CTI and ITI intervals) were the same as Chapter 3 (see sections 2.2.4 and 3.3.3), so here I will provide details specific to this study only. See **Figure 5.1** for a representation of the task procedure.
In this study, all four tasks involved presenting greyscale pictures at the centre of the screen, required semantic processing of these stimuli, and allowed binary yes/no responses. The four tasks were:

- Outdoor / indoor discrimination task (external task 1): participants had to decide if the picture depicted an outdoors scene, as opposed to an indoors scene.
- Natural / man-made discrimination task (external task 2): participants had to decide if the picture depicted a natural scene, as opposed to a man-made scene.
- Pleasantness task (internal task 1): participants had to decide whether the picture was pleasant for them or not.
- Self-relatedness task (internal task 2): participants had to decide if they related or associated with the scene in the picture.

The proportion of switch and repetition trials was the same as Chapter 3, although this experiment included 400 trials, 100 for each of the four tasks. Participants had a self-paced break every 100 trials (once every ~13 minutes).
The size of picture stimuli was scaled based on screen size, while maintaining the original aspect ratio (60% x 45% of screen size).

5.2.4. Stimuli

Stimuli were 401 pictures carefully selected from the IAPS database (Lang et al., 2008) to be suitable for the tasks. I created four lists of pictures (one for each task with 100 stimuli each) balanced for valence, arousal and visual complexity. Valence and arousal ratings were available from the IAPS tech report. All four lists had the same number of positive (IAPS ratings M = 7.02; SD = 0.32), neutral (M = 5.43; SD = 0.29) and negative (M = 3.50; SD = 0.47) pictures. Arousal ratings did not exceed 1 standard deviation above the mean (mean arousal = 4.822; max arousal = 5.975), valence

ratings did not exceed 2 standard deviations above and below the mean (min valence = 2.52; max valence = 7.65; full range of valence ratings in IAPS = 1.31–8.34).

I calculated the JPEG compression error as a proxy of visual complexity under the assumption that, when compressing image files, complex images tend to result in larger files and to generate higher compression error compared to simpler images (Machado et al., 2015). JPEG compression error was calculated as follows:

$$Complexity(i) = rmse\big(i, f(i)\big) \times \frac{s\big(f(i)\big)}{s(i)}$$

where *i* is the image, *rmse* is the root mean square error, *f* is the compression scheme, and *s* is the image size.

Using 1x4 ANOVAs, I checked that the 4 lists were not significantly different from each other in terms of valence ($F(3,397)=0.09$; $p=0.96$), arousal ($F(3,397)=1.1$; $p=0.34$) and complexity ($F(3,397)=0.55$; $p=0.64$). Importantly, all pictures were rendered greyscale and matched for mean luminance and contrast using the SHINE Toolbox (Willenbockel et al., 2010).

To ensure balanced responses to the two external tasks, the list associated to the outdoor/indoor discrimination task contained half outdoor and half indoor scenes, while the list associated to the natural/man-made discrimination task contained half natural and half man-made scenes. By definition, it was not possible to ensure a similar balance for the internal tasks since they require subjective responses that likely vary across participants. For each participant, each picture only appeared once, with no repetitions either within or between the four lists.

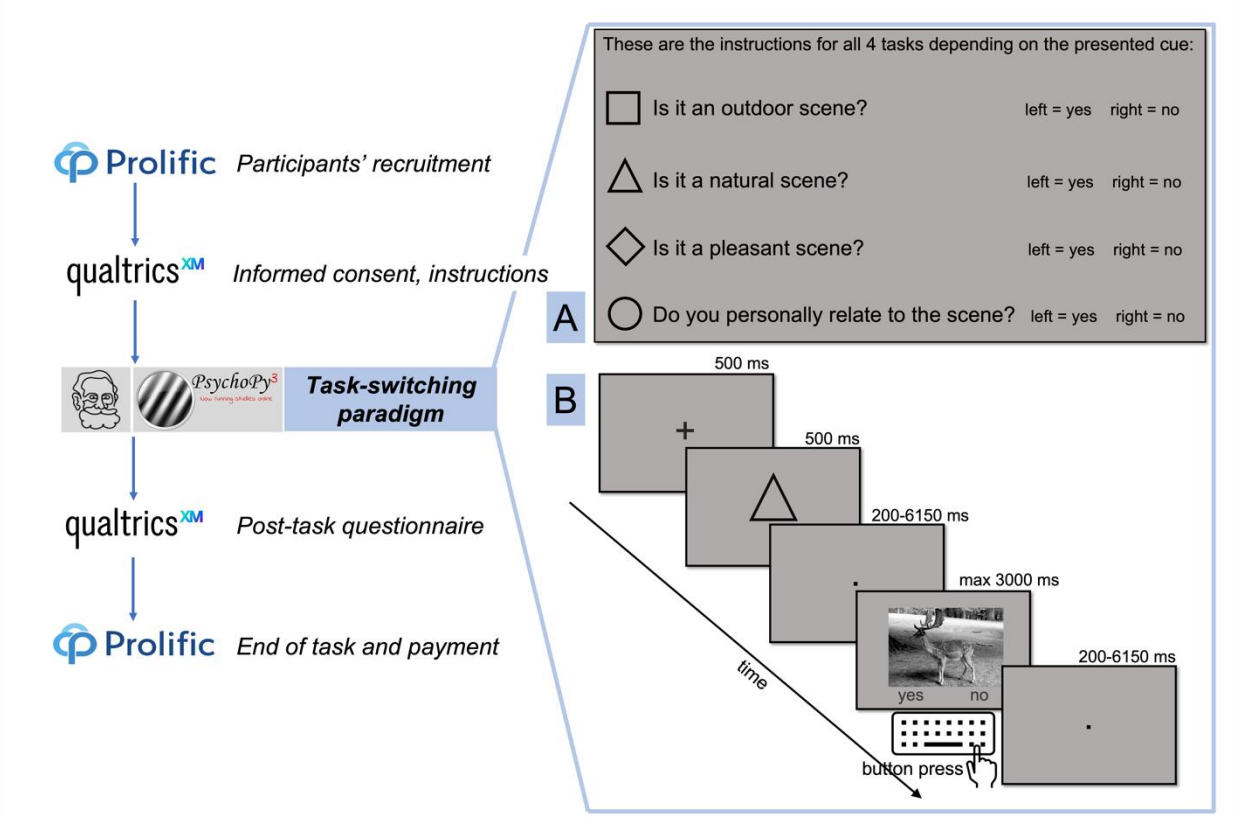

Figure 5.1. Online study pipeline (left) and details of main experiment (right) including an instruction screen showing one of the 4 possible cue-task mappings (A) and the structure of a single trial (B).

5.2.5. Statistical Analysis

I analysed data using JASP 0.16.3 (JASP Team 2020). The analysis pipeline was the same as Chapter 3, as also described in the General Methods (section 2.3.2). I excluded 15 participants from the analyses (final n = 201) because they either failed to respond to >10% of trials, or their accuracy for any of the 4 task conditions fell below 60%. For each participant I removed outlier trials as defined by the Tukey's method (Tukey, 1977) and trials with RT < 200 ms (Schmitz & Voss, 2014; Verschooren, Schindler, et al., 2019), which resulted in an average of 2.61% (± 1.26) discarded trials per participant, in addition to the trials discarded due to incorrect responses (9.39% ± 5.50). I analysed RTs for each of the following trial types: repetitions of internal tasks, repetitions of external tasks, within-domain switches (internal-to-internal and external-to-external), between-domain switches (from internal to external and vice versa).

I performed frequentist and Bayesian statistics on mean RTs for accurate trials only and excluded the data from the training phase. I included all participants in the current analyses, and report the analyses without outlier participants in Appendix C. A more in depth explanation of all analytical choices is provided in Chapter 3 (section 3.3.5).

5.2.5.1. Pre-registered analyses

As in Chapter 3, I performed a 2x2 rANOVA with domain (internal, external) and trial type (repetitions, switches) as factors, to investigate the overall presence of switch costs as per *Hypothesis 1*, as well as in the internal domain, as per *Hypothesis 2*. In this analysis, an absence of interaction between domain and trial type would provide support for our preregistered *Hypothesis 3*, although a significant interaction would replicate our previous study (Chapter 3; Calzolari et al., 2022). I also performed a 2x2 rANOVA with factors domain (internal, external) and switch type (within-domain, between-domains) on the switch costs to test for *Hypothesis 4* and *Hypothesis 5*. I checked for the overall level of task difficulty irrespective of switch costs with a 1x4 rANOVA on RTs in repetition trials only and, finally, checked for the nuanced effects of each task on switch costs with a 4x2 rANOVA.

5.2.5.2. Exploratory analyses

As in Chapter 3, I performed one sample t-tests comparing all switch types in the 2x2 and 4x2 rANOVAs to 0 to make sure that the switch cost effects detected in the main analyses were not solely driven by one specific switch type. In the case of switches within the internal domain, this complemented the main test for *Hypothesis 2*.
In addition, to check if switch costs were influenced by task difficulty (regardless of domain and task conditions), I grouped specific switch subtypes into 2 categories (hard-to-easy, easy-to-hard) based on the results from the 1x4 ANOVA on task repetitions (see **Figure 5.3A**). In particular, if a switch type involved going from a task with faster RTs to a task with slower RTs according to the ANOVA on task repetitions, that switch was categorized as easy-to-hard (and vice versa for switches from tasks with slow RTs to tasks with faster responses). This was similar to Chapter 3, although here there were no neutral switch types, thus I could simply use a paired samples t-

test (frequentist and Bayesian) on switch costs to compare the easy-to-hard and hard-to-easy conditions. In this study, I could not find a subset of participants who displayed no differences in task difficulty. Therefore, in this Chapter I did not repeat the pre-registered analyses on a smaller sample, as I did in Chapter 3.

Finally, I performed a 2x3 rANOVA with factors domain (internal, external) and CTI length (short, medium, long) on switch costs, to account for the effect of varied durations for task preparation. Short (200 – 1250 ms), medium (1600 – 3000 ms) and long CTIs (3350 – 6150 ms) were divided as done in Chapter 3. This ANOVA was followed by one-sample t-tests for each of the 6 switch cost conditions to check whether switch costs were present across all CTI durations.

5.3. Results

As mentioned in the Methods section, here I report results from all participants, including outliers. Please refer to Appendix C for the equivalent tests without outliers.

5.3.1. Accuracy

Participants' accuracy was high overall (90.85% ± 5.62). The mean accuracy for the external tasks (judgement of outdoor and natural scene) was 94.43% (± 5.24) and 89.05% (± 7.03) respectively. The mean accuracy of internal tasks (pleasantness and relatedness judgements) was 91.25% (± 7.31) and 88.66% (± 8.11) respectively.

5.3.2. Switch costs

I applied the Bayesian stopping rule and found that the Bayesian t-test comparing switches and repetitions held very strong evidence for the presence of overall switch costs (BF_{10}=1.611e+32; $t(200)=15.30$, $p<.001$, $d=1.08$), supporting *Hypothesis 1* (**Figure 5.2A**).

In accordance with this, the 2x2 rANOVA with factors domain and trial type on RTs (**Figure 5.2B**) also resulted in a significant main effect of trial type (BF_{10}=1.974e+32,

$F(1,200)=238.51$, $p<.001$, $\eta_p^2=0.54$), with repetitions significantly faster than switches (*Hypothesis 1*). The main effect of domain was also significant, showing that external tasks led to faster RTs than internal tasks ($BF_{10}=4.492e+32$, $F(1,200)=238.74$, $p<.001$, $\eta_p^2=0.54$). Finally, I found a significant interaction between domain and trial type ($BF_{10}=49.07$, $F(1,200)=12.48$, $p<.001$, $\eta_p^2=0.06$), led by the fact that, while the RTs for switches towards internal tasks were significantly greater than those towards external tasks, the switch costs in the external domain were greater than in the internal domain. This finding disproves *Hypothesis 3* but is in line with our previous findings. Post-hoc t-tests confirmed that significant switch costs were present in both the external ($BF_{10}=9.907e+27$, $t=14.07$, $p_{bonf}<.001$) and the internal domain ($BF_{10}=1.623e+15$, $t=9.51$, $p_{bonf}<.001$), in accordance with *Hypothesis 2*.

5.3.3. Additional costs in between-domain switches

The 2x2 rANOVA with factors domain and switch type (**Figure 5.2C**) on switch costs (i.e., mean RTs for switch trials minus repetition trials) revealed a significant main effect of domain (greater costs for switches to external than to internal tasks; $BF_{10}=32.003$, $F(1,200)=11.92$, $p<.001$, $\eta_p^2=0.056$), but no effect of switch type ($BF_{10}=0.358$, $F(1,200)=3.72$, $p=.07$, $\eta_p^2=0.016$). Therefore, I did not find evidence in favour of *Hypothesis 4*. I also found no significant interaction between domain and switch type ($BF_{01}=7.403$, and $F(1,200)=0.055$, $p=.815$, $\eta_p^2=2.748e\text{-}4$). Nonetheless, all types of switch cost were significantly different from repetitions (i.e., significantly greater than 0 in the one-sample t-tests, all $p<.001$; see Table C1a in Appendix C including the switches within the internal domain ($BF_{10}=2.019e+9$, $t=7.41$, $p<.001$, $d=0.52$) and the switches from external to internal domain ($BF_{10}=7.572e+12$, $t=8.78$, $p<.001$, $d=0.62$). This further supported *Hypothesis 2* in showing that the effects found in the previous rANOVA were not solely driven by one particular switch type.

Relatedly, the 4x2 rANOVA on switch costs with factors trial type and task (**Figure 5.2D**) revealed a significant main effect of task ($BF_{10}=3.722$, $F(3,600)=4.85$, $p=.002$, $\eta_p^2=0.024$), but no main effect of switch type, approaching significance in the frequentist analyses but carrying strong Bayesian evidence in favour for a lack of effect

(BF$_{01}$=3.226 and F(1,200)=3.841, p=.051, η_p^2=0.019). Similarly to the previous rANOVA, there was no significant interaction (BF$_{01}$=58.004 and F(3,600)=1.109, p=.345, η_p^2=0.006). Notably, all eight types of switch cost were significant (i.e., greater than 0 in the one-sample t-tests; Table C1b in Appendix C).

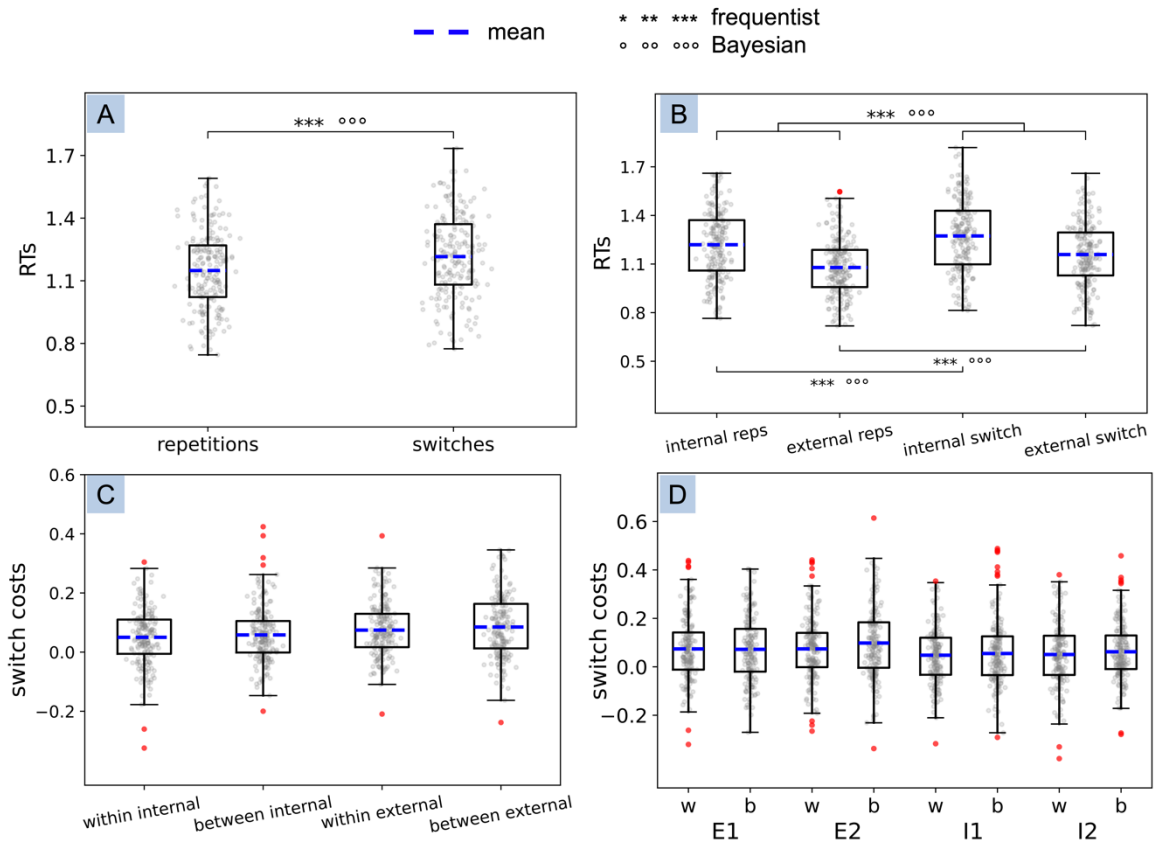

Figure 5.2. Boxplots representing data from all pre-registered statistical analyses. (A) Comparison of all repetitions versus all switches (overall switch costs); (B) main effect of trial type and post-hoc t-tests from the 2x2 rANOVA with factors domain (internal, external) and trial type (switches, repetitions) that measures the switch costs in each domain; (C) data from the 2x2 rANOVA on switch costs with factors domain and switch type (within, between domain) (D) data from the 4x2 rANOVA on switch costs with factors task and switch type. Outlier participants appear as red dots. These were included in all results reported in the main text (see Appendix C for results excluding outliers). The mean is represented as a blue dashed line. The whiskers represent the range between minimum and maximum i.e., the variability outside the upper and lower quartiles. * p<.05; ** p<.01, *** p<.001, ° BF10>3 (substantial evidence), °° BF10 >10

(strong evidence), °°° BF10 > (very strong evidence).

5.3.4. Difficulty of task repetitions

I found a significant main effect in the 1x4 rANOVA (**Figure 5.3A**; Table C3 in Appendix C) comparing RTs for repetitions in each task (BF_{10}=5.543e+69, F(2.319,463.894)=152.49, p<.001, η_p^2=0.43 with Greenhouse-Geisser sphericity correction), which highlighted potential intrinsic differences in difficulty between task conditions, against our expectations. Indeed, all post-hoc t-tests across tasks resulted significant (see Table C3 for details). In particular, the external task 1 (indoor/outdoor discrimination) induced the fastest RTs, followed by external task 2 (natural/man-made discrimination) and internal task 1 (pleasantness judgement). Internal task 2 (relatedness judgement) held the slowest RTs.

Table 5.1 displays means and standard deviations for all conditions of all pre-registered analyses (RTs after subtraction of task repetitions are reported, where relevant. See Table C4 for the raw RTs).

	Repetitions	Combined switches	Within domain	Between domains
All	1.149 (0.182)	1.216 (0.198)		
Internal	1.219 (0.211)	1.273 (0.220)	0.050 (0.096)	0.058 (0.094)
External	1.078 (0.175)	1.159 (0.197)	0.074 (0.089)	0.085 (0.104)
E1	1.042 (0.177)		0.074 (0.130)	0.072 (0.134)
E2	1.115 (0.192)		0.074 (0.128)	0.098 (0.144)
I1	1.205 (0.210)		0.048 (0.118)	0.055 (0.138)
I2	1.233 (0.226)		0.051 (0.130)	0.062 (0.119)

Table 5.1. Mean and SD for all conditions in the pre-registered analyses. All units are seconds. E1: external task 1 (indoor/outdoor discrimination); E2: external task 2 (natural/man-made discrimination); I1: internal task 1 (pleasantness judgement); I2:

internal task 2 (relatedness judgement).

5.3.5. Switch costs grouped by difficulty

The t-test on switch costs comparing easy-to-hard and hard-to-easy switches (grouped according to the differences in task difficulty in the previous 1x4 rANOVA) was significant but with anecdotal Bayesian evidence (BF_{10}=2.108; *t*(200)=2.603, *p*=.01, *d*=0.184), indicating that the magnitude of switch costs might have been influenced by task difficulty (**Figure 5.3**).

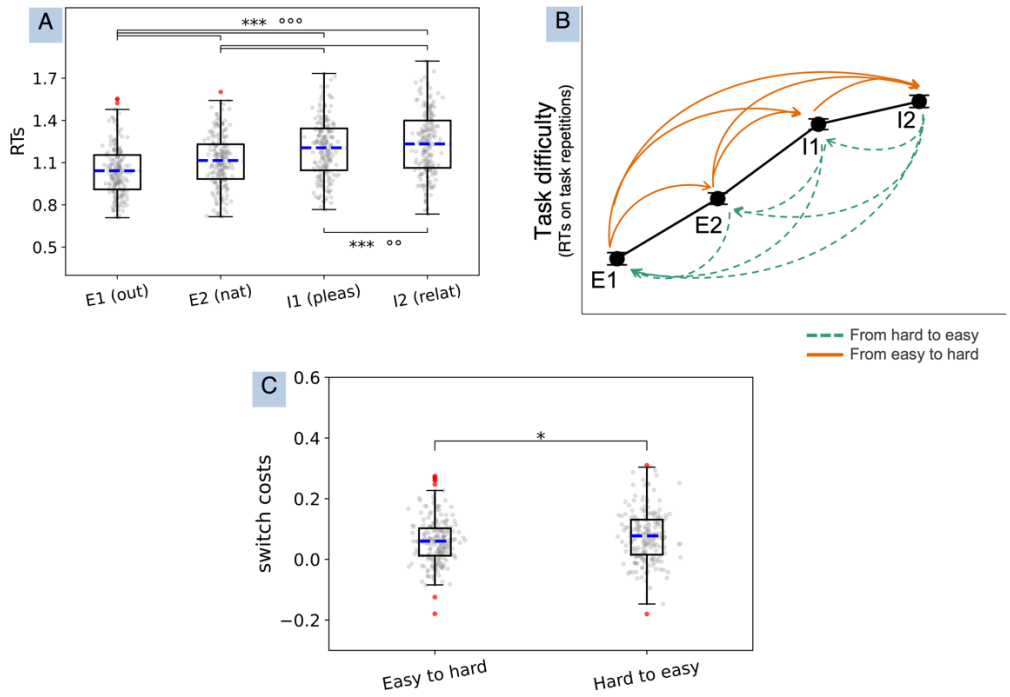

Figure 5.3. (A) 1x4 ANOVA with task repetitions, to measure task difficulty irrespective of switch costs. (B) Categorisation of each switch subtype in light of the level of difficulty of each task, as found in A. (C) Boxplots showing the results from the t-test comparing switch costs grouped as easy-to-hard or hard-to-easy. Outlier participants appear as red dots (these were not removed from analyses). The mean is represented as a blue dashed line. The whiskers represent the range between minimum and maximum i.e., the variability outside the upper and lower quartiles. * *p*<.05; ** *p*<.01, *** *p*<.001, ° BF10>3 (substantial evidence), °° BF10 >10 (strong evidence), °°° BF10

> (very strong evidence).

5.3.6. Effects of CTI duration

The 2x3 rANOVA on switch costs with factors domain and CTI (**Figure 5.4**) showed a significant main effect of CTI (BF_{10}=6.544e+8, $F(2,400)=28.632$, $p<.001$, $\eta_p^2=0.125$) and domain (greater switch costs in the external as compared to internal domain; BF_{10}=18.976, $F(1,200)=11.605$, $p<.001$, $\eta_p^2=0.055$), but strong evidence for the lack of an interaction (BF_{01}=33.45, $F(2,400)=0.45$, $p=.634$, $\eta_p^2=0.002$). Post-hoc t-tests revealed greater switch costs in short CTIs compared to both medium (BF_{10}=446165.672, $t=5.827$, $p_{bonf}<.001$) and long CTIs (BF_{10}=7.748e+8, $t=7.095$, $p_{bonf}<.001$), but no difference between medium and long CTIs (BF_{10}=0.145, $t=1.268$, $p_{bonf}=.616$). This pattern was present both in the internal (short vs medium: BF_{10}=18032.713, $t=4.851$, $p_{bonf}<.001$; short vs long: BF_{10}=960580.49, $t=5.324$, $p_{bonf}<.001$; medium vs long: BF_{01}=10.87, $t=0.473$, $p_{bonf}=1$) and external domain (short vs medium: BF_{10}=10.775, $t=3.57$, $p_{bonf}=.006$; short vs long: BF_{10}=456.521, $t=4.93$, $p_{bonf}<.001$; medium vs long: BF_{01}=5.319, $t=1.36$, $p_{bonf}=1$). Switch costs were significantly greater than 0 in all CTI durations, as measured by the one-sample t-tests (all $p<.001$). **Table 5.2** includes the descriptive statistics of all conditions in this analysis (RTs after subtraction of task repetitions are reported; see Table C6 in Appendix C for the raw RTs).

	Internal	**External**
Short CTIs	0.089 (0.117)	0.108 (0.142)
Medium CTIs	0.039 (0.105)	0.072 (0.116)
Long CTIs	0.035 (0.108)	0.058 (0.110)

Table 5.2. Mean and SD for all conditions in the 2x3 rANOVA. All units are seconds.

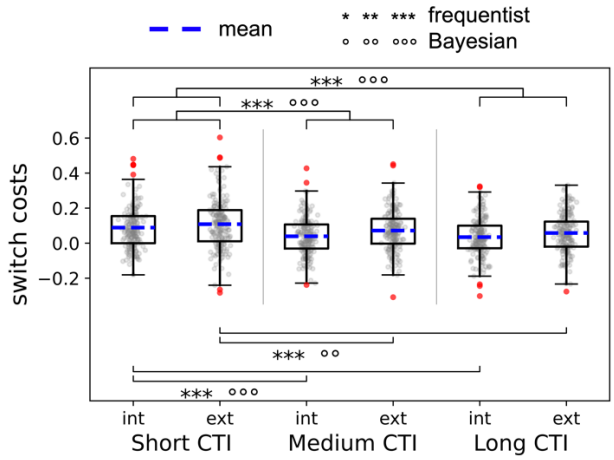

Figure 5.4. Boxplots representing the data from the analysis on the effects of CTI duration. The figure shows the post-hoc t-tests from the 2x3 rANOVA on switch costs with factors domain (internal, external) and CTI (short, medium, long). Outlier participants appear as red dots. These were included in all results reported in the main text (see Appendix C for results excluding outliers). The mean is represented as a blue dashed line. The whiskers represent the range between minimum and maximum i.e., the variability outside the upper and lower quartiles. * p<.05; ** p<.01, *** p<.001, ° BF10>3 (substantial evidence), °° BF10 >10 (strong evidence), °°° BF10 > (very strong evidence).

5.4. Discussion

The present study investigated the behavioural signatures of switching within and between externally and internally oriented cognitive tasks. Crucially, the aim of the current experiment was to test if I could generalise the novel effects I found in the previous behavioural study (Chapter 3; Calzolari et al., 2022) to a different range of internal and external tasks and employing different stimuli. In particular, the key reason for using different tasks was to test the presence of switch costs and additional between-domain costs in a context where both external and internal tasks required semantic stimulus processing. In the previous study (Chapter 3; Calzolari et al., 2022), external and internal domains were characterised by task rules with distinct levels of linguistic processing, where internally oriented tasks required deeper semantic access

and retrieval as compared to externally oriented tasks requiring working memory (to find the third or the penultimate letter) and simple letter recognition (consonant or vowel). Given this imbalance, I designed the current experiment to match the level of stimulus processing across domains (general encoding of the picture scenes and their meaning).

In accordance with Chapters 3 and 4, the results showed strong evidence of switch costs i.e., slower RTs when switching tasks compared to repeating the same task, both in the external and the internal domain. I also found a significant interaction between domain and trial type, as before. However, I was unable to replicate the presence of additional costs for switching between domains as compared to within each domain.

First, I proved that this version of the paradigm is also appropriate for the investigation of task-switching, since I found strong evidence for the presence of switch costs regardless of domain or task, as per *Hypothesis 1*. Moreover, I replicated the main result from my previous study – the presence of switch costs when participants switched towards internally oriented tasks (Chapter 3; Calzolari et al., 2022). The fact that I replicated this important finding strengthens previous conclusions and indicates that self-referential processing is characterised by similar features of cognitive flexibility as externally oriented tasks. In particular, one of the most recent theories suggests that switch costs arise from the need to control the interference from previously relevant tasks as well as the need to actively reconfigure the task-set (Vandierendonck et al., 2010; Yeung et al., 2006). I hereby show that these control processes can be engaged by self-reference as well, when in a goal-directed context. In addition, I also found an interaction between domain and trial type, which could indicate the presence of distinct but interconnected cognitive systems for the control of external and internal processes. This interaction was present in our prior behavioural study as well (Chapter 3; Calzolari et al., 2022), against my initial predictions (*Hypothesis 3*), and fits with the idea that task-specific components are also engaged during cognitive control, as found in previous research where the effects of preparatory time and task predictability affected both switches and repetitions (Altmann, 2004; Dreisbach et al., 2002). This view is also in line with the neuroimaging data from Chapter 4 showing domain-specific brain activation in preparation of external (dorsal attention network) and internal (i.e., default mode network) tasks

along with a joint activation of areas associated with domain-general control (e.g., IPL and dorsal precuneus) in preparation of switches towards tasks from both domains.

Related to such interaction effect, it is important to emphasise that the magnitude of switch costs was greater in the external domain (as per the prior study), even though the switches towards internal tasks induced the slowest RTs among all conditions (where instead in Chapter 3 the switches to external tasks held the slowest RTs). The fact that the relative proportion of switch costs in the two domains was similar across studies (greater costs in the external domain as compared to internal) despite the main effect of domain having opposite direction in the two studies provides a further validation of our core interpretation and points towards the presence of a strong generalisable effect of domain-switching, regardless of specific task demands.

The different direction for the main effect of domain likely reflects differences in the specific tasks used that might not relate to the nature of external or internal processing per se, but rather to the level of difficulty of each task. While this clearly shows that there are a number of different aspects that can influence the behavioural outcomes of these paradigms, the fact that I found consistent switch cost effects which displayed a similar balance across domains is once again reassuring in regard to our interpretation of switch costs.

However, against my predictions and contrary to what I previously found, I did not observe significant additional costs in response to between-domain switching (as compared to within-domain). It is possible that the behavioural manifestations of the additional processes required to switch between domains are more sensitive to the influence of specific task requirements, as more task components will likely differ across tasks from different cognitive domains, and different domains might engage different forms of task switching (C. M. Arrington et al., 2003; Ravizza & Carter, 2008; Rushworth et al., 2005).

As already explained earlier, the current study differs from the previous in terms of the depth of stimulus processing required by external and internal domains, which was unbalanced in Chapter 3. It is possible that such difference might have aided and boosted the behavioural costs of switching between domains in the previous study, and was instead absent in the current one. While this does not invalidate the hypothesis I had, it is plausible that the impact that specific stimulus and task properties have on switch costs hindered the signs of shifting across domain qualities, which more likely take place during task preparation. This idea comes from an

influential theory of task switching (two-stage reconfiguration account) which distinguishes between two key components of cognitive control, namely goal shifting and rule activation (Rubinstein et al., 2001). In cued switching paradigms, participants are able to prepare and shift to the currently relevant abstract goal before stimulus presentation. However, according to the theory, the activation of specific response rules is postponed until the stimulus is presented, which is thought to explain the presence of residual switch costs even after long preparation times (Vandierendonck et al., 2010). In fact, while the CTI analysis confirmed that short preparation time (200-1250 ms) significantly increased switch costs as compared to medium and long intervals, (as often reported in the literature, e.g., Monsell & Mizon, 2006), in this study switch costs were always significant even after long preparatory intervals. Importantly, this pattern was present in both the external and the internal domain, with no interaction between domain and CTI duration, thus still supporting the presence of certain features of cognitive control that are common across both external and internal domain.

As already described in previous chapters, Verschooren and colleagues suggested that switching between perceptual and working memory tasks elicited switch costs with a similar magnitude to switching within each of those domains (Verschooren et al., 2019). They interpreted those results in light of the resource-sharing account, suggesting that the control of external (perceptual) and internal (working memory) domains stems from the same cognitive resource which gets reallocated to one or the other domain based on current needs. While I agree that there are domain-general features of cognitive control that can be activated during switching towards different cognitive domains, our previous neuroimaging evidence (Chapter 4) point towards the activation of both domain-general and domain-specific neural pathways during task preparation, suggesting that distinct resources are also recruited during switch preparation depending on which cognitive sets become relevant. Further tests aimed at distinguishing between our view and alternative accounts (e.g. Verschooren et al., 2019) are needed, specifically to understand whether these mechanisms differ if self-referential processing is involved or not. Nonetheless, this work still constitutes an advancement towards understanding the complex nuances of cognitive control and its interface with internal processing.

Furthermore, contrary to my expectations, task difficulty appeared to have had a noticeable influence on switch costs in the current study. In fact, while I previously

found that switch costs were not significantly different when grouped according to task difficulty (see paragraph ‘Switch costs grouped by difficulty’ in Results section of Chapter 3), here I noticed a significant difference between ‘easy-to-hard’ and ‘hard-to-easy’ switch types. This might have been due to the greater imbalance between tasks in this paradigm as compared to the paradigm with written word stimuli. In the previous study, I was able to randomly select a pool of participants that showed no differences in difficulty across task repetitions, which allowed to perform the pre-registered analyses on a balanced subset of participants. Here, this procedure was not feasible due to the greater imbalance between task repetitions. This can be quantitatively confirmed by the extremely strong Bayesian evidence in favour of a difference in the 1x4 ANOVA on task repetitions, 1.15e54 times stronger than the evidence for the same analysis in our previous study. In fact, all tasks induced significantly different RTs as compared to each other, with the internal tasks having slower RTs than external ones (contrary to our previous study where one of the externally oriented tasks held the slowest RTs). It is however likely that these intrinsic task differences do not relate to the different level of stimulus processing induced by the tasks (which was a greater issue in the previous paradigm, as explained earlier), but instead reflect how effortful retrieving the correct response is. Previous research suggested that the complexity of visual stimuli can impact the ability to efficiently inhibit task-irrelevant features (i.e. details embedded in the pictorial stimuli) during task-switching, enhancing the chance of distraction and of irrelevant attentional shifts (Schuch et al., 2020). It is thus plausible that the use of complex stimuli in the current study (pictures instead of words) made the retrieval of subjective information more time-consuming as compared to the discriminations of external feature (e.g., whether a scene is indoor or outdoor). While it is unlikely that this affected the reliability of my interpretations regarding switch costs, this second study highlights the overall need for a further exploration of what stimulus features and task requirements affect domain-switching, and how.

Related to the potential influence of task characteristics, the current study suffers from the limitation that the stimulus list was fixed and equal for all participants, who thus all saw the same pictures in the same conditions, in a randomly shuffled order. Future studies might aim at having a more varied set of stimuli to reduce the potential effect of specific stimuli, or perhaps employ simpler stimuli whose features can easily be controlled and manipulated, to allow more systematic and fine-grained testing on the

effect of task and stimulus affordances on (between-domain) switch costs.

5.5. Conclusions

We were able to replicate the core findings on the nature of switch costs in the internal and external domain even in the case of different task requirements and stimuli. However, we were not able to replicate the presence of additional costs in between-domain switching, suggesting that this might be more sensitive to specific task requirements and features. Nonetheless, taken together, our results support the model we originally proposed, suggesting the presence of two cognitive systems for the control of external and internal tasks, which communicate and share domain-general features. Further research is required to assess whether between-domain switches necessitate of a more effortful reallocation of cognitive resources across control systems, and whether this consistently translates into measurable behavioural costs.

Chapter 6

CHAPTER 6 : AN EXPLORATION OF RESTING-STATE BRAIN ACTIVITY IN EARLY AND LATE CHRONOTYPES USING CHANGE-POINT DETECTION.

6.1. Introduction

When at rest, the brain is functionally organised into distinct large-scale networks defined by temporally correlated regions (Hutchison et al., 2013). These patterns of functional connectivity (FC) appear to resemble the activation elicited by tasks and cognitive processes (Gilson et al., 2018; Gonzalez-Castillo et al., 2015; Laird et al., 2011; Smith et al., 2009), suggesting a mechanism of reconfiguration between rest and task which allows cognition and behaviour to emerge in a context-dependent manner (Cohen & D'Esposito, 2016). Among these networks, the default mode network (DMN) has been linked to self-referential processing, mind-wandering and autobiographical memory, and was shown to be anticorrelated with lateral frontoparietal networks subserving external attention and working memory (DAN) and executive control (ECN), likely under the coordinating influence of the salience network (SN) (Buckner et al., 2008; Fox et al., 2005; Seeley et al., 2007). Importantly, the mediodorsal (MD) thalamus has been proposed as part of the SN network and presents strong connectivity with DMN, DAN and ECN regions, thus potentially playing an important role in a wide range of high-order cognitive functions, including cognitive flexibility, and in coordinating the exchange of information across relevant networks (K. Li et al., 2022).

In previous chapters I adopted a task-switching perspective to investigate the goal-directed reorganisation of cognitive systems for internal and external processes (Chapters 3 and 5) and their underlying neural systems during such cognitive changes (Chapter 4) for the first time. However, detecting and investigating similar switch points in resting-state would allow us to further characterise the intrinsic cognitive landscape of the brain when unconstrained by task demands.

Further to the above, thalamocortical connectivity is thought to be pivotal for the

regulation of general and directed arousal via modulation of the noradrenergic system, which in turn appears to greatly influence cognition, as found by studies of sleep deprivation (Tomasi et al., 2009). While sleep deprivation is a serious issue that is known to affect people with sleep disturbances and night work shifts, mild chronic sleep restriction can also be experienced by late chronotypes. Chronotype is defined as the temporal preference for sleep, with early and late chronotypes having a propensity towards advanced or delayed sleep (and wakefulness) periods, respectively (Roenneberg et al., 2007). Extreme chronotypes (late in particular) can frequently experience a mismatch between their circadian rhythms and external demands from work or school schedules (Giannotti et al., 2002; Wittmann et al., 2006), which often creates sleep disturbances and/or chronic sleep restriction and has a detrimental impact on physical and mental health (Wittmann et al., 2006). Despite this being a widely acknowledged issue, the effects of different chronotypes and the implications of cumulative sleep debt on brain networks have been scarcely investigated. Only recently, research found that late chronotype scores correlated with a reduced stationary connectivity within regions of the DMN and between DMN and SN regions as compared to early chronotypes (Facer-Childs et al., 2019, 2021; Horne & Norbury, 2018; Wang et al., 2022). However, the exact influence of arousal as dictated by circadian rhythms and chronotype on dynamic network reconfiguration is still largely unknown.

Most studies have investigated resting-state networks using stationary analysis approaches that measure average brain activity (BOLD, FC, graph measures, etc…) over the entire scan length of several minutes, and presuppose the interactions between brain regions are constant over time – a convenient assumption that has been however discredited with a fair degree of certainty (Calhoun et al., 2014; Kopell et al., 2014). While this has been addressed by adopting a dynamic FC approach, the vast majority of dynamic FC studies employed the sliding windows method, which suffers from some key limitations such as the arbitrary choice of a fixed window length, shape and overlap, and has no solid grounding in neurobiological principles (Hutchison et al., 2013).

Alternative methods have been developed, which allow changes in functional connectivity networks to be found without the need to segment the data with fixed parameters established a priori. One of these methods is change-point detection. Change-point detection is a broad term that refers to a number of search methods that

find abrupt changes in timeseries, irrespective of the nature of that time series. There exist a multitude of different approaches to change-point detection, of which some such as FreSpeD, Dynamic Connectivity Regression and Network Change Point Detection have been specifically developed for neuroimaging data (Cribben et al., 2012; Cribben & Yu, 2017; Schröder & Ombao, 2019). However, most of these methods have issues with the detection of change-points in multivariate time-series, and use binary segmentation which finds one single change-point at a time and is not sensitive to small frequent changes, as well as being limited in the number of brain regions they can handle.

In this study I used a recently proposed method called cross covariance isolate detect (CCID) which, as compared to previous methods, can detect even small frequent changes, is computationally fast, and can provide information regarding which brain regions are associated with each change-point (Anastasiou et al., 2022).

Using CCID, I sought to identify changes across regions of the networks subserving and coordinating external and internal cognition (as explained above) in a data-driven manner. I wanted to then explore the brain activation around the identified changes using general linear models (GLM), as well as the connectivity between them using dynamic FC and graph theory, in addition to descriptive measures such as number and distribution of change-points. I further wished to investigate how these measures could change across early and late chronotypes at different times of day.

Overall, I expected to observe thalamic (along with SN) activation associated with change-points, specifically in MD thalamus. I also hypothesised patterns of anticorrelation between DMN and DAN/ECN networks, potentially accompanied by dynamic connectivity changes from SN and thalamic regions towards those networks. Moreover, I expected the MD thalamus (and other SN regions) to demonstrate connector hub properties (i.e., high centrality measures) in the graph analysis. Further, I explored whether I could find differences in whole-brain activation and dynamic FC between early and late chronotypes, and whether the effect of chronotype would interact with the time of day. I particularly expected late chronotypes to show differential activity/connectivity measures overall, and especially in the morning.

6.2. Materials and methods

The initial methodological steps of data acquisition and preprocessing mentioned here are also described in more detail in previous publications (Facer-Childs et al., 2019, 2021). The analysis approach is different in the current study and will be described fully.

6.2.1. Participants

Participants were recruited via emails and advertisements across campus, were asked to fill in a medical history form and the Munich Chronotype Questionnaire (MCTQ), and were screened for MR safety. Participants were considered suitable for the study if they were eligible to undergo MRI scanning, reported no diagnosis of sleep, neurological or psychiatric disorders and were not taking medications that could affect sleep. Eligible participants who were also categorised as Early or Late Chronotypes according to the MCTQ scores (corrected mid sleep on free days, MSF_{SC}) were then invited to take part in the main study. The chronotype categorisation was corroborated by actigraphy monitoring (analysis of sleep and wake-up times) and by biological circadian phase markers (dim light melatonin onset and peak time of the cortisol awakening response, obtained through saliva samples), which confirmed a distinction between early and late Circadian Phenotypes (Facer-Childs et al., 2019). I will nonetheless refer to Chronotypes throughout the study.

A final sample of 38 healthy participants (mean age = 22.7 ± 4.2 years; 24 females, 14 males) took part in the study, of which 16 were Early (mean age 24.7 ± 4.6 years; 9 females, 7 males; MSF_{SC} 02:24 ± 00:10 h) and 22 were Late (mean age 21.3 ± 3.3 years; 15 females, 7 males; MSF_{SC} 06:52 ± 00:17 h) chronotypes (Facer-Childs et al., 2019). Participants gave written informed consent before participating, and received compensation (cash) after taking part. The University of Birmingham's Science, Technology, Engineering and Mathematics Ethical Review Committee provided approval for the study.

6.2.2. Experimental design and procedure

Participants underwent three MRI sessions at the Birmingham University Imaging Centre (BUIC), after completing questionnaires, sleep diaries, and the aforementioned saliva sampling and actigraphy (Facer-Childs et al., 2019). MRI sessions were always carried out at 2 pm and 8 pm of the same day, then at 8 am of the following day. We will refer to these sessions as 'afternoon', 'evening' and 'morning' sessions, respectively. This allowed participants to wake up naturally on the first day, but induced sleep deprivation in the Late Chronotype group in the second day of testing. Participants slept at home in between the two days. In each session, the researcher obtained a structural and a 15-minutes resting-state scan. After MRI, participants also performed cognitive tests (not discussed here) including psychomotor vigilance and Stroop tasks, as well as the Karolinska Sleepiness Scale and a questionnaire to check for their activities in between sessions e.g., food and caffeine intake, exercise, exposure to indoor and outdoor light (Facer-Childs et al., 2019).

6.2.3. MRI acquisition

All data were acquired on a 3T Philips Achieva scanner at BUIC using a 32-channel head coil. Eye-open resting-state data were collected with a whole-brain EPI sequence (450 volumes per run, 32 slices, TR = 2000 ms, TE = 35 ms, voxel size = 3x3x4 mm, flip angle = 80°, matrix size = 80x80x32). T1-weighted images were also obtained for anatomical co-registration, with parameters TR = 8400 ms, TE = 3.8 ms, voxel size = 1x1x1 mm, flip angle = 8°, matrix size = 288x288x175. Participants' respiratory and cardiac activity were acquired during scanning using a respiratory belt and pulse oximeter, respectively. Their eyes were monitored by means of a camera in the scanner to ensure they kept their eyes open and did not fall asleep. On one occasion, the functional scan was restarted because the participant kept their eyes closed for more than 15 seconds (i.e., half of a 30s epoch according to the standard sleep staging approach; Berry et al., 2015) (Facer-Childs et al., 2019).

6.2.4. fMRI preprocessing

fMRI preprocessing was performed using UF^{2}C (http://www.lniunicamp.com/uf2c; de Campos et al., 2020), TAPAS PhysIO toolbox (Kasper et al., 2017) and SPM12 (Ashburner et al., 2016) implemented in MATLAB (MathWorks, USA). Standard preprocessing steps were followed: motion correction (6 rigid body transformation), temporal filtering (high-pass >0.008 Hz, low-pass <0.1 Hz), coregistration and normalisation to MNI space, smoothing with a 6-mm Gaussian kernel, detrending. Physiological noise modelling was performed using RETROICOR (Fourier expansion of cardiac and respiratory phase), heart rate variability and respiratory volume per time, which produced 18 regressors of no interest which were regressed out along with motion, average white matter and CSF signal. Motion censoring was performed to exclude scans with mean Framewise Displacement of 0.5 mm, which resulted in deleting one scan (afternoon session from the Early Chronotype group; final n for Early chronotype = 15). Motion parameters did not significantly differ between Early and Late chronotypes (Facer-Childs et al., 2019).

6.2.5. Statistical analysis

6.2.5.1. Timeseries extraction

I used SPM12 to extract the time-series of 57 regions of interest (ROI) using masks from the FIND lab atlas of functional ROIs (https://findlab.stanford.edu/functional_ROIs.html; Shirer et al., 2012). In particular, I extracted all ROIs from 7 large-scale resting-state networks: dorsal and ventral DMN (encompassing the posterior cingulate/medial prefrontal cortex and the retrosplenial/medial temporal lobe areas, respectively), left and right executive control (ECN; including dorsolateral PFC and parietal cortices), visuospatial network (i.e, the dorsal attention network or DAN, including intraparietal sulcus and frontal eye fields), anterior and posterior salience network (SN; including anterior insula / dorsal anterior cingulate cortex and posterior insula, respectively). See **Figure 6.1A** for a representation of the masks and Table D1 in Appendix D for the full list of regions.

Throughout the rest of the chapter, the visuospatial network will be referred to as dorsal attention network (DAN), to keep consistency with the rest of the thesis.

6.2.5.2. Change-point detection

I used the cross-covariance isolate detect (CCID) method to perform change-point detection on the extracted timeseries (Anastasiou et al., 2022). CCID is a novel approach to change-point detection which applies the Isolate-Detect principle (Anastasiou & Fryzlewicz, 2021) on the data's cross-covariance structure, as thoroughly described in the original paper by Anastasiou and colleagues (Anastasiou et al., 2022).

In brief, CCID first involves the conversion of ROI timeseries into local wavelet periodograms and cross-periodograms, i.e., estimate of spectral density of the timeseries and their cross-covariance, using the Locally Stationary Wavelet (LSW) model. This step allows to whiten the data to avoid spurious change-points due to autocorrelation, and better prepares the data for the subsequent segmentation into intervals. The ROI timeseries are aggregated together using the L_2 (Euclidean distance) or L_∞ (infinity) metric. In particular, for this study, I chose the L_∞ metric as it was shown to be less conservative than L_2 (providing more change-points) (Anastasiou et al., 2022). The Isolate-Detect algorithm then segments the data into all possible intervals (half intervals starting from the left expanding to the right and vice versa for the other half, ordered in an alternating way, as shown in **Figure 6.1B**) and starts testing from the first one, assessing all points in that interval. As typically done in change-point detection (Grigg et al., 2003), CCID assesses the change-point using a scaled cumulative sum (CUSUM) statistic on the transformed data (periodograms) which, given a certain interval, compares the mean of each side of the candidate points in that interval. A datapoint is considered a change-point if the scaled CUSUM value exceeds a given threshold (we kept the default parameter as per Anastasiou et al., 2022). If no change-point is found in an interval, the algorithm moves on to the next, and so on (as for intervals 1, 2, 3, 4 and 5 in **Figure 6.1B**, first line). If a change-point is found (e.g., interval 6 in **Figure 6.1B**), the algorithm assesses the data next to the interval where the change-point was found, i.e., from the end (if right-expanding) or

from the start (if left-expanding) of that interval, and assesses expanding intervals from there until all gaps are filled (**Figure 6.1B**, second line).

I performed CCID as described above using the R package 'ccid' (function *detect.th*; Anastasiou et al., 2022) on RStudio 2021.9.1.372 (RStudio Team, 2021) with approach "infinity" (L∞) and default parameters. In doing so, I obtained the location and number of change-points for each subject and session. Importantly, I performed three variations of CCID: (a) one with all 57 ROIs and no minimum distance between change-points, meaning that the algorithm was unconstrained and allowed to keep change-points even when directly next to each other in time, (b) one with all 57 ROIs and a minimum distance of 5 datapoints (5 TRs, equal to 10 seconds;), and (c) a final one with 53 ROIs (4 thalamic ROIs were left out), and 5 TR minimum distance between change-points. When a minimum distance is specified, the algorithm prunes away some of the original change-points if they are closer than the specified distance. I set the minimum distance parameter in order to keep meaningful changes only, taking the sluggishness of the haemodynamic response into account (Buxton et al., 2004). In the case of version *c*, I decided to obtain change-points that were not associated with thalamic activity in order to use them as onsets in a general linear model (GLM, see section 6.2.5.3 below), to explore whether I could find thalamic activation in the GLM without the risk of double-dipping.

I used version *a* to first explore the unconstrained nature of change-points. I plotted the changes' location and distribution (kernel density) for each group and session, and explored which regions were more often associated with them (this feature is only available when the minimum distance is not greater than 1 TR). I also explored whether there were any differences in the number of change-points across groups and sessions. Because this is count data, I used a Generalised Linear Model with Poisson distribution (i.e. Poisson regression, a common solution for count data; Inouye et al., 2017), including group, session and their interaction in the model, using the R package lme4 (Bates et al., 2015). I also double-checked these results with a 2x3 mixed ANOVA (after checking for ANOVA assumptions), using JASP 0.16.1 (JASP Team 2022). I then used a permutation test of equality (using *sm.density.compare()* in RStudio) to assess differences in the change-points' distribution.

When applied without specifying a minimum distance between change-points, the CCID threshold approach also provides information on which connections (cross

periodograms) are associated with each change-point, i.e., which pairs of ROIs each change originates from. This is done a posteriori by matching the multivariate results with a univariate version of CCID that is applied to each timeseries individually (see Anastasiou et al., 2022 for details the CCID algorithm and this post-processing procedure). I summarised this information by counting the occurrence of each ROI pair across change-points for each subject and session and averaged the counts across subjects in each condition (group and time of day) as well as overall, in order to assess which connections were more commonly associated with change-points in our data.

6.2.5.3. GLM analysis

I conducted a whole-brain GLM analysis in SPM12 (Ashburner et al., 2016; K. J. Friston et al., 1994), using the change-points detected with CCID as onsets in order to explore whether changes in the large-scale networks we included are governed by common brain activation patterns. In particular, for this analysis I employed the change-points obtained from 53 ROIs (excluding the thalamic regions) and with minimum distance of 5 TRs (*version c* explained in section *2.5.2*).
I performed two versions of the GLM:
(1) In one version I performed a comparison across sessions and groups to assess for potential differences in BOLD activation due to chronotype and time of day. To do so, I computed a first-level (single-subject) GLM where I averaged across events in each session and subject. Then, I performed a second-level GLM with a flexible factorial design including sessions (afternoon, evening and morning) as a within-subject factor and group (early and late chronotypes) as a between-subject factor. For this design I specified the following T-contrasts: Early > Late, Late > Early, Evening > Afternoon, Morning > Afternoon, interaction between Early > Late and Evening > Afternoon, interaction between Late > Early and Morning > Afternoon. The specific comparisons across sessions and the interactions were selected considering the afternoon session as a baseline where neither chronotype would be sleep deprived, while I expected early chronotypes to be potentially more tired during the evening scan, and the late chronotype to be more tired during the morning scan.

(2) In another GLM version, I instead simply computed the average across all sessions and groups, to explore possible general patterns of brain activation regardless of chronotype and time of day. In this version, in the first (single-subject) level of the GLM I simply averaged across events as well as across sessions within each subject. I then performed a one-sample t-test to average across participants in the second-level GLM.

In both GLM versions, I used event onsets with a duration of 0, and tested five different events in time (each with a separate GLM): events occurring 3 TRs before each change-point, 2 TRs before, 1 TR before, during each change-point (i.e., change-points were used as event onsets), 1 TR after each change-point (**Figure 6.1C**). This was done to fully explore the activation around change-points having no previous knowledge about when exactly change-related activity would arise. I report activation as statistically significant if it survived family-wise error (FWE) correction with $p<0.05$ at the voxel level, and otherwise clearly specify uncorrected subthreshold observations.

6.2.5.4. Dynamic functional connectivity

I also employed a novel approach to perform a dynamic FC analysis (**Figure 6.1D**). Instead of dividing the resting-state data (57 ROIs) into canonical sliding windows with fixed length and overlap, I utilised the change-points we found with 5 TRs of minimum distance (*version b* explained in section 6.2.5.2) to segment the data into individually defined windows with variable length, based on change-point detection. This approach was implemented to overcome the well-known limitations of the sliding windows method, namely the arbitrary choice of window length and overlap (Preti et al., 2017), in favour of a more data-driven approach.

I then followed the standard procedure implemented in the GIFT toolbox (https://trendscenter.org/software/gift/) for computing dynamic FC analyses (Allen et al., 2012; S. M. Smith et al., 2011). Specifically, after segmenting the data for each subject and session, I estimated the regularised inverse covariance matrix of each segment using the graphical LASSO (gLASSO) algorithm with L1 penalty (Friedman et al., 2008). This allowed to obtain sparse FC matrices, in line with the suggested economic organisation of brain networks (Bullmore & Sporns, 2009). I then computed

k-means clustering (with 1000 iterations) to partition all the segments of data into 4 clusters, i.e., FC states, based on their distance from the cluster means (centroids). I estimated the optimal number of states using the Elbow criterion on the cluster validity index (ratio of within- to between-cluster distance), as done in previous seminal dynamic FC studies (Allen et al., 2012; Damaraju et al., 2014). This estimation works by plotting the cluster validity index as a function of the number of clusters, and choosing the number of clusters which corresponds to the curve ('elbow') of the plot, since from that point onwards increasing the number of clusters will not considerably change the index (Vergara et al., 2020).To perform these steps, I used custom MATLAB code adapted from the code available in the GIFT toolbox.

From this procedure I obtained 4 FC states overall, as well as a state vector for each subject and session indicating which segments belonged to which state. With this information, I visually described the 4 states, and performed T-tests on the median FC values in each state (Damaraju et al., 2014), the transition probabilities, and the frequency of occurrence of each state to compare these across groups and/or sessions. More specifically, for each of these variables (median FC values, transition probability, frequency of occurrence) I performed the following T-test comparisons: Early > Late (group effect), Early Evening > Early Afternoon, Late Morning > Late Afternoon, Early Evening > Late Evening, Early Morning > Late Morning. I corrected for multiple comparisons using the False Discovery Rate (FDR), as previously done (Damaraju et al., 2014).

6.2.5.5. Graph metrics

Finally, I also extracted graph metrics from the segmented data (**Figure 6.1E**), with the specific aim of testing whether the thalamus displayed connector hub properties when dynamically exploring the FC graphs.

I used the data from 57 ROIs and with a minimum distance of 5 TRs between change-points (*version b* explained in section 6.2.5.2). I first segmented the data using the change-points as separator (between-changepoint segments). I then obtained a filtered 57x57 adjacency matrix (Pearson's correlation coefficient matrix) for each segment using the Triangulated Maximally Filtered Graph (TMFG) filtering method, available through the NetworkToolbox package in R, as per previous graph analyses

on data segmented with change-point detection (Mancho-Fora, Montalà-Flaquer, Farràs-Permanyer, Zarabozo-Hurtado, et al., 2020). The TMFG algorithm starts by including the 4 nodes that have highest sum of correlations greater than the average correlation in the matrix, and then iteratively finds other nodes with the highest sum of correlations to a set of 3 connected nodes that were already included in the network (until every node is connected), resulting in a sparse weighted undirected graph (Massara et al., 2017). For each matrix I then calculated the following graph metrics, again using the R package NetworkToolbox: nodal degree, strength, betweenness, eigenvector and nodal impact. These centrality measures provide information regarding the importance of each node in relation to the other nodes of the network. In particular, they allow to identify hubs, i.e., nodes that play a central role in shaping the activity of the network (Power et al., 2013). Degree centrality is given by the number of edges (connections) of a node, while node strength refers to the combined weight of a node's connections. Both constitute simple and commonly used measures to spot hubs (Sporns, 2018). Betweenness conveys the number of shortest paths passing through a given node, with the idea that nodes that can connect various portions of the network (i.e., with high betweenness) are the most influential (Rubinov & Sporns, 2010). Eigenvector centrality allows to rank each node based not only on the number but also on the quality of its connections (e.g., a node with few connections to high-ranking nodes may have higher eigencentrality as compared to one with a larger number of less important connections; Lohmann et al., 2010). Finally, nodal impact measures how much the network's mean distance changes without a certain node (Kenett et al., 2011).

For each of these metrics, I calculated the average across segments and subsequently the average across sessions and groups, and plotted the mean values for each node. Node values that exceeded the threshold of 1 standard deviation (SD) above the mean of all nodes were considered as an indicator of the importance of those nodes in relation to the metrics, as per previous graph theory studies (Sporns et al., 2007; van den Heuvel & Sporns, 2011). As a quality check, I performed the same procedure over each full run (non-segmented data).

I performed no comparisons across groups or sessions for these metrics as I simply sought to characterise common network properties with our novel approach, and given the scarce differences found between conditions in the previous analyses (see Results section).

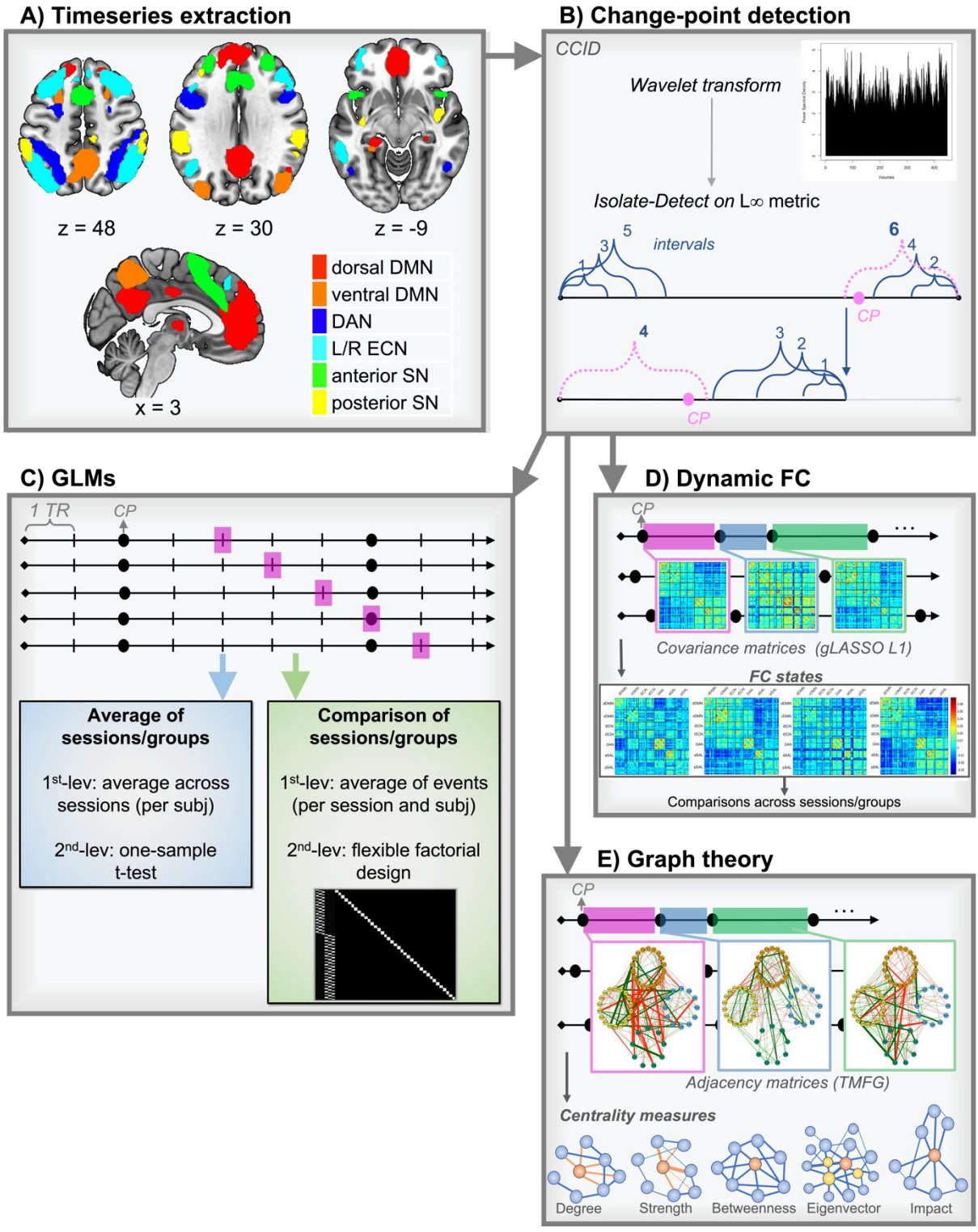

Figure 6.1. Analysis pipeline. A) Extraction of 57 ROIs from 7 intrinsic resting-state networks (dorsal and ventral DMN, left and right ECN, DAN, anterior and posterior SN) using masks from the FIND lab atlas (Shirer et al., 2012). B) Change-point detection using the cross-covariance isolate detect (CCID) method (Anastasiou et al., 2022). C) GLMs performed using single event onsets (onsets at either 3 TR, 2 TR or

1 TR before each change-point, on the change-point, or 1 TR after). In one version, I first averaged across sessions (1st level) and then computed the average across subjects (2nd level, one-sample t-test). In another version, I used a flexible factorial design at the second level to compare activation across sessions (afternoon, evening, morning) and groups (early and late chronotypes). D) I segmented data using the change-points and performed a dynamic FC analysis following the standard procedure in the GIFT toolbox: I obtained an inverse regularised covariance matrix for each segment using gLASSO with L1 penalty, then performed k-means clustering to obtain 4 functional connectivity (FC) states. I then explored differences across groups and sessions by performing t-tests on the median FC values, frequency of occurrence and transition probability from each FC state. E) I computed an adjacency matrix for each segment using the Triangulated Maximally Filtered Graph (TMFG) filtering method (Massara et al., 2017) and then computed centrality graph measures such as degree, strength, betweenness, eigenvector and impact, displaying the averaged values across segments, sessions and subjects, and considering nodes that surpassed a threshold of 1 SD above the mean as having high centrality values.

6.3. Results

6.3.1. Change-point detection

On average, when no minimum distance was set (*version a*), CCID returned ~14 change-points per subject and session (mean, SD and range across sessions and groups: 14.05 ± 2.99, 5-22). The average distance between change-points (in TRs) across all participants was 30.51 TRs (± 7.63). **Table 6.1** below reports the number of change-points as well as the average distance between change-points for each group and session (also plotted in **Figure 6.2**).

Change-points count						
Group	**Early**			**Late**		
Session	**Afternoon**	**Evening**	**Morning**	**Afternoon**	**Evening**	**Morning**
Mean	15.13	13.47	13.87	14	13.59	14.32
SD	2.61	3.10	3.33	2.64	3.57	2.71

Min	11	7	8	9	5	10
Max	20	18	21	18	22	20
Distance between change-points (TR)						
Group	**Early**			**Late**		
Session	**Afternoon**	**Evening**	**Morning**	**Afternoon**	**Evening**	**Morning**
Mean	28.19	32.13	30.58	30.24	31.91	29.82
SD	4.13	10.43	8.35	6.26	9.79	5.61
Min	22.10	20.44	19.76	21.06	19.82	20.65
Max	36.55	61	46.75	42.89	68.40	40.70

Table 6.1. (Top) Number of change-points per group and session. (Bottom) Distance (in TRs) between change-points per group and session. Mean, SD, minimum and maximum values of both measures are reported.

The Poisson regression showed that not group, not session, nor their interaction could significantly change the number of change-points, as shown by the coefficients in **Table 6.2** below and related p-values.

	Estimate coeff	**SE**	**Z**	**p**
(Intercept)	2.71690	0.06637	40.934	<2e-16
Group (Late)	-0.07784	0.08748	-0.890	0.374
Session (Evening)	-0.11668	0.09673	-1.206	0.228
Session (Morning)	-0.08741	0.09598	-0.911	0.362
Group (Late): Session (Evening)	0.08703	0.12628	0.689	0.491
Group (Late): Session (Morning)	0.10988	0.12504	0.879	0.380

Table 6.2. Generalised Linear Model (Poisson distribution) looking at the effect of group, session and interaction on the change-points count (Early chronotypes in afternoon session as intercept).

The ANOVA returned the same results (i.e., no significant differences across groups nor sessions, and no interaction; see Appendix D, Table D2).
The distribution of change-points (**Figure 6.3**) was also not significantly different across sessions and groups (p = 0.98).

See the Appendix D (Table D3) for information on *version b* with minimum distance = 5 TRs.

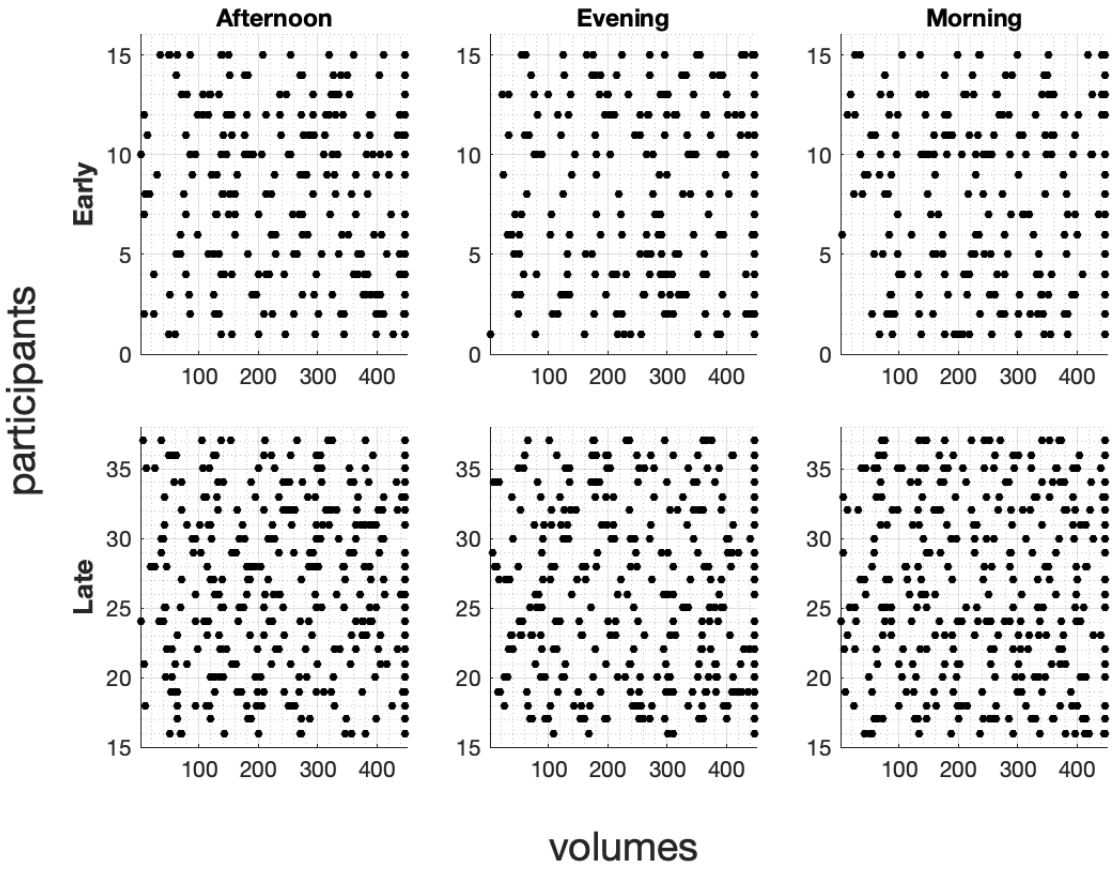

Figure 6.2. Representation of change-points (black dots) in each subject. Plots are separated for groups (Early and Late chronotypes) and sessions (afternoon, evening, and morning session). In each plot, each subject is one line in the y axis (subjects 1-15 belonging to the Early group, subjects 16-37 belonging to the Late group), with the scan volumes on the x axis.

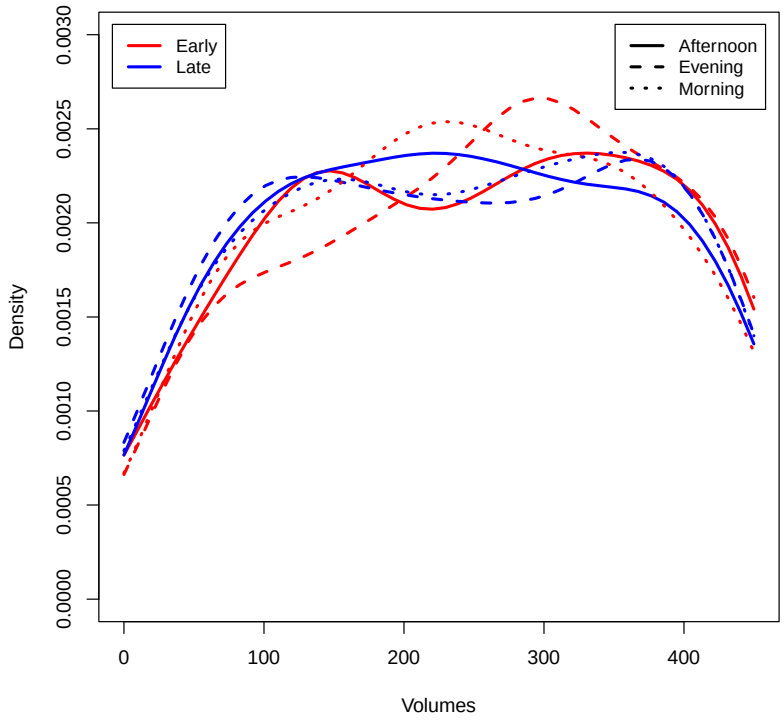

Figure 6.3. Kernel density plot of change-points in each group and session.

When observing the number of occurrences of each pairwise connection (count of ROI pairs associated with the change-points), I noted that all connections were involved with a seemingly uniform number of occurrences throughout, except fewer instances of changes between the ECN and the rest of the networks, as well as between the middle occipital lobe and the other regions (**Figure 6.4A**). This pattern was maintained in the Late chronotype group throughout all sessions and in the morning session in particular, where the fewer occurrences of ECN connections were more noticeable as compared to the morning session of Early chronotypes (**Figure 6.4B**). Early chronotypes instead displayed a more uniform engagement of connections. Interestingly, Early chronotypes also displayed a generally higher number of connectivity changes in the evening session (between dorsal DMN and DAN in particular; **Figure 6.4B**).

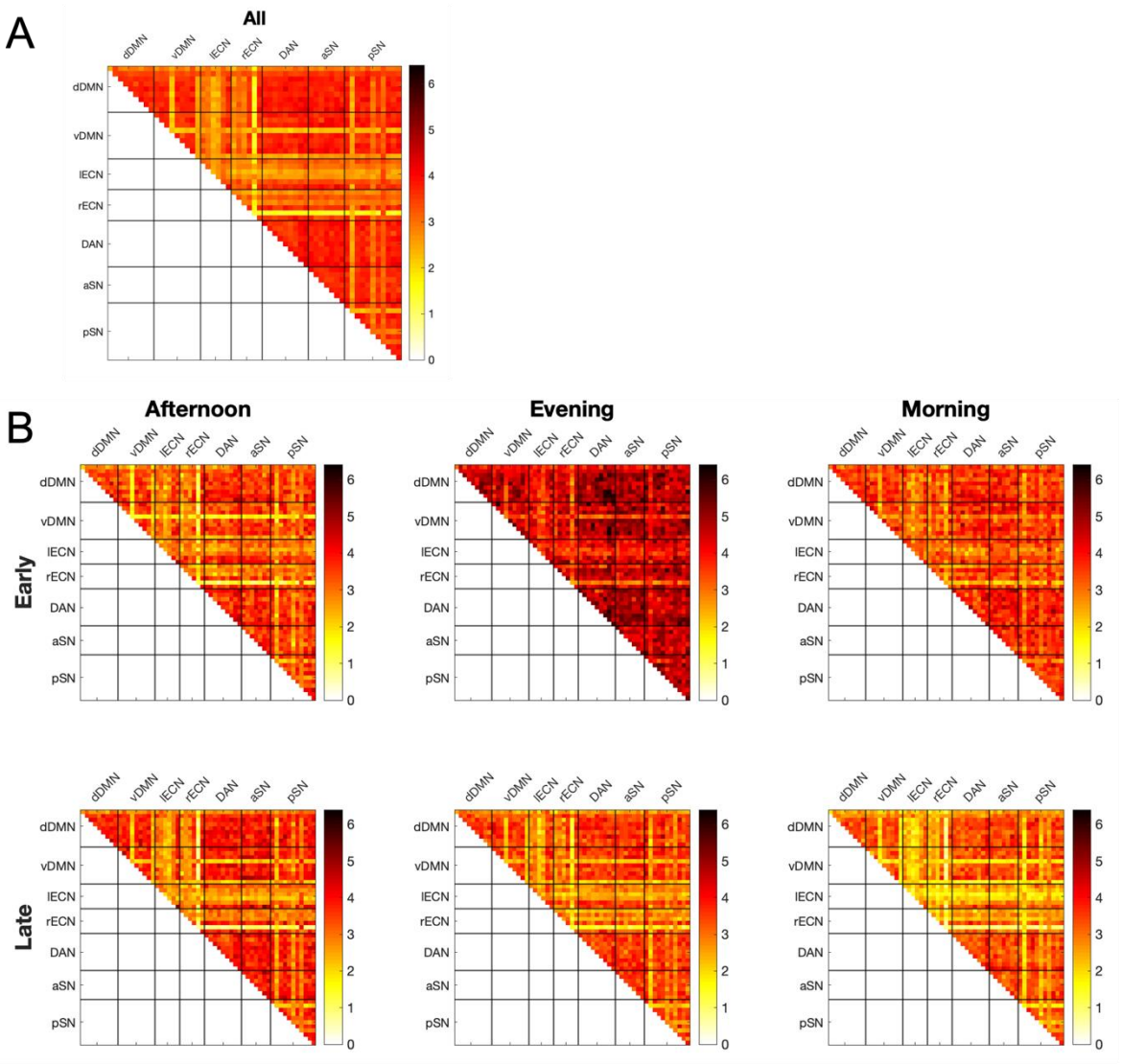

Figure 6.4. Average count of how many times each connection (ROI pair) was associated with a change-point (information available from the CCID threshold approach with no restrictions on the minimum distance between change-points). A) Average count across all conditions; B) separate mean counts for each chronotype (Early, Late) and session (afternoon, evening, morning). Abbreviations: dDMN, vDMN = dorsal and ventral Default Mode network; lECN, rECN = left and right Executive Control network; DAN = Dorsal Attention network; aSN, pSN = anterior and posterior Salience network.

6.3.2. GLM analysis

6.3.2.1. Comparison across chronotypes and time of day

I found no clusters of activation greater than 1 voxel at any of the tested onsets (no differences at 3 TR, 2 TR, 1 TR before the change-points, on the change-points, nor 1 TR after the change-points) in any of the comparisons (Early>Late, Late>Early, Evening>Afternoon, Morning>Afternoon, interaction of Early>Late and Evening>Afternoon, interaction of Late>Early and Morning>Afternoon). In **Figure 6.5** we only show the activation maps at $p < .001$ uncorrected for the GLM comparisons with change-points as onsets (see Table D4 in Appendix D for the full list of uncorrected results), as an example.

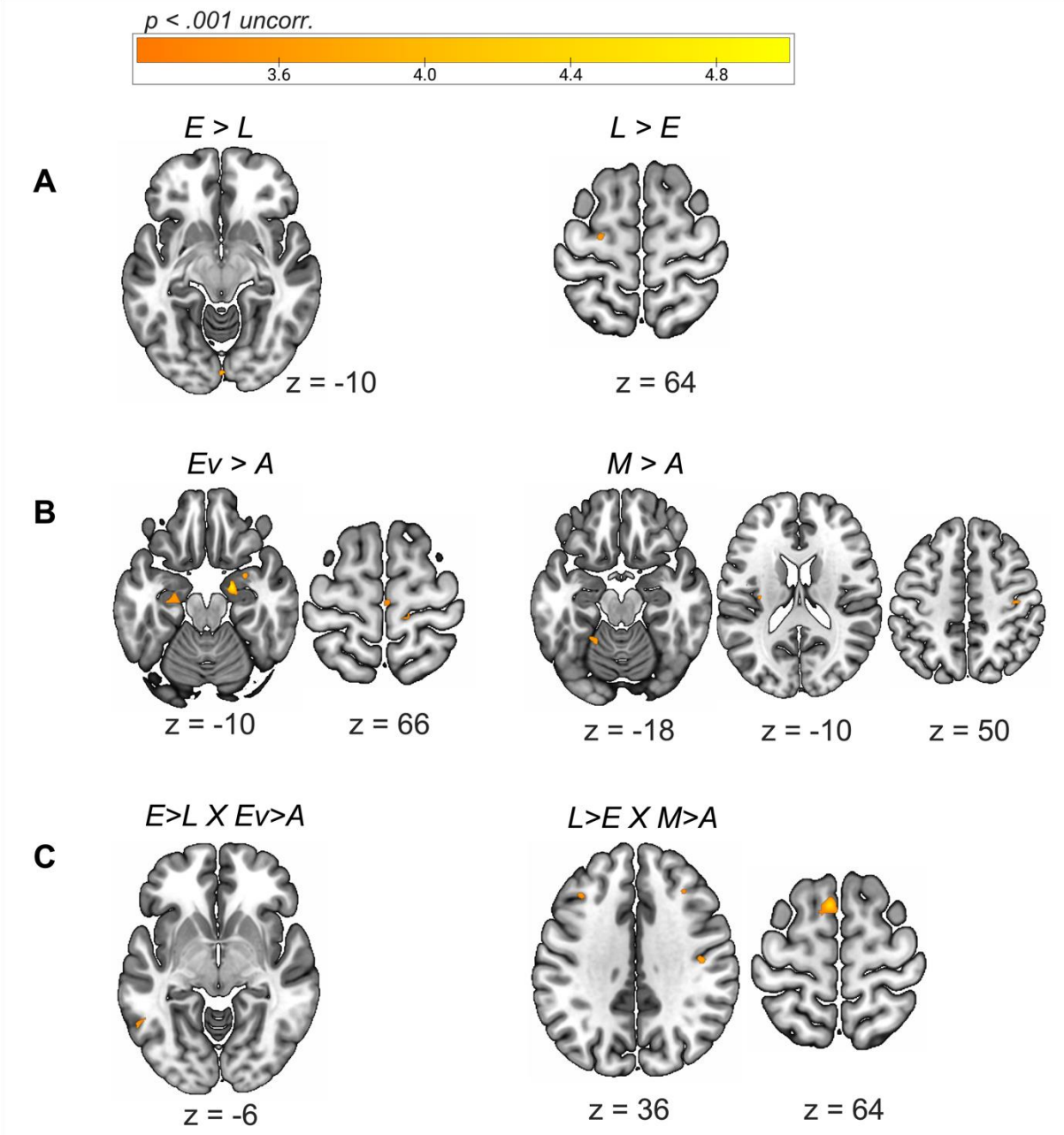

Figure 6.5. Brain activation at the group level (flexible factorial design) for the whole-brain comparisons between groups and sessions after averaging across change-point events. A) Comparison across groups: Early > Late (left) and Late > Early (right); B) Comparison across sessions: Evening > Afternoon (left) and Morning > Afternoon (right); C) interactions between groups and sessions: interaction of Early > Late and Evening > Afternoon (left), interaction of Late > Early and Morning > Afternoon (right). The activation maps are shown at p<.001 uncorrected and rendered on a standard template (mni152 template in MRIcroGL). For each slice, the relative MNI coordinate is reported. Abbreviations: E = Early chronotypes; L = Late chronotypes; A= afternoon session; Ev = evening session; M = morning session.

6.3.2.2. Average across all conditions

I also found no statistically significant activation at any of the tested onsets (no differences at 3 TR, 2 TR, 1 TR before the change-points, on the change-points, nor 1 TR after the change-points) when averaging across sessions and groups. For this reason, in Figure 6 we show the activation maps at $p < .001$ uncorrected for the GLMs on each tested onsets (see Table D5 in Appendix D for the full list of uncorrected results).

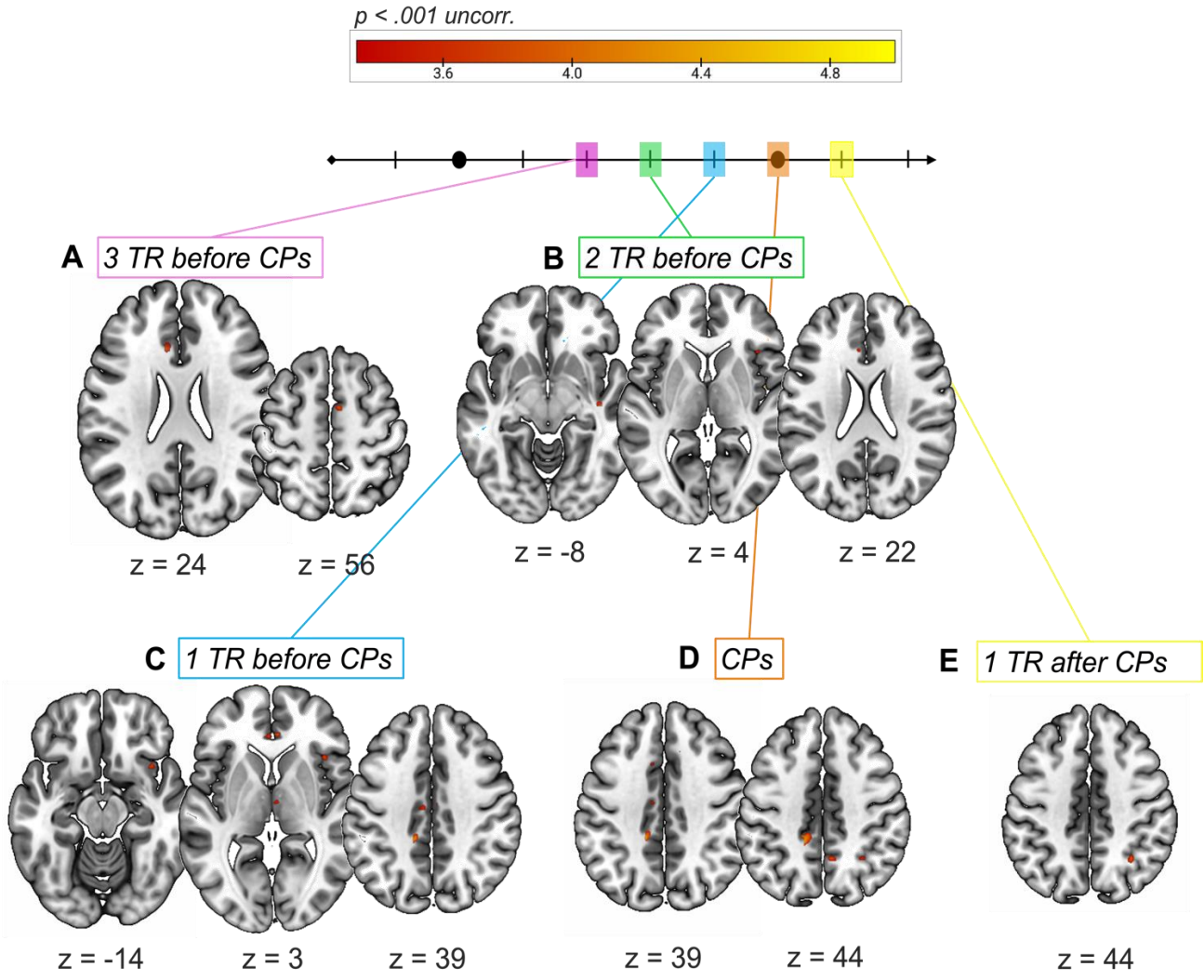

Figure 6.6. Brain activation at the group level (one-sample t-test) for the whole-brain GLMs that averaged across groups and sessions after averaging across various event

onsets: A) 3 TR before each change-point, B) 2 TR before each change-point, C) 1 TR before each change-point, D) change-points, E) 1 TR after each change-point. The activation maps are shown at p<.001 uncorrected and rendered on a standard template (mni152 template in MRIcroGL). For each slice, the MNI z-coordinate is reported.

6.3.3. Dynamic functional connectivity

Estimating the number of clusters with the Elbow criterion suggested 4 as the optimal number of clusters (**Figure 6.7**).

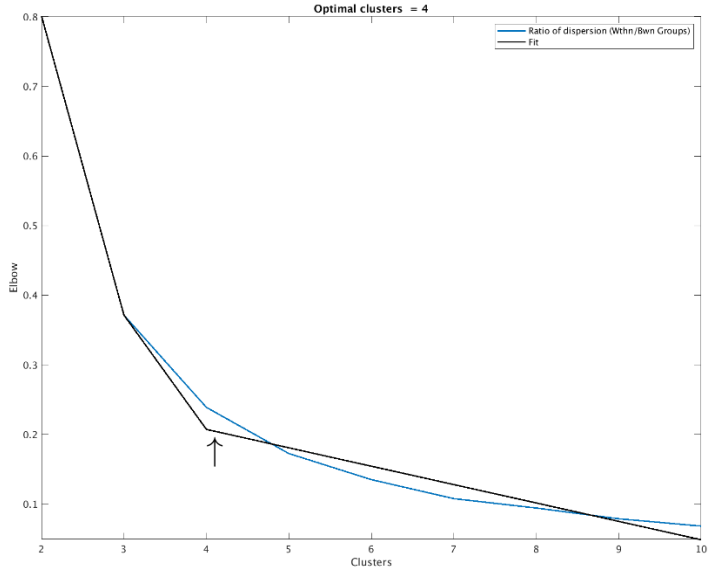

Figure 6.7. Plot showing the optimal number of clusters according to the Elbow criterion.

K-means clustering over the segmented data thus returned 4 functional connectivity states (clusters), displayed in **Figure 6.8**. All states showed connectivity values within the absolute value of 0.1. I will describe them as strong/weak patterns relatively to the states' overall trend. As a quality check, the same analysis performed using the classic sliding windows approach (with 33 s windows and 1 s overlap, as per default parameters in the GIFT toolbox) returned similar connectivity values (< 0.1), suggesting that this is an intrinsic feature of this data set rather than of the specific

analysis.

State 1 occurred on 18% of segments throughout subjects and sessions, and can be described as a state of generally weak (positive and negative) connectivity across all regions, alongside strong positive connectivity among regions within the DAN (visuospatial network) and within the anterior SN. Regions of the DAN were also negatively correlated with regions of the dorsal DMN. State 2 had an occurrence of 27% and was characterised by overall (weak) positive correlations within and between dorsal DMN, ventral DMN, left and right ECN and DAN (although there was a pattern of weak negative correlation between DAN and dorsal DMN). Anterior and posterior SN were negatively correlated with DMN and ECN, and were positively correlated within and between themselves. The occurrence for State 3 was 18%. This state was similar to State 1, presenting a general pattern of weak positive correlations across the whole network, except for a noticeable negative pattern between subcortical regions and the rest of the network. Specifically, I noticed a marked negative correlation between portions of cerebellum (lobule VI of crus I belonging to ECN, DAN and SN) and thalamus (mediodorsal thalamus in dorsal DMN) and all other regions. State 4 had the highest occurrence (37%) and displayed a pattern of positive correlation within each subnetwork (especially within some regions in dorsal DMN, DAN and anterior SN), between DMN and ECN, and between DAN and SN. Moreover, in this state DAN and SN were negatively correlated with dorsal DMN and, to a lesser extent, with ventral DMN and ECN.

Figure 6.9 shows the state vector for each subject and session, delineating which segments belonged to which FC state.

I found no significant differences in FC values in any of the tested comparisons (i.e., nothing survived the FDR correction for multiple comparisons). In other words, for each of the 4 FC states, connectivity did not differ between groups nor sessions. In **Figure 6.10**, I represent the median FC values of early and late chronotypes, and the results of the T-test for each state. See Appendix D for a depiction of the other non-significant comparisons (Early Evening vs Early Afternoon, Late Morning vs Late Afternoon, Early Evening vs Late Evening, Early Morning vs Late Morning; Figure D1, D2, D3 and D4, respectively).

I also found no significant differences across groups or sessions when comparing the frequency of occurrence of each FC state (see detailed statistical results in Table D6 and D7 of Appendix D).

There were few differences in transition probability across sessions: State 3-to-State 3 probability was significantly higher for Early chronotypes in the Evening session compared to the Afternoon session (Early-A = 0.331±0.385; Early-E = 0.767±0.329; $t(14)=3.647$, $p=0.0026$). The same was true for State 4-to-State 4 probability (Early-A = 0.394±0.299; Early-E = 0.575±0.290; $t(14)=3.491$, $p=0.0036$). The mean transition probabilities across the whole sample are represented in **Figure 6.11**.

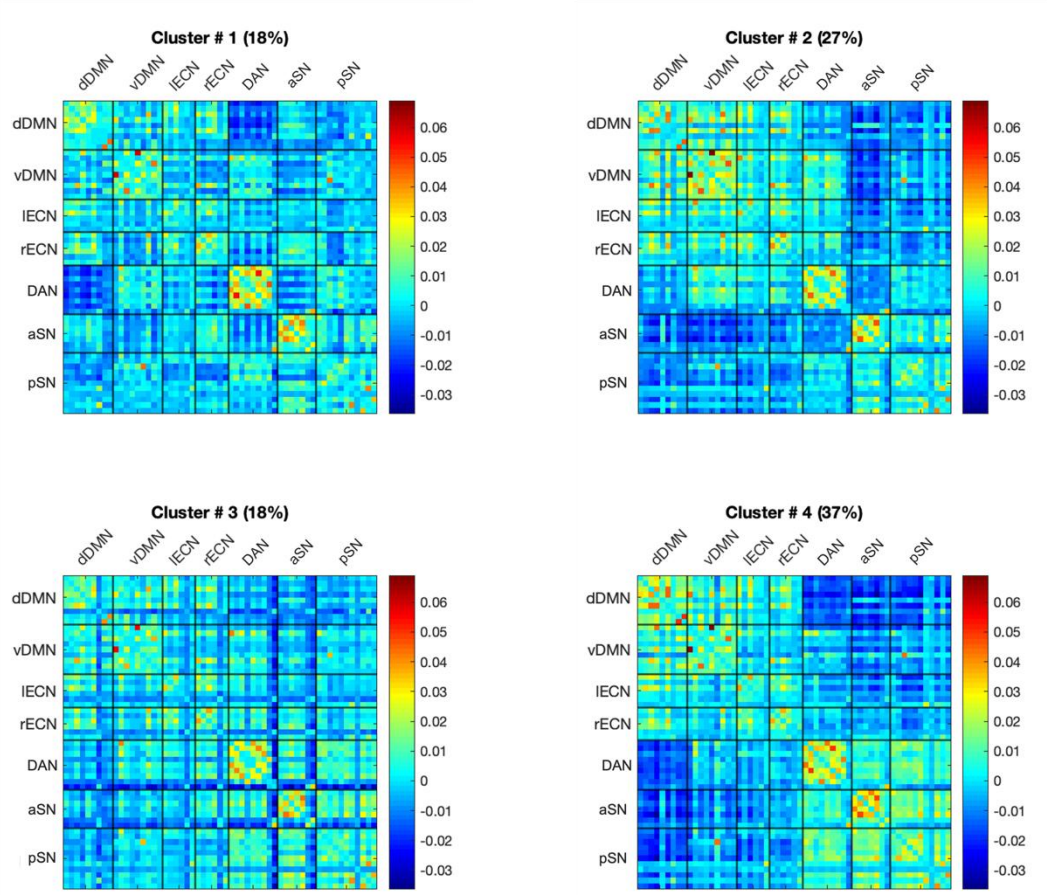

Figure 6.8. FC states obtained via K-means clustering of segmented resting-state data. Each row (and each column) displays the connectivity values between one region and the other regions of the network. Intrinsic resting-state networks (dorsal and ventral DMN, left and right ECN, DAN, anterior and posterior SN) are labelled and outlined by black lines. Abbreviations: dDMN, vDMN = dorsal and ventral Default Mode network; lECN, rECN = left and right Executive Control network; DAN = Dorsal Attention network; aSN, pSN = anterior and posterior Salience network.

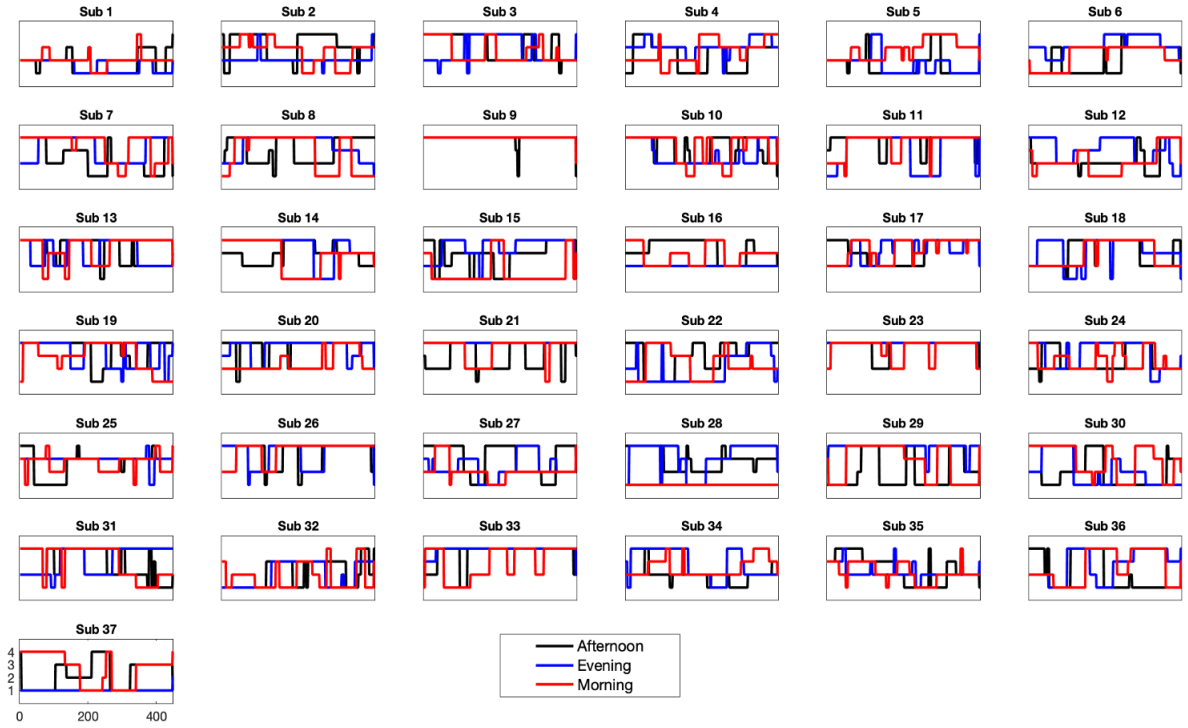

Figure 6.9. State vector indicating the FC state each segment belongs to. FC states are on the y axis, scan volumes are on the x axis. Each plot represents the vectors of one subject, with sessions coded with black (afternoon), blue (evening) and red lines (morning).

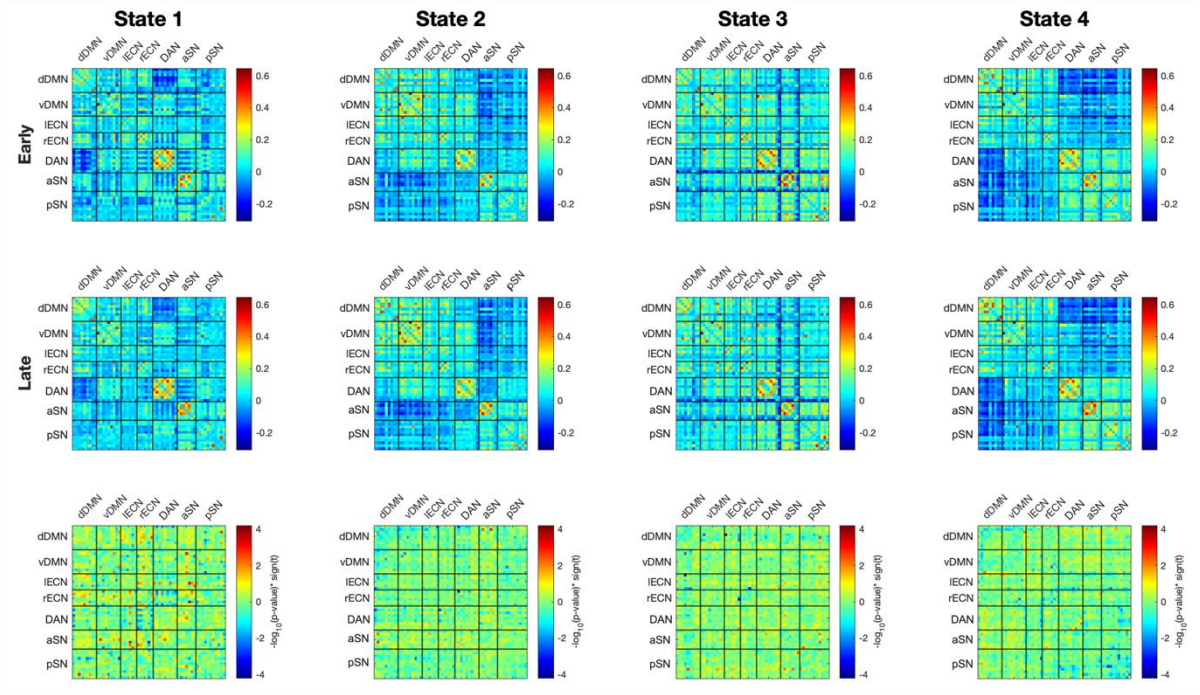

Figure 6.10. Median FC values of Early (top row) and Late (middle row) chronotypes, and the results of the T-test for each state (bottom row). Results are reported as the negative log10 of p-values (when t values > 0), as done in previous seminal papers and implemented in the GIFT toolbox (Damaraju et al., 2014). No median FC value survived the comparison upon FDR correction. Abbreviations: dDMN, vDMN = dorsal and ventral Default Mode network; lECN, rECN = left and right Executive Control network; DAN = Dorsal Attention network; aSN, pSN = anterior and posterior Salience network.

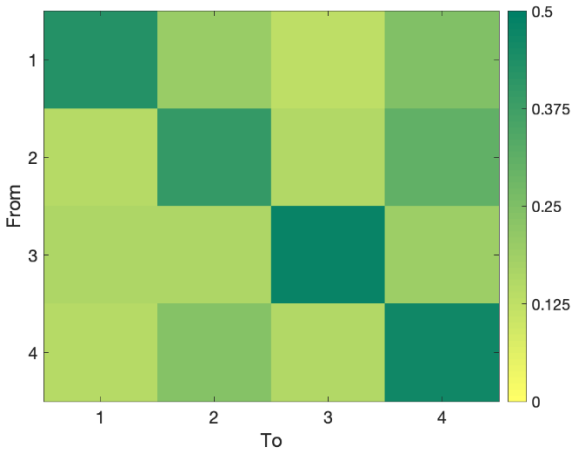

Figure 6.11. Mean group probability of transition from each FC state to the others.

6.3.4. Graph metrics

I identified a subset of nodes that displayed high centrality values in the measures we investigated (**Figure 6.12**). Overall, the right angular gyrus (belonging to the dorsal DMN) was the only node that showed values higher than 1 SD above the mean values of all nodes in all the centrality measures we investigated (degree, strength, betweenness, eigenvector, impact), as summarised in **Table 6.3**.

The right anterior insula, precuneus/posterior cingulate complex and the right superior frontal gyrus (dorsal DMN portion) also scored higher than threshold on four out of the five measures (degree, strength, betweenness and impact for the insula, and degree, betweenness, eigenvector and impact for precuneus and superior frontal gyrus).

The left angular gyrus and the medial PFC/anterior cingulate area scored 1 SD higher than the mean for degree, strength and eigenvector centrality.

Finally, the right superior and middle frontal gyrus (portions belonging to ventral DMN and ECN) scored higher than threshold on betweenness, eigenvector and impact measures.

See Figure D5 in Appendix D for the results from the same procedure over full runs (non-segmented data).

I also obtained a graphical representation of the weighted undirected graphs from each segment of each participant (see an example from one participant in **Figure 6.13**) using the R package 'qgraph' (Epskamp et al., 2012). For display purposes, I grouped portions of the same subnetworks together (e.g., ventral and dorsal DMN to form the DMN, left and right ECN to form ECN, anterior and posterior SN to form SN). This only constitutes a proof of principle and was done to demonstrate that this procedure can highlight the variations in correlation patterns within and between subnetworks at various time periods (i.e., dynamically), as informed by the change-points. See Figure D6 in Appendix D for a summary undirected graph from the stationary analysis which displays strong functional connections within the DMN as well as between the DMN and other subnetworks (in accordance with results from the segmented analysis).

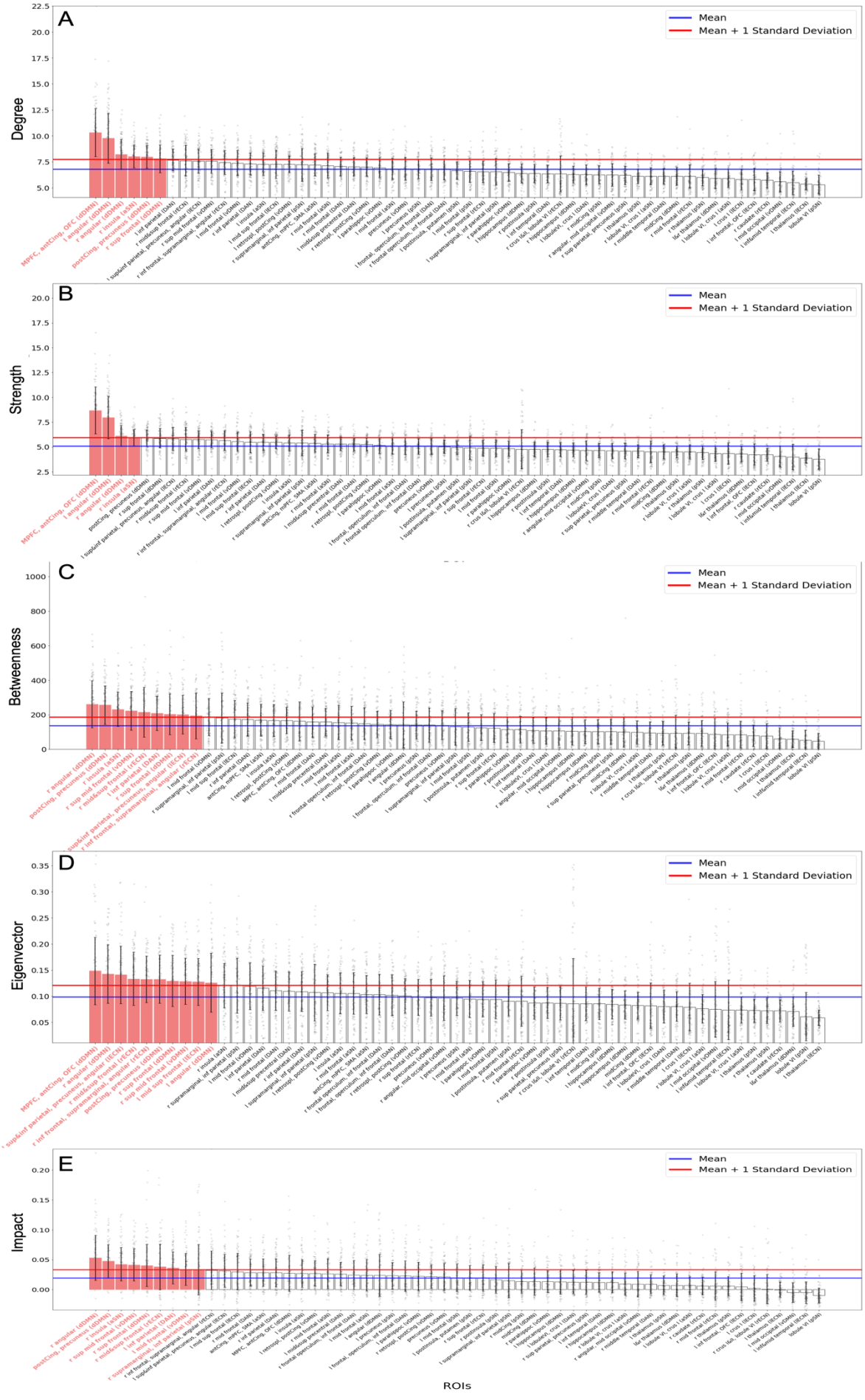
A
Degree
Mean
Mean + 1 Standard Deviation
B
Strength
C
Betweenness
D
Eigenvector
E
Impact
ROIs

Figure 6.12. Graph analysis on segmented data. Mean values of centrality measures for each of the 57 nodes (x axis), after calculating the measures for each segment of each session and subject. From the top: A) degree, B) strength, C) betweenness, D) eigenvector, E) impact. Node values were sorted in descending order to display all nodes with highest score (in red) first. The blue lines indicate the mean across nodes, and the red lines indicate 1 SD above the mean (threshold).

Region	Network	**Degree**	**Strength**	**Betweenness**	**Eigenv.**	**Impact**
mPFC / anterior Cingulate, OFC	dDMN	**X**	**X**		**X**	
right angular gyrus	dDMN	**X**	**X**	**X**	**X**	**X**
left angular gyrus	dDMN	**X**	**X**		**X**	
right anterior insula	aSN	**X**	**X**	**X**		**X**
precuneus / posterior Cingulate	dDMN	**X**		**X**	**X**	**X**
right superior frontal gyrus	dDMN	**X**		**X**	**X**	**X**
right superior & mid frontal gyrus	vDMN			**X**	**X**	**X**
mid & superior frontal gyrus	rECN			**X**	**X**	**X**
mid & superior frontal gyrus	lECN				**X**	
sup & inf parietal, precuneus, angular g	lECN			**X**	**X**	
inf frontal, supramarginal, angular g	rECN			**X**	**X**	
left inferior parietal	DAN			**X**		**X**
left mid frontal	vDMN					**X**
right supramarginal, inferior parietal	pSN					**X**

Table 6.3. Regions with values higher than 1 SD above the mean of at least one centrality measure. The table highlights which regions exceed the 1 SD threshold for which measures, summarising the main information from Figure 11. Abbreviations: dDMN, vDMN = dorsal and ventral Default Mode network; lECN, rECN = left and right Executive Control network; DAN = Dorsal Attention network; aSN, pSN = anterior and posterior Salience network.

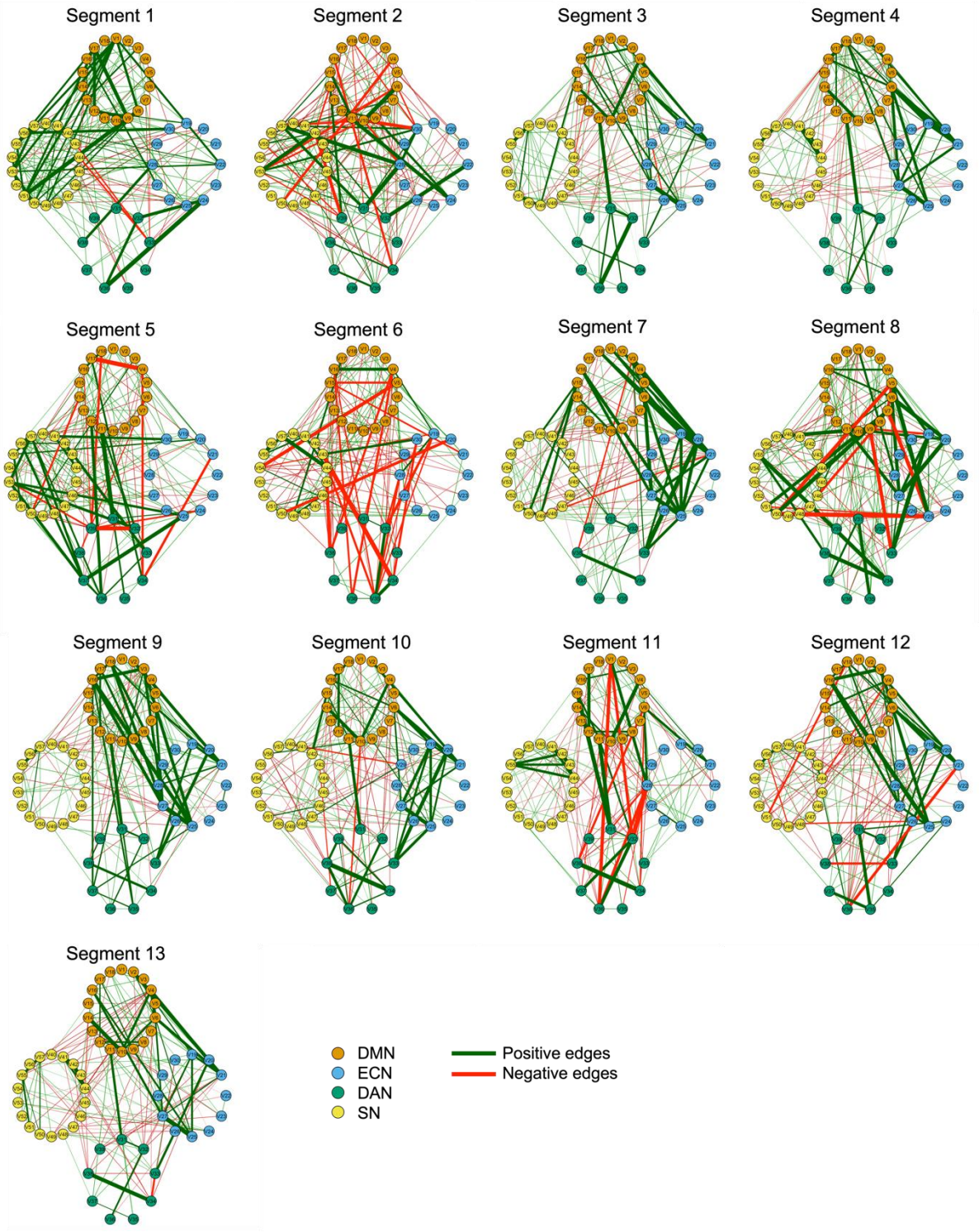

Figure 6.13. Example of weighted undirected graph from one participant (sub-08, afternoon session). Graphs were made with the R package 'qgraph' (Epskamp et al., 2012). Green edges represent positive correlation coefficients, while red edges represent negative correlation coefficients. Abbreviations: DMN = Default Mode network (both dorsal and ventral portions); ECN = Executive Control network (left and right); DAN = Dorsal Attention network; SN = Salience network (anterior and posterior

portions).

6.4. Discussion

In this study, I analysed resting-state fMRI data from participants identified as early or late chronotypes at different times of day (afternoon and evening of day 1, then morning of the following day). I first extracted 57 ROIs from 7 intrinsic networks, and identified change-points in the time-series of each individual using the novel cross-covariance isolate-detect method (CCID; Anastasiou et al., 2022). I then investigated the BOLD response associated with the change-points, as well as dynamic FC and graph measures from the segmented data. My aim was to spot and characterise the changes within and across the functional networks subserving internal and external cognition and cognitive control when unconstrained by task demands. I wanted to understand whether the MD thalamus had a role in those dynamic changes, while assessing potential variations due to arousal differences across chronotypes and time of day.

The logic behind performing change-point detection on these data was to try and identify instances of network reconfiguration during rest which, by definition, lacks specific triggering events that are identifiable a priori (Shakil et al., 2016). Since resting-state networks are thought to undergo state transitions and fluctuations that resemble those elicited by task-switching and changes in goal-directed cognitive content (Gilson et al., 2018; Gonzalez-Castillo et al., 2015; Sporns, 2018), using CCID allowed me to explore resting-state data in a way that would conceptually parallel my previous task-switching data (Chapter 4).

First, I found a uniform number and distribution of change-points across conditions. Changes occurred (on average) every minute, which sits within the range of low frequency resting-state fluctuations between 0.01 - 0.1 Hz (Fransson, 2005), suggesting CCID is capturing fluctuations traditionally associated with intrinsic neural activity (Leopold & Maier, 2012).

According to the CCID timeseries matching procedure, change-points were overall induced by widespread changes across regions (Figure 4). With regards to this, it is interesting to notice that – while different chronotypes did not differ in terms of change-

points number and distribution – they displayed somewhat different occurrence patterns at different times of day (albeit not statistically tested). Late chronotypes showed decreased exchange with the ECN with respect to early chronotypes, especially in the morning session, which might suggest the presence of less efficient communication with executive control regions, akin to the effects of sleep deprivation (Lombardo et al., 2020; Pesoli et al., 2022). Conversely, early chronotypes displayed a generally higher count of pairwise connections (i.e., richer network reorganisation during change-points), especially in the evening session and between DMN and DAN. I speculate that this could relate to the increased network integration normally occurring in the evening due to the circadian fluctuations of resting-state activity (Farahani et al., 2022).

Unexpectedly, the GLM analysis did not return significant results after the correction for multiple comparisons, and generally showed very little activation both when comparing and averaging across groups/sessions, even at a liberal threshold of $p<.001$ uncorrected. Despite the scarce findings, I wish to briefly comment on the (uncorrected) group activation after averaging across participants and sessions (Figure 6). This was initially located around the bilateral anterior cingulate and right anterior insular cortices (3, 2 and 1 TR before each change-point), as well as the right mediodorsal thalamus (1 TR before each change-point). During change-points, activation shifted towards left mid cingulate cortex and bilateral ventral precuneus, and finally towards the right angular gyrus 1 TR after the changes. Although this evidence only comes from weak BOLD activation in distinct GLMs, I speculate such sequential activity patterns might reflect the interlinked communication across regions which gives rise to broad network reconfigurations during change-points. Anterior cingulate and insula constitute the main components of SN, and are tightly connected with mediodorsal thalamus and precuneus, as well as other frontoparietal regions (K. Li et al., 2022; Menon & Uddin, 2010; Sridharan et al., 2008). The mid cingulate cortex is also connected to specific portions of the anterior insula, and was shown to respond to monitoring of the environment, response selection and task-set implementation (Jamadar et al., 2010; K. S. Taylor et al., 2009). Finally, the ventral precuneus contains a wide network of connections, including mid cingulate and insular cortices, thalamus and angular gyrus (Zhang & Li, 2012).

I believe the generally weak activation in the GLMs might be due to the fact that, by averaging across all change-points, I joined together events that actually involved a number of different regions, and thus obtained no clearcut activity patterns (i.e., not all change points will be associated with activity or FC changes in the same regions). This would also align with the findings from the CCID timeseries matching procedure, showing multiple pairwise connections associated with the change-points (although I would expect some to be more important or driving than others). Moreover, despite including a high number of regions and obtaining a higher number of change-points per subject compared to previous research (Anastasiou et al., 2022; Mancho-Fora, Montalà-Flaquer, Farràs-Permanyer, Zarabozo-Hurtado, et al., 2020), I had to average across ~14 datapoints per participant, which might not be enough to obtain strong activation (i.e., low number of events). In other words, the lack of significant results might be due to the presence of few change-points emerging from a multitude of brain changes. A possible solution for future research would be to employ longer runs with shorter TRs which would allow to gather more datapoints and identify more change-points. These could then be divided into groups according to the type of pairwise changes associated with them (e.g., within networks, across DMN and attentional networks, and so on), something I was not able to do here due to the small number of events. In addition, since CCID constitutes a novel approach to finding onsets for GLM analysis, I had no a priori knowledge on how to select the onsets in relation to change-points, e.g., whether to average across a few TRs around the change-points (and how many), or if to search for relevant activation before the changes (and how long before). I thus opted for testing out 5 different events in an exploratory manner (3 TRs, 2 TRs and 1 TR before each change-point, on the change-points and 1 TR after each change-point).
Future research might attempt other solutions (e.g., averaging across multiple TRs and/or comparing the activation before and after change-points).

As a second analysis, I investigated dynamic FC within temporal segments defined by the change points. Using k-means clustering, I identified 4 FC states recurring among the segmented data and found patterns of positive and negative correlations that have been previously linked with functional brain reorganisation (Allen et al., 2012). State 1 was mostly characterised by a positive correlation within DMN, DAN and SN, and a negative correlation between DAN and dorsal DMN, in accordance with traditional

accounts supporting the anticorrelation between these two networks (Fox et al., 2005). States 2 and 4 instead showed a pattern of positive correlation between DMN subnetworks and ECN, both anticorrelated with anterior and posterior SN. This seems to contrast with the traditional tripartite model that predicts an anticorrelation between DMN and ECN (Menon & Uddin, 2010; Sridharan et al., 2008), in favour of a more variable pattern of co-activation and disengagement of these networks, mediating changes in cognitive content (Chang & Glover, 2010; Kelly et al., 2008b; Pessoa, 2014). The main difference between States 2 and 4 resides in the correlations with the DAN, first weakly anticorrelated with DMN and anterior SN while positively correlated with ECN (State 2), then anticorrelated with both DMN and ECN but positively correlated with SN (State 4). Taking this evidence together, I could speculate a relationship between the strength of DMN-DAN anticorrelation and the correlation between SN and DAN, in accordance with studies on sustained attention and mind-wandering (Gao & Lin, 2012; Kucyi et al., 2016). State 3 was instead characterised by generally weak correlations across the network, except for a marked negative correlation between subcortical (cerebellum and thalamus) and cortical regions. This might resemble the states found by Allen et al. (2012), hiding a positive correlation between those subcortical regions and somatosensory cortices (which I did not include in our analysis). These states were not significantly different across chronotypes or time of day, indicating that the dynamic FC patterns in these high-order networks are mainly preserved in healthy participants who only differ by chronotype.
All in all, I did not observe relevant differences in change-points distribution, BOLD activity or dynamic FC between conditions (chronotype and their interaction with time of day). The literature on the effects of chronotype and circadian rhythms on resting-state brain activity is scarce, very recent, and presents mixed results. Some studies reported changes in stationary DMN connectivity in late chronotypes (Facer-Childs et al., 2019), while other studies only found FC changes due to circadian rhythms, but not due to chronotype (Fafrowicz et al., 2019; Farahani et al., 2022). Based on our results, we argue that different chronotypes still share similar resting-state brain dynamics. More subtle differences in brain activity linked to sleep debt in late chronotypes might however emerge with task-fMRI designs, in the presence of cognitive and attentional effort (Fafrowicz et al., 2009; Schmidt et al., 2015). In this regard, an interesting future development would be to test our task-switching paradigm on early and late chronotypes, in order to investigate connectivity differences while

they explicitly engage in cognitive switching between attentional and introspective tasks (respectively engaging DAN and DMN networks as shown in Chapter 4). A similar study using well-rested and sleep deprived individuals was indeed part of the pre-COVID plans for this thesis.

In the graph analysis, I found that regions mostly belonging to the dorsal DMN network such as medial PFC, bilateral angular gyrus, precuneus/posterior cingulate complex and right superior frontal gyrus displayed higher centrality values than the rest of the nodes. The right anterior insula was also prevalent in almost all measures (degree, strength, betweenness, impact). However, against my predictions, the thalamus did not present high centrality characteristics. Previous studies employing voxel-wise graph theory techniques also identified portions of the DMN, anterior insula and frontal cortex as globally connected hubs, and described subcortical regions as weak segregated hubs with shorter connections (Tomasi & Volkow, 2011; van den Heuvel et al., 2012). Within the DMN, precuneus, angular gyrus and mPFC were often reported as prominent cortical hubs with high global brain connectivity (Buckner et al., 2009; Cole et al., 2010; Tomasi & Volkow, 2011). In particular, the precuneus was appointed as the most connected hub in previous studies (Tomasi & Volkow, 2011), and its connectivity with portions of the superior frontal gyrus were shown to flexibly change between task and rest (Ciuciu et al., 2014). Relatedly, the superior frontal gyrus is thought to be a key node of the DMN, with connections to multiple frontoparietal regions linked to executive control functions (Spreng et al., 2013). Similarly, the anterior insula is known to have a flexible connectivity profile which enables the interface between other high-order resting-state networks (DMN and ECN/DAN; Gao & Lin, 2012; Menon & Uddin, 2010), with some studies proposing the role of causal outflow hub, transiently coupling with a variety of cortical and subcortical regions (Molnar-Szakacs & Uddin, 2022; Nomi et al., 2016). Instead, the results on subcortical hubs in the literature are mixed, with some describing subcortical regions as weak segregated hubs (Tomasi & Volkow, 2011), and others showing hub properties in portions of thalamus, cerebellum and basal ganglia (Cole et al., 2010; van den Heuvel & Sporns, 2011). We could speculate that the reason why we saw higher centrality measures in DMN here (instead of thalamic regions and more prevalently than SN regions) is because we performed our graph analysis on the segments between change-points. Another option would have been to take segments

around each change-point and focus on known periods of network reconfiguration, although with the added issue of choosing how many datapoints to include around each change-point. Given the current evidence, I am tempted to speculate that, while regions such as insula, thalamus and precuneus might serve as hubs during network reconfiguration (BOLD response few TRs before and during change-points), a great deal of information is received and integrated by the DMN on the longer run (between change-points), as shown by the activation of the angular gyrus right after each change-point. This aligns with effective connectivity and graph theory studies which identified insula and other executive control regions as 'driving' hubs, and DMN regions (including right angular gyrus, but particularly precuneus) as 'driven' hubs that receive information from other regions (Liao et al., 2011; Yan & He, 2011). In particular, the right angular gyrus (which scored high in all centrality measures) has been previously defined as a cross-modal hub integrating multisensory information with predictions from prior experience, and being linked with a plethora of cognitive functions such as manipulation of mental representations, semantic and memory processing (Seghier, 2013; Wei et al., 2019). Moreover, different subnuclei in the angular gyrus showed preferential structural connectivity towards other DMN regions (posterior portion) or regions of the attentional network (anterior portion) (Uddin et al., 2010), supporting the current interpretation based on centrality measures and BOLD activation.

As a quality check, I performed a stationary (non-segmented) version of the graph analysis and observed that the range of values of all graph measures were similar, and that the right angular gyrus showed high centrality values in both versions, with some minor differences in the order/values of other regions. Perhaps my segmented approach has the advantage of weighting and highlighting the nodes that are more important for each network reconfiguration (i.e., after each change-point). Future work should attempt to perform a 'more dynamic' version of this analysis, e.g., by assessing the timeseries resulting from tracking the changes in graph metrics over time (Sporns, 2018). However, as there is currently a lack of examples on how to employ (group-level) dynamic graph theory to change-point detection, this study constitutes a first exploration in that direction.

There are a few general limitations to the use of change-point detection that should be considered when interpreting these results.

For this study, I selected a change-point detection method (CCID) that would allow me to find “switch points” across pairs of regions in a data-driven manner. While very promising, there are still uncertainties regarding the optimisation of change-point detection techniques for group-level analyses of neuroimaging data (Cribben et al., 2013; Lindquist et al., 2007). This study was thus exploratory and comprised a range of different measures (GLM, dynamic FC, graph theory) that I felt could provide a more complete characterisation of brain dynamics under change-point detection.

Moreover, while CCID resolves the main disadvantage of the sliding windows approach (fixed window length selected a priori), it includes the possibility to choose the minimum distance between change-points, which introduces another type of arbitrary parameter choice. Other researchers selected wider gaps between change-points (Mancho-Fora, Montalà-Flaquer, Farràs-Permanyer, Zarabozo-Hurtado, et al., 2020). I opted for a minimum distance of 10 s (5 TRs) in order to account for the sluggishness of the BOLD response (Buxton et al., 2004), and did not choose a larger distance in order to balance between having meaningful data segments and having enough change-points, while not excessively constraining the detection (which in the case of CCID is purposefully made to detect potential transient changes of small magnitude; Anastasiou et al., 2022) in the absence of strong reasons for it. In any case, the distance between the resulting change-points was on average above 30 TRs (~60 s), which is within the recommended range for performing meaningful dynamic FC analyses with standard approaches (Leonardi & Van De Ville, 2015). Further attempts should still aim at exploring how different choices for this parameter affect results.

An alternative solution that could solve some of the issues highlighted in this discussion (while overcoming the limitations of standard dynamic FC approaches) is the use of Hidden Markov Models (HMM). HMM are probabilistic generative models that employ Bayesian inference to infer reoccurring correlation patterns (brain states) at fast and unconstrained temporal scales (Vidaurre et al., 2017). Future studies could employ HMM instead of or in addition to change-point detection to better characterise the switches across large-scale networks, and in particular their temporal organisation (Vidaurre et al., 2017).

6.5. Conclusions

Overall, I employed a data-driven approach for the identification of changes in brain functional connectivity common to and across different times of day in healthy participants identified as early and late chronotypes. I used this information to analyse the BOLD changes across large-scale networks and their dynamic functional connectivity using different methodological approaches (k-means, graph measures). Results show no differences across chronotypes at different times of day, and demonstrate weak common activation around the change-points (involving MD thalamus, precuneus and SN regions) as well as dynamic FC patterns and graph measures. Despite some inconsistent results, I demonstrate that change-point detection could potentially provide additional useful information after further exploration of this technique.

Chapter 7

CHAPTER 7 : GENERAL DISCUSSION

7.1 Summary of aims and results

This thesis aimed to investigate the behavioural and neural correlates of cognitive switching across self-referential processes and processing of external stimulus features. While it is well accepted that our brain constantly shifts between internal and external monitoring both during tasks as well as at rest, no task-switching studies have looked at performance and brain changes when switching from and to self-referential processing. Using two task designs that I developed, I focused on analysing the behavioural performance (Chapters 3 and 5) and the preparatory fMRI activity (Chapter 4) associated with switching not only within externally oriented tasks, but also within self-referential tasks and between these two domains. In Chapter 3 and 4 I employed a cued task-switching paradigm which included two self-referential (personality and bodily sensations judgements) and two externally oriented (vowel and consonant identification) tasks on written trait and bodily adjectives. In Chapter 5, I used the same paradigm structure, but with pleasantness and self-reference judgments, and indoor/outdoor and nature/man-made discrimination of pictorial stimuli. In all studies, I found higher RTs for switches compared to repetitions, in both external and internal domains. I also found an interaction between domain and trial type for which tasks in the external domain displayed greater switch costs than those in the internal domain. In Chapter 3 I also found greater switch costs for between-domain switches compared to switches within each domain, but did not replicate this in Chapters 4 and 5. All four types of switch costs were significant, including those within the internal domain in all 3 Chapters.

In terms of fMRI activation, in Chapter 4 I found that preparing to perform internal tasks activated a set of DMN regions as compared to preparing for external tasks, regardless of trial type. Conversely, preparing to perform external tasks activated DAN regions, as compared to internal tasks. Overall, switch preparation activated left-lateralised DAN regions with more ventrolateral peaks as well as dorsal precuneus, posterior cingulate and SMA. Preparing towards all switch types (within each domain, and between domains) always activated the left dorsal precuneus. Comparing across

switch types (between and within domains) did not return major cortical clusters of activation.

In addition to the task studies, I explored whether I could define and investigate the switches across frontoparietal networks underlying internal and external cognition during resting-state, using change-point detection and subsequent GLM and functional connectivity analyses (Chapter 6). To this end, I used a dataset of resting-state data from early and late chronotypes at three different times of day (afternoon, evening and morning). This allowed me to also investigate the potential influence of sleep preference and (indirectly) of related chronic sleep restrictions on network dynamics, in lieu of studying arousal with sleep deprivation as per the original plans before COVID-19. I successfully identified “switch points” among regions of the high-order frontoparietal networks involved in external and internal cognition and cognitive control (approximately 14 change-points per participant). When using the change-points as GLM onsets, no clusters survived correction, but I nonetheless observed interesting uncorrected activation which started in SN regions (anterior/mid cingulate and insular cortices), mediodorsal thalamus, and then transferred to DMN regions (ventral precuneus and angular gyrus). Moreover, 4 FC states emerged from the dynamic FC analysis, picturing a variable correlation pattern between SN and the other networks, between DMN and DAN/ECN, and between cortical and subcortical regions. Finally, the graph analysis revealed high centrality measures in DMN regions and right anterior insula. Overall, there were no significant differences across chronotypes in any of the above measures, indicating the observed network change properties were not influenced by sleep preference.

7.2 Interpretation of results

7.2.1 Cognitive flexibility and self-referential processing

In all three task studies (Chapters 3-5), I found increased RTs when participants switched across tasks as compared to repeating the same task, and found that this held true for each switch type across domains (within external tasks, within internal tasks, from external to internal and vice versa). The presence of switch costs to the

internal domain and their smaller magnitude relative to costs in the external domain appear to be reliable effects since I have replicated them in two different paradigms with different tasks and stimuli (Chapters 3-4 vs 5), both online and in-person (Chapters 3 and 5 vs 4). This demonstrates the presence of switch costs in self-referential processing for the first time, suggesting that the control of this type of internal process follows similar (although not identical) dynamics to the control of external processes, thus highlighting the presence of a common control system for internal and external processes, as well as potentially domain-specific control features. This suggestion aligns with findings from the neuroimaging literature which report preparatory activation in frontoparietal areas, modulated by the types of switching and tasks involved (Chiu & Yantis, 2009; Ruge et al., 2013), and with the well-known distinction between the functional networks underlying external and internal processing (Dixon et al., 2017; Vanhaudenhuyse et al., 2011). The neuroimaging results I observed in Chapter 4 in fact support this view: they show domain-specific activation in preparation of external and internal tasks (regardless of trial type), along with a dynamic pattern of causal directed communication across regions from DAN/ECN and DMN depending on domain and trial type (as found by DCM). Relatedly, I found common activation in preparation of switches to either domain mainly in dorsal precuneus and IPL, which clearly reflects a general involvement of working memory (DAN) and executive control regions (dorsal precuneus, IFG) while participants retain information on which task to perform, and prepare to execute it. In particular, the omnipresent engagement of the dorsal precuneus in all types of switch preparation suggests an important role of this region in supporting general cognitive control, specifically in the context of switching across external and internal domains.

Overall, these studies represent a useful addition to the fields of self-processing as well as task-switching. Similarly, I expanded on the study of task-switching by addressing the scarce focus on the shifts within and between internal and external domains, incorporating self-reflection in the investigation of cognitive flexibility. In particular, investigating self-referential cognition from a goal-directed perspective, instead of solely viewing it as a process that is detached from and/or unrelated to the current situation, allows to obtain additional information regarding its function in every-day life and its integration with external signals. The constant shift between external

and internal monitoring and the anticorrelation between the underlying networks are well-established phenomena, but internal cognition has been often studied within resting-state or inattentive state (e.g., mind-wandering) contexts, in contrast to adaptive and goal-directed cognition. Still, both external and internal information are required for guiding behaviour in every-day life. These two views do not oppose each other, but rather look at a very complex and non-trivial process from different perspectives. Previous literature indeed suggests that internal and external information can compete with each other in certain instances, but might require integration and interaction in other occasions (e.g. biasing of external attention by episodic memory, creative thinking, mentalizing; Dixon et al., 2014). In fact, while a plethora of studies described DMN functions as mainly stimulus-independent and spontaneous (Christoff et al., 2009; Greicius et al., 2003), others also highlighted that the wide variety of processes subserved by DMN have an important role in decision making processes. For instance, autobiographical memory and planning, as well as social cognition all require some degree of internal focus while highly contributing to guiding adaptive behaviour (Smallwood et al., 2021; Spreng et al., 2010). Further examples of this include circumstances such as meditation, where the introspective sphere becomes the focus of goal-directed attention and cognition, in some cases reducing the anticorrelation between DMN and DAN (Josipovic et al., 2012).

7.2.2 Theoretical considerations

From a theoretical perspective, studies on behavioural switch costs associated the increased RTs after switching with either reconfiguration of the new task-set, interference from previous irrelevant task-sets, or a mixture of both processes (Vandierendonck et al., 2010). Recent studies suggested a hybrid account including reconfiguration and interference as two slides of the same coin as the most exhaustive. Given that I employed variable jittered CTIs, although these experiments were not designed to discriminate across theoretical frameworks, I can speculate that the behavioural effects I observed are more likely related to a mixture of residual, unfinished and/or delayed configuration processes (S. Brown et al., 2006), since participants were not able to establish a specific control strategy due to the unexpected length of intervals (De Baene & Brass, 2014; Vandierendonck et al., 2010). The GLM

results in Chapter 4 showed clear advanced preparation in regions traditionally associated with either external or internal processing, suggesting the presence of a reconfiguration process activating task goals and features of the upcoming task (Slagter et al., 2007; Wylie et al., 2006). Additionally though, switching across the two domains (internal to external and vice versa) potentially included residual activation from the irrelevant domain. Moreover, DCM results display an intriguing balance between excitation of task-relevant regions and inhibition of task-irrelevant ones. For instance, the model suggested inhibitory inputs enter in DAN parietal areas and exert inhibitory modulations among DAN areas during preparation of internal task repetitions, possibly indicating a successfully suppressed interference from irrelevant task representations. Therefore, it is plausible to speculate the presence of both reconfiguration and interference contributions during switch preparation.

7.2.3 Switching across and within domains: the role of task parameters

When I explored the possible presence of additional costs when switching across domains as compared to within each domain, only the first behavioural study (Chapter 3) returned significant results. The fMRI study (Chapter 4) showed a trend in the expected direction, but the second behavioural study (Chapter 5) even showed anecdotal Bayesian evidence for the null hypothesis. Initially, the promising results from the first study suggested that additional reconfiguration steps were taking place during switches across domains. Specifically, I speculated that the additional time could reflect the more effortful switch across domain-specific systems, possibly mediated by a domain-general control. However, taking all results together, I cannot draw definite conclusions about the additional costs of switching between domains. Instead, the mixed results obtained across the three studies suggest that differences in the task requirements across external and internal tasks may have driven the additional costs. First of all, the neuroimaging findings in Chapter 4 show very weak differences across switch types (when directly comparing switches within and between domains). While this might be due to the small number of trials, it could also potentially suggest differences in exogenous reconfiguration (i.e., post-stimulus task-rule activation) rather than differences in advanced preparation. In fact, in previous studies, different types of task-switching (i.e., switching across S-R mappings and switching

across visual stimulus features) displayed the same cue-locked ERPs while showing differential stimulus-locked ERPs, suggesting task parameters might affect task execution more (Rushworth et al., 2002, 2005).

It is possible that differences in task similarity, as defined by the amount of processing components shared by tasks (Arrington et al., 2003) have influenced these differences in the results across the chapters. Specifically, in the study design I employed in Chapters 3 and 4, there is likely an aspect of task similarity within domains and dissimilarity across domains, as the two external tasks both involve low-level letter identification while the two internal tasks involve higher-level semantic judgements. This imbalance, rather than a true difference between internal and external processing, might have potentially driven the effects of between-domain switching (i.e., additional costs). While such imbalance might be partially intrinsic to the definition of internal and external domain in certain cases, there might also be ways to improve the task similarity in terms of stimulus processing across the two domains. This is in fact the main reason I developed the second task paradigm, which I used in Chapter 5. Specifically, I used pictures due to the availability in the literature of validated tasks involving semantic stimulus encoding, e.g., employing indoor/outdoor, living/non-living and natural/man-made discrimination tasks on complex pictures (Dosenbach et al., 2006; Gusnard et al., 2001; R. Smith et al., 2016). However, while pictorial stimuli allowed me to overcome the processing dissimilarity issue, they introduced a greater imbalance in task difficulty (as measured by RTs in task repetitions). This could be due to the fact that pictures required further interpretation in the case of subjective self-referential tasks, as compared to more immediate scene classification based on objective scene features. Moreover, pictures potentially have a higher number of cognitive and attentional affordances and induce stronger imagery than words (Holmes et al., 2008; Wilford et al., 2021), especially in the case of complex photographs as used in Chapter 5. This might have introduced more variability in the way participants perform the tasks (e.g. in terms of strategy, focus points,...), especially in the case of subjective judgments like pleasantness and relatedness. Perhaps future studies could explore the possibility to use externally oriented semantic tasks with word stimuli too, for instance by expanding on the list of trait stimuli to include adjectives related to specific ‘external’ sensory modalities. This would allow the use of semantic discrimination tasks in the external condition as well (e.g. “does it relate to vision?” versus “does it relate to hearing?” on words like ‘bright’, ‘small’, ‘loud’,

‘noisy’, etc...), but would require further complication of the design: since the words suggested above cannot be used for internally oriented tasks, the stimuli in this paradigm would have to consist of pairs of words (one for the external and one for the internal conditions), and participants might have to understand which word to attend to based on task instructions. If tested and refined, this might still help with overcoming the dissimilarity across domains while using simple and versatile word stimuli. All these considerations highlight the inherent difficulty of carefully balancing a task design which tries to merge processes that are greatly different by nature.

7.2.4 Goal-directed vs spontaneous switching and thalamic contributions

Further to the task-switching approach, I also explored network changes at rest using change-point detection (Chapter 6). By focusing my analysis on ROIs from high-order networks involved in external and internal cognition and cognitive control, I detected change-points related to changes in pairwise connectivity within and between those networks. The findings from this work are largely different from those of Chapter 4, as it is to be expected due to the differences in brain states (task vs rest) and analytical approaches. Specifically, in Chapter 4 I observed strong activation of specific dorsal parietal regions (e.g., left IPL) and precuneus, which is likely specialised to the context of switching across goal-directed external and internal tasks with advanced preparation. Instead, in Chapter 6 I found weak evidence of a common activation pattern in SN and DMN regions around network change-points. This highlights the flexibility of our cognitive and neural system in adapting to different global and directed states, despite the involvement of similar networks or regions. In fact, according to influential neuroscientific viewpoints (McIntosh, 2004; Pessoa, 2014), the functional engagement of regions (and consequent creation of functional networks and subnetworks) likely adapts based on the context in which they are operating, giving rise to multiple intersecting network configurations.

It is worth highlighting that in both task and rest studies (Chapters 4 and 6), I expected to find an involvement of the MD thalamus in switching across cognitive domains and across networks. This hypothesis stemmed from its widespread connections to high-order networks, especially SN and DMN (Hwang et al., 2017; Li et al., 2022), and convincing evidence from animal studies (and some evidence from humans)

implicating this nucleus in cognitive flexibility, working memory and decision-making (Monchi et al., 2001; Peräkylä et al., 2017; Pergola et al., 2018; Rikhye et al., 2018). However, we only found a small cluster of activation in ventrolateral thalamus in preparation of external switches (Chapter 4), and a few voxels (uncorrected) activating in 1 TR before resting-state change-points (Chapter 6). The former hints at a possible involvement of the thalamus in relation to working memory updates. The latter could hint at an early engagement of the SN in initiating broad network reconfiguration, which would then travel to the MD thalamus and further passed to DMN regions (as discussed in Chapter 6). Such a pattern could indicate that cortico-cortical resting-state communication is mediated by the thalamus, as suggested by Hwang and colleagues which described the thalamus as an integrative hub for a variety of brain networks and cognitive functions (Hwang et al., 2017). I can further speculate that a similar mechanism might be taking place during cognitive switching (Chapter 4), where perhaps the transient contribution of the MD thalamus is simply weaker and less detectable than steady cortical responses.

The lack of stronger activation patterns in Chapter 6 might respond to averaging across multiple different changes which are not necessarily driven or preceded by the same exact activations. While it is possible that the mediodorsal thalamus is truly not (or scarcely) engaged in switching dynamics, or that our study designs could not optimally capture its transient contribution, the difficulties associated with imaging this region might have also affected the results. It has been previously suggested that thalamic activation is transient and not often detected due to the sluggishness of the canonical HRF and other limitations of functional MR imaging of subcortical structures (Isherwood et al., 2021; Lewis et al., 2015; R. Li et al., 2021). In fact, activity in subcortical structures is more difficult to capture than in cortical regions due to their smaller size, their greater susceptibility to physiological noise, and their reduced signal-to-noise ratio due to the distance from receiver coils (Forstmann et al., 2017; Lewis et al., 2018; Risk et al., 2021; Sclocco et al., 2018). While there are specific MRI sequence parameters that can be adopted to increase the signal-to-noise ratio in the thalamus (e.g., restricting the field of view), these would in turn detriment the imaging of cortical areas, making them unsuitable for the mechanistic study of thalamocortical communication (particularly with frontoparietal networks) that are of interest here (Risk et al., 2021). Moreover, subcortical structures like thalamus and basal ganglia show substantial variations in HRF speed, amplitude and nonlinearity (Lewis et al., 2018;

Yen et al., 2011). For instance, in the visual system, superior colliculus and lateral geniculate nucleus were found to follow a faster and narrower HRF as compared to V1 (Lewis et al., 2018). The presence of different HRF in subcortical areas is thought to influence both fast event-related task designs as well as resting-state functional connectivity studies (Lewis et al., 2018; Wager et al., 2005). In fact, faster HRFs were shown to increase the frequency power of the resting-state BOLD signal beyond the typical 0.1 Hz cut-off (J. E. Chen & Glover, 2015), possibly leading to incorrect assumptions and false negatives (Handwerker et al., 2004; Lindquist et al., 2009). This might have potentially concealed a stronger thalamic activation in my resting-state analysis (Chapter 6), given the low-pass filter to 0.1 Hz. I nonetheless opted for the use of the canonical HRF in my GLM analyses as per the majority of studies in the literature, so that the results from our novel task design (Chapter 4) and analyses (Chapter 6) would be comparable to previous work. However, future studies that aim at investigating thalamic functions should try to estimate the HRF magnitude, latency and duration to boost statistical power, for instance by using a finite impulse response basis set or non-linear techniques (e.g., inverse logit model), as suggested by previous methodological comparisons (Lindquist et al., 2009).

7.2.5 Effects of chronotype on resting-state reconfiguration

The activation and connectivity states discussed in Chapter 6 did not appear to change significantly between early and late chronotypes at different times of day (except for a few uncorrected voxels). I was interested in understanding whether the chronic sleep restriction that is usually observed in late chronotypes (especially in morning hours) might have an impact on brain dynamics, akin to sleep deprivation. This is particularly important since the literature on brain changes in this regard is recent and, despite the ongoing interest on this topic, there are still scarce findings available. To the best of my knowledge, there are no chronotype studies using dynamic FC or change-point detection, but only static FC or whole-brain activation approaches (Facer-Childs et al., 2019; Horne & Norbury, 2018; Tian et al., 2020). Previous findings on this same dataset indicated increased static connectivity among DMN regions, regions of the motor network, and increased connectivity between DMN and SN in early chronotypes as compared to late chronotypes (Facer-Childs et al., 2019, 2021). However, the

results in Chapter 6 appear to suggest that these overall differences do not automatically translate into transient differences in activation or dynamic states. Another explanation is that change-point detection in this case was not suitable to fully capture the potential dynamic differences across chronotypes. Further research on this intriguing question is still needed, as well as research establishing whether extreme chronotypes present signs of brain changes related to chronic sleep loss or disturbances.

7.3 Limitations

In addition to the above-mentioned considerations regarding differences in stimulus processing and difficulty across domains, and the difficulties of imaging the thalamus with fMRI, there are some further methodological considerations and limitations related to the empirical chapters in this thesis.

First, as discussed earlier, both the study designs I developed (Chapter 3 and 5) suffer from an imbalance in task difficulty which, despite the mixed findings, was shown to influence switch costs (Rubinstein et al., 2001; Yeung & Monsell, 2003). In this thesis I controlled for task difficulty with additional analyses, but future studies should aim at solving or minimising the issue. For instance, akin to what done by (Verschooren, Schindler et al., 2019) a possibility would be to have a block design in which half blocks focus on switches towards one domain only (either external or internal) and the other half focus on switches towards the other domain. Specifically, half of the blocks would allow the comparison of behavioural performances to the same internally oriented task after a repetition, a within-domain switch or a between-domain switch, while the other half would allow the same comparison but in the external domain. However, while minimising the issue of task difficulty (as the analyses would focus on the performance to one task only in each domain), this design would not allow to directly compare the two domains (i.e., switches within the internal domain cannot be compared to switches within the external domain, and same for between-domain switches).

Second, I kept a jittered and highly variable CTI in all three Chapters to keep consistency across studies, as this was needed in the fMRI study to allow a proper separation between cue-related and stimulus-related activation (De Baene & Brass,

2011; Sidlauskaite et al., 2014). While I found that this choice of CTI did not affect the interaction between domain and switch costs, the presence of long CTIs did reduce the overall magnitude of switch costs, as expected (Monsell, 2003). Future work that might specifically focus on behavioural performances and not on neural correlates could make use of shorter and more uniform CTIs to allow for more consistent and robust switch costs beyond residual costs (Kiesel et al., 2010).

In terms of analytical considerations, I employed repeated measures ANOVA and T-tests for my behavioural analyses. This choice was guided by the overarching presence of ANOVA approaches in the psychological and neuroscientific literature (including that of task-switching studies, e.g., Verschooren, Schindler et al., 2019), as well as by the simplicity and reliability of these models (V. A. Brown, 2021). However, in recent years there has been a general shift in the scientific community towards the use of general linear mixed models (LMM), slowly taking hold in psychology too. In rmANOVA, data from multiple trials are aggregated together and the focus is on the difference across means, which however leads to losing some valuable information about the variability within participants or trials (V. A. Brown, 2021). Instead, LMMs allow to analyse conditions of interest (fixed factors) while concurrently considering the variability within and between participants (or trials) by including random factors (V. A. Brown, 2021; Magezi, 2015). As a result, while ANOVA focuses on quantitative differences between conditions under multiple strict assumptions (e.g., sphericity and no missing data, beyond the basic common assumptions in all linear regression models), LMMs can be used to emphasise individual patterns of change and model individual differences, while also accommodating for missing or unbalanced data (Hesselmann, 2018; Krueger & Tian, 2004). LMMs are thus more flexible than rmANOVA but also more complex, and require careful non-trivial considerations prior to fitting (e.g. when and if to model a variable with random intercept and/or slope) as well as when interpreting results (Magezi, 2015). In certain conditions, non-optimal LMM models were shown to yield more false positive results than rmANOVA (Hesselmann, 2018). Our analysis choices were made at the point of pre-registration, opting for the use of more trivial methods given the novelty of task designs and research questions. Future studies could however explore LMMs, which would allow the inclusion of single-trial RTs (or switch costs) and for the modelling of participants as random effects.

It is also worth mentioning some key limitations regarding the use of DCM. Like most modelling approaches, DCM results and their validity highly depend on the initial feature selection and model definition (e.g., selection of number and size of ROIs, model space and parameters), and thus requires careful considerations about study design and research questions (Daunizeau et al., 2011). In particular, choosing of a model set is increasingly difficult the more ROIs are included in the model (as the degrees of freedom also increase). It is thus important to remember that, while there potentially exist infinite models that could explain the data, DCM provides an informative simplification of complex dynamics, rather than reflecting the ground truth (Stephan et al., 2010). In Chapter 4, I included a high number of ROIs, which, while providing a more complete picture of frontoparietal changes, made it hard to formally define a comprehensive model space. I thus opted for the use of a greedy search over all possible reduced models which is considered a more exploratory approach (Zeidman, Jafarian, Seghier, et al., 2019). Using fewer ROIs (e.g., 3 or 4) would have allowed to specifying families of models to be compared with each other more easily, thus providing solutions that are more hypothesis-driven (Daunizeau et al., 2011; Stephan et al., 2010). Moreover, my study design did not involve a clear distinction between driving and modulatory effects, which made it hard (and possibly deceptive) to interpret the C matrix (i.e., driving inputs). To make the most of the potential of this analysis, future studies should aim at optimising the task design for DCM (e.g., factorial designs with clear driving and modulatory factors) and framing the experimental questions in terms of model comparison.

Finally, as already mentioned, the aim of this project was to characterise network switching both in case of induced switching due to task demands (Chapter 4) and during rest (Chapter 6), but I had to investigate these two dynamics separately due to the disruption brought by the pandemic to in-person testing. However, a better option would have been to collect task and resting-state data from the same participants (e.g., in two scanning sessions) in order to better relate task-induced and resting-state network switching as part of the same study design (Liu et al., 2022; Vanhaudenhuyse et al., 2011). For instance, it would have been useful to correlate the BOLD activation of regions involved in domain switching with their resting FC, to systematically link resting-state activity with the activity evoked by cognitive changes (Ito et al., 2017).

In this regard, a very intriguing approach would be to adapt the study designs I implemented in this thesis to investigate voluntary task switching, and link it with

resting-state dynamics. Voluntary task switching is a variant of the traditional task-switching paradigms in which participants are not guided in the task selection (e.g., via external prompts or fixed trial sequences) but are instead instructed to simply select one task in each trial (C. M. Arrington & Yates, 2009). This procedure requires participants to control their own performance in the absence of external guidance, and thus task choice becomes another behavioural measure along with RTs and accuracy. For the purpose of this thesis, I wanted to control the number of switches and tasks performed in order to have more uniform performances across participants and investigate this type of cognitive switching more systematically, thus inducing switches in an experimentally controlled manner. However, voluntary switching would more closely resemble resting-state fluctuations in cognitive content (see Vanhaudenhuyse et al., 2011 for a conceptually similar line of research), and mirror every-day dynamics in which humans switch their cognitive focus either spontaneously or with intent, allowing the investigation of a qualitatively different type of control that was not explored here.

7.4 Future directions

There are a number of interesting avenues for expanding on the current research. First, before the COVID pandemic, we intended to use non-invasive stimulation to determine the causal effect of the key regions involved in cognitive switching. This could be easily achieved with transcranial direct current stimulation (tDCS), which could be placed over parietal areas (e.g., IPL, as found in Chapter 4). A protocol including task performance before and after tDCS across sessions where anodal and sham tDCS is delivered would allow to shed light onto the causal role of the stimulated area on task performance. Since tDCS is likely to deliver current over large scalp areas due to the electrode size and current dispersion, using high-definition (HD) tDCS for this purpose would allow to deliver more focal stimulation and thus facilitate the targeting of a specific task-relevant area with reduced confounding from nearby regions (Filmer et al., 2020).

Instead, given the specific hypotheses we had regarding thalamic contributions, and given the difficulty of imaging this structure with fMRI, a potential option to indirectly

investigate the influence of thalamocortical pathways on cognitive control (and thus potentially boost their contribution) is to use transcutaneous auricular vagus nerve stimulation (taVNS). taVNS is an extremely simple and safe non-invasive neuromodulation technique which consists in placing small surface electrodes on the outer ear (e.g., tragus) in order to stimulate the auricular branch of the vagus nerve with a small amount of electrical current (Yakunina et al., 2017). Recent literature showed that taVNS allows for the investigation of causal dynamics between the stimulated neurotransmitter systems (cholinergic, GABAergic and noradrenergic) and cognitive processes, since it reaches specific brainstem nuclei (locus coeruleus, raphe, and nucleus of the solitary tract) and propagates to thalamus, hippocampus, insula, amygdala, prefrontal and motor cortex (Colzato & Beste, 2020). With regards to cognitive flexibility, taVNS was shown to induce effects on inhibitory control, conflict adaptation and set-shifting, for instance diminishing dual-task interference and reducing behavioural switch costs, even after one session of online stimulation (Beste et al., 2016; Borges et al., 2020; Fischer et al., 2018). Given these promising findings, taVNS could be used in concomitance with one of the study designs I employed in this thesis (or a modified/improved version of it) to see if and how vagus nerve stimulation can impact performance during switching within and across internal and external domains.

On a different note, before the pandemic we intended to investigate the effects of arousal on cognitive changes. First, we planned to use of pupillometry to assess changes in alertness during cognitive switching. Pupillometry is considered a proxy of locus coeruleus (LC) and noradrenergic activity, since LC activity positively correlates with pupil diameter (Mathot, 2018). Moreover, pupillary unrest (fluctuations in pupil diameter) was shown to correlate with increased activity in thalamus, SN and ECN regions during drowsiness, as well as resting-state BOLD fluctuations in the DMN, suggesting that pupillometry might track fluctuations in thalamocortical activity and changes in tonic alertness (M. Schneider et al., 2016; Yellin et al., 2015). Relatedly, pupillometry has been used as indirect marker of mind-wandering and attentional lapses (Konishi et al., 2017; Pelagatti et al., 2018; Smallwood et al., 2011). Crucially, previous studies used pupillometric signatures related to different arousal states to discriminate between different mind-wandering states, such that in a context requiring external attention, mind-wandering was associated with a low arousal state whereas, in a context that required internal focus, the arousal level was the same between mind-

wandering and on-task thoughts (Unsworth & Robison, 2018). These results suggest that arousal level and current context could guide attention towards internal processes or external environment, and that these complex dynamics can be traced using pupillary responses. These interesting findings, in addition to the fact that pupillometry was also used in task-switching paradigms to track mental effort (Pajkossy et al., 2017; Rondeel et al., 2015), suggest that pupillometry might prove a useful tool to complement behavioural performance and provide information on the arousal state associated with changes in cognitive content. This would be an important addition because the level of alertness and the ability to maintain it during switch trials is known to affect task-switching performances (Arrington & Yates, 2009). Relatedly, it could also help with tracking and further assessing the level of task difficulty beyond RTs.

Further to this, sleep deprivation can be used to investigate the relationship between cognition and arousal by introducing a large manipulation of general arousal. As explained in section 1.5.2 of the Introduction chapter, some studies showed that even one night of total or partial sleep deprivation can affect the dynamics between DMN, DAN and ECN both at rest and during tasks, as well as behavioural performances during attentional shifting (De Havas et al., 2012; Gujar et al., 2009; Heuer et al., 2004; Sämann et al., 2010; Whitney et al., 2017). Investigating the behavioural and neural changes induced by sleep deprivation during domain switching (with the tasks I employed in this thesis) could thus expand on the relationship between arousal and the balance between external and internal monitoring. This was in fact included in our original plans before the pandemic.

Finally, I wish to mention that the study approach proposed in this thesis (Chapters 3-5) could have potential implications for the investigation of a number of clinical conditions that are characterised by an imbalance between external and internal cognition. For instance, patients with disorders of consciousness (DOC) such as vegetative state and minimally conscious state are known to have impaired awareness of themselves and their surroundings which, along with low arousal levels, is at the core of their symptomatology (Laureys et al., 2007). Studies found DOC patients can display hyperactive external awareness (as indexed by increased activation of ECN and SN regions) and hypoactive internal awareness (as reflected by reduced DMN activation and connectivity between thalamus and DMN) as compared to healthy controls (Fernández-Espejo et al., 2012; J.-H. He et al., 2014). While using my study designs for the assessment of this type of imbalance in DOC patients would not be

possible, given the great cognitive effort required by the task, a later use of domain-switching during or after recovery from DOC could potentially help with tracking and/or boosting the improvement of patients' cognitive abilities with regards to the adaptive reorienting of external and internal awareness.

Moving on with a different example, anxiety and depression are often associated with an inflexible self-focused attention, such as in the case of worry and rumination (De Lissnyder et al., 2012; Hughes et al., 2008). In fact, the presence of such symptoms has been previously shown to correlate with duration and severity of generalised anxiety and major depressive disorder, and to negatively affect problem solving and task performance (De Lissnyder et al., 2012). The use of a domain-switching paradigm like the ones employed in this thesis could potentially shed more light onto the maladaptive imbalance between external and internal monitoring in these conditions. Finally, due to the inclusion of interoceptive sensibility, my first task design (Chapters 3 and 4) could prove helpful in investigating domain switching in conditions that display low interoceptive abilities such as anorexia, bulimia nervosa and schizophrenia (Prentice & Murphy, 2022).

7.5 Conclusions

Overall, this thesis aimed to investigate the behavioural and neural correlates of cognitive switching across the internal and external domains, as well as to identify switches in the networks underlying these cognitive processes during rest. Throughout this research, I provided evidence for the presence of behavioural switch costs in the self-referential domain for the first time, to the best of my knowledge, and found that precuneus and lateral parietal regions were involved in the preparation of switches both towards external and internal tasks, along with domain-specific preparation in DAN and DMN networks. In doing so, I developed and tested novel task-switching paradigms that could prove useful for further advancements in the field of self-referential processing and task-switching. Lastly, I found evidence (although only uncorrected for multiple comparisons) of the activation of anterior and mid cingulate, anterior insula, mediodorsal thalamus, ventral precuneus and right angular gyrus before and/or during resting-state change-points across frontoparietal and

control networks (DMN, DAN, ECN and SN), with no difference across chronotypes. This provided a novel way of approaching the study of changes across resting-state networks underlying high-order cognition, and suggests that sleep preferences do not affect network-switching dynamics. The communication and interaction of external and internal domains during adaptive cognitive changes is still an elusive and complicated question. Moreover, many parameters dependent on task design and analysis choices can influence results. Nonetheless, this work adds value to the vast literature on task-switching and to the data-driven investigation of resting-state dynamics among the networks subserving internal and external cognition. Our findings and approaches open new potential avenues to advance research on these topics.

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APPENDIX

Appendix A[1]

[back to Chapter 3]

Additional result tables

		frequentist				Bayesian
		t	**df**	**p**	**Cohen's d**	**BF_{10}**
a)	**within internal**	8.203	199	< .001	0.580	2.141e+11
	between internal	15.612		< .001	1.104	1.251e+33
	within external	17.867		< .001	1.263	7.059e+39
	between external	16.432		< .001	1.162	3.720e+35
b)	**E1, within**	11.102	199	< .001	0.785	6.195e+19
	E1, between	13.687		< .001	0.968	3.614e+27
	E2, within	14.235		< .001	1.007	1.668e+29
	E2, between	11.826		< .001	0.836	8.733e+21
	I1, within	4.624		< .001	0.327	3543.073
	I1, between	12.001		< .001	0.849	2.929e+22
	I2, within	7.353		< .001	0.520	2.851e+9
	I2, between	10.600		< .001	0.750	2.091e+18

Table A1. One sample t-tests over switch types after subtracting repetitions to check that all switch types in the 2x2 (a) and 4x2 (b) rANOVAs were significantly different from task repetitions (=0). Includes all participants.

[1]As published in Neuroscience of Consciousness:

Calzolari, S., Boneva, S., & Fernández-Espejo, D. (2022). Investigating the shift between externally and internally oriented cognition: a novel task-switching paradigm. Neuroscience of Consciousness, 2022(1), niac016.

			frequentist		Bayesian
			t	p_{bonf}	BF_{10}
E1, within	**-**	**E1, between****	-3.766	0.005	51.150
E2, within	**-**	**E2, between****	0.385	1.000	0.085
I1, within	**-**	**I1, between****	-6.480	< .001	1.257e+7
I2, within	**-**	**I2, between****	-3.546	0.012	29.122

** Frequentist p-value adjusted for comparing a family of 28

Table A2. Post-hoc t-tests (frequentist and Bayesian) from the 4x2 repeated measures ANOVA with factors task and switch type performed on switch costs (with subtraction of task repetitions), Includes all participants. E1: external task 1 (consonant finding); E2: external task 2 (vowel finding); I1: internal task 1 (personality task); I2: internal task 2 (current sensations).

			frequentist		Bayesian
			t	p_{bonf}	BF_{10}
E1/consonants	**-**	**E2/vowels**	7.787	< .001	1.637e+17
		I1/personality	5.986	< .001	6.993.178
		I2/sensations	8.840	< .001	2.296e+9
E2/vowels	**-**	**I1/personality**	-1.801	0.433	0.335
		I2/sensations	1.053	1.000	0.133
I1/personality	**-**	**I2/sensations**	2.854	0.027	1077.291

[a] *Greenhouse-Geisser correction was applied due to violated assumption of sphericity (p < .05)*
Note. Frequentist p-value adjusted for comparing a family of 6 (*)

Table A3. Post-hoc t-tests from the 1x4 repeated measures ANOVA (frequentist and Bayesian) on task repetitions. This was used to check whether there was an intrinsic difference in task difficulty, irrespective of switch costs. Includes all participants.

	Within domain	Between domains	Hard-to-easy switches	Neutral switches	Easy-to-hard switches
			1.179 (0.198)	1.199 (0.192)	1.243 (0.203)
Internal	1.135 (0.190)	1.195 (0.201)			
External	1.239 (0.221)	1.261 (0.232)			
E1	1.271 (0.243)	1.315 (0.261)			
E2	1.209 (0.238)	1.204 (0.237)			
I1	1.137 (0.208)	1.213 (0.216)			
I2	1.133 (0.208)	1.175 (0.227)			

Table A4. Descriptive statistics of RTs for all conditions in the 2x2 ANOVA (domain x switch type), 4x2 ANOVA (task x switch type) and 1x3 ANOVA (difficulty) on switch costs. Includes all participants. E1: external task 1 (consonant finding); E2: external task 2 (vowel finding); I1: internal task 1 (personality task); I2: internal task 2 (current sensations).

	Within domain	Between domains
Internal	1.119 (0.176)	1.185 (0.187)
External	1.168 (0.214)	1.199 (0.237)
E1	1.185 (0.224)	1.238 (0.260)
E2	1.151 (0.229)	1.155 (0.247)
I1	1.116 (0.190)	1.206 (0.207)
I2	1.126 (0.212)	1.162 (0.202)

Table A5. Descriptive statistics of RTs for all conditions in the 2x2 (domain x switch type) and 4x2 ANOVAs (task x switch type) when analysing a balanced subset of 70 participants. E1: external task 1 (consonant finding); E2: external task 2 (vowel finding); I1: internal task 1 (personality task); I2: internal task 2 (current sensations).

		Internal	External
Short CTIs	**Repetitions**	1.090 (0.187)	1.143 (0.213)
	Switches	1.215 (0.219)	1.319 (0.259)
Medium CTIs	**Repetitions**	1.071 (0.183)	1.099 (0.194)
	Switches	1.146 (0.195)	1.214 (0.213)
Long CTIs	**Repetitions**	1.082 (0.185)	1.118 (0.208)
	Switches	1.137 (0.189)	1.223 (0.228)

Table A6. Descriptive statistics of RTs for all conditions in the 2x3 (domain x CTI) ANOVA. E1: external task 1 (consonant finding); E2: external task 2 (vowel finding); I1: internal task 1 (personality task); I2: internal task 2 (current sensations).

	frequentist				Bayesian
	t	df	p	Cohen's d	BF_{10}
internal switches – short CTIs	14.050	199	< .001	0.993	2.284e+28
internal switches – medium CTIs	9.837		< .001	0.696	6.613e+15
internal switches – long CTIs	6.930		< .001	0.490	1.323e+8
external switches – short CTIs	18.875		< .001	1.335	6.443e+42

external switches – medium CTIs	14.537		< .001	1.028	6.888e+29
external switches – long CTIs	13.161		< .001	0.931	4.592e+25

Table A7. One sample t-tests over internal and external switches in each CTI condition (after subtracting repetitions) to check that all switch costs in the 2x3 rANOVA were significantly different from task repetitions (=0). Includes all participants.

Statistical analyses after removing outlier participants

Switch costs

			frequentist				Bayesian
			t	**df**	**p**	**Cohen's d**	**BF_{10}**
repetitions *(1.097±0.166)*	-	**switches** (*1.204±0.181*	-22.117	197	< .001	-1.572	1.227e+52

Note. The alternative hypothesis specifies that repeats is smaller than switches.

Table A8. Paired Samples T-test (frequentist and Bayesian) for finding overall switch costs (all repetitions versus all switches), when excluding 2 outlier participants.

			frequentist			Bayesian
			df	**F**	**p**	**η^2_p**	**BF_{10}**
domain			1,191	24.020	< .001	0.112	3.254e+60
trial type			1,191	482.533	< .001	0.716	7.059e+38
domain ✻ trial type			1,191	40.452	< .001	0.175	27.642
				t	**p_{bonf}**	**BF_{10}**
internal *(1.118±0.167)*	-	**external** *(1.168±0.184)*		-4.901	< .001	1.918e+7
repetitions *(1.097±0.166)*	-	**switches** (*1.204±0.181)*		-21.967	< .001	3.932e+74
int. repeat. *(1.076±0.166)*		**ext. repeat.*** *(1.103±0.176)*		-2.462	0.087	2.010
	-	**int. switch.*** *(1.160±0.177)*		-13.747	< .001	3.689e+29
		ext. switch.* *(1.234±0.202)*		-13.901	< .001	5.043e+25
ext. repeat. *(1.103±0.176)*		**int. switch.*** *(1.160±0.177)*		-5.059	< .001	36893.923
	-	**ext. switch.*** *(1.234±0.202)*		-21.385	< .001	1.336e+46
int. switch. *(1.160±0.177)*	-	**ext. switch.*** *(1.234±0.202)*		-6.763	< .001	1.133e+7

Note. Frequentist p-value adjusted for comparing a family of 6 (*)
Underlined comparisons signal a change in significance with respect to the analysis with all participants (int rep vs ext rep including all participants: p = .004)

Table A9. 2x2 repeated measures ANOVA (frequentist and Bayesian) with factors domain and trial type, to assess the presence and nature of switch costs in the two cognitive domains. 8 outlier participants were excluded.

Additional costs in between-domain switches

			frequentist			Bayesian
			df	**F**	**p**	**η^2_p**	**BF_{10}**
domain			1,186	32.696	< .001	0.150	2.893e+7
switch type			1,186	52.976	< .001	0.222	1.838e+7
domain ✻ switch type			1,186	10.587	0.001	0.054	8.175
					t	**p_{bonf}**	**BF_{10}**
internal *(0.083±0.075)*	-	**external** *(0.125±0.079)*			-5.718	< .001	9.485e+6
within *(0.083±0.063)*	-	**between** *(0.125±0.077)*			-7.278	< .001	1.623e+9
within int. *(0.053±0.092)*	-	**within ext.*** *(0.113±0.080)*			-6.513	< .001	2.045e+8
		between int.* *(0.113±0.092)*			**-7.450**	**< .001**	**1.081e+10**
within ext. *(0.113±0.080)*	-	**between ext.*** *(0.136±0.112)*			**-2.853**	**0.027**	**3.182**
between int. *(0.113±0.092)*	-	**between ext.*** *(0.136±0.112)*			-2.527	0.072	1.231

Note. Frequentist p-value adjusted for comparing a family of 6 (*)
Underlined comparisons signal a change in significance with respect to the analysis with all participants

Table A10. 2x2 repeated measures ANOVA (frequentist and Bayesian) with factors domain and switch type performed on the switch costs (mean switches after subtraction of mean repetitions for each subject), to explore the extra costs of switching across domains versus switching while staying within the same domain. 13 outlier participants were excluded.

	frequentist				Bayesian
	df	**F**	**p**	**η^2_p**	**BF_{10}**
task [a]	2.858,462.959	17.775	< .001	0.099	6.609e+9
switch type	1,162	56.404	< .001	0.258	6.602e+8
task ✻ switch type	2.974,481.733	7.152	< .001	0.042	21.176

			t	p_{bonf}	BF_{10}
E1 *(0.120±0.106)*	-	**E2*** *(0.129±0.101)*	-0.936	1.000	0.105
		I1* *(0.073±0.085)*	4.913	< .001	17773.654
		I2* *(0.078±0.090)*	4.364	< .001	1257.844
E2 *(0.129±0.101)*	-	**I1*** *(0.073±0.085)*	5.849	< .001	3.475e+6
		I2* *(0.078±0.090)*	5.299	< .001	362652.970
I1 *(0.073±0.085)*	-	**I2*** *(0.078±0.090)*	-0.549	1.000	0.076
within *(0.078±0.059)*	-	**between** *(0.122±0.080)*	-7.510	< .001	4.105e+10
E1, within *(0.098±0.107)*	-	**E1, between**** *(0.142±0.151)*	-3.856	0.004	48.924
E2, within *(0.127±0.107)*	-	**E2, between**** *(0.131±0.141)*	-0.358	1.000	0.093
I1, within *(0.034±0.100)*	-	**I1, between**** *(0.111±0.119)*	-6.775	< .001	1.264e+8
I2, within *(0.053±0.114)*	-	**I2, between**** *(0.103±0.114)*	-4.423	< .001	1449.261

[a] *Greenhouse-Geisser correction was applied due to violated assumption of sphericity (p < .05)*
Note. Frequentist p-value adjusted for comparing a family of 6 (*) or 28 (**)
Underlined comparisons signal a change in significance with respect to the analysis with all participants

Table A11. 4x2 repeated measures ANOVA (frequentist and Bayesian) with factors task and switch type performed on switch costs (with subtraction of task repetitions), to aid previous analyses in understanding the role of specific tasks in shaping the costs of switching between and within domains. 37 outlier participants excluded.

		frequentist				Bayesian
		t	**df**	**p**	**Cohen's d**	BF_{10}
a)	**within internal**	7.905	186	< .001	0.578	2.862e+10
	between internal	16.811		< .001	1.229	6.859e+35
	within external	19.353		< .001	1.415	1.034e+43
	between external	16.598		< .001	1.214	1.676e+35
b)	**E1, within**	11.729	162	< .001	0.919	1.901e+20
	E1, between	11.969		< .001	0.938	8.604e+20
	E2, within	15.098		< .001	1.183	2.897e+29
	E2, between	11.886		< .001	0.931	5.099e+20
	I1, within	4.342		< .001	0.340	564.543
	I1, between	11.929		< .001	0.934	6.685e+20
	I2, within	5.914		< .001	0.463	513324.314
	I2, between	11.567		< .001	0.906	6.904e+19

Table A12. One sample t-tests over switch types after subtracting repetitions to check that all switch types in the 2x2 (a) and 4x2 (b) rANOVAs were significantly different

from task repetitions (=0). 13 (a) and 37 (b) outlier participants were excluded from the two analyses, respectively.

Difficulty of task repetitions

			frequentist			Bayesian
		df	**F**	**p**	**η^2_p**	**BF_{10}**
task repetition[a]		2.147, 403.568	29.502	< .001	0.136	5.015e+14
				t	**p_{bonf}**	**BF_{10}**
E1/consonants *(1.139±0.190)*	-	**E2/vowels** *(1.055±0.170)*		8.259	< .001	3.970e+16
	-	**I1/personality** *(1.090±0.174)*		4.867	< .001	257.241
	-	**I2/sensations** *(1.057±0.169)*		7.988	< .001	4.127e+7
E2/vowels *(11.055±0.170)*	-	**I1/personality** *(1.090±0.174)*		-3.391	0 .001	17.161
	-	**I2/sensations** *(1.048±0.157)*		-0.271	1.000	0.084
I1/personality *(1.090±0.174)*	-	**I2/sensations** *(1.057±0.169)*		3.121	0.011	645.084

[a] *Greenhouse-Geisser correction was applied due to violated assumption of sphericity (p < .05)*
Note. Frequentist p-value adjusted for comparing a family of 6 (*)
Underlined comparisons signal a change in significance with respect to the analysis with all participants

Table A13. Main analysis and post-hoc t-tests from the 1x4 repeated measures ANOVA (frequentist and Bayesian) with factor task repetition. This was used to check whether there was an intrinsic difference in task difficulty, irrespective of switch costs. 11 outlier participants were removed from this analysis.

Switch costs grouped by difficulty

		frequentist			Bayesian
	df	**F**	**p**	**η^2_p**	**BF_{10}**
Switch difficulty[a]	1.857, 358.361	2.528	0.085	0.013	0.212

[a] *Greenhouse-Geisser correction was applied due to violated assumption of sphericity (p < .05)*
M±SD: hard-to-easy = 0.106±0.089; neutral = 0.120±0.095; easy-to-hard = 0.102±0.098

Table A14. 1x3 repeated measures ANOVA (frequentist and Bayesian) on switch costs with factor switch difficulty. This was used to check whether switch costs were influenced by task difficulty, irrespective of domain. 6 outlier participants were removed from this analysis.

Effects of CTI duration

			frequentist			Bayesian
			df	F	p	η^2_p	BF_{10}
domain			1	35.609	< .001	0.167	9.679e+9
CTI			2	56.347	< .001	0.240	4.165e+18
domain ✻ CTI			2	0.674	0.510	0.004	0.033 (BF_{01}=30.537)
					t	p_{bonf}	BF_{10}
internal *(0.085±0.074)*	-	**external** *(0.127±0.080)*			-5.967	< .001	3.799e+10
short *(0.145±0.092)*	-	**medium*** *(0.092±0.072)*			8.066	< .001	6.202e+12
		long* *(0.079±0.074)*			10.010	< .001	6.319e+19
medium *(0.113±0.080)*	-	**long*** *(0.136±0.112)*			1.945	0.158	0.624
int. short *(0.120±0.114)*	-	**int. medium**** *(0.073±0.093)*			5.490	< .001	10842.976
		int. long** *(0.060±0.098)*			6.932	< .001	6.367e+7
int. medium *(0.073±0.093)*	-	**int. long**** *(0.060±0.098)*			1.442	1.000	0.228
ext. short *(0.170±0.117)*	-	**ext. medium*** *(0.112±0.095)*			6.762	< .001	1.745e+8
		ext. long** *(0.099±0.095)*			8.274	< .001	9.506e+10
ext. medium *(0.112±0.095)*	-	**ext. long**** *(0.099±0.095)*			1.512	1.000	0.325

Note. Frequentist p-value adjusted for comparing a family of 3 (*)
Note. Frequentist p-value adjusted for comparing a family of 15 (**)
Underlined comparisons signal a change in significance with respect to the analysis with all participants

Table A15. 2x3 repeated measures ANOVA (frequentist and Bayesian) on switch costs with factors domain and CTI, to assess the influence of CTI duration on the magnitude of switch costs. 21 outlier participants were excluded.

	frequentist				Bayesian
	t	df	p	Cohen's d	BF_{10}
internal short	14.141	178	< .001	1.057	4.895e+27
internal medium	10.510		< .001	0.786	2.218e+17
internal long	8.277		< .001	0.619	2.172e+11
external short	19.410		< .001	1.451	2.492e+42
external medium	15.656		< .001	1.170	1.026e+32
external long	13.862		< .001	1.036	7.750e+26

Table A16. One sample t-tests over all conditions of the 2x3 rANOVA (domain x CTI), to check that all the switch costs were significantly different from task repetitions (=0). 21 outlier participants were excluded from the analysis.

Appendix B

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	frequentist				Bayesian
	t	**df**	**p**	**Cohen's d**	**BF_{10}**
within internal	4.675	29	< .001	0.854	396.799
between internal	5.747		< .001	1.049	6035.418
within external	6.918		< .001	1.263	115045.595
between external	6.914		< .001	1.262	113990.771

Table B1. One sample t-tests over switch types after subtracting repetitions to check that all switch types in the 2x2 rANOVA were significantly different from task repetitions (=0).

	Repetitions	**Combined switches**	**Within-domain sw.**	**Between-domain sw.**
Internal	1.161 (0.220)	1.252 (0.235)	1.231 (0.256)	1.274 (0.223)
External	1.099 (0.168)	1.250 (0.205)	1.224 (0.207)	1.272 (0.230)

Table B2. Descriptive statistics (mean and SD) of RTs for all conditions in the 2x2 rANOVA (domain x switch type).

Contrast	Region (AAL3)	Peak Coordinates			Voxels per cluster	z-score	Peak $p_{FWE\text{-}corr}$	Cluster $p_{FWE\text{-}corr}$
A) RI > RE	L Inferior Temporal	-47	5.5	-35	238	6.859	<.001	.000
	R Crus I (Uvula)	30.5	-84.5	-32.5	383	6.841	<.001	.000
	L Inferior Orbitofrontal	-49.5	30.5	-5	327	6.411	<.001	.000
	L Medial Superior Frontal	-4.5	50.5	22.5	374	6.377	<.001	.000
	L Middle Temporal	-54.5	-34.5	0	35	6.053	<.001	<.001
	L Superior Frontal	-12	38	50	58	6.005	<.001	<.001
	Undefined	-9.5	0.5	7.5	44	5.960	<.001	<.001
	L Mid / Post Cingulate	-9.5	-42	35	61	5.945	<.001	<.001
	L Crus II (Uvula)	-29.5	-84.5	-35	20	5.813	<.001	<.001
	L Inf Frontal, pars triangularis	-52	20.5	22.5	12	5.545	.001	<.001
	L Rectus	-2	45.5	-20	24	5.469	.002	<.001
	L Middle Cingulate	-4.5	-12	37.5	7	5.461	.002	<.001
	L Lingual / Parahippocampal	-9.5	-42	0	5	5.377	.004	<.001
	Undefined	-12	-24.5	-7.5	4	5.342	.004	.001
	L Supramarginal / Mid Temporal	-52	-54.5	22.5	6	5.341	.004	<.001
	L Superior Occipital / Cuneus	-12	-99.5	17.5	7	5.329	.005	<.001
	R Cerebellar Tonsil	5.5	-52	-45	3	5.326	.005	.003
	R Inf Frontal, pars triangularis	55.5	30.5	-2.5	12	5.256	.007	<.001
	L Amygdala / Parahippocampal	-24.5	-7	-15	7	5.225	.008	<.001
	L Cuneus	-2	-77	32.5	6	5.214	.009	<.001
	L Superior Frontal	-19.5	33	42.5	3	5.170	.011	.003
	R Mid Temporal Pole / STG	40.5	13	-37.5	4	5.140	.013	.001
	R SMA	8	18	62.5	3	5.064	.020	.003
	L Amygdala / Parahippocampal	-29.5	-4.5	-20	3	5.034	.023	.003

	L Superior Frontal	-19.5	25.5	45	4	5.032	.023	.001
B) RE > RI	R Superior Parietal / Precuneus	18	-64.5	55	635	6.615	<.001	.000
	L Inferior Parietal	-34.5	-42	45	671	6.523	<.001	.000
	L Superior Frontal	-24.5	-4.5	50	36	5.846	<.001	<.001
	R Superior Frontal	33	0.5	60	13	5.379	.004	<.001
	L Inf Semi-Lunar Lobule	-29.5	-69.5	-52.5	4	5.160	.012	.001
C) SI > SE	L Precuneus	-4.5	-52	7.5	278	6.571	<.001	.000
	L Inf Frontal, pars Orbitalis	-49.5	30.5	-5	375	6.494	<.001	.000
	L Angular	-49.5	-57	25	103	6.403	<.001	<000
	R Superior Temporal Pole	45.5	20.5	-30	11	6.240	<.001	<.001
	L Rectus	-2	33	-17.5	21	6.102	<.001	<.001
	L SMA	-4.5	20.5	62.5	25	5.977	<.001	<.001
	L Middle Temporal	-52	-37	0	19	5.866	<.001	<.001
	L Superior Frontal	-12	50.5	30	59	5.851	<.001	<.001
	L Superior Frontal	-19.5	33	45	22	5.739	<.001	<.001
	L pre-Anterior Cingulate	-9.5	43	12.5	9	5.643	<.001	<.001
	L Middle Temporal Pole	-47	13	-35	142	5.594	.001	.000
	R Crus II	15.5	-87	-32.5	25	5.504	.002	<.001
	R Middle Temporal	58	-4.5	-20	8	5.360	.004	<.001
	L Cuneus	-12	-925	25	5	5.262	.007	<.001
	L Mid Frontal	-34.5	18	50	3	5.120	.014	.002
	L Inf Orbitofrontal	-32	33	-7.5	4	5.022	.024	.001
D) SE > SI	L Superior Frontal	-24.5	-4.5	50	58	6.478	<.001	<.001
	L Mid Occipital	-27	-64.5	32.5	199	6.147	<.001	.000
	L Inferior Parietal	-34.5	-39.5	42.5	59	5.895	<.001	<.001
	R Middle Frontal	25.5	0.5	50	41	5.836	<.001	<.001

R Supramarginal / IPL	45.5	-34.5	42.5	22	5.716	<.001	<.001
R Angular/ Sup Par Lobule	25.5	-62	47.5	39	5.433	.003	<.001

Table B3. Results from the second-level GLM analyses (one-sample t-test) testing for the group effects of domain on brain activation. Specific contrasts include: internal repetitions vs external repetitions, external repetitions vs internal repetitions, switches to internal vs switches to external, switches to external vs switches to internal. Results survived a threshold of $p < 0.05$ with family wise error (FWE) correction. Abbreviations: RI = repetition of internal tasks; RE = repetition of external tasks; SI = all switches towards internal tasks; SE = all switches towards external tasks.

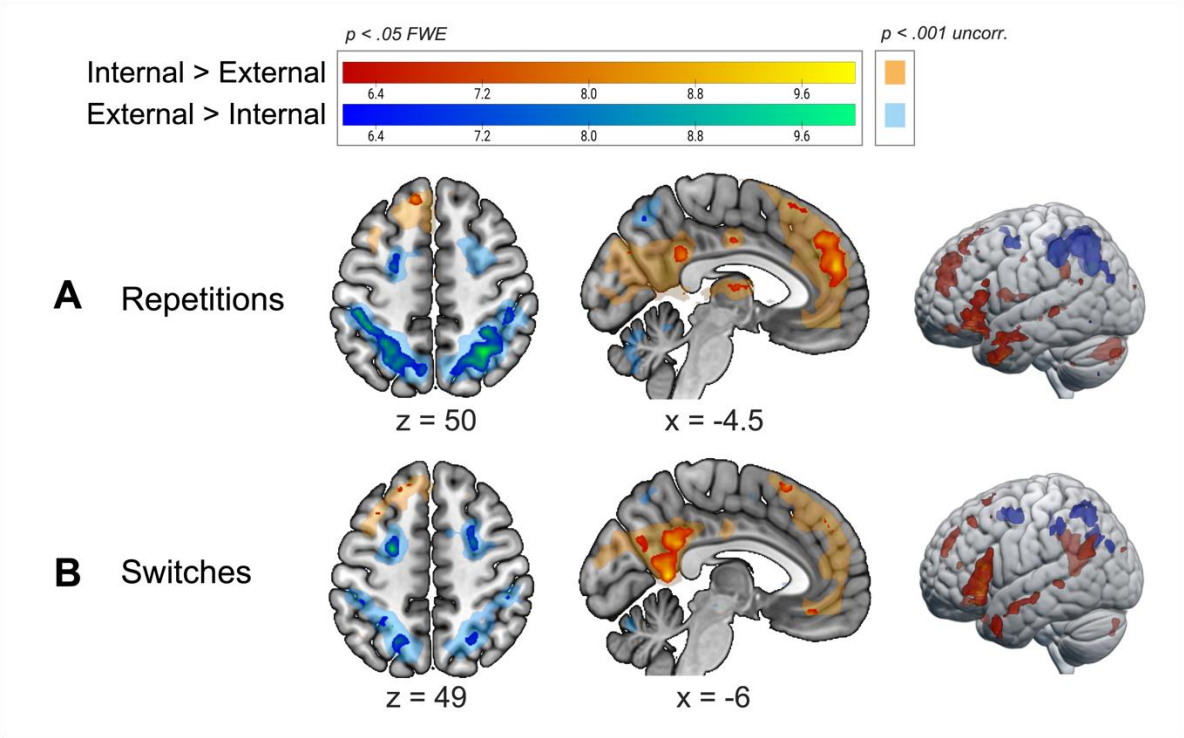

Figure B1. Brain activation at the group level (one-sample t-test) for the whole-brain comparisons between domains for each trial type. Specifically, the first-level GLMs compared 'internal > external' and 'external > internal' for both repetitions only (A) and switches only (B) on a multi-run model for each subject (4 runs of task per participant). The activation maps are shown at p<0.05 FWE-corrected (bright colours; warm scale = internal > external; cold scale = external > internal) and rendered on a standard template (mni152 template in MRIcroGL). Uncorrected activation maps at *p*<.001 are also shown for representational purposes with faint, transparent colours. For each slice, the relative MNI coordinate is reported.

A Matrix – Average effective connectivity

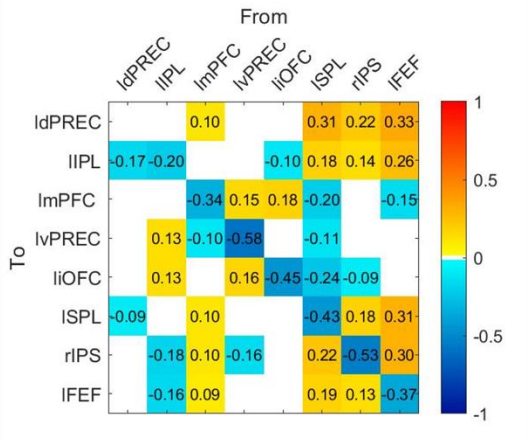

Figure B2. Estimated average effective connectivity across experimental conditions (A matrix). We report the connections that exceeded the 95% posterior probability threshold in the PEB analysis. Warm colours in the extrinsic connections indicate more excitation as compared to baseline (i.e., rest), cold colours signal more inhibition compared to baseline. Note that self-connections are log-scaled and always inhibitory, so warm colours indicate a reduction in inhibition and cold colours indicate increased inhibition. Abbreviations: *lm*PFC = left middle prefrontal cortex; *lv*PREC = left ventral precuneus; *li*OFC = left inferior orbitofrontal cortex; *l*SPL = left superior parietal lobule; rIPS = right intraparietal sulcus; *l*FEF = left frontal eye fields; *l*IPL = left inferior parietal lobule; *ld*PREC = left dorsal precuneus.

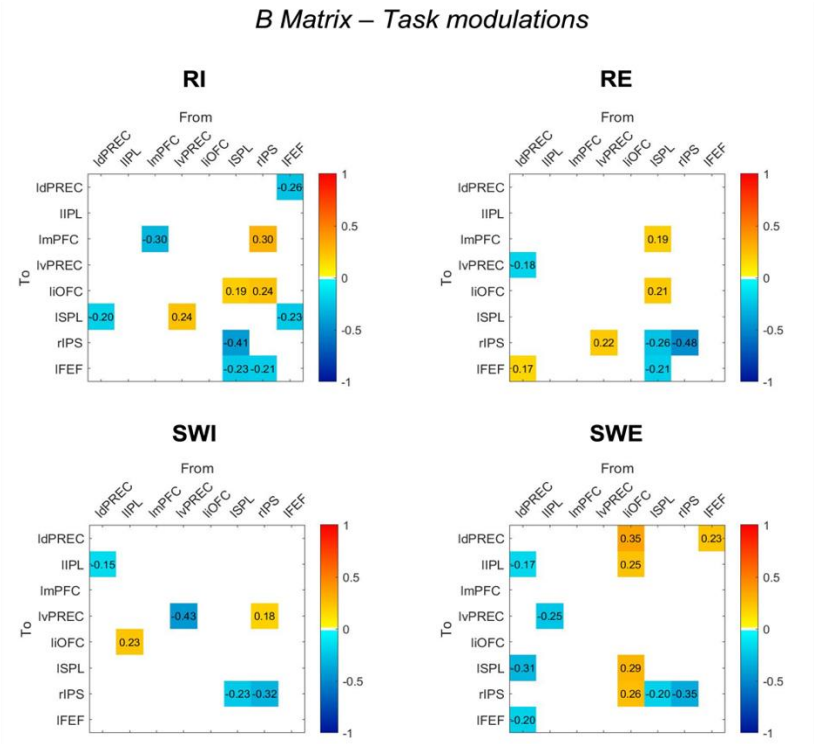

Figure B3. Modulatory effects of each task condition (B matrix). We report the connections that exceeded the 95% posterior probability threshold in the PEB analysis. Warm colours in the extrinsic connections indicate more excitation as a result of the task condition, while cold colours signal more inhibition as an effect of task. In the case of self-connections, the modulation is interpreted as increased (warm colours) or decreased (cold colours) inhibition, which means self-connections become less or more sensitive (respectively) to inputs from the rest of the network as a result of task influence. Abbreviations: RI = internal repetitions; RE = external repetitions; SWI = switches to internal; SWE = switches to external; *lm*PFC = left middle prefrontal cortex; *lv*PREC = left ventral precuneus; *li*OFC = left inferior orbitofrontal cortex; *l*SPL = left superior parietal lobule; rIPS = right intraparietal sulcus; *l*FEF = left frontal eye fields; *l*IPL = left inferior parietal lobule; *ld*PREC = left dorsal precuneus.

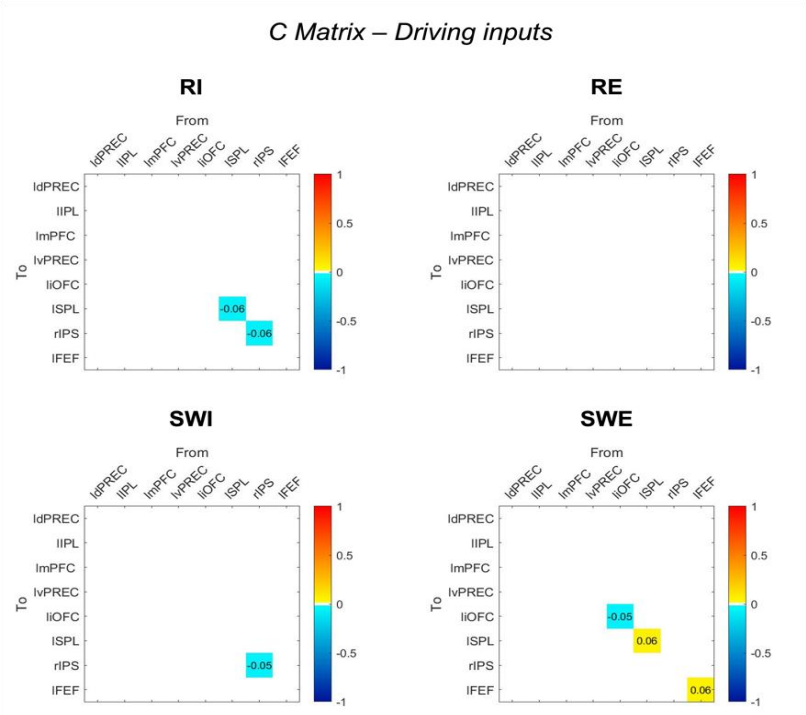

Figure B4. Driving inputs from the task (C matrix), representing where each task condition enters the network. We report the connections that exceeded the 95% posterior probability threshold in the PEB analysis. Warm colours indicate a positive drive from task condition while cold colours indicate a negative drive. By definition, driving inputs are only present in self-connections. Abbreviations: RI = internal repetitions; RE = external repetitions; SWI = switches to internal; SWE = switches to external; *lm*PFC = left middle prefrontal cortex; *lv*PREC = left ventral precuneus; *li*OFC = left inferior orbitofrontal cortex; *l*SPL = left superior parietal lobule; rIPS = right intraparietal sulcus; *l*FEF = left frontal eye fields; *l*IPL = left inferior parietal lobule; *ld*PREC = left dorsal precuneus.

Additional comments on the nature of fMRI activation in specific switch types.

Interestingly, when looking at the effect of switching in each domain separately, we observed that the above-mentioned activity was mostly driven by switches towards internal tasks (as compared to internal task repetitions), while switches towards external tasks only induced a minimal portion of that same activation (mostly limited to small clusters in left IPL and precuneus). Nonetheless, the DCM results on task-

induced modulations showed that switching preparation in both domains elicits widespread modulations among parietal areas (or from frontal to parietal), in contrast with the preparation of task repetitions which appear to target frontal regions instead (i.e., modulations from parietal towards frontal regions). This potentially indicates that, during task repetitions, more frontal regions are involved in the maintenance of current task rules while, during switching, the parietal cortex is engaged in the retrieval and reconfiguration of currently relevant action sets (Philipp et al., 2013). In addition, the preparation of switches towards internal tasks caused parietal inhibitory modulations which resulted in excitatory connections to DMN and language regions (ventral precuneus and iOFC), whereas switches to the external domain mostly induced an excitatory modulation from iOFC towards all DAN parietal regions. This clearly highlights a pattern of dynamic communication between frontoparietal networks depending on the domain to be accessed, which is accompanied by the consistent involvement of dorsal and ventral precuneus to aid connectivity modulations.

The smaller GLM effect associated with all switches towards external tasks is likely due to the differential effect we subsequently observed between different switch types as compared to repetitions. In fact, while the switches within the external domain elicited a marked activation of left IPL, SPL, bilateral precuneus and left middle frontal gyrus, the switches from internal to external domain only induced changes in the cerebellum. Conversely, when looking at each switch type in the internal domain, we observed the opposite pattern: while the switches within the internal domain (compared to internal repetitions) mostly resulted in the activation of the left inferior OFC (pars triangularis) and precuneus, the switches from external to internal tasks resulted in a wide cluster of activation in left IPL and SPL as well as precuneus. A potential explanation for these heterogeneous results is that, while within-domain switches require activation in domain-specific circuits, the preparatory activity of between-domain switches instead includes residual activation from the other domain (previous trial). This view would suggest the presence of task-set inertia, i.e., that switching also involves the presence of residual activity from task-irrelevant processes, competing for behavioural control and thus interfering with performance (Qiao et al., 2017; Wylie et al., 2004).

Appendix C

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Additional result tables

		frequentist				Bayesian
		t	df	p	Cohen's d	BF_{10}
a)	**within internal**	7.412	200	< .001	0.523	2.019e+9
	between internal	8.778		< .001	0.619	7.572e+12
	within external	11.786		< .001	0.831	3.524e+21
	between external	11.539		< .001	0.814	6.448e+20
b)	**E1, within**	8.071	200	< .001	0.569	1.975e+11
	E1, between	7.616		< .001	0.537	1.315e+10
	E2, within	8.167		< .001	0.576	3.503e+11
	E2, between	9.691		< .001	0.684	5.253e+15
	I1, within	5.773		< .001	0.407	638220.268
	I1, between	5.642		< .001	0.398	337431.689
	I2, within	5.526		< .001	0.390	194397.659
	I2, between	7.415		< .001	0.523	4.119e+9

Table C1. One sample t-tests over switch types after subtracting repetitions to check that all switch types in the 2x2 (a) and 4x2 (b) rANOVAs were significantly different from task repetitions (=0). Includes all participants.

			frequentist		Bayesian
			t	p_{bonf}	BF_{10}
E1, within	-	**E1, between****	0.163	1.000	0.080
E2, within	-	**E2, between****	-2.354	0.527	1.172
I1, within	-	**I1, between****	-0.685	1.000	0.099
I2, within	-	**I2, between****	-1.099	1.000	0.150

** Frequentist p-value adjusted for comparing a family of 28

Table C2. Post-hoc t-tests (frequentist and Bayesian) from the 4x2 repeated measures ANOVA with factors task and switch type performed on switch costs (with subtraction of task repetitions), Includes all participants. E1: external task 1 (indoor/outdoor discrimination); E2: external task 2 (natural/man-made

discrimination); I1: internal task 1 (pleasantness judgement); I2: internal task 2 (relatedness judgement).

			frequentist		Bayesian
			t	p_{bonf}	BF_{10}
E1		**E2**	-7.310	< .001	8.928e+12
	-	**I1**	-16.347	< .001	1.985e+34
		I2	-19.118	< .001	2.009e+34
E2		**I1**	-9.037	< .001	2.238e+12
	-	**I2**	-11.808	< .001	3.814e+19
I1	**-**	**I2**	-2.771	0.035	35.308

[a] *Greenhouse-Geisser correction was applied due to violated assumption of sphericity (p < .05)*
Note. Frequentist p-value adjusted for comparing a family of 6 (*)

Table C3. Post-hoc t-tests from the 1x4 repeated measures ANOVA (frequentist and Bayesian) on task repetitions. This was used to check whether there was an intrinsic difference in task difficulty, irrespective of switch costs. Includes all participants. E1: external task 1 (indoor/outdoor discrimination); E2: external task 2 (natural/man-made discrimination); I1: internal task 1 (pleasantness judgement); I2: internal task 2 (relatedness judgement).

	Within domain	Between domains	Hard-to-easy switches	Easy-to-hard switches
			1.171 (0.200)	1.264 (0.216)
Internal	1.269 (0.227)	1.277 (0.225)		
External	1.153 (0.200)	1.163 (0.208)		
E1	1.116 (0.213)	1.115 (0.218)		
E2	1.189 (0.221)	1.214 (0.237)		
I1	1.253 (0.234)	1.260 (0.238)		
I2	1.284 (0.243)	1.295 (0.245)		

Table C4. Descriptive statistics of RTs for all conditions in the 2x2 ANOVA (domain x switch type), 4x2 ANOVA (task x switch type) and 1x3 ANOVA (difficulty) on switch costs. Includes all participants. E1: external task 1 (indoor/outdoor discrimination); E2: external task 2 (natural/man-made discrimination); I1: internal task 1 (pleasantness judgement); I2: internal task 2 (relatedness judgement).

		Internal	External
Short CTIs	**Repetitions**	1.231 (0.220)	1.093 (0.190)
	Switches	1.319 (0.247)	1.202 (0.230)
Medium CTIs	**Repetitions**	1.202 (0.209)	1.065 (0.177)
	Switches	1.241 (0.214)	1.137 (0.204)
Long CTIs	**Repetitions**	1.223 (0.220)	1.080 (0.182)
	Switches	1.258 (0.229)	1.138 (0.200)

Table C5. Descriptive statistics of RTs for all conditions in the 2x3 (domain x CTI) ANOVA. E1: external task 1 (indoor/outdoor discrimination); E2: external task 2 (natural/man-made discrimination); I1: internal task 1 (pleasantness judgement); I2: internal task 2 (relatedness judgement).

	frequentist				Bayesian
	t	**df**	**p**	**Cohen's d**	**BF_{10}**
internal switches – short CTIs	10.757	200	< .001	0.759	3.132e+18
internal switches – medium CTIs	5.334		< .001	0.376	39626.617
internal switches – long CTIs	4.530		< .001	0.320	1208.247
external switches – short CTIs	10.836		< .001	0.64	5.336e+18
external switches – medium CTIs	8.830		< .001	0.623	1.048e+13
external switches – long CTIs	7.459		< .001	0.526	2.645e+9

Table C6. One sample t-tests over internal and external switches in each CTI condition (after subtracting repetitions) to check that all switch costs in the 2x3 rANOVA were significantly different from task repetitions (=0). Includes all participants.

Statistical analyses after removing outlier participants

Switch costs

	frequentist				Bayesian
	df	**F**	**p**	**η^2_p**	**BF_{10}**
domain	1,198	234.991	< .001	0.543	1.651e+32
trial type	1,198	233.374	< .001	0.541	4.492e+31

domain ✻ trial type			1,198	13.432	< .001	0.064	67.502
					t	**p_{bonf}**	**BF_{10}**
internal	**-**	**external**			15.329	< .001	2.361e+57
repetitions	-	**switches**			-15.277	< .001	4.466e+42
int. repeat. *(1.215±0.208)*	**-**	**ext. repeat.*** *(1.074±0.169)*			15.500	< .001	1.525e+32
		int. switch.* *(1.268±0.216)*			-9.305	< .001	4.668e+14
		ext. switch.* *(1.154±0.192)*			6.482	< .001	2.868e+7
ext. repeat. *(1.074±0.169)*	**-**	**int. switch.*** *(1.268±0.216)*			-20.670	< .001	2.844e+46
		ext. switch.* *(1.154±0.192)*			-14.035	< .001	5.072e+27
int. switch. *(1.268±0.216)*	**-**	**ext. switch.*** *(1.154±0.192)*			12.532	< .001	1.463e+24

Note. Frequentist p-value adjusted for comparing a family of 6 (*)
Underlined comparisons signal a change in significance with respect to the analysis with all participants

Table C7. 2x2 repeated measures ANOVA (frequentist and Bayesian) with factors domain and trial type, to assess the presence and nature of switch costs in the two cognitive domains. 2 outlier participants were excluded.

Additional costs in between-domain switches

			frequentist				**Bayesian**
			df	**F**	**p**	**η^2_p**	**BF_{10}**
domain			1,189	18.053	< .001	0.087	513.257
switch type			1,189	1.742	.188	0.009	0.191
domain ✻ switch type			1,189	0.454	0.501	0.002	0.142
					t	**p_{bonf}**	**BF_{10}**
internal	**-**	**external**			-4.249	< .001	8801.445
within	**-**	**between**			-1.320	.188	0.144
within int. *(0.050±0.087)*	**-**	**within ext.*** *(0.077±0.084)*			-3.143	.011	7.844
		between int.* *(0.054±0.083)*			**-0.498**	**1.000**	**0.092**
within ext. *(0.077±0.084)*	**-**	**between ext.*** *(0.087±0.102)*			**-1.423**	**.934**	**0.210**
between int. *(0.054±0.083)*	**-**	**between ext.*** *(0.087±0.102)*			-3.898	< .001	143.556

Note. Frequentist p-value adjusted for comparing a family of 6 (*)
Underlined comparisons signal a change in significance with respect to the analysis with all participants

Table C8. 2x2 repeated measures ANOVA (frequentist and Bayesian) with factors domain and switch type performed on the switch costs (mean switches after subtraction of mean repetitions for each subject), to explore the extra costs of switching across domains versus switching while staying within the same domain. 11 outlier participants were excluded.

			frequentist			Bayesian
			df	F	p	η^2_p	BF_{10}
task			3,510	6.222	< .001	0.035	24.987
switch type			1,170	0.303	.582	0.002	0.077
task ✻ switch type			3,510	70.833	.476	0.005	0.017
					t	p_{bonf}	BF_{10}
E1	-	**E2***			-1.146	1.000	0.129
		I1*			2.966	.019	12.494
		I2*			1.267	1.000	0.155
E2	-	**I1***			4.112	< .001	1167.978
		I2*			2.413	.097	2.802
I1	-	**I2***			-1.699	.539	0.559
within	-	**between**			-0.551	.582	0.050
E1, within *(0.073±0.115)*	-	**E1, between**** *(0.068±0.132)*			0.417	1.000	0.092
E2, within *(0.073±0.110)*	-	**E2, between**** *(0.090±0.136)*			-1.580	1.000	0.262
I1, within *(0.043±0.108)*	-	**I1, between**** *(0.040±0.111)*			0.309	1.000	0.090
I2, within *(0.057±0.120)*	-	**I2, between**** *(0.059±0.098)*			-0.230	1.000	0.088

[a] *Greenhouse-Geisser correction was applied due to violated assumption of sphericity (p < .05)*

Note. Frequentist p-value adjusted for comparing a family of 6 (*) or 28 (**)

Underlined comparisons signal a change in significance with respect to the analysis with all participants

Table C9. 4x2 repeated measures ANOVA (frequentist and Bayesian) with factors task and switch type performed on switch costs (with subtraction of task repetitions), to aid previous analyses in understanding the role of specific tasks in shaping the costs of switching between and within domains. 30 outlier participants excluded. E1: external task 1 (indoor/outdoor discrimination); E2: external task 2 (natural/man-made

discrimination); I1: internal task 1 (pleasantness judgement); I2: internal task 2 (relatedness judgement).

		frequentist				Bayesian
		t	**df**	**p**	**Cohen's d**	**BF_{10}**
a)	**within internal**	7.978	189	< .001	0.579	4.645e+10
	between internal	8.993		< .001	0.652	2.205e+13
	within external	12.612		< .001	0.915	4.819e+23
	between external	11.811		< .001	0.857	2.140e+21
b)	**E1, within**	8.229	170	< .001	0.629	1.361e+11
	E1, between	6.789		< .001	0.519	84.541e+7
	E2, within	8.743		< .001	0.669	2.805e+12
	E2, between	8.662		< .001	0.662	1.739e+12
	I1, within	5.222		< .001	0.399	21803.507
	I1, between	4.733		< .001	0.362	2693.994
	I2, within	6.225		< .001	0.476	2.502e+6
	I2, between	7.886		< .001	0.603	1.889e+10

Table C10. One sample t-tests over switch types after subtracting repetitions to check that all switch types in the 2x2 (a) and 4x2 (b) rANOVAs were significantly different from task repetitions (=0). 11 (A) and 30 (B) outlier participants were excluded from the two analyses, respectively. E1: external task 1 (indoor/outdoor discrimination); E2: external task 2 (natural/man-made discrimination); I1: internal task 1 (pleasantness judgement); I2: internal task 2 (relatedness judgement).

Difficulty of task repetitions

			frequentist			Bayesian
			df	**F**	**p**	**η^2_p**	**BF_{10}**
task repetition[a]			2.296, 449.927	152.595	< .001	0.438	2.696e+69
					t	**p_{bonf}**	**BF_{10}**
E1 *(1.034±0.167)*	-	**E2** *(1.107±0.184)*			-7.226	< .001	8.323e+12
		I1 *(1.198±0.205)*			-16.333	< .001	2.110e+34
		I2 *(1.226±0.223)*			-19.103	< .001	8.233e+33
E2 *(1.107±0.184)*	-	**I1** *(1.198±0.205)*			-9.107	< .001	2.476e+12

		I2 *(1.226±0.223)*	-11.877	< .001	3.242e+19
I1 *(1.198±0.205)*	-	**I2** *(1.226±0.223)*	-2.770	0.035	35.111

[a] *Greenhouse-Geisser correction was applied due to violated assumption of sphericity (p < .05)*

Note. Frequentist p-value adjusted for comparing a family of 6 (*)

Underlined comparisons signal a change in significance with respect to the analysis with all participants

Table C11. Main analysis and post-hoc t-tests from the 1x4 repeated measures ANOVA (frequentist and Bayesian) with factor task repetition. This was used to check whether there was an intrinsic difference in task difficulty, irrespective of switch costs. 4 outlier participants were removed from this analysis. E1: external task 1 (indoor/outdoor discrimination); E2: external task 2 (natural/man-made discrimination); I1: internal task 1 (pleasantness judgement); I2: internal task 2 (relatedness judgement).

Switch costs grouped by difficulty

	frequentist				Bayesian
	t	**df**	**p**	**Cohen's d**	**BF_{10}**
Hard-to-easy – Easy-to-hard	3.174	190	0.002	0.230	10.185

M±SD: hard-to-easy = 0.077±0.082; easy-to-hard = 0.057±0.065

Table C12. T-test (frequentist and Bayesian) comparing the switch costs of hard-to-easy and easy-to-hard switches. This was used to check whether switch costs were influenced by task difficulty, irrespective of domain. 10 outlier participants were removed from this analysis.

Effects of CTI duration

	frequentist				Bayesian
	df	**F**	**p**	**η^2_p**	**BF_{10}**
domain	1,181	16.308	< .001	0.083	167.426
CTI	2,362	20.503	< .001	0.102	920922.811
domain ✻ CTI	2,362	0.381	0.683	0.002	0.030
			t	**p_{bonf}**	**BF_{10}**

internal	**-**	**external**	-4.038	< .001	2955.569
short	**-**	**medium***	5.137	< .001	23406.291
		long*	5.880	< .001	3.116e+6
medium	**-**	**long***	0.743	1.000	0.080
int. short *(0.074±0.098)*	**-**	**int. medium**** *(0.036±0.098)*	3.922	.001	217.503
		int. long** *(0.036±0.096)*	3.890	.002	1658.620
int. medium *(0.036±0.098)*	**-**	**int. long**** *(0.036±0.096)*	-0.032	1.000	0.083
ext. short *(0.104±0.126)*	**-**	**ext. medium*** *(0.069±0.105)*	3.602	.005	15.455
		ext. long** *(0.058±0.107)*	4.722	< .001	337.334
ext. medium *(0.069±0.105)*	**-**	**ext. long**** *(0.058±0.107)*	1.120	1.000	0.141

Note. Frequentist p-value adjusted for comparing a family of 3 (*)
Note. Frequentist p-value adjusted for comparing a family of 15 (**)
Underlined comparisons signal a change in significance with respect to the analysis with all participants

Table C13. 2x3 repeated measures ANOVA (frequentist and Bayesian) on switch costs with factors domain and CTI, to assess the influence of CTI duration on the magnitude of switch costs. 19 outlier participants were excluded.

	frequentist				**Bayesian**
	t	**df**	**p**	**Cohen's d**	**BF_{10}**
internal short	10.103	181	< .001	0.749	3.132e+18
internal medium	4.937		< .001	0.366	39626.617
internal long	5.076		< .001	0.376	1208.247
external short	11.093		< .001	0.822	5.336e+18
external medium	8.879		< .001	0.658	1.048e+13
external long	7.311		< .001	0.542	8.893e+8

Table C14. One sample t-tests over all conditions of the 2x3 rANOVA (domain x CTI), to check that all the switch costs were significantly different from task repetitions (=0). 19 outlier participants were excluded from the analysis.

Appendix D

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Network	ROI	N
Dorsal DMN	Medial Prefrontal / Anterior Cingulate / Orbitofrontal Cortex	1
	L Angular Gyrus	2
	R Superior Frontal Gyrus	3
	Posterior Cingulate / Precuneus	4
	Midcingulate Cortex	5
	R Angular Gyrus	6
	L and R Thalamus (mediodorsal)	7
	L Hippocampus	8
	R Hippocampus	9
Ventral DMN	L Retrosplenial / Posterior Cingulate Cortex	10
	L Middle Frontal Gyrus	11
	L Parahippocampal Gyrus	12
	L Middle Occipital Gyrus	13
	R Retrosplenial / Posterior Cingulate Cortex	14
	Precuneus	15
	R Superior Frontal / Middle Frontal Gyrus	16
	R Parahippocampal Gyrus	17
	R Angular Gyrus / Middle Occipital Gyrus	18
L ECN	L Middle Frontal / Superior Frontal Gyrus	19
	L Inferior Frontal / Orbitofrontal Gyrus	20
	L Superior Parietal / Inferior Parietal / Precuneus / Angular Gyrus	21
	L Inferior Temporal / Middle Temporal Gyrus	22
	R Crus I	23
	L Thalamus	24
R ECN	R Middle Frontal / Superior Frontal Gyrus	25
	R Middle Frontal Gyrus	26
	R Inferior Parietal / Supramarginal / Angular Gyrus	27
	R Superior Frontal Gyrus	28
	L Crus I / Crus II / Lobule VI	29
	R Caudate	30
DAN (visuospatial)	L Middle Frontal / Superior Frontal / Precentral Gyrus	31
	L Inferior Parietal Sulcus	32
	L Frontal Operculum / Inferior Frontal Gyrus	33
	L Inferior Temporal Gyrus	34
	R Middle Frontal Gyrus	35
	R Inferior Parietal Lobule	36
	R Frontal Operculum / Inferior Frontal Gyrus	37
	R Middle Temporal Gyrus	38
	R Lobule VI / Crus I	39
Anterior Salience	L Middle Frontal Gyrus	40
	L Insula	41

	Anterior Cingulate / Medial Prefrontal / Supplementary Motor Area	42
	R Middle Frontal Gyrus	43
	R Insula	44
	L Lobule VI / Crus I	45
	R Lobule VI / Crus I	46
Posterior Salience	L Middle Frontal Gyrus	47
	L Supramarginal / Inferior Parietal Gyrus	48
	L Precuneus	49
	R Midcingulate Cortex	50
	R Superior Parietal Gyrus / Precuneus	51
	R Supramarginal / Inferior Parietal Gyrus	52
	L Thalamus	53
	L Lobule VI	54
	L Posterior Insula / Putamen	55
	R Thalamus	56
	R Posterior Insula	57

Table D1. List of all 57 ROIs used in our analyses. The ROIs and their subdivision into intrinsic networks are taken from the FIND lab atlas of functional ROIs, as described in (Shirer et al., 2012) (see their Supplementary Material for a complete list of all 90 ROIs and their subdivision into networks).

Change-point detection (no minimum distance)

	df	F	p	η^2_p
Group	1, 35	0.068	0.796	0.002
Session	2,70	1.414	0.250	0.039
Group*Session	2,70	0.917	0.405	0.026

Table D2. 2x3 ANOVA on change-points count (group x session).

Change-point detection (minimum distance = 5 TRs)

When a minimum distance of 5 TRs was set (*version b*), CCID returned an average of ~13.06 (± 2.66) change-points per subject and session. The average distance (in TRs) between change-points was 32.59 TRs (± 7.39). Table D1 below displays number of change-points and distance in TRs across change-points per each group and session.

Change-points count						
Group	**Early**			**Late**		
Session	**Afternoon**	**Evening**	**Morning**	**Afternoon**	**Evening**	**Morning**
Mean	13.93	12.73	12.93	13	13.55	13.55
SD	2.31	2.63	3.01	2.92	2.79	2.79
Min	11	7	8	9	5	10
Max	18	16	20	17	19	19
Distance between change-points (TR)						
Group	**Early**			**Late**		
Session	**Afternoon**	**Evening**	**Morning**	**Afternoon**	**Evening**	**Morning**
Mean	30.56	33.57	32.47	32.35	34.53	31.66
SD	4.31	9.95	7.75	6.06	9.13	6.31
Min	24.31	23	20.75	23.69	22.95	21.74
Max	36.75	61	46.75	44.44	68.40	44.40

Table D3. (Top) Number of change-points per group and session. (Bottom) Distance (in TRs) between change-points per group and session. Mean, SD, minimum and maximum values of both measures are reported.

Contrast	Region (AAL3)	Peak Coordinates			Voxels per cluster	z-score	Peak p_{uncorr}	Cluster p_{uncorr}
K) Early > Late	L Calcarine	0	-90	-10	11	3.879	<.001	.313
L) Late > Early	L Precentral	-24	-16	64	7	3.511	<.001	.423
	R Precuneus / Sup Occipital	24	-74	34	3	3.382	<.001	.614
M) Evening > Afternoon	R Parahippocampal	18	-6	-20	50	4.537	<.001	.041
	R Mid Temporal	44	6	-34	22	3.979	<.001	.158
	R Hippocampus	18	-34	0	19	3.942	<.001	.188
	L Vermis	-2	-50	-14	22	3.901	<.001	.158
	R Amygdala	28	2	-22	10	3.842	<.001	.336
	L Postcentral	-64	-10	18	5	3.768	<.001	.503
	L Mid Temporal	-46	2	-28	5	3.578	<.001	.503
	L Hippocampus	-24	-16	-20	29	3.557	<.001	.109
	R Inf Temporal	40	-4	-34	3	3.485	<.001	.614
	R Orbitofrontal	34	34	-14	7	3.417	<.001	.423
	R Paracentral Lobule	12	-32	66	22	3.409	<.001	.158
	R Supplementary Motor Area	2	-22	66	10	3.395	<.001	.336
	L Crus II	-16	-84	-32	6	3.273	<.001	.460
	L Paracentral Lobule	-2	-28	60	5	3.246	<.001	.503
	R Precentral	16	-20	78	3	3.201	<.001	.614
N) Morning > Afternoon	L Culmen	-20	-52	-18	15	3.672	<.001	.240
	L Insula (Rolandic Opercular)	-44	-8	18	4	3.501	<.001	.553
	R Precentral	40	-18	50	15	3.492	<.001	.240

	R Superior Frontal	18	-16	74	4	3.358	<.001	.553
	L Insula	-34	-18	18	5	3.349	<.001	.503
O)	**Interaction Early > Late X Evening > Afternoon**							
	L Inferior Temporal	-58	-58	-6	12	3.589	<.001	.292
P)	**Interaction Late > Early X Morning > Afternoon**							
	L Supplementary Motor Area	-6	10	64	75	4.334	<.001	.015
	L Inf Frontal (pars triangularis)	-36	26	30	37	4.057	<.001	.074
	R Postcentral	44	-16	36	16	3.671	<.001	.225
	R Insula	36	-14	14	12	3.605	<.001	.292
	R Mid Frontal	32	30	34	11	3.509	<.001	.313
	L Postcentral	-50	-10	42	44	3.499	<.001	.054
	Undefined	26	-30	0	4	3.472	<.001	.553
	L Crus I	-26	-68	-36	19	3.434	<.001	.188
	Undefined	2	-6	-8	3	3.208	<.001	.614

Table D4. Results from the second-level GLM analyses (flexible factorial design) testing for the difference across chronotypes and time of day as well as their interaction after averaging across all change-points (used as event onsets). Specific contrasts include: A) Early vs Late chronotypes, B) Late vs Early, C) Evening vs Afternoon sessions, D) Morning vs Afternoon, E) interaction of Early vs Late and Evening vs Afternoon, F) interaction of Late vs Early and Morning vs Afternoon. Results are thresholded at $p < .001$ with no correction for multiple comparisons.

Contrast	Region (AAL3)	Peak Coordinates			Voxels per cluster	z-score	Peak p_{uncorr}	Cluster p_{uncorr}
A) Group average, 3 TR before CPs	L Anterior Cingulate	-10	24	24	11	3.653	<.001	.199
	R Supplementary Motor Area	6	0	56	14	3.597	<.001	.150
	R Superior Temporal Pole	38	12	-22	8	3.591	<.001	.271
	L Mid Cingulate	-8	-22	42	5	3.237	.001	.385
B) Group average, 2 TR before CPs	Undefined	38	-2	-12	6	3.559	<.001	.356
	R Insula	40	-16	-8	9	3.519	<.001	.259
	L Sup Anterior Cingulate	-6	26	22	4	3.410	<.001	.455
	Undefined	38	22	4	5	3.351	<.001	.401
	R Insula	26	-14	-10	4	3.345	<.001	.455
	R Anterior Cingulate	2	36	4	3	3.146	.001	.522
C) Group average, 1 TR before CPs	L Mid Cingulate	-12	-38	40	22	4.462	<.001	.085
	R pre-Anterior Cingulate	2	38	6	54	4.058	<.001	.011
	R Insula	36	14	-14	9	3.544	<.001	.257
	R Insula	42	20	2	8	3.544	<.001	.285
	L Mid Cingulate	-6	-44	50	5	3.535	<.001	.400
	L Superior Frontal	-18	6	54	9	3.469	<.001	.257
	L Mid Cingulate	-6	-14	38	9	3.453	<.001	.257
	L pre-Anterior Cingulate	0	38	20	4	3.450	<.001	.454

	R Mediodorsal Thalamus	4	-10	0	9	3.367	<.001	.257
	R Supramarginal	64	-38	34	6	3.302	<.001	.355
	R Mid Cingulate	4	-12	40	4	3.301	<.001	.454
	Undefined	34	-24	-6	4	3.252	.001	.454
	L Mid Cingulate	0	8	32	3	3.190	.001	.521
D) Group average, CPs	L Mid Cingulate / Precuneus	-14	-40	40	81	4.403	<.001	.002
	Undefined	4	-2	-2	29	3.779	<.001	.048
	R Precuneus	14	-50	16	6	3.634	<.001	.345
	L Mid Cingulate	-10	16	38	12	3.588	<.001	.185
	R Precuneus	6	-54	44	14	3.555	<.001	.154
	L Mid Cingulate	-8	-10	38	8	3.540	<.001	.275
	R Postcentral	38	-38	54	4	3.434	<.001	.444
	L Mid Cingulate	-8	-6	38	3	3.429	<.001	.511
	R Angular	48	-48	26	9	3.426	<.001	.248
	L Insula	-34	-6	16	4	3.425	<.001	.444
	R Angular	30	-54	42	8	3.422	<.001	.275
	L Posterior Cingulate	-6	-44	24	4	3.307	<.001	.444
E) Group average, 1 TR after CPs	R Angular / IPL	32	-56	44	12	3.635	<.001	.190
	R Middle Temporal Gyrus	36	-64	28	10	3.602	<.001	.230
	Undefined	0	-2	0	5	3.508	<.001	.396
	L Post Cingulate / Precuneus	-8	-50	16	4	3.258	.001	.450

Table D5. Results from the second-level GLM analyses (one-sample t-test) testing for the average across chronotypes and time of

day after averaging across different event onsets: A) 3 TR before each change-point, B) 2 TR before each change-point, C) 1 TR before each change-point, D) change-points, E) 1 TR after each change-point. Results are thresholded at $p < .001$ with no correction for multiple comparisons (no results survived $p<.05$ with family-wise correction).

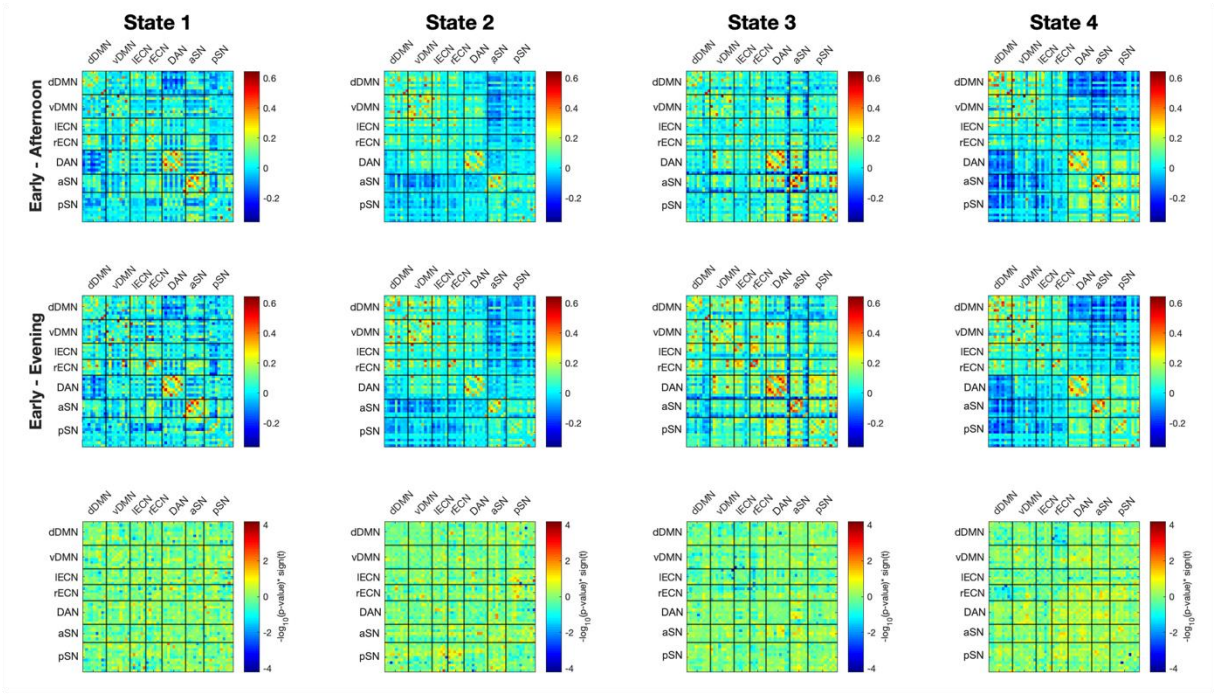

Figure D1. Median FC values for the afternoon (top row) and evening sessions (middle row) of Early chronotypes, and the results of the T-test for each state (bottom row). Results are reported as the negative log10 of p-values (when t values > 0). No FC value survived FDR correction.

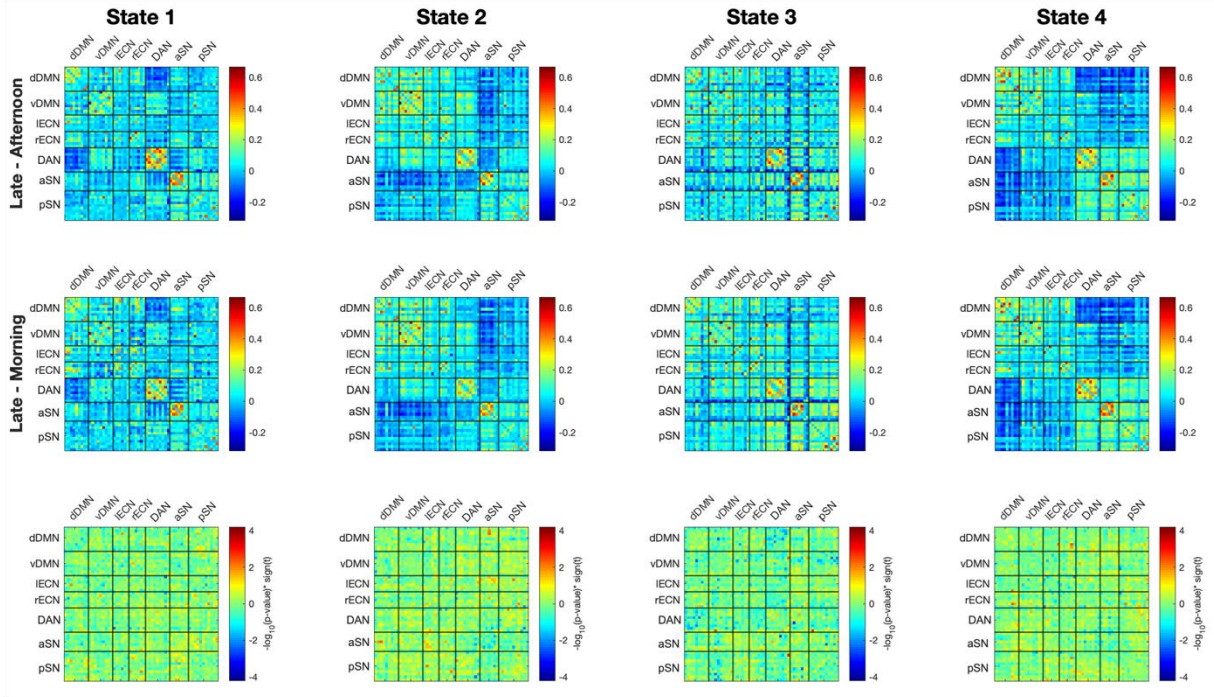

Figure D2. Median FC values for the afternoon (top row) and morning sessions (middle row) of Late chronotypes, and the results of the T-test for each state (bottom row). Results are reported as the negative log10 of p-values (when t values > 0). No FC value survived FDR correction.

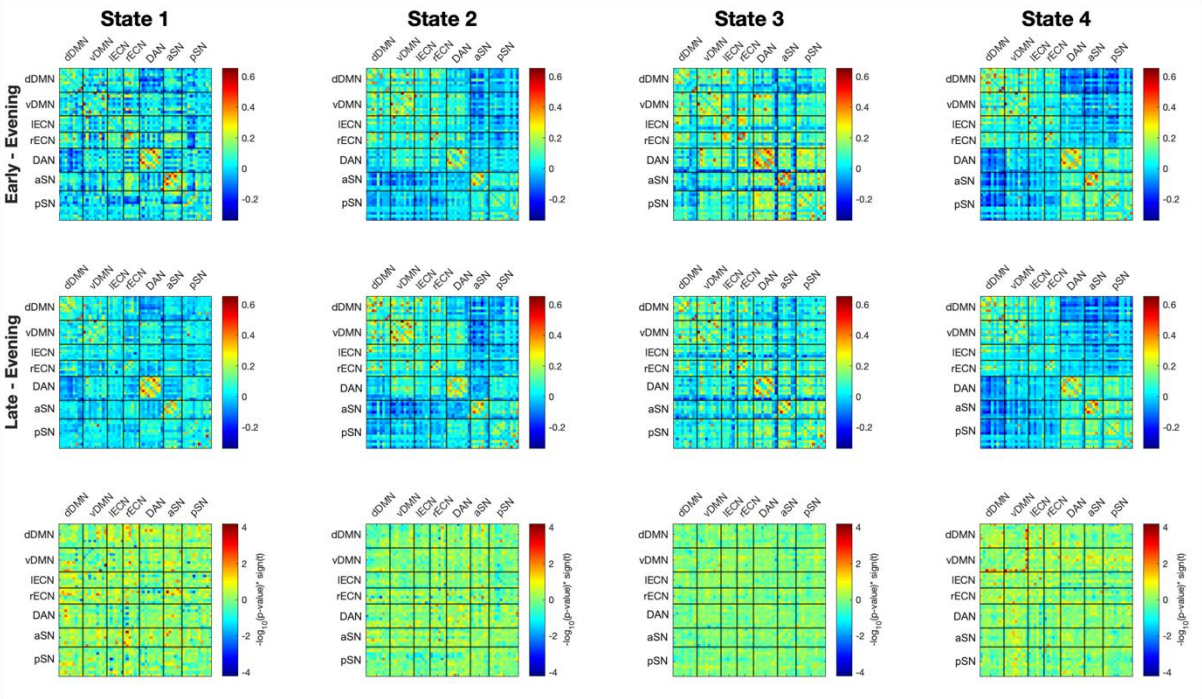

Figure D3. Median FC values for the evening session of Early (top row) and Late (middle row) chronotypes, and the results of the T-test for each state (bottom row). Results are reported as the negative log10 of p-values (when t values > 0). No FC value survived FDR correction.

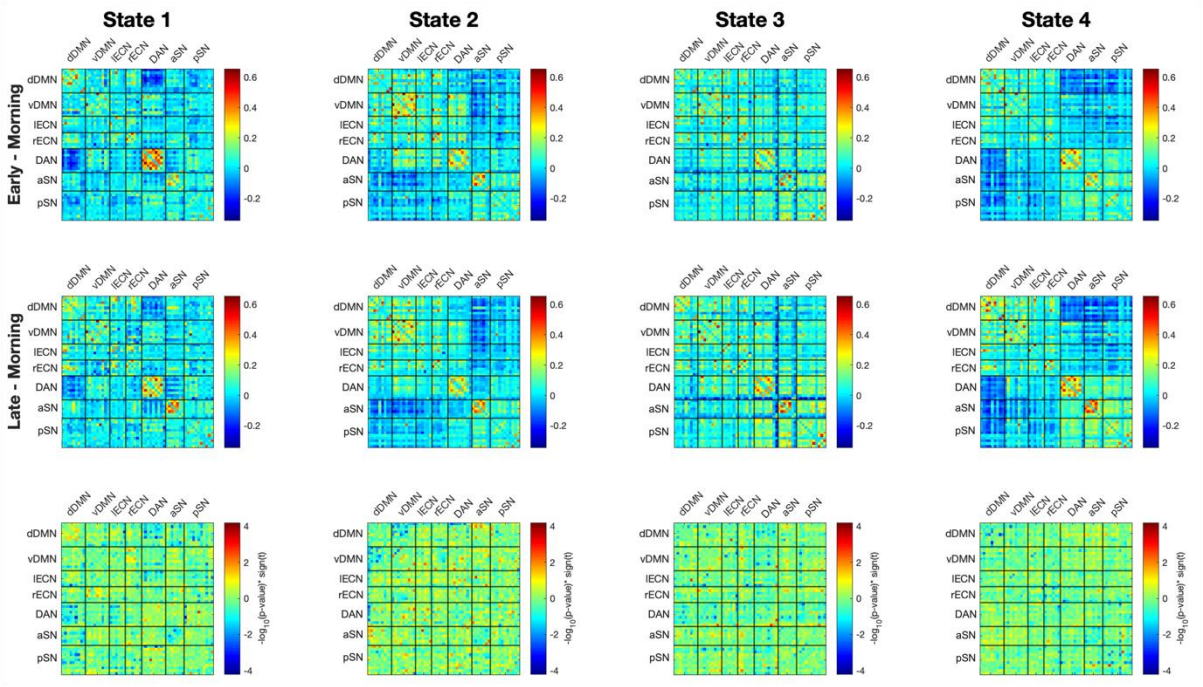

Figure D4. Median FC values for the morning session of Early (top row) and Late (middle row) chronotypes, and the results of the T-test for each state (bottom row). Results are reported as the negative log10 of p-values (when t values > 0). No FC value survived FDR correction.

	M(±SD)			
	State 1	**State 2**	**State 3**	**State 4**
Early	7.133 (±4.257)	11.867 (±7.090)	8.133 (±7.120)	15.467 (±8.659)
Late	7.682 (±6.395)	11.091 (±6.179)	7.273 (±6.009)	15.864 (±8.155)
Early-A	3.067 (±3.150)	3.467 (±3.137)	3.133 (±2.748)	5.267 (±3.654)
Early-E	1.600 (±1.920)	4.333 (±3.200)	2.600 (±3.719)	5.200 (±2.757)
Early-M	2.467 (±2.031)	4.067 (±3.011)	2.400 (±2.261)	5.000 (±4.018)
Late-A	2.727 (±2.585)	3.909 (±2.959)	2.000 (±2.582)	5.364 (±3.140)
Late-E	2.409 (±2.922)	2.909 (±2.114)	2.227 (±2.349)	5.818 (±4.171)
Late-M	2.545 (±3.035)	4.273 (±2.865)	3.045 (±2.734)	4.682 (±2.552)

Table D6. Mean and standard deviation for the frequency of occurrence of each FC state in each group and session.

	State 1		State 2		State 3		State 4	
	t	***p***	***t***	***p***	***t***	***p***	***t***	***p***
Early vs Late	0.291	0.773	0.353	0.726	0.397	0.694	0.142	0.888
Early-E vs Early-A	2.011	0.064	0.840	0.415	0.939	0.364	0.079	0.938
Late-M vs Late-A	0.232	0.819	0.530	0.601	1.829	0.082	0.941	0.358
Early-E vs Late-E	0.941	0.353	1.634	0.111	0.374	0.710	0.503	0.618
Early-M vs Late-M	0.088	0.931	0.210	0.835	0.754	0.456	0.295	0.770

Table D7. Results from t-tests on the frequency of occurrence of each FC state across groups and sessions.

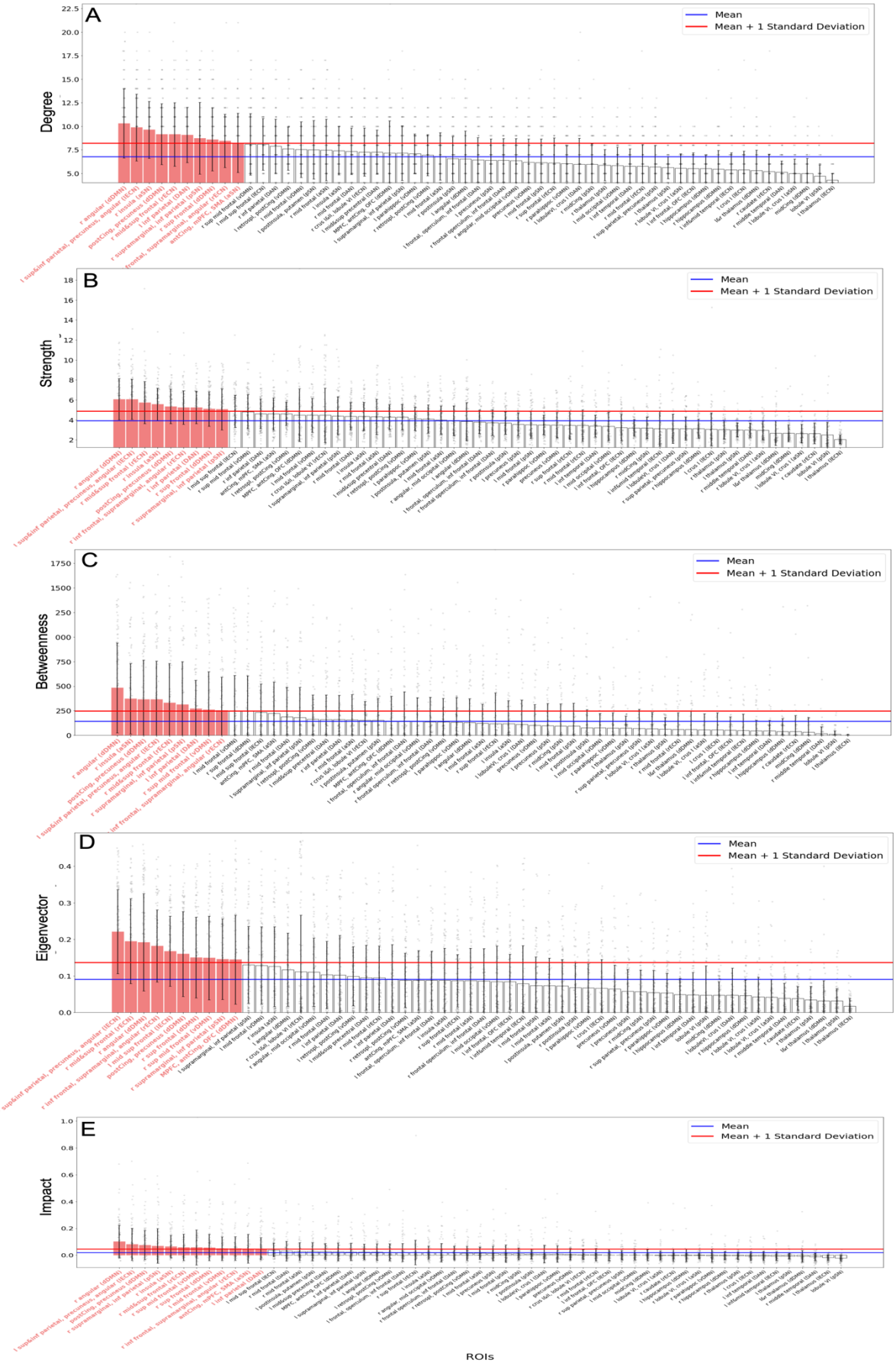
A
Degree
Mean
Mean + 1 Standard Deviation
B
Strength
Mean
Mean + 1 Standard Deviation
C
Betweenness
Mean
Mean + 1 Standard Deviation
D
Eigenvector
Mean
Mean + 1 Standard Deviation
E
Impact
Mean
Mean + 1 Standard Deviation
ROIs

Figure D5. Graph analysis on stationary (non-segmented) data. Mean values of centrality measures for each of the 57 nodes (x axis). From the top: A) degree, B) strength, C) betweenness, D) eigenvector, E) impact. Node values were sorted in descending order to display all nodes with highest score (in red) first. The blue lines indicate the mean across nodes, and the red lines indicate 1 SD above the mean (threshold).

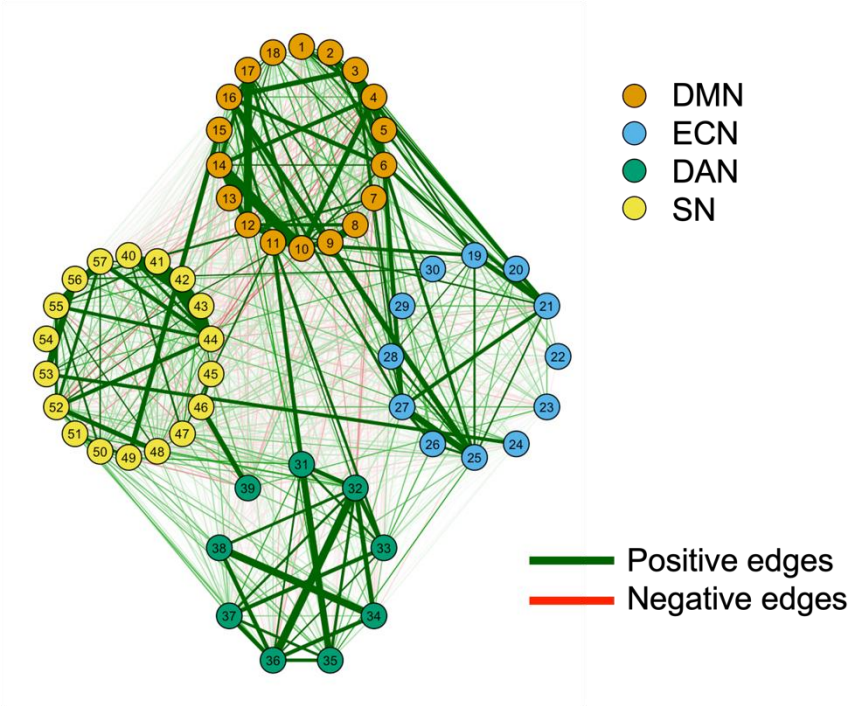

Figure D6. Weighted undirected graph from the averaged adjacency matrices from the analysis of full runs (non-segmented data). The graph shows the average correlation pattern among the 57 nodes. Green edges represent positive correlation coefficients, while red edges represent negative correlation coefficients. Abbreviations: DMN = Default Mode network (both dorsal and ventral portions); ECN = Executive Control network (left and right); DAN = Dorsal Attention network; SN = Salience network (anterior and posterior portions).