RE-EXAMINING THE ROLE OF THE DEFAULT NETWORK

DURING CONTROLLED PROCESSING

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ABSTRACT

Activation of the default network (DN) during externally-directed cognitive control tasks has been associated with off-task behaviors and poor task performance. Recently, evidence has suggested that DN activation may be associated with better cognitive control when access to stored representational knowledge, a putative DN function,, is congruent with task goals (Spreng et al., 2014). Near-ceiling behavioral performance in this earlier study precluded analysis of incorrect trials. We address this limitation by increasing cognitive control demands. Healthy young adults (N=28) were scanned using fMRI while performing a working memory task. Famous and anonymous face stimuli were used to contrast high versus low access to stored representational knowledge, respectively. Differential DN activation was observed during correct and incorrect trials when famous faces were goal-relevant, or distractors. These results provide further evidence that the DN is not a 'task negative' network, but can support cognitive control when access to stored representations is goal-congruent.

Dedication

This thesis is dedicated to B.G, for her unequivocal support lays the foundation for my assiduous

efforts.

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The Default Network and Controlled Processing

The default network (DN) is a collection of functionally-connected brain regions including the medial prefrontal cortex (MPFC), posterior cingulate cortex (PCC), lateral and medial temporal lobes (MTL), and the posterior inferior parietal lobules (IPL; Buckner, Krienen, Castellanos, Diaz & Yeo, 2008). The DN is active during internally-directed cognitive processes, such as self-generated thought and mentalizing, and is associated with attention to personally relevant stimuli, such as familiar faces (Andrews-Hanna, Smallwood & Spreng, 2014; Leveroni et al., 2000). Activity within the DN is reduced during controlled processing and engagement of this network has been shown to disrupt externally-focused, goal-directed behaviour (Raichle et al., 2011; Shulman et al., 1997; Sonuga-Barke & Castellanos, 2007, but see: Spreng et al., 2014). For this reason, the DN has been described as a "task negative" network, associated with poor performance on externally-directed cognitive control tasks, off-task behaviours, and mind-wandering. Indeed, reduced suppression of this network during cognitive control tasks is considered a marker of cognitive dysfunction (Anticevic et al., 2012**;** Christoff, Gordon, Smallwood, Smith & Schooler, 2009; Spreng, 2012; Whitfield-Gabrieli & Ford, 2012). While the DN is associated with internally-mediated processes, and poor task performance when engaged during externally-directed tasks, the dorsal attention network (DAN) is associated with positive task performance during tasks requiring externally-directed attention (Corbetta, Kincade & Shulman, 2002; Ptak and Schnider, 2010). The DAN encompasses the dorsolateral prefrontal cortex (DLPFC), frontal eye fields (FEF), inferior precentral sulcus (IPCS), intraparietal sulcus (IPS), middle temporal motion complex (MT), and superior parietal lobule (SPL; Corbetta et al., 2002; Vossel, Geng & Fink, 2014). The dorsal attention and default networks are anti-correlated

both during both task and rest (Fox et al., 2005; Kelly, Udin, Biswal, Castellanos & Milham, 2008; McKiernan, Kaufman, Kucera-Thompson & Binder, 2003). Tasks requiring external attention are associated with DAN activation and suppression of the DN (Buckner et al., 2008; Gusnard and Raichle, 2001) and internal processes are associated with DN activation (Andrews-Hanna, Smallwood & Spreng, 2014).

Research investigating the role of the DN in cognitive functioning is ongoing, with recent findings contradicting previous claims that DN activity disrupts performance on externally-focused tasks (Anticevic et al., 2012; Mason et al., 2007; Weissman, Roberts, Visscher & Woldorff, 2006). These studies have provided preliminary evidence that the DN can facilitate controlled processing when the demands of the task are congruent with the functions of the DN (i.e., they depend on access to stored representation, or are personally relevant; Crittenden, Mitchell & Duncan, 2015; Konishi, McLaren, Engen, & Smallwood, 2005; Meyer, Spunt, Berkman & Taylor, 2002; Spreng & Grady, 2010; Spreng, Stevens, Chamberlain, Gilmore & Schacter, 2010; Spreng et al., 2014). This suggests that the DN may not be a "task negative" network (Spreng, 2012), but rather, activation of the DN may facilitate goal-directed cognition when external task-demands are congruent with DN functions.

The ability of the DN to facilitate controlled processing may also rely upon interactions among brain networks. During controlled processing of stimuli with personal relevance, DN regions increase functional connectivity with the frontoparietal-control network (FPCN; Spreng, Stevens, Chamberlain, Gilmore & Schacter, 2010; Gerlach, Spreng, Gilmore & Schacter, 2011; St. Jacques, Kragel & Rubin, 2011), a network of regions associated with cognitive control functions, including conflict monitoring, reasoning, and planning (Kroger et al., 2002; van den Heuvel et al., 2003; Wager, Jonides & Reading, 2004). The FPCN encompasses the rostrolateral

prefrontal cortex (RLPFC), middle frontal gyrus (MFG), precuneus (PCu), anterior extent of the IPL, dorsal anterior cingulate cortex (dACC), and the anterior insula (aINS; Vincent et al., 2008; Spreng, et al., 2010). Spreng et al., (2010) used a common planning task to contrast DN activity when planning was externally-focused (i.e., Tower of London task; Shallice, 1982) or internally-focused (i.e., autobiographical planning for one's personal goals). The FPCN coupled with the DAN during the Tower of London task and with the DN during an autobiographical planning task that required access to internal representations to plan for future goals. The FPCN is anatomically interposed between the DAN and the DN, and may serve to flexibly couple with these networks to support cognitive performance, depending on task demands (i.e., externally-versus internally-focused tasks; Spreng et al., 2010). Indeed, specific nodes within the FPCN, such as the MFG, left aINS, dACC, and superior medial prefrontal cortex (sMPFC), demonstrate functional connectivity with the DN and DAN (Spreng, Sepulcre, Turner, Stevens & Schacter, 2013). Spreng et al. (2013) suggest that activation of these *dual-aligned* nodes enables the FPCN to flexibly couple with either the DAN or DN and may serve as hubs for interactions among the three networks (i.e., FPCN, DN, & DAN) – shifting attentional focus from internal to externally directed processes. While studies have revealed specialised associations across different networks, such as the DN with internally-directed processes (Andrews-Hanna, Smallwood & Spreng, 2014; Leveroni et al., 2000), and the dorsal attention network (DAN) with externally-mediated processes (Corbetta & Shulman, 2002; Corbetta et al., 2002; Ptak and Schnider, 2010), inter-network connections, and interactions may be necessary to support complex cognition (McIntosh, 2000; Spreng, et al., 2013). Cognitive control may depend upon inter-network coupling to support cognitive performance.

A recent study by Spreng et al., (2014) examined the role of the DN during an externally directed N-back working memory task. The N-back task is a visual working memory task associated with engagement of frontal and parietal cortices (Jonides et al., 1993; Owen, McMillan, Laird & Bullmore, 2005). The authors manipulated access to stored representational knowledge during working memory by incorporating DN congruent (famous faces) and DN incongruent (anonymous faces) stimuli (Spreng et al., 2014). Famous faces initiate access to stored representations (e.g., name, occupation, movie roles) and have been shown to reliably activate regions of the DN (Gobbini and Haxby, 2007). Previous studies demonstrating that DN activity during an externally-directed controlled processing task is associated with poor task performance have used stimuli that are devoid of personal meaning, such as shapes or blocks (Weissman et al., 2006). In the Spreng et al. (2014) study, personally meaningful stimuli (i.e., famous faces) were used to investigate whether activation of the DN could support externally directed controlled processing (i.e., working memory). Indeed, this was the case. Famous face working memory trials, in contrast to anonymous face trials, were associated with activity within the DN. Further, accuracy for famous face working memory was higher than anonymous face trials, suggesting that activation within the DN may facilitate task performance under DN-congruent conditions. In contrast to famous faces, anonymous face matches engaged frontal and parietal brain regions associated with external attention. Meyer and colleagues (2012) also demonstrated that DN activation was associated with enhanced performance on a social working memory task which required maintenance and online manipulation of social information. Participants were required to rank order friends based on a given trait, and working memory load was defined as the number of friends to be ranked on a given trial. Social working memory load was associated with parametric increases in activity in frontoparietal and DN regions. Taken

together, these results suggest that the DN can facilitate performance during an externally-directed task, but only when stimuli activate internal representations.

Other reports have postulated a role for the DN during externally-directed, controlled processing tasks. A recent study by Konishi et al., (2015) demonstrated that the DN is active during cognitive control when stimuli to be processed are not accessible to perceptual processing and must rely on mnemonic processes. The DN has also been implicated in task switching, a specific cognitive control function necessary to reorient processing resources from external perceptual processing to perform internally-directed tasks such as retrieving items from memory, engaging in creative or imaginative thought, or considering the perspective of others (i.e., theory of mind; Crittenden et al., 2015). This reorienting or shifting of task context has also been associated with interactions among large-scale brain networks, including the DN (Spreng et al., 2013).

Once thought to disrupt performance during cognitive processing (Anticevic et al., 2012; Mason et al., 2007; Weissman et al., 2006), recent studies have elucidated the role of the DN during the processing of familiar stimuli (Leveroni et al., 2000), social and traditional working memory tasks (Konishi et al., 2015; Meyer et al., 2012; Spreng et al., 2014), problem-solving (Spreng et al., 2010), and task switching (Crittenden et al., 2015). Taken together these studies challenge the characterization of the DN as a 'task negative' network and posit a more active role for these brain regions in cognitive control. Both stimulus properties and cognitive context appear to play a role (Meyer et al., 2012; Spreng et al., 2010; Spreng et al., 2014). The DN can facilitate controlled processing when stimuli have personal meaning (Meyer et al., 2012; Spreng et al., 2014) or when cognitive task demands are personally relevant (Spreng et al., 2010). The engagement of the DN during controlled processing may also be mediated by inter-network

interactions, specifically the FPCN coupling with the DN (Spreng et al., 2010; Spreng et al., 2013).

Default Network Subsystems

The DN can be structurally and functionally divided into three subsystems, each serving differing, and overlapping, processes: the medial temporal subsystem, the dorsomedial subsystem, and the core subsystem (Andrews-Hanna, Reidler, Sepulcre, Pulin & Buckner, 2010).

Medial temporal subsystem. The medial temporal subsystem is comprised of the hippocampus (HC), parahippocampal gyrus (PHG), the retrosplenial cortex (RSC), the posterior IPL and the ventromedial prefrontal cortex (vmPFC). This subsystem is supported by white matter tracts connecting the MTL, RSC, and angular gyrus (AG; Schmahmann, Pandya, Wang, et al., 2007;Kobayashi, & Amaral,2003). The medial temporal subsystem is recognized to have a role in mental simulation, imagination, and memory (Andrews-Hanna, 2012; Bar et al., 2007; Buckner et al., 2008; Hassabis & Maquire 2007; Schacter et al., 2012). Specifically, this system is associated with episodic recollection, contextual retrieval, and simulating the future. It is reliably activated during tasks that require participants to view objects with strong contextual associations and use associative conceptual knowledge to guide decision making (Bar, 2007; Kumaran, Summerfield, Hassabis & Maquire 2007). This system works in tandem with the dorsal medial subsystem when access to past internal representations are required (e.g., mentalizing about the future requires knowledge of people within the mentalized situation; Rabin, Gilboa, Stuss, Mar & Rosenbaum, 2010; Spreng & Grady, 2010). The core role of this sub system is to update, and track, knowledge that is not within the immediate perceptual environment.

Dorsal medial subsystem. The dorsal medial subsystem is comprised of the dorsal medial prefrontal cortex (dmPFC), the temporoparietal junction (TPJ), the lateral temporal cortex, and the temporal pole. This subsystem is supported by connections between the inferior parietal lobe and lateral temporal lobe via the middle longitudinal fasciculus. This subsystem is heavily involved in mentalizing, the process in which we attend to the mental states of ourselves, and others around us (Frith & Frith, 2003; Liebeman 2007; Mar, 2011; Saxe, 2006; Schilbach, Eickhoff, Rotarska-Jagiela, Fink & Vogeley, 2008). It has been suggested that this subsystem contributes to social cognition by allowing individuals to access, and use, social conceptual knowledge to reflect on the thought processes of oneself and others. The dmPFC has been associated with social-processing tasks such as discriminating between representations of individuals (Hassabis et al., 2014). The right TPJ has been associated with reflecting on the beliefs of other people (Saxe, 2011). The inferior frontal and lateral temporal regions have been associated with social tasks that involve the semantic/conceptual aspect of mentalizing (Binder & Desai, 2011; Binder, Desai, Graves, & Conant, 2009; Seghier, 2013). This subsystem typically couples with the DLPFC when social tasks require executive control (Liberman, 2007). For example, Meyer et al. (2012) found that, during a social working memory task, working memory load was associated with parametric increases in default network, and DLPFC activity. Taken together, there is evidence to suggest that, overall, this subsystem is involved in social cognitive processes, with contributions from each brain region.

Core subsystem. The core system of the default network is comprised of the anterior medial prefrontal cortex (amPFC) and the PCC. This system is supported by connections between the PCC and amPFC via the cingulum bundle. The PCC is considered a key node in the DN and reliably activates across all tasks that require self-generated thought and is suggested to

be an important zone of integration within the DN (e.g., episodic/autobiographical memory, future thinking, mentalizing, spatial navigation; Binder et al., 2009; Brewer, Garrison, & Whitfield-Gabrieli, 2013; Qin & Northoff, 2011). The dorsal region of the PCC has been associated with monitoring socially behaviourally relevant stimuli and environmental changes (Leech, Kamourieh, Beckmann & Sharp, 2011; Pearson, Heilbronner, Barack, Hayden & Platt, 2011). Other important zones of integration of the DN, that reliably activate across nearly all self-generated thought tasks, include the anterior lateral temporal cortex and the AG (Mar, 2011; Ranganath & Ritchey, 2012). It has been suggested that the AG may serve as a cross-modal hub allowing internal and external representations to interact (Binder & Desai, 2011; Seghier, 2013). The amPFC is most associated with self-related processing (e.g., when individuals reference information to themselves or access personal knowledge; Andrews-Hanna, 2012; D'Argembeau, 2013). This area also becomes active when individuals make value decisions pertaining to personally significant others (Benoit, Gilbert, Volle, & Burgess, 2010; Krienen, Tu, & Buckner, 2010). The amPFC has extensive connections with both the dorsal medial subsystem, and the medial temporal subsystem (Andrews-Hanna et al., 2010). Overall, the core system is best thought of as a zone of integration that allows interaction amongst the other two subsystems.

Familiar Face Processing Network

Haxby, Hoffman & Gobbini (2000) suggest that the human neural system supporting face perception consists of two subsystems: the core system, and the extended system. The core subsystem is associated with brain regions sub-serving distinct perceptual functions: the inferior occipital gyri (IOG), associated with the early perception of facial features, the superior temporal sulcus (STS), associated with the recognition of expression, and the lateral fusiform gyrus (FG), associated with the recognition of unique facial identity. The early perception of facial features is

necessary for processing the recognition of expression and identity. Recognition of identity relies on static properties of faces, such as unique facial structure. In contrast, recognition of expression relies on dynamic properties, such as gaze or facial expression (Haxby et al., 2000). Behaviourally, recognition of identity and expression are dissociable - familiarity, and repetition priming, facilitate performance on facial identity, but not expression, matching tasks (Ellis, Young & Flude, 1990; Young et al., 1986). In contrast to the core subsystem, the extended subsystem is associated with a set of brain regions implicated in processing the social properties of faces: the intraparietal sulcus with identification of direction of gaze, the auditory cortex with pre-lexical speech perception (i.e., lip reading), the limbic system with processing of emotional expression, and the anterior temporal cortex with retrieval of autobiographical information (Hoffman & Haxby, 2000; Puce, Allison, Bentin, Gore & McCarthy, 1998; George et al., 1999; Haxby et al., 2000; Sergent, Ohta, & MacDonald, 1992; Streit et al., 1999). These two subsystems serve distinct functions. Facial perception begins in the core subsystem, which engages perceptual information, followed by further processing in the extended subsystem, which identifies socially relevant information.

While all facial perception engages the core subsystem, the familiarity of a face impacts the engagement of the extended system. In contrast to unfamiliar faces, viewing familiar faces (e.g., a famous face) engages a *person-knowledge extended system*. The person-knowledge extended system encompasses brain regions associated with theory of mind, semantic and episodic retrieval, and emotion (i.e., the amygdala, anterior paracingulate, anterior and medial temporal cortex, posterior STS, & PCC; Gobbini, Leibenluft, Santidago & Haxby, 2004; Leveroni et al., 2000). Engagement of the person-knowledge subsystem may represent inter-connected representations affiliated with our knowledge of a familiar face. These rich neural

representations can enhance visual encoding (Bruce & Young, 1986; Balas, Cox, & Conwell, 2007). Indeed, greater familiarity of a face facilitates performance on recognition tasks (Jackson & Raymond, 2008). In contrast, recognition of unfamiliar faces is easily disrupted by changes in viewpoint (Bruce et al., 1999; Hill, Schyns, & Akamatsu, 1997), poor lighting (Hill & Bruce, 1996; Johnston, Hill, & Carman, 1992) and image/video quality (Burton, Wilson, Cowan, & Bruce 1999). While facial perception begins in the core system, processing in the extended system is modulated by familiarity. Engagement of the person knowledge extended system is isolated to the processing of familiarity, suggesting a unique face neural network for familiar faces.

Memory Systems: Recollection and Familiarity

Dual process theories suggest that recognition memory consists of two distinct processes: recollection, and familiarity (Jacoby, 1991; Joordens & Hockley, 2000; Mandler, 1980; Reder et al., 2000; Yonelinas, 1994, 2002). Recollection refers to the recovery of qualitative information about a specific event. For example, recalling the identity of a person, and the context in which you first encountered them. Familiarity is the subjective feeling of recognizing an event, without remembering specific details. For example, knowing that you have met someone before, without remembering specific details regarding your first encounter. There is evidence to suggest that recollection and familiarity are dissociable processes. Suggesting processing speed is increased when engaging familiar, versus recollective processes, individuals are significantly faster when discriminating events based on familiarity, rather than the contextual details (Hintzman & Caulton, 1997; Gronlund, Edwards, & Ohrt, 1997; Hintzman, Caulton, & Levin, 1998). During recognition tests, distinct receiver operating characteristics (ROCs) are observed when plotting hit rates against false alarm rates. Familiarity is associated with a curvilinear function, whereas

recollection is associated with a linear function (Kelley & Wixted, 2001; Glanzer, Kim, Hilford, & Adams, 1999; Yonelinas, 1994, 1999; Yonelinas, Dobbins, Szymanski, Dhaliwal, & King, 1996). Familiarity and recollection evoke distinct event-related potentials (ERPs), suggesting engagement of separate brain processes (Curran, 2000; Düzel,Yonelinas, Mangun, Heinze, & Tulving, 1997; Smith, 1993; Klimesch, Doppelmayr, Yoneli-nas, Kroll, Lazzara, Rohm, & Gruber, 2001). Further, brain injuries result in differing impairments on familiarity and recollection processes. For example, recollection is disproportionately impaired in amnesic patients (Aggleton & Shaw, 1996; Aggleton et al., 2000; Carlesimo, 1994). Indeed, theoretical, neural, and behavioural research support recollection and familiarity as two dissociable cognitive processes involved in recognition memory.

Neural systems. Neuroimaging studies on recognition memory suggests that recollection and familiarity are supported by engagement of the medial temporal and frontal lobes (Yonelina, 2002). In the medial temporal lobe, the hippocampal region is critical for recollection, whereas the surrounding structures in the medial and inferior temporal lobe are associated with familiarity processes (e.g., the parahippocampal cortex; Aggleton & Brown, 1999; Eichenbaum, Otto, & Cohen, 1993). Indeed, damage severing the HC from surrounding structures primarily disrupts the associative elements of recollection, whereas extensive MTL damage impairs both recollective and familiarity processes (Gilboa et al., 2006). Analysis of neural activation patterns associated with recognition memory elucidate recollection and familiarity processes differentially engaging MTL regions (Skinner & Fernandes, 2007). Recollection has been associated with increased activation in the PHG and HC, whereas familiarity is associated with decreased activation in the right HC. Engagement of MTL regions during recollective and familiarity processes is typically associated with memory storage (Squire & Zola-Morgan, 1991;

Aggleton & Brown, 1999). Whereas the MTL is implicated in memory storage, the frontal lobe is implicated in the *retrieval* of semantic and episodic memory (Tulving & Markowitsch, 1998). Episodic memory gives rise to the conscious experience of "remembering" (i.e., recollection), and semantic memory gives rise to the conscious experience of "knowing" (i.e., the feeling of familiarity; Tulving, 1985; Yonelina, 2002). A recent meta-analysis suggests that familiarity and recollection are associated with differentiated, and overlapping activation patterns within the frontal lobes. While both recollection and familiarity processes activate the right DLPFC, recollection is associated with additional activity in the bilateral anterior, and superior, frontal lobes (Skinner & Fernandes, 2007). Dissociable neural correlates suggests process-dependent activation within medial temporal and frontal lobe regions during familiarity and recollection processes (Aggleton & Brown, 1999; Skinner & Fernandes, 2007; Yonelina, 2002). The medial temporal lobes are implicated in memory storage (Squire & Zola-Morgan, 1991; Aggleton & Brown, 1999) and retrieval processes engage the frontal lobes (Tulving & Markowitsch, 1998).

Current Study

Study rationale and research aims

Activation of the DN during externally-directed controlled processing has been associated with off-task behaviour and poor task performance (Andrews-Hanna, Smallwood & Spreng, 2014). However, previous studies have typically used stimuli that do not require an internal focus or access to stored internal representations (Weissman et al., 2006). It follows then, that activation of the DN in these studies has been associated with off-task behaviour. A study by Spreng et al. (2014) provided preliminary evidence that activation of the DN is associated with successful performance during an externally-directed controlled processing task when stimuli (famous faces) engage stored representational knowledge. This suggests that the

DN may not be a "task negative" network, but, rather, may facilitate performance under DN-congruent conditions. However, performance on the previous task was near ceiling, precluding investigation of the association between DN activity and task performance. Here we use a more challenging 3-back faces task to directly examine the impact of DN activity on performance by examining correct and incorrect trials separately. The overall aim of the study is to extend previous work by Spreng and colleagues (2014) to directly investigate the contribution of DN activity to externally-directed cognitive control.

Hypotheses

We investigate whether default network activity will facilitate controlled processing under conditions that require access to stored representations. We hypothesize that when access to stored representations can be used to support cognitive control (e.g., famous faces that serve as targets), DN activity will be associated with better task performance. In contrast, when access to stored representations is not goal-relevant (i.e. distracting), default network activity will be associated with off task behavior and poor task performance.

Methods

Participants

Twenty-eight healthy, young adult participants (18-35 years of age) were recruited from the undergraduate research pool at Cornell University. All participants were healthy, with normal or corrected-to-normal vision. Informed consent was obtained, and the experiment was conducted in accordance with the York University Office of Research Ethics and the Institutional Ethics Review Board at Cornell University. Three participants were excluded. One due to an fMRI artefact, one because of a response box malfunction, and a third because of poor famous

face recognition (< 10 famous faces recognized). After exclusions, 25 participants remained ($M_{age} = 21$; 64% female).

Study Design

Participants completed a practice session of a working memory task, and then underwent MRI scanning while completing eight runs of a working memory task. After scanning, participants completed a recognition task for the face stimuli from the working memory task, where they were asked to judge the 'famousness' of each image.

Tasks

Practice task. This task consisted of a series of screens explaining the working memory task rules (see below). Participants were required to complete practice blocks of each task condition. The first two blocks of the practice task were non-timed 1-back and 3-back blocks (see N-back task). During the first two blocks, stimuli were presented for an unlimited time period (i.e., stimuli did not cycle without a participant response). Afterwards, participants were required to complete four blocks of a 1-back, and 3-back task (approximately 15 minutes; see below for stimuli presentation details). Within each block was one 1-back, and one 3-back task. Participants did not proceed until they had reached 80% accuracy on the 1-back, and 60% on the 3-back task or had failed the practice task three times.

N-back task. This task consisted of 1-back, 3-back, and rest blocks, across eight runs. Within each run was one 1-back, three 3-back, and four rest blocks. For the 1-back condition, participants were required to press a button when the face they saw was the same face presented one image before, and press another button when the face they saw was not the same face presented one image before. For the 3-back portion, participants were required to press a button

when the face they saw was the same face presented three images before, and press another button when the face they saw was not the same face presented three images before. For our rest condition, between working memory blocks, participants were presented with a fixation cross for 14 seconds. The task was approximately one hour (i.e., seven minutes per run). Each run consisted of 152 non-repeating faces (114 anonymous and 38 famous faces). Each face was presented for 750 ms, followed by a 1250 ms fixation cross. Conditions of interest for the 1-back were anonymous-anonymous faces (AA; $n = 64$) and famous-famous faces (FF; $n = 40$) pairs. Conditions of interest for the 3-back were anonymous-famous-famous-anonymous faces (AFFA $n = 72$), and famous-anonymous-anonymous-famous faces (FAAF $n = 72$), quadruplets. These quadruplets were chosen as they are balanced for stimuli (i.e., famous and anonymous faces). Each pair and quadruplet was separated by an anonymous face (see Figure 1).

Recognition task. This task consisted of 304 famous and 480 anonymous faces from the working memory task. Participants were shown each face and asked to decide if the face was famous, or not famous. The purpose of this task was to exclude unrecognized famous faces from the n-back famous face trials.

Stimuli

Images of famous faces were gathered via google images. Images of anonymous faces were gathered via open-source model databases. Face stimuli were edited using Photoshop. First, images were grey-scaled and cropped using oval selection. Background around face stimuli were removed. Last, brightness was adjusted to similar levels across all images.

Data Analysis

  MRI data collection and preprocessing. Brain imaging data were acquired with a 3T GE Discovery MR750 MRI scanner (GE Healthcare, Milwaukee, WI) with a 32-channel receive-only phased array head coil at the Cornell Magnetic Resonance Imaging Facility, in Ithaca. Anatomical scans were acquired using a T1-weighted volumetric MRI Magnetization Prepared Rapid Gradient Echo (MP-RAGE; TR = 7.7ms; TE = 3.4ms; 7° flip angle; 1.0mm isotropic voxels, 176 slices). Eight 7m 18s experimental runs of blood-oxygen-level-dependent (BOLD) functional scans were acquired with a T2*-weighted echo-planar imaging (EPI) pulse sequence (TR = 2000 ms; TE = 25 ms; 80° flip angle; 49 axial slices; 3.0 mm isotropic voxels).

  Anatomical data were skull stripped and segmented using Freesurfer. All fMRI data were processed using AFNI (Cox, 1996). The first four volumes from each run were excluded to allow for T1-equilibration effects. All functional data underwent slice-timing correction, despiking, motion correction, and white matter, ventricle, and drainage vessel regression. Functional data were then co-registered with their skull-stripped anatomical image, and aligned to Montreal Neurological Institute (MNI) space. Lastly, functional data were smoothed using a 6 mm full half-width at half maximum kernel (FWHM).

  Partial least squares. One of the statistical techniques that was used to analyze neuroimaging data was Partial Least Squares (PLS). This method of analysis is a data-driven multivariate statistical technique that reveals patterns of activity that are associated with each condition of our study design (PLS; Krishnan et al., 2011; McIntosh et al., 1996). For analysis of the n-back task we inputted working memory and rest blocks as conditions of interest. Each participant had 32 working memory blocks, using a block length of 44 seconds, and 32 rest

blocks, using a block length of 14 seconds. For our famous and anonymous face analysis, the first instance of viewing an anonymous and famous face were compared. Because participants viewed more anonymous, than famous faces, anonymous faces were randomly chosen until they matched the number of famous faces for each participant. Famous faces and anonymous faces were inputted as conditions of interest, and a trial block time of two seconds was used. For the analysis of our 1-back task, our conditions of interest, FF and AA, were inputted using a trial block time of four seconds. For the analysis of our 3-back task, our conditions of interest, FAAF and AFFA, were inputted using a trial block time of eight seconds. The results of this analysis reveal latent variables (LVs) that are associated with patterns of brain activity that differentiate conditions of interest. Each voxel is given a singular value weight for each LV, known as salience, which is proportional to the covariance of activity with the task contrast on a given LV. Composite brain activity scores for each participant, on each LV, are calculated by multiplying the salience by the BOLD signal value in a given voxel, and calculating the mean across all voxels. Brain scores are then used to examine similarities and differences in brain activity across conditions of interest. Greater activity in brain areas with positive, or negative, weights on an LV will yield positive, or negative, mean scores for each condition across participants. To determine differences in activity across conditions, confidence intervals (95%) for the mean composite brain activity score in each condition are calculated from bootstrap. Significant differences are determined by lack of overlap between confidence intervals. This method of analysis is able to avoid the problem of multiple statistical comparisons because the decomposition and associated resampling techniques consider all voxels simultaneously. This technique is able to identify voxels with co-varying activity, making it methodologically suitable for the investigation of large-scale brain networks. Significance of LVs were determined by 500 permutation tests, using

resampling without replacement. The significance of each voxel's contribution to a LV was provided by bootstrapping the resampled data 500 times, with replacement, to estimate the SE of the salience of each voxel on the LV. A bootstrap ratio (BSR), calculated as the ratio of each salience to its SE, was thresholded at ±2.58 (equivalent to $p < 0.01$). A cluster size of 20 voxels was used, removing any activation/deactivation less than 20 voxels from each LV.

Analyses

Recognition task. For each participant, a trial was excluded if they did not recognize one or more famous faces. For example, if a participant did not recognize the first famous face of a FAAF trials, the trial was excluded. After exclusion, the number of trials included in each analysis were: 1-back correct (FF, $M = 28$, $SD = 7$) and 3-back correct (AFFA, $M = 24$, $SD = 13$; FAAF, $M = 32$, $SD = 12$) and incorrect conditions (AFFA, $M = 13$, $SD = 5$; FAAF, $M = 11.32$, $SD = 5$).

N-back task. Using PLS, baseline rest activity and n-back task activity were inputted as conditions of interest. This analysis was conducted to validate the faces n-back task via activation of brain regions associated with working memory (i.e., bilateral parietal cortex, aINS, dACC and the bilateral FG (FG; Spreng et al., 2014).

Anonymous and famous faces. The first instances of famous and anonymous faces were analyzed using PLS. For our analysis, anonymous faces were randomly chosen until they matched the number of famous faces for each participant. This analysis was conducted to determine if the famous and anonymous faces were eliciting neural activity in accordance with previous studies. Famous faces engage more regions of the DN, such as the MPFC, medial and

lateral temporal lobes and PCC, whereas anonymous faces engage more FPCN and DAN regions, such as the superior parietal cortex (Leveroni et al., 2000; Spreng et al., 2014)**.**

Specific Hypotheses

(i) We hypothesized that performance would be higher when famous faces served as targets. To investigate whether performance would be better for famous versus anonymous face matches, univariate statistics were used to identify the main effect of stimulus type (famous and anonymous) and working memory condition (1-back & 3-back). We then used a priori paired sample t-tests to identify differences in accuracy and reaction time amongst our 1-back (FF & AA) and 3-back (AFFA & FAAF) conditions of interest.

(ii) We hypothesized that when famous faces served as targets, DN activity would be associated with correct trial performance. To investigate whether DN activity would be greater during working memory for famous versus anonymous faces, we used multivariate analyses (PLS) to identify whole-brain patterns of activity for famous versus anonymous face match correct trials: FF vs. AA (1-back); FAAF vs. AFFA (3-back).

(iii) We hypothesized that when famous faces served as targets, DN activity would be associated with correct trials performance. When hypothesized that when anonymous faces served as targets, misses would be associated with DN activity. To investigate whether default network activity during the working memory task was associated with task performance, we used PLS analyses to contrast hits versus misses during the famous and anonymous 3-back working memory trials (i.e. FAAF and AFFA).

Results

Behavioral

Accuracy. We defined accuracy as number of hits in proportion to misses. An analysis of variance was conducted using fame and working memory as factors. For fame, AA and AFFA were combined as one factor level, and FF and FAAF as another. For working memory, 1-back and 3-back conditions were used as factor levels. Significant effects for fame ($F(1, 24) = 27.13$, $p < .001$, $\eta^2 = 0.53$) and working memory ($F(1, 24) = 200.16$, $p = < .001$, $\eta^2 = 0.89$) were observed. There was no significant interaction between working memory and fame. Planned comparisons revealed that working memory was better for fame target trials, AA ($M = 87.81$, $SD = 7.52$) vs. FF ($M = 93.90$, $SD = 4.63$), $t(24) = 4.83$, $p < .001$); AFFA ($M = 64.91$, $SD = 10.48$) vs. FAAF ($M = 71.57$, $SD = 10.981$, $t(24) = -3.05$, $p = .005$).

Reaction time. An analysis of variance was conducted using fame and working memory as factors. For fame, AA and AFFA were combined as one factor level, and FF and FAAF as another. For working memory, 1-back and 3-back conditions were used as factor levels. Significant effects for fame ($F(1, 24) = 11.56$, $p = .002$, $\eta^2 = 0.33$) and working memory were observed ($F(1, 24) = 71.04$, $p = < .001$, $\eta^2 = 0.75$). There was no significant interaction between working memory and fame. Planned comparisons revealed that reaction time was not significantly faster for fame target trials during the 1-back task, AA ($M = 546.03$, $SD = 81.75$) vs. FF ($M = 537.28$, $SD = 85.74$), $t(24) = -1.47$, $p = .155$), but was significantly faster for fame target trials during the 3-back task, AFFA ($M = 625.05$, $SD = 96.89$) vs. FAAF ($M = 602.50$, $SD = 94.13$, $t(24) = 3.97$, $p < .001$).

Functional Neuroimaging

We conducted preliminary analyses to assess the main effects of our primary task manipulations: (1) working memory vs. rest and (2) famous versus anonymous working memory conditions. A contrast of working memory versus rest conditions (collapsed across 1- and 3-back conditions) revealed a significant latent variable dissociating activity between the two conditions ($p < .001$). Consistent with previous work (Spreng et al., 2014), working memory was associated with activity in the bilateral prefrontal and parietal brain regions, dACC and bilateral fusiform gyrus. Regions associated with the rest condition included: PCC, MPFC and IPL (see Table 1 and Figure 3). Next, we analyzed patterns of brain response that differentiated viewing the first instance of a famous versus an anonymous face. The contrast revealed a significant latent variable ($p = .004$). Viewing famous faces was associated with activity in orbitofrontal prefrontal cortex (OPFC), vmPFC, DLPFC, anterior prefrontal cortex, SPL, posterior IPL, portions of the anterior and lateral temporal lobes, PCC and visual associative areas. Viewing anonymous faces was associated with activity in DLPFC, dACC, insula, anterior portion of the IPL, SPL, portions of the lateral temporal lobes, TPJ, PCu, MT, and visual association areas (see Table 2 and Figure 3).

We hypothesized that DN activity would be associated with better working memory performance during the famous face target trials as these stimuli should activate stored associations that would support task performance. For our 1-back condition, multivariate analysis revealed a pattern of brain activity dissociating FF and AA hits ($p < .002$). For the FF condition, regions included the MPFC, PCC, posterior IPL, TPJ, PHG, HC, dACC and insula. For the AA condition, regions included the PCC, lateral temporal lobes, FEF, DLPFC, TPJ, MFG, anterior IPL and anterior PFC (see Table 3 and Figure 5). For the 3-back working memory

conditions, FAAF and AFFA were dissociated (p = .038). FAAF hits were associated with activity in VMPFC, lateral & medial temporal lobes, dACC, MFG, RLPFC, DLPFC, IPCS, MT and bilateral FG. AFFA hits regions included the MFG, insula & SPL (see Table 4 and Figure 6).

We postulated that errors might be caused by a failure of the FPCN to couple with the appropriate network (i.e., the DAN for anonymous faces, and the DN for famous faces; Spreng et al., 2013). To address this question we first analyzed each stimulus condition separately. Contrasting FAAF hits versus misses revealed a significant LV (p < .001). Famous face hits were associated with activity in dorsal PCC, lateral temporal lobes, HC, insula, dACC, DLPFC, TPJ, bilateral intraparietal sulcus (IPS), bilateral SPL and bilateral FG. Famous face misses were associated with activity in the PHG, PCC, MPFC, MFG, anterior IPL, SFG, and left FG (see Table 5 and Figure 7). AFFA hits versus misses also revealed a significant LV (p = .046). Anonymous face hits were associated with activity in the MFG, anterior cingulate cortex (ACC), aINS, IPL, DLPFC, FEF, IPS, & right FG. Anonymous face misses were associated with activity in the lateral temporal lobe, AG, PCu, SPL & MT (see Table 6 and Figure 7). Next, we directly contrasted 3-back famous and anonymous misses. Our analysis revealed a significant pattern of activity dissociating FAAF and AFFA miss conditions (p = .002). Activity associated with famous face misses included the MPFC, posterior IPL, PCC, MFG, FEF & anterior IPL. For anonymous face misses, activity was observed in the HC, lateral temporal lobes, PCC, ACC, anterior IPL, PCu & left FG (see Table 7 and Figure 6).

Discussion

Default network activity has been associated with mind wandering, and poor performance on cognitive control tasks (Weissman et al., 2006; Mason et al., 2007). Previous studies investigating the role of the DN during cognitive control tasks have typically used stimuli that

are devoid of personal meaning. When stimuli can access stored representations (e.g., familiar faces), they reliably engage the DN (Leveroni et al., 2000). Spreng et al., (2014) provided preliminary evidence suggesting the activation of the DN during cognitive control can facilitate access to goal-congruent stored representational knowledge. In this earlier study, near-ceiling behavioural performance limited analysis of DN activity and connectivity to correct trials. In the current study, we directly addressed this limitation. Specifically, we increased working memory demands to investigate how DN activity was associated with cognitive control performance when access to representational knowledge was goal-relevant or irrelevant. The inclusion of this more demanding cognitive control condition facilitated analysis of correct and incorrect trials, allowing us to directly examine how the DN activity is associated with cognitive control performance. Consistent with previous findings, working memory engaged regions of both the DAN and FPCN, while viewing famous relative to anonymous faces primarily engaged DN regions (see Tables 1-2; Spreng et al., 2014). Critically, activation of the DN, particularly the medial temporal lobe subsystem, was differentially associated with task performance based on the goal relevance of stored representations. Consistent with our primary hypothesis, activity in these regions was associated with correct trials when fame was goal-relevant and incorrect trials when famous faces were distractors.

Working memory performance is modulated by stimulus familiarity

Our behavioural analyses were consistent with previous reports, as visual working memory was facilitated for famous/familiar faces when compared to anonymous/unfamiliar faces (Jackson & Raymond, 2008; Spreng et al., 2014). Participants were significantly more accurate when matching famous, compared to anonymous, faces, across task demands. Reaction times were significantly faster for famous, compared to anonymous faces during our 3-back condition,

and approached statistical significance during our 1-back condition (see Figure 2). The facilitative effect of familiarity on accuracy, but not reaction time, was consistent across working memory conditions. The rapid stimulus presentation rate suggests that this facilitation may have occurred automatically as opposed to relying on conscious retrieval of long-term memory representations. Todorov, Gobbini, Evans, & Haxby (2007) investigated facial perception and spontaneous retrieval and found that minimal behavioural information, and poor explicit information about a face, is sufficient to elicit automatic mental representations. Jackson & Raymond (2008) reported that visual working memory for faces is enhanced if visual representations of the stimuli are accessible in long-term memory. Here, we included only those famous faces that were recognized by participants – confirming that participants had pre-existing knowledge of visual stimuli. Thus, our finding demonstrating that working memory was improved by fame is consistent with this earlier study and suggests that automatic access to stored representations is sufficient to enhance cognitive control processing.

Default network activity is modulated by stimulus familiarity during cognitive control

We investigated the pattern of activity that dissociated correct famous and correct anonymous face trials. For our 1-back condition, correct famous face trials engaged regions of the DN (e.g., MPFC, posterior IPL, PHG, HC, and PCC), whereas correct anonymous face trials engaged regions of the DAN (FEF, DLPFC & SPL) and FPCN (RLPFC, MFG & aINS; see Table 3). During our 3-back condition, correct famous face trials were associated with regions of the DN (vmPFC, portions of the lateral and medial temporal lobes), FPCN (dACC, MFG, RLPFC), and the DAN (DLPFC, inferior precentral sulcus, and visual area MT), whereas correct anonymous face trials were associated with a pattern of activity encompassing the FPCN (bilateral MFG & insula), and DAN (bilateral SPL) regions (see Table 4). Across working

memory demands, correct famous face trials recruited regions of the DN *and* accuracy for famous face trials was significantly higher in comparison to anonymous face matches. This suggests that DN activity may facilitate task performance. This is in contrast to previous studies suggesting that DN activity is associated with poor task performance (Raichle et al., 2011; Shulman et al., 1997; Sonuga-Barke & Castellanos, 2007). The DN was not active during correct anonymous face trials at any level of working memory demand. This is in-line with previous findings suggesting that the DN may facilitate working memory *only* when task demands are congruent with DN activity (Meyer et al., 2012; Spreng et al., 2014).

Spreng et al., (2014) used a 2-back faces task and reported that correct famous face trials were associated with DN activity. While we observed a similar pattern for the 1-back working memory condition, during the more demanding 3-back condition, increased activity in the DAN and FPCN was observed. This suggests that as task difficulty increases, brain regions associated with attention and cognitive control are recruited. Jonides, Schumacher & Smith (1993) observed, during an n-back task, increases in activity in brain regions associated with attention as working memory load increased. Similarly, Meyer et al., (2012) observed increased activation in frontoparietal *and* DN areas as working memory load increased. Consistent with these previous reports, DN activity was also associated with positive performance for DN-congruent stimuli across both 1- and 3-back working memory conditions.

In line with our hypothesis, when stimuli can access long-term stored representations, DN activity is associated with positive task performance. However, default network activity in isolation may be insufficient for correct task performance as the cognitive demands of the task increase. Increasing working memory demand is associated with greater activation in brain regions associated with attention (Jonides et al., 1993; Meyer et al., 2012). During our 1-back

trials, correct famous face trials were associated with DN activity. As working memory load increased, correct famous face trials were associated with DN, FPCN, and DAN activity. Previous studies that have reported that the DN is associated with poor performance have typically used stimuli devoid of personal meaning, such as blocks or shapes (Weissman et al., 2006). In line with recent findings, we observed that DN activity was associated with positive task performance, but *only* when stimuli were personally relevant (Meyer et al., 2012; Spreng et al., 2010; Spreng et al., 2014).

Default network interactions associated with cognitive control performance

The aim of this study was to extend previous research investigating DN contributions to cognitive control (Spreng et al., 2014) by manipulating both stimulus familiarity and working memory demands. By increasing task demands, we were able to investigate neural activity associated with correct, and importantly, incorrect, trials. Based on previous findings of DN interactions during cognitive control tasks involving personally meaningful stimuli (Spreng et al., 2010), we postulated that DN network coupling might modulate performance during working memory. We observed a pattern of neural activity that dissociated correct from incorrect famous face trials during our 3-back condition (see Table 7 and Figure 6). Correct famous face trials were associated with a pattern of activity encompassing regions of the FPCN, DAN, and DN. Incorrect famous face trials were associated with a pattern of activity encompassing the DN and FPCN. While correct and incorrect trials were both associated with regions of the DN, correct trials showed greater recruitment of DAN and FPCN regions. Correct famous face trials were associated with DN activity in the PCC, lateral and medial temporal lobes, and HC. In contrast, incorrect trials were associated with a more circumscribed DN pattern encompassing the PHC, PCC and MPFC (see Figure 6).

Previous studies investigating working memory for personally significant stimuli have found increases in activity within DN regions during correct trials (Meyer et al., 2012; Spreng et al., 2014). In our study, DAN, DN, and FPCN activity were associated with correct working memory performance for famous stimuli. Co-activation of the DN and DAN during correct famous face trials is in contrast to previous studies reporting that the DN and DAN are anti-correlated at rest, and during goal-directed tasks (Fox et al., 2005). Spreng et al. (2013) identified the dACC, MFG, aINS, and sMPFC as dual-aligned nodes within the FPCN that may flexibly couple with either the DAN or DN to support cognitive performance. We observed activity within dACC and sMPFC regions during correct famous face trials, suggesting that dual-aligned nodes identified by Spreng et al. (2013) may support coupling of the FPCN with the DN and the DAN. We observed activity within the MFG, another dual-aligned node, and the DN during incorrect famous face trials. This suggests that during incorrect famous face trials the FPCN co-activated with the DN, but not the DAN. Spreng et al., (2013) suggested dual-aligned nodes may allow attentional focus to shift from internally- to externally-directed cognition. During famous face trials, our task allows for associations between external perceptual features and internal stored representations to facilitate performance (i.e., recognition of famous faces). Correct performance during famous face trials may be facilitated by a shift from internal processes (i.e., recognition of famous faces, and recollection of prior knowledge), to an external focus (i.e., responding to the n-back task). Internal processes responsible for the facilitative effects of familiarity may be associated with activity within the DN, whereas external-attention processes essential for positive task performance are facilitated by the DAN. Our results support this process as being mediated by the FPCN (Spreng et al., 2013). Failure of the FPCN to couple with the DN to facilitate internal stored representations may reduce the facilitative effects of

familiarity, whereas failure to couple with the DAN, and shift attention externally, may result in poor performance. Indeed, there is an absence of DAN activity during incorrect famous face trials. Poor performance during famous face trials may be explained by a failure to shift focus externally, evidenced by an absence of DAN activity.

Previous studies suggest that the DN facilitates cognitive performance when stimuli access stored representations, and impairs performance when stimuli are devoid of personal meaning (Weissman et al., 2006; Spreng et al., 2014). During correct anonymous face trials, there was an absence of DN activity. We observed FPCN and DAN activity during correct, in contrast to incorrect, anonymous face trials. This is in line with previous studies reporting correct performance for unfamiliar stimuli being associated with activity within attentional networks, but not the DN (Weissman et al., 2006; Spreng et al., 2014). Similar to correct famous face trials, we observed activity within dual-aligned nodes of the FPCN, the MFG and dACC, in addition to DAN activity during correct anonymous face trials. Our results suggests coupling of the DAN and FPCN through the MFG and dACC during correct anonymous face trials (Spreng et al., 2013). Incorrect anonymous face trials were associated with partial recruitment of the DN, FPCN, and DAN. Absence of core DN nodes, such as the MPFC or PCC, typically associated with mind wandering (McGuire et al., 1996; Smallwood et al., 2011), and the presence of regions associated with attention, suggests incorrect performance on anonymous face trials was not due to mind wandering. While famous face trials allow for associations between external perceptual features and internal stored representations to facilitate performance, during anonymous face trials, famous faces serve as distractors. Default network areas recruited during incorrect anonymous face trials overlap with regions associated with the episodic aspects of the DN, such as episodic retrieval (e.g., the right lateral temporal lobe and AG; Andrews-Hanna et al., 2010;

Rugg & Vilberg, 2013). This suggests that participants may have spontaneously engaged stored representations of famous faces (Todorov et al., 2007), impairing performance. During incorrect anonymous face trials, participants were attending to anonymous faces (exemplified by DAN activity), but were distracted by famous faces (exemplified by DN activity). Additionally, a reduction in FPCN activity suggests participants failed to fully engage, or couple, with the appropriate network during incorrect anonymous face trials (i.e., the DAN).

Previous studies have reported that the FPCN, coupled with the DN, is associated with positive task performance during a personally relevant (i.e., autobiographical) problem solving task (Spreng et al., 2010). In this study, we observed that co-activation of the FPCN with the DN *and* DAN is associated with positive task performance for famous face stimuli during a demanding working memory task. During a demanding working memory task, co-activation of the FPCN with *only* the DN was associated with poor task performance during famous face trials. This suggests that as working memory demands increase, co-activation of the FPCN with the DN, in isolation from the DAN, is insufficient for positive task performance when stimuli evoke stored representations (Todorov et al., 2007). Our findings are line with previous studies implicating the DAN and DN during working memory performance for stimuli that access stored representations (Meyer et al., 2012). When stimuli are devoid of personal meaning, activity within regions of the DAN and FPCN is associated with positive task performance. Incorrect anonymous face trials were associated with partial recruitment of the DN, DAN, and FPCN.

Default network areas recruited during incorrect anonymous face trials overlap with regions associated with the medial temporal lobe regions in the DN that are associated with mnemonic and associative processing (Andrews-Hanna et al., 2010). Engagement of these regions by famous face stimuli may facilitate or impair performance depending on trial type.

That is, when famous faces serve as targets, stored representations may facilitate performance, when famous faces serve as distractors, stored representations may impair performance. Additionally, reduction in FPCN activity during incorrect anonymous face trials suggests participants failed to fully couple with the appropriate network (i.e., the DAN). Our results suggest network interactions may serve as an explanatory mechanism for correct, and incorrect trials. Importantly, co-activation of the FPCN with the DN and DAN supports working memory performance *only* when stimuli access stored representations. When stimuli are devoid of personal meaning, positive task performance is associated with activity within the FPCN and DAN.

Recruitment of DN subsystems during controlled processing

Incorrect famous, and anonymous face trials were associated with activity within the DN and FPCN. Our analysis revealed a distinct pattern of DN subsystem activity for each condition. Incorrect anonymous face trials recruited regions that overlapped with the DN medial temporal subsystem, a system associated with the episodic features of the DN (i.e., mental simulation, imagination, episodic recollection and contextual retrieval; Andrews-Hanna et al., 2010). Activity within nodes of the DN during incorrect famous face trials overlapped with the core subsystem of the DN, a system associated with social monitoring, judgments, and self-generated thought tasks (Binder et al., 2009; Brewer, Garrison, & Whitfield-Gabrieli, 2013; Qin & Northoff, 2011). Activity within the medial temporal subsystem during incorrect anonymous face trials suggests participants were engaging in episodic processes associated with the DN (Andrews-Hanna et al., 2010). As famous faces are distracting during anonymous face trials, participants may have been engaging stored representations of famous faces. In our analysis of correct and incorrect famous face trials, correct trials were associated with DN activity

overlapping with regions of the medial temporal subsystem. When famous faces were congruent with task demands (i.e., famous face trials), DN medial temporal subsystem activity facilitated task performance. When famous faces were incongruent with task demands (i.e., anonymous face trials) recollection of stored representations, which elicited medial temporal subsystem activity, served to distract participants, leading to errors.

Activity within the core subsystem during incorrect famous face trials may suggest participants were distracted or engaged in internal processes such as mind-wandering, or day dreaming (McGuire et al., 1996; Smallwood et al., 2011). Alternatively, by failing to engage nodes of the DN associated with the episodic features of the DN, participants may not have spontaneously retrieved stored representations of targets (i.e., famous faces). Todorov et al., (2007) found that when participants could recall information about familiar faces (recalled familiar faces), versus when participants failed to retrieve information about a familiar face (unrecalled familiar face), perceptions of recalled familiar faces were associated with more activity in lateral and medial temporal lobe regions – areas overlapping with the medial temporal subsystem. Absence of medial temporal subsystem activity suggests that during incorrect famous face trials participants failed to retrieve stored representations of famous face stimuli. By failing to retrieve stored representations, targets may have been perceived as unfamiliar faces. Perception of familiar faces as unfamiliar would diminish the facilitative effects of familiarity on cognitive performance (Jackson & Raymond, 2008), explaining errors on famous face trials.

Our results suggest that in both conditions different subsystems of the DN are coupled with the FPCN, providing evidence for distinct roles of DN subsystems during controlled processing (Andrews-Hanna et al., 2010). The role of each subsystem may be mediated by task demands. Core subsystem activity during incorrect famous face trials may be associated with

mind wandering (Andrews-Hanna et al., 2010; McGuire et al., 1996; Smallwood et al., 2011). Indeed, previous research suggests inefficient processing of stimuli is associated with activity in regions of the DN overlapping with some regions of the core subsystem (Weissman et al., 2006). We observed that co-activation of the DN with the FPCN facilitates task performance for famous face stimuli. Division of the DN into subsystems elucidates the relationship between the DN and the FPCN during controlled processing. When recall of stored representations can facilitate performance, as is the case during famous face trials, correct famous face trials are associated with coupling of the FPCN with the medial temporal subsystem. Failure to engage the medial temporal subsystem may impair performance when engagement of stored representations can facilitate performance, evidenced during incorrect famous face trials. When the recall of stored representations may serve to distract, as is the case during anonymous face trials, incorrect anonymous face trials are associated with activity within the medial temporal subsystem. While past studies have found that the DN is associated with positive (Meyer et al., 2012: Spreng et al., 2010; Spreng et al., 2014) or negative (Weissman et al., 2006) task performance, our results suggests that specific subsystems of the DN can facilitate (i.e., the medial temporal subsystem) or impair (i.e., the core subsystem) task performance depending on task goals. The association between the medial temporal subsystem and positive task performance is reliant on task demands. Coupling of the medial temporal subsystem of the FPCN can facilitate task performance, but *only* when targets access stored representations.

Limitations and Future Directions

A potential limitation of the study relates to our interpretation of our famous face 1-back trials. During our 1-back correct famous face trials, compared to our anonymous face trials, we observed DN activity. Interpretation of our 1-back famous face trials may be confounded by stimuli properties because famous faces naturally elicit DN activity (Leveroni et al., 2000). It is important, however, to consider that this pattern of neural activity arises in the context of a continuous working memory performance task. That is, activation of this network is associated with poor performance during externally-directed cognitive tasks (Weissman et al., 2006). Given that our 3-back famous face trials were associated with DN activity, matched for stimulus type (i.e., AFFA vs. FAAF), and consistent with previous results (Spreng et al., 2014), it is unlikely that the DN activation observed during our 1-back is only due to the perception of famous face stimuli. Another limitation of our study is the number of trials used for analysis per participant. In this study, with the exception of match trials, we never repeated an anonymous or famous face. We removed trials where participants did not recognize a famous face. We excluded these trials to ensure we accurately manipulated familiarity. Including unrecognized famous faces limits the scope of our interpretations. That is, we cannot accurately interpret familiar stimuli as modulating network activity if we include unrecognized familiar stimuli in our analysis. By removing trials we excluded approximately 50% of our famous face trials, on average, during our 3-back task. This is a potential limitation when interpreting the results of our famous and anonymous face analysis. Indeed, our anonymous face hit and miss contrasts revealed expected activity for hits, but not for misses. Our anonymous face misses were not associated with widespread DN activity, typically seen in previous studies (Weissman et al., 2006). This may be due to limited statistical power given the imperative to include only recognized famous stimuli.

Last, we did not directly control for degree of familiarity in this study. That is, some famous faces may have been more familiar than others. In our study, we manipulated task difficulty across two stimulus types: famous, and anonymous faces. We observed that familiarity can enhance task performance, and is associated with DN activity. It is unclear if task performance, and DN activity, is modulated by level of familiarity during a demanding cognitive task. Familiarity has been shown to modulate activity in regions of the DN in a recognition task, with more familiar faces associated with greater activation in the anterior paracingulate cortex, and posterior superior temporal sulcus (Gobbini & Haxby, 2007). One hypothesis is that increases in familiarity might coincide with parametric increases in activity in DN regions during a working memory task. Future studies should investigate the effect of multiple levels of familiarity on modulating DN activity during a cognitive task.

Conclusion

The purpose of this study was to examine the role of the DN during externally-directed cognitive control. We built upon previous research suggesting activation of the DN during working memory can facilitate task performance by manipulating working memory difficulty and analyzing both correct and incorrect trials (Spreng et al., 2014). Across working memory demands, activity within the DN was associated with positive task performance when target stimuli were able to access stored representations. Further, accuracy was significantly higher for famous versus anonymous face trials. This suggests that when stimuli automatically or spontaneously accessed long-term stored representations (Todorov et al., 2007), the DN may facilitate controlled processing. Previous studies have found that, as working memory load increases, activation in brain regions associated with attention concurrently increase (Jonides et al., 1993; Meyer et al., 2012). In our study, as working memory demands increased, we observed

recruitment of attention networks (i.e., FPCN and DAN) during famous and anonymous face trials. Importantly, when stimuli activated stored representations (i.e., famous faces), engagement of the DN, in addition to attentional networks, was associated with positive task performance.

We further postulated that coupling may serve as a neural mechanism supporting the role of the DN during controlled processing. Coupling of the FPCN with the DN, or DAN, to facilitate task performance has been demonstrated in previous research (Spreng et al., 2010). Spreng et al., (2013) identified nodes within the FPCN that may flexibly couple with the DAN or DN to support goal-directed cognition. We observed co-activation of dual-aligned nodes (Spreng et al., 2013) with DN and DAN activity during correct famous, and anonymous face trials. Activation of dual-aligned nodes with DN and DAN activity supports the idea of coupling as an underlying mechanism facilitating controlled processing. Recruitment of regions of the DAN, in conjunction with FPCN and DN during a continuous performance task is a novel finding. We suggest that as cognitive demand on an externally-directed task involving familiar stimuli increases, co-activation of the DAN and DN, supported through dual-aligned nodes of the FPCN, is necessary for positive task performance.

A core rationale of our study was to investigate the relationship between DN activation and cognitive control by contrasting brain activity during correct *and* incorrect trials. Our analysis revealed a distinct pattern of DN subsystem activity during incorrect trials for famous and anonymous faces. Correct famous, and incorrect anonymous, face trials recruited regions of the medial temporal subsystem, a system associated with the episodic processes of the DN (Andrews-Hanna et al., 2010). Incorrect famous face trials recruited regions of the core subsystem, a system associated with mind wandering, and daydreaming (McGuire et al., 1996; Smallwood et al., 2011). Our results suggest that distinct subsystems of the DN may support, or

impair cognitive performance. As observed during our incorrect famous face trials, core subsystem activity in isolation from medial temporal subsystem activity may be insufficient to support controlled processing when stimuli access stored representations. When famous face stimuli served as targets, activation of the medial temporal subsystem activity was necessary for accurate performance. In contrast, when famous face stimuli served as distractors, medial temporal subsystem activity was associated with poor task performance, suggesting that the DN can support externally-directed cognitive control, but only when task demands are congruent with DN functions.

Consistent with our overall hypothesis, when stimuli automatically, or spontaneously, access long-term stored representations, as is the case in famous face matches, DN activity facilitates task performance. As task demands increase, recruitment of attention and cognitive control networks is necessary for correct performance on famous, and anonymous face trials. We predicted that DN activity would be associated with correct performance when stimuli accessed stored representations. Our results, however, suggests that different subsystems of the DN may be associated with differing task performance (i.e., correct, and incorrect trials), across task demands. We provided evidence suggesting that coupling may serve as a mechanism supporting the role of DN during controlled processing. Our results support the importance of DN activation and interactions with other brain networks to support externally-directed cognitive control. These results demonstrate that the DN is not simply a "task negative" network. The DN, FPCN, and DAN interact to facilitate controlled processing. Both the nature of the stimuli and task demands determine the extent and impact of DN engagement during externally-directed cognitive control.

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Table 1. Peak activation coordinates for rest and sustained task performance (n-back)

Lat	Region	x	y	z	BSR
B	Medial PFC	0	40	-4	7.74
L	Superior Frontal Gyrus	-20	40	32	4.95
	Inferior Frontal Gyrus	-44	-36	-2	3.93
L	Premotor Cortex	-18	12	52	3.59
R	Primary Motor Cortex	46	-16	48	4.97
	Posterior Insula	-38	-16	-6	4.86
L	Inferior Parietal Lobule	-66	-32	32	5.26
R	Inferior Parietal Lobule	66	-24	30	5.87
B	Superior Parietal Lobule	16	-56	68	7.06
B	Posterior Cingulate	-14	-40	40	5.71
B	Visual Association Cortex	-12	-82	28	10.91
		54	-70	24	4.02
		-58	-58	-14	3.28
L	Cerebellum	-20	-40	-32	4.95
R	Cerebellum	8	-56	-58	4.54

Faces n-back > Rest

Lat	Region	x	y	z	BSR
R	Frontal Pole	2	62	-22	-4.70
R	Inferior Frontal Gyrus	30	46	-18	-3.99
L	Dorsolateral Prefrontal Cortex	-36	58	10	-5.61
R		20	58	32	-3.33
R		14	68	18	-3.12
R	Frontal Eye Fields	36	12	52	-7.48
L		-32	2	52	-4.57
B	Anterior Cingulate	2	22	42	-10.03
R	Primary Motor Cortex	12	-38	66	-3.80
R	Anterior Inferior Parietal Lobule	50	-46	52	-7.25
L	Anterior Inferior Parietal Lobule	-58	-52	26	-3.36
L	Anterior Temporal Lobe	-42	-10	-42	-3.83
L	Posterior Superior Temporal Sulcus	-50	-54	6	-4.61
R	Fusiform Gyrus	44	-60	-18	-5.92
L	Fusiform Gyrus	-44	-62	-26	-10.55

Note. See Figure 2 for rest and sustained working memory performance brain activation maps

Table 2. Peak activation coordinates for viewing the first instance of famous and anonymous faces

Lat	Region	Coordinates			
		x	y	z	BSR
Famous > Anonymous					
R	Orbitofrontal Cortex	34	36	-18	6.57
L	Ventromedial Prefrontal Cortex	-8	46	-22	4.93
R	Ventromedial Prefrontal Cortex	16	56	-14	4.27
R	Medial Frontal gyrus	16	54	4	4.40
		16	38	36	5.66
R	Anterior Prefrontal Cortex	12	72	-9	3.82
L	Anterior Prefrontal Cortex	-16	56	2	4.27
L	Premotor Cortex	-38	-2	42	3.22
L	Inferior Frontal Gyrus	-38	24	10	5.41
R	Inferior Frontal Gyrus	42	10	30	3.99
R	Dorsolateral Prefrontal Cortex	46	32	10	5.04
L	Dorsolateral Prefrontal Cortex	-16	28	46	5.54
		-16	44	42	3.89
L	Superior Parietal Lobule	-36	-66	56	3.74
R	Posterior Inferior parietal Lobule	44	-58	22	4.08
L	Middle Temporal Gyrus	-52	-14	-18	5.27
R	Middle Temporal Gyrus	60	0	-30	3.16
R	Inferior Temporal Gyrus	36	-10	-42	3.21
L	Posterior Cingulate Cortex	-10	-54	18	6.17
		-2	-32	38	4.65
R	Basal Ganglia	20	8	24	4.84
R	Thalamus	4	-16	2	5.31
		4	6	-10	5.18
L	Fusiform Gyrus	-30	-52	-12	4.48
R	Fusiform Gyrus	38	-52	4	3.62
R	Visual Association Cortex	36	-70	14	3.00
L	Visual Association Cortex	-42	-80	6	5.37
R	Associative Visual Cortex	48	-78	-2	4.80
R	Cerebellum	38	-40	-28	4.15
Anonymous > Famous					
L	Dorsolateral Prefrontal Cortex	-36	36	24	-5.33
R	Dorsolateral Prefrontal Cortex	46	44	14	-4.65
L	Inferior Frontal Gyrus	-54	6	12	-3.77
R	Inferior Frontal Gyrus	44	44	-2	-3.33
B	Dorsal Anterior Cingulate	0	6	30	-6.60
R	Premotor Cortex	2	-12	64	-6.23

R	Premotor Cortex	56	6	28	-5.62
R	Premotor Cortex	18	6	56	-3.58
L	Premotor Cortex	-24	-6	52	-3.93
L	Premotor Cortex	-56	6	30	-4.54
L	Anterior Insula	-28	18	-10	-4.98
R	Anterior Insula	40	12	-6	-4.12
L	Posterior Insula	-34	-12	-4	-3.51
R	Posterior Insula	46	0	4	-3.42
R	Anterior Caudate	14	18	-8	-4.39
L	Putamen	-18	16	-8	-3.88
		-22	4	-14	-3.75
R	Anterior Inferior Parietal Lobule	40	-38	44	-3.33
R	Superior Parietal Lobule	34	-46	64	-3.92
R	Primary Sensory Cortex	58	-12	30	-5.55
R	Somatosensory Association Cortex	9	-36	52	-4.28
L	Precuneus	-6	-52	54	-4.68
		-14	-64	42	-3.82
L	Temporo-parietal Junction	-62	-12	16	-3.54
L	Superior Temporal Gyrus	-62	-8	6	-3.35
R	Superior Temporal Gyrus	44	-4	-14	-3.16
R	Middle Temporal Gyrus	60	-22	-6	-4.18
R	Middle Temporal Gyrus	50	-29	-16	-3.72
R	Middle Temporal Gyrus	48	-46	-5	-4.65
L	Middle Temporal Gyrus	-56	-34	14	-6.80
L	Ventral Posterior Cingulate	-12	-28	34	-3.84
L	Primary Visual Cortex	-10	-88	0	-3.06
L	Visual Area MT	-52	-64	4	-4.65
L	Visual Association Cortex	-2	-100	-2	-4.63
R	Visual Association Cortex	8	-82	26	-4.44
R	Visual Association Cortex	-14	-66	-10	-3.64
R	Cerebellum	22	-60	-40	-4.13
R	Cerebellum	14	-60	-26	-4.07
R	Cerebellum	32	-18	66	-3.66
R	Cerebellum	12	-66	-50	-3.67
R	Cerebellum	28	-54	-34	-3.97
R	Cerebellum	2	-74	-46	-3.79

Note. See Figure 3 for brain activation maps corresponding to the first instance of viewing a famous, and anonymous face

Table 3. Peak activation coordinates for correct famous (FF) and anonymous (AA) face 1-back trials

Lat	Region	Coordinates			
		X	y	z	BSR
FF > AA					
R	Medial Prefrontal Cortex	8	72	8	-3.62
L	Superior Medial Prefrontal Cortex	-10	64	22	-3.37
L	Dorsal Anterior Cingulate	-16	42	14	-4.89
L	Posterior Inferior Parietal Lobule	-48	-70	32	-2.93
L	Parahippocampal Cortex	-28	-40	-16	-4.23
R	Parahippocampal Cortex	18	-30	-20	-3.11
L	Hippocampus	-24	-22	-4	-5.17
R	Temporoparietal Junction	36	-48	2	-4.01
R	Posterior Cingulate	6	-48	20	-3.34
R	Putamen	22	0	24	-4.86
L	Putamen	-24	-2	30	-3.37
L	Brainstem	-4	-16	-8	-3.03
L	Cerebellum	-14	-38	-34	-3.73
AA > FF					
R	Anterior PFC	28	46	12	3.23
L	Dorsolateral Prefrontal Cortex	-44	34	34	3.69
		-48	10	38	3.59
R	Frontal Eye Fields	28	-12	48	6.75
R	Middle Frontal gyrus	42	38	14	4.00
L	Premotor Area	-12	-24	48	3.17
R	Supplementary Motor Area	2	6	46	5.52
L	Supplementary Motor Area	-6	-4	68	3.35
L	Anterior Insula	-26	24	-4	5.91
R	Anterior Insula	34	18	-2	6.01
R	Insula	32	-26	22	3.70
L	Insula	-30	-26	8	3.52
R	Thalamus	10	-24	4	6.00
L	Premotor Cortex	-54	0	46	3.86
L	Superior Temporal Lobe	-52	-22	0	4.90
R	Superior Temporal Lobe	64	-16	-6	4.00
R	Posterior Inferior lateral Temporal lobe	60	-36	-20	3.18
L	Posterior Superior Temporal Sulcus	-50	-54	6	6.48
R	Posterior Superior Temporal Sulcus	60	-50	-2	4.95

R	Striatum	14	-14	-12	3.68
L	Somatosensory Cortex	-22	-18	72	4.86
		-12	-46	64	3.37
R	Supramarginal gyrus	36	-50	30	3.37
L	Superior Parietal Lobule	-38	-42	54	7.25
R	Anterior Inferior Parietal Lobule	50	-34	48	5.25
R	TPJ	66	-40	30	3.62
L	Precuneus	-2	-36	50	3.01
R	Retrosplenial Cortex	14	-62	10	2.98
L	Cuneus	0	-68	12	3.65
R	Posterior Occipital Lobe	22	-94	0	4.64
		18	-84	-14	3.43
L	Posterior Occipital Lobe	-32	-76	10	3.31
L	Lateral Occipital lobe	-44	-88	-2	3.64
R	Fusiform Gyrus	44	-48	-10	4.92
R	Striatum	16	14	-8	5.06
L	Amygdala	-24	-12	-6	3.77
L	Cerebellum	-4	-80	-40	4.07
		-2	-60	-18	4.03
		-30	-74	-28	3.91
		-48	-60	-26	3.47
		-18	-74	-48	4.78
		-22	-48	-52	3.82
R	Cerebellum	6	-46	-60	3.35
		26	-64	-52	5.32

Note. See Figure 4 for correct 1-back famous and anonymous face trial brain activation maps

Table 4. Peak activation coordinates for correct famous (FAAF) and anonymous (AFFA) face 3-back trials

Lat	Region	Coordinates			
		X	y	z	BSR
FAAF > AFFA					
B	Ventromedial PFC	0	46	-24	3.21
L	Rostral-lateral PFC	-26	68	10	3.55
R	Dorsolateral PFC	44	26	20	5.23
L	Dorsolateral PFC	-42	50	12	4.41
L	Middle Frontal Gyrus	-22	40	12	4/51
L	Inferior Frontal Gyrus	-56	24	18	4.07
L	Inferior Precentral Sulcus	-36	4	34	3.45
L	Dorsal Anterior Cingulate	-12	14	36	5.83
R	Superior Temporal Sulcus	36	-62	26	4.03
R	Temporal Sulcus	64	-54	10	3.00
L	Parahippocampal Cortex	-54	-40	-10	3.81
R	Medial Temporal Lobe	30	0	-36	3.77
R	Parahippocampal Gyrus	38	-26	-22	3.06
L	Lateral Temporal Lobe	-66	-18	2	4.33
R	Temporoparietal Junction	54	-44	26	3.20
		54	-56	10	2.96
R	Amygdala	24	-6	-20	2.98
R	Visual Area MT	42	-56	6	3.17
L	Visual Area MT	-46	-82	6	3.13
L	Putamen	-28	0	16	3.67
R	Thalamus	4	-6	14	3.30
L	Thalamus	-16	-14	12	3.18
L	Fusiform Gyrus	-42	-60	-22	6.55
R	Fusiform Gyrus	40	-52	-26	5.20
R	Posterior Occipital Lobe	32	-94	2	5.26
		10	-98	0	3.67
L	Cerebellum	-2	-48	-38	5.02
R		2	-80	-26	3.64
AFFA > FAAF					
R	Middle Frontal Gyrus	26	58	12	-4.99
L	Middle Frontal Gyrus	-18	14	54	-3.56
L	Inferior Frontal Gyrus	-48	18	4	-3.38
R	Premotor Area	30	-18	58	-3.72
L	Premotor Area	-18	-8	66	-3.22
R	Superior Parietal Lobule	28	-32	64	-3.85
L	Superior Parietal Lobule	-26	-38	64	-3.60
R	Sensorimotor Cortex	16	-6	56	-4.43
L	Posterior Superior Temporal	-50	-26	12	-3.81

	Gyrus				
R	Posterior Superior Temporal	38	-38	10	-3.76
	Gyrus				
R	Thalamus	22	-20	-2	-4.32
R	Hypothalamus	10	-8	-6	-3.80
L	Insula	-34	-2	-4	-4.15
L	Cerebellum	-10	-58	-62	-3.38
R	Cerebellum	36	-46	-54	-3.72
	Cerebellum	14	-54	-54	-4.29
	Cerebellum	28	-58	-58	-4.80

Note. See Figure 5 for correct 3-back famous and anonymous face trial brain activation maps

Table 5. Peak activation coordinates for famous face hit, and miss 3-back trials

Lat	Region	Coordinates			
		x	y	z	BSR
Hits > Misses					
L	Dorsal Medial Prefrontal Cortex	-8	66	18	3.44
R	Dorsolateral Prefrontal Cortex	52	40	16	3.13
L	Supplementary Motor Area	-8	-12	56	6.45
		-8	-18	74	4.09
		-12	18	66	4.09
L	Primary Motor Cortex	-32	-24	70	5.27
R	Primary Motor Cortex	36	4	34	5.22
		28	-14	68	3.47
L	Premotor Area	-60	4	30	4.16
L	Inferior Frontal Gyrus	-60	8	18	3.24
R	Premotor Area	36	-4	62	3.68
L	Anterior Cingulate	-8	16	36	5.16
R	Insula	40	2	-12	3.48
L	Striatum	-14	16	-8	4.63
R	Thalamus	6	-12	8	3.36
R	Anterior Hippocampus	36	12	-24	5.17
L	Hippocampus	-20	-20	-24	4.46
R	Superior Temporal Sulcus	66	-44	6	4.57
R	Lateral Temporal Cortex	62	2	-6	3.93
		62	-28	6	3.54
		64	-12	6	3.38
L	Lateral Temporal Cortex	-62	-14	-8	4.82
		-58	-34	16	2.97
		-52	2	-6.0	4.75
		-58	-34	16	2.97
R	Medial Temporal Cortex	38	-14	-36	4.33
L	Medial Temporal Cortex	-58	-48	4	3.81
R	Temporo-parietal Junction	52	-44	22	3.67
L	Dorsal Posterior Cingulate	-4	-26	46	3.97
R	Superior Parietal Lobule	24	-74	56	3.42
R	Somatosensory Cortex	48	-22	38	3.60
R	Intraparietal Sulcus	36	-62	34	3.74
L	Intraparietal Sulcus	-32	-58	44	3.18
L	Intraparietal Sulcus	-26	-72	30	3.00
R	Lingual Gyrus	20	-54	0	5.16
L	Fusiform Gyrus	-38	-66	-20	8.57
R	Fusiform Gyrus	44	-66	-18	6.08
R	Visual Association Area	2	-80	30	3.43
R	Medial Occipital Cortex	12	-70	12	3.44
B	Ventromedial Occipital Cortex	0	-84	-14	3.38

R	Cerebellum	4	-74	-32	3.20
L	Cerebellum	-28	-68	-58	3.37
		-14	-38	-46	3.96
L	Brainstem	-2	-30	-44	4.43
Misses > Hits					
L	Middle Frontal Gyrus	-24	24	40	-3.54
R	Superior Frontal Gyrus	18	24	50	-3.54
R	Medial Prefrontal Cortex	12	48	4	-3.47
L	Medial Prefrontal Cortex	-16	58	-2	-3.47
R	Anterior Inferior Parietal Lobule	58	-40	48	-3.04
R	Dorsal Posterior Cingulate	8	-34	44	-3.74
L	Parahippocampal Cortex	-38	-52	-4	-4.00

Note. See Figure 6 for 3-back correct and incorrect, famous face trial brain activation maps

Lat	Region	Coordinates			
		x	y	z	BSR
Hits > Misses					
R	Middle Frontal Gyrus	34	2	36	-3.79
R	Dorsolateral Prefrontal Cortex	30	50	4	-3.76
L	Inferior Frontal Gyrus	-52	22	-8	-5.39
L	Frontal Eye Fields	-24	-2	48	-4.11
B	Primary Motor Cortex	0	0	68	-3.96
B	Supplementary Motor Area	0	10	54	-3.11
L	Anterior Cingulate	-6	26	38	-4.47
R	Anterior Insula	32	18	2	-4.22
L	Anterior Insula	-32	18	-4	-4.26
R	Putamen	-18	0	4	-4.02
R	Striatum	14	12	-8	-4.08
R	Superior Temporal Sulcus	52	-34	2	-4.51
L	Inferior Temporal Gyrus	-52	-60	-18	-2.73
		-66	-46	0	-2.90
R	Inferior Temporal Gyrus	58	-40	-18	3.67
R	Anterior Inferior Parietal Lobule	52	-34	44	-4.39
R	Intraparietal Sulcus	34	-42	42	-5.25
L	Intraparietal Sulcus	-30	-58	50	-4.84
R	Fusiform Gyrus	48	-64	-18	-4.08
R	Posterior Occipital Cortex	32	-92	-18	-4.06
L	Brainstem	-10	-18	-14	-3.84
L	Cerebellum	-12	-76	-28	-3.4
		-38	-50	-36	-3.62
R	Cerebellum	40	-60	-38	-4.73
		38	-56	-60	-4.10
		16	-38	-36	-3.62
		14	-56	-30	-3.04
Misses > Hits					
R	Premotor Cortex	40	-14	36	3.61
R	Inferior Frontal Gyrus	60	14	14	3.28
L	Supplementary Motor Area	-16	-10	58	4.21
L	Cingulate Gyrus	-14	-24	32	4.34
R	Angular Gyrus	40	-68	26	3.32
R	Lateral Temporal Cortex	54	-2	-28	4.05
R	Middle Temporal Gyrus	34	-56	16	4.43
R	Supramarginal Gyrus	50	-16	22	3.91
L	Supramarginal Gyrus	-48	-18	26	4.39
		-42	-34	24	3.64
L	Supramarginal Gyrus	-66	-22	32	3.56

R	Somatosensory Cortex	2	-32	68	3.01
R	Superior Parietal Lobule	18	-48	72	3.53
R	Temporo-parietal Junction	48	-42	28	4.05
L	Visual Area MT	-34	-76	24	4.85
R	Precuneus	6	-44	62	3.62
L	Precuneus	-2	-68	28	3.62
R	Brainstem	6	-34	-22	3.55
L	Cerebellum	-34	-80	-40	3.66

Note. See Figure 6 for 3-back correct and incorrect, anonymous face trial brain activation maps

Table 7. Peak activation coordinates for incorrect famous (FAAF) and anonymous (AFFA) face 3-back trials

Lat	Region	Coordinates			BSR
		x	y	z	
FAAF > AFFA					
R	Medial Prefrontal Cortex	14	50	4	-3.93
L	Dorsomedial Prefrontal Cortex	-4	50	40	-4.20
R	Dorsomedial Prefrontal Cortex	40	-50	28	-3.23
L	Frontal Eye Fields	-26	24	42	-3.87
R	Middle Frontal Gyrus	36	12	36	-3.36
L	Precuneus	-12	-56	48	-3.91
R	Anterior Inferior Parietal Lobule	54	-36	42	3.49
R	Posterior Inferior Parietal Lobule	50	-58	42	-3.41
L	Posterior Inferior Parietal Lobule	-44	-56	46	-3.87
R	Posterior Cingulate Cortex	8	-34	40	-3.24
R	Basal Ganglia	16	2	2	-3.29
L	Cerebellum	-26	-78	-50	-3.50
AFFA > FAAF					
L	Supplementary Motor Area	-22	-16	58	5.56
L	Premotor Cortex	-60	4	30	3.32
R	Premotor Cortex	62	4	32	4.36
		54	-4	48	3.58
R	Anterior Cingulate	10	8	38	4.98
B	Anterior Cingulate	0	30	22	3.52
R	Insula	50	-16	22	6.52
L	Posterior Insula	-42	0	6	3.47
R	Posterior Insula	42	-2	-8	3.30
L	Caudate	-16	28	4	3.50
L	Temporoparietal Junction	-44	-24	12	5.03
R	Hippocampus	26	-26	-16	4.26
		24	-48	0	4.13
		14	-32	8	3.86
		34	-8	-26	3.51
		20	-12	-26	3.49
R	Superior Temporal Cortex	68	-28	0	5.44
		58	-40	22	5.19
		60	-24	-16	3.47
		-52	0	-6	5.14
R	Superior Parietal Lobule	8	-38	70	5.33
L	Anterior Inferior Parietal	-44	-28	38	3.45

	Lobule				
R	Cuneus	6	-84	28	3.93
R	Precuneus	24	-58	20	5.05
L	Posterior Cingulate	-8	-18	42	3.46
R	Ventral Posterior Cingulate	16	-76	16	3.04
L	Fusiform Gyrus	-38	-82	-20	3.48
R	Retrosplenial Cortex	46	-70	26	3.03
L	Visual Association Area	-16	-104	-4	3.51
R	Visual Cortex	10	-86	-6	4.29
		28	-82	8	3.70
		14	-90	12	3.44
B	Periaqueductal Grey	-2	-30	-6	3.70
R	Cerebellum	26	-46	-34	4.86
		44	-44	-32	3.62
		10	-54	-8	3.23
L	Cerebellum	-20	-68	-32	4.13
		-44	-70	-24	3.69
		-4	-62	-6	3.75
		-38	-42	-36	3.85
		-12	-34	-36	3.87

Note. See Figure 5 for 3-back famous and anonymous face trial brain activation maps
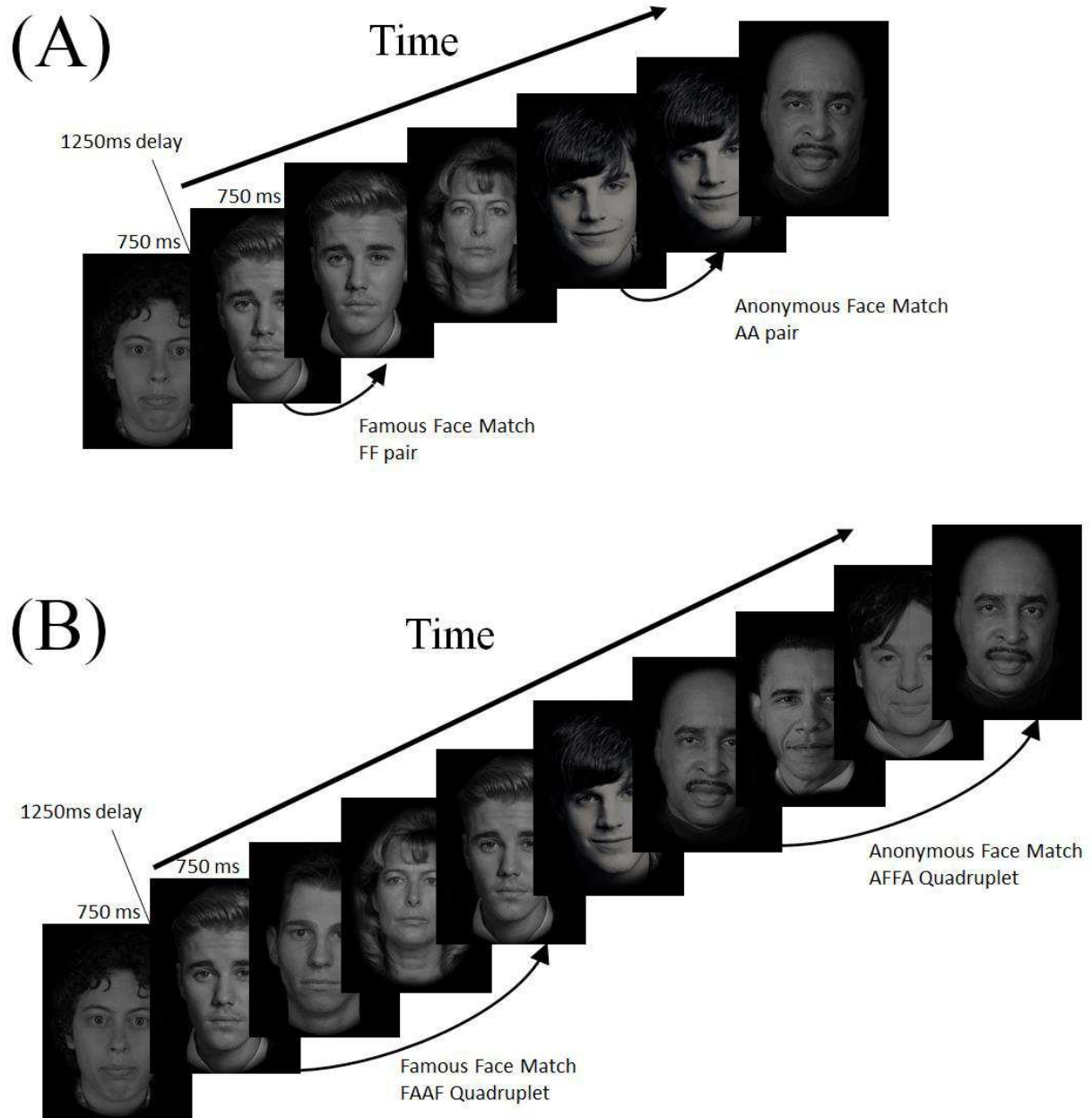
Figure 1. Time series of the (A) 1-back and (B) 3-back working memory task.

(A)

(B)
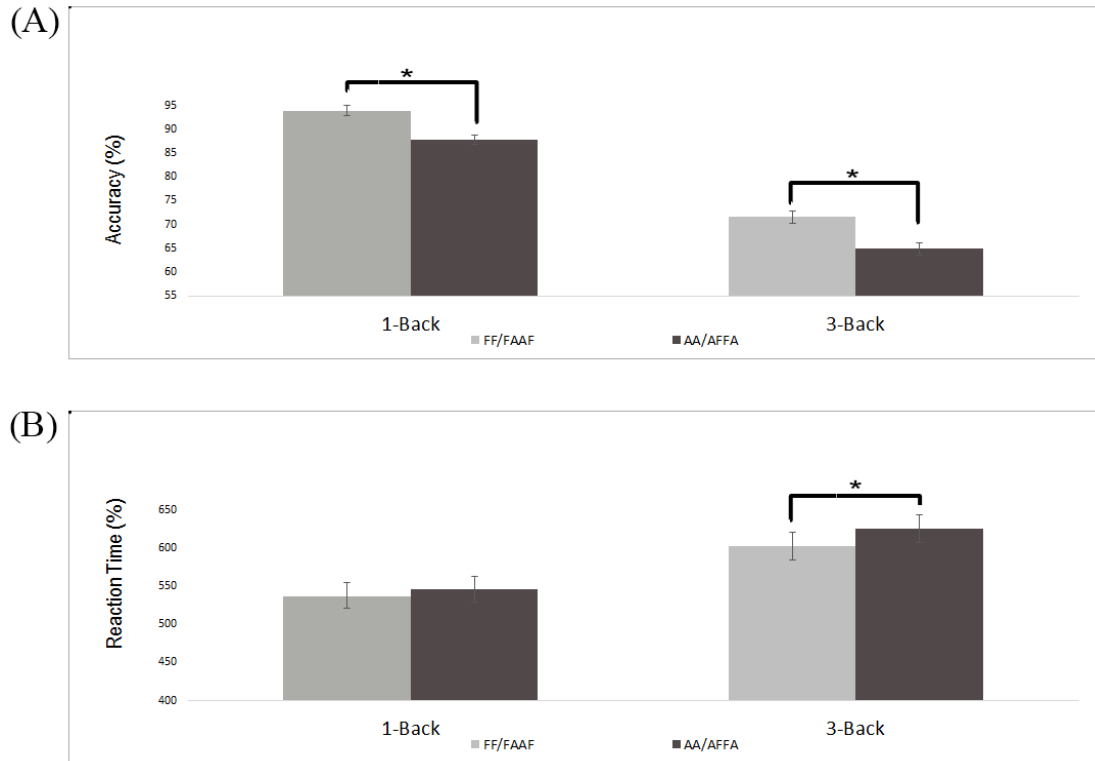
Figure 2. Univariate statistics for the 1- and 3-back task for (A) accuracy (FF vs. AA: $t(24) =$ 4.83, $p < .001$), FAAF vs. AFFA $t(24) = 3.05$, $p = .005$) and (B) reaction time (FAAF vs. AFFA: $t(24) = 3.97$, $p < .001$).
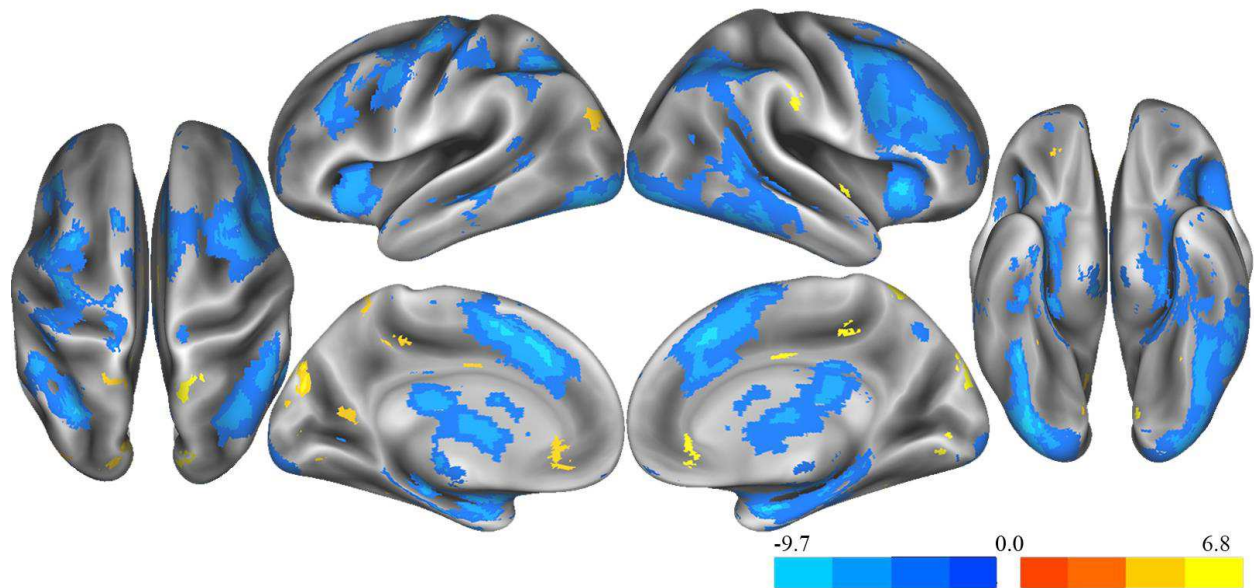
Figure 3. Transient and sustained brain activity dissociating rest (warm colour) and n-back (cold colour) conditions. Brain activity corresponds to bootstrap ratio values, the ratio of voxel salience to the bootstrapped standard error. See Table 1 for peak activation coordinates.
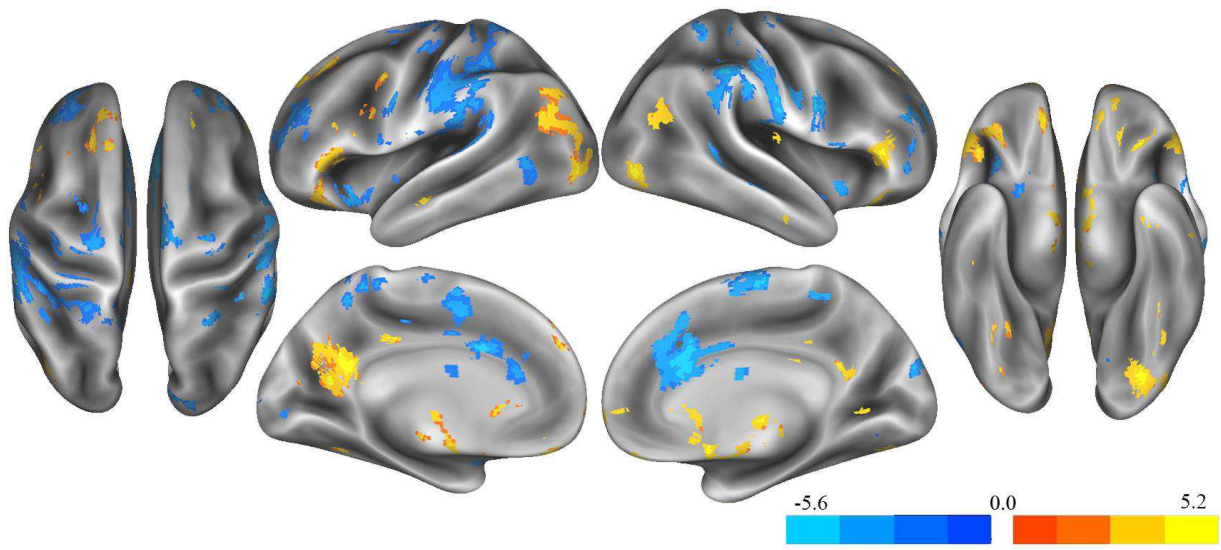
Figure 4. Transient brain activity dissociating the first instance of a famous (warm colours) and anonymous (cold colours) face. Brain activity corresponds to bootstrap ratio values, the ratio of voxel salience to the bootstrapped standard error. See Table 2 for peak activation coordinates.
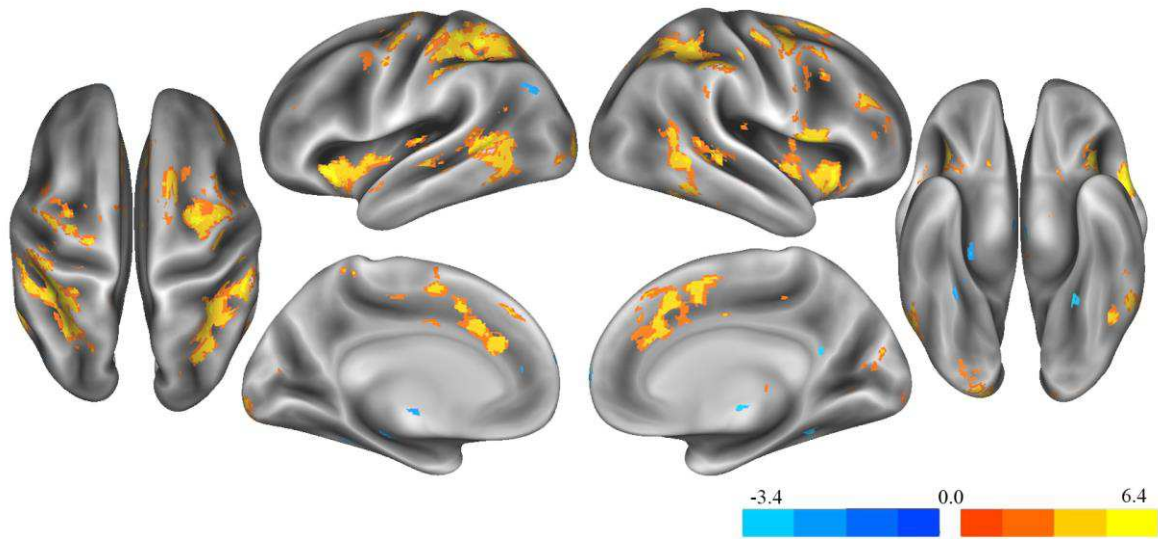
Figure 5. Transient brain activity dissociating 1-back anonymous (warm colours) and famous (cold colour) matches. Brain activity corresponds to bootstrap ratio values, the ratio of voxel salience to the bootstrapped standard error. See Table 3 for peak activation coordinates.
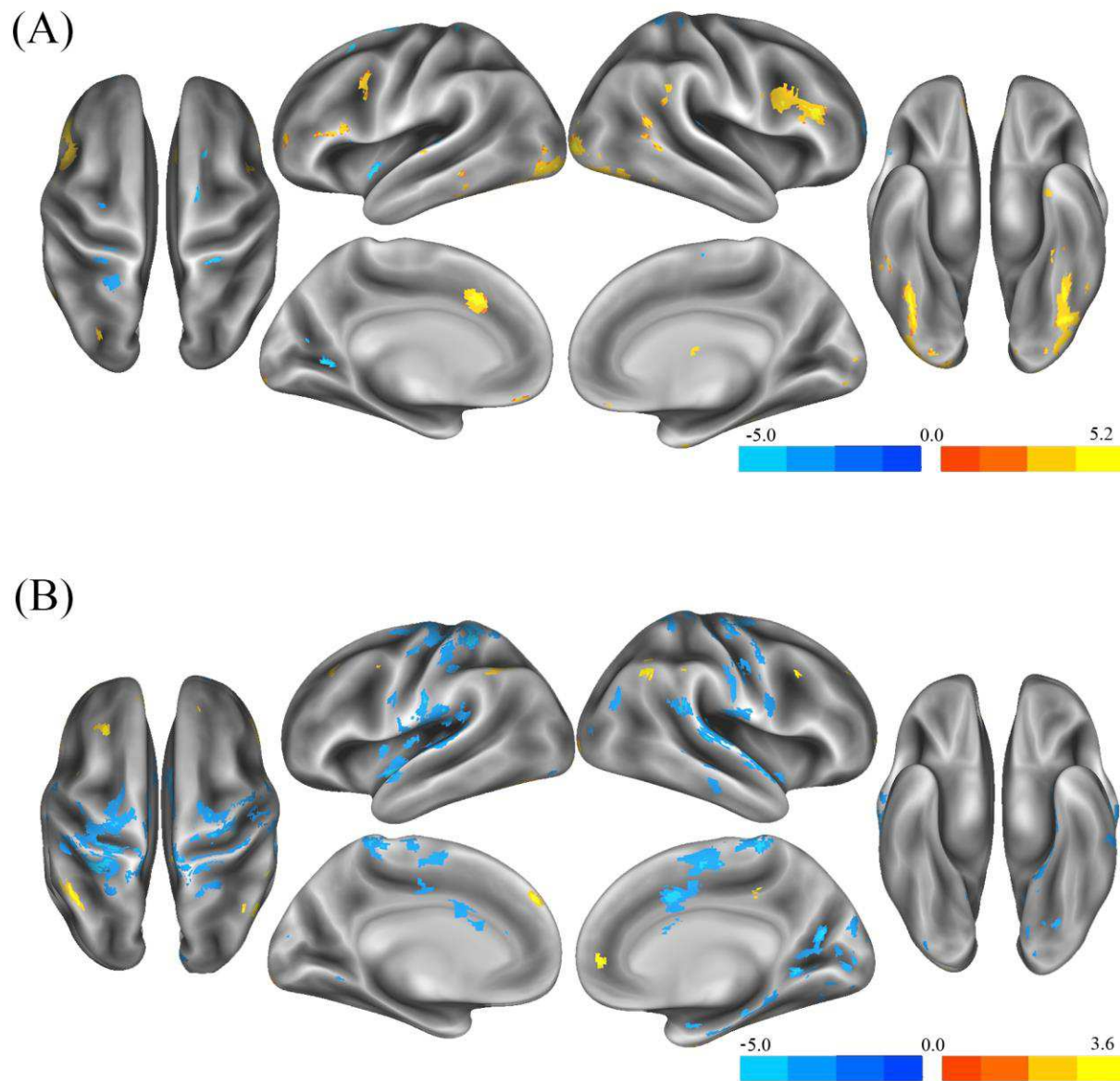
Figure 6. Transient brain activity dissociating 3-back famous and anonymous trials. (A) Transient brain activity dissociating famous (warm colour) and anonymous (cold colour) hits. See Table 4 for peak activation coordinates. (B) Transient brain activity dissociating famous (warm colour) and anonymous (cold colour) misses. See Table 7 for peak activation coordinates. Brain activity corresponds to bootstrap ratio values, the ratio of voxel salience to the bootstrapped standard error.
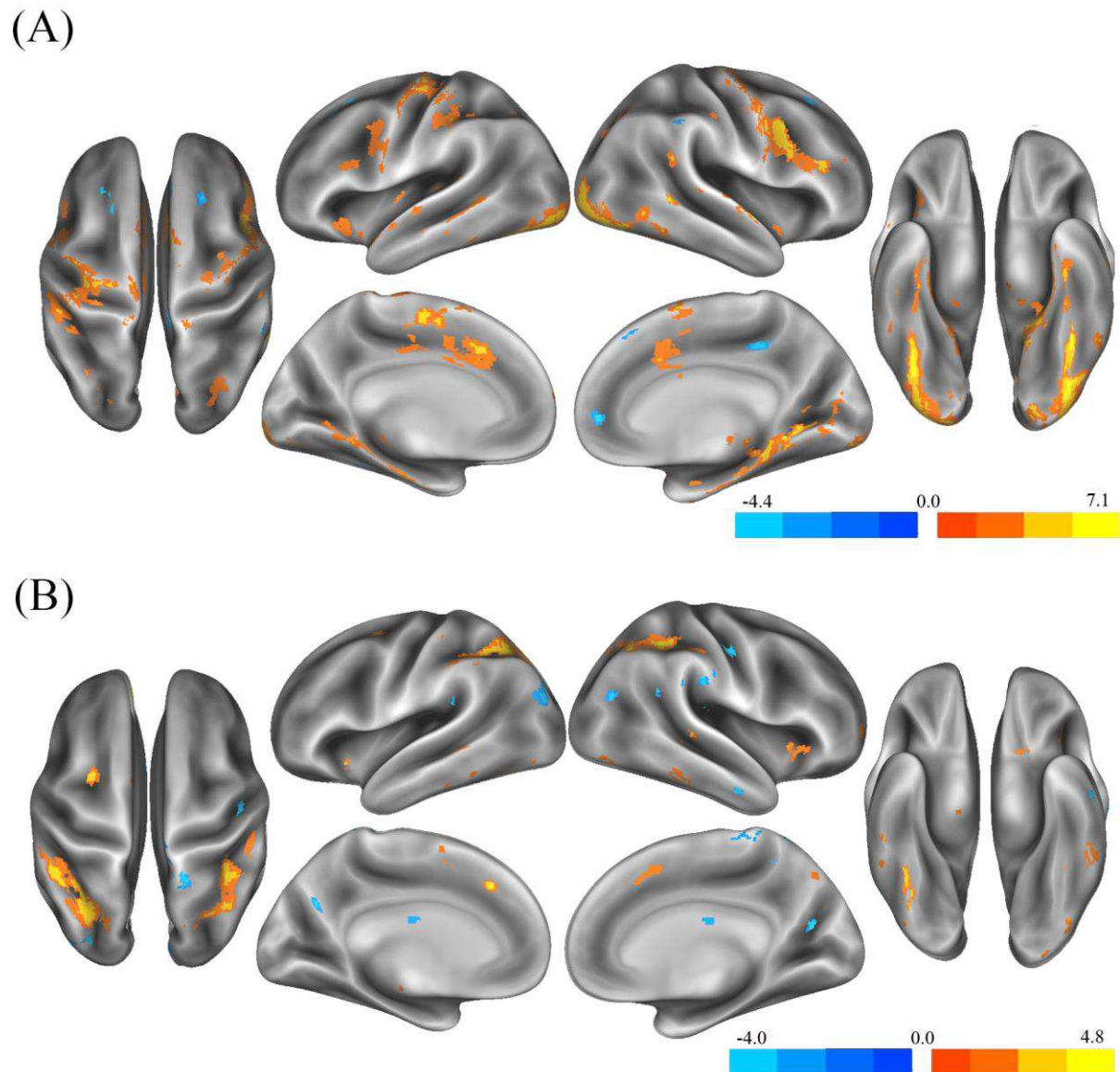
Figure 7. Transient brain activity for famous and anonymous face 3-back trials. (A) Transient brain activity dissociating famous hits (warm colours) and misses (cold colours). See Table 5 for peak activation coordinates. (B) Transient brain activity dissociating anonymous hits (warm colours) and misses (cold colours). See Table 6 for peak activation coordinates. Brain activity corresponds to bootstrap ratio values, the ratio of voxel salience to the bootstrapped standard error.