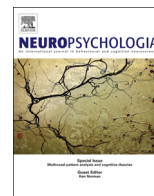




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A framework for understanding the relationship between externally and internally directed cognition

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ABSTRACT

Externally directed cognition (EDC) involves attending to stimuli in the external environment, whereas internally directed cognition (IDC) involves attending internally to thoughts, memories and mental imagery. To date, most studies have focused on the competition or trade-offs between these modes of cognition. However, both EDC and IDC include a variety of cognitive states that differ along multiple dimensions. These dimensions may influence the way in which EDC and IDC relate to each other. In this review, we present a novel framework that considers whether cognitive resources are oriented externally or internally, and also whether a given cognitive state involves intentional (i.e., voluntary) or spontaneous (i.e., involuntary) processing. Within this framework, we examine the conditions under which EDC and IDC are expected to either compete, or co-occur without interference. We argue that EDC and IDC are not inherently antagonistic, but when both involve higher levels of intentionality they are increasingly likely to compete, due to the capacity limitations of intentional processing. In contrast, if one or both involve spontaneous processing, EDC and IDC can co-occur with minimal interference given that involuntary processes are not subject to the same capacity constraints. A review of the brain regions implicated in EDC and IDC suggests that their neural substrates are partially segregated and partially convergent. Both EDC and IDC recruit the lateral prefrontal cortex (PFC) during intentional processing, and may therefore compete over the processes and representational space it supports. However, at lower levels of intentionality, EDC and IDC rely on largely distinct neural structures, which may enable their co-occurrence without interference. The proposal that EDC and IDC can in some cases co-occur, provides a framework for understanding the complex mental states that underlie theory of mind, creativity, the influence of self-evaluative processing on cognitive control, and memory-guided attention.

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1. Introduction

At one moment, our attention could be directed externally to a conversation with a friend, and at the next moment, it could be directed internally to plans for the coming evening. This common situation illustrates a key distinction between externally and internally directed cognition (EDC and IDC, respectively). Cognitive neuroscience research has traditionally focused on EDC, utilizing selective attention, cognitive control, and other tasks that involve processing and responding to externally presented stimuli. More recently, however, IDC has gained more widespread appreciation with the discovery of the default mode network (DMN). The DMN

is a collection of regions that are suppressed during a variety of tasks that demand external attention (Shulman et al., 1997), and are activated during the 'resting state' (Gusnard & Raichle, 2001), which is ostensibly dominated by internally directed self-referential cognitive processes (Buckner, Andrews-Hanna, & Schacter, 2008). IDC has also garnered interest with the growing scientific investigation of mind wandering — a prevalent form of cognition characterized by an internal train of thought that is often unrelated to the immediate sensory environment, and that usually competes with externally directed task performance (Christoff, 2012; Christoff, Gordon, Smallwood, Smith, & Schooler, 2009; Kam & Handy, 2013; Kane & McVay, 2012; Killingsworth & Gilbert, 2010; Mason et al., 2007; Schooler et al., 2011).

At first glance, EDC and IDC may appear to be mutually exclusive modes of cognition vying for the same cognitive resources, and it is often assumed that when one of these modes is operating, the other is automatically suppressed. This perspective is based on empirical work which has demonstrated that: (1) periods of mind wandering are associated with errors in externally directed task performance

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(e.g., reading comprehension) (Allen et al., 2013; Kam & Handy, 2014; Smallwood, McSpadden, & Schooler, 2008; Smallwood & Schooler, 2006); (2) activation in DMN regions is associated with errors in performance on EDC tasks (Christoff, et al., 2009; Foster, Dastjerdi, & Parvizi, 2012; Weissman, Roberts, Visscher, & Woldorff, 2006); (3) BOLD signal fluctuations in the DMN are negatively correlated with BOLD signal fluctuations in neural systems engaged by external attention (e.g., frontal eye fields and intraparietal sulcus) (M. Fox et al., 2005) and also negatively correlated with BOLD signal fluctuations in extrastriate, primary somatosensory, and motor cortices (Christoff, 2012); and (4) periods of off-task relative to on-task thought are associated with reduced task-related visual and auditory ERP responses (Kam et al., 2011). Although suggestive of an antagonistic relationship, these trade-offs between EDC and IDC do not reveal the complete story.

EDC and IDC represent a variety of cognitive states that differ along multiple dimensions, and these dimensions may influence the way in which EDC and IDC relate to each other. Here we argue that one relevant dimension is the level of intentionality involved. In this review, we propose specific working definitions for EDC and IDC, and then propose a basic framework that considers not only whether cognitive resources are externally or internally directed, but also whether a given cognitive state involves intentional or spontaneous processing. This framework is predicated on prior work which has argued that distinctions between EDC and IDC, and between intentional and spontaneous processing, are central organizing principles in cognitive and social neuroscience (Buckner et al., 2008; Chun, Golomb, & Turk-Browne, 2011; M.D. Fox et al., 2005; Gusnard & Raichle, 2001; Lieberman, 2007; Schneider & Shiffrin, 1977). Furthermore, models of attention have long suggested that distinct neural systems may be involved in reflexive (spontaneous) shifts of attention versus executive (intentional) control of attention (Corbetta & Shulman, 2002; Petersen & Posner, 2012; Posner & Dehaene, 1994). However, prior work did not specifically address the nature of the interactions between EDC and IDC, which is the topic of the present review. Based on our theoretical framework, we specify the conditions under which EDC and IDC may compete for the same resources or may co-occur with minimal competition and interference. Specifically, we propose that EDC and IDC are increasingly likely to compete when both involve higher levels of intentionality due to the capacity limitations of controlled, volitional processing, but can co-occur with minimal interference if one or both involve spontaneous processing. We argue that the co-occurrence of EDC and IDC is necessary for some of the most complex and valuable cognitive states humans can experience, including those underlying mentalizing, creativity, the influence of self-evaluative thinking on cognitive control, and the adaptive biasing of external attention by episodic memory. Furthermore, we review the neural basis of EDC and IDC, and suggest that they are supported by partially segregated and partially convergent processing streams, which may explain why EDC and IDC compete with one another in some situations, but co-occur without competition in others. Finally, we examine some implications of the current framework and highlight important avenues for future research.

2. Defining externally and internally directed cognition

2.1. Externally directed cognition (EDC)

EDC involves attention directed externally (i.e., ‘outside of the head or body’) to stimuli present in the external world, thoughts about an attended external stimulus, semantic processing involved in interpreting an external stimulus, and actions directed at external stimuli (Chun et al., 2011; Lieberman, 2007). In all cases, attention is directed outward at information coming in through the senses. Our definition is similar to that articulated by Chun et al. (2011), but differs with regard to high-level cognitive processes (e.g., cognitive control). Unlike their account, we propose that cognitive control is an example of EDC given that an external stimulus is often the focus of attention. Thus, EDC has a necessary condition: an external stimulus must be present. While EDC may occur during stimulation from all five sensory modalities, it is especially likely to occur during stimulation from the “distal” senses (vision and audition) which draw attention outward to the external world.

2.2. Internally directed cognition (IDC)

IDC involves attention directed internally (i.e., ‘inside the head or body’) to thoughts and other information that has been previously stored in long-term or working memory. It includes episodic memory retrieval (attention focused internally on re-living a past experience), simulation of future events, stimulus-independent thought streams (often dominated by self-referential content), mental imagery, and dreaming (Andrews-Hanna, 2012; Buckner et al., 2008; Fox, Nijeboer, Solomonova, Domhoff, & Christoff, 2013; Lieberman, 2007). IDC can operate in the presence or absence of external stimuli, and can be triggered by external stimuli or internal factors, but in all cases involves processing that is largely decoupled from the external perceptual environment (Schooler et al., 2011).

2.3. Mixtures of externally and internally directed cognition

The vast majority of cognitive states likely involve some mixture of externally and internally directed cognition. This mixture could take the form of EDC and IDC rapidly alternating in time as the result of a competition over limited resources, or a mixture of EDC and IDC co-occurring without interference. For instance, alternating EDC and IDC may occur while driving to a novel destination; there may be rapid shifts between focusing externally on the road and other cars, and focusing internally to remember the directions. In contrast, the co-occurrence of EDC and IDC often takes place during interpersonal interactions. While engaged in a conversation, attention may be directed externally to the words being spoken by a friend, but simultaneously directed internally to inferences about their mental state and interpretations of the meaning of their words. Specifying the conditions under which EDC and IDC either compete or co-occur is the main goal of this paper.

Table 1
A framework of cognitive states.

	Externally directed cognition	Internally directed cognition
Spontaneous	Example: stimulus-driven attentional re-orienting in response to a salient external stimulus	Example: mind wandering without awareness
Intentional	Example: top-down attentional orienting to a task relevant external stimulus or location	Example: directed thinking about future plans, such as how to get out of debt

3. A theoretical framework of cognitive states

In this section, we present a theoretical framework (Table 1) that addresses the following variables: (1) whether a cognitive state involves EDC or IDC; and (2) whether the cognitive state involves intentional or spontaneous processing.

Intentional cognitive processing (largely synonymous with controlled, directed, or top-down processing) involves the voluntary control of attention, is subjectively effortful, has a limited capacity, and allows for flexible responses to the environment (Corbetta & Shulman, 2002; Lieberman, 2007; Miller & Cohen, 2001; Schneider & Shiffrin, 1977). It often involves the representation of current and desired states, and the deliberate instantiation of appropriate mental operations and actions to transform the former into the latter. Intentional processing is often required in situations that are non-routine (i.e., novel), trigger multiple response alternatives, and require attentional control to ensure that the most appropriate response is selected (Miller & Cohen, 2001). We use the term 'intentional' instead of 'goal-directed' because there is some evidence that the latter is not antithetical to spontaneous cognition; for example, processes aimed at accomplishing task-related goals can be spontaneously driven by non-consciously perceived stimuli (Dijksterhuis & Aarts, 2010; Lau & Passingham, 2007; Pessiglione et al., 2007). Therefore, both intentional and spontaneous processing can be goal-directed.

Spontaneous cognitive processing (largely synonymous with stimulus-driven or bottom-up processing) occurs involuntarily, is subjectively effortless, may be driven by salient stimuli, memories, or emotions, and is typically difficult to suppress (Corbetta & Shulman, 2002; Lieberman, 2007; Schneider & Shiffrin, 1977). Although spontaneous cognitive processing is often impervious to cognitive load, it sometimes can tax limited attentional resources, as in the case of mind wandering (Smallwood & Schooler, 2006). Having said that, mind wandering is not always spontaneous; individuals often direct the flow of thoughts they are immersed in. Therefore, more work is necessary to determine whether all forms of mind wandering tax attentional resources, or whether this effect is limited to directed mind wandering. Nevertheless, for the purposes of the present paper, the term 'spontaneous' includes processes that would be called 'automatic' (i.e., that are largely unaffected by cognitive load), but it is not limited to them.

In the following subsections, we highlight some examples of EDC and IDC states as a function of intentionality. This is by no means an exhaustive set of examples. Moreover, it could be argued that some of the examples for spontaneous processing do require some element of directed attention, or show sensitivity to task demands, however, the important point is that these examples clearly require *less* intentionality than the examples that illustrate intentional processing. We use 'intentional' and 'spontaneous' as useful organizing terms, and do not intend to convey the idea that they are dichotomous categories per se. In actuality, cognitive processes probably vary along a continuous space of intentionality.

3.1. Examples of mainly externally directed cognition

3.1.1. Spontaneous EDC

This category includes cognitive states in which an external stimulus is the focus of attention, and is processed largely spontaneously. As one example, this cognitive state occurs during stimulus-driven attentional re-orienting (Corbetta & Shulman, 2002). For example, suddenly appearing stimuli tend to reflexively capture attention (Yantis & Hillstrom, 1994). Priming studies have also demonstrated that non-consciously perceived stimuli can be spontaneously processed, sometimes up to a semantic level (e.g., Dehaene et al., 1998; Greenwald, Draine, & Abrams, 1996).

3.1.2. Intentional EDC

This category includes cognitive states in which an external stimulus is processed voluntarily (i.e., with the aid of attentional control). This category is frequently examined using selective attention tasks in which participants voluntarily shift attention to one out of many spatial locations or objects on the basis of an informative cue (Buschman & Miller, 2007; Corbetta & Shulman, 2002). Another example is classic cognitive control tasks (e.g., Stroop, Flanker, etc.) in which rules are used to intentionally respond to external stimuli that are the current focus of attention (Miller & Cohen, 2001). These tasks often involve the concurrent presentation of multiple stimuli that afford competing response tendencies, and thus demand a high level of externally directed attention to the task relevant stimulus in order to guide the selection of the correct response (Egner & Hirsch, 2005).

3.2. Examples of mainly internally directed cognition

3.2.1. Spontaneous IDC

This category includes cognitive states in which attention is directed internally and driven involuntarily. A common phenomenon during 'rest', and during easy or well-practiced EDC tasks is the tendency to 'zone out' and spontaneously think of things unrelated to the task, especially recent past events, future plans, and social relationships (Andrews-Hanna, Reidler, Huang, & Buckner, 2010; Christoff, 2012; Mar, Mason, & Litvack, 2012). This phenomenon – often referred to as mind wandering – can be assessed by asking participants to perform a boring or over-practiced EDC task and periodically sampling their experience using thought probes. These probes can ask a number of questions such as whether participants' attention is on-task or off-task, and if the latter, if they were aware or unaware of their mind wandering (Christoff et al., 2009). If the participant is unaware of their mind wandering, this represents a clear case of what we call spontaneous IDC. Other examples include the involuntary retrieval of task-irrelevant information from episodic memory (Kuhl, Johnson, & Chun, 2013), and the spontaneous thoughts and audiovisual imagery that constitute night-time dream experiences (Fox et al., 2013).

3.2.2. Intentional IDC

This category includes cognitive states in which attention is oriented internally, and is voluntarily directed. For example, when not otherwise engaged in a task, individuals often spend considerable time intentionally thinking about the past or future, for example, planning how to get out of debt (Addis, Wong, & Schacter, 2007; Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010). As another example, when individuals are performing a boring task they may intentionally 'tune out' and let their mind wander away from the task. The phenomenon of 'tuning out' involves awareness of mind wandering (Schooler et al., 2011), and may be associated with intentionality if the individual is directing the flow of thoughts. Theory of mind (ToM) or 'mentalizing' tasks also fall into this category, as they often involve voluntarily generating inferences about the mental state of other individuals (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001; Saxe & Kanwisher, 2003). It should be noted that mentalizing does not always require intentionality (Senju, Southgate, White, & Frith, 2009).

3.3. Conditions under which EDC and IDC compete or co-occur

This section provides a theoretical framework for understanding the conditions under which EDC and IDC either compete, or co-occur with minimal interference. A key feature of our

framework is appreciating the fact that the brain has a fundamental capacity limitation with respect to intentional processing (Schneider & Shiffrin, 1977). This is likely because intentional processing draws upon limited attentional/working memory resources that prioritize information processing (Desimone & Duncan, 1995). Intentional processing involves the specification of currently relevant information (e.g., an external stimulus, or particular thought) maintained within working memory, and the top-down propagation of this information to distributed brain regions in order to coordinate processing in accordance with one's intention. Correspondingly, brain activity is amplified in neural circuits representing relevant information and is suppressed in neural circuits representing irrelevant information (Desimone & Duncan, 1995; Miller & Cohen, 2001).

In contrast to the common view that EDC and IDC are mutually antagonistic or necessarily compete for expression, we propose that there is no *inherent* competition between them. Instead, we suggest that the relationship between EDC and IDC depends on the extent to which they draw upon capacity-limited intentional processes. More specifically, we propose that EDC and IDC are antagonistic when *both* involve a high degree of intentionality. For example, our account predicts that interference should arise if trying to intentionally search for a friend in a crowd, while simultaneously attending internally to plan a future event, or volitionally re-live an episodic memory. We are unaware of any existing studies that have specifically examined this idea. There are abundant studies, however, that have provided clear evidence that mind wandering – an IDC process that utilizes limited attentional resources – strongly competes with intentional EDC processes including text comprehension, top-down selective attention to visual target stimuli, and the capacity to inhibit a pre-potent response to infrequent 'No-go' stimuli (Allen et al., 2013; Kam & Handy, 2014; Kane & McVay, 2012; Smallwood et al., 2008; Smallwood & Schooler, 2006). Importantly, we suggest that attentional resources are not devoted to EDC or IDC in an all-or-none fashion, but rather, can be divided between EDC and IDC in any proportion. However, the simultaneous operation of capacity-limited EDC and IDC processes will be less efficient and subject to interference, consistent with the observed findings of competition between EDC and IDC in behavioral and neuroimaging studies (Allen et al., 2013; Christoff, 2012; Christoff et al., 2009; Foster et al., 2012; M. Fox et al., 2005; Kam et al., 2011; Kam & Handy, 2014; Schooler et al., 2011; Smallwood et al., 2008; Smallwood & Schooler, 2006; Weissman et al., 2006).

Our proposal suggests that EDC and IDC can co-occur without interference if one or both involve a spontaneous process (particularly those that are automatic and do not tax limited attentional resources). Consistent with this idea, mind wandering does not interfere with the capacity to process unexpected auditory tones that involuntarily capture external attention (Kam, Dao, Stanculescu, Tildesley, & Handy, 2013). One possibility is that mind wandering actually stops briefly to allow such externally directed processing to occur. However, highly practiced (i.e., automatized) EDC tasks can be performed with little disruption despite the presence of frequent mind wandering (Smallwood & Schooler, 2006), suggesting that they can co-occur with minimal interference. The nature of mind wandering itself may differ to some degree in the presence of a task. However, it is clear that the extent to which mind wandering competes with EDC task performance depends on whether the performance has become automatized, or instead requires intentional processing (Smallwood & Schooler, 2006).

ToM or mentalizing tasks provide another example of simultaneous EDC and IDC with minimal interference. In some ToM tasks, participants are asked to infer the mental state of another individual based on perceptual information alone, or in combination with additional contextual information (Baron-Cohen et al., 2001;

Lieberman, 2007). In such cases, there is likely to be external attention to the individual in question and observable cues (e.g., eye gaze, facial expression, biological motion, etc.), as well as internal attention to inferences about that person's mental state. Whereas mental state inference is thought to require intentionality, the perception of biological motion and facial expression is thought to occur relatively automatically (Batty & Taylor, 2003; Lieberman, 2007). These findings are consistent with our proposal that EDC and IDC can co-occur with minimal interference as long as one or both involve a spontaneous process.

Some aspects of creativity, such as the process of generating novel ideas, is thought to rely on a mind-set characterized by largely spontaneous processing (Ellamil, Dobson, Beeman, & Christoff, 2012; Fox & Christoff, 2014; Limb & Braun, 2008), and seems to involve the co-occurrence of EDC and IDC with minimal interference. For example, the generation of new ideas during the creation of a novel work of art or musical composition entails externally directed attention to the work being produced (which may or may not involve intentionality), and largely involuntary IDC processes that support the spontaneous retrieval and integration of prior knowledge stored in long term memory in order to generate new ideas (Ellamil et al., 2012; Limb & Braun, 2008).

One limitation of the examples noted above is that it is difficult to know for certain whether EDC and IDC were occurring simultaneously, or whether there were rapid shifts between them. However, a recent study has provided compelling evidence that EDC and IDC can co-occur without interference by examining the effect of spontaneous self-evaluative thoughts on cognitive control performance (Bengtsson, Dolan, & Passingham, 2010). In this study, participants were first implicitly primed to activate self-evaluative thoughts related to being 'clever' or being 'stupid'. Then participants performed an *N*-back working memory task, which primarily requires externally focused attention to determine whether a current letter is the same as the letter that appeared two letters back. The results demonstrated greater post-error slowing during the *N*-back task – an index of adaptive EDC performance monitoring – after being primed to think of themselves as clever versus stupid (Bengtsson et al., 2010). Relative to a baseline condition, the clever priming condition led to greater post-error slowing, whereas the stupid priming condition led to less post-error slowing, suggesting that cognitive control was enhanced or impaired depending on the content of self-evaluative thinking (Bengtsson et al., 2010). These findings clearly suggest that IDC and EDC can be simultaneously activated without interference in some cases, given that self-evaluative thinking related to being clever actually *improved* EDC task performance. Supporting the idea of co-occurrence, the clever priming condition was associated with increased neural activation during error trials in the paracingulate/dorsal MPFC, a region that contributes to internally oriented self-reflection (Bengtsson et al., 2010; see also Bengtsson, Lau, & Passingham, 2009). This suggests that self-evaluative thinking was occurring throughout the cognitive control task, and was likely occurring spontaneously given the implicit nature of the priming procedure.

4. EDC and IDC processing at the neural level

In this section, we review the brain regions and networks implicated in EDC and IDC (Fig. 1). The following section builds on this background, and outlines how the dynamic relationship between EDC and IDC may play out at the neural level.

4.1. The neural basis of EDC

Fig. 1B illustrates brain areas that are primarily involved in EDC. These areas include primary and associative visual and auditory

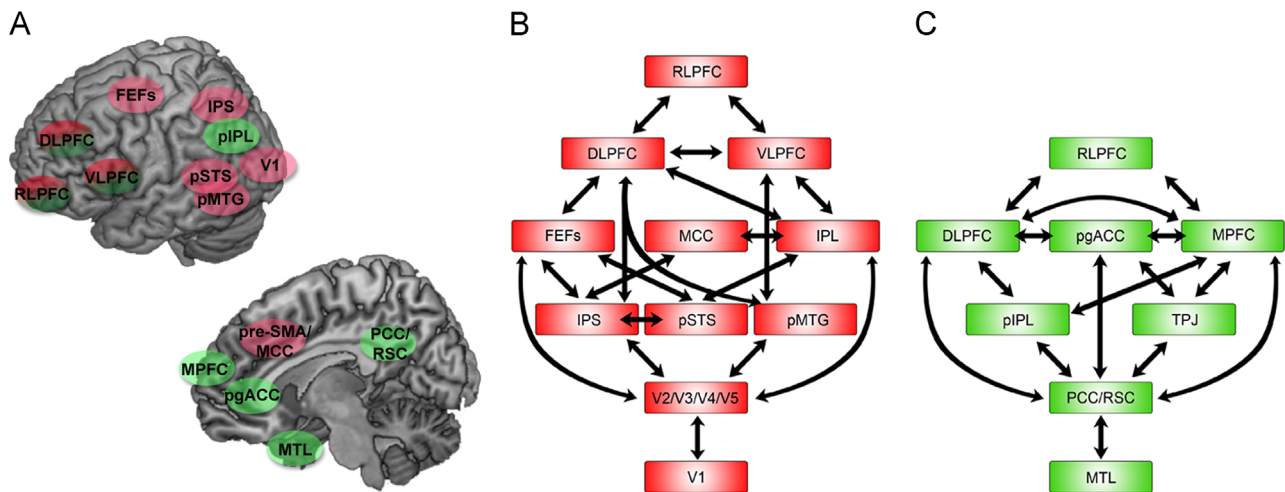


Fig. 1. Illustration of EDC and IDC brain regions and simplified pathways: (A) brain regions relevant to EDC (denoted in red) and IDC (denoted in green). Regions within the lateral prefrontal cortex are denoted in red and green to signify their involvement in both EDC and IDC. (B) Schematic model of the organization of the EDC processing stream. (C) Schematic model of the organization of the IDC processing stream. IPS=intraparietal sulcus, pMTG=posterior middle temporal gyrus, pSTS=posterior superior temporal sulcus, IPL=inferior parietal lobule, MCC=mid-cingulate cortex, FEFs=frontal eye fields, DLPFC=dorsolateral prefrontal cortex, VLPFC=ventrolateral prefrontal cortex, RLPFC=rostrolateral prefrontal cortex, MPFC=medial prefrontal cortex, MTL=medial temporal lobe, PCC/RSC=posterior cingulate cortex/retrosplenial cortex, TPJ=temporoparietal junction, pIPL=posterior inferior parietal lobule, pgACC=pregenual anterior cingulate cortex.

cortices that gather information from the external environment, and primary motor and premotor areas that organize actions directed at external stimuli. Additionally, the posterior superior temporal sulcus (pSTS) plays a role in detecting biological motion from visual cues (Allison, Puce, & McCarthy, 2000), while the frontal eye fields (FEFs) and intraparietal sulcus (IPS) are fundamentally involved in regulating external attention by enhancing the processing of behaviorally relevant spatial locations and sensory stimuli (Corbetta & Shulman, 2002; Gottlieb, Kusunoki, & Goldberg, 1998; Kastner, Pinsk, De Weerd, Desimone, & Ungerleider, 1999; Moore & Armstrong, 2003). Finally, cognitive control tasks involve the use of rules to appropriately respond (or inhibit a response) to external stimuli, and additionally draw upon the lateral prefrontal cortex (PFC), anterior mid-cingulate cortex (aMCC; often referred to as the dorsal anterior cingulate cortex), anterior insula, pre-supplementary motor area (pre-SMA), posterior middle temporal gyrus (pMTG), and a large area of the inferior parietal lobule (IPL) (Braver, 2012; Bunge, Kahn, Wallis, Miller, & Wagner, 2003; Cole & Schneider, 2007; Dixon & Christoff, 2012; Dosenbach et al., 2006; Duncan, 2010; Kerns et al., 2004). In some cases, cognitive control tasks may tap into IDC (e.g., when participants focus on information maintained in working memory), however, attention is predominantly directed at external stimuli in the majority of these tasks.

Moving from primary sensory cortices to the lateral PFC, there is progressively greater involvement in intentional EDC processes. For example, electrophysiological recordings of neuronal timing suggest that bottom-up (involuntary) shifts of attention towards external stimuli are driven by the IPS, whereas top-down (intentional) shifts of attention are driven by the lateral PFC/FEFs (Buschman & Miller, 2007). Additionally, the pMTG appears to provide long-term storage of rules, whereas the lateral PFC supports the active (intentional) use of these rules (Bunge et al., 2003; Donohue, Wendelken, Crone, & Bunge, 2005), and rule information is transmitted in a top-down manner from the lateral PFC to the parietal cortex (Crowe et al., 2013). Furthermore, lateral PFC rule activation is strongest when learning a new task and then decreases over time as performance becomes more automatic (Duncan, 2010; Poldrack et al., 2005; Toni, Ramnani, Josephs, Ashburner, & Passingham, 2001). Finally, within the lateral PFC itself, there is a tendency for activation to spread from caudal (BA 44, 8, and 9) to rostral (BA 46 and 10) as EDC task demands and

rule complexity increase and greater intentionality is ostensibly required (Badre & D'Esposito, 2009; Christoff & Gabrieli, 2000; Christoff et al., 2001; Koechlin & Summerfield, 2007; Petrides, 2005). In sum, the lateral PFC flexibly represents currently relevant task information that prioritizes and drives information processing in sensory and motor regions toward a common goal (Miller & Cohen, 2001).

4.2. The neural basis of IDC

Fig. 1C highlights key brain areas that are reliably associated with IDC. During periods of waking rest, or boring tasks, individuals tend to engage in self-referential thinking about events of the recent past and immediate future, especially those involving social relationships and other current concerns (Andrews-Hanna, 2012; Andrews-Hanna et al., 2010; Fox et al., 2013; Klinger, 2008; Mar et al., 2012). These periods are associated with activation of the DMN, which includes the posterior cingulate cortex/retrosplenial cortex (PCC/RSC), the pregenual anterior cingulate cortex (pgACC), a wide swath of medial prefrontal cortex (MPFC), the posterior IPL, the temporoparietal junction (TPJ), and also the hippocampus and surrounding medial temporal lobe (MTL) regions (Andrews-Hanna, 2012; Buckner et al., 2008; Christoff et al., 2009; Christoff, Ream, & Gabrieli, 2004; Greicius, Krasnow, Reiss, & Menon, 2003; Gusnard & Raichle, 2001; Mason et al., 2007; Raichle et al., 2001). The DMN and MTL are also recruited by tasks that specifically involve IDC, including episodic memory retrieval (Andrews-Hanna, Saxe, & Yarkoni, 2014; Spreng, Mar, & Kim, 2009), simulating future events (D'Argembeau et al., 2010; Schacter, Addis, & Buckner, 2007; Spreng et al., 2010), and explicit reflection on the mental states and personality characteristics of the self and others (Andrews-Hanna et al., 2014; D'Argembeau et al., 2005, 2010; Fletcher et al., 1995; Mitchell, Macrae, & Banaji, 2006; Northoff & Bermpohl, 2004; Ochsner et al., 2005; Schmitz & Johnson, 2007).

Caudal DMN regions (MTL, RSC/PCC, and pIPL) appear to be involved in relatively spontaneous IDC processing. For example, during episodic memory retrieval, the MTL spontaneously reactivates both task relevant and task irrelevant information (e.g., Kuhl et al., 2013), and both the MTL and PCC/RSC are involved in the spontaneous replay of recent experiences during waking rest and sleep (Karlssoon & Frank, 2009; Rasch & Born, 2007). Furthermore,

a recent theory suggests that the IPL is involved in the bottom-up (spontaneous) capture of attention by episodic memories (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008). Together, these regions may contribute to the spontaneous generation of mental imagery, conceptual knowledge, and thoughts based on prior experience (Andrews-Hanna, 2012; Buckner et al., 2008; Christoff et al., 2004; Ellamil et al., 2012). In contrast, rostral DMN regions (pgACC, and dorsal and rostral MPFC) have a closer relationship with intentional IDC processes, including explicit reflection on thoughts, feelings, and attributes of the self and others (Amodio & Frith, 2006; Jenkins & Mitchell, 2011; Lane, Fink, Chau, & Dolan, 1997; Schmitz & Johnson, 2007). Of course, some aspects of self-evaluative processing may occur relatively spontaneously, and may also draw upon the MPFC (Schmitz & Johnson, 2007).

Finally, the lateral PFC has an underappreciated role in IDC. The lateral PFC is activated during the resting state (Christoff et al., 2004) and during mind wandering (Christoff et al., 2009; Dumontheil, Gilbert, Frith, & Burgess, 2010; Stawarczyk, Majerus, Maquet, & D'Argembeau, 2011), and also exhibits positively correlated activation with DMN regions during rest (Leech, Kamourieh, Beckmann, & Sharp, 2011) and various other tasks (Dixon & Christoff, 2012; Ellamil et al., 2012; Spreng et al., 2010). Notably, the lateral PFC may be especially involved in IDC processes that are more intentional in nature. For example, the lateral PFC is activated when volitionally thinking about future autobiographical plans (Spreng et al., 2010), constructing a future event in mind (Addis et al., 2007), generating inferences about other's mental states (Mar, 2011), and during voluntary episodic memory retrieval (Barredo, Oztekin, & Badre, 2013). Furthermore, dorsal/rostral lateral PFC activation correlates with the depth of mental state inference during strategic economic tasks (Bhatt, Lohrenz, Camerer, & Montague, 2010; Yoshida, Seymour, Friston, & Dolan, 2010), and participants can learn to regulate activation within RLPFC (BA 10) by intentionally directing attention inward to their thoughts in conjunction with real-time fMRI neurofeedback (McCaig, Dixon, Keramatian, Liu, & Christoff, 2011).

5. The neural basis of the competition and co-occurrence of EDC and IDC

The empirical findings reviewed above suggest that EDC and IDC involve partially segregated, yet partially convergent processing streams. This pattern supports the framework proposed here, and is also consistent with the seminal proposal of Mesulam (1998, 2000). As illustrated in Fig. 2, Mesulam suggested that at one extreme, the external environment is registered by primary sensory areas and is elaborated upon in modality-specific association cortices, and at the other extreme, information about the internal milieu is registered by the hypothalamus, and is elaborated upon in limbic regions (amygdala, hippocampus, etc.). Interposed between these two extremes are paralimbic (temporal pole, caudal OFC, insula, etc.) and heteromodal association areas (e.g., lateral PFC) that bridge the internal and external environments (Mesulam, 1998, 2000).

Although Mesulam (1998, 2000) focused on visceral/emotional processes in the case of IDC, our framework is generally similar to his model, particularly the idea of a confluence of EDC and IDC processing in the lateral PFC. We further build on this idea by articulating the role of intentionality. As noted above, when EDC or IDC processing occurs spontaneously, activation is driven by, and is often confined to 'lower-order' regions (primary/associative visual areas, pSTS, and IPS in the case of EDC; the MTL, PCC/RSC, and pIPL in the case of IDC). Because there are distinct EDC-specific and IDC-specific 'lower-order' neural structures, this could allow for the parallel operation of spontaneous EDC and IDC processes.

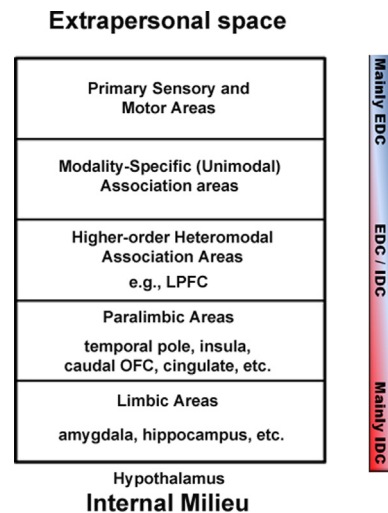


Fig. 2. Segregation and convergence of EDC and IDC processing streams. This image, adapted from Mesulam (2000), illustrates that the EDC and IDC processing streams begin with segregated neural structures, and then converge on heteromodal association areas (including the lateral PFC).

The data reviewed earlier suggests that EDC and IDC processing streams converge on 'higher-order' brain regions, especially the lateral PFC during intentional processing (see Figs. 1 and 2). The lateral PFC has a unique ability for adaptive coding, that is, representing a diverse array of currently relevant information (Duncan, 2001; Miller & Cohen, 2001), and hence, may be involved in the intentional specification of the behavioral relevance of a particular external stimulus or train of thought. Accordingly, competition will arise during concurrent intentional EDC and IDC, as both draw upon the capacity-limited processes of the lateral PFC to intentionally specify behavioral relevance and transmit this information to 'lower-order' neural structures in order to co-ordinate processing in disparate regions towards a common goal (Miller & Cohen, 2001). Consistent with this idea, electrophysiological recordings have demonstrated that neural activation occurs earlier in the lateral PFC as compared to more caudal regions (e.g., the parietal cortex) during top-down (intentional) processing (e.g. Buschman & Miller, 2007; Crowe et al., 2013). Therefore, intentional EDC processes that recruit the lateral PFC (e.g., most cognitive control tasks) should interfere with intentional IDC processes that recruit the lateral PFC (e.g., autobiographical future planning). Moreover, although mind wandering often occurs spontaneously, it does utilize limited attentional resources (Smallwood & Schooler, 2006) and recruits the lateral PFC (Christoff et al., 2009), and may therefore interfere with intentional EDC tasks. In support of this idea, mind wandering disrupts demanding EDC tasks such as reading comprehension (Smallwood et al., 2008), selective attention to targets while suppressing interference from competing stimuli (Kam & Handy, 2014), and response inhibition (Allen et al., 2013) – all of which rely on the lateral PFC (Aron, Robbins, & Poldrack, 2004; Egner & Hirsch, 2005; Keller, Carpenter, & Just, 2001; MacDonald, Cohen, Stenger, & Carter, 2000).

On the other hand, a central feature of our framework is the suggestion that intentional EDC processes supported by the lateral PFC should be able to operate in parallel with automatic IDC processes that do not recruit the lateral PFC (and vice versa). Supporting this idea, the frequency of mind wandering tends to increase during well-practiced (automatized) EDC tasks, yet it has minimal adverse effects on performance (Smallwood & Schooler, 2006). This is likely because lateral PFC involvement decreases as a task becomes automatic (Poldrack et al., 2005). Additionally, a true co-occurrence of EDC and IDC may take place during some instances of theory of mind. This may be possible because

intentionally thinking about others' mental states draws upon the lateral PFC, MPFC, and TPJ (Amodio & Frith, 2006; Bhatt et al., 2010; Mar, 2011; Saxe & Kanwisher, 2003), whereas the relatively spontaneous processing of external cues (e.g., biological motion, facial expression, etc.) that inform such inferences is mainly supported by caudal EDC-related regions such as the posterior superior temporal sulcus and does not require the lateral PFC (Allison et al., 2000; Lieberman, 2007; Mar, 2011; Pitcher, Dilks, Saxe, Triantafyllou, & Kanwisher, 2011).

Furthermore, the simultaneous operation of EDC and IDC has been demonstrated in studies documenting the influence of spontaneous self-evaluative thinking on cognitive control (*N*-back) performance (Bengtsson et al., 2009, 2010). The *N*-back task involves intentional EDC processes and recruits the lateral PFC in addition to other EDC-related regions (Owen, McMillan, Laird, & Bullmore, 2005). On the other hand, the influence of spontaneous self-evaluative thinking was specifically associated with activation of the paracingulate/dorsal MPFC in these studies (Bengtsson et al., 2010, 2009). These results suggest that cognitive control and spontaneous self-evaluative thinking may be supported by distinct brain regions, and this may allow for their co-occurrence, as outlined in our framework.

Finally, creativity provides an additional example of how EDC and IDC processes that rely on different brain regions can co-occur without interference. One study had participants create novel artwork for a book cover and found activation of IDC-related regions (e.g., MTL) which may have reflected the spontaneous retrieval and integration of previously stored information in order to generate novel ideas (Ellamil et al., 2012). There was also activation of EDC-related regions (e.g., superior parietal cortex, fusiform gyrus, occipital-temporal cortex, premotor cortex) which may have reflected externally directed attention to the visual artwork being produced and to the actions producing the work (Ellamil et al., 2012). Similarly, another study found that jazz piano improvisation was associated with activation of both IDC-related areas (e.g., medial PFC) and EDC-related brain regions (e.g., pMTG, fusiform gyrus, primary sensory-motor cortices) (Limb & Braun, 2008). EDC-related regions may have been involved in producing and listening to the music, while IDC-related regions may have been involved in self-evaluative processing and creating novel note sequences. Further reinforcing the idea that IDC and EDC were co-occurring in these studies, the study of visual art creativity found that the lateral PFC demonstrated widespread positive functional connectivity (i.e., temporally correlated activation) with both EDC-related regions and IDC-related regions during the creative process (Ellamil et al., 2012). Acknowledging the temporal resolution limitations of fMRI, these data suggest that patterns of activation related to EDC and IDC fluctuated in concert with one another. Such findings are consistent with the notion of co-occurrence, rather than with the notion of a rapid alternation between EDC and IDC, supporting the framework articulated here.

6. Implications of the framework

6.1. Flexible shifting of attention

It is increasingly recognized that the capacity to flexibly shift between and coordinate internally and externally directed cognition is critical for adaptive cognitive functioning (Allen et al., 2013; Buckner et al., 2008). Dysfunction of this shifting capacity may contribute to the cognitive decline associated with aging, as well as with neurological and psychiatric conditions including anxiety, depression, schizophrenia, autism, and Alzheimer's (Beck & Clark, 1997; Buckner et al., 2008; Nolen-Hoeksema, 1991; Watkins & Teasdale, 2004). For example, in the case of depression, individuals often have difficulty shifting attention away from spontaneous (as

well as voluntary) negative thinking about the self and one's depressive symptoms (Nolen-Hoeksema, 1991). Our review suggests that the lateral PFC is involved in both EDC and IDC in the case of intentional processing, and may therefore play a critical role in shifting attention between these two modes of cognition based on its pattern of functional coupling with other brain regions. In support of this idea, Spreng et al. (2010) demonstrated that a frontoparietal network including the lateral PFC exhibited significant functional connectivity with EDC regions when performing a Tower of Hanoi task requiring externally directed visuospatial attention, but coupled more strongly with IDC regions during an autobiographical future planning task requiring internally directed attention. Others have also suggested that the lateral PFC may play a key role in mediating interactions between internally and externally directed processing (Burgess, Dumontheil, & Gilbert, 2007; Vincent, Kahn, Snyder, Raichle, & Buckner, 2008). As such, the lateral PFC would appear to be a prime target for interventions aimed at improving the ability to voluntarily shift the focus of attention between the internal and external world, and to avoid getting stuck in maladaptive thought patterns that may interfere with normal cognitive functioning. This may be one means by which meditation training exerts its beneficial effects on clinical symptoms of anxiety and depression (Hofmann, Sawyer, Witt, & Oh, 2010; Khoury et al., 2013; Segal, Williams, & Teasdale, 2013), given that meditation practice is associated with structural and functional changes in the lateral PFC (e.g., Farb et al., 2007; Fox et al., 2014). In fact a key facet of mindfulness meditation practice is to pay attention to the breath, and to repeatedly shift attention back to the breath whenever attention has strayed to extraneous thoughts or to external stimuli (e.g., sounds from the surrounding environment). Over time, this practice may enhance the capacity to intentionally shift between EDC and IDC.

6.2. The influence of self-referential thinking on EDC

There is a large literature documenting the substantial impact of self-concept on behavior (Markus & Wurf, 1987; McConnell, 2011). Currently activated self-related thoughts influence attention, decision making, affect, and other cognitive operations especially in demanding situations. The suggestion that EDC and IDC can operate simultaneously in some cases can be used as a framework for understanding the influence of self-concept. In particular, spontaneous self-referential thoughts may not necessarily compete with EDC for attentional resources, but rather, may directly influence the efficacy of EDC processes. Supporting this possibility, cognitive control performance is not necessarily disrupted by the activation of self-evaluative thoughts; rather it can be hindered or facilitated depending on the content of the self-related thinking (Bengtsson et al., 2010, 2009). To date, cognitive neuroscience studies of EDC have largely ignored the potential impact of self-evaluative thinking on task performance. However, this may be an important source of individual variation in the efficacy of cognitive control, and may play out in terms of specific types of interactions between EDC regions and the MPFC (and perhaps other default mode network regions as well). Examining these interactions would be a fruitful avenue for future research.

6.3. Co-operation between externally and internally directed cognition

Several of the topics addressed above — creativity, mentalizing, and the influence of self-evaluative thinking on cognitive control — raise the intriguing possibility of not just co-occurrence, but *co-operation*, between EDC and IDC processes in the service of higher-order goals related to the external world or inner well-being

(Fox & Christoff, 2014). Some of the most essential mental states humans are capable of experiencing seem to involve such cooperative or facilitative interactions between EDC and IDC. Take creativity, for example. In the context of musical improvisation by a jazz quartet, there is a spontaneously generated stream of musical ideas (involving internally oriented retrieval and re-combination of knowledge stored in memory), the translation of such ideas into motor activity expressed through an instrument resulting in external sounds (eliciting EDC), and also the simultaneous monitoring of other band members, the overall harmonic and rhythmic patterns of the group, exchanged looks and cues from audience members, and so on. In this example, EDC and IDC are not simply co-occurring independently, but rather, are actively co-ordinated. Our framework suggests that such facilitative interactions are quite possible as long as one mode of cognition is occurring relatively spontaneously (as it thought to be the case during some aspects of creativity) (Limb & Braun, 2008). There is much to be learned about the nature of co-ordinated EDC-IDC interactions and the factors that support such co-ordination. One relevant factor may be meta-cognition, which may facilitate the selection of useful and congruent information arising from EDC and IDC processes (see Fox & Christoff, 2014 for a discussion on meta-cognition and creativity).

6.4. Memory-guided attention

One area of inquiry that has received growing interest in recent years is memory-guided attention. There is solid evidence supporting the idea that episodic memory can exert an adaptive influence on visual search by directing external attention to important locations learned in the past (Chun & Turk-Browne, 2007; Summerfield, Lepsien, Gitelman, Mesulam, & Nobre, 2006). For example, we would be much faster to locate a glass for water in our own house relative to a friend's house for the simple reason that we can use episodic memory to limit the search space in our own house: we can use prior experience to know which cabinet contains glasses. In addition to the influence of explicit episodic memories, there is also evidence that implicitly acquired memories of the spatial layout of the environment can also guide the deployment of external attention (Chun & Jiang, 1998; Dixon, Zelazo, & De Rosa, 2010). Memory-guided attention is another clear example of facilitative EDC-IDC interactions. However, these studies have yet to address the influence of intentionality. Our framework predicts that spontaneously retrieved episodic memories can operate concurrently with intentional visual search and provide an 'on-line' adaptive bias that rapidly guides attention to a target location. In contrast, our framework predicts that intentionally retrieved memories should interrupt visual search, and lead to an alternation between IDC and EDC that results in accurate, but slower visual search. This hypothesis remains to be tested.

7. Conclusions

In this review, we have proposed that EDC and IDC are not intrinsically antagonistic, but rather, that their relationship depends on processing demands. Specifically, we suggest that EDC and IDC can co-occur with minimal interference – and may even co-operate with one another – when one or both involve spontaneous processing. The reason for this is that largely distinct neural structures that support IDC and EDC during spontaneous processing. On the other hand, we suggest that EDC and IDC tend to interfere with one another when both involve intentional processing, as both then draw upon the capacity-limited resources of the lateral PFC to specify the behavioral relevance of a stimulus or train of thought. The proposal that EDC and IDC can in some cases co-occur, provides a useful framework for understanding the

complex mental states that underlie mentalizing, creativity, the influence of self-evaluative processing on cognitive control, and memory-guided attention.

Future research examining EDC and IDC should strive to articulate whether intentional or spontaneous processing is being examined, and to not fall into the trap of conflating EDC with intentional (goal-directed) processing, and IDC with spontaneous (unconstrained) processing (see Spreng, 2012). When using terms such as mind wandering, stimulus-independent thought, day-dreaming, task-unrelated thought, and so on, it is important to explicitly specify (as much as possible) whether processing is spontaneous or intentional. Similarly, it cannot be assumed that cognitive processes occurring during the 'resting state' are necessarily spontaneous. Participants appear to direct their own musings just as much as they let themselves get carried away by spontaneous streams of thought (Klinger, 2008).

Additionally, it will be important for future work to incorporate interoceptive and emotional processes into frameworks of EDC-IDC interactions. Emotional processing is a particularly interesting case because it may often involve the co-occurrence of EDC and IDC, with attention being directed externally to the emotion-eliciting stimulus itself, and also internally to thoughts and feelings elicited by those stimuli. Furthermore, considering dimensions other than intentionality may also be useful for discerning the relationship between EDC and IDC. For example, the level of awareness involved (ranging from unconscious processing to meta-awareness) may influence whether or not interference arises between EDC and IDC (see also Fox and Christoff, 2014). Finally, we have emphasized the critical role of the lateral PFC in bridging internally and externally directed cognition, but other regions may also play a central role. For example, there is some evidence that the anterior insula may play a role in mediating interactions between internal and external processing (Sridharan, Levitin, & Menon, 2008). In sum, much progress has been made in understanding the relationship between EDC and IDC, and future work geared toward the detailed analysis of interactions at the cognitive and neural level will clarify how competition and co-operation between these modes of cognition give rise to important mental functions that contribute to adaptive human behavior.

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References

- Addis, D. R., Wong, A. T., & Schacter, D. L. (2007). Remembering the past and imagining the future: Common and distinct neural substrates during event construction and elaboration. *Neuropsychologia*, 45(7), 1363–1377.
- Allen, M., Smallwood, J., Christensen, J., Gramm, D., Rasmussen, B., Jensen, C. G., et al. (2013). The balanced mind: The variability of task-unrelated thoughts predicts error monitoring. *Frontiers in Human Neuroscience*, 7, 743.
- Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: Role of the STS region. *Trends in Cognitive Sciences*, 4(7), 267–278.
- Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: The medial frontal cortex and social cognition. *Nature Reviews in Neuroscience*, 7(4), 268–277.
- Andrews-Hanna, J. R. (2012). The brain's default network and its adaptive role in internal mentation. *Neuroscientist*, 18(3), 251–270.
- Andrews-Hanna, J. R., Reidler, J. S., Huang, C., & Buckner, R. L. (2010). Evidence for the default network's role in spontaneous cognition. *Journal of Neurophysiology*, 104(1), 322–335.

- Andrews-Hanna, J. R., Saxe, R., & Yarkoni, T. (2014). Contributions of episodic retrieval and mentalizing to autobiographical thought: Evidence from functional neuroimaging, resting-state connectivity, and fMRI meta-analyses. *Neuroimage*.
- Aron, A. R., Robbins, T. W., & Poldrack, R. A. (2004). Inhibition and the right inferior frontal cortex. *Trends in Cognitive Sciences*, 8(4), 170–177.
- Badre, D., & D'Esposito, M. (2009). Is the rostro-caudal axis of the frontal lobe hierarchical? *Nature Reviews Neuroscience*, 10(9), 659–669.
- Baron-Cohen, S., Wheelwright, S., Hill, J., Raste, Y., & Plumb, I. (2001). The "Reading the Mind in the Eyes" Test revised version: A study with normal adults, and adults with Asperger syndrome or high-functioning autism. *Journal of Child Psychology and Psychiatry*, 42(2), 241–251.
- Barredo, J., Oztekin, I., & Badre, D. (2013). Ventral fronto-temporal pathway supporting cognitive control of episodic memory retrieval. *Cerebral Cortex*.
- Batty, M., & Taylor, M. J. (2003). Early processing of the six basic facial emotional expressions. *Brain Research Cognitive Brain Research*, 17(3), 613–620.
- Beck, A. T., & Clark, D. A. (1997). An information processing model of anxiety: Automatic and strategic processes. *Behaviour Research and Therapy*, 35(1), 49–58.
- Bengtsson, S. L., Dolan, R. J., & Passingham, R. E. (2010). Priming for self-esteem influences the monitoring of one's own performance. *Social Cognitive and Affective Neuroscience*, 6(4), 417–425.
- Bengtsson, S. L., Lau, H. C., & Passingham, R. E. (2009). Motivation to do well enhances responses to errors and self-monitoring. *Cerebral Cortex*, 19(4), 797–804.
- Bhatt, M. A., Lohrenz, T., Camerer, C. F., & Montague, P. R. (2010). Neural signatures of strategic types in a two-person bargaining game. *Proceedings of the National Academy of Sciences of the United States of America*, 107(46), 19720–19725.
- Braver, T. S. (2012). The variable nature of cognitive control: A dual mechanisms framework. *Trends in Cognitive Sciences*, 16(2), 106–113.
- Buckner, R. L., Andrews-Hanna, J. R., & Schacter, D. L. (2008). The brain's default network: Anatomy, function, and relevance to disease. *Annals of the New York Academy of Sciences*, 1124, 1–38.
- Bunge, S. A., Kahn, I., Wallis, J. D., Miller, E. K., & Wagner, A. D. (2003). Neural circuits subserving the retrieval and maintenance of abstract rules. *Journal of Neurophysiology*, 90(5), 3419–3428.
- Burgess, P. W., Dumontheil, I., & Gilbert, S. J. (2007). The gateway hypothesis of rostral prefrontal cortex (area 10) function. *Trends in Cognitive Sciences*, 11(7), 290–298.
- Buschman, T. J., & Miller, E. K. (2007). Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science*, 315(5820), 1860–1862.
- Cabeza, R., Ciaramelli, E., Olson, I. R., & Moscovitch, M. (2008). The parietal cortex and episodic memory: An attentional account. *Nature Reviews in Neuroscience*, 9(8), 613–625.
- Christoff, K. (2012). Undirected thought: Neural determinants and correlates. *Brain Research*, 1428, 51–59.
- Christoff, K., & Gabrieli, J. D. E. (2000). The frontopolar cortex and human cognition: Evidence for a rostrocaudal hierarchical organization within the human prefrontal cortex. *Psychobiology*, 28(2), 168–186.
- Christoff, K., Gordon, A. M., Smallwood, J., Smith, R., & Schooler, J. W. (2009). Experience sampling during fMRI reveals default network and executive system contributions to mind wandering. *Proceedings of the National Academy of Sciences of the United States of America*, 106(21), 8719–8724.
- Christoff, K., Prabhakaran, V., Dorfman, J., Zhao, Z., Kroger, J. K., Holyoak, K. J., et al. (2001). Rostrolateral prefrontal cortex involvement in relational integration during reasoning. *NeuroImage*, 14(5), 1136–1149.
- Christoff, K., Ream, J. M., & Gabrieli, J. D. (2004). Neural basis of spontaneous thought processes. *Cortex; A Journal Devoted to the Study of the Nervous System and Behavior*, 40(4–5), 623–630.
- Chun, M. M., Golomb, J. D., & Turk-Browne, N. B. (2011). A taxonomy of external and internal attention. *Annual Review of Psychology*, 62, 73–101.
- Chun, M. M., & Jiang, Y. (1998). Contextual cueing: Implicit learning and memory of visual context guides spatial attention. *Cognitive Psychology*, 36(1), 28–71.
- Chun, M. M., & Turk-Browne, N. B. (2007). Interactions between attention and memory. *Current Opinions in Neurobiology*, 17(2), 177–184.
- Cole, M. W., Bagic, A., Kass, R., & Schneider, W. (2010). Prefrontal dynamics underlying rapid instructed task learning reverse with practice. *Journal of Neuroscience*, 30(42), 14245–14254.
- Cole, M. W., & Schneider, W. (2007). The cognitive control network: Integrated cortical regions with dissociable functions. *NeuroImage*, 37(1), 343–360.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews in Neuroscience*, 3(3), 201–215.
- Crowe, D. A., Goodwin, S. J., Blackman, R. K., Sakellari, S., Sponheim, S. R., Macdonald, A. W., III, et al. (2013). Prefrontal neurons transmit signals to parietal neurons that reflect executive control of cognition. *Nature Neuroscience*, 16(10), 1484–1491.
- D'Argembeau, A., Collette, F., Van der Linden, M., Laureys, S., Del Fiore, G., Degueldre, C., et al. (2005). Self-referential reflective activity and its relationship with rest: A PET study. *NeuroImage*, 25(2), 616–624.
- D'Argembeau, A., Stawarczyk, D., Majerus, S., Collette, F., Van der Linden, M., Feyers, D., et al. (2010). The neural basis of personal goal processing when envisioning future events. *Journal of Cognitive Neuroscience*, 22(8), 1701–1713.
- Dehaene, S., Naccache, L., Le Clec, H. G., Koechlin, E., Mueller, M., Dehaene-Lambertz, G., et al. (1998). Imaging unconscious semantic priming. *Nature*, 395(6702), 597–600.
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, 18, 193–222.
- Dijksterhuis, A., & Aarts, H. (2010). Goals, attention, and (un)consciousness. *Annual Review of Psychology*, 61, 467–490.
- Dixon, M. L., & Christoff, K. (2012). The decision to engage cognitive control is driven by expected reward-value: Neural and behavioral evidence. *PLoS One*, 7(12), e51637.
- Dixon, M. L., Zelazo, P. D., & De Rosa, E. (2010). Evidence for intact memory-guided attention in school-aged children. *Developmental Science*, 13(1), 161–169.
- Donohue, S. E., Wendelken, C., Crone, E. A., & Bunge, S. A. (2005). Retrieving rules for behavior from long-term memory. *NeuroImage*, 26(4), 1140–1149.
- Dosenbach, N. U., Visscher, K. M., Palmer, E. D., Miezin, F. M., Wenger, K. K., Kang, H. C., et al. (2006). A core system for the implementation of task sets. *Neuron*, 50(5), 799–812.
- Dumontheil, I., Gilbert, S. J., Frith, C. D., & Burgess, P. W. (2010). Recruitment of lateral rostral prefrontal cortex in spontaneous and task-related thoughts. *Quarterly Journal of Experimental Psychology (Hove)*, 63(9), 1740–1756.
- Duncan, J. (2001). An adaptive coding model of neural function in prefrontal cortex. *Nature Review Neuroscience*, 2(11), 820–829.
- Duncan, J. (2010). The multiple-demand (MD) system of the primate brain: mental programs for intelligent behaviour. *Trends in Cognitive Sciences*, 14(4), 172–179.
- Egner, T., & Hirsch, J. (2005). Cognitive control mechanisms resolve conflict through cortical amplification of task-relevant information. *Nature Neuroscience*, 8(12), 1784–1790.
- Ellamil, M., Dobszon, C., Beeman, M., & Christoff, K. (2012). Evaluative and generative modes of thought during the creative process. *NeuroImage*, 59(2), 1783–1794.
- Farb, N. A., Segal, Z. V., Mayberg, H., Bean, J., McKeon, D., Fatima, Z., et al. (2007). Attending to the present: Mindfulness meditation reveals distinct neural modes of self-reference. *Social, Cognitive and Affective Neuroscience*, 2(4), 313–322.
- Fletcher, P. C., Happe, F., Frith, U., Baker, S. C., Dolan, R. J., Frackowiak, R. S., et al. (1995). Other minds in the brain: A functional imaging study of "theory of mind" in story comprehension. *Cognition*, 57(2), 109–128.
- Foster, B. L., Dastjerdi, M., & Parvizi, J. (2012). Neural populations in human posteromedial cortex display opposing responses during memory and numerical processing. *Proceedings of the National Academy of Sciences of the United States of America*, 109(38), 15514–15519.
- Fox, K., & Christoff, K. (2014). Metacognitive facilitation of spontaneous thought processes: When metacognition helps the wandering mind find its way. In: S. M. Fleming, & C. D. Frith (Eds.), *The cognitive neuroscience of metacognition* (pp. 293–319). Berlin, Heidelberg: Springer.
- Fox, K., Nijeboer, S., Dixon, M. L., Floman, J. L., Ellamil, M., Rumak, S. P., et al. (2014). Is meditation associated with altered brain structure? A systematic review and meta-analysis of morphometric neuroimaging in meditation practitioners. *Neuroscience & Biobehavioral Reviews*.
- Fox, K., Nijeboer, S., Solomonova, E., Domhoff, G. W., & Christoff, K. (2013). Dreaming as mind wandering: Evidence from functional neuroimaging and first-person content reports. *Frontiers in Human Neuroscience*, 7, 412.
- Fox, M., Snyder, A. Z., Vincent, J. L., Corbetta, M., Van Essen, D. C., & Raichle, M. E. (2005). The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proceedings of the National Academy of Sciences of the United States of America*, 102(27), 9673–9678.
- Fox, M. D., Snyder, A. Z., Vincent, J. L., Corbetta, M., Van Essen, D. C., & Raichle, M. E. (2005). The human brain is intrinsically organized into dynamic, anticorrelated functional networks. *Proceedings of the National Academy of Sciences of the United States of America*, 102(27), 9673–9678.
- Gottlieb, J. P., Kusunoki, M., & Goldberg, M. E. (1998). The representation of visual salience in monkey parietal cortex. *Nature*, 391(6666), 481–484.
- Greenwald, A. G., Draine, S. C., & Abrams, R. L. (1996). Three cognitive markers of unconscious semantic activation. *Science*, 273(5282), 1699–1702.
- Greicius, M. D., Krasnow, B., Reiss, A. L., & Menon, V. (2003). Functional connectivity in the resting brain: A network analysis of the default mode hypothesis. *Proceedings of the National Academy of Sciences of the United States of America*, 100(1), 253–258.
- Gusnard, D. A., & Raichle, M. E. (2001). Searching for a baseline: Functional imaging and the resting human brain. *Nature Reviews Neuroscience*, 2(10), 685–694.
- Hofmann, S. G., Sawyer, A. T., Witt, A. A., & Oh, D. (2010). The effect of mindfulness-based therapy on anxiety and depression: A meta-analytic review. *Journal of Consulting and Clinical Psychology*, 78(2), 169–183.
- Jenkins, A. C., & Mitchell, J. P. (2011). Medial prefrontal cortex subserves diverse forms of self-reflection. *Social Neuroscience*, 6(3), 211–218.
- Kam, J. W., Dao, E., Farley, J., Fitzpatrick, K., Smallwood, J., Schooler, J. W., et al. (2011). Slow fluctuations in attentional control of sensory cortex. *Journal of Cognitive Neuroscience*, 23(2), 460–470.
- Kam, J. W., Dao, E., Stanculescu, M., Tildesley, H., & Handy, T. C. (2013). Mind wandering and the adaptive control of attentional resources. *Journal of Cognitive Neuroscience*, 25(6), 952–960.
- Kam, J. W., & Handy, T. C. (2013). The neurocognitive consequences of the wandering mind: A mechanistic account of sensory-motor decoupling. *Frontiers in Psychology*, 4, 725.
- Kam, J. W., & Handy, T. C. (2014). Differential recruitment of executive resources during mind wandering. *Consciousness and Cognition*, 26C, 51–63.
- Kane, M. J., & McVay, J. C. (2012). What mind wandering reveals about executive-control abilities and failures. *Current Directions in Psychological Science*, 21(5), 348–354.
- Karlsson, M. P., & Frank, L. M. (2009). Awake replay of remote experiences in the hippocampus. *Nature Neuroscience*, 12(7), 913–918.
- Kastner, S., Pinsk, M. A., De Weerd, P., Desimone, R., & Ungerleider, L. G. (1999). Increased activity in human visual cortex during directed attention in the absence of visual stimulation. *Neuron*, 22(4), 751–761.

- Keller, T. A., Carpenter, P. A., & Just, M. A. (2001). The neural bases of sentence comprehension: A fMRI examination of syntactic and lexical processing. *Cerebral Cortex*, *11*(3), 223–237.
- Kerns, J. G., Cohen, J. D., MacDonald, A. W., 3rd, Cho, R. Y., Stenger, V. A., & Carter, C. S. (2004). Anterior cingulate conflict monitoring and adjustments in control. *Science*, *303*(5660), 1023–1026.
- Khoury, B., Lecomte, T., Fortin, G., Masse, M., Therien, P., Bouchard, V., et al. (2013). Mindfulness-based therapy: A comprehensive meta-analysis. *Clinical Psychology Review*, *33*(6), 763–771.
- Killingsworth, M. A., & Gilbert, D. T. (2010). A wandering mind is an unhappy mind. *Science*, *330*(6006), 932.
- Klinger, E. (2008). 15 Daydreaming and fantasizing: Thought flow and motivation In K. D. Markman, W. M. P. Klein & J. A. Suh (Eds.), *Handbook of imagination and mental simulation*.
- Koechlin, E., & Summerfield, C. (2007). An information theoretical approach to prefrontal executive function. *Trends in Cognitive Sciences*, *11*(6), 229–235.
- Kuhl, B. A., Johnson, M. K., & Chun, M. M. (2013). Dissociable neural mechanisms for goal-directed versus incidental memory reactivation. *Journal of Neuroscience*, *33*(41), 16099–16109.
- Lane, R. D., Fink, G. R., Chau, P. M., & Dolan, R. J. (1997). Neural activation during selective attention to subjective emotional responses. *Neuroreport*, *8*(18), 3969–3972.
- Lau, H. C., & Passingham, R. E. (2007). Unconscious activation of the cognitive control system in the human prefrontal cortex. *Journal of Neuroscience*, *27*(21), 5805–5811.
- Leech, R., Kamourieh, S., Beckmann, C. F., & Sharp, D. J. (2011). Fractionating the default mode network: Distinct contributions of the ventral and dorsal posterior cingulate cortex to cognitive control. *Journal of Neuroscience*, *31*(9), 3217–3224.
- Lieberman, M. D. (2007). Social cognitive neuroscience: A review of core processes. *Annual Review of Psychology*, *58*, 259–289.
- Limb, C. J., & Braun, A. R. (2008). Neural substrates of spontaneous musical performance: An fMRI study of jazz improvisation. *PLoS One*, *3*(2), e1679.
- MacDonald, A. W., III, Cohen, J. D., Stenger, V. A., & Carter, C. S. (2000). Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science*, *288*(5472), 1835–1838.
- Mar, R. A. (2011). The neural bases of social cognition and story comprehension. *Annual Review of Psychology*, *62*, 103–134.
- Mar, R. A., Mason, M. F., & Litvack, A. (2012). How daydreaming relates to life satisfaction, loneliness, and social support: The importance of gender and daydream content. *Consciousness and Cognition*, *21*(1), 401–407.
- Markus, H., & Wurf, E. (1987). The dynamic self-concept: A social psychological perspective. *Annual Review of Psychology*, *38*(1), 299–337.
- Mason, M. F., Norton, M. I., Van Horn, J. D., Wegner, D. M., Grafton, S. T., & Macrae, C. N. (2007). Wandering minds: The default network and stimulus-independent thought. *Science*, *315*(5810), 393–395.
- McCaig, R. G., Dixon, M., Keramatian, K., Liu, I., & Christoff, K. (2011). Improved modulation of rostrolateral prefrontal cortex using real-time fMRI training and meta-cognitive awareness. *Neuroimage*, *55*(3), 1298–1305.
- McConnell, A. R. (2011). The multiple self-aspects framework: Self-concept representation and its implications. *Personality and Social Psychology Review*, *15*(1), 3–27.
- Mesulam, M. (1998). From sensation to cognition. *Brain*, *121*(Part 6), 1013–1052.
- Mesulam, M. (2000). *Principles of behavioral and cognitive neurology*. New York, NY: Oxford University Press.
- Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*, *24*, 167–202.
- Mitchell, J. P., Macrae, C. N., & Banaji, M. R. (2006). Dissociable medial prefrontal contributions to judgments of similar and dissimilar others. *Neuron*, *50*(4), 655–663.
- Moore, T., & Armstrong, K. M. (2003). Selective gating of visual signals by microstimulation of frontal cortex. *Nature*, *421*(6921), 370–373.
- Nolen-Hoeksema, S. (1991). Responses to depression and their effects on the duration of depressive episodes. *Journal of Abnormal Psychology*, *100*(4), 569–582.
- Northoff, G., & Bermpohl, F. (2004). Cortical midline structures and the self. *Trends in Cognitive Sciences*, *8*(3), 102–107.
- Ochsner, K. N., Beer, J. S., Robertson, E. R., Cooper, J. C., Gabrieli, J. D., Kihlstrom, J. F., et al. (2005). The neural correlates of direct and reflected self-knowledge. *Neuroimage*, *28*(4), 797–814.
- Owen, A. M., McMillan, K. M., Laird, A. R., & Bullmore, E. (2005). N-back working memory paradigm: A meta-analysis of normative functional neuroimaging studies. *Human Brain Mapping*, *25*(1), 46–59.
- Pessiglione, M., Schmidt, L., Draganski, B., Kalisch, R., Lau, H., Dolan, R. J., et al. (2007). How the brain translates money into force: A neuroimaging study of subliminal motivation. *Science*, *316*(5826), 904–906.
- Petersen, S. E., & Posner, M. I. (2012). The attention system of the human brain: 20 years after. *Annual Review of Neuroscience*, *35*, 73–89.
- Petrides, M. (2005). Lateral prefrontal cortex: Architectonic and functional organization. *Philosophical Transactions of the Royal Society of London B: Biological Science*, *360*(1456), 781–795.
- Pitcher, D., Dilks, D. D., Saxe, R. R., Triantafyllou, C., & Kanwisher, N. (2011). Differential selectivity for dynamic versus static information in face-selective cortical regions. *Neuroimage*, *56*(4), 2356–2363.
- Poldrack, R. A., Sabb, F. W., Foerde, K., Tom, S. M., Asarnow, R. F., Bookheimer, S. Y., et al. (2005). The neural correlates of motor skill automaticity. *Journal of Neuroscience*, *25*(22), 5356–5364.
- Posner, M. I., & Dehaene, S. (1994). Attentional networks. *Trends in Neurosciences*, *17*(2), 75–79.
- Raichle, M. E., MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(2), 676–682.
- Rasch, B., & Born, J. (2007). Maintaining memories by reactivation. *Current Opinion in Neurobiology*, *17*(6), 698–703.
- Saxe, R., & Kanwisher, N. (2003). People thinking about thinking people. The role of the temporo-parietal junction in “theory of mind”. *Neuroimage*, *19*(4), 1835–1842.
- Schacter, D. L., Addis, D. R., & Buckner, R. L. (2007). Remembering the past to imagine the future: The prospective brain. *Nature Reviews Neuroscience*, *8*(9), 657–661.
- Schmitz, T. W., & Johnson, S. C. (2007). Relevance to self: A brief review and framework of neural systems underlying appraisal. *Neuroscience & Biobehavioral Reviews*, *31*(4), 585–596.
- Schneider, W., & Shiffrin, R. M. (1977). Controlled and automatic human information processing: I. Detection, search, and attention. *Psychological Review*, *84*, 1–66.
- Schooler, J. W., Smallwood, J., Christoff, K., Handy, T. C., Reichle, E. D., & Sayette, M. A. (2011). Meta-awareness, perceptual decoupling and the wandering mind. *Trends in Cognitive Sciences*, *15*(7), 319–326.
- Segal, Z. V., Williams, J. M. G., & Teasdale, J. D. (2013). *Mindfulness-based cognitive therapy for depression* (2nd ed.). New York: Guilford Press.
- Senju, A., Southgate, V., White, S., & Frith, U. (2009). Mindblind eyes: An absence of spontaneous theory of mind in Asperger syndrome. *Science*, *325*(5942), 883–885.
- Shulman, G. L., Fiez, J. A., Corbetta, M., Buckner, R. L., Miezin, F. M., Raichle, M. E., et al. (1997). Common blood flow changes across visual tasks: II. Decreases in cerebral cortex. *Journal of Cognitive Neuroscience*, *9*(5), 648–663.
- Smallwood, J., McSpadden, M., & Schooler, J. W. (2008). When attention matters: The curious incident of the wandering mind. *Memory and Cognition*, *36*(6), 1144–1150.
- Smallwood, J., & Schooler, J. W. (2006). The restless mind. *Psychological Bulletin*, *132*(6), 946–958.
- Spreng, R. N. (2012). The fallacy of a “task-negative” network. *Frontiers in Psychology*, *3*, 145.
- Spreng, R. N., Mar, R. A., & Kim, A. S. (2009). The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: A quantitative meta-analysis. *Journal of Cognitive Neuroscience*, *21*(3), 489–510.
- Spreng, R. N., Stevens, W. D., Chamberlain, J. P., Gilmore, A. W., & Schacter, D. L. (2010). Default network activity, coupled with the frontoparietal control network, supports goal-directed cognition. *Neuroimage*, *53*(1), 303–317.
- Sridharan, D., Levitin, D. J., & Menon, V. (2008). A critical role for the right fronto-insular cortex in switching between central-executive and default-mode networks. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(34), 12569–12574.
- Stawarczyk, D., Majerus, S., Maquet, P., & D’Argembeau, A. (2011). Neural correlates of ongoing conscious experience: Both task-unrelatedness and stimulus-independence are related to default network activity. *PLoS One*, *6*(2), e16997.
- Summerfield, J. J., Lepsien, J., Gitelman, D. R., Mesulam, M. M., & Nobre, A. C. (2006). Orienting attention based on long-term memory experience. *Neuron*, *49*(6), 905–916.
- Toni, I., Ramnani, N., Josephs, O., Ashburner, J., & Passingham, R. E. (2001). Learning arbitrary visuomotor associations: Temporal dynamic of brain activity. *Neuroimage*, *14*(5), 1048–1057.
- Vincent, J. L., Kahn, I., Snyder, A. Z., Raichle, M. E., & Buckner, R. L. (2008). Evidence for a frontoparietal control system revealed by intrinsic functional connectivity. *Journal of Neurophysiology*, *100*(6), 3328–3342.
- Watkins, E., & Teasdale, J. D. (2004). Adaptive and maladaptive self-focus in depression. *Journal of Affective Disorders*, *82*(1), 1–8.
- Weissman, D. H., Roberts, K. C., Visscher, K. M., & Woldorff, M. G. (2006). The neural bases of momentary lapses in attention. *Nature Neuroscience*, *9*(7), 971–978.
- Yantis, S., & Hillstrom, A. P. (1994). Stimulus-driven attentional capture: Evidence from equiluminant visual objects. *Journal of Experimental Psychology: Human Perception and Performance*, *20*(1), 95–107.
- Yoshida, W., Seymour, B., Friston, K. J., & Dolan, R. J. (2010). Neural mechanisms of belief inference during cooperative games. *Journal of Neuroscience*, *30*(32), 10744–10751.