# CHAPTER **13**

### The Neuroscience of Spontaneous Thought: An Evolving Interdisciplinary Field

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### Abstract

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An often-overlooked characteristic of the human mind is its propensity to wander. Despite growing interest in the science of mind-wandering, most studies operationalize mind-wandering by its task-unrelated *contents*, which may be orthogonal to the *processes* constraining how thoughts are evoked and unfold over time. This chapter emphasizes the importance of incorporating such processes into current definitions of mind-wandering, and proposes that mind-wandering and other forms of spontaneous thought (such as dreaming and creativity) are mental states that arise and transition relatively freely due to an absence of constraints on cognition. The chapter reviews existing psychological, philosophical, and neuroscientific research on spontaneous though through the lens of this framework, and calls for additional research into the dynamic properties of the mind and brain.

Key Words: spontaneous thought, mind-wandering, task-unrelated, dreaming, creativity

### An Introduction to an Evolving Interdisciplinary Field

A mere 10 years ago, the idea of an edited volume on spontaneous thought might have seemed farfetched. Yet fast-forward to 2018, and the topic once considered a "fringe" or "pseudo" science—has begun to thrive in mainstream research. This growing scientific interest in spontaneous mental activity was sparked by several independent findings from psychology and neuroscience research that have recently been synthesized under the heading of a new field: *the neuroscience of spontaneous thought* (see Christoff, Irving, Fox, Spreng, & Andrews-Hanna, 2016, for a recent review).

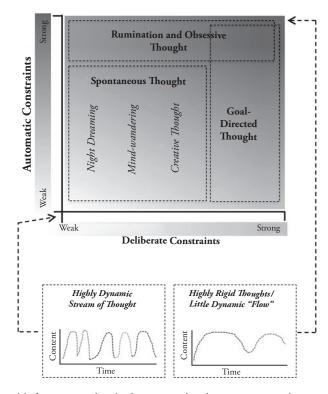
Beginning in the 1960s, findings from the psychology literature demonstrated that cognition often unfolds independent from the here and now (Singer & McCraven, 1961; Kane, Brown, & McVay, 2007; Killingsworth & Gilbert, 2010; Klinger & Cox, 1987), and subsequent studies have shown that these *task-unrelated* or *stimulusindependent thoughts* exhibit complex relationships with attention (Antrobus, Singer, & Greenberg, 1966; McVay & Kane, 2010; Smallwood & Schooler, 2006; Teasdale et al., 1995) and well-being (Giambra & Traynor, 1978; McMillan, Kaufman, & Singer, 2013; Watkins, 2008). In parallel, neuroscientists discovered that a set of regions known as the *default network* becomes more active when participants disengage from a wide variety of tasks (Raichle et al., 2001; Shulman et al., 1997a), leading to a plethora of studies attempting to uncover the network's functional roles (reviewed in Buckner, Andrews-Hanna, & Schacter, 2008). Subsequently, the introduction of resting state functional connectivity (RSFC) into mainstream neuroscience research (i.e., Fox et al., 2005; Greicius, Krasnow, Reiss, & Menon, 2003) demonstrated that intricate maps of the brain's functional network architecture could be derived from an fMRI scan while individuals rested quietly in the scanner (reviewed in Fox & Raichle, 2007). Collectively, these findings revealed that a set of brain regions becomes engaged in coordinated ways when individuals are left alone undisturbed.

Neuroscientists therefore started to question: "What is so special about periods of rest?"

In this chapter, we highlight how our understanding of the neuroscience of spontaneous thought has benefited greatly from integrating these parallel findings across psychological and neuroscientific levels of analysis, as well as related fields such as the philosophy of mind-wandering (Carruthers, 2015; Dorsch, 2015; Irving, 2016; Irving & Thompson, Chapter 8 in this volume; Metzinger, 2013; Metzinger, 2015; Sripada, Chapter 3 in this volume; Sripada, 2016). Realizing that the mind is always active-spontaneously associating, simulating, remembering, predicting, mentalizing, and evaluating-suggests that the default network's coordinated activity during periods of wakeful rest may be neither a coincidence nor indicative of a state of idleness. Similarly, the recent discovery that regions associated with executive control become engaged during mind-wandering<sup>1</sup> (Christoff, Gordon, Smallwood, Smith, & Schooler, 2009; Fox, Spreng, Ellamil, Andrews-Hanna, & Christoff, 2015) sheds important light on the complex behavioral relationships between mind-wandering and executive function. Here we discuss how interdisciplinary cross-talk led to evolving views on how to define, measure, and understand the significance of spontaneous thought, and how these inquiries continue to spark new questions for future research on this elusive phenomenon.

### Evolving Definitions of Spontaneous Thought

Although the phrase "spontaneous thought" is often equated with "mind-wandering" throughout the literature, we recently proposed that mindwandering is but one member of a larger class of spontaneous processes that also includes nighttime dreaming, as well as aspects of creativity (Christoff et al., 2016; Figure 13.1). We defined spontaneous



**Figure 13.1.** A dynamic model of spontaneous thought. Spontaneous thought spans a conceptual space, inclusive of night dreaming, mind-wandering, and creative thought, that is relatively free from two kinds of constraints: (1) deliberate constraints (*x*-axis), and (2) automatic constraints (*y*-axis). According to this model, adapted and extended from Christoff and colleagues (2016), ruminative and obsessive thought are not truly spontaneous in nature due to strong bottom-up, "automatic" constraints that bias their content. The dynamics of thought—the way thoughts unfold and flow over time—represent an important element of this model. As shown in the bottom left box, thoughts that are free from both kinds of constraints should transition relatively quickly and span different phenomenological content (represented by different gray colors). Conversely, excessively constrained thoughts should have longer durations with similar content (bottom right box). (See Color Insert)

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thought as "a mental state, or a sequence of mental states, that arise relatively freely due to an absence of strong constraints on the contents of each state and on the transitions from one mental state to another" (p. 719). Three key components of this definition are largely overlooked by prior research (see also Irving, 2016, for a philosophical theory that incorporates similar developments). First, the definition suggests that thoughts arising in a spontaneous or unintentional fashion should not be equated with thoughts arising deliberately, even when such thoughts have similar (e.g., task-unrelated) contents. Second, this definition contrasts thoughts that arise spontaneously from those that are constrained through automatic sources, such as perceptual and affective salience. Third, if spontaneous thoughts unfold relatively free from constraints, they should flow in a flexible and dynamic manner.

Although these principles may seem inherent to the term "spontaneity," the bulk of the mindwandering literature characterizes the phenomenon by its *contents*, rather than the *processes* by which thoughts are evoked (i.e., Smallwood & Schooler, 2006). For years, mind-wandering has been defined as being either unrelated to the task at hand (as a task-unrelated thought) (e.g., Giambra, 1989), or as independent from external stimuli (as a stimulusindependent thought) (e.g., Teasdale et al., 1995). While more recent taxonomies suggest that true episodes of mind-wandering are thoughts that are both task-unrelated and stimulus-independent (Stawarczyk et al., 2011a), such definitions do not consider the manner in which thoughts are evoked, nor how they unfold over time (but see Christoff, 2012; Irving, 2016; Irving & Thompson, Chapter 8 in this volume; Klinger, 1971; McMillan et al., 2013; Seli, Carriere, & Smilek, 2015a; Smallwood & Schooler, 2015; Stan & Christoff, Chapter 5 in this volume).

The distinction between spontaneous versus deliberate thought is critical in many respects. For one, recent research suggests that unintentional versus intentional task-unrelated thoughts show dissociable effects across a variety of behavioral and clinical contexts (Seli, Risko, Purdon, & Smilek, 2016a). For example, intentional task-unrelated thoughts are most frequent in easy compared to difficult tasks, while unintentional thoughts are most frequent in difficult compared to easy tasks (Seli, Risko, & Smilek, 2016b). Further, greater endorsement of unintentional thinking, as measured with a trait questionnaire, positively predicts symptoms of both deficit hyperactivity disorder (ADHD; Seli, Smallwood, Cheyne, & Smilek, 2015b) and obsessive-compulsive disorder (OCD; Seli, Risko, Smilek, & Schacter, 2016c), despite the finding that intentional task-unrelated thoughts do not show significant relationships with symptoms of these disorders. Moreover, intentional task-unrelated thoughts positively predict aspects of trait mindfulness, while unintentional thoughts negatively predict the same mindfulness construct (Seli et al., 2015a). The distinction between unintentional and intentional task-unrelated thinking may also prove important when interpreting existing neuroscience research, as discussed later in this chapter.

Another key dimension of spontaneous thought, foreshadowed by William James as the flowing "stream" in the stream of consciousness (James, 1890), is the manner in which thoughts unfold over time. According to the definition of Christoff and colleagues (2016), thoughts that concern a narrow topic, and remain fixated on this narrow topic over AQ: Please time, are not spontaneous in nature because of the excessive constraints that influence how one tran-& Schooler. sitions from one thought to another. As discussed earlier, a train of thought can be constrained in two ways (Christoff et al., 2016; Irving, 2016). One type of constraint that can limit the flow of thought list. Please is deliberate in nature-that is, evoked intentionprovide the ally using top-down control, as when one chooses to remain focused on a particular topic for an extended period of time. Another type of constraint is automatic in nature—as when a habitual thought pattern or salient perceptual stimulus biases one's thoughts toward a specific topic in a bottom-up manner. This temporal variability, largely overlooked by prior research, has important clinical relevance. For example, excessive automatic constraints could characterize ruminative thoughts (see DuPre & Spreng, Chapter 36 in this volume)-a common symptom of depression and anxiety (Nolen-Hoeksema, Wisco, & Lyubomirsky, 2008; Watkins, 2008). In contrast, thoughts with excessive variability may characterize ADHD or aspects of psychosis (Christoff et al., 2016). The dynamics of spontaneous thoughts may have additional implications for recent neuroscientific findings (see discussion later in this chapter).

Although this section has given much weight to process models of spontaneous thought, the content of spontaneous thought is also key, and variability in thought content over time is an important manifestation of its dynamic flow. Additionally, numerous studies have shown that task-unrelated thoughts can have a diverse

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array of content, including emotional, temporal, and social content that may differ within and between individuals in ways that relate to well-being (Klinger, 2009; Singer & Antrobus, 1966; Smallwood & Andrews-Hanna, 2013). For example, although meta-analyses of behavioral studies show that task-unrelated thoughts have a slightly positive bias on average (Fox et al., 2014; Fox et al., in preparation), symptoms of depression have been linked to more negative and selffocused thoughts (Andrews-Hanna et al., 2013; Giambra & Traynor, 1978). Additionally, while task-unrelated thoughts can sometimes predict worse subsequent mood (Killingsworth & Gilbert, 2010, but see Mason, Brown, Mar, & Smallwood, 2013; Poerio, Totterdell, & Miles, 2013), taskunrelated thoughts pertaining to the future predict better subsequent mood (Ruby, Smallwood, Engen, & Singer, 2013). According to the content regulation hypothesis proposed by Smallwood and Andrews-Hanna (Smallwood & Andrews-Hanna, 2013; Andrews-Hanna, Smallwood, & Spreng, 2014), an ability to limit one's task-unrelated thoughts to largely positive, constructive content is thought to be a critical factor governing its costs and benefits.

### Evolving Approaches to Measuring the Neuroscience of Spontaneous Thought

Thus far, this chapter has introduced a new field-the neuroscience of spontaneous thoughtand has discussed how the definition of spontaneous thought (and mind-wandering, in particular) has evolved in recent years. Before synthesizing findings from research on this topic, it is worth discussing how the neural underpinnings of spontaneous thought are commonly measured. The element of spontaneity poses a unique challenge inherent to its experimental study. How can one measure a process that, by definition, cannot be directly experimentally induced, as doing so would introduce deliberate constraints on cognition that conflict with spontaneity? And how can one isolate stretches of spontaneous thought, when they arise at unpredictable times, independently of immediate perceptual input and experimental demands, and often unbeknownst to the person having those thoughts? This section reviews evolving approaches to measuring the neural underpinnings of spontaneous thought, and evaluates such approaches in light of the definitions discussed in the previous section.

### Early Neuroscience Research Measured Spontaneous Thoughts Accidentally and Indirectly

Although the field of psychology had begun to address the challenges inherent to the measurement of spontaneous thought by the 1990s, historical biases and demands for rigorous experimental control pressured the neuroscience field to focus on externally-oriented processes with measurable behavioral manifestations (Callard, Smallwood, & Margulies, 2012). As a result, the neuroscience of spontaneous thought trailed behind for decades (but see early efforts by Ingvar, 1979; Andreasen et al., 1995; McGuire et al., 1996; Binder et al., 1999). Given these biases, it may not seem surprising that the *default network*, a brain system now widely appreciated for its role in internally directed thought (Buckner, Andrews-Hanna, Schacter, 2008), was discovered entirely accidentally. This groundbreaking discovery followed a meta-analysis of nine different positron emission tomography (PET) studies of "human visual information processing," each with passive control conditions in which participants fixated on a crosshair or passively viewed the same stimuli (Shulman et al., 1997a, 1997b). To the surprise of the researchers, relatively few regions would exhibit common patterns of blood flow increases across the experimental tasks (Shulman et al., 1997b), while a robust set of regions would show the opposite contrast of passive fixation > active tasks (Shulman et al., 1997a). The network that emerged in this second comparison was coined the "default mode of brain function" by Raichle and colleagues in 2001 (Raichle et al., 2001).

Although these two manuscripts brought initial attention to the default mode and introduced several hypotheses regarding the default network's functional significance during periods of awake rest, including the generation of "unconstrained verbally-mediated thoughts" (Shulman et al., 1997a), the studies did not assess the frequency or nature of ongoing thoughts during periods of rest. Despite the efforts of these groups, many subsequent studies assumed the default network and the resting state reflected an idle state with little contribution to active forms of cognition. This assumption was perhaps most apparent throughout the literature on resting state functional connectivity MRI (rs-fcMRI), a technique that examines temporally correlated fMRI activity patterns during extended periods of awake rest (reviewed in Fox & Raichle, 2007). In 2003, fMRI activity time courses from key regions of the default

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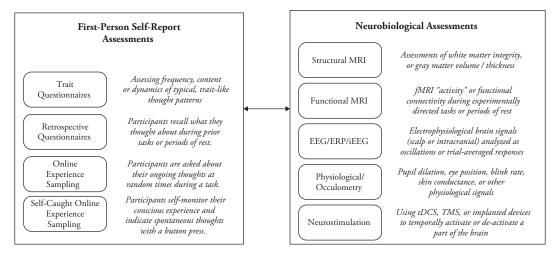
mode were shown to temporally correlate at low frequencies during the resting state, forming a brain system known as the *default mode network*, or default network (Greicius et al., 2003; Greicius, Srivastava, Reiss, & Menon, 2004). Several other large-scale brain systems have been subsequently identified using principles of rs-fcMRI (Yeo et al., 2011; Power et al., 2011; Doucet et al., 2011). A commonly held assumption of rs-fcMRI was that patterns of connectivity are *intrinsic* in nature, reflecting a long history of firing and wiring (Fox & Raichle, 2007). Periods of awake rest were used to evoke resting state correlations because cognition was assumed to be at a minimum during this unconstrained state, and low temporal frequencies were isolated partially to ensure that task-related activity was filtered out, despite later findings that unconstrained thoughts unfold at similar frequencies (Klinger, 2009; Vanhaudenhuyse et al., 2010).

Thus, groundbreaking discoveries from neuroscience research in the first decade of the 2000s revealed that periods of awake rest were associated with increased activity in a set of regions that came to be known as the default mode network. Scientists became curious about periods of rest, prompting a synthesis of the psychological literature on unconstrained cognition and mind-wandering. These initial efforts revealed that the absence of experimental tasks should not be equated with the absence of cognition (Andreasen et al., 1995; Binder et al., 1999; Buckner, Andrews-Hanna, & Schacter, 2008; Christoff, Ream, & Gabrieli, 2004), and set the stage for an explosion of research to come.

### Measuring the Neuroscience of Spontaneous Thought in the Modern Age

The appreciation that thoughts frequently unfold in the absence of internal and external constraints on cognition led to a plethora of neuroimaging and electrophysiological studies attempting to more precisely characterize their neural underpinnings. Here we review mainstream methods to measure the neuroscience of spontaneous thought (Figure 13.2).

One common method examines individual difference relationships between covert neurocognitive measures (such as fMRI activity, strength of rs-fcMRI correlations between brain regions, structural MRI, neurophysiological/occulometric measures, electroencephalography [EEG] and event related potentials [ERP]) and participant scores on trait questionnaires assessing the typical nature of spontaneous thoughts in daily life. Examples of such questionnaires include the Imaginal Process Inventory (Singer & Antrobus, 1966), the Mind-Wandering Questionnaire (Mrazek et al., 2013), and the recent Mind Excessively Wandering Scale (Mowlem et al., 2016). Scores on these and other trait questionnaires are correlated across participants with individual differences in brain activity or connectivity during experimental tasks (Mason



**Figure 13.2.** Methods to assess the neuroscience of spontaneous thought in humans. Left panel: Many different first-person approaches are used to assess the nature of trait- or state-like thought patterns, although most existing studies do not differentiate between spontaneous and constrained forms of thinking. Right panel: Neuroimaging, psychophysiological, and occulometric approaches are increasingly being employed to covertly assess the neurocognitive correlates of spontaneous thought. MRI = magnetic resonance imaging; EEG = electroencephalography; ERP = event-related potential; iEEG = intracranial EEG; tDCS = transcranial direct current stimulation; TMS: transcranial magnetic stimulation.

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et al., 2007) or periods of rest (Kucyi & Davis, 2014). Of particular interest given evolving definitions of spontaneous thought are two additional scales that separately assess the tendency for individuals to engage in intentional and unintentional forms of thought: the Mind-Wandering Deliberate Scale and the Mind-Wandering Spontaneous Scale (Carriere et al., 2013; Seli, Carriere, & Smilek, 2015a). Additionally, the "Mentation Rate" and "Absorption in Daydreams" subscales of the Imaginal Process Inventory (Singer & Antrobus, 1966) focus on the dynamics of spontaneous and deliberate thought (e.g., how quickly one's thoughts transition from topic to topic versus how likely thoughts are to remain focused on a specific topic). Several clinically oriented questionnaires may indirectly measure the dynamics of thought, insofar as they plausibly measure automatic constraints on thought processes. These inventories include the Ruminative Response Scale (Roberts, Gilboa, & Gotlib, 1998; Treynor, Gonzalez, & Nolen-Hoeksema, 2003), the Rumination-Reflection Questionnaire (Trapnell & Campbell, 1999), the Cognitive Intrusions Questionnaire (Freeston, 1991), and the Intrusive Thoughts Questionnaires (Edwards & Dickerson, 1987). Recent studies have begun to examine relationships between these clinically focused traits and individual differences in brain activity or connectivity (Hamilton et al., 2011; Kaiser et al., 2015; Ordaz et al., 2017).

Relating neurobiological measures to trait questionnaires has the advantage of allowing researchers to assess more stable properties of mind-wandering, but may not provide an accurate assessment of participants' thoughts during the tasks or rest periods for which neurobiological measures are derived. For example, Berman et al. (2014) found that group differences in functional connectivity between depressed and non-depressed individuals were much more substantial following a rumination induction period than during a baseline resting state, suggesting that spontaneous cognition may not always track trait measures. To overcome this limitation, researchers commonly administer retrospective questionnaires after task paradigms or periods of rest in which neurobiological measures are simultaneously recorded. Retrospective questionnaires require participants to retrospectively reflect on their phenomenological experience during those paradigms, and answer a series of self-report questions characterizing the nature of their thoughts during that time. This approach was originally implemented in conjunction with neuroimaging on an informal

verbal basis, prompting Andreasen and colleagues to coin the ironic acronym Random Episodic Silent Thought (REST) to emphasize that periods of rest often involve autobiographical memory recall and future thought (Andreasen et al., 1995). In 1996, McGuire and colleagues (McGuire et al., 1996) used a retrospective questionnaire to assess participants' frequency of task-unrelated thoughts following task and rest conditions, and examined which brain regions tracked individual differences in the frequency of task-unrelated thoughts (see also Andrews-Hanna, Reidler, Huang, Randy, & Buckner, 2010a). More than a decade later, a retrospective Resting State Questionnaire was developed to quantify the content and form of thoughts during resting state scans (Delamillieure et al., 2010), and a similar questionnaire was administered in a different study that linked individual differences in thought content to individual differences in functional connectivity during rest (Andrews-Hanna et al., 2010a; see also Doucet et al., 2012; Gorgolewski et al., 2014). Across these studies, participants reported spending a large proportion of time engaging in stimulus-independent thoughts, with thoughts about the future being especially frequent. Retrospective questionnaires have also been used in conjunction with methods assessing pupillometry (Smallwood, Brown, Baird, & Schooler, 2012a) and EEG (Barron, Riby, Greer, & Smallwood, 2011). Collectively, retrospective questionnaires have the potential to reveal the frequency and content of spontaneous thoughts without disrupting ongoing cognition or biasing subsequent attention. A drawback of this approach is that participants may not remember the contents of their thoughts when assessed minutes later, and reported thoughts might be influenced by biases in memory. Additionally, since retrospective questionnaires often ask participants to average multiple thoughts across extended periods of time, they are not ideal approaches to examine the way in which thoughts precisely unfold over time.

Online experience sampling approaches have the potential to overcome many of the limitations of retrospective questionnaires by assessing the nature of thoughts at different moments throughout a task. This approach had gained popularity in psychology (Giambra, 1989; Teasdale et al., 1995), and had initially been adopted for use in simulated scanning environments to approximate the frequency of task-unrelated thoughts in identical paradigms conducted in the scanner (Andrews-Hanna et al., 2010a; Binder et al., 1999; McKiernan, D'Angelo,

Kaufman, & Binder, 2006). It was not until 2009, however, that experience sampling probes were incorporated directly into neuroimaging paradigms, allowing researchers to compare patterns of brain activity associated with epochs of on-task versus offtask thought, and examine correspondences with disruptions in behavioral performance (Christoff, Gordon, Smallwood, Smith, & Schooler, 2009a). Since then, additional studies have adopted similar online experience sampling approaches during periods of rest (Tusche, Smallwood, Bernhardt, & Singer, 2014; Van Calster et al., 2016; Vanhaudenhuyse et al., 2010) or external tasks (Kucyi, Salomons, & Davis, 2013; Stawarczyk, Majerus, Maquet, & D'Argembeau, 2011b), and the approach has also gained popularity in the EEG (Baird et al., 2014; Kam et al., 2011; Kam et al., 2013; Kirschner et al., 2012; Smallwood et al., 2008) and structural MRI literature (Bernhardt et al., 2014). Note, however, that while most studies ask participants whether they characterized their thoughts as ontask or off-task, some studies have additionally asked about participants' meta-awareness of their thoughts (i.e., Christoff et al., 2009a), or whether their thoughts were dependent or independent of external stimuli (Kucyi, Salomons, & Davis, 2014; Stawarczyk et al., 2011b). These questions, as well as questions assessing other measures of phenomenological content, are important because participants are often unaware of their ongoing mental activity (Fox & Christoff, 2015; Schooler et al., 2011). Furthermore, a sizable proportion of offtask thoughts pertain to external distractions and involve unique neural underpinnings (Stawarczyk et al., 2011b). Critically, to our knowledge, no neuroscientific study has directly assessed, using online experience sampling approaches, whether participants' thoughts arose in a spontaneous or constrained fashion. Thus, as discussed in the next section, existing neuroimaging research may present an incomplete picture, and resolving the neuroscience of spontaneous versus deliberate (and automatically constrained) thought marks an important direction for future research.

One twist on the online experience sampling approach allows participants to press a button the moment they become aware of a spontaneous thought arising. Participants then answer questions characterizing their thought, and subsequently return their attention back to the ongoing task (e.g., focusing on one's breath). This *self-caught online thought sampling* approach gives researchers the opportunity to analyze patterns of brain activity before, during, and after moments of awareness of thought, differentiating brain regions involved in the generation and awareness of task-unrelated and/or spontaneous thoughts (Ellamil et al., 2016; see also Hasenkamp et al., 2012, and Hasenkamp, Chapter 39 in this volume). Related approaches have been adopted for non-meditators as well (Vanhaudenhuyse et al., 2010), offering additional insight into the dynamics of thinking.

### Evolving Insight into the Neurobiological Basis of Spontaneous Thought

As discussed in the previous section, neurocognitive research over the last several years has witnessed evolving methodological approaches to characterizing brain systems and tracking the frequency and phenomenology of spontaneous thought. Indirect or inferential approaches have begun to be complemented by real-time assessments that are less influenced by biases and failures of memory. Avenues for future research include novel approaches that could assess spontaneous thoughts covertly without interrupting the participant or relying on self-report, as well as methods that could examine the causal role of brain regions in the generation or dynamics of spontaneous thought (see discussion later in this chapter). In this section, we ask what can be gleaned from the research outlined in the preceding on the neuroscience of spontaneous thought (see also Kam & Handy, Chapter 19 in this volume, for a summary of ERP research).

## *The Role of the Brain's Default Network in Mind-Wandering*

As discussed previously, early neuroimaging studies observed that short breaks in between blocks of externally directed tasks led to blood flow increases in brain regions that would be come to be known as the default network.<sup>2</sup> Subsequent rs-fcMRI studies determined that activity fluctuations within these structures are temporally correlated during rest (i.e., Fox et al., 2005; Greicius et al., 2003). Clustering the magnitude of interregional associations during rest and tasks revealed that the default network can be further parceled into two subsystems that converge on core hubs (Andrews-Hanna et al., 2010b; Yeo et al., 2011). A ventrally positioned medial temporal subsystem includes the hippocampal formation and parahippocampal cortex, as well as two cortical regions that exhibit direct anatomical connections with the medial temporal lobe: ventral angular gyrus and retrosplenial cortex. A dorsal medial subsystem includes structures spanning the

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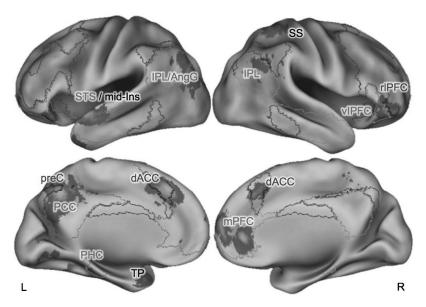
dorsal medial prefrontal cortex (mPFC), the temporoparietal junction, the lateral superior and inferior prefrontal gyrus, and the middle temporal gyrus extending into the temporal pole. These subsystems are strongly interconnected with a set of core hubs centered on the anterior mPFC, the posterior cingulate cortex, the dorsal angular gyrus, the superior frontal sulcus, and right anterior temporal cortex. The default network also includes aspects of Crus I and II of the cerebellum (Buckner, Krienen, Castellanos, Diaz, & Yeo, 2011), and subcortical regions such as aspects of the dorsal and ventral striatum (Choi, Yeo, & Buckner, 2012). Thus, structural and functional MRI research suggests that the default network is a large brain system with interacting components that converge on key association cortices.

Although early neuroimaging studies did not explicitly assess participants' mental states during periods of "rest" that give rise to default network activity, links between unconstrained thinking and the default network were observed across several subsequent studies employing a variety of methodological approaches (but see Raichle, 2016). For example, retrospective questionnaires and online experience sampling approaches revealed that conditions in which participants reported high frequencies of task-unrelated thought were associated with greater default network activity (Andrews-Hanna et al., 2010a; Mason et al., 2007; McKieran et al., 2006), that off-task trials activated the default network to a greater degree than on-task trials (Christoff et al., 2009a; Stawarczyk et al., 2011b), and that stimulus-independent thoughts during the resting state activated the default network to a greater degree than epochs in which participants were focused on external perceptions (Preminger, Harmelech, & Malach, 2011; Stawarczyk et al., 2011b; Van Calster et al., 2016; Vanhaudenhuyse et al., 2010). Additionally, individual difference analyses revealed positive associations between default network activity during ongoing tasks and mind-wandering as assessed with trait questionnaires and retrospective measures (Mason et al., 2007). Conversely, experienced meditators, as compared to novices, show less default network activity and experience fewer taskunrelated thoughts while meditating (Brewer et al., 2011). Links between task-unrelated thinking and the default network also extend to individual differences in rs-fcMRI measures (Andrews-Hanna et al., 2010a; Doucet et al., 2012; Gorgolewski et al., 2014; O'Callaghan, Shine, Lewis, Andrews-Hanna, & Irish, 2015; Smallwood et al., 2016; Wang et al.,

2009), and structural MRI measures such as cortical thickness (Bernhardt et al., 2014; Golchert et al., 2017). In 2015, much of the work outlined in the preceding was synthesized in two formal fMRI meta-analyses of mind-wandering (Fox et al., 2015; Stawarczyk & D'Argembeau, 2015). These metaanalyses revealed that several regions throughout the default network—particularly regions associated with the default network core—were reliably associated with mind-wandering across studies employing diverse populations and methodological approaches (Figure 13.3), but also regions outside the DN (see the following).

Although the default network is now widely appreciated for its role in spontaneous thought, the precise functional contributions of the specific regions involved remain unclear, particularly because the studies included in the meta-analysis defined mind-wandering by its task-unrelated and/ or stimulus-independent nature, rather than by its spontaneous dynamic processes. One intriguing possibility is that different regions, subsystems, or multivariate patterns within the default network support the conceptual content and/or form characterizing spontaneous thoughts (Andrews-Hanna et al., 2010; Andrews-Hanna, Smallwood, & Spreng, 2014; Gorgolweski et al., 2014; Smallwood et al., 2016; Tusche et al., 2014). For instance, specific patterns of default network activity might differentiate a positive spontaneous thought about one's upcoming wedding from a negative memory about an ex-partner, or a thought of any other conceptual nature. This possibility is supported by evidence from a variety of task-related and rs-fcMRI studies suggesting that the medial temporal subsystem might support contextual, visuospatial, and temporal aspects of memory and imaginationimportant for constructing a mental scene (Addis, Pan, Vu, Laiser, & Schacter, 2009; Andrews-Hanna et al., 2010b; Bar, 2007; Bar, Aminoff, Mason, & Fenske, 2007; Hassabis & Maguire, 2009)whereas the dorsal medial subsystem may support a variety of socio-emotional content (Andrews-Hanna, Saxe, & Yarkoni, 2014; Hyatt, Calhoun, Pearlson, & Assaf, 2015; Lieberman, 2007; Spreng & Andrews-Hanna, 2014). The widespread connectivity of core hub regions, combined with their involvement in a variety of self-generated processes, well position these regions to integrate disparate conceptual information when computing the overarching significance or importance of a particular thought (Andrews-Hanna, Smallwood, & Spreng, 2014; Smallwood et al., 2016)-a process that may

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**Figure 13.3.** Meta-analytic findings reveal neuroimaging correlates of task-unrelated and/or stimulus-independent thought. A meta-analysis of 10 fMRI studies demonstrates that many regions within the brain's default network (outlined in dark black, using 7-network parcellations from Yeo et al., 2011) and the frontoparietal control network (outlined in light black) are reliably engaged across studies of task-unrelated and/or stimulus-independent thought. Regions within the default network include: medial prefrontal cortex (mPFC), posterior cingulate cortex (PCC), parahippocampal cortex (PHC, a part of the medial temporal subsystem; see Yeo et al., 2011), inferior parietal lobule (IPL), angular gyrus (AngG), superior temporal sulcus (STS), and ventral lateral PFC (vIPFC). Regions within the frontoparietal control network include: rostral lateral prefrontal cortex (rIPFC), dorsal anterior cingulate cortex (dACC), and precuneus (preC). Regions spanning other networks include mid insula (mid-Ins), somatosensory cortex (SS), and temporal pole (TP, extending into the dorsal medial subsystem of the default network). Note that the fMRI studies included in the meta-analysis do not differentiate between spontaneous and constrained forms of thinking, so it is unclear which regions are involved in spontaneous thought, and which are involved in exerting constraints on those thoughts (see text). (See Color Insert)

partly determine the thought's dynamics, or the way in which it unfolds over time.

It is also possible that specific components of the default network directly contribute to the generation of spontaneous thoughts in a more domaingeneral manner, yet interact with other default regions, such as the lateral temporal cortex, to elaborate thoughts with specific conceptual content (e.g., Szpunar, Jing, Benoit, & Schacter, 2015). Evidence from human neuroimaging, intracranial recordings, rodent neurophysiology, and lesion work suggests that the hippocampus and nearby medial temporal structures may be prime candidates for such components (for reviews, see Christoff et al., 2016; Fox, Andrews-Hanna, & Christoff, 2016). In particular, activity in the hippocampus, parahippocampal cortex, and other aspects of the medial temporal subsystem emerge early in the dynamics of spontaneous thought-just prior to the moment of subjective awareness-consistent with a role in the initiation, as opposed to the elaboration and/or evaluation, of spontaneous thought (Ellamil et al.,

2016; Gelbard-Sagiv, Mukamel, Harel, Malach, & Fried, 2008). Additionally, reviews of human intracranial recording studies suggest that spontaneous thoughts, memories, and other dreamlike experiences are elicited more than half the time following electrical stimulation of regions within the medial temporal lobe-considerably more than any other cortical region assessed (reviewed in Selimbeyoglu & Parvizi, 2010; Fox et al., 2016). In rats, hippocampal place cells-neurons with spatial receptive fields that track where a rat is in its environment (O'Keefe & Nadel, 1978)—also spontaneously fire independent of immediate perceptual input, including during brief epochs of "rest" when the rat stops navigating its environment (Foster & Wilson, 2006). This spontaneous hippocampal firing has been linked to replay of prior experiences (Diba & Buzsaki, 2007; Foster & Wilson, 2006), pre-play of upcoming experiences (Dragoi & Tonegawa, 2011, 2013), and even to patterns suggestive of simulations of entirely novel experiences (Gupta, van der Meer, Touretzky, & Redish, 2010). In humans,

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spontaneous hippocampal activity and connectivity during periods of rest following periods of learning predict the degree to which studied material is encoded into long-term memory (Tambini, Ketz, & Davachi, 2010), and periods of rest as well as sleep are considered critical for memory consolidation and problem-solving (Dewar, Alber, Butler, Cowan, & Della Sala, 2012; Dewar, Alber, Cowan, & Della Sala, 2014; Stickgold, 2005; Wagner, Gais, Haider, Verleger, & Born, 2004). Finally, damage to the medial temporal lobe in hippocampal amnesia and Alzheimer's disease is associated with profound deficits in both memory and imagination (Hassabis, Kumaran, Vann, & Maguire, 2007; Irish & Piolino, 2016), although the effect of such lesions on spontaneous thought has yet to be investigated, to our knowledge. In sum, multiple sources of evidence from human and nonhuman animals suggest that the medial temporal lobe may play a key role in the initiation of a spontaneous thought. The medial temporal lobe is densely interconnected with cortical structures throughout the medial temporal subsystem as well as several core default network regions such as the lateral temporal cortex (Lavenex & Amaral, 2000; Suzuki & Amaral, 1994), thought to play an important role in conceptual knowledge and elaboration (Patterson, Nestor, & Rogers, 2007; Rice, Lambon Ralph, & Hoffman, 2015). Thus, it is likely that the medial temporal lobe does not operate in isolation, and we suspect its connectivity with distant cortical regions within and outside the default network are important determinants of the phenomenological content, form, dynamics, and conscious awareness of spontaneous thought.

### The Role of the Frontoparietal Control Network in Mind-Wandering

Although the role of the default network in spontaneous thought has now gained support from a considerable body of research, neuroimaging meta-analyses of mind-wandering also reveal reliable involvement of several regions outside the default network (Figure 13.3) (Fox et al., 2015; but see Stawarczyk & D'Argembeau, 2015). Most notable are aspects of the frontoparietal control network (FPCN), a set of regions spanning association cortices such as the lateral prefrontal cortex, dorsal anterior cingulate/pre-supplementary motor area, and anterior inferior parietal lobe (Vincent, Kahn, Snyder, Raichle, & Buckner, 2008; Yeo et al., 2011). The FPCN is thought to allow individuals to flexibly allocate attentional resources toward external stimuli and/or internal representations (i.e., thoughts,

memories, and emotions), and to integrate relevant information from external and internal sources of information in the service of immediate and longterm goals (Cole et al., 2013; Spreng, Sepulcre, Turner, Stevens, & Schacter, 2013; Vincent et al., 2008). While the involvement of the FPCN in taskunrelated and/or stimulus-independent thought may seem surprising given that mind-wandering is often assumed to reflect a failure of control (Kane & McVay, 2012; McVay & Kane, 2010), a closer look at the data points to many possible explanations that mark important avenues for future research.

First, the majority of studies define mindwandering by its task-unrelated and/or stimulusindependent contents, and consequently lump spontaneous and deliberate thoughts together when conducting analyses. It is therefore possible that the FPCN comes online only when individuals experience deliberate task-unrelated thoughts. There are two ways to interpret this claim, which arise from the two ways to distinguish spontaneous from deliberate thoughts. First, it is possible that the FPCN comes online only when participants deliberately disengage from ongoing tasks, and that thoughts arising without intention may not involve the FPCN at all (Seli et al., 2016b). Second, it is possible that the FPCN comes online only when participants deliberately constrain the course that their thoughts take as they unfold over time. In this sense, transient FPCN activity may reflect the deliberate re-allocation of attention away from the task at hand and/or the sustained pursuit of internal goals that are irrelevant to the task at hand. Similarly, sustained patterns of FPCN activity may help participants shield their internal thoughts from less personallyvsignificant distractions, including the sounds of the scanning environment, other thoughts deemed less important, or even the task itself. Despite the injunctions to participants to stay alert and focused on external stimuli in paradigms, such as the Sustained Attention to Response Task (SART), participants may consider real-world issues such as an upcoming exam, a weekend trip, or an unresolved conflict with a friend as more pressing "tasks," which may therefore vie for attention in potentially adaptive ways (Andrews-Hanna, 2012; Baars, 2010; McMillan et al., 2013). Nevertheless, recent findings provide support for the idea that the FPCN might play an important role in deliberate (but not necessarily spontaneous) task-unrelated thinking. Golchert and colleagues (2017) used a trait questionnaire to assess the frequency with which participants engaged in deliberate and

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spontaneous forms of task-unrelated thought. Participants who engaged in more frequent deliberate thinking exhibited greater functional integration between the FPCN and the DN, and greater cortical thickness in aspects of the FPCN.

Another explanation for the FPCN's involvement in spontaneous and/or deliberate taskunrelated thought concerns the phenomenological content characterizing periods of spontaneous or deliberate thought. Behavioral and neuroimaging studies exploring the content of task-unrelated thoughts suggest that adults spend a considerable proportion of time engaged in prospectively oriented thoughts, including thoughts about future goals, and in planning how to achieve those goals (Andrews-Hanna et al., 2010a; Andrews-Hanna et al., 2013; Baird, Smallwood, & Schooler, 2011; Song & Wang, 2012; Stawarczyk et al., 2011a; Stawarczyk et al., 2013). Support for this idea comes from neuroimaging studies using task paradigms in which participants are explicitly asked to plan for their future. In these autobiographical planning contexts, both the default network and the FPCN become engaged in a tightly coordinated manner (Gerlach, Spreng, Gilmore, & Schacter, 2011; Gerlach, Spreng, Madore, & Schacter, 2014; Spreng & Andrews-Hanna, 2015; Spreng, Stevens, W. D., Chamberlain, J. P., Gilmore, A. W., & Schacter, 2010). One intriguing question is whether thoughts pertaining to upcoming goals can occur and/or unfold in a spontaneous fashion, as suggested by Klinger's current concern hypothesis (Klinger, 1971, 2009). If so, would such thoughts recruit activity within the FPCN?

The nature of the task paradigms employed in mind-wandering studies may also partly explain why activity within the FPCN is often associated with task-unrelated thoughts. Most neuroscience research assesses mind-wandering retrospectively or with online experience sampling probes during easy behavioral paradigms in which participants can maintain a minimal level of performance while simultaneously allocating their attention toward the task at hand and their (potentially) spontaneous thoughts. Thus, easy tasks-including resting state paradigms and the SART task-may encourage dual-task situations where participants simultaneously direct their attention externally and internally, or rapidly switch between internal and external modes of attention. Both types of processes may recruit the FPCN in a regulatory manner to help coordinate attention across tasks. Conversely, maintaining reasonable levels of performance during

difficult behavioral paradigms may require that participants be continuously focused on the task at hand. In these scenarios, occasional off-task trials may be more likely to manifest as decreases in FPCN activity, reflecting lapses in attention marked by a failure of control. Paralleling these findings, behavioral studies of mind-wandering reveal complex relationships between mind-wandering and executive function that appear to partly depend on the difficulty of the ongoing task (Smallwood & Andrews-Hanna, 2013). For example, participants who frequently experience task-unrelated thoughts during easy tasks have higher working memory capacity (Levinson, Smallwood, & Davidson, 2012), suggesting that they are simultaneously able to have task-unrelated thoughts while maintaining acceptable performance on the task. Conversely, participants who frequently experience task-unrelated thoughts during difficult tasks tend to exhibit poorer working memory capacity (Kane & McVay, 2012; Unsworth & McMillan, 2013). These findings prompted Smallwood and Andrews-Hanna to propose the context regulation hypothesis, suggesting that the costs and benefits of mind-wandering partly depend on an individual's ability to constrain task-unrelated thoughts to easy or unimportant contexts (Andrews-Hanna, Smallwood, & Spreng, 2014; Smallwood & Andrews-Hanna, 2013). In light of these observations, future studies could consider examining patterns of activity associated with task-unrelated thoughts across tasks that vary in difficulty.

Finally, it is important to note that not all regions within the FPCN are reliably engaged across studies of mind-wandering: Whereas rostral lateral PFC (rlPFC) and dorsal anterior cingulate cortex (dACC)/pre-SMA are among those present, metaanalyses of mind-wandering show that the dorsolateral prefrontal cortex (dlPFC), posterior PFC, and anterior inferior parietal lobe are not reliably engaged across studies (Fox et al., 2015). The rlPFC has been linked to metacognitive awareness of one's thoughts, attention, and performance (Fleming & Dolan, 2012; McCaig, Dixon, Keramatian, Liu, & Christoff, 2011), so activity in the rlPFC could reflect the monitoring processes encouraged by online experience sampling tasks (but see Christoff et al., 2009a). Furthermore, dACC/pre-SMA may play an important role in the detection of internal conflict elicited when mind-wandering during the presence of an ongoing task, or in computing tradeoffs in the expected values of being on-task versus off-task.

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Intriguingly, according to some theories of pre-

frontal cortex function, the prefrontal cortex is orga-

nized along a rostro-caudal gradient, where more

anterior regions become engaged by more abstract

or temporally extended conditions that often rely

"Seung-Schik et al., 2003" not found in reference list; please provide.

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on internal processes such as episodic memory and maintenance of long-term goals (Badre & D'Esposito, 2009; Christoff & Gabrieli, 2000; Christoff, Keramatian, Gordon, Smith, & Mädler, 2009b; Christoff, Ream, Geddes, & Gabrieli, 2003; Dixon, Fox, & Christoff, 2014; O'Reilly, 2010). Conversely, posterior PFC regions tend to respond to more specific task demands, such as learning specific stimulus-response contingencies, biasing attention toward one stimulus attribute and away from another, or flexibly adjusting one's attention following errors in performance (Badre & D'Esposito, 2009; Christoff et al., 2009b; O'Reilly, 2010). It is therefore possible that the FPCN activation during mind-wandering represents a form of abstract control that is compatible with a considerable degree of dynamic spontaneity. Because abstract goals (e.g., "do well as an academic") place few constraints on how one is to achieve or think about them, one's thoughts may be directed toward such a goal, while still spontaneously wandering to a broad range of ideas (Irving, 2016). This hypothesis makes testable predictions: Periods of spontaneous task-unrelated thought (measured through online thought sampling) that are loosely constrained to an abstract goal should be associated with more anterior PFC activation, whereas periods of task-unrelated thought that are deliberately constrained to a specific goal should be associated with more posterior PFC activation.

In sum, although the functional contributions of the FPCN are unclear, different regions or patterns within and across regions likely play different roles and are likely influenced by a variety of factors (see Christoff et al., 2016, for a similar point).

### The Role of Additional Brain Regions

A synthesis of existing neuroscience research on mind-wandering would be incomplete without discussing the involvement of additional regions outside the default and frontoparietal networks, including the lingual gyrus, somatosensory cortex, and posterior insula (Figure 13.3). Collectively, these regions may be associated with the sensory and embodied perception of task-unrelated thoughts. Many individuals characterize their thoughts during awake rest as unfolding in the form of mental *images* (Delamillieure et al., 2010), and the lingual gyrus may support the visual nature of such thoughts. The lingual gyrus is reliably observed during a variety of visual and mental imagery tasks-including when individuals are dreaming (Fox, Nijeboer, Solomonova, Domhoff, & Christoff, 2013), or asked to recall their past and imagine their future (Addis et al., 2009)-and lesions to this region are associated with an impaired ability to engage in visual imagery and reduced levels of dreaming (Solms, 1997, 2000). Similarly, the somatosensory cortex and posterior insula, associated with tactile sensation, tactile imagery, and interoceptive awareness (Craig, 2003; Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004; Seung-Schik et al., 2003), could relate to the frequently reported thoughts about the body (Delamillieure et al., 2010; Diaz et al., 2013) and/or distracting external sensations. Interestingly, there is some evidence from rs-fcMRI that individuals who characterize their thoughts as having more visual imagery during periods of rest show heightened connectivity between visual regions, including the lingual gyrus, somatosensory cortices, and posterior insula (Doucet et al., 2012), perhaps reflecting attention toward sensorimotor and perceptual characteristics of unconstrained thinking.

### *The Role of Default and Frontoparietal Networks in Dreaming and Creative Thought*

In this section, we have synthesized research investigating the neuroscience of spontaneous thought, focusing on studies defining mind-wandering largely by its contents (since studies defining mindwandering by its spontaneity are scarce). Whereas some expected findings have emerged from this synthesis-namely, the involvement of the default network-other findings-namely, the involvement of the FPCN-are more surprising, inviting several distinct hypotheses regarding their precise role in spontaneous thought. We now turn to neuroscience research examining two cognitive processes closely related to spontaneous thought-namely, dreaming and creative thinking-and ask whether our knowledge of these mental states can shed light on the role of the FPCN in mind-wandering and spontaneous thought more broadly.

According to the dynamic process model of spontaneous thought illustrated in Figure 13.1, dreaming is considered more spontaneous than mind-wandering due to an absence of many constraints on the contents and flow of mental states during this period, resulting in the bizarre, improbable, and highly dynamic characteristics of

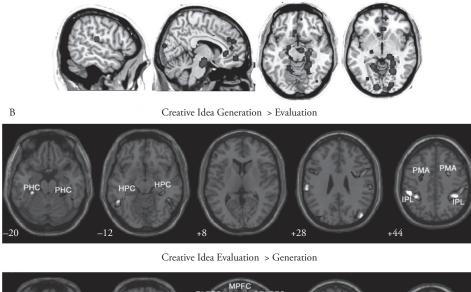
dreams (Hobson, Pace-Schott, & Stickgold, 2000). Conversely, creative thought is considered less spontaneous than mind-wandering because it usually unfolds in the service of a specific goal (e.g., to generate a creative idea, solution, or product), and involves more deliberate processes of selecting a creative solution, evaluating its utility, and revising it if necessary (Beaty, Benedek, Kaufman, & Silvia, 2015). Creative insight also involves aspects of metacognitive awareness (Armbruster, 1989), as individuals who lack awareness of their creative ideas may be unable to benefit from them. Consequently, assuming that activity within the FPCN during mind-wandering at least partially reflects the deliberate nature of task-unrelated thoughts, and/or the metacognitive awareness that often accompanies

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them, one might expect that dreams would show activity reductions in the FPCN (consistent with lack of cognitive control and metacognitive awareness), while creative thinking might evoke increases in FPCN activity, particularly during later evaluative stages of the creative process.

A synthesis of neuroimaging literature on dreaming supports the role of the FPCN in deliberate constraints and metacognitive awareness (Fox et al., 2013). Compared to periods of relaxed wakefulness, REM sleep is associated with enhanced activity throughout the default network's medial temporal subsystem, and reductions in activity throughout the FPCN, consistent with the bizarre nature of dreams and a lack of awareness while dreaming (Figure 13.4A). Interestingly, lucid dreamers-individuals



REM Sleep (Likely Dreaming ) > Awake Rest

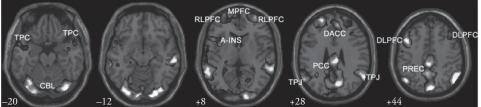


Figure 13.4. Neural underpinnings of night dreaming and creative thought. (A) A meta-analysis of neuroimaging studies on REM sleep (a sleep stage characterized by dreaming) reveals greater activity in a number of brain regions compared to awake rest. Among others, these include medial temporal and medial prefrontal regions within the default network, and visual cortex. (B) Creative thinking is associated with distinct temporal activity dynamics. The medial temporal lobe becomes engaged to a greater degree early in the creative process while generating a creative idea. Other regions within the default network, as well as key frontoparietal control network regions, become engaged to a greater degree during later stages of creative thinking, when evaluating creative ideas. A-INS = anterior insula; dACC = dorsal anterior cingulate cortex; DLPFC = dorsal lateral prefrontal cortex; CBL = cerebellum; HPC = hippocampus; IPL = inferior parietal lobule; MPFC = medial prefrontal cortex; PHC = parahippocampus; PMA = premotor area (PMA); PCC = posterior cingulate cortex; PREC = precuneus; TPC = temporopolar cortex; TPJ = temporoparietal junction. Figures adapted from Fox et al., 2015 (A), and Ellamil et al., 2011 (B). (See Color Insert)

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who are aware of their dreams while dreaming, and are often able to deliberately control how their dreams unfold—have enhanced gray matter volume throughout rostrolateral and medial PFC (Filevich, Dresler, Brick, & Kühn, 2015), and also exhibit enhanced rIPFC activity during tasks in which participants are explicitly asked to monitor the contents of their thoughts (Filevich et al., 2015). The FPCN is also widely recruited during lucid REM sleep as compared to non-lucid REM sleep (Dresler et al., 2012).

Conversely, many creative tasks, including tasks of divergent thinking, poetry generation, and creative idea generation, show initial activity within the medial temporal subsystem and the posterior cingulate cortex, followed by enhanced activity and connectivity of FPCN regions when deliberate constraints must be implemented to hone in on creative ideas, or evaluate and revise creative products (Figure 13.4B) (Beaty et al., 2015; Beaty, Benedek, Silvia, & Schacter, 2016; Ellamil, Dobson, Beeman, & Christoff, 2011; Liu et al., 2015). Thus, evidence from neuroscience research on dreaming and creative thinking suggests that the involvement of the FPCN in mind-wandering-and spontaneous forms of thinking more broadly-might reflect deliberate control processes that serve to constrain the content and flow of mental states by guiding and suppressing their spontaneity (Fox & Christoff, 2014). In short, the growing body of neuroscience findings on mind-wandering may reflect an intricate balance of spontaneous and deliberate cognitive processes, and it remains a task for future research to unravel the common or distinct neural underpinnings of each.

### New Promises for Future Inquiry into the Neuroscience of Spontaneous Thought

In this chapter, we have synthesized an interdisciplinary field of inquiry—the *neuroscience of spontaneous thought*—and have discussed how definitions of spontaneous thought, approaches to measure spontaneous thought, and knowledge of brain systems supporting such thoughts have rapidly evolved in a few short years. New definitions rely less on the task-unrelated and stimulus-independent content that had long dominated the literature, and more on the processes that govern their initiation, as well as the temporal dynamics that characterize their flow; measurement approaches have shifted from indirect to more direct approaches in which thoughts are assessed much closer to the time at which they occur; and recent neuroscience findings emphasize the importance of regions outside the default network—such as the FPCN, sensorimotor networks, and posterior insula.

With exciting theoretical and methodological progress come many new questions and avenues for future research. One timely research direction regards assessing the forgotten dynamics of spontaneous thought (Christoff et al., 2016; Irving, 2016). To this end, online experience sampling approaches could be used in conjunction with dynamic rsfcMRI (Calhoun, Miller, Pearlson, & Adalı, 2014) to elucidate how spontaneous thoughts and their corresponding neural underpinnings unfold and change over time (Zabelina & Andrews-Hanna, 2016). These approaches may also shed light on key mechanisms underlying a variety of mental health disorders (e.g., Kaiser et al., 2015).

Another direction for future research includes differentiating between spontaneous and deliberate thoughts at both the behavioral and neural level, and re-synthesizing existing research in light of subsequent findings. Relatedly, there is some suggestion that spontaneous thoughts can be further characterized by the unintentional manner in which they are *initiated* (i.e., Seli et al., 2016b), as well as the unconstrained nature in which they unfold over time (Christoff et al., 2016; Irving, 2016; see also Stan & Christoff, Chapter 34 in this volume). Although the initiation and dynamics of spontaneous thought are likely correlated, they are conceptually distinct (Smallwood, 2013). They are likely correlated because top-down constraints on thought are typically (perhaps always) initiated with deliberate intent. Yet they are conceptually distinct for two reasons. For one, it seems possible to unintentionally initiate automatic constraints on the spontaneous dynamics of thought. For example, a depressed patient might unintentionally begin to ruminate. Furthermore, it seems possible to intentionally initiate a thought process with spontaneous dynamics. During a boring lecture, for example, one might intentionally let one's mind wander in an unconstrained manner. To help determine the relationship between these two ways of characterizing spontaneous thought, future research could design questionnaires that directly assess the tendency to have thoughts whose dynamics are unconstrained, compared to the tendency to *initiate* thoughts unintentionally. Researchers could then relate both forms of spontaneity to individual differences in brain activity and connectivity.

Additionally, although this chapter has largely focused on the role of deliberate constraints in

restricting the contents and flow of thought, another type of constraint can also limit its spontaneity. Affective and perceptual biases in attention are examples of *automatic constraints* that serve to capture and hold one's attention on specific sources of information (see earlier discussion in this chapter; Christoff et al., 2016; Irving, 2016; Irving & Thompson, Chapter 8 in this volume; Todd et al., 2012). Although little is known about the relationship between automatic constraints and spontaneous thought, preliminary evidence from clinical literature on depression and anxiety implicates an important role of the brain's salience network (McMenamin, Langeslag, Sirbu, Padmala, & Pessoa, 2014; Ordaz et al., 2017; Seeley et al., 2007; reviewed in Christoff et al., 2016).

Future research would also benefit from developing new methods to covertly assess spontaneous thoughts without relying on self-report. Despite the usefulness of the introspective approaches discussed in the preceding, self-report assessments come with several limitations. Participants are sometimes unaware of their own mental activity, and most studies do not assess participants' subjective level of awareness. Participants may also interpret questions and use self-report scales in different ways, sometimes being sensitive to perceived experimenter expectations. Additionally, the act of requiring participants to introspect about their mental activity may interfere with the natural course of cognition, and may bias participants to think in particular ways. To overcome some of these limitations, analysis methods such as machine learning algorithms could be applied in future work to covertly predict the nature of mental activity based on voxelwise patterns of brain activity (i.e., with multivoxel pattern analysis; Kragel, Knodt, Hariri, & LaBar, 2016; Tusche et al., 2014), and/or concurrent behavioral, occulometric, neurophysiological, or neuroendocrine measures. Additionally, these approaches could eventually be used in conjunction with realtime fMRI to train people to become more aware of their thinking patterns (e.g., McCaig et al., 2011; McDonald et al., 2017; see also Garrison et al., 2013a; Garrison et al., 2013b), and improve their ability to stay on task, or engage in productive forms of spontaneous thought.

Finally, although neuroimaging and behavioral approaches can offer insight into the neural underpinnings of spontaneous thought, these approaches are correlational at best, and are unable to reveal whether patterns of brain activity play a causal role in the initiation or dynamics of spontaneous thought. Future research should therefore make use of methods such as transcranial magnetic stimulation (TMS) or transcranial direct current stimulation (TDCS) to transiently disrupt or enhance activity in certain brain regions (Axelrod, Rees, Lavidor, & Bar, 2015), and neuropsychological studies should consider assessing if and how spontaneous thoughts become altered in patients with focal cortical or subcortical lesions. Toward this in reference end, intracranial electroencephalography also marks list; please a promising area of future research (reviewed in Selimbeyoglu and Parvizi, 2010; Fox et al., 2016).

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An old sufi parable attributed to Mulla Nasrudin might serve as an analogy for the history of research on spontaneous thought. A police officer approaches a drunk man who's searching for something beneath a lamppost, "What are you looking for?" "My keys, Sir," the drunk man replies. The police officer helps to look for a few minutes. Finding nothing, the officer asks, "Are you sure you lost them under the lamppost?" "No," says the drunk, "I lost them in the park." "Then why are you searching here?!?" "Because there's a light." Like the drunk man, the field of psychology may have neglected spontaneous thought for over a century because it is shrouded in darkness. From Behaviorism through the Cognitive Revolution, the field looked for psychological processes under the light of experimental tasks. Methodological innovations in neuroscience and psychology moved our gaze a little further, but still we look only at those forms of "mind-wandering" that can be illuminated by their contents. Now it's time to break out the flashlights, to step into the darkness wherein lies the dynamics of spontaneous thought.

### Acknowledgments

We extend our gratitude to Evan Thompson, Randy Buckner, Jonathan Smallwood, Matt Dixon, Rebecca Todd, Chandra Sripada, and Dasha Zabelina for helpful feedback and scholarly discussion on our teams' recently published manuscripts featured in the present chapter. A Brain and Behavioral Research Foundation Grant supported J. R. A.-H. while preparing this chapter. K. C. was supported by grants from the Natural Sciences and Engineering Research Council (NSERC) (RGPIN 327317-11) and the Canadian Institutes of Health Research (CIHR) (MOP-115197). Z. C. I. was supported by a Social Sciences and Humanities Research Council of Canada (SSHRC) postdoctoral fellowship, the Balzan Styles of Reasoning Project, and a Templeton Integrated Philosophy and Self

JESSICA R. ANDREWS-HANNA ET AL. 157 Control grant. R. N. S. was supported by an Alzheimer's Association grant (NIRG-14-320049). K. C. R. F. was supported by a Vanier Canada Graduate Scholarship.

#### Notes

- In the first section, we discuss how the definition of mindwandering varies throughout the literature, leading to disparate interpretations of existing experimental findings. Note that while we use the term "mind-wandering" loosely in this chapter, we are sensitive to these different interpretations and discuss them at length when possible.
- Strictly speaking, we have argued that mind-wandering is a form of spontaneous thought, and so we cannot be sure that these studies are measuring mind-wandering properly defined (as we discuss throughout this section when interpreting current findings).

### References

- Addis, D. R., Pan, L., Vu, M.-A., Laiser, N., & Schacter, D. L. (2009). Constructive episodic simulation of the future and the past: Distinct subsystems of a core brain network mediate imagining and remembering. *Neuropsychologia*, 47, 2222–2238.
- Andreasen, N. C., O'Leary, D. S., Cizadlo, T., Arndt, S., Rezai, K., Watkins, G. L., . . . Hichwa, R. D. (1995). Remembering the past: Two facets of episodic memory explored with positron emission tomography. *American Journal of Psychiatry*, 152, 1576–1585.
- Andrews-Hanna, J. R. (2012). The brain's default network and its adaptive role in internal mentation. *The Neuroscientist: A Review Journal Bringing Neurobiology, Neurology and Psychiatry*, 18, 251–270.
- Andrews-Hanna, J. R., Kaiser, R. H., Turner, A. E. J., Reineberg,
  A. E., Godinez, D., Dimidjian, S., & Banich, M. T. (2013).
  A penny for your thoughts: Dimensions of self-generated thought content and relationships with individual differences in emotional wellbeing. *Frontiers in Psychology*, *4*, 1–13.
- Andrews-Hanna, J. R., Reidler, J. S., Huang, C., Randy, L., & Buckner, R. L. (2010). Evidence for the default network's role in spontaneous cognition. *Journal of Neurophysiology*, 104, 322–335.
- Andrews-Hanna, J. R., Reidler, J. S., Sepulcre, J., Poulin, R., & Buckner, R. L. (2010). Functional-anatomic fractionation of the brain's default network. *Neuron*, 65, 550–562.
- 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*, 91C, 324–335.
- Andrews-Hanna, J. R., Smallwood, J., & Spreng, R. N. (2014). The default network and self-generated thought: Component processes, dynamic control, and clinical relevance. *Annals of the New York Academy of Sciences*, 1316, 29–52.
- Antrobus, J. S., Singer, J. L., & Greenberg, S. (1966). Studies in the stream of consciousness: Experimental enhancement and suppression of spontaneous cognitive processes. *Perceptual* and Motor Skills, 23, 399–417.
- Armbruster, B. B. (1989). Metacognition in creativity. In J. A. Glover, R. R. Ronning, & C. Reynolds (Eds.), *Handbook* of creativity (pp. 177–182). New York, NY: Springer Science+Business Media.

- Axelrod, V., Rees, G., Lavidor, M., & Bar, M. (2015). Increasing propensity to mind-wander with transcranial direct current stimulation. *Proceedings of the National Academy of Sciences of the U S A*, 112(11), 3314–3319.
- Baars, B. J. (2010). Spontaneous repetitive thoughts can be adaptive: Postscript on "mind wandering." *Psychological Bulletin*, 136, 208–210.
- Badre, D., & Esposito, M. D. (2009). Is the rostro-caudal axis of the frontal lobe hierarchical?, *Nature Reviews Neuroscience*, *10*(9), 659–669.
- Baird, B., Smallwood, J., Lutz, A., & Schooler, J. W. (2014). The decoupled mind: Mind-wandering disrupts cortical phase-locking to perceptual events. *Journal of Cognitive Neuroscience*, 26, 2596–2607.
- Baird, B., Smallwood, J., & Schooler, J. W. (2011). Back to the future: Autobiographical planning and the functionality of mind-wandering. *Consciousness and Cognition*, 20, 1604–1611.
- Bar, M. (2007). The proactive brain: Using analogies and associations to generate predictions. *Trends in Cognitive Sciences*, 11, 280–289.
- Bar, M., Aminoff, E., Mason, M., & Fenske, M. (2007). The units of thought. *Hippocampus*, 17(6), 420–428.
- Barron, E., Riby, L. M., Greer, J., & Smallwood, J. (2011). Absorbed in thought: The effect of mind wandering on the processing of relevant and irrelevant events. *Psychological Science*, 22(5), 596–601.
- Beaty, R. E., Benedek, M., Kaufman, S. B., & Silvia, P. J. (2015). Default and executive network coupling supports creative idea production. *Scientific Reports*, 5, 10964.
- Beaty, R. E., Benedek, M., Silvia, P. J., & Schacter, D. L. (2016). Creative cognition and brain network dynamics. *Trends in Cognitive Sciences*, 20(2), 87–95.
- Berman, M. G., Misic, B., Buschkuehl, M., Kross, E., Deldin, P. J., Peltier, S., . . . Jonides, J. (2014). Does resting-state connectivity reflect depressive rumination? A tale of two analyses. *NeuroImage*, 103, 267–279.
- Bernhardt, B. C., Smallwood, J., Tusche, A., Ruby, F. J. M., Engen, H. G., Steinbeis, N., & Singer, T. (2014). Medial prefrontal and anterior cingulate cortical thickness predicts shared individual differences in self-generated thought and temporal discounting. *NeuroImage*, 90, 290–297.
- Binder, J. R., Frost, J. A., Hammeke, T. A., Bellgowan, P. S. F., Rao, S. M., & Cox, R. W. (1999). Conceptual processing during the conscious resting state: A functional MRI study. *Journal of Cognitive Neuroscience*, 11(1), 80–95.
- Braboszcz, C., & Delorme, A. (2011). Lost in thoughts: Neural markers of low alertness during mind wandering. *NeuroImage*, 54, 3040–3047.
- Brewer, J. A., Worhunsky, P. D., Gray, J. R., Tang, Y.-Y., Weber, J., & Kober, H. (2011). Meditation experience is associated with differences in default mode network activity and connectivity. *Proceedings of the National Academy of Sciences of the* USA, 108(50), 20254–20259.
- 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.
- Buckner, R. L., Krienen, F. M., Castellanos, A., Diaz, J. C., & Yeo, B. T. T. (2011). The organization of the human cerebellum estimated by intrinsic functional connectivity. *Journal of Neurophysiology*, 106, 2322–2345.

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- Calhoun, V. D., Miller, R., Pearlson, G., & Adalı, T. (2014). The chronnectome: Time-varying connectivity networks as the next frontier in fMRI data discovery. *Neuron*, *84*, 262–274.
- Callard, F., Smallwood, J., & Margulies, D. S. (2012). Default positions: How neuroscience's historical legacy has hampered investigation of the resting mind. *Frontiers in Psychology*, 3, 321.
- Carriere, J. S. A., Seli, P., & Smilek, D. (2013). Wandering in both mind and body: Individual differences in mind wandering and inattention predict fidgeting. *Canadian Journal* of Experimental Psychology/Revue Canadienne de Psychologie Expérimentale, 67, 19–31.
- Carruthers, P. (2015). The centered mind: What the science of working memory shows us about the nature of human thought. Oxford: Oxford University Press.
- Choi, E. Y., Yeo, B. T. T., & Buckner, R. L. (2012). The organization of the human striatum estimated by intrinsic functional connectivity. *Journal of Neurophysiology*, 108, 2242–2263.
- 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. (2009a). Experience sampling during fMRI reveals default network and executive system contributions to mind wandering. *Proceedings of the National Academy of Sciences of the U S A*, 106, 8719–8724.
- Christoff, K., Irving, Z. C., Fox, K. C. R., Spreng, R. N., & Andrews-hanna, J. R. (2016). Mind-wandering as spontaneous thought: A dynamic framework. *Nature Reviews Neuroscience*, 17(11), 718–731.
- Christoff, K., Keramatian, K., Gordon, A. M., Smith, R., & Mädler, B. (2009b). Prefrontal organization of cognitive control according to levels of abstraction. *Brain Research*, *1286*, 94–105.
- Christoff, K., Ream, J. M., Gabrieli, J. D. E., & Unit, B. S. (2004). Neural basis of spontaneous thought process. *Cortex*, 40, 623–630.
- Christoff, K., Ream, J. M., Geddes, L. P. T., & Gabrieli, J. D. E. (2003). Evaluating self-generated information: Anterior prefrontal contributions to human cognition. *Behavioral Neuroscience*, 117, 1161–1168.
- Cole, M. W., Reynolds, J. R., Power, J. D., Repovs, G., Anticevic, A., & Braver, T. S. (2013). Multi-task connectivity reveals flexible hubs for adaptive task control. *Nature Neuroscience*, 16, 1348–1355.
- Craig, A. (Bud). (2003). Interoception: The sense of the physiological condition of the body. *Current Opinion in Neurobiology*, 13, 500–505.
- Critchley, H. D., Wiens, S., Rotshtein, P., Ohman, A., & Dolan, R. J. (2004). Neural systems supporting interoceptive awareness. *Nature Neuroscience*, 7, 189–195.
- Delamillieure, P., Doucet, G., Mazoyer, B., Turbelin, M., Delcroix, N., Mellet, E., . . . Joliot, M. (2010). The resting state questionnaire: An introspective questionnaire for evaluation of inner experience during the conscious resting state. *Brain Research Bulletin*, *81*, 565–573.
- Dewar, M., Alber, J., Butler, C., Cowan, N., & Della Sala, S. (2012). Brief wakeful resting boosts new memories over the long term. *Psychological Science*, 23, 955–960.

- Dewar, M., Alber, J., Cowan, N., & Della Sala, S. (2014). Boosting long-term memory via wakeful rest: intentional rehearsal is not necessary, consolidation is sufficient. *PloS One*, 9, e109542.
- Diaz, B. A., Van Der Sluis, S., Moens, S., Benjamins, J. S., Migliorati, F., Stoffers, D., . . . Linkenkaer-Hansen, K. (2013). The Amsterdam Resting-State Questionnaire reveals multiple phenotypes of resting-state cognition. *Frontiers in Human Neuroscience*, 7, 1–15.
- Diba, K., & Buzsáki, G. (2007). Forward and reverse hippocampal place-cell sequences during ripples. *Nature Neuroscience*, 10, 1241–1242.
- Dixon, M. L., Fox, K. C. R., & Christoff, K. (2014). A framework for understanding the relationship between externally and internally directed cognition. *Neuropsychologia*, 62, 321–330.
- Dorsch, F. (2015). Focused daydreaming and mind-wandering. *Review of Philosophy and Psychology*, 6, 791–813.
- Doucet, G., Naveau, M., Petit, L., Delcroix, N., Zago, L., Crivello, F., . . . Joliot, M. (2011). Brain activity at rest: A multiscale hierarchical functional organization. *Journal of Neurophysiology*, 105(6), 2753–2763.
- Doucet, G., Naveau, M., Petit, L., Zago, L., Crivello, F., Jobard, G., . . . Joliot, M. (2012). Patterns of hemodynamic lowfrequency oscillations in the brain are modulated by the nature of free thought during rest. *NeuroImage*, 59, 3194–200.
- Dragoi, G., & Tonegawa, S. (2011). Preplay of future place cell sequences by hippocampal cellular assemblies. *Nature*, 469, 397–401.
- Dragoi, G., & Tonegawa, S. (2013). Distinct preplay of multiple novel spatial experiences in the rat. *Proceedings of the National Academy of Sciences of the US A*, 110, 9100–5.
- Dresler, M., Wehrle, R., Spoormaker, V. I., Koch, S. P., Holsboer, F., Steiger, A., . . . Czisch, M. (2012). Neural correlates of dream lucidity obtained from contrasting lucid versus nonlucid REM sleep: A combined EEG/fMRI case study. *Sleep*, 35, 1017–20.
- Edwards, S., & Dickerson, M. (1987). Intrusive unwanted thoughts: A two-stage model of control. *British Journal of Medical Psychology*, 60, 317–328.
- Ellamil, M., Dobson, C., Beeman, M., & Christoff, K. (2011). Evaluative and generative modes of thought during the creative process. *NeuroImage*, 59, 1783–1794.
- Ellamil, M., Fox, K. C. R., Dixon, M. L., Pritchard, S., Todd, R. M., Thompson, E., & Christoff, K. (2016). Dynamics of neural recruitment surrounding the spontaneous arising of thoughts in experienced mindfulness practitioners. *NeuroImage*, 136, 186–196.
- Filevich, E., Dresler, M., Brick, T. R., & Kühn, S. (2015). Metacognitive mechanisms underlying lucid dreaming. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, 35, 1082–1088.
- Fleming, S. M., & Dolan, R. J. (2012). The neural basis of metacognitive ability. *Philosophical Transactions of the Royal Society* of London. Series B, Biological Sciences, 367, 1338–1349.
- Foster, D. J., & Wilson, M. A. (2006). Reverse replay of behavioral sequences in hippocampal place cells during the awake state. *Nature*, 440, 680–683.
- Fox, K. C. R., Andrews-Hanna, J. R., & Christoff, K. (2016). The neurobiology of self-generated thought from cells to systems: Integrating evidence from lesion studies, human intracranial electrophysiology, neurochemistry, and neuroendocrinology. *Neuroscience*, 335, 134–150.

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- Fox, K. C. R., & 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). New York: Springer.
- Fox, K. C. R., Nijeboer, S., Dixon, M. L., Floman, J. L., Ellamil, M., Rumak, S. P., . . . Christoff, K. (2014). Is meditation associated with altered brain structure? A systematic review and meta-analysis of morphometric neuroimaging in meditation practitioners. *Neuroscience & Biobehavioral Reviews*, 43, 48–73.
- Fox, K. C. R., Nijeboer, S., Solomonova, E., Domhoff, G. W., & Christoff, K. (2013). Dreaming as mind wandering: Evidence from functional neuroimaging and firstperson content reports. *Frontiers in Human Neuroscience*, 7, 1–18.
- Fox, K. C. R., Spreng, R. N., Ellamil, M., Andrews-Hanna, J. R., & Christoff, K. (2015). The wandering brain: Meta-analysis of functional neuroimaging studies of mind-wandering and related spontaneous thought processes. *NeuroImage*, 111, 611–621.
- Fox, K. C. R., Thompson, E., Andrews-Hanna, J. R., & Christoff, K. (2014). Is thinking really aversive? A commentary on Wilson et al.'s "Just think: the challenges of the disengaged mind." *Frontiers in Psychology*, *5*, 1427.
- Fox, M. D., & Raichle, M. E. (2007). Spontaneous fluctuations in brain activity observed with functional magnetic resonance imaging. *Nature Reviews Neuroscience*, 8, 700–711.
- 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 U S A*, 102, 9673–9678.
- Freeston, M. H., Ladouceur, R., Thibodeau, N., & Gagnon, F. (1991). Cognitive intrusions in a non-clinical population. I. Response style, subjective experience, and appraisal. *Behavior Research and Therapy*, 29, 585–597.
- Garrison, K. A., Scheinost, D., Worhunsky, P. D., Elwafi, H. M., Thornhill, T. A, Thompson, E., . . . Brewer, J. A. (2013a). Real-time fMRI links subjective experience with brain activity during focused attention. *NeuroImage*, 81, 110–118.
- Garrison, K. A., Santoyo, J. F., Davis, J. H., Thornhill IV, T. A., Kerr, C. E., & Brewer, J. A. (2013b). Effortless awareness: Using real time neurofeedback to investigate correlates of posterior cingulate cortex activity in meditators' selfreport. *Frontiers in Human Neuroscience*, 7, 1–9.
- Gelbard-Sagiv, H., Mukamel, R., Harel, M., Malach, R., & Fried, I. (2008). Internally generated reactivation of single neurons in human hippocampus during free recall. *Science*, 322(5898), 96–101.
- Gerlach, K. D., Spreng, R. N., Gilmore, A. W., & Schacter, D. L. (2011). Solving future problems: Default network and executive activity associated with goal-directed mental simulations. *NeuroImage*, 55, 1816–1824.
- Gerlach, K. D., Spreng, R. N., Madore, K. P., & Schacter, D. L. (2014). Future planning: Default network activity couples with frontoparietal control network and reward-processing regions during process and outcome simulations. *Social Cognitive and Affective Neuroscience*, 9, 1942–1951.
- Giambra, L. M. (1989). Task-unrelated-thought frequency as a function of age: A laboratory study. *Psychology and Aging*, 4, 136–143.

- Giambra, L. M., & Traynor, T. D. (1978). Depression and daydreaming: An analysis based on self-ratings. *Journal of Clinical Psychology*, 34, 14–25.
- Golchert, J., Smallwood, J., Jefferies, E., Seli, P., Huntenburg, J. M., Liem, F., . . . Margulies, D. S. (2017). Individual variation in intentionality in the mind-wandering state is reflected in the integration of the default-mode, fronto-parietal, and limbic networks. *NeuroImage*, 146, 226–235.
- Gorgolewski, K. J., Lurie, D., Urchs, S., Kipping, J. a, Craddock, R. C., Milham, M. P., . . . Smallwood, J. (2014). A correspondence between individual differences in the brain's intrinsic functional architecture and the content and form of self-generated thoughts. *PloS One*, 9, e97176.
- 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 U S A, 100, 253–258.*
- Greicius, M. D., Srivastava, G., Reiss, A. L., & Menon, V. (2004). Default-mode network activity distinguishes Alzheimer's disease from healthy aging: evidence from functional MRI. *Proceedings of the National Academy of Sciences of the U S A*, 101, 4637–4642.
- Gupta, A. S., van der Meer, M. A. A., Touretzky, D. S., & Redish, A. D. (2010). Hippocampal replay is not a simple function of experience. *Neuron*, 65, 695–705.
- Hamilton, J. P., Furman, D. J., Chang, C., Thomason, M. E., Dennis, E., & Gotlib, I. H. (2011). Default-mode and task-positive network activity in major depressive disorder: Implications for adaptive and maladaptive rumination. *Biological Psychiatry*, 70, 327–333.
- Hasenkamp, W., Wilson-Mendenhall, C. D., Duncan, E., & Barsalou, L. W. (2012). Mind wandering and attention during focused meditation: A fine-grained temporal analysis of fluctuating cognitive states. *NeuroImage*, 59, 750–760.
- Hassabis, D., Kumaran, D., Vann, S. D., & Maguire, E. A. (2007). Patients with hippocampal amnesia cannot imagine new experiences. *Proceedings of the National Academy of Sciences of the U S A*, 104, 1726–1731.
- Hassabis, D., & Maguire, E. a. (2009). The construction system of the brain. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, 364, 1263–1271.
- Hobson, J. A., Pace-schott, E. F., & Stickgold, R. (2000). Dreaming and the brain : Toward a cognitive neuroscience of conscious states. *Behavioral and Brain Sciences*, 23, 793–1121.
- Hyatt, C. J., Calhoun, V. D., Pearlson, G. D., & Assaf, M. (2015). Specific default mode subnetworks support mentalizing as revealed through opposing network recruitment by social and semantic FMRI tasks. *Human Brain Mapping*, 36, 3047–63.
- Ingvar, D. H. (1979). "Hyperfrontal" distribution of the cerebral grey matter flow in resting wakefulness: on the functional anatomy of the conscious state. Acta Neurologica Scandinavica, 60(1), 12–25.
- Irish, M., & Piolino, P. (2016). Impaired capacity for prospection in the dementias: Theoretical and clinical implications. *The British Journal of Clinical Psychology/The British Psychological Society*, 55, 49–68.
- Irving, Z. C. (2016). Mind-wandering is unguided attention: Accounting for the "purposeful" wanderer. *Philosophical Studies*, 173, 547.
- Kaiser, R. H., Whitfield-Gabrieli, S., Dillon, D. G., Goer, F., Beltzer, M., Minkel, J., . . . Pizzagalli, D. A. (2015). Dynamic

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resting-state functional connectivity in major depression. *Neuropsychopharmacology*, 1–9.

- Kam, J. W. Y., Dao, E., Farley, J., Fitzpatrick, K., Smallwood, J., Schooler, J. W., & Handy, T. C. (2011). Slow fluctuations in attentional control of sensory cortex. *Journal of Cognitive Neuroscience*, 23, 460–470.
- Kam, J. W. Y., Dao, E., Stanciulescu, M., Tildesley, H., & Handy, T. C. (2013). Mind wandering and the adaptive control of attentional resources. *Journal of Cognitive Neuroscience*, 25, 952–960.
- Kane, M. J., Brown, L. H., McVay, J. C., Silvia, P. J., Myin-Germeys, I., & Kwapil, T. R. (2007). For whom the mind wanders, and when: An experience-sampling study of working memory and executive control in daily life. *Psychological Science*, 18, 614–621.
- Kane, M. J., & McVay, J. C. (2012). What mind wandering reveals about executive-control abilities and failures. *Current Directions in Psychological Science*, 21, 348–354.
- Killingsworth, M. A., & Gilbert, D. T. (2010). A wandering mind is an unhappy mind. *Science*, *330*, 932.
- Kirschner, A., Kam, J. W. Y., Handy, T. C., & Ward, L. M. (2012). Differential synchronization in default and taskspecific networks of the human brain. *Frontiers in Human Neuroscience*, 6, 139.
- Klinger, E. (1971). Structure and functions of fantasy. Bognor Regis, UK: John Wiley & Sons.
- Klinger, E. (2009). Daydreaming and fantasizing: thought flow and motivation. In K. D. Markman, W. M. P. Klein, & J. A. Suhr (Eds.), *Handbook of Imagination and Mental Stimulation* (pp. 225–239). New York: Psychology Press, Taylor & Francis Group.
- Klinger, E., & Cox, W. (1987). Dimensions of thought flow in everyday life. *Imagination, Cognition & Personality*, 7, 105–128.
- Kragel, P. A, Knodt, A. R., Hariri, A. R., & LaBar, K. S. (2016). Decoding spontaneous emotional states in the human brain. *PLoS Biology*, 14, e2000106.
- Kucyi, A., & Davis, K. D. (2014). Dynamic functional connectivity of the default mode network tracks daydrearning. *NeuroImage*, 100, 471–480.
- Kucyi, A., Salomons, T. V, & Davis, K. D. (2013). Mind wandering away from pain dynamically engages antinociceptive and default mode brain networks. *Proceedings of the National Academy of Sciences of the U S A*, 110(46), 18692–18697.
- Lavenex, P., & Amaral, D. G. (2000). Hippocampal- neocortical interaction: A hierarchy of associativity. *Hippocampus*, 10(4), 420–430.
- Levinson, D. B., Smallwood, J., & Davidson, R. J. (2012). The persistence of thought: Evidence for a role of working memory in the maintenance of task-unrelated thinking. *Psychological Science*, 23(4), 375–380.
- Lieberman, M. D. (2007). Social cognitive neuroscience: A review of core processes. *Annual Review of Psychology*, 58, 259–289.
- Liu, S., Erkkinen, M. G., Healey, M. L., Xu, Y., Swett, K. E., Chow, H. M., & Braun, A. R. (2015). Brain activity and connectivity during poetry composition: Toward a multidimensional model of the creative process. *Human Brain Mapping*, 36, 3351–3372.
- 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 (New York, N.Y.)*, 315, 393–395.

- Mason, M. F., Brown, K., Mar, R. A., & Smallwood, J. (2013). Driver of discontent or escape vehicle: the affective consequences of mindwandering. *Frontiers in Psychology*, 4, 477.
- 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, 1298–1305.
- McDonald, A. et al., (2017). The real-time fMRI neurofeedback based stratification of default network regulation neuroimaging data repository. *NeuroImage*, 146, 157–170.
- McGuire, P. K., Paulesu, E., Frackowiak, R. S., & Frith, C. D. (1996). Brain activity during stimulus independent thought. *Neuroreport*, 7, 2095–2099.
- McKiernan, K. A., D'Angelo, B. R., Kaufman, J. N., & Binder, J. R. (2006). Interrupting the "stream of consciousness": An fMRI investigation. *NeuroImage*, 29, 1185–1191.
- McMenamin, B. W., Langeslag, S. J. E., Sirbu, M., Padmala, S., & Pessoa, L. (2014). Network organization unfolds over time during periods of anxious anticipation. *Journal of Neuroscience*, 34(34), 11261–11273.
- McMillan, R. L., Kaufman, S. B., & Singer, J. L. (2013). Ode to positive constructive daydreaming. *Frontiers in Psychology*, 4, 626.
- McVay, J. C., & Kane, M. J. (2010). Does mind wandering reflect executive function or executive failure? Comment on Smallwood and Schooler (2006) and Watkins (2008). *Psychological Bulletin, 136*, 188–197; discussion 198–207.
- Metzinger, T. (2013). The myth of cognitive agency: Subpersonal thinking as a cyclically recurring loss of mental autonomy. *Frontiers in Psychology*, 4, 931.
- Metzinger, T. (2015). M-Autonomy. Journal of Consciousness Studies, 22, 270-302.
- Mowlem, F. D., Skirrow, C., Reid, P., Maltezos, S., Nijjar, S. K., Merwood, A., . . . Asherson, P. (2016). Validation of the Mind Excessively Wandering Scale and the relationship of mind wandering to impairment in adult ADHD. *Journal of Attention Disorders*. doi: 10.1177/1087054716651927
- Mrazek, M. D., Phillips, D. T., Franklin, M. S., Broadway, J. M., & Schooler, J. W. (2013). Young and restless: Validation of the mind-wandering questionnaire (MWQ) reveals disruptive impact of mind-wandering for youth. *Frontiers in Psychology*, 4, 560.
- Nolen-Hoeksema, S., Wisco, B. E., & Lyubomirsky, S. (2008). Rethinking rumination. *Perspectives on Psychological Science*, 3, 400–424.
- O'Callaghan, C., Shine, J. M., Lewis, S. J. G., Andrews-Hanna, J. R., & Irish, M. (2015). Shaped by our thoughts: A new task to assess spontaneous cognition and its associated neural correlates in the default network. *Brain and Cognition*, *93*, 1–10.
- O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map.* Oxford: Oxford University Press.
- O'Reilly, R. C. (2010). The what and how of prefrontal cortical organization. *Trends in Neurosciences*, 33, 355–361.
- Ordaz, S. J., Lemoult, J., Colich, N. L., Prasad, G., Pollak, M., Price, A., . . . Gotlib, I. H. (2017). Ruminative brooding is associated with salience network coherence in early pubertal youth. *Social Cognitive and Affective Neuroscience*, 12(2), 298–310.
- Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience*, 8, 976–987.

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- Preminger, S., Harmelech, T., & Malach, R. (2011). Stimulusfree thoughts induce differential activation in the human default network. *NeuroImage*, 54, 1692–1702.
- Poerio, G. L., Totterdell, P., & Miles, E. (2013). Mind-wandering and negative mood: Does one thing really lead to another? *Consciousness and Cognition*, 22(4), 1412–1421.
- Power, J. D., Cohen, A. L., Nelson, S. M., Wig, G. S., Barnes, K. A., Church, J. A., . . . Petersen, S. E. (2011). Functional network organization of the human brain. *Neuron*, 72(4), 665–678.
- 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 U S A*, 98, 676–682.
- Rice, G. E., Lambon Ralph, M. A., & Hoffman, P. (2015). The roles of left versus right anterior temporal lobes in conceptual knowledge: An ALE meta-analysis of 97 functional neuroimaging studies. *Cerebral Cortex (New York, N.Y. : 1991)*, 25, 4374–4391.
- Roberts, J. E., Gilboa, E., & Gotlib, I. H. (1998). Ruminative response style and vulnerability to episodes of dysphoria: Gender, neuroticism, and episode duration. *Therapy*, 22, 401–423.
- Ruby, F. J. M., Smallwood, J., Engen, H., & Singer, T. (2013). How self-generated thought shapes mood—the relation between mind-wandering and mood depends on the sociotemporal content of thoughts. *PLoS ONE*, 8(10), e77554.
- 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, 319–326.
- Seeley, W. W., Menon, V., Schatzberg, A. F., Keller, J., Glover, G. H., Kenna, H., . . . Greicius, M. D. (2007). Dissociable intrinsic connectivity networks for salience processing and executive control networks. *Journal of Neuroscience*, 27(9), 2349–2356.
- Seli, P., Carriere, J. S. A., & Smilek, D. (2015a). Not all mind wandering is created equal: Dissociating deliberate from spontaneous mind wandering. *Psychological Research*, 79, 750–758.
- Seli, P., Risko, E. F., Purdon, C., & Smilek, D. (2016a). Intrusive thoughts: Linking spontaneous mind wandering and OCD symptomatology. *Psychological Research*. doi: 10.1007/ s00426-016-0756-3
- Seli, P., Risko, E. F., & Smilek, D. (2016b). On the necessity of distinguishing between unintentional and intentional mind wandering. *Psychological Science*, 27, 685–691.
- Seli, P., Risko, E. F., Smilek, D., & Schacter, D. L. (2016c). Mind-wandering with and without intention. *Trends in Cognitive Sciences*, 20, 605–617.
- Seli, P., Smallwood, J., Cheyne, J. A., & Smilek, D. (2015b). On the relation of mind wandering and ADHD symptomatology. *Psychonomic Bulletin & Review*, 22, 629–636.
- Selimbeyoglu, A., & Parvizi, J. (2010). Electrical stimulation of the human brain: Perceptual and behavioral phenomena reported in the old and new literature. *Frontiers in Human Neuroscience*, 4, 46.
- Shulman, G. L., Fiez, J. A., Corbetta, M., Buckner, R. L., Miezen, F. M., Raichle, M. E., & Petersen, S. E. (1997a). Common blood flow changes across visual tasks: II. Decreases in cerebral cortex. *Journal of Cognitive Neuroscience*, 9(5), 648–663.
- Shulman, G. L., Corbetta, M., Buckner, R. L., Fiez, J. A., Miezin, F. M., Raichle, M. E., & Petersen, S. E. (1997b).

Common blood flow changes across visual tasks: I. Increases in subcortical structures and cerebellum but not in nonvisual cortex. *Journal of Cognitive Neuroscience*, 9(5), 624–647.

- Singer, J. L., & Antrobus, J. S. (n.d.). *Imaginal processes inventory*. New York: Center for Research in Cognition and Affect Graduate Center, City University of New York.
- Singer, J. L., & McCraven, V. G. (1961). Some characteristics of adult daydreaming. *The Journal of Psychology*, 51, 151–164.
- Smallwood, J., & Andrews-Hanna, J. (2013). Not all minds that wander are lost: The importance of a balanced perspective on the mind-wandering state. *Frontiers in Psychology*, 4, 1–6.
- Smallwood, J., Beach, E., Schooler, J. W., & Handy, T. C. (2008). Going AWOL in the brain: Mind wandering reduces cortical analysis of external events. *Journal of Cognitive Neuroscience*, 20, 458–469.
- Smallwood, J., Brown, K., Baird, B., & Schooler, J. W. (2012a). Cooperation between the default mode network and the frontal-parietal network in the production of an internal train of thought. *Brain Research*, 1428, 60–70.
- Smallwood, J., Brown, K. S., Baird, B., Mrazek, M. D., Franklin, M. S., & Schooler, J. W. (2012b). Insulation for daydreams: A role for tonic norepinephrine in the facilitation of internally guided thought. *PloS One*, 7, 1–5.
- Smallwood, J. (2013). Distinguishing how from why the mind wanders: A process–occurrence framework for selfgenerated mental activity. *Psychological Bulletin*, 139(3), 519–535.
- Smallwood, J., Karapanagiotidis, T., Ruby, F., Medea, B., de Caso, I., Konishi, M., . . . Jefferies, E. (2016). Representing representation: Integration between the temporal lobe and the posterior cingulate influences the content and form of spontaneous thought. *PloS One*, 11, e0152272.
- Smallwood, J., & Schooler, J. W. (2015). The science of mind wandering: Empirically navigating the stream of consciousness. *Annual Review of Psychology*, 66, 487–518.
- Solms, M. (1997). The Neuropsychology of Dreams: A Clinicoanatomical Study. Hillsdale, NJ: Erlbaum.
- Solms, M. (2000). Dreaming and REM sleep are controlled by different brain mechanisms. *Behavioral and Brain Sciences*, 23(6), 843–850.
- Song, X., & Wang, X. (2012). Mind wandering in Chinese daily lives: An experience sampling study. *PloS One*, 7, e44423.
- Spreng, R. N., & Andrews-Hanna, J. R. (2015). The default network and social cognition. In A. W. Toga (Ed.), *Brain* mapping: An encyclopedic reference (Vol. 1316, pp. 165–169). Amsterdam: Academic Press, Elsevier.
- Spreng, R. N., Sepulcre, J., Turner, G. R., Stevens, W. D., & Schacter, D. L. (2013). Intrinsic architecture underlying the relations among the default, dorsal attention, and frontoparietal control networks of the human brain. *Journal of Cognitive Neuroscience*, 25, 74–86.
- 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, 303–17.
- Sripada, C. (2016). Imaginative guidance: A mind forever wandering. In *Homo Prospectus*. New York City: Oxford University Press.
- Stawarczyk, D., Cassol, H., & D'Argembeau, A. (2013). Phenomenology of future-oriented mind-wandering episodes. *Frontiers in Psychology*, 4, 1–12.
- Stawarczyk, D., & D'Argembeau, A. (2015). Neural correlates of personal goal processing during episodic future thinking

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and mind-wandering: An ALE meta-analysis. *Human Brain Mapping*, *36*, 2928–2947.

- Stawarczyk, D., Majerus, S., Maj, M., Van der Linden, M., & D'Argembeau, A. (2011a). Mind-wandering: Phenomenology and function as assessed with a novel experience sampling method. *Acta Psychologica*, 136, 370–381.
- Stawarczyk, D., Majerus, S., Maquet, P., & D'Argembeau, A. (2011b). Neural correlates of ongoing conscious experience: Both task-unrelatedness and stimulus-independence are related to default network activity. *PloS One*, 6, e16997.
- Stickgold, R. (2005). Sleep-dependent memory consolidation. Nature, 437, 1272–1278.
- Suzuki, W. A., & Amaral, D. G. (1994). Perirhinal and parahippocampal cortices of the macaque monkey: Cortical afferents. *Journal of Comparative Neurology*, 350, 497–533.
- Szpunar, K. K., Jing, H. G., Benoit, R. G., & Schacter, D. L. (2015). Repetition-related reductions in neural activity during emotional simulations of future events. *PloS One*, 10, e0138354.
- Tambini, A., Ketz, N., & Davachi, L. (2010). Enhanced brain correlations during rest are related to memory for recent experiences. *Neuron*, 65, 280–290.
- Teasdale, J. D., Dritschel, B. H., Taylor, M. J., Proctor, L., Lloyd, C. A., Nimmo-Smith, I., & Baddeley, A. D. (1995). Stimulus-independent thought depends on central executive resources. *Memory & Cognition*, 23, 551–559.
- Trapnell, P. D., & Campbell, J. D. (1999). Private selfconsciousness and the five-factor model of personality: Distinguishing rumination from reflection. *Journal of Personality and Social Psychology*, 76, 284–304.
- Treynor, W., Gonzalez, R., & Nolen-Hoeksema, S. (2003). Rumination reconsidered: A psychometric analysis. *Therapy*, 27, 247–259.
- Tusche, A., Smallwood, J., Bernhardt, B. C., & Singer, T. (2014). Classifying the wandering mind: Revealing the affective content of thoughts during task-free rest periods. *NeuroImage*, 97, 107–16.

- Unsworth, N., & McMillan, B. D. (2013). Mind wandering and reading comprehension: Examining the roles of working memory capacity, interest, motivation, and topic experience. *Journal of Experimental Psychology. Learning, Memory, and Cognition*, 39, 832–842.
- Van Calster, L. Van, Argembeau, A. D., Salmon, E., Peters, F. & Majerus, S. (2016). Fluctuations of attentional networks and default mode network during the resting state reflect variations in cognitive states: Evidence from a novel resting-state experience sampling method. *Journal of Cognitive Neuroscience*, 29(1), 95–113.
- Vanhaudenhuyse, A., Noirhomme, Q., Tshibanda, L. J.-F., Bruno, M.-A., Boveroux, P., Schnakers, C., . . . Boly, M. (2010). Default network connectivity reflects the level of consciousness in non-communicative brain-damaged patients. *Brain*, 133, 161–171.
- 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, 3328–3342.
- Wagner, U., Gais, S., Haider, H., Verleger, R., & Born, J. (2004). Sleep inspires insight. *Nature*, 427, 21–24.
- Wang, K., Yu, C., Xu, L., Qin, W., Li, K., Xu, L., & Jiang, T. (2009). Offline memory reprocessing: Involvement of the brain's default network in spontaneous thought processes. *PloS One*, 4, e4867.
- Watkins, E. R. (2008). Constructive and unconstructive repetitive thought. *Psychological Bulletin*, 134(2), 163–206.
- Yeo, B. T. T., Krienen, F. M., Sepulcre, J., Sabuncu, M. R., Lashkari, D., Hollinshead, M., . . . Buckner, R. L. (2011). The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *Journal of Neurophysiology*, *106*, 1125–1165.
- Zabelina, D. L., & Andrews-Hanna, J. R. (2016). Dynamic network interactions supporting internally-oriented cognition. *Current Opinion in Neurobiology*, 40, 86–93.

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