

## Review

# The wandering brain: Meta-analysis of functional neuroimaging studies of mind-wandering and related spontaneous thought processes



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## ABSTRACT

The neural basis and cognitive functions of various spontaneous thought processes, particularly mind-wandering, are increasingly being investigated. Although strong links have been drawn between the occurrence of spontaneous thought processes and activation in brain regions comprising the default mode network (DMN), spontaneous thought also appears to recruit other, non-DMN regions just as consistently. Here we present the first quantitative meta-analysis of neuroimaging studies of spontaneous thought and mind-wandering in order to address the question of their neural correlates. Examining 24 functional neuroimaging studies of spontaneous thought processes, we conducted a meta-analysis using activation likelihood estimation (ALE). A number of key DMN areas showed consistent recruitment across studies, including medial prefrontal cortex, posterior cingulate cortex, medial temporal lobe, and bilateral inferior parietal lobule. Numerous non-DMN regions, however, were also consistently recruited, including rostrolateral prefrontal cortex, dorsal anterior cingulate cortex, insula, temporopolar cortex, secondary somatosensory cortex, and lingual gyrus. These meta-analytic results indicate that DMN activation alone is insufficient to adequately capture the neural basis of spontaneous thought; frontoparietal control network areas, and other non-DMN regions, appear to be equally central. We conclude that further progress in the cognitive and clinical neuroscience of spontaneous thought will therefore require a re-balancing of our view of the contributions of various regions and networks throughout the brain, and beyond the DMN.

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## Introduction

Beneath the surface of our everyday behavior flows a stream of spontaneous thoughts, emotions, and memories. These undirected forms of thought are usually referred to as daydreaming, stimulus-independent thought, or mind-wandering (Christoff, 2012; Christoff et al., 2004, 2009; Fox and Christoff, 2014; Killingsworth and Gilbert, 2010; Mason et al., 2007; McGuire et al., 1996; Singer, 1966; Singer and Antrobus, 1972; Smallwood and Schooler, 2006, 2014). The term *mind-wandering* should in no way suggest that spontaneous forms of thought are *random* or *meaningless*, however. In fact, first-person content reports indicate that, however inexplicable its origin may seem, spontaneous thought is strongly related to one's goals, concerns, and experiences in everyday life (Andrews-Hanna et al., 2014b; Christoff et al., 2011; Fox and Christoff, 2014; Fox et al., 2013; Klinger, 2008; McMillan et al., 2013; Smallwood and Andrews-Hanna, 2013). Spontaneous thought, then, refers to the type of thought that we recognize as our own creation without yet understanding its ontogeny or purpose – if any (for more detailed discussions, see Christoff et al., 2011; Fox and Christoff, 2014).

Cognitive psychology and neuroscience have so far focused the bulk of their efforts on studying goal-directed thought (Christoff, 2012, 2013; Fox and Christoff, 2014). As important as such processes are, however, the past few decades have seen a growing recognition that spontaneous mental processes are extremely common during restful waking states and minimally-demanding tasks (Kane et al., 2007; Killingsworth and Gilbert, 2010; Singer, 1966). Any cognitive process that occurs so frequently and ubiquitously is of inherent interest to cognitive neuroscientists, but there are other reasons for developing a more complete model of the neural correlates of these spontaneous thought processes. Spontaneous thought processes appear to play a role at the extreme poles of human flourishing and clinical conditions: in creative thinking and problem-solving on the one hand (Baird et al., 2012; Ellamil et al., 2012), and in depressive rumination, post-traumatic stress disorder, and other mental health disorders on the other (Andrews-Hanna et al., 2014b; Berman et al., 2011; Ehlers et al., 2004; Nolen-Hoeksema, 2000; Whitfield-Gabrieli and Ford, 2012).

The growing appreciation of the importance of spontaneous cognition has coincided with the parallel discovery that a consistent 'default mode' of brain function characterizes the human resting state in functional neuroimaging experiments (Buckner et al., 2008; Gusnard et al., 2001; Raichle, 2010; Raichle et al., 2001; Raichle and Snyder, 2007; Shulman et al., 1997). The hypothesized connection (Gusnard et al., 2001; Raichle et al., 2001) between spontaneous thought processes and activation of the default mode network (DMN) has now been widely validated in cognitive and clinical neuroscience (Dixon et al., 2014; Fox and Christoff, 2014). However, this relationship has come to overshadow the possible contribution of non-DMN regions to spontaneous thought. Our own empirical neuroimaging work (Andrews-Hanna et al., 2010a; Christoff, 2012; Christoff et al., 2004, 2009), as well as that of many other research groups (Binder et al., 1999; D'Argembeau et al., 2005; Dumontheil et al., 2010; Mason et al., 2007; McGuire et al., 1996; McKiernan et al., 2006; Spiers and Maguire, 2006a; Stawarczyk et al., 2011b; Wang et al., 2009), has consistently shown recruitment of non-DMN regions during mind-wandering and related forms of spontaneous thought. Yet the robustness of these findings has remained largely unacknowledged and, until now, unexamined by systematic whole-brain meta-analysis. As a consequence, activity in a

few selected DMN regions-of-interest (ROIs) continues to be used as the standard, and by implication, sufficient neural indicator of mind-wandering in both healthy (Stawarczyk et al., 2011b; Vanhaudenhuyse et al., 2011) and clinical (Anticevic et al., 2012; Berman et al., 2011; Whitfield-Gabrieli and Ford, 2012) populations.

Restricting analyses to DMN regions is problematic for at least two other reasons. For one, the subjective variety of spontaneous thought modes (which can include memory recall, planning for the future, hypothetical imaginings, mentalizing, and so on) suggest correspondingly complex and variegated neural correlates (Andrews-Hanna et al., 2013; Dixon et al., 2014; Fox and Christoff, 2014; Fox et al., 2013); a simple DMN-mind-wandering mapping is unlikely to fulfill this criterion. Moreover, despite its involvement in spontaneous thought, the DMN is implicated in many cognitive processes that may not be spontaneous, such as famous face recognition (Spreng et al., 2014). It therefore seems likely that other brain areas and/or networks play a role in spontaneous thought.

Here we present a meta-analysis that specifically aimed to assess the consistency of recruitment of various regions throughout the brain during spontaneous thought processes. Rather than focusing on DMN contributions, we took a whole-brain approach to carry out a quantitative meta-analysis of the 24 functional neuroimaging studies of mind-wandering and related spontaneous thought processes published to date (see Table 1 for a list of the studies).

## Methods

### Search strategy

To identify neuroimaging studies related to mind wandering and spontaneous thought, we conducted a comprehensive and systematic search of the literature using MEDLINE (<http://www.pubmed.com>), Google Scholar (<http://scholar.google.com>), and PsycINFO (<http://www.apa.org/pub/databases/psycinfo/index.aspx>) for papers containing the words 'mind-wandering'; 'mind wandering'; 'spontaneous thought'; 'stimulus-independent thought'; 'task-unrelated thought'; or 'daydreaming,' from October 2014 to 1996, the year the first explicit functional neuroimaging study of spontaneous thought was published (McGuire et al., 1996). This list of articles was further refined by searching within results for studies that contained any of the words or phrases 'magnetic resonance imaging', 'MRI', 'positron emission tomography,' 'neuroimaging,' or 'brain' within the title or abstract. Of the candidate studies, every abstract was read to confirm whether functional neuroimaging methods to study mind-wandering or related spontaneous thought processes was employed (see details of inclusion and exclusion criteria in the next section). The reference lists of each included study, as well as those of several major reviews (Andrews-Hanna, 2012; Andrews-Hanna et al., 2014b; Christoff, 2012), were also searched, to ensure completeness.

### Study inclusion and exclusion criteria

All studies using functional neuroimaging (i.e., functional magnetic resonance imaging (fMRI) or positron emission tomography (PET)) were considered, but studies using purely morphometric neuroimaging methods to study mind-wandering (e.g., cortical thickness in Bernhardt et al., 2014) were not included. Using the search strategy detailed above, a total of 24 studies were collected (Table 1).

**Table 1**  
Functional neuroimaging studies examining various forms of mind-wandering or spontaneous thought.

Study	Analysis	Peak foci	Design	N	Mind-wandering measure <sup>a</sup>	Spontaneous thought type
<b>McGuire et al. (1996)</b>	WB & ROI	5	Blocked	5/6	Retrospective	Verbal stimulus-independent thoughts during rest
<b>Binder et al. (1999)</b>	WB	8	Blocked	14	Inferential	Task-unrelated thought during rest
<b>Christoff et al. (2004)</b>	WB	15	Blocked	12	Assumptive	Spontaneous thought during rest
<b>D'Argembeau et al. (2005)</b>	WB	9	Blocked	13	Retrospective	Spontaneous thought during rest
McKiernan et al. (2006)	ROI	–	Blocked	30	Inferential	Task-unrelated thought during auditory task
<b>Spiers &amp; Maguire (2006b)</b>	WB & ROI	24	ER	20	Retrospective (Online)	Spontaneous mentalizing during navigation task
<b>Mason et al. (2007)</b>	WB resting state → Functionally-defined ROIs	20	Blocked	19	Inferential and Questionnaire	Mind-wandering during highly practiced task
<b>Christoff et al. (2009)</b>	WB	34	ER	15	Online	Mind-wandering during SART
<b>Wang et al. (2009)</b>	WB & ROI	8	Blocked	13	Questionnaire	Spontaneous thought during rest
Andrews-Hanna et al. (2010a)	ROI; seed-based FC	–	Blocked	30/139	Surprise retrospective	Spontaneous thought during passive fixation
<b>Dumontheil et al. (2010)</b>	WB	20	Blocked	16	Retrospective	Task-unrelated thought during various simple tasks
<b>Stawarczyk et al. (2011b)</b>	ROI/Supp. WB	14	ER	22	Online	Mind-wandering during SART
Vanhaudenhuyse et al. (2011)	ROI	–	ER	22	Online	Intensity of internal awareness during rest
Christoff (2012)	ROI; seed-based FC	–	ER	15	Online	Mind-wandering during SART
Hasenkamp et al. (2012)	WB	–	ER	14	Online	Mind-wandering during meditation
Hasenkamp and Barsalou (2012)	ROI; seed-based FC	–	ER	14	Online	Mind-wandering during meditation
Allen et al. (2013)	ROI	–	ER	21/21	Online	Task-unrelated thought during EAT
Kucyi et al. (2013)	WB	–	Blocked	51	Online	Mind-wandering during painful stimuli
Moss et al. (2013)	Functional localizer- defined ROIs	–	Blocked	15	Retrospective	Mind-wandering during reading
Smallwood et al. (2013b)	WB	–	ER	16	Assumptive	Stimulus-independent thought during various tasks
Smallwood et al. (2013a)	ROI	–	Blocked	42	Online	Mind-wandering during reading
Gorgolewski et al. (2014)	WB	–	Blocked	166	Retrospective	Self-generated thought during rest
Kucyi and Davis (2014)	ROI	–	Blocked	51	Online	Mind-wandering during painful stimuli
Tusche et al. (2014)	ROI	–	ER	30	Online	Self-generated thought during rest

All studies were conducted using fMRI, except McGuire et al. (1996) and D'Argembeau et al. (2005), which used PET. *N* = sample size (experimental/control group, if applicable). Studies employing whole-brain analyses that were included in the meta-analysis are listed in bold font. The number of peak activation foci contributed from each study is indicated in the third column. EAT: Error Awareness Task; ER: event-related; FC: functional connectivity; ROI: region of interest; SART: Sustained Attention to Response Task; Supp.: supplemental; WB: whole-brain.

<sup>a</sup> See *Methods* for a discussion of mind-wandering measures.

Only reports published in peer-reviewed journals were included (results from abstracts, presented talks, etc., were excluded). To be included, studies had to: (i) report specific peak foci of activation in either Talairach or Montreal Neurological Institute (MNI) space; (ii) report group results (case studies of single subjects were excluded); and (iii) involve healthy, non-clinical, 'normal' populations.

A fourth criterion was employed to ensure that some form of spontaneous thought was taking place: included studies had to (iv) employ some form of retrospective, online, or questionnaire self-report measure that indicated frequency or depth of spontaneous thought processes (a single exception to this criterion was allowed for an early fMRI study, because it was otherwise specifically designed to detect activations associated with spontaneous thought (Christoff et al., 2004); exclusion of this study did not appreciably alter the meta-analytic results, but its inclusion increased the power of our analysis). This criterion avoids the widespread reverse inference that is particularly present in this field (Christoff and Owen, 2006; Poldrack, 2006), where DMN activity is frequently interpreted as indirect evidence of mind-wandering-like processes (in the absence of any reports to that effect from participants themselves). This criterion also allowed for comparison of spontaneous thought frequency across multiple conditions, and therefore for a common feature across all the contrasts and studies included here (despite difference in comparison/control conditions; see below). All contrasts included in this meta-analysis represent a comparison between some state of *higher* spontaneous thought frequency with a corresponding period or task involving *lower* spontaneous thought frequency, or, similarly, regions where higher activity predicted higher rates of mind-wandering. Furthermore, all these spontaneous thought frequency ratings are derived directly from questionnaires, experience sampling probes, and so on, rather than based on assumptions about when spontaneous thought frequency should be higher or lower. The mind-wandering measures employed included (a) post-scan *retrospective* reports (e.g., D'Argembeau et al., 2005; McGuire et al., 1996); (b) *online*, trial-by-trial first-person reports of whether spontaneous

thoughts were occurring or not (e.g., Christoff et al., 2009; Stawarczyk et al., 2011b); and (c) *questionnaires* purporting to measure 'trait' levels of fantasy and spontaneous thought (e.g., Wang et al., 2009). A final method was (d) *inferential*, in that mind-wandering scores on a given block or task for a group tested only behaviorally were assumed to hold for a separate group of participants tested in the scanner (e.g., Mason et al., 2007). Details for each study are provided in Table 2.

As a fifth criterion studies had to (v) report whole-brain results. Studies that reported activation foci in ways other than 3D coordinate space were excluded (e.g. ROI analysis) as they are not compatible with the activation likelihood estimation (ALE) analysis approach. Further, ROI findings tend to be biased toward the DMN, reinforcing the false notion that the DMN is specifically (or exclusively) involved in mind-wandering.

Studies satisfying all five criteria (and therefore included in the meta-analysis) are listed in bold font in Table 2. A total of 10 of the 24 studies were included; failure to satisfy criterion (v) accounted for the majority of exclusions (details in Table 2). Two studies (Hasenkamp et al., 2012; Kucyi et al., 2013) met all five criteria, but involved other potentially confounding factors. The first (Hasenkamp et al., 2012) employed a population of expert meditation practitioners, who may have altered frequency of mind-wandering (Mrzcek et al., 2013), as well as altered brain activity during periods of rest with high levels of mind-wandering (Brewer et al., 2011). The second study (Kucyi et al., 2013) examined the relationship between mind-wandering and pain, administering painful electrical nerve stimulation during the sessions where mind-wandering was reported, again presenting a potential confound. To avoid these confounds affecting our meta-analytic results these studies were excluded (although their inclusion did not appreciably impact the present findings).

One study by Spiers and Maguire (2006a) was followed up with a similar study using the same subjects, dataset, and baseline condition, but somewhat different spontaneous mental activity as the condition of interest (Spiers and Maguire, 2006b). As inclusion of both studies

**Table 2**  
Brain areas consistently activated by mind-wandering and related spontaneous thought processes.

Region	Cluster size (mm <sup>3</sup> )	Peak ALE value	Peak in MNI space (x, y, z)	Brodman area	Studies contributing to cluster
<i>Frontal lobe</i>					
Dorsal anterior cingulate cortex	2920	0.0144	−5, 27, 39 (Fig. 2a)	32	a, e, g, h
R dorsolateral/rostrolateral prefrontal cortex	1656	0.0085	45, 43, −8 (Figs. 2e, g)	46/10	d, i
L ventrolateral prefrontal cortex	1320	0.0090	−35, 10, −26 (Fig. 2d)	47/11	c, g, j
Rostromedial prefrontal cortex	1256	0.0081	3, 61, 13 (Fig. 2b)	10/9	e, f
Medial prefrontal cortex; anterior cingulate cortex	1080	0.0089	4, 42, 3 (Fig. 2b)	24/32	f, g
<i>Parietal lobe</i>					
Precuneus; posterior cingulate cortex	3784	0.0123	−8, −56, 39 (Fig. 2a)	7/31	b, d, f, g, h, j
L inferior parietal lobule; angular gyrus	2616	0.0092	−46, −72, 25 (Fig. 2d)	39	b, e, f, g, h
R inferior parietal lobule; supramarginal gyrus	1808	0.0098	56, −51, 33 (Fig. 2f)	40/39	d, f, i
R secondary somatosensory cortex	1416	0.0097	24, −39, 56 (Fig. 2i)	5/40	c, e, g
<i>Temporal lobe</i>					
L parahippocampus	3496	0.0196	−27, −37, −18 (Fig. 2h)	36	b, c, f, g, h
L temporopolar cortex	2608	0.0116	−50, −1, −5 (Fig. 2g)	38	f, g, i
L mid-insula	1032	0.0126	−42, 29, −12 (Fig. 2g)	13	e, j
<i>Occipital lobe</i>					
L lingual gyrus	1936	0.0092	−15, −66, 5 (Fig. 2c)	19/18/30	c, e, g, j

Significant meta-analytic clusters, with peak coordinates, for spontaneous thought > control conditions. BA: Brodmann area. a: McGuire et al. (1996); b: Binder et al. (1999); c: Christoff et al. (2004); d: D'Argembeau et al. (2005); e: Spiers & Maguire (2006b); f: Mason et al. (2007); g: Christoff et al. (2009); h: Wang et al. (2009); i: Dumontheil et al. (2010); j: Stawarczyk et al. (2011b).

would involve completely overlapping, non-independent samples and data, only one study was included. The former study involved spontaneous mentalizing, which is very common during mind-wandering and related forms of spontaneous cognition (Fox et al., 2013), and so was retained. The latter study instead investigated spontaneous route-planning during virtual navigation, which bears much less resemblance to the various other forms of spontaneous thought examined here, and so was not included in the meta-analysis.

#### Adjustment of peak coordinates

Some included studies reported results in Talairach coordinates. For consistency, we converted all coordinates to MNI space using non-linear transformations in the WFU PickAtlas software package (Maldjian et al., 2003).

A small but substantial number of peak foci ( $n = 15$ ) were reported at coordinates that lay outside of the template brain images used within the activation likelihood estimation meta-analysis software, GingerALE. To avoid data loss, we performed a minimum linear translation of these peak coordinates in MNI space to fit within the GingerALE template mask. In all cases these translations were minimal (mean = 3.87 mm; range: 1–10 mm), and in no case did adjusted peak foci subsequently fall within a different brain region from that listed in the results tables of the original publication. Full details of these translations, including the original and adjusted foci, are available in the online Supplementary materials (Table S1).

#### Activation likelihood estimation (ALE) meta-analysis

We used a quantitative, random-effects meta-analytic method known as activation likelihood estimation (ALE) (Eickhoff et al., 2009, 2012; Laird et al., 2005; Turkeltaub et al., 2002, 2012) implemented in the software program GingerALE 2.3.1 (San Antonio, TX: UT Health Science Center Research Imaging Institute). The most recent ALE algorithm tests for above-chance clustering of peak foci from different experiments included in the meta-analysis (Eickhoff et al., 2009, 2012) by comparing actual activation foci locations/clustering with a null distribution that includes the same number of peak foci distributed randomly throughout the brain's gray matter. Included activation foci were smoothed using a full-width half maximum (FWHM) Gaussian kernel dependent on the sample size (subjects) of the experiment from which foci were drawn (larger sample → smaller smoothing kernel –

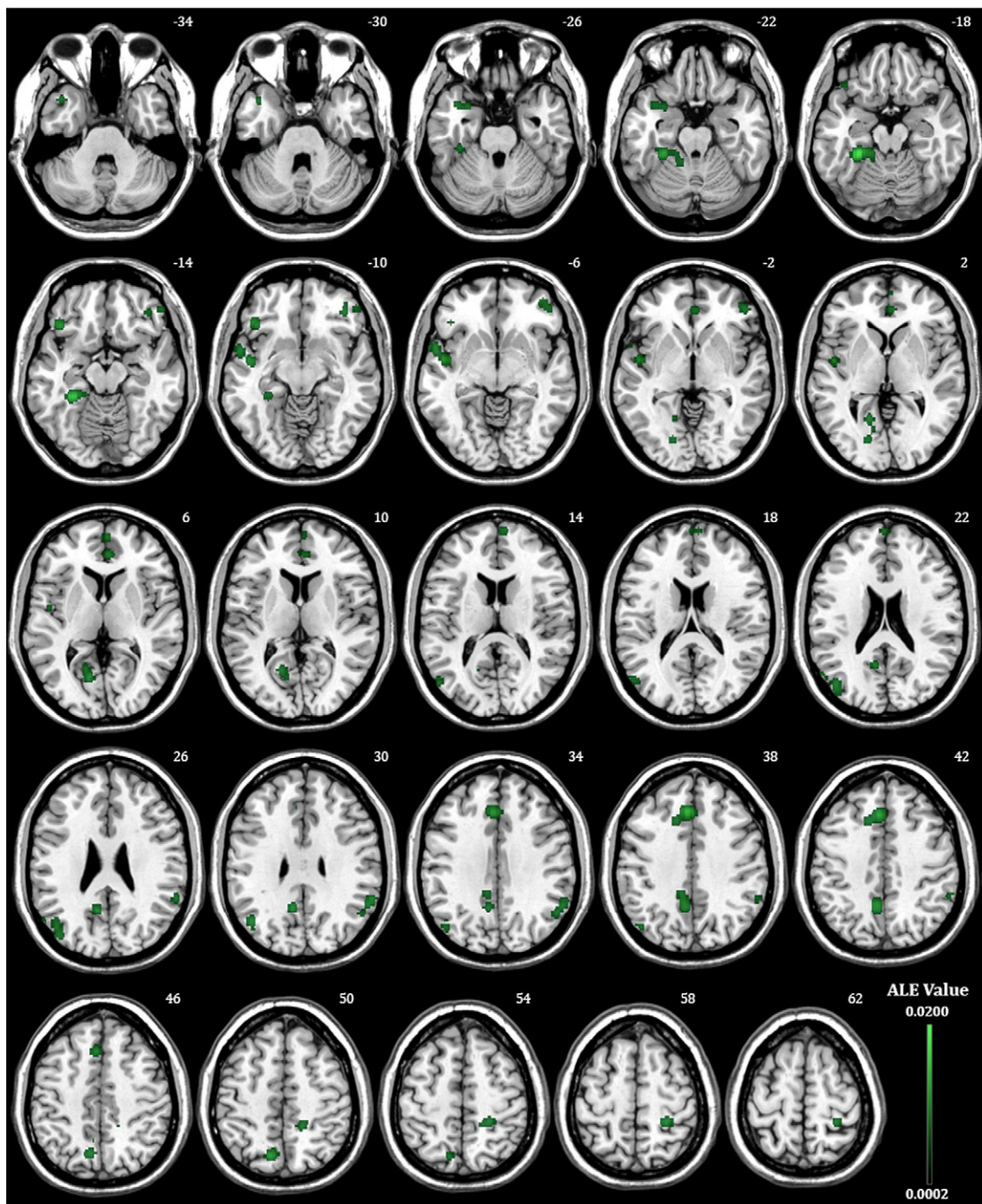
empirically determined by Eickhoff et al., 2009, 2012). Resulting statistical maps show clusters where convergence between activation foci is greater than would be expected by chance (i.e., if foci from each experiment were distributed independently).

We analyzed a total of 157 foci from 10 neuroimaging studies (studies in bold font in Table 1). Statistical maps were thresholded using a false discovery rate (FDR – see Genovese et al., 2002) of  $q = .05$  and a cluster threshold of  $k = 1000 \text{ mm}^3$ . We used this relatively liberal statistical threshold, but high cluster threshold, in order to better visualize results and to ensure that cross-study convergence was not neglected in this relatively small-sample meta-analysis. Similar results were found at more conservative statistical thresholds. Region classifications follow those indicated in the Multi-Image Analysis GUI ('Mango') image-viewing software (UT Health Science Center Research Imaging Institute) used to visualize the meta-analytic results. The Duvernoy neuroanatomical atlas was also consulted (Duvernoy et al., 1991). Fig. 1 and Fig. 2 were created in the mricron software package (<http://www.mccauslandcenter.sc.edu/mricro/mricron/index.html>; (Rorden et al., 2007)). Fig. 3 was created by overlaying our meta-analytic statistical map onto a surface brain projection using the Caret software (Van Essen, 2005), with network demarcations derived from resting-state functional connectivity MRI in a sample of 1000 adults (Yeo et al., 2011).

## Results

We found 13 regions to be reliably involved in mind wandering and spontaneous thought (Table 2; Fig. 1). These regions included all major hubs of the DMN: rostromedial prefrontal cortex, medial prefrontal cortex/anterior cingulate cortex, precuneus/posterior cingulate cortex, bilateral inferior parietal lobule, and left medial temporal lobe/parahippocampal cortex (extending somewhat into the cerebellum). We also found significant clusters outside the DMN, including the dorsal anterior cingulate cortex, right dorsolateral/rostrolateral prefrontal cortex, left ventrolateral prefrontal cortex, secondary somatosensory cortex, left temporopolar cortex, left mid insula, and left lingual gyrus. A detailed representation of the results is presented in Fig. 1, which shows all significant meta-analytic differences in their entirety through 25 horizontal slices. A more focused representation is given in Fig. 2, which, for added clarity, depicts the peak of each significant meta-analytic cluster from the viewpoint/orientation most common for each given region.





**Fig. 1.** Meta-analytic activations associated with mind-wandering and related spontaneous thought processes throughout the entire brain. Horizontal slices presented with 3 mm skip. Color bar indicates ALE likelihood values (see [Methods](#)). White numbers denote vertical stereotactic coordinates (z) in MNI space. See [Table 2](#) for detailed quantitative results.

## Discussion

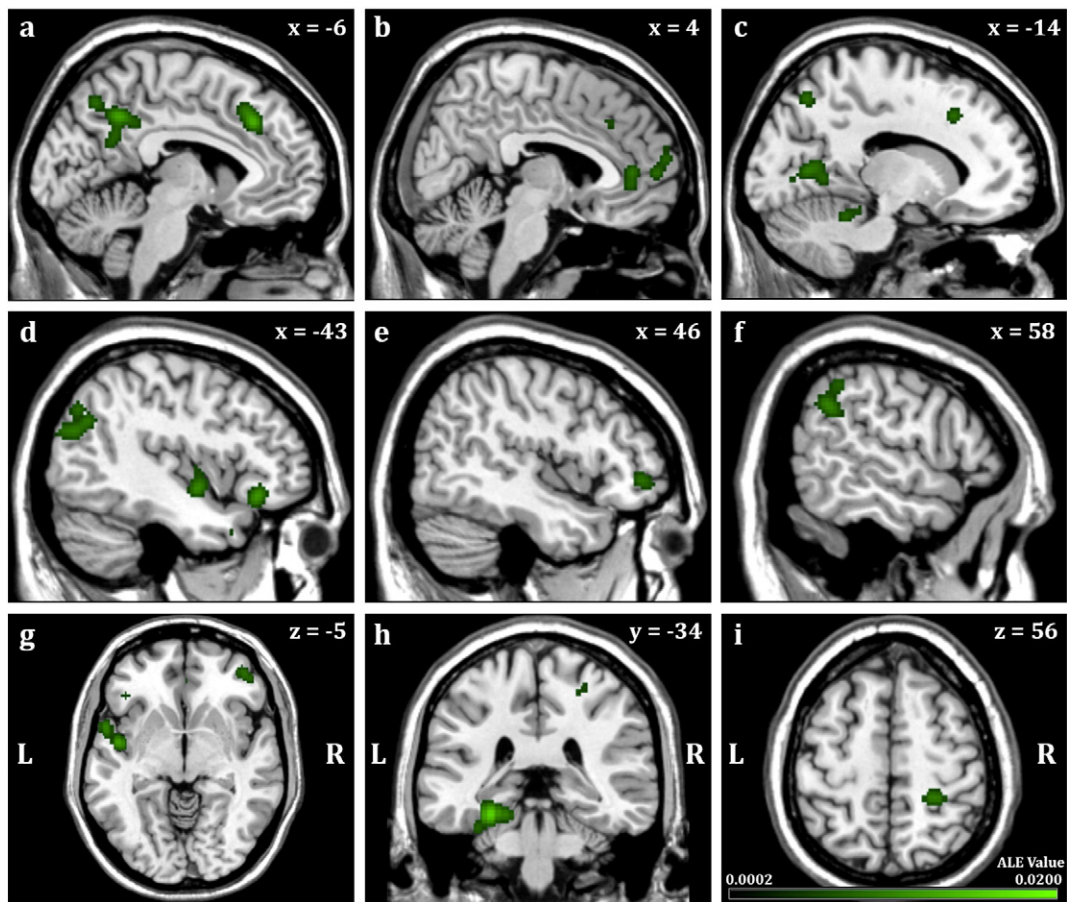
### Overview

The aim of the present meta-analysis was to impartially interrogate whole-brain neuroimaging results of various forms of spontaneous thought to investigate (i) the extent to which the DMN is implicated and (ii) the extent to which regions and brain networks outside the boundaries of the DMN are involved. Our quantitative meta-analysis revealed consistent activations throughout the brain ([Figs. 1 and 2](#)), but predominantly in limbic, paralimbic, and association cortices. Primary sensory cortices were conspicuously absent, although clusters were observed in secondary visual and somatosensory areas. The wide cortical distribution of these meta-analytic findings likely reflects the

corresponding diversity of mental processes and content denoted by the umbrella terms ‘mind-wandering’ and ‘spontaneous thought’. Far from indicating a definitive set of neural correlates for spontaneous thought, the results suggest that numerous forms of spontaneous thought could be differentiated at the neural level (see below).

### Default mode network involvement in spontaneous thought

Our meta-analysis provided strong evidence that the DMN, which characterizes the ‘resting’ state, is involved in spontaneous thought processes of various kinds – an idea with a lengthy precedent. In some of the very earliest human neuroimaging studies, resting brain activity was already proposed to contribute to the internal stream of thinking ([Ingvar, 1979](#)). Additionally, a potential role of the DMN in mind-wandering-like



**Fig. 2.** Peaks of each meta-analytic cluster of activation associated with mind-wandering and related spontaneous thought processes. Peaks for each of 13 significant meta-analytic clusters of activation associated with mind-wandering and related spontaneous thought processes. (a) Posterior cingulate cortex/precuneus and dorsal anterior cingulate cortex. (b) Medial prefrontal cortex/anterior cingulate cortex and rostromedial prefrontal cortex. (c) Left lingual gyrus (largest cluster). (d) From left to right: left inferior parietal lobule/angular gyrus; left mid-insula; and left ventrolateral prefrontal cortex. (e) Right rostralateral/dorsolateral prefrontal cortex. (f) Right inferior parietal lobule/supramarginal gyrus. (g) Left temporopolar cortex and mid-insula; right rostralateral/dorsolateral prefrontal cortex. (h) Left parahippocampus/medial temporal lobe, extending into the cerebellum. (i) Right secondary somatosensory cortex. Color bar indicates ALE likelihood values (see Methods). See Table 2 and Fig. 1 for more detailed results. Stereotactic coordinates (x, y, z) are in MNI space. L: left; R: right.

processes was discussed in the first major publications relating to this network (Andreasen et al., 1995; Gusnard et al., 2001; McGuire et al., 1996; Raichle et al., 2001). We found strong evidence in support of this notion, with meta-analytic clusters in almost all DMN regions: rostromedial prefrontal cortex (BA 9/10), anterior cingulate cortex (BA 24/32), ventrolateral prefrontal cortex (BA 47/11), posterior cingulate cortex (BA 31), bilateral posterior inferior parietal lobule (BA 39/40), and the medial temporal lobe (especially the parahippocampus/BA 36). All of these meta-analytic clusters overlap with regions that are widely thought of as being part of the DMN (Buckner et al., 2008; Yeo et al., 2011).

Recent work has shown that the DMN can be parcellated into multiple component subsystems (Andrews-Hanna et al., 2010b, 2014b; Yeo et al., 2011). A *medial temporal subsystem* comprises most of the clusters observed here: medial temporal lobe, retrosplenial cortex, ventromedial prefrontal cortex, and posterior inferior parietal lobule; a *dorsal medial subsystem* comprises the dorsomedial prefrontal cortex, temporoparietal junction, lateral temporal cortex, and temporopolar cortex. The anterior medial prefrontal cortex and posterior cingulate cortex appear to act as major hubs interacting with and connecting these two subsystems.

Evidence from meta-analyses of the task-based literature suggests that these default network components may support different cognitive functions (Andrews-Hanna et al., 2014b). The medial temporal subsystem is activated during episodic memory recall and future thinking tasks, and is hypothesized to play a role in retrieving past information

and flexibly binding this information into a coherent mental scene (e.g., Hassabis and Maguire, 2007; Schacter et al., 2012). In contrast, the dorsal medial subsystem activates during social tasks, particularly those that involve internal/reflective processing such as mentalizing (i.e., inferring the mental states of other people, and evaluating one's own; Andrews-Hanna et al., 2014a; Lieberman, 2007; Schilbach et al., 2012). Consistent with a central, hub-like role, the anterior medial prefrontal cortex and posterior cingulate cortex activate across a wide range of tasks, including mnemonic and social tasks, and those involving self-related processing. These regions may allow us to assess the personal significance of a variety of external and internal sources of information and construct an overarching personal meaning (D'Argembeau, 2013; Roy et al., 2012).

Paralleling the task-related literature, there is considerable evidence from phenomenological studies that mind-wandering is a heterogeneous set of cognitive processes, evoking multiple types of content that vary both within and across individuals (Andrews-Hanna et al., 2014b; Smallwood and Schooler, 2006, 2014). A clear prediction for future studies, then, is that activity in different default network subsystems during mind-wandering might be associated with different types of mental content. Below, we discuss this possibility further.

#### *Frontoparietal control network involvement in spontaneous thought*

Mind-wandering and related spontaneous thought processes consistently recruited many regions of the frontoparietal control network



(Vincent et al., 2008; Yeo et al., 2011), including the dorsal anterior cingulate cortex (BA 32), right rostrolateral/dorsolateral prefrontal cortex (BA 10/46), right anterior inferior parietal lobule (BA 39/40), and precuneus (BA 7) (Table 2; Figs. 1–3). The frontoparietal control network plays a central role in goal-directed cognition (Niendam et al., 2012). This role extends from classic measures of executive functioning to personally relevant goal-directed tasks, such as planning for the future (Gerlach et al., 2014; Spreng et al., 2010). In the latter capacity, it tends to be activated in unison with DMN areas, so we discuss its potential role in spontaneous thought in the following section, which addresses DMN-frontoparietal control network coupling in the generation of spontaneous thought.

#### *Coupling of the default mode and frontoparietal control networks*

Many meta-analytic clusters fell within the borders of either the default mode (Buckner et al., 2008; Raichle et al., 2001; Shulman et al., 1997) or fronto-parietal control network (Spreng et al., 2013; Vincent et al., 2008; Yeo et al., 2011). We visualize the extent of this overlap by plotting our meta-analytic clusters on an ‘inflated’ brain template with border outlines for both networks in Fig. 3. The borders of the two networks are based on previously published, large-scale ( $n = 1000$ ) resting state datasets (Yeo et al., 2011), whereas the green clusters of activation represent our whole-brain meta-analytic results (from Table 2; Fig. 1).

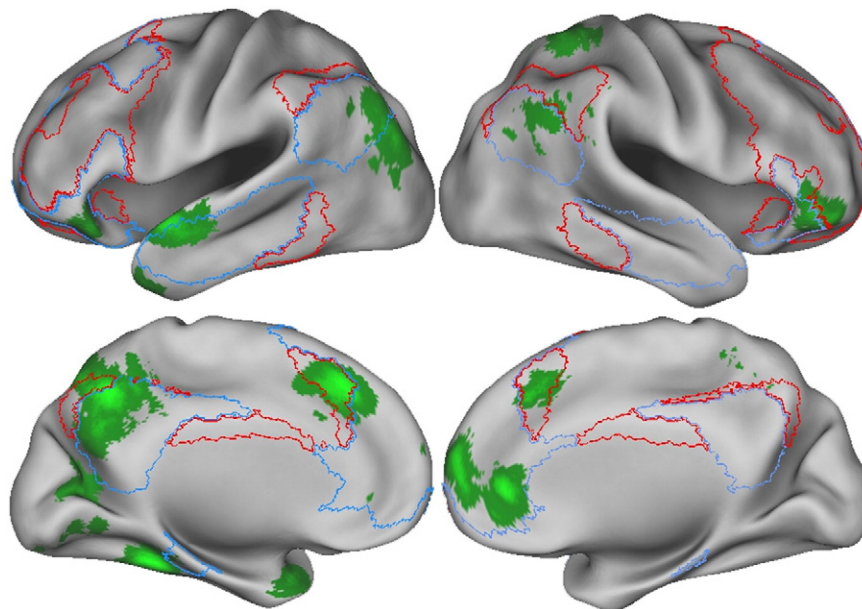
Although our meta-analytic results cannot directly address the temporal correlation of these brain activations, such results are consistent with observations of temporal coupling of DMN and fronto-parietal control network areas (e.g., Christoff, 2012; Spreng et al., 2010). Spontaneous thought is not the only cognitive process, however, to exhibit co-activation of, and functional connectivity (i.e., temporal coupling) between, the default mode and frontoparietal control networks. Similar findings have been observed in autobiographical memory recall (Spreng et al., 2009), mentalizing or ‘theory of mind’ (Spiers and Maguire, 2006a; Spreng et al., 2009), creative generation and evaluation of artwork (Ellamil et al., 2012), and goal-directed prospection (Gerlach et al., 2014; Spreng et al., 2009). Intriguingly, memory recall,

mentalizing, creative recombination of ideas, and thoughts about the future mark the dominant themes of spontaneous thought content from the subjective point of view (reviewed in Fox et al., 2013; Klinger, 2008), making these overlapping brain activations intriguing avenues for future research. Resting-state functional connectivity analysis has revealed that there is an extensive intrinsic architecture to support dynamic interactions between the default and frontoparietal control networks (Spreng et al., 2013). The coupled recruitment of these two networks might represent a dynamic interplay whereby executive control regions guide, evaluate, and select among the various spontaneous streams of thoughts, memories, and imaginings offered up to consciousness by the DMN (Andrews-Hanna et al., 2014b; Fox and Christoff, 2014; Fox et al., in press).

#### *Activations outside the default mode and frontoparietal control networks*

The co-activation or flexible coupling of the DMN and fronto-parietal control networks is not sufficient to explain all the consistent activations associated with spontaneous thought: numerous other areas need to be accounted for, including right secondary somatosensory cortices (BA 5/40), the left mid-insula (BA 13), and the left lingual gyrus (BA 19/18/30), and possibly the temporopolar cortex (BA 38; the inclusion, or not, of this region within the DMN remains controversial, and the cluster we observed lies outside the typically-defined DMN area; see Fig. 3). The cluster in the left medial temporal lobe also extended somewhat into the cerebellum. First-person reports of the subjective content of spontaneous thought shed some light on the potential role of these regions, however: a large proportion of mind-wandering content involves faint-to-immersive visual imagery in one form or another (Delamillieure et al., 2010), and thoughts centering on the body (including exteroceptive and interoceptive information) are also very common (Fox et al., 2013; Klinger, 2008).

The secondary somatosensory cortex and the insula represent two of the major cortical centers for processing exteroceptive and interoceptive body information, respectively (Craig, 2004, 2009; Critchley et al., 2004; Farb et al., 2013; Penfield and Boldrey, 1937; Penfield and Rasmussen, 1950). Although the role of the insula, in particular, may



**Fig. 3.** Mind-wandering/spontaneous thought brain activations contrasted with the default mode network and frontoparietal control network. Significant meta-analytic clusters associated with mind-wandering and related spontaneous thought processes (green clusters) juxtaposed with outlines of the default mode network (blue) and the frontoparietal control network (red). Meta-analytic mind-wandering activations overlap considerably with both networks, but also include regions beyond both networks (e.g., in temporopolar cortex, insula, secondary somatosensory areas, and downstream visual areas in the lingual gyrus). DMN and frontoparietal control network masks based on aggregate data from 1000 subjects as reported by Yeo et al. (2011).

be more complex due to its involvement in such a wide variety of processes (Singer et al., 2009), a role for these regions in the 'somatic' experiences of spontaneous thought is one possibility.

The lingual gyrus is a downstream visual area of the occipital lobe involved in 'higher' visual processing (Corbetta et al., 1990; Zeki et al., 1991). Beyond its unambiguous role in color vision, our recent work has shown that this area is consistently recruited during nighttime dreaming (Domhoff and Fox, 2015; Fox et al., 2013) – which is almost universally visual in nature (Schredl, 2010; Schwartz, 2000). Further, neurological lesions in this area often lead to an inability to create visual imagery and cessation of all visual dream imagery, but with otherwise normal continuation of dreaming (Solms, 1997, 2000) – the classic Charcot–Wilbrand syndrome (Charcot, 1883; Critchley, 1953; Wilbrand, 1887). Following a detailed comparison of both subjective reports and neural recruitment, we have further argued that nighttime dreaming shows striking similarities to waking spontaneous waking thought (Domhoff and Fox, 2015; Fox et al., 2013), of which the common recruitment of the lingual gyrus and the similarly high frequency of visual imagery are but two instances. Although, as with the insula, the role of the lingual gyrus in spontaneous thought may have many nuances, one possible explanation is involvement in the often-intensive visual imagery accompanying spontaneous thinking of various kinds (Domhoff and Fox, 2015; Fox et al., 2013).

Finally, we observed a significant cluster in the left temporopolar cortex (BA 38). Although relatively poorly understood compared to other neocortical regions, the temporopolar cortex appears to play a strong role in integrated emotional processing involving visceral responses, as well as 'theory of mind' (or mentalizing) (Olson et al., 2007). These putative roles for the observed temporopolar cortex cluster are consistent with the findings that both mentalizing, and a wide range of complex emotions, are ubiquitous features of spontaneous thought (Fox et al., 2013, 2014; Klinger, 2008).

#### *Neural correlates of specific spontaneous thought content*

Subjective reports suggest a great variety of mind-wandering content, from seemingly pointless fantasizing, to complex planning for the future, to the generation of creative ideas (Andrews-Hanna et al., 2013, 2014b; Baird et al., 2011, 2012; Christoff, 2012; Delamillieure et al., 2010; Diaz et al., 2013; Dixon et al., 2014; Ellamil et al., 2012; Fox et al., 2013; Klinger, 2008; Stawarczyk et al., 2011a, 2013). It therefore seems likely that different forms and content of mind-wandering entail at least partially dissociable neural correlates. Some important empirical and theoretical steps have already been taken toward delineating such functional specificity: for instance, Tusche et al. (2014) investigated the emotional content of unconstrained thoughts during task-free rest periods using multivariate pattern analysis. They found that patterns of activity within medial prefrontal cortex predicted the valence (positive vs. negative) of thoughts – not just during the initial session, but even at a follow-up scanning session one week later. Other researchers, instead of directly contrasting one type of thought with another, have instead used various measures of intrinsic connectivity throughout the brain to attempt to predict either the content (Gorgolewski et al., 2014) or frequency (Kucyi and Davis, 2014; Wang et al., 2009) of spontaneous thought. Although all of these results remain tentative, the investigation of specific functional roles for the various brain networks and regions involved has undoubtedly begun in earnest.

#### *Temporal brain dynamics of spontaneous thought*

A putative discussion of the functional role(s) of each region and network would be incomplete without consideration of the specific temporal sequence whereby some regions or networks may contribute to the initial generation of thoughts, and others to their subsequent elaboration and evaluation (Andrews-Hanna et al., 2014b; Fox et al.,

under review). In addition to functional differences related to content and emotional valence, there are likely subtle but important differences in the timing with which these regions are recruited. For example, if spontaneous thoughts are predominantly generated in medial temporal lobe structures, as is strongly suggested by neurophysiological investigations in humans (e.g., Penfield and Perot, 1963; Vignal et al., 2007), these brain structures may come online first during a mind-wandering episode. If DMN regions reflect the initial affective and self-referential elaboration of the spontaneously generated thoughts, they may come online second. Finally, if regions of the frontoparietal control network reflect further subsequent elaboration, monitoring, or control of mind-wandering, they may be recruited last. These ideas remain speculative, however; further investigations of the temporal dynamics of mind-wandering are crucial for advancing our understanding of this phenomenon, and will ultimately require the combined use of modalities with higher temporal resolution than fMRI, such as electroencephalography (EEG) and magnetoencephalography (MEG). Such investigations would be most meaningfully and beneficially conducted within a framework that takes a balanced whole-brain approach to the contribution of different brain networks and regions, and does not restrict analyses to just a few DMN regions-of-interest. An appreciation of the highly varied neural basis revealed here (Table 2) should help us to begin to better model the momentary fluctuations and temporal trajectory of spontaneous streams of thought.

#### *Implications for clinical disorders of spontaneous thought*

Above, we discussed the idea that the DMN (especially medial temporal lobe structures) may contribute to the actual arising of memories and the stream of associated thoughts and imaginings. Higher executive areas may, on the other hand, subsequently evaluate, monitor, and guide the flow of these thoughts toward desirable and beneficial outcomes (Fox and Christoff, 2014; Fox et al., in press). Given the evidence that spontaneous thought involves a coupling of both DMN and frontoparietal control network regions in normal, healthy subjects, important implications arise for clinical disorders of spontaneous thought.

For instance, preferential (or over-) activation of DMN regions in isolation, with minimal or attenuated contributions from executive areas, might characterize dysfunctional forms of spontaneous thought, such as depressive rumination or the spontaneous and debilitating re-experiencing characteristic of post-traumatic stress disorder (Fox et al., under review). Conversely, an over-involvement of frontoparietal control areas might characterize conditions like obsessive-compulsive disorder, where fleeting thoughts and urges are acted upon repeatedly and with determination. If the distributed neural basis of spontaneous thought is not appreciated, and DMN regions are preferentially or exclusively investigated, links between such clinical disorders of spontaneous thought and non-DMN brain regions might be missed.

Two highly-cited studies of depression (Berman et al., 2011; Hamilton et al., 2011) exemplify this potential pitfall: both found links between DMN activity and frequency of depressive rumination, but neither explored potential links with non-DMN areas, particularly executive areas of the frontoparietal control network. Yet one of these groups' meta-analysis (Hamilton et al., 2012) has shown that several regions beyond the DMN show abnormal activity in depression, including the dorsolateral prefrontal cortex, insula, and dorsal anterior cingulate cortex (note that the two latter regions are consistently recruited by spontaneous thought – Table 2). In contrast, a recent study that did explore whole-brain relationships (Hach et al., 2014) found that depressed patients showed altered patterns of functional connectivity across numerous non-DMN areas, including the dorsal anterior cingulate cortex, as well as both the dorsolateral and the rostrolateral prefrontal cortex (all regions of the frontoparietal control network). Although the study investigated deliberate past- and future-oriented thought, and did not directly address 'spontaneous' forms of cognition, similar differences in neural recruitment could also characterize the



spontaneous thoughts of depressed patients. Such possibilities are clearly worthy of further investigation with an unbiased, whole-brain approach, not only for depression but also for other clinical conditions characterized by disorders of spontaneous thought.

#### Limitations of the meta-analysis

A number of limitations of the present meta-analytic methods, as well as of the primary research literature meta-analyzed, should be kept in mind. First, differences in baselines and other control conditions across studies are a source of heterogeneity. Collapsing across numerous different baselines or control conditions is a common, indeed inevitable, practice in any large meta-analysis of functional neuroimaging studies (Salimi-Khorshidi et al., 2009; Svoboda et al., 2006; Wager et al., 2007, 2009). Nonetheless, the heterogeneity attributable to the many different study designs concatenated here should be kept in mind.

Another concern is the wide variety of questionnaire and thought-sampling methods employed to determine the content and frequency of spontaneous thought. Although we would argue that subtle distinctions between different kinds of spontaneous thought are premature at this point, it should be acknowledged that various distinctive forms of spontaneous cognition might eventually be differentiable both phenomenologically, and potentially also at the neural level. The present meta-analysis, collapsing over these potentially distinguishable forms of spontaneous cognition, is meant merely as a preliminary effort at synthesis.

A third point is the fairly small sample size of studies included in the meta-analysis. Compared with processes like memory or attention, very little neuroimaging research has investigated spontaneous thought processes, and of this already small pool many studies have not employed agnostic, whole-brain analyses suitable for inclusion in a quantitative meta-analysis. As such, our meta-analytic results are based on a relatively small (if rigorous, and rigorously selected) set of studies, and should therefore be interpreted with caution. Future work may both extend and further clarify the results presented here.

#### Conclusions and future directions

The primary aim of this meta-analysis was to provide a quantitative overview of the brain regions and networks consistently recruited by mind-wandering and related forms of spontaneous thought. We found that a wide variety of regions throughout all lobes and both hemispheres appear to be reliably recruited. Most of these regions fall within boundaries of the default mode or frontoparietal control networks, suggesting that these networks, as presently conceptualized, form an important part of the neural signature accompanying, spontaneous thought of various kinds. A number of other reliably activated regions are not so easily subsumed under either of these networks (e.g., the insula, the somatosensory cortices, and the lingual gyrus), suggesting that future work may need to look beyond the typical delineation of these two networks' contributions in order to construct a full account of the neural recruitment associated with spontaneous thought.

The study of deliberate, goal-oriented, and externally-directed mental activity has been of paramount concern to cognitive neuroscientists over the past few decades (Dixon et al., 2014). Although this work has been, and remains, critical in advancing our understanding of brain function, its dominance has led to the relative neglect among researchers of spontaneous forms of cognition. To continue without redressing this imbalance in our scientific focus would be to ignore some of the most remarkable and complex processes of which our brains are capable. A deeper investigation of more fleeting, spontaneous forms of cognition will be necessary to move cognitive neuroscience toward a neurobiological understanding of higher mental functions like creativity and imagination. To paraphrase William James (James, 1985): No account of cognition in its totality can be final which leaves these other forms of consciousness quite disregarded.

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