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

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Abstract

■ Neuroimaging studies have revealed the recruitment of a range of neural networks during the resting state, which might reflect a variety of cognitive experiences and processes occurring in an individual's mind. In this study, we focused on the default mode network (DMN) and attentional networks and investigated their association with distinct mental states when participants are not performing an explicit task. To investigate the range of possible cognitive experiences more directly, this study proposes a novel method of resting-state fMRI experience sampling, informed by a phenomenological investigation of the fluctuation of mental states during the resting state. We hypothesized that DMN activity would increase as a function of internal mentation and that the activity of dorsal and ventral networks would indicate states of top–down versus bottom–up attention at rest. Results showed that dorsal attention network activity fluctuated as a function of subjective reports of attentional control, providing evidence that activity of this network reflects the perceived recruitment of controlled attentional processes during spontaneous cognition. Activity of the DMN increased when participants reported to be in a subjective state of internal mentation, but not when they reported to be in a state of perception. This study provides direct evidence for a link between fluctuations of resting-state neural activity and fluctuations in specific cognitive processes. ■

INTRODUCTION

While at rest, different brain networks are in operation (van de Ven, Formisano, Prvulovic, Roeder, & Linden, 2004; Biswal et al., 1995). Investigating cognitive processes operating in this context represents a challenge, as there is no direct way to observe mental experiences that happen during rest. Previous research has tried to link cognition to resting-state networks using postscan questionnaires (Diaz et al., 2013; Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010; Delamillieure, Doucet, & Mazoyer, 2010), but these might be biased because of selective memory and/or lack of awareness of certain experiences (Schooler et al., 2011). For example, people may have distorted memories of their previous experience and may sometimes not notice that they were mind wandering (Smallwood & Schooler, 2015). Furthermore, these questionnaires do not allow examination of the neural correlates of intraindividual variations in cognitive experiences. A method based on the online sampling of experience at various points in time during the resting state is required to relate fluctuations in cognitive experiences to cerebral activity, although online sampling may present other biases, which will be discussed below. Here we propose a novel method combining an empirical model of subjective experiences at rest, derived from a preliminary behavioral study, with experience sampling during resting-state fMRI. Our specific aim is to explore the cognitive functions of three brain networks that are commonly observed in resting-state fMRI, the default mode network (DMN), the dorsal attention network (DAN), and the ventral attention network (VAN).

One of the major networks observed during the resting state is the DMN (Buckner, Andrews-Hanna, & Schacter, 2008). This network encompasses the medial pFC, posterior cingulate cortex/precuneus, posterior inferior parietal lobes, lateral temporal cortex, and hippocampal formation. However, the specific function of this network during the resting state remains unclear. In task-based studies, the DMN has been associated with various forms of internal mentation, such as envisioning the future and autobiographical memory (D'Argembeau et al., 2014; Spreng & Grady, 2010; Buckner et al., 2008; Schacter, Addis, & Buckner, 2008). DMN activity has also been shown to increase when participants report mind wandering during various tasks (Fox, Nathan Spreng, Ellamil, Andrews-Hanna, & Christoff, 2015; Stawarczyk & D'Argembeau,

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2015; Andrews-Hanna, Smallwood, & Spreng, 2014; Stawarczyk, Majerus, Maquet, & D'Argembeau, 2011; Christoff, Gordon, Smallwood, Smith, & Schooler, 2009; McGuire, Paulesu, Frackowiak, & Frith, 1996). The similarity of DMN areas observed in resting-state, mind-wandering, and task-based studies involving internal mentation has led some authors to suggest that DMN activity at rest may be the result of various spontaneous thinking processes (Andrews-Hanna et al., 2014; Andrews-Hanna, 2012; Anticevic, Cole, & Murray, 2012). For example, the processes engaged when people are explicitly instructed to plan the future or think about the past may in part be similar to spontaneous thinking processes arising at rest.

In task-based studies, the DMN interacts with multiple networks (Fox et al., 2015), including attention-related networks (Spreng, Sepulcre, Turner, Stevens, & Schacter, 2013). These attentional networks consist, on the one hand, of a DAN encompassing the inferior parietal sulcus, FEFs, and the right middle frontal gyrus, which is involved in top–down, goal-directed attentional control (Majerus et al., 2012; Corbetta & Shulman, 2002). On the other hand, a VAN encompassing the TPJ and the OFC is involved in bottom–up, stimulus-driven attention, that is, the processing of unexpected, novel, and salient stimuli (Asplund, Todd, Snyder, & Marois, 2010; Marois, Leung, & Gore, 2000). At rest, the intervention of these networks has also been observed (Fox, Corbetta, Snyder, Vincent, & Raichle, 2006). More specifically, it has been shown that the DAN correlates negatively with the DMN (Boly et al., 2009; Fox et al., 2005) and interacts with a frontoparietal control network during the resting state, which has been proposed to play a role in the switching between internal and external cognition (Spreng et al., 2013; Smallwood, Brown, Baird, & Schooler, 2012; Spreng, Stevens, Chamberlain, Gilmore, & Schacter, 2010). In addition, the VAN has been shown to be segregated from the DAN during rest (Fox et al., 2006). These findings suggest that top–down and bottom–up attentional processes may both operate at rest. When not performing an explicit task, we can explore the environment with our senses in a controlled way (top–down attention) or our attention can suddenly be attracted by an unexpected stimulus (bottom–up attention). In the same vein, internal mentation can also be associated with top–down and bottom–up attention (Cabeza, Ciaramelli, & Moscovitch, 2012; Christoff, 2012; Chun, 2011; Gilbert, Simons, Frith, & Burgess, 2006): for example, a person can suddenly think about an event that pops up into his or her mind and then continue reflecting on this event in a more goal-driven and deliberate manner. We also tend to engage into top–down oriented thoughts in relation to our personal goals and current concerns (Gerlach, Spreng, Madore, & Schacter, 2014; Spreng & Levine, 2013).

To date, the functions of brain networks operating during the resting state (i.e., when no experimental task is proposed), such as the DMN, DAN, and VAN, have been mainly inferred from studies that have investigated the neural correlates of cognitive processes in particular task contexts. Although this approach is clearly valuable for formulating specific hypotheses on the role of particular networks in supporting different aspects of cognitive activity during the resting state, a complete understanding of neurocognitive mechanisms operating at rest requires that these hypotheses are tested more directly by examining the relationships between variations of neural activity and cognitive states under task-free conditions. To provide direct evidence for the cognitive dimensions associated with resting-state networks, a few studies have tried to link resting-state activity with cognitive processes using postscan questionnaires or experience sampling methods. Postscan questionnaires are retrospective questionnaires asking participants, at the end of an fMRI session, to review the conscious experiences they had during the acquisition of fMRI data (Gorgolewski et al., 2014; Doucet et al., 2012; Andrews-Hanna, Reidler, Huang, & Buckner, 2010). Although this method allows the collection of information about possible experiences without interfering with the resting state, retrospective assessments may sometimes be biased. First, participants may have selective memory for particular kinds of experiences, and other experiences may be remembered inaccurately. Second, participants may not notice (i.e., may not be "meta-aware") that they are having particular experiences (Schooler et al., 2011); hence, these experiences are unlikely to be reported in the postscan questionnaire. Finally, participants are often asked to rate their experiences over an extended scanning period (frequently a duration of approximately 7 min), and thus, the postscan reports cannot be associated with specific neural events and their fluctuation during the resting-state scanning period. Instead, the relationship between network activity and cognitive experience is examined at a global level by correlating interindividual variations in brain activity with interinvidual variations in cognitive experience. Thus, the observed correlations might in part be due to (unmeasured) individual differences (e.g., in personality traits) that impact cognitive experience.

Another method, experience sampling, allows the online evaluation of subjective experience using probes that are presented to participants at variable and unpredictable time points during the scanning period. This method invites participants to rate their cognitive experiences using categories or scales and has mainly been used to probe cognitive experiences occurring during completion of a task (i.e., mind wandering; Stawarczyk, Majerus, Maquet, et al., 2011; Christoff et al., 2009). Experience sampling thus assesses cognitive experiences more directly than retrospective reports, although it can also present some disadvantages. Experience sampling may suffer from a selection bias in that only participants who have reported sufficient observations can be analyzed. Furthermore, using experience sampling can create a disruption in the natural activity of the brain.

Thus, retrospective and experience sampling methods have both advantages and disadvantages and may be complementary, although they sometimes provide similar findings (i.e., a reduced P3b amplitude for task unrelated thoughts in both experience sampling (Smallwood, Beach, Schooler, & Handy, 2008) and retrospective methods (Barron, Riby, Greer, & Smallwood, 2011). To our knowledge, only one fMRI study has used experience sampling during the resting state, and it focused exclusively on the internal versus external orientation of subjective cognitive experiences (Vanhaudenhuyse et al., 2011). Internal awareness reports were linked to activity of an "intrinsic system" involving parts of the DMN, whereas external awareness was associated with a lateral frontoparietal "extrinsic system" closely corresponding to the DAN.

Although continuous experience sampling eliminates some postscan response biases, the types of experiences that are assessed are typically defined in an a priori manner. When using response categories defined by a priori assumptions about what resting-state cognition should be, experiences that do not fit into the classification system may be underreported or erroneously classified, leading to biased and potentially unrealistic experience sampling results. In this study, we present a novel experience sampling method aimed at providing a direct and unbiased investigation of the cognitive events and attentional states associated with fluctuations of the DMN, DAN, and VAN during the resting state. We focus on the DMN given that it is the main and most robust network observed during the resting state and given its likely association with internal thoughts happening during spontaneous cognition (Andrews-Hanna et al., 2014; Andrews-Hanna, 2012; Anticevic et al., 2012). Furthermore, we also focused on the VAN and DAN given their reported interactions with the DMN. It is likely that attentional states fluctuate during the resting state (Fox et al., 2005), and they may be associated with specific types of cognitive events; sudden, intrusive, stimulus-related thoughts may solicit stimulus-driven attention, whereas prolonged thoughts on a given problem may solicit task-related attention. We developed an experience sampling classification model informed by a preliminary behavioral study in which cognitive experiences at rest were collected in a fully unconstrained manner. The information gathered in this behavioral study was then used to construct an unbiased and realistic experience sampling model for use in a subsequent resting state–fMRI experiment.

STUDY 1—CONSTRUCTION OF THE EXPERIENCE SAMPLING CLASSIFICATION MODEL

To develop an unbiased and realistic model of possible cognitive experiences during the resting state, a preliminary behavioral study was conducted using two unconstrained experience sampling methods. The first method was a "think aloud" procedure (Ericsson & Simon, 1998), allowing a free, continuous expression of one's experiences at rest. Second, because the continuous monitoring of inner thoughts and speech output could potentially bias resting-state experience sampling, we also included a second condition based on discontinuous, cued experience sampling. Collected experiences were analyzed and classified using a "bottom–up" approach, and the resulting categories were then compared with dimensions identified in previous studies on mind wandering (Andrews-Hanna et al., 2014; Diaz et al., 2013; Ward & Wegner, 2013; Stawarczyk, Majerus, Maj, Van der Linden, & D'Argembeau, 2011; Delamillieure et al., 2010; Spreng & Grady, 2010) to finally generate a set of categories that covered all events reported by the participants.

Methods

Participants

Eighteen (11 women and 7 men) French-speaking adults from the university community, aged between 19 and 30 ($M = 25.28$, $SD = 3.04$) years, participated in the experiment. The participants were randomly assigned to one of the two data collection methods (continuous thinking aloud, cued experience sampling), resulting in nine participants per condition. None of the participants declared having a history of psychiatric or neurological disorders, and they gave their written informed consent to take part and to have the session audio recorded. The ethics committee of the University Hospital Center of Liège approved the study.

Materials and Procedure

Participants were invited to lie on their back on an air-inflated mattress and rest with eyes open during 30 min in a quiet room with dimmed lights. Instructions varied depending on the group the participants were assigned to. The first group reported the experiences they had during rest using the thinking aloud method (Ericsson & Simon, 1998), which consists of continuous verbal description of any experience occurring during the resting period. An audiorecorder was placed near the participant, but out of sight, to record the participants' verbal productions for later transcription. The second group of participants was asked to report their experiences at rest only when they heard a probe sound (tone of 1000 Hz presented at 70 dB for 1 sec). The participants of this group were instructed to describe the experience(s) they had during the 10 sec preceding the probe sound. This description had no specific time limit but was instructed to last for not longer than 10 sec. The probe sound occurred 40 times at fixed random time interval ranging from 30 to 60 sec. The investigator remained present in the room but out of sight of the participant. When participants did not want to disclose the content of an experience because it was too intimate, they were instructed to say "private." This prevented participants from inventing experiences to cover up intimate experiences they did not want to report. There were no other restrictions or indications for content reporting, and participants were reminded that there was no need to talk/to report when they did not experience any cognitive event. This further allowed us to code the absence of cognitive experience.

Analysis

Transcriptions of the audio recordings were analyzed and categorized according to several dimensions. Importantly, the categories were not defined in an a priori manner but relied on a bottom–up procedure based on the frequency of occurrence of reported experiences. For example, the experience "I was thinking about tomorrow" would be labeled as a thought, independent of the immediate environment, and pertaining to the future. When a label had a minimum of 20 observations and was reported by at least five participants, the label was given the status of a category. For example, the label "thought" was frequently observed and thus received the category status. The resulting categories we obtained from this method were then compared and associated, when applicable, with existing dimensions used in other studies on spontaneous cognition and mind wandering (Ward & Wegner, 2013; Stawarczyk, Majerus, Maj, et al., 2011; Vanhaudenhuyse et al., 2011; Andrews-Hanna, Reidler, Sepulcre, et al., 2010; Spreng & Grady, 2010). This procedure led to a comprehensive model of cognitive experiences at rest where every possible experience could be classified in four categories (see Figure 1). All cognitive experiences were then categorized in these four categories by the first author. To test interrater reliability, another independent judge also classified 100 randomly selected cognitive experiences obtained from both sampling methods. This judge received a training session to ensure the classification was clearly understood. Interrated agreement was assessed using Cohen's kappa score (Cohen, 1968). There was very good interrater agreement between the two judges ($K = 0.80$).

Results and Discussion

A total of 1525 experiences were collected. The amount of observations differed between the two groups, as the continuous thinking aloud condition inevitably led to more responses ($n = 980$) than the sampling method ($n = 545$). We analyzed and categorized each of the observations (see Figure 2). A large set of experiences that were observed in both conditions could be summarized under the label "thought" ($M = 79.86\%$, $SD = 17.41$), such as "I am thinking about the picture on the wall" or "I was thinking about a book I was reading last night…." A further subdivision among thoughts could be observed, separating thoughts related to the environment ($M = 30.21\%$, $SD = 13.64$; experience sampling: $M = 27.75\%$, $SD = 8.55$; thinking aloud: $M = 32.39\%$, $SD = 17.23$) from thoughts unrelated to the immediate environment ($M = 49.65\%$, $SD = 23.17$; experience sampling: $M = 54.50\%$, $SD = 19.29$; thinking aloud: $M = 45.34\%$, $SD = 26.53$). Another important type of experiences were

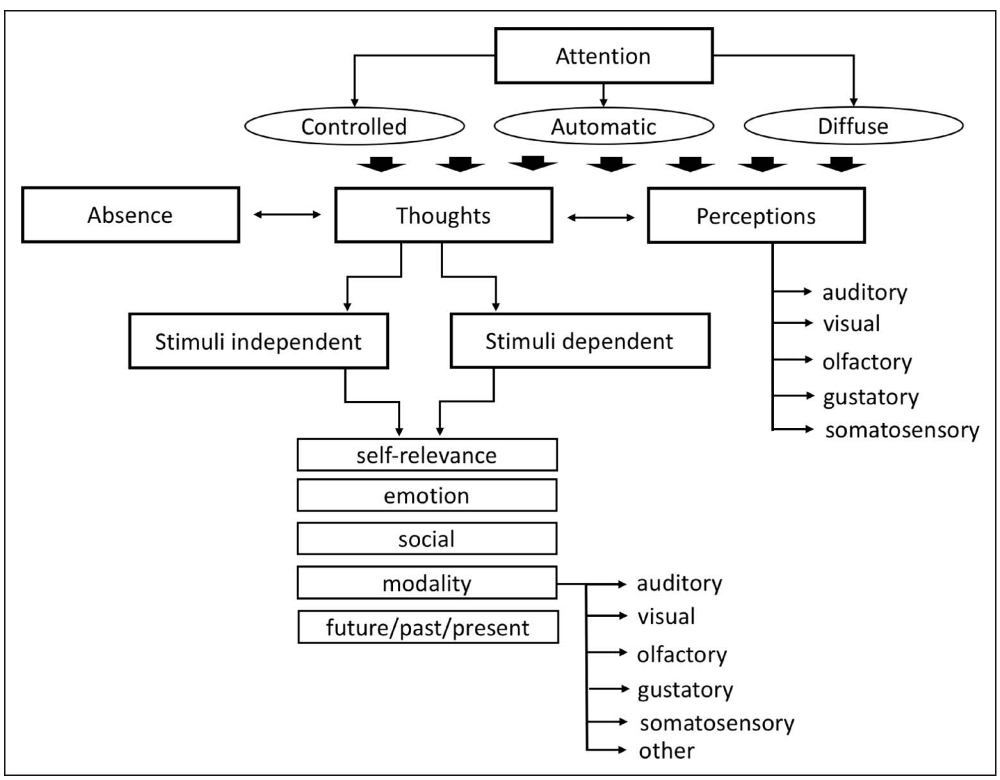

Figure 1. Cognitive experience model obtained from the unconstrained experience reports collected in Study 1. The category "modality" refers to the different representations of a thought. The "other" category of the thought's modality was selected when participants could not report how they represented their thoughts with one or more of the five senses (i.e., unsymbolized thinking; Hurlburt & Akhter, 2008).

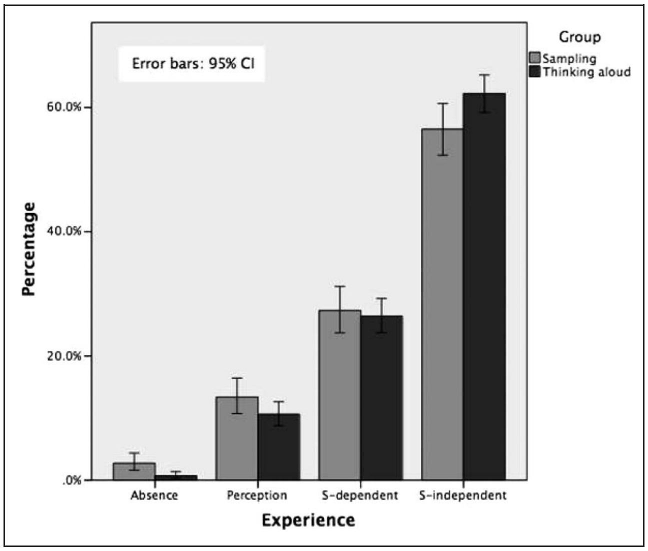

Figure 2. Frequency of different types of cognitive experiences in the two reporting conditions of Study 1.

categorized as "perceptions" (M = 17.68%, SD = 15.71; experience sampling: M = 14.53%, SD = 14.60; thinking aloud: M = 20.49%, SD = 17.23) for which participants reported sensorial acknowledgment of one or more stimuli while no thought was experienced. These perceptions were diverse and involved one or more of the five senses, for example: "I was simply looking at the picture, without thinking." A minor set of experiences could be labeled as "absence," where participants reported having "an empty mind" or "thinking about nothing" (M = 2.35%, SD = 3.3), although it should be acknowledged that this category might also reflect a lack of meta-awareness of thought content rather than an absence of content per se.

In summary, most experiences collected with both sampling methods were categorized as "thoughts," which is in line with previous studies investigating resting-state cognition (Diaz et al., 2013; Andrews-Hanna, 2012). For thought experiences, there were several possible subdivisions, for which the degree of awareness of the immediate environment was a dominant characteristic (i.e., stimulus-dependent vs. stimulus-independent thought). A category named "perceptions" was also distinguished, which consisted of experiences involving perceptions without thoughts. The observation of this category along with the two categories of thoughts (related or unrelated to the environment) is an important finding, as "perceptions" may have been confounded with environment-related thoughts in previous studies using a priori categories. These studies indeed simply distinguished between externally and internally oriented cognition (Demertzi et al., 2011; Vanhaudenhuyse et al., 2011) without considering possible mixed states, where internal mentation is simultaneously accompanied by some awareness of the external environment. Our results also showed the presence of a distinct category termed "absence," which was nevertheless relatively rare in this study.

The categories identified by our bottom–up characterization of resting-state cognition in this study led us to construct a summary model of mental experiences for use in the subsequent rs-fMRI study. This model, presented in Figure 1, distinguishes four broad categories of experiences: "absence," "perceptions," "stimulus-dependent thoughts," and "stimulus-independent thoughts." Other subdivisions of thoughts, based on temporality, self-relevance, emotional valence, or the sensory modality of perceptions were further observed, as shown in Figure 1. However, these subdivisions were not retained for the rs-fMRI study reported in Study 2 because of their relative low frequency of occurrence, preventing reliable estimation of associated neural activity.

Variations in attentional states were also observed in the resting-state cognitive events collected in this study, although their explicit description did not occur frequently, probably because participants may rarely be spontaneously aware of their attentional state. A number of participants mentioned experiencing a sudden shift of attention toward stimuli in the environment or toward an intrusive thought, which could broadly be attributed to bottom–up attentional processes. Some participants also described controlled, top–down attentional processes, such as when intentionally focusing their attention when solving a problem. Finally, a loose attentional state (Cohen & Dennett, 2011; De Brigard & Prinz, 2010) was occasionally reported where participants described having no particular goal in mind but were still broadly attentive to their experience (i.e., participants were not in a state of drowsiness but reported loose thoughts with no specific focus, such as fantasizing about the next vacation, but not planning it, jumping from one thought to another without a specific goal in mind). On the basis of these descriptions and given the focus of the present research on both default mode and attentional networks during resting-state cognition, the following attentional category labels were added to the model: bottom–up attention, top–down attention, and diffuse attention. The percentages of attentional states are not reported, as these would provide a biased representation of their actual frequency. Indeed, spontaneously reported information about these states was only available for a minority of cognitive events.

STUDY 2—NEURAL CORRELATES OF COGNITIVE EXPERIENCES AT REST

The summary model obtained from Study 1 was used to probe cognitive experiences and to investigate their association with DMN, DAN, and VAN fluctuations during an rs-fMRI paradigm. Given our focus on three well-defined neural networks, an ROI approach was used. Coordinates of main DMN structures reported repeatedly across studies on mind wandering and rs-fMRI studies were selected. Similarly, coordinates of important structures observed multiple times in studies on attention networks, separating top–down and bottom–up attention, were selected as ROIs. The ROI approach was further complemented by a whole-brain analysis. Participants reported their cognitive experiences and attentional states when probed during rest, using a decision tree classification system based on the cognitive experiences model developed in Study 1. The reported experiences were regressed to resting-state BOLD activity acquired before the probes.

Methods

Participants

Forty-five right-handed (32 women and 13 men), French-speaking, adult university students or graduates with at least a high school diploma, aged between 19 and 31 years (M = 24.45, SD = 3.05), participated in the experiment. None of the participants declared having a history of psychiatric or neurological disorder and gave their written informed consent to take part. There was no overlap in participants between Studies 1 and 2. The ethics committee of the University Hospital Center of Liège approved the study. Of the 45 participants, 3 interrupted the rs-fMRI session. Scans of the remaining participants were screened for motion artifacts and time series with motion exceeding 3 mm (translation) or 3° (rotation) were discarded. This was the case for two participants, resulting in a total of 40 analyzable participants.

Resting-state Paradigm

While at rest in the MRI scanner, probes were sent at randomly distributed times varying between 30 and 60 sec, inviting participants to report their experience. The delay between probes was specifically chosen to offer a sufficient amount of time for the participants to regain a resting state between two successive probes (as indicated by participants in the probe group in Study 1). The duration of the resting-state scan varied from 48 to 58 min, depending on the participants' answers and RT. Experience sampling probes consisted of the appearance of an exclamation mark during 1000 msec, inviting the participant to review and characterize the cognitive event(s) he or she just experienced. Several screens were presented in succession so the participant could communicate the nature of the experience based on the model developed in Study 1 (see Figure 1). The first screen offered four categories for a broad characterization of the cognitive experience. These four categories were "absence," "perception," "stimulus-dependent thought," and "stimulus-independent thought." An absence was defined as a mind blanking or empty state of mind. Perceptions represented the acknowledgment of a stimulus through one or more senses, without any internal thought. Thoughts were distinguished as stimulus-dependent thoughts, where an awareness of the immediate environment was present, or stimulus-independent thoughts, where there was no awareness of the immediate environment. The participants used two response boxes, one in each hand. Participants used an egocentric mental projection of their fingers onto the screen so that each finger corresponded to a specific category (see Figure 3). To probe the attentional state associated with each experience, a final display appeared, except when the participant had responded "absence" on the previous display. Participants indicated whether their attention was "controlled," "diffuse," "automatic" (bottom–up), or if they were in a somnolent state (referring to a state of drowsiness). We also considered the situation of a diffuse attention without a particular goal in mind, as this state had been identified

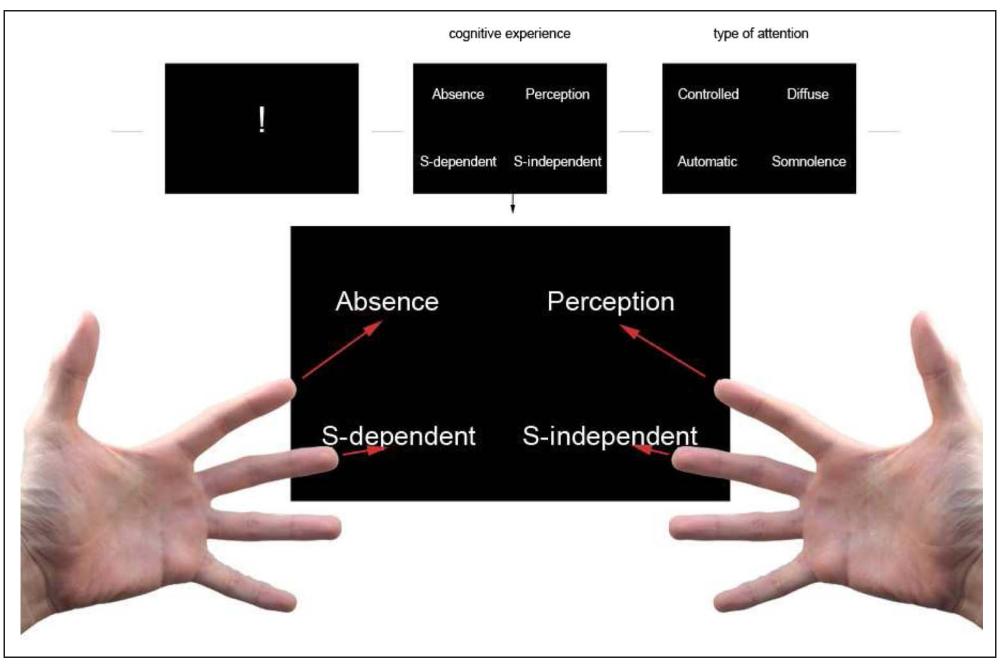

Figure 3. Response mechanism for the fMRI experience sampling probes. The figure illustrates the exclamation point appearing during rest, indicating the need to report the last perceived experience, followed by the two response screens. An example of response modality is given for the first response screen and shows the egocentric mental projection of the fingers onto the screen so that each finger corresponds to a specific category.

in Study 1. This state of "diffuse attention" implies that attention is not precisely oriented on a specific internal or external stimulus in an either top–down or bottom–up manner, but the participant is nevertheless in an alert state (Cohen & Dennett, 2011; De Brigard & Prinz, 2010). Because the diffuse attentional state is a state that can be considered to be somewhere between task-related and stimulus-related attention, we could expect weak recruitment of both DAN and VAN networks in this condition. We also included a somnolence category, as somnolence is likely to occur during extended periods of resting state (Fox & Christoff, 2014; Gruberger, Maron-Katz, Sharon, Hendler, & Ben-Simon, 2013). Both the cognitive experience and the attentional state decision displays had a maximum duration of 6000 msec each; a nonresponse was recorded if the participant did not respond within this 6000-msec period. A total of 50 probes were sent during the fMRI acquisition, presenting an adequate trade-off to ensure sufficient temporal separation of the probes while also avoiding discomfort of the participants which may have occurred for sessions lasting more than 1 hr.

Participants first took part in an information session preceding the fMRI session by at least 24 hr (ranging from 24 hr to 10 days). In this information session, an explanation of the experience sampling classification was given, and participants were introduced to the cognitive experience model and the different types of attention distinguished in this model. Every category was explained and illustrated with examples. This was followed by a training session outside the scanner, using laptop computer and an external numeric keypad to simulate the response box of the MRI scanner. Participants were instructed to rest, eyes open, in front of the computer. Upon appearance of an exclamation mark, the participant had to classify the cognitive experience they had just before the appearance of the exclamation mark using the same classification procedure as explained above, but responses were not registered. The probes were separated by randomly distributed numbers in an interval of 30–60 sec as for the fMRI session.

During the training session, participants were allowed to ask questions during the resting-state experience sampling procedure. They were also briefed on the importance of classifying the last perceived experience before the probe (rather than any previous experience they might have had since the last probe) to maximize the probability that the analyzed cerebral activity time window would match the reported experience. In the same way, it was made clear to participants that there were no a priori expectations from the researchers regarding reported experiences and there was no right or wrong answer. Participants were also instructed that it would be normal to have thoughts about the ongoing experiment and that these thoughts, if present, should not be discarded. This further encouraged authentic and realistic experience sampling reports. Participants were interrupted midway their training session and inquired about their last experience classification to discuss their classification. This gave the opportunity to the experimenter to ensure the classification procedure was understood correctly. They were also informed that, in doubt, they could communicate their experience at any given time to discuss its classification. A second, brief information session was held just before the fMRI scan to ensure participants had fully understood and could remember the classification procedure and had no further questions.

MRI

Experiments were carried out on a 3-T head-only scanner (Magnetom Allegra, Siemens Medical Solutions, Erlangen, Germany) operated with the standard transmit–receive quadrature head coil. fMRI data were acquired using a T2*-weighted gradient-echo EPI sequence with the following parameters: repetition time (TR) = 2040 msec, echo time (TE) = 30 msec, field of view (FOV) = 192 × 192 mm^2, 64 × 64 matrix, 34 axial slices with 3 mm thickness and 25% interslice gap to cover most of the brain. The three initial volumes were discarded to avoid T1 saturation effects. Field maps were generated from a double echo gradient-recalled sequence (TR = 517 msec, TE = 4.92 and 7.38 msec, FOV = 230 × 230 mm^2, 64 × 64 matrix, 34 transverse slices with 3 mm thickness and 25% gap, flip angle = 90°, bandwidth = 260 Hz/pixel) and used to correct echo-planar images for geometric distortion because of field inhomogeneities. A high-resolution T1-weighted MP-RAGE image was acquired for anatomical reference (TR = 1960 msec, TE = 4.4 msec, inversion time = 1100 msec, FOV = 230 × 173 mm, matrix size = 256 × 192 × 176, voxel size = 0.9 × 0.9 × 0.9 mm). In each session, between 1412 and 1692 functional volumes were acquired (M = 1574, SD = 59), depending on the resting period duration between probes and on RTs of the participant. Restraining the participant's head using a vacuum cushion minimized head movement. Stimuli were displayed on a screen positioned at the rear of the scanner, which the participant could comfortably see using a head coil mounted mirror.

Analysis

fMRI data were preprocessed and analyzed using SPM8 software (Wellcome Department of Imaging Neuroscience, www.fil.ion.ucl.ac.uk/spm) implemented in MATLAB (Mathworks, Inc., Sherbom, MA). EPI time series were corrected for slice-timing and for motion and distortion using "Realign and Unwarp" (Andersson, Hutton, Ashburner, Turner, & Friston, 2001) using the generated field map together with the FieldMap toolbox (Hutton et al., 2002) provided in SPM8. A mean realigned functional image was then calculated by averaging all the realigned and unwarped functional scans and the structural T1 image was coregistered to this mean functional image (rigid body transformation optimized to maximize the normalized mutual information between the two images). The mapping from subject to MNI space was estimated from the structural image with the “unified segmentation” approach (Ashburner & Friston, 2005). The warping parameters were then separately applied to the functional and structural images to produce normalized images of resolution $2 \times 2 \times 2$ mm^3 and $1 \times 1 \times 1$ mm^3, respectively. Finally, the warped functional images were spatially smoothed with a Gaussian kernel of 8 mm FWHM.

For each participant, brain responses were estimated at each voxel, using a general linear model with event-related regressors. Two models were designed. A first model assessed the activity related to cognitive experiences, whereas a second model assessed the activity related to attentional states. The creation of two separate design matrices was necessary, given that a number of onsets would be shared between some types of cognitive experiences and attentional states if they were included in the same design matrix. Brain activity of interest corresponded to the epoch-related regressor modeling the five scans (10.2 sec) before the probe. This temporal window was chosen following the result of the “think aloud” condition of Study 1, showing that experiences fluctuated relatively slowly, such that more than one experience rarely occurred in a 10-sec time window. Furthermore, this time frame is commonly used in mind-wandering studies (e.g., Henríquez, Chica, Billeke, & Bartolomeo, 2016). This activity was then associated with the categories that were reported by the participant. Because of this unconstrained event-related design, category distribution could not be controlled beforehand, leading to the risk of some categories not appearing sufficiently frequently to allow for reliable statistical analysis. This was the case for the categories “absence” (6.48%) and “automatic” (bottom–up) attention state (6.29%). Although there were too few observations to conduct meaningful analyses for these categories, they were nevertheless modeled as covariates of no interest. On the basis of previous research by Stawarczyk, Majerus, Maquet, et al. (2011), participants who did not meet the requirements of at least three observations for the remaining three categories, at either the level of cognitive experiences or attentional states, were withdrawn from the respective analyses. It is important to note that participants generally presented a much higher amount of events than this minimum, as shown in Table 1. This resulted in the inclusion of 30 participants of the 40 participants for the analysis of each model. Note that these 30 participants were not the same for both models. Both models shared 27 participants who had enough observations to qualify for both designs. Erroneous responses (i.e., nonresponses and invalid responses, such as when two buttons were pressed simultaneously), probe and classification displays, and button press responses were also modeled in the design matrices. The design matrices also included the realignment parameters as regressors to account for any residual movement-related effect. A high pass filter was implemented using a cutoff period of 128 sec. For both models, three linear contrasts corresponding to the three distinct categories of each model were created. The resulting set of voxel values constituted a map of t statistics. The contrast images were then entered in second-level analyses, corresponding to ANOVA random effects models and a series of linear contrasts of interest were created. In the SPM approach, unequal numbers of trials per condition are not considered to significantly distort the estimation of the BOLD response, given that the regressor for which the betas are estimated relies on the same number of data points irrespective of the number of trials per condition; an increase in the number of trials makes the estimation more precise but does not necessarily lead to higher beta values. However, to rule out any effect resulting from the unequal number of events per condition, we calculated a ratio of the amount of observations for each category per participant by dividing the number of observations for a category by the total number of observations across categories (see also Luft, Meeson, Welchman, & Kourtzi, 2015, for a similar approach). We then used this ratio as a covariate in the second-level design. allowing us to control, at the interindividual level, for potential differences in the precision of the parameter estimates associated with the unequal number of events. For the analysis of cognitive experiences, a voxel-wise one-way ANOVA with three levels (perception, stimulus-dependent thought, and stimulus-independent thought) was performed. A voxel-wise one-way ANOVA with three levels (somnolence, diffuse, and controlled) was also performed for the analysis of attentional states.

Table 1. Mean and Standard Deviation of Reported Cognitive Experiences and Attention Types in Study 2

	Mean	*SD*	*Min*	*Max*
Controlled attention	10.39	4.66	3	20
Diffuse attention	16.03	8.25	3	39
Somnolence	14.68	7.04	3	29
Stimulus dependent	16.19	6.62	6	29
Stimulus independent	18.34	7.68	6	35
Perception	11.10	5.62	3	26

Because our aim was to identify activity in the three resting-state networks of interest, coordinates most frequently reported for each network of interest were selected from the literature on the DMN and attention networks, and a mean was calculated in case of multiple coordinates for the same functional region (this was the case of the left posterior intraparietal sulcus [IPS]). Each coordinate of interest was used as a center for a 10-mm radius sphere. Eight coordinates were selected for the DMN and included the medial pFC (0, 52, −5), posterior cingulate cortex/precuneus (−8, −56, 26), left posterior inferior parietal lobe (−44, −76, 40), left retrospenial cortex (−14, 52, 8), left parahippocampal cortex (−28, −40, −12), left middle temporal lobe (−60, −24, −18), and the inferior temporal gyrus (−68, −36, −4; 51, −13, −25; Andrews-Hanna, Reidler, Sepulcre, et al., 2010; Spreng et al., 2010; Toro, Fox, & Paus, 2008; Gilbert et al., 2007; Mason et al., 2007). Six coordinates were selected for the DAN and included the IPS (24, −56, 46; −25, −57, 46), the FEF (27, −8, 50; −25, −8, 50), the right middle frontal gyrus (34, 45, 19), and the anterior inferior parietal lobe (−52, −49, 47), although this latter structure is included in the frontoparietal control network by some authors, its role in controlled attention for spontaneous cognition has been observed (Majerus et al., 2012; Stawarczyk, Majerus, Maquet, et al., 2011; Asplund et al., 2010; Walther, Goya-Maldonado, Stippich, Weisbrod, & Kaiser, 2010; Chiu & Yantis, 2009; Vincent, Kahn, Snyder, Raichle, & Buckner, 2008; Weissman, Roberts, Visscher, & Woldorff, 2006; Serences et al., 2005; Corbetta & Shulman, 2002). Lastly, four coordinates were selected for the VAN and included the TPJ (52, −52, 25; −52, −53, 23) and the OFC (34, 27, −10; −37, 27, −8; Majerus et al., 2012; Asplund et al., 2010; Todd, Fougnie, & Marois, 2005). Three masks of interest regrouping every spheres for each respective network were created (see Figure 4) using the Marsbar toolbox (marsbar.sourceforge.net). Reported results were corrected for multiple comparisons with cluster and voxel significance levels set at $p < .05$ (FWE corrected) for each of the three masks; the corrections for the multiple comparison ensured that false positives were not more likely for networks that included a larger number of ROIs as compared with networks with a smaller number of ROIs. The ROI analysis approach was complemented by a whole-brain analysis.

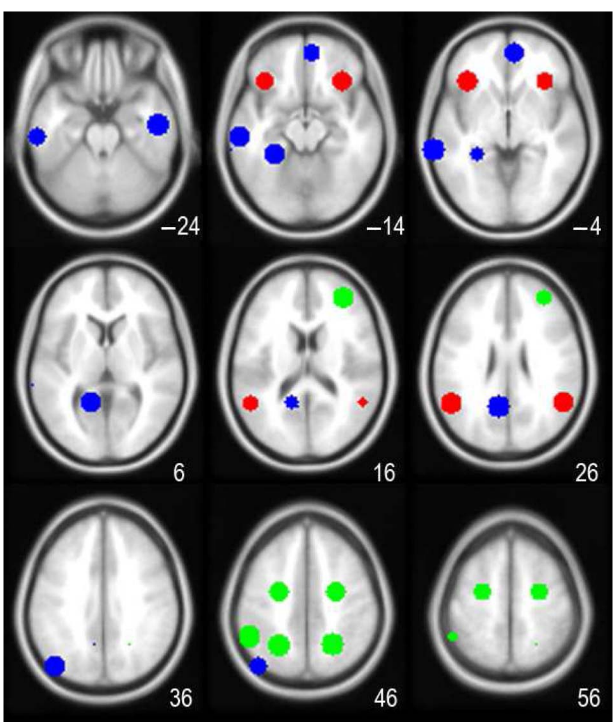

Figure 4. Graphical representation of ROIs on axial slices. The DMN is represented in blue, the DAN in green, and the VAN in red.

Results and Discussion

When probed during the rs-fMRI, the participants reported having an absence for merely 6% of the probes. This amount of absences is low, although slightly higher than the mean percentage observed in Study 1 according to the Wilcoxon signed-rank test, $Z = -.46, p < .001$. Other reported cognitive experiences consisted of 18% of perceptions, 31% of stimulus-dependent thoughts, and 42% of stimulus-independent thoughts. Compared with Study 1, there were no significant differences in percentages of perceptions, $Z = -.46$, $p = .645$, stimulus-dependent thoughts, $Z = -.92$, $p = .927$, and stimulus-independent thoughts, $Z = -1.04$, $p = .301$. Regarding attentional processes, participants reported being in a state of controlled attention for 18% of the probes, of diffuse attention for 37%, and of automatic attention for only 7%, and they reported being in somnolent state for 28% of probes. Both "absence" and "automatic attention" categories were not further analyzed because of their very low frequency of reporting. Relationships of reported frequency between cognitive experiences and attention are depicted in Table 2.

First, we examined the global effects in the ROIs associated with the three types of cognitive experiences (see Table 4 and Figure 5). The experience of perceptions was positively associated with activity in the right middle frontal gyrus and the OFC bilaterally, which were part of the DAN and VAN, respectively. No significant activity was observed in the DMN. Additional structures such as the superior temporal gyri, the supramarginal gyri, the left middle frontal gyrus, the right middle cingulate gyrus, the right putamen, and the left angular gyrus were observed in the whole-brain analysis. The experience of stimulus-independent thoughts was associated with increased activity in two regions of the DMN (the medial pFC and right inferior temporal gyrus) of the eight ROIs and one region of the VAN (OFC). Additional structures observed in the whole-brain analysis included the precental gyrus, the supplementary motor cortex, and the superior temporal gyrus of the right hemisphere. The experience of stimulus-dependent thoughts was associated with increased activity in five regions of the DMN (inferior temporal gyri, medial pFC, left middle temporal gyrus, and left parahippocampal cortex), as well as one region of the DAN (anterior inferior parietal lobe) and four regions of the VAN (TPJs and OFC bilaterally; see Table 4). The whole-brain analysis revealed additional activity in the precentral gyri, the angular gyri, the superior temporal gyri, the right supplementary motor cortex, the right inferior frontal gyrus, the right posterior insula, and the left caudate.

Table 2. Associated Frequencies (%) of Reported Attention Types and Cognitive Experiences

	Cognitive Experience			*Attentional State*		
	Stimulus Dependent	*Stimulus Independent*	*Perceptions*	*Controlled Attention*	*Diffuse Attention*	*Somnolence*
Associated Frequency						
Controlled attention	25	13	41			
Diffuse attention	36	45	22			
Somnolence	34	35	25			
Stimulus dependent				36.5	32	35
Stimulus independent				27	56	49
Perception				36.5	12	16

Absence and automatic attention have been omitted in this table.

To further investigate these results, we performed between-category contrasts. When contrasting "stimulus-dependent thought" and "stimulus-independent thought" categories to the "perception" category, we observed significant activity in three regions of the DMN encompassing the medial pFC, the left middle temporal gyrus, and the left inferior temporal gyri (see Table 5). The differential effect of the two thought categories relative to the perception category was also associated with increased activity in the right TPJ, part of the VAN network of interest, alongside the left postcentral gyrus and the right angular gyrus revealed by the whole-brain analysis. When the inverse contrast (perception vs. stimuli dependent and independent thoughts) was performed, no significant differential activity was observed. Finally, when directly contrasting the "stimulus-independent thought" and the "stimulus-dependent thought" categories, we did not find any differential activation, neither in the DMN or in other networks of interest.

Second, we examined global effects associated with each of the three attentional categories, using simple t contrasts (see Table 3 and Figure 6). Controlled attention was associated with activity in three regions of the DAN (left anterior inferior parietal lobule, right middle frontal gyrus, right FEF) of the six ROIs, whereas the whole-brain analysis revealed additional activity of the precentral gyrus. Interestingly, the controlled attention condition was also associated with increased activity in all the regions of the VAN (TPJ and OFC bilaterally). No ROI showed decreased activity for the controlled attention category. For the diffuse attention category, we observed a significant increase in the right OFC, a region associated with the VAN. The simple effect of somnolence was associated with increased activity in a subset of regions of the DMN (medial pFC, left parahippocampal cortex, and right middle temporal gyrus) and the VAN (left TPJ and right OFC). The whole-brain analysis revealed additional activity of the precentral, middle temporal, and the superior frontal gyri of the right hemisphere.

The specificity of the effects associated with the different attentional conditions was assessed by conducting several between-conditions t contrasts. When contrasting the "controlled attention" category to the "diffuse attention" and "somnolence" categories (see Table 5), we observed significant activity of the right middle frontal gyrus, which is part of the DAN. Additional activity in the right post- and precentral gyrus, the left posterior insula, and the left lingual gyrus was observed in the whole-brain analysis. No other direct contrast (other than mentioned in Table 5 and seen in Figure 7) led to significant activation differences. Similar results were obtained when analyzing data from the 27 participants who qualified for both the attentional and cognitive experience designs (see Methods section).

GENERAL DISCUSSION

This study aimed at investigating the cognitive dimensions associated with three resting-state networks (DMN, DAN, and VAN) using a novel experience sampling method. At the behavioral level, we observed that the majority of resting-state experiences consisted of thoughts and perceptions (while absences were rare) that could be accompanied by different attentional states. Neuroimaging data showed that reports of experiencing thoughts at rest were accompanied by an increase of activity in multiple regions of the DMN. We further observed a link between subjective experiences of attentional control during rest and increased activity of the DAN. These results demonstrate that particular cognitive experiences and attentional states are linked to fluctuations of brain activity during the resting state.

A first important finding is the observation of an association between fluctuations in subjectively experienced attentional states and neural activity in attentional networks during rest. More specifically, we found that the subjective experience of conscious attentional control during the resting state was associated with DAN activity. Until now, such

Table 3. Summary of the Main Effect of Reported Attention Types Revealed by the ROI Analysis

Region	*Laterality*	*Number of Voxels*	*x*	*y*	*z*	*Network*	*Z Score*
Controlled Attention							
Precentral gyrus	R	610	50	2	46	-	6.86
Anterior inferior parietal lobe	L	138	−56	−48	38	DAN	5.26
Middle frontal gyrus	R	250	30	44	24	DAN	4.93
			28	50	16		4.23
FEF	R	71	20	−14	52	DAN	4.18
			20	−4	54		3.96
Inferior temporal gyrus	R	146	54	−4	−22	DMN	4.51
			50	−8	−18		4.38
TPJ	L	332	−48	−58	16	VAN	5.01
			−56	−48	30		4.96
			−50	−46	26		3.64
TPJ	R	158	58	−46	26	VAN	4.95
			50	−44	22		4.34
			48	−52	16		4.29
			46	−46	20		3.87
OFC	R	217	34	28	−2	VAN	4.59
			38	24	−14		3.63
			34	18	−14		3.52
OFC	L	213	−30	26	−14	VAN	4.16
			−42	26	−14		3.82
			−38	20	−14		3.71
Diffuse Attention							
OFC	R	103	32	30	−2	VAN	4.63
Somnolence							
Precentral gyrus	R	425	50	2	46	-	4.70
Middle temporal gyrus	R	177	46	−44	8	-	4.64
Medial pFC		189	0	46	−10	DMN	4.48
			8	44	−10		4.09
			12	48	−14		3.93
			8	46	−14		3.93
Parahippocampal cortex	L	95	−28	−50	−12	DMN	4.13
			−24	−32	−16		3.75
Superior frontal gyrus	R	363	2	8	66	-	3.92
Middle temporal gyrus	R	85	56	−18	−18	DMN	3.78
TPJ	L	94	−48	−54	16	VAN	3.98
OFC	R	30	34	30	−2	VAN	3.57

All regions are significant at $p < .05$, corrected for multiple comparisons at cluster level (FWE-corrected). ROIs that are indicated in **bold** are significant at $p < .05$, corrected for multiple comparisons at peak and cluster level (FWE-corrected) over small VOI. R = right, L = left.

Table 4. Summary of the Main Effect of Reported Cognitive Experiences Revealed by the ROI Analysis

Region	*Laterality*	*Number of Voxels*	*x*	*y*	*z*	*Network*	*Z Score*
Perceptions							
Superior temporal gyrus	R	1994	54	4	6	–	5.56
Middle frontal gyrus	L	668	−30	38	24	–	5.02
Middle cingulate gyrus	R	1184	8	16	34	–	4.77
Putamen	R	401	18	14	−2	–	4.66
OFC	R	68	38	26	−2	VAN	4.56
Supramarginal gyrus	L	301	−64	−32	24	–	4.54
Supramarginal gyrus	R	838	66	−34	22	–	4.45
Superior temporal gyrus	L	297	−52	0	6	–	4.39
Angular gyrus	L	294	−42	−64	10	–	4.20
Middle frontal gyrus	R	75	34	48	24	DAN	3.78
OFC	L	36	30	24	−2	VAN	3.83
Stimulus-dependent Thoughts							
Precentral gyrus	R	659	50	4	48	–	6.97
Angular gyrus	L	159	−38	−64	12	–	5.96
Angular gyrus	R	346	40	−58	16	–	5.91
Supplementary motor cortex	R	146	6	8	62	–	5.37
Inferior temporal gyrus	R	210	46	−12	−18	DMN	5.48
Inferior frontal gyrus	R	44	50	18	10	–	5.36
Superior temporal gyrus	R	220	62	−40	18	–	5.26
Superior temporal gyrus	L	82	−42	14	−14	–	5.17
Precentral gyrus	L	57	−44	−4	48	–	5.11
Posterior insula	R	112	42	−10	−12	–	5.05
Medial pFC		257	14	50	−10	DMN	5.03
			0	48	−12		3.79
Caudate	L	33	−12	4	4	–	4.96
Middle temporal gyrus	L	147	−54	−18	−14	DMN	4.27
			−62	−20	−20		4.24
			−64	−24	−16		3.92
			−54	−30	−14		3.72
Parahippocampal cortex	L	161	−28	−50	−12	DMN	4.44
			−34	−40	−20		4.16
			−32	−34	−18		4.14
			−30	−48	−16		4.02
Inferior temporal gyrus	L	76	−64	−44	0	DMN	3.96
			−60	−40	−8		3.96
			−60	−36	−6		3.94
Anterior inferior parietal lobe	L	132	−54	−46	30	DAN	4.48
TPJ	R	249	58	−46	30	VAN	4.97
			44	−54	30		4.27

Table 4. (*continued*)

Region	*Laterality*	*Number of Voxels*	*x*	*y*	*z*	*Network*	*Z Score*
OFC	L	213	−40	18	−10	VAN	4.93
			−34	24	0		4.14
OFC	R	296	30	26	−2	VAN	4.48
			40	22	−4		4.25
			28	22	−14		3.82
			28	−32	−16		3.68
			26	28	−14		3.71
			40	22	−16		3.45
TPJ	L	224	−44	−50	18	VAN	4.28
			−52	−44	26		4.20
			−58	−54	18		3.86
			−58	−46	20		3.71
			−52	−46	30		3.45
Stimulus-independent Thoughts							
Precentral gyrus	R	160	50	4	48	–	6.12
Supplementary motor cortex	R	120	8	10	60	–	5.67
Medial pFC		258	0	48	−12	DMN	5.55
			10	50	−14		5.49
Superior temporal gyrus	R	61	52	−44	16	–	5.09
OFC	R	36	34	28	2	VAN	4.93
Inferior temporal gyrus	R	82	54	−10	−20	DMN	4.36

All regions are significant at $p < .05$, corrected for multiple comparisons at cluster level (FWE-corrected). ROIs that are indicated in **bold** are significant at $p < .05$, corrected for multiple comparisons at peak and cluster level (FWE corrected) over small VOI. R = right, L = left.

an association had been postulated based on the similarities observed between the attentional network activations observed in task-based studies and those identified by functional connectivity patterns in resting-state studies (Fox et al., 2006). Here we provide direct evidence for an association between fluctuations in attentional states and in attentional network neural activity during the resting state. Although the DAN activity observed in this study included parts of the left anterior inferior parietal lobule, activity in a more posterior part of the IPS, considered to be a central part of the DAN in task-based studies (Corbetta & Shulman, 2002), was not observed. Interestingly, IPS involvement was also absent in previous studies using whole-brain independent component analysis to identify attentional networks in resting-state networks (e.g., Allen et al., 2014; Schöpf et al., 2010). In task-based studies, IPS activity is observed mostly in situations of external attentional control, especially when switching between several external stimuli or when memorizing a list of external stimuli (Majerus et al., 2012; Shulman et al., 2009). Most studies on selective attention have neglected situations in which attention is focused on internally generated contents (Forster & Lavie, 2014); these are precisely one of the situations explored in this study. A further unexpected finding was the observation of activity in the VAN not only for the global effect of controlled attention but also for the global effects of other attentional categories. Given that the VAN is considered to reflect attentional processes associated with the detection of salient stimuli (Corbetta & Shulman, 2002), the pervasiveness of VAN activity in this study might reflect the frequent detection of salient cognitive events and the task-associated monitoring of the environment for appearance of the exclamation mark. However, these montoring and detection processes might not be conscious, given the very low reports of bottom–up, stimulus-driven attentional states. Furthermore, the right TPJ, a region of the VAN, unexpectedly showed an increase in activation for thoughts compared with perceptions. The TPJ has been associated with multimodal conceptual representations, which might be more involved in thoughts than perceptions, particularly for concepts associated with social information in the case of the right TPJ (Chow et al., 2013; Pannese & Hirsch, 2011; see Seghier, 2012, for a review). This is indeed in line with the results of Study 1, where a

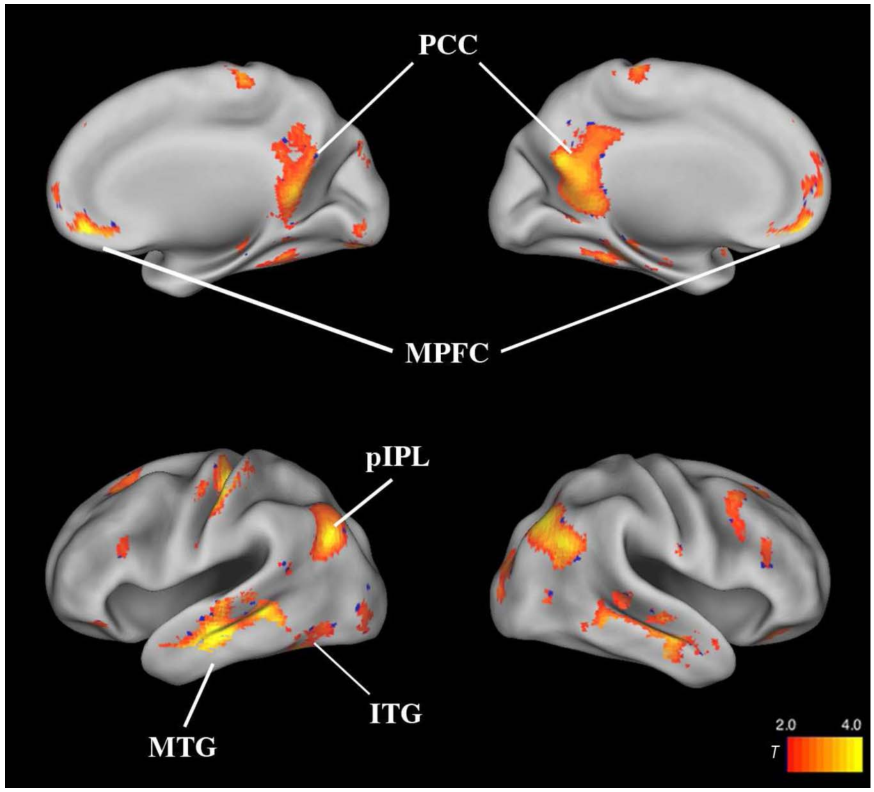

Figure 5. Brain activity involved in thoughts when contrasted to perceptions. Regions are displayed at $p < .001$, uncorrected with a minimum cluster size of 20 voxels, with the color bar representing the T score. PCC = posterior cingulate cortex, MPFC = medial pFC, pIPL = posterior inferior parietal lobe, ITG = inferior temporal gyrus, MTG = middle temporal lobe.

majority of thought-related reports involved social contents.

Another major finding of this study is the observation of a direct association between activity in regions of the DMN (such as the medial pFC, the left inferior temporal gyrus, and left middle temporal gyrus) and the subjective report of stimulus-dependent and stimulus-independent thoughts. In task-based studies, these regions have been consistently associated with self-generated thoughts (Andrews-Hanna et al., 2014; Andrews-Hanna, Reidler, Huang, et al., 2010; Buckner et al., 2008). Interestingly, in this study, the DMN showed activity in association with self-generated thoughts in general, regardless of the presence or absence of their link to the external environment. These findings are in line with recent task-based studies showing activation of the medial pFC when processing external stimuli in a task that also activates a representation in memory, in opposition to stimuli that only depend on immediate perceptual input (comparable to the "perception" category of this study; Konishi, McLaren, Engen, & Smallwood, 2015; Spreng et al., 2014).

In the Introduction, we had suggested that intrusive thoughts, which involve DMN activity, could be associated with increased stimulus-driven attention, whereas prolonged thoughts, also involving DMN activity, may be associated with increased task-related attention, suggesting that the DMN interacts with attentional networks during cognitive processing. This suggestion was partially supported by our findings, with the occurrence of stimulus-dependent thoughts being associated with activity in all four regions of the VAN whereas the stimulus-independent condition was associated with activity only in a small part of the VAN. However, no differential activation in the VAN or the DAN was observed when directly contrasting the stimulus-dependent and stimulus-independent thought conditions, so possible interactions between attentional states and cognitive events associated with DMN activity need to be further explored in future studies.

The whole-brain analysis identified additional brain regions that showed fluctuations as a function of cognitive experiences. Pre- and postcentral gyri were the most consistently activated additional brain regions and, in the resting state literature, have been linked to the somatomotor resting state network (Allen et al., 2014; Damoiseaux et al., 2006). These activations appeared most strongly for contrasts involving the controlled attention condition. The pre- and postcentral gyri have been observed in studies on attention and working memory (Li, Christ, & Cowan, 2014; Guida, Gobet, Tardieu, & Nicolas, 2012; Corbetta & Shulman, 2002). Furthermore, the right precentral gyrus has been linked to an extension of the FEF of the DAN (Fox et al., 2005). These regions might thus play a role in top–down attention.

More generally, this study directly demonstrates the role of the DMN in thought generation and processing during the resting state. Spreng and Grady (2010) stressed the need for novel techniques to understand DMN activity and its relation to cognition. The paradigm developed in

Table 5. Summary of Contrasts of Reported Attention Types and Cognitive Experiences Revealed by the Whole-brain and ROI Analysis

Region	*Laterality*	*Number of Voxels*	*x*	*y*	*z*	*Network*	*Z-score*
Controlled Attention versus Other Types of Attention							
Postcentral gyrus	R	714	50	−16	24	–	4.68
Posterior insula	L	443	−40	−12	−8	–	4.34
	R	843	32	22	0	–	4.31
Precentral gyrus	R	450	20	−16	58	–	4.20
Middle frontal gyrus	R	66	28	44	24	DAN	3.89
Lingual gyrus	L	430	−10	−74	−6	–	3.83
Controlled Attention versus Diffuse Attention							
Posterior insula	L	693	−38	−14	−6	–	4.70
Middle cingulate gyrus	R	1156	8	−22	44	–	4.63
Postcentral gyrus	R	876	50	−16	24	–	4.57
Posterior insula	R	522	52	24	32	–	4.50
Anterior inferior parietal lobe	L	51	−58	−50	40	DAN	3.73
			−54	−50	38		3.61
Controlled Attention versus Somnolence							
Lingual gyrus	L	339	−12	−82	4	–	3.90
Middle frontal gyrus	R	89	32	46	26	DAN	3.89
Thoughts versus Perceptions							
Inferior temporal gyrus	L	93	−62	−38	0	DMN	4.53
Postcentral gyrus	L	345	−50	−18	52	–	4.49
Medial pFC		117	2	50	−12	DMN	4.37
			0	58	−12		4.13
Angular gyrus	R	368	38	−54	20	–	4.16
Middle temporal gyrus	L	93	−58	−16	−14	DMN	3.91
			−64	−22	−16		3.72
			−62	−20	−20		3.71
TPJ	R	53	54	−60	30	VAN	3.68
Stimulus-dependent versus Perceptions							
Angular gyrus	L	617	38	−54	20	–	4.49
Postcentral gyrus	L	385	−50	−18	52	–	3.85
Inferior temporal gyrus	L	119	−62	−38	0	DMN	4.35
Middle temporal gyrus	L	292	−54	−42	−12	DMN	4.15
			−64	−42	0		4.00

Table 5. (*continued*)

Region	*Laterality*	*Number of Voxels*	*x*	*y*	*z*	*Network*	*Z-score*
Middle temporal gyrus	L	99	−62	−20	−20	DMN	4.00
			−64	−22	−16		3.95
			−58	−16	−14		3.88
			−54	−16	−18		3.81
Stimulus-independent versus Perceptions							
Medial pFC		96	2	50	−12	DMN	4.30
			0	50	−12		4.12
Posterior cingulate cortex/precuneus		123	−10	−52	18	DMN	3.79

All regions are significant at $p < .05$, corrected for multiple comparisons at cluster level (FWE corrected). ROIs that are indicated in **bold** are significant at $p < .05$, corrected for multiple comparisons at peak and cluster level (FWE corrected) over small VOI. R = right, L = left.

this study is a step in that direction. However, some limitations of this study need to be mentioned. First, only a small set of the different cognitive experiences occurring during rest could be sampled in the present fMRI study, because of the fact that many experiences occurred at a too low frequency. Second, our rs-fMRI study used global categories that can be subdivided into smaller categories, and hence, it only gives a relatively coarse account of the cognitive richness of experiences occurring during the resting state and their associated neural substrates. Also, the relatively small amount of probes provides a limited amount of observations to construct the general linear model for fMRI analysis. A greater number of observations would increase statistical power. To achieve this, a longer experience-sampling session would be necessary, but it should be noted that increasing the amount of time spent in the scanner would likely increase discomfort and might also increase drowsiness. Finally, even though the online experience sampling method used in this study was likely to put the participants in a state of conscious monitoring of their cognitive experiences in comparison with methods using postscan questionnaires, we cannot exclude the possibility that participants were not aware of some of the cognitive experiences they had. However, most of these

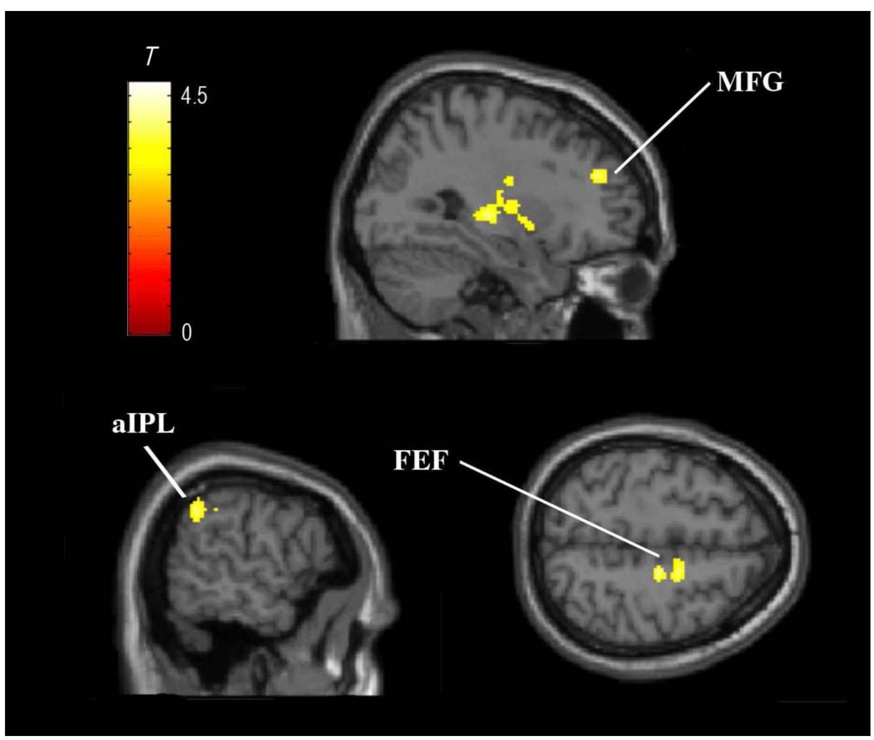

Figure 6. Brain activity involved in controlled attention when contrasted to other attentional states. Regions are displayed at $p < .001$, uncorrected with a minimum cluster size of 20 voxels, with the color bar representing the T score. MFG = middle frontal gyrus, aIPL = anterior inferior parietal lobe.

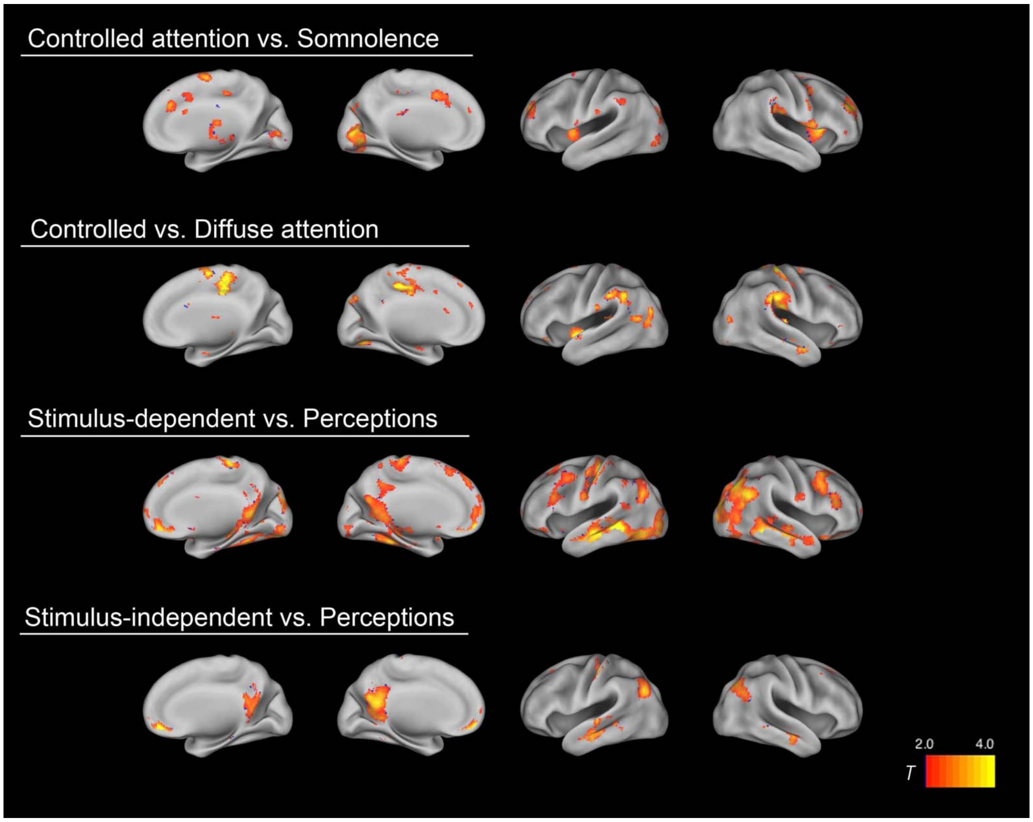

Figure 7. Brain activity associated with between-condition *t* contrasts. Regions are displayed at $p < .001$, uncorrected with a minimum cluster size of 20 voxels, with the color bar representing the *T* score.

"unconscious" events would likely have been classified as reflecting an "absence." As already noted, reports of "absences" were relatively rare.

In summary, this study provides direct evidence that fluctuations in the activity of the DMN and attentional networks are related to specific cognitive experiences and attentional states at rest. More specifically, activity in regions of the DMN were related to the occurrence of internal thoughts, independent of their integration with the external environment, and activity in the DAN increased when attentional control was reported. Future research using a similar approach could shed light on the functions of other resting-state networks and, ultimately, on the functional dynamics and interactions of the resting brain.

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