

# The Phenomenal Contents and Neural Correlates of Spontaneous Thoughts across Wakefulness, NREM Sleep, and REM Sleep

Lampros Perogamvros<sup>1,2,3</sup>, Benjamin Baird<sup>1</sup>, Mitja Seibold<sup>4</sup>, Brady Riedner<sup>1</sup>, Melanie Boly<sup>1</sup>, and Giulio Tononi<sup>1</sup>

## Abstract

Thoughts occur during wake as well as during dreaming sleep. Using experience sampling combined with high-density EEG, we investigated the phenomenal qualities and neural correlates of spontaneously occurring thoughts across wakefulness, non-rapid eye movement (NREM) sleep, and REM sleep. Across all states, thoughts were associated with activation of a region of the midcingulate cortex. Thoughts during wakefulness additionally involved a medial prefrontal region, which

was associated with metacognitive thoughts during wake. Phenomenologically, waking thoughts had more metacognitive content than thoughts during both NREM and REM sleep, whereas thoughts during REM sleep had a more social content. Together, these results point to a core neural substrate for thoughts, regardless of behavioral state, within the midcingulate cortex, and suggest that medial prefrontal regions may contribute to metacognitive content in waking thoughts. ■

## INTRODUCTION

Thoughts are a central feature of waking life, whether they are directed toward accomplishing a particular task or whether they occur spontaneously. Experience sampling experiments have found that spontaneous thoughts during wakefulness occur often, with a frequency of occurrence of as high as 30–50% (Killingsworth & Gilbert, 2010; Kane et al., 2007). Although the underlying neural mechanisms of thought are not well understood, neuroimaging studies using fMRI and PET have found neural correlates of spontaneous thought in a network of areas including the default mode network (DMN) and the executive control network (reviewed in Fox, Spreng, Ellamil, Andrews-Hanna, & Christoff, 2015).

Thoughts occur not only in wakefulness but also during sleep, often in combination with perceptual experiences, in the form of dreams. Although there may be differences between thoughts that occur during wakefulness and dreaming, including reduced metacognitive insight (Nir & Tononi, 2010), several studies have suggested that the overall phenomenology of consciousness is remarkably similar across sleep and wake (Kahan & LaBerge, 2011; Kahan, LaBerge, Levitan, & Zimbardo, 1997). For example, both states draw on proximal and distal memory sources (Fox, Nijeboer, Solomonova,

Domhoff, & Christoff, 2013; Nielsen & Stenstrom, 2005) and frequently involve thoughts regarding daily personal concerns (Andrews-Hanna, Reidler, Huang, & Buckner, 2010; Smallwood, Fitzgerald, Miles, & Phillips, 2009; Cartwright, Agargun, Kirkby, & Friedman, 2006; Nielsen & Stenstrom, 2005). The continuity of cognition across wake and sleep has led some researchers to suggest that there may be a common neurophysiological substrate of thought across waking and dreaming (Domhoff & Fox, 2015; Fox et al., 2013; Wamsley, 2013; Llinas & Pare, 1991).

Physiologically, an important distinguishing feature of sleep and wakefulness is that during sleep individuals are largely disconnected from the environment, and as a consequence, external sensory stimuli have little influence on the content of experience. However, it is interesting to note that a similar reduction in cortical responses to the external environment, as measured by an attenuation of sensory-evoked responses or reduced phase-locking to perceptual stimuli, has also been observed during mind-wandering (Baird, Smallwood, Lutz, & Schooler, 2014; Braboszcz & Delorme, 2011; Kam et al., 2011; Smallwood, Beach, Schooler, & Handy, 2008). Another distinguishing feature of sleep and wake thought is that, outside of rare instances of lucidity (LaBerge, Nagel, Dement, & Zarcone, 1981), dreaming participants have little or no deliberate cognitive control over the content of thought, which is not always the case during wake, even during mind-wandering (Christoff, Irving, Fox, Spreng, & Andrews-Hanna, 2016).

<sup>1</sup>University of Wisconsin-Madison, <sup>2</sup>Geneva University Hospitals,

<sup>3</sup>University of Geneva, <sup>4</sup>University of Amsterdam

To the best of our knowledge, no study to date has simultaneously investigated the phenomenal content and neural correlates of thought across wakefulness and sleep states. Although thoughts across wakefulness and sleep exhibit some continuity of content, they occur within brain states having very different neurophysiological and neuromodulatory profiles (Jones, 2005). It is therefore an open question whether there is a core neural substrate to thought across wakefulness and sleep. In this study, we aimed at examining the neural substrate and phenomenology of thought across quiet resting wakefulness, non-rapid eye movements (NREM) sleep, and REM sleep. Throughout all three states, brain activity was continuously recorded using high-density EEG (hd-EEG), and participants were intermittently prompted to report the contents of consciousness using thought sampling (wake; Smallwood & Schooler, 2006; Klinger & Cox, 1987) or serial awakenings (sleep; Siclari, Larocque, Postle, & Tononi, 2013).

## METHODS

### Study Participants

Sixty-nine healthy individuals (23 men, age =  $43.14 \pm 12.94$  years, 25–64 [mean  $\pm$  SD, range]) participated in the experiment. All participants had no history of neurological disorder. Signed informed consent was obtained from all participants before the experiment, and ethical approval for the study was obtained from the University of Wisconsin-Madison institutional review board.

### Procedures

#### *Spontaneous Thought Task during Wakefulness*

Participants were asked to rest their eyes on a fixation cross in the center of a computer screen for approximately 30 min. At pseudorandom intervals (approximately once per minute), participants were prompted with a sound and were instructed to report the last thing going through their mind (any images, thoughts, feelings, emotions) just before the sound. Following this open-ended report, they were asked to rate the content of their experience on a thought scale (thinking or reasoning) ranging from 0 (*no thoughts*) to 5 (*maximally thought-like*). Participants were also asked to rate on a scale from 0 (*absence*) to 5 (*maximum*) the degree of the cognitive effort in their experience (e.g., trying to think through a problem or accomplish a particular task). Examples of what we operationally defined as “thoughts” were given to participants before testing, which included, for example, invariant concepts, ideas, memories, and decisions.

#### *Serial Awakenings during Sleep*

Experience sampling during sleep was accomplished using the “serial awakening” method, which is described

in detail elsewhere (Siclari et al., 2013). In brief, participants were awakened throughout the night while sleeping in the sleep laboratory and were asked to report whether, just before the awakening, they were dreaming of anything. If participants reported having a dream experience, they were asked to describe its most recent content (“the last thing going through your mind before the alarm sound”) and then underwent a structured interview via intercom. Specifically, participants were again asked to rate their experience on a “thought” scale ranging from 0 (*no thoughts*) to 5 (*maximally thought-like*), as well as to rate their experience on several other dimensions, including their level of voluntary control over the content of the experience, the richness and complexity of the experience, the cognitive effort put in the experience, the duration and capacity to recall the experience. Awakenings were performed at intervals of at least 20 min, in N2 or REM sleep, using a computerized alarm sound. Participants were required to have been asleep for a minimum of 10 min and must have been in a stable sleep stage for a minimum of 5 min for an awakening to occur.

#### *Content Analysis*

To phenomenologically compare thoughts in wakefulness with those in NREM and REM sleep, reports that were scored by participants between 3 and 5 on the thought scale (see Procedures) were considered high-thought reports. High-thought reports were additionally classified by two independent raters in eight categories on a scale from 0 (*absence of the category*) to 5 (*maximum in this category*): (1) metacognition, (2) social focus, (3) positive emotions, (4) negative emotions, (5) past focus, (6) present focus, (7) future focus, and (8) bizarreness. The definitions of these categories are given in Table A1. In total, 264 dream reports (157 in N2 and 107 in REM sleep) and 869 waking reports were scored. Of those, 141 dream reports (71 in N2 and 70 in REM sleep) and 652 waking reports were high-thought trials. The average interrater reliability was 79% for waking data and 82% for dream data, representing an acceptable interrater reliability for both states (Hallgren, 2012; Schredl, 2010b). Because of the non-normal distribution of the data (Shapiro–Wilk normality test  $p < .05$ ; Table A2), Wilcoxon signed-rank tests were performed between averaged scores for each participant on each of the categories for high-thought trials in wakefulness versus N2 sleep, wakefulness versus REM sleep, and N2 versus REM sleep. Wilcoxon signed-rank tests were also performed for the “cognitive effort” category, which was another dimension in which participants self-evaluated in both wakefulness and sleep. Finally, scores in certain categories in which participants self-evaluated during sleep (voluntary control over the content of the experience, richness and complexity of the experience, recall of the experience, duration of the experience) in the N2 and REM reports were averaged

for each of the 69 participants, and Wilcoxon signed-rank tests were performed between N2 and REM sleep scores for each participant. Multiple comparisons were performed for the 31 independent tests using the Holm–Bonferroni method (Holm, 1979), and  $p$  values were adjusted at a  $p < .05$  significance level. To study the relation between the cognitive effort and thought variables across states, a linear mixed model was used to account for repeated measures with varied numbers of repeated observations within participants. Mixed model construction and mixed model bootstrapping were performed with the lme4 package (Bates, Maechler, Bolker, & Walker, 2015) in the R environment (R Development Core Team, 2006).

### Participants Selected for the hd-EEG Analysis

From the initial group of 69 participants, 13 individuals were selected for the EEG analysis of wake and N2 stages (six men, age =  $40.6 \pm 11.9$  years, 25–59 [mean  $\pm$  SD, range]). We selected participants from this data set who had trials with both low level of thoughts (0–2) and trials with high level of thoughts (3–5) in both wakefulness and N2 sleep. Ten different participants were included in the EEG analysis of REM sleep (6 men, age =  $37.7 \pm 11.5$  years, 27–64 [mean  $\pm$  SD, range]) based on the same criterion.

### EEG Recordings

Recordings were made at the University of Wisconsin–Madison Center for Sleep Medicine and Sleep Research (WisconsinSleep) using a 256-channel hd-EEG system (Electrical Geodesics, Inc., Eugene, OR) combined with Alice Sleepware (Philips Respironics, Murrysville, PA). Additional polysomnography channels were used to record and monitor eye movements and submental electromyography during sleep. Sleep scoring was performed over 30-sec epochs according to standard criteria (Iber, Ancoli-Israel, Chesson, & Quan, 2007).

### EEG Preprocessing

The EEG signal was sampled at 500 Hz and band-pass filtered offline between 1 and 50 Hz. The 1-Hz high-pass threshold was used due to sweating artifacts in some participants, which caused intermittent high-amplitude ( $>300$   $\mu$ V) slow frequency oscillatory activity around 0.3 Hz. Noisy channels and epochs containing artifactual activity were visually identified and removed. Ocular, muscular, and electrocardiograph artifacts were removed with independent component analysis using EEGLAB routines (Delorme & Makeig, 2004). Only independent component analysis components with specific activity patterns and component maps characteristic of artifactual activity were removed (Jung et al., 2000). Previously removed noisy channels were interpolated using spherical

splines (EEGLAB). Finally, EEG data were referenced to the average of all electrodes.

### EEG Signal Analysis

#### Source Localization

The cleaned, filtered, and average-referenced EEG signal corresponding to the 20 sec before the alarm sound in both wakefulness and sleep was extracted and analysed at the source level. Source modeling was performed using the GeoSource software (Electrical Geodesics, Inc.). A four-shell head model based on the Montreal Neurological Institute atlas and a standard coregistered set of electrode positions were used to construct the forward model. The source space was restricted to 2447 dipoles in three dimensions that were distributed over  $7 \times 7 \times 7$  mm cortical voxels. The inverse matrix was computed using the standardized low-resolution brain electromagnetic tomography constraint. A Tikhonov regularization procedure ( $\lambda = 10^{-1}$ ) was applied to account for the variability in the signal-to-noise ratio (Pascual-Marqui, 2002). We computed spectral power density using the Welch's modified periodogram method (implemented with the *pwelch* function in MATLAB; The MathWorks, Inc., Natick, MA) in 2-sec Hamming windows (8 segments, 50% overlap) to decompose the source signals into frequency bands of interest before taking the norm across dimension to produce a single power value for each dipole.

### Statistical Analysis

Statistical analysis was carried out in MATLAB. To compare brain activity between low-thought and high-thought trials, source-space power was averaged within standard frequency bands (Delta: 1–4 Hz, Theta: 4–8 Hz, Alpha: 8–12 Hz, Sigma: 12–18 Hz, Beta: 18–25 Hz, Gamma: 25–50 Hz). We then averaged the power values within low-thought and high-thought trials for each participant and for each frequency band and stage (wakefulness, N2 sleep, and REM sleep) separately. Group level analyses used paired two-sample  $t$  tests (two-tailed) between the low-thought and high-thought conditions in wake, NREM sleep, and REM sleep, tests that were performed separately for each frequency band and thresholded at corrected  $p < .05$  using nonparametric threshold-free cluster enhancement (TFCE; weighing parameters  $E = 0.5$  and  $H = 2$ ; Mensen & Khatami, 2013; Smith & Nichols, 2009).

## RESULTS

### Phenomenological Results

We examined potential differences and similarities in the phenomenology of thoughts across wake and sleep states. High-thought trials were found to be more

frequent in wake (75%), compared with N2 sleep (45%) and REM sleep (65%). Mean values across the phenomenological categories are shown in Table A3. Higher scores on the thought scale were significantly associated with reported higher cognitive effort across all three states ( $\beta = 0.36, p < .0001$ ) and in each state separately (wake:  $\beta = 0.37, p < .0001$ ; N2:  $\beta = 0.42, p < .0001$ ; REM:  $\beta = 0.41, p < .0001$ ).

#### Wakefulness versus N2 Sleep

Thoughts in wakefulness were rated significantly higher than thoughts occurring in N2 sleep in metacognition ( $p = .01, Z = 3.51$ ; Table 1). No other significant differences were found in the comparisons at a Holm–Bonferroni corrected significance level.

#### Wakefulness versus REM Sleep

Thoughts in wakefulness were significantly higher than thoughts occurring in REM sleep in metacognition ( $p = .008, Z = 3.58$ ). REM thoughts were significantly higher in social focus ( $p = .001, Z = -4.06$ ) and in positive emotions ( $p = .002, Z = -3.92$ ; Table 1). Thoughts in REM sleep were also rated more “effortful” than thoughts in wakefulness ( $p = .02, Z = -3.29$ ). No other significant differences were found in the comparisons at a Holm–Bonferroni corrected significance level.

#### N2 Sleep versus REM Sleep

REM thoughts contained significantly higher cognitive effort ( $p = .04, Z = -3.05$ ) than N2 thoughts. REM thoughts also lasted longer ( $p = .001, Z = -4.25$ ), were more easily recalled ( $p = .0001, Z = -4.48$ ), and were more rich and complex ( $p = .0001, Z = -4.84$ ), than N2 thoughts. No other significant differences were found in the comparisons at a Holm–Bonferroni corrected significance level.

#### Topographical Results

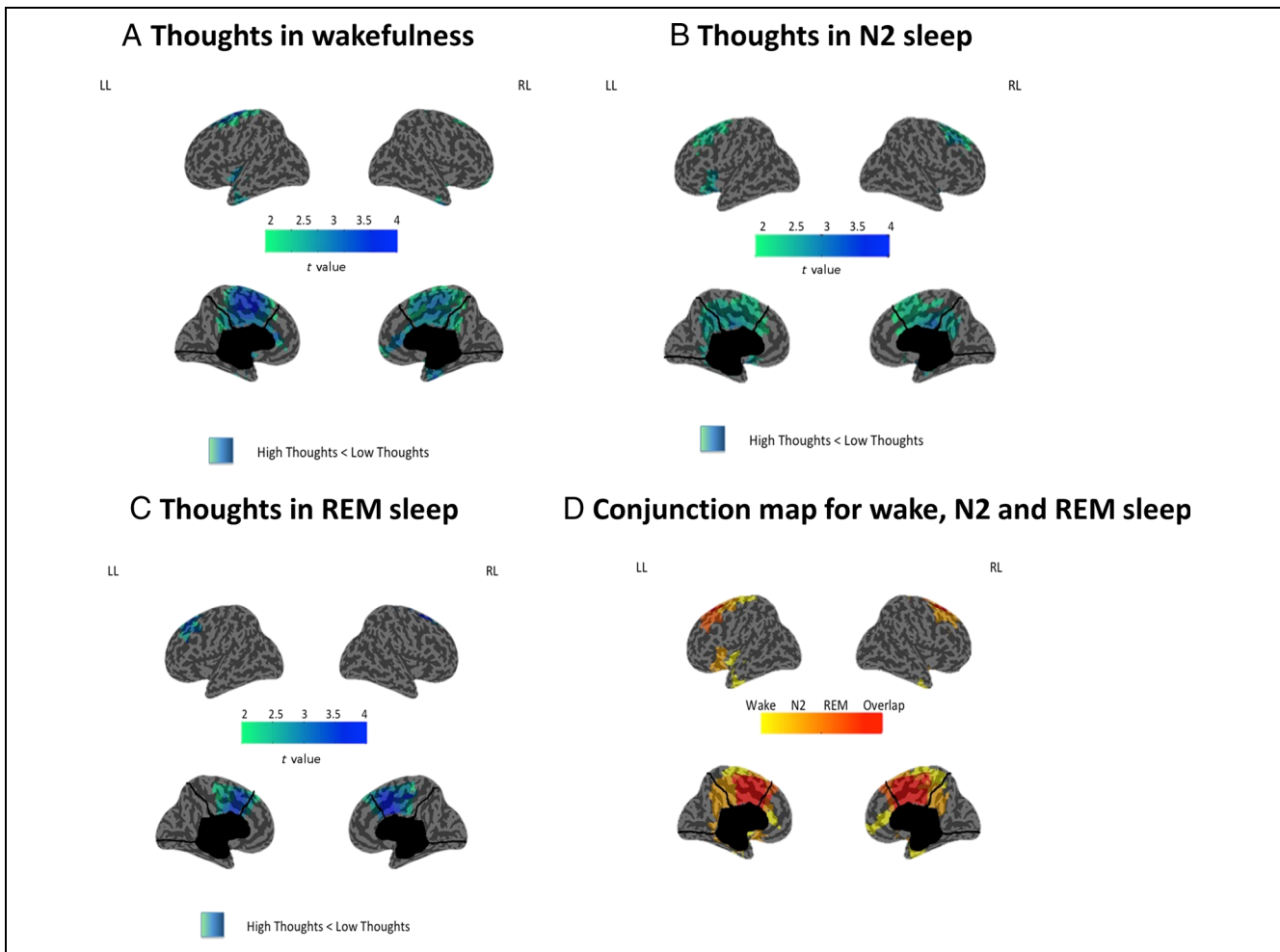
Across all three states (wakefulness, REM sleep, and NREM sleep), we found that high-thought reports compared with low-thought reports had decreased delta power (1–4 Hz), which was maximal over the midcingulate cortex (Figure 1). No significant changes were found for other frequency bands. During wake, topographical differences extended to the posterior cingulate cortex, premotor cortex, and the medial prefrontal cortex (mPFC; Figure 1A). In N2 sleep, decreased delta power in high-thought reports compared with low-thought reports was again maximal over the midcingulate cortex and again included posterior cingulate cortex and premotor cortex but did not extend to frontal cortex (Figure 1B). In REM sleep, decreased delta power during high-thought reports was again maximal over the midcingulate cortex but had a more restricted topography, which did not include either

**Table 1.** Phenomenological Analysis of Thoughts across Wakefulness and Sleep in All Participants

	Wake vs. N2		Wake vs. REM		N2 vs. REM	
	<i>P</i> <sub>uncor</sub>	<i>P</i> <sub>cor</sub>	<i>P</i> <sub>uncor</sub>	<i>P</i> <sub>cor</sub>	<i>P</i> <sub>uncor</sub>	<i>P</i> <sub>cor</sub>
Metacognition	.0004	.01*	.0003	.008*	.66	1
Social focus	.03	.63	.00004	.001*	.19	1
Positive emotions	.74	1	.00008	.002*	.003	.06
Negative emotions	.90	1	1	1	.04	.8
Past focus	.88	1	.29	1	.26	1
Present focus	.76	1	.08	1	.38	1
Future focus	.60	1	.26	1	.39	1
Bizarreness	.94	1	.27	1	.32	1
Cognitive effort	.80	1	.001	.02*	.002	.04*
Duration	n/a	n/a	n/a	n/a	.00002	.001*
Richness/complexity	n/a	n/a	n/a	n/a	.00001	.0001*
Voluntary control	n/a	n/a	n/a	n/a	.91	1
Recall of experience	n/a	n/a	n/a	n/a	.000007	.0001*

Wilcoxon signed-rank tests between high-thought trials in wakefulness, N2 sleep, and REM sleep.

\*Significant difference after correction for multiple comparisons for 31 independent tests using the Holm–Bonferroni method and adjustment of *p* values at a .05 significance level.



**Figure 1.** The neural correlates of thoughts across wakefulness and sleep. Inflated cortical maps illustrating the cortical distribution of  $t$  values (two-tailed, paired  $t$  tests,  $p < .05$ , TFCE-corrected) for the contrast between trials with high thought and low thought at the source level for delta power (1–4 Hz) for (A) wakefulness ( $n = 13$ ), (B) N2 sleep ( $n = 13$ ), (C) REM sleep ( $n = 10$ ). (D) Conjunction map showing the differences (yellow to orange) and overlap (red) of the topographical maps contrasting high-thought and low-thought trials across wakefulness, N2 sleep, REM sleep.

posterior cingulate cortex or frontal cortex (Figure 1C). A conjunction map showing the differences and overlap of the topographical maps contrasting high-thought and low-thought trials across the three states is shown in Figure 1D. The midcingulate cortex is a region of overlap among all three states.

#### *Metacognitive versus Nonmetacognitive Thoughts in Wake*

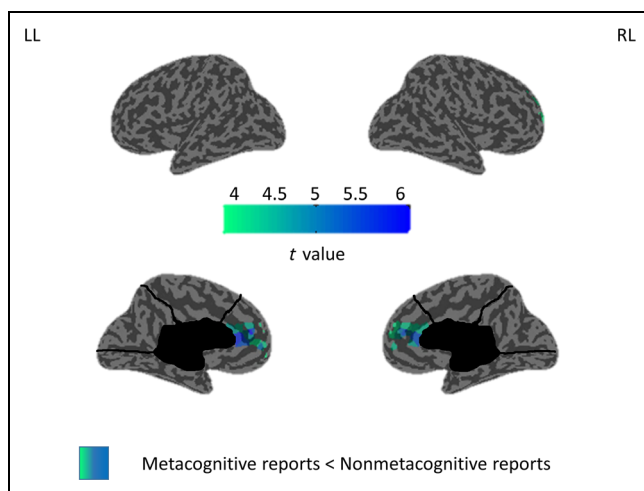
Given that metacognition was a major phenomenological difference in thoughts between wakefulness and sleep, we performed a supplementary EEG analysis, in which we compared metacognitive thoughts (averaged score 1–5 between the two independent scorers in the “metacognition” category), with thoughts involving no metacognition (score 0) in wakefulness. We found higher delta power (1–4 Hz) over a frontal region corresponding to the mPFC in the reports with no metacognition compared with the metacognitive trials (Figure 2). No significant changes were found for other frequency bands.

## DISCUSSION

In this study, we investigated the neural correlates of spontaneous thought across wakefulness, NREM sleep, and REM sleep. The results indicate that experiences characterized by high levels of thought were associated with the activation of the midcingulate region across all three states. Waking thoughts also involved a medial prefrontal region, whose activation was associated with higher metacognitive content than dreaming thoughts. Aside from metacognitive content, spontaneous thoughts in wakefulness did not differ from thoughts in NREM and REM sleep in most phenomenological categories.

### **The Phenomenology of Spontaneous Thoughts in Wake, NREM Sleep, and REM Sleep**

Content analysis revealed that thoughts in wakefulness did not differ from thoughts in NREM and REM sleep in most categories. First, the proportion of episodic memories and thoughts about the present or future were similar



**Figure 2.** Metacognitive versus nonmetacognitive reports in wake. Inflated cortical map illustrating the topographical distribution of  $t$  values for the contrast between trials with no metacognition and metacognition at the source level for delta power (1–4 Hz) in wake (last 20 sec before the alarm sound). Only significant differences at the  $p < .05$  level, obtained after correction for multiple comparisons, are shown (two-tailed, paired  $t$  tests, seven participants).

across states. This result is consistent with the idea that dreaming, similar to daydreaming, frequently involves past memories, current concerns, and future plans (Wamsley, 2013; Perogamvros & Schwartz, 2012; Baird, Smallwood, & Schooler, 2011). Moreover, we did not observe a difference in bizarreness between waking and dreaming thoughts. Although we are hesitant to overinterpret a null effect, one possible implication of this result is that, although dreaming, particularly REM dreaming, frequently involves bizarre elements (Schredl, 2010a), thoughts in particular may be less bizarre and more consistent across sleep and wake states (Fox et al., 2013; Wamsley, 2013; Domhoff, 2007) than previously acknowledged (Williams, Merritt, Rittenhouse, & Hobson, 1992).

However, waking thoughts differed from dreaming thoughts, whether occurring in NREM sleep or in REM sleep, by having higher metacognitive content. This finding is partly consistent with previous work (Kahan & LaBerge, 2011), which found that metacognition about one's own thoughts, feelings, and behavior was one of the few dimensions in which reported dreaming and waking experiences differ. Our results suggest that the higher metacognitive content of waking thoughts may be related to the involvement of the mPFC (Figure 1D). Metacognitive reports compared with nonmetacognitive reports in wake (Figure 2) were associated with activation (reduced delta) of mPFC, consistent with previous studies, which have found mPFC involvement in metacognition (e.g., Baird, Smallwood, Gorgolewski, & Margulies, 2013; Fleming, Huijgen, & Dolan, 2012). The implication of this structure in metacognition is also supported by a recent study that found increased functional connectivity between the hippocampus and mPFC during a metacognitive process of

imagining events from the future or past of the individual (Karapanagiotidis, Bernhardt, Jefferies, & Smallwood, 2017). Further investigation will be needed to determine whether these frontal regions are directly involved in experiential aspects of metacognitive thinking or are instead recruited when metacognition poses additional cognitive demands with no direct experiential correspondence.

We also observed that REM dreaming thoughts have greater social focus than waking thoughts, as reported previously (McNamara, McLaren, Smith, Brown, & Stickgold, 2005). A possible explanation for this finding is that typical dreams expose the person to richer environments with more opportunities for diverse social interactions than typical daydreams. Dreaming exposure to rich social stimuli may permit an offline enhancement of social cognition (Revonsuo, Tuominen, & Valli, 2015) and of the so-called theory of mind (Fox et al., 2013; Perogamvros, Dang-Vu, Desseilles, & Schwartz, 2013). Another interesting finding is that cognitive effort was higher in REM dreaming than in wakefulness and NREM dreaming, even though thinking was more frequent in wake than N2/REM sleep.

### The Neural Correlates of Spontaneous Thought in Wake, NREM Sleep, and REM Sleep

The present experiment highlights a midcingulate region as a neural correlate of spontaneous thought across wakefulness, NREM sleep, and REM sleep. Decreased delta power was consistently observed in this region when participants reported that their experience involved thinking both during an experience-sampling task in wakefulness and during serial awakenings from sleep. The negative peak of slow waves in the EEG delta frequency range ( $<4$  Hz) is associated with neuronal down states, during which neurons become hyperpolarized and cease firing (Steriade, Timofeev, & Grenier, 2001), as confirmed by intracranial recordings in humans (Nir et al., 2011). In contrast, EEG activation, associated with decreased delta power, is associated with the recovery of neural activity (Nir et al., 2011). The occurrence of bistability and neuronal down states have been linked to the loss of consciousness during both sleep and anesthesia (Sachdev et al., 2015; Purdon et al., 2013; Tononi & Massimini, 2008). Because down states lead to the breakdown of stable causal interactions among neurons (Pigorini et al., 2015), a cortical area undergoing down states is hypothesized to not contribute specific contents to conscious experiences (Tononi, Boly, Massimini, & Koch, 2016). Thus, our findings suggest that conscious thoughts are less likely to be reported when midcingulate regions are at least partially inactivated as indicated by the occurrence of slow waves. Although the occurrence of bistability between “ON” and “OFF” periods is typical of NREM sleep, recent studies have demonstrated the occurrence of local EEG fluctuations in both the delta (Sachdev et al., 2015) and theta range (Bernardi et al., 2015; Hung

et al., 2013) in awake humans, often associated with transient behavioral impairments (Bernardi et al., 2015). Similar local low-frequency fluctuations have been observed in rodents, where they are associated with neuronal OFF periods and behavioral misses (Vyazovskiy et al., 2011). Moreover, local slow waves and neuronal OFF periods have been recently discovered also in REM sleep (Funk, Honjoh, Rodriguez, Cirelli, & Tononi, 2016).

So far, studies examining the neural correlates of spontaneous thoughts had focused on the waking state (reviewed in Fox et al., 2015) and employed fMRI or PET, methods that have lower temporal resolution than hd-EEG. Brain areas related to spontaneous thought processes were mainly part of the DMN, which encompasses mPFC, precuneus/posterior cingulate cortex, and bilateral inferior parietal lobule, as well as the medial-temporal lobe/parahippocampal cortex (O'Callaghan, Shine, Lewis, Andrews-Hanna, & Irish, 2015; Bernhardt et al., 2014; Stawarczyk, Majerus, Maquet, & D'Argembeau, 2011; Dumoutheil, Gilbert, Frith, & Burgess, 2010; Christoff, Gordon, Smallwood, Smith, & Schooler, 2009; Pagnoni, Cekic, & Guo, 2008; Mason et al., 2007; McKiernan, D'Angelo, Kaufman, & Binder, 2006; Christoff, Ream, & Gabrieli, 2004). However, non-DMN structures have also been implicated in spontaneous thought processes, such as the dorsal ACC, midcingulate cortex, secondary somatosensory cortex, insula, rostralateral pFC, and temporopolar cortex (Fox et al., 2015; Christoff et al., 2009), as well as dorsolateral pFC (Smallwood, Brown, Baird, & Schooler, 2012).

By considering the neural correlates of spontaneous thought across wake, NREM sleep, and REM sleep, our study highlights a more restricted brain region centered on midcingulate cortex bilaterally. This region, which corresponds to large part of Brodmann's area 24 (Palomero-Gallagher, Vogt, Schleicher, Mayberg, & Zilles, 2009), lies anatomically between the anterior and the posterior cingulate cortex (Palomero-Gallagher et al., 2009; Vogt, Hof, & Vogt, 2004). Functional studies have previously associated neural activity in this region with various unconscious or conscious processes such as conflict monitoring (Carter et al., 1998), readiness for action (Hoffstaedter, Grefkes, Zilles, & Eickhoff, 2013), reward processing (Parvizi, Rangarajan, Shirer, Desai, & Greicius, 2013; Bush et al., 2002; Shima & Tanji, 1998), and processing of pain and negative affect (Shackman et al., 2011). Consistent with our findings, fMRI studies had also found that midcingulate cortex is recruited, along with other regions, during spontaneous thought in wakefulness (Bernhardt et al., 2014; Hasenkamp, Wilson-Mendenhall, Duncan, & Barsalou, 2012; Christoff et al., 2009). Specifically, Christoff et al. (2009) demonstrated that episodes of mind-wandering showed activation of the midcingulate cortex, precuneus, and TPJ when compared with task-related episodes. Hasenkamp et al. (2012) also observed activity in the midcingulate cortex during self-reported mind-wandering. Complementing these results, Bernhardt

et al. (2014) found that task-unrelated thoughts under low-demanding conditions were associated with increased cortical thickness of mPFC and midcingulate cortex. In our experiments, midcingulate cortex was highlighted by hd-EEG contrasts between high and low spontaneous thought across all three behavioral states of wake, NREM sleep, and REM sleep. Moreover, midcingulate cortex was the only region to emerge as a neural correlate of spontaneous thought during REM sleep. Contrasts within NREM sleep highlighted again midcingulate cortex as well as an adjacent region of posterior cingulate cortex. Contrasts within wake added premotor cortex, posterior cingulate cortex, and mPFC. The more restricted and specific neural correlates of thought were observed with contrasts within sleep. This finding is consistent with the prediction that sleep reduces confounding factors extraneous to conscious thought, because sleeping participants, unlike awake ones, are disconnected from the external environment, perform no task, and have little or no cognitive control over the content and form of the thought experience.

The fact that midcingulate cortex alone and not adjacent posterior cingulate cortex emerged as a neural correlate of spontaneous thought in REM sleep deserves some comment. It has been suggested that posterior cingulate cortex, a core region of the DMN, may support internally generated thought (Fox et al., 2015; Leech, Kamourieh, Beckmann, & Sharp, 2011), due to its capacity to integrate information from different long-term memory systems of the temporal lobe (Smallwood et al., 2016; Andrews-Hanna et al., 2010). Our results in wake and NREM also point to posterior cingulate cortex as a possible neural correlate of spontaneous thought. During REM sleep, however, posterior cingulate cortex is deactivated compared with wakefulness or NREM states (Fox et al., 2013; Braun et al., 1997; Maquet et al., 1996). Because individuals are still perfectly capable of spontaneous thought during REM sleep, one interpretation of these results is that the recruitment of posterior cingulate cortex may not be a necessary condition for having conscious thoughts, and its involvement in thought may be indirect. Alternatively, thought-related changes in activity in the posterior cingulate region may still occur during REM sleep but may be dampened and thus more difficult to detect. Yet another possibility is that REM sleep thoughts may lack some specific features mediated by posterior cingulate cortex; however, in the current analysis, we did not observe consistent differences between REM thoughts and both N2 and wake thoughts along a single content dimension.

The midcingulate cortex, especially its anterior portion, has been associated with the so-called salience network, which mediates appropriate responses to environmental or internal stimuli of significant valence (Parvizi et al., 2013; Seeley et al., 2007; Bush et al., 2002; Shima & Tanji, 1998; Williams & Goldman-Rakic, 1998). High activity in this region could mean that the content of high-thought trials is more salient for the participant than the one of low-thought

trials. This region also receives dopaminergic input from the ventral tegmental area (Hollerman & Schultz, 1998), in line with suggestions that dreaming may be related to the activation of cortical and subcortical reward structures, as in the Reward Activation Model (Perogamvros & Schwartz, 2012). Combined EEG/fMRI studies of dreaming are needed to further investigate the hypothesis that cortical and subcortical reward structures may be implicated in dreaming, because hd-EEG is inadequate for accurately localizing current sources in deep structures. Similarly, a possible involvement of subcortical structures in the medial-temporal lobe (hippocampus, parahippocampus) in triggering spontaneous thoughts (Christoff et al., 2016; Ellamil et al., 2016) cannot be ruled out. On the other hand, cortical regions such as the inferior parietal lobule and posterior insula, which had been proposed as possible early generators of thought (Ellamil et al., 2016), were not highlighted by our contrasts even though they are typically accessible to hd-EEG.

In summary, hd-EEG topographical contrasts as well as content analysis support the conclusion that conscious thoughts share similar phenomenological features and

neural correlates across wakefulness, NREM, and REM sleep, despite the otherwise different neurophysiological profiles of these states. This finding is broadly consistent with the claim that common brain regions are involved in both daydreaming and dreaming (or rather, in REM sleep, as most neuroimaging studies so far did not investigate dreaming per se; Domhoff & Fox, 2015; Fox et al., 2013; Nir & Tononi, 2010; Llinas & Pare, 1991). However, our results also point to several important differences in thoughts across waking and sleep states. The most notable one is that significant differences in prefrontal activation were not observed during NREM and REM sleep thoughts, in contrast to thoughts during wake. Correspondingly, the frequency of metacognitive thoughts is also reduced in dreams, whereas the metacognitive content of thoughts during wake is associated with the activation of mPFC. Together, these observations point to the hypothesis that prefrontal regions may either support specific types of conscious thoughts (i.e., those involving metacognitive content) or support unconscious functions that support metacognitive thoughts (Fleming, Dolan, & Frith, 2012).



## APPENDIX

**Table A1.** Definitions of Categories Used for Scoring Dream and Waking Thoughts

Metacognition: thinking or reflecting about one's experience
Social focus: experience related to other people or social entities
Positive emotions: presence of positive emotions, such as happiness, excitement, curiosity, etc.
Negative emotions: presence of negative emotions, such as sadness, anger, boredom, etc.
Past focus: experience related to one's autobiographical (episodic) past events
Present focus: thoughts about something that is happening right now
Future focus: thoughts about the future
Bizarreness: presence of impossible, unlikely or inconsistent features in the experience

**Table A2.** Shapiro–Wilk Normality Test for the Categories Used in Content Analysis

	Shapiro–Wilk	
	Statistic	Sig.
Metacognition N2	.221	<.001*
Metacognition wake	.872	.055
Metacognition REM	.188	<.001*
Social N2	.687	<.001*
Social wake	.941	.467
Social REM	.911	.021*
Positive emotion N2	.791	.005*
Positive emotion W	.875	.060
Positive emotion REM	.932	.067
Negative emotion N2	.446	<.001*
Negative emotion W	.689	<.001*
Negative emotion REM	.690	<.001*
Past N2	.576	<.001*
Past W	.820	.12*
Past REM	.592	<.001*
Present N2	.953	.652
Present W	.948	.573
Present REM	.890	.007
Future N2	.635	<.001*
Future W	.858	.037
Future REM	.557	<.001*
Bizarre N2	.458	<.001*
Bizarre W	.615	<.001*
Bizarre REM	.580	<.001*

Several variables have non-normal distribution (marked with \* $p < .05$ ).

**Table A3.** Mean Numbers (Scores) and Standard Deviations of Number of Words in the Report as well as Content Categories across Wake, N2 Sleep, and REM Sleep

	Wake	N2	REM
Words	15.8 ( $\pm 10.8$ )	14.1 ( $\pm 7.3$ )	16.1 ( $\pm 8.4$ )
Metacognition	0.27 ( $\pm 0.25$ )	0.03 ( $\pm 0.14$ )	0.007 ( $\pm 0.04$ )
Social focus	0.88 ( $\pm 0.76$ )	1.66 ( $\pm 1.66$ )	2.69 ( $\pm 1.74$ )
Positive emotions	0.61 ( $\pm 0.55$ )	0.73 ( $\pm 1.01$ )	1.90 ( $\pm 1.35$ )
Negative emotions	0.62 ( $\pm 0.57$ )	0.50 ( $\pm 0.86$ )	1.09 ( $\pm 0.73$ )
Past focus	0.56 ( $\pm 0.43$ )	0.61 ( $\pm 0.51$ )	0.47 ( $\pm 0.92$ )
Present focus	1.88 ( $\pm 0.69$ )	1.95 ( $\pm 0.68$ )	2.30 ( $\pm 0.75$ )
Future focus	0.63 ( $\pm 0.59$ )	0.55 ( $\pm 1.09$ )	0.45 ( $\pm 0.91$ )
Bizarreness	0.11 ( $\pm 0.25$ )	0.17 ( $\pm 0.47$ )	0.21 ( $\pm 0.69$ )
Cognitive effort	0.76 ( $\pm 0.67$ )	0.94 ( $\pm 0.89$ )	1.98 ( $\pm 1.29$ )
Duration	n/a	3.03 ( $\pm 0.79$ )	3.53 ( $\pm 0.87$ )
Richness/complexity	n/a	2.35 ( $\pm 0.81$ )	3.06 ( $\pm 0.88$ )
Recall of experience	n/a	2.67 ( $\pm 0.91$ )	3.24 ( $\pm 0.90$ )
Voluntary control	n/a	0.56 ( $\pm 0.80$ )	0.58 ( $\pm 0.86$ )

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Reprint requests should be sent to Giulio Tononi, Department of Psychiatry, University of Wisconsin-Madison, 6001 Research Park Blvd., Madison, WI 53719, or via e-mail: gtononi@wisc.edu.

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