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Dynamics of neural recruitment surrounding the spontaneous arising of thoughts in experienced mindfulness practitioners

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ABSTRACT

Thoughts arise spontaneously in our minds with remarkable frequency, but tracking the brain systems associated with the early inception of a thought has proved challenging. Here we addressed this issue by taking advantage of the heightened introspective ability of experienced mindfulness practitioners to observe the onset of their spontaneously arising thoughts. We found subtle differences in timing among the many regions typically recruited by spontaneous thought. In some of these regions, fMRI signal peaked prior to the spontaneous arising of a thought — most notably in the medial temporal lobe and inferior parietal lobule. In contrast, activation in the medial prefrontal, temporopolar, mid-insular, lateral prefrontal, and dorsal anterior cingulate cortices peaked together with or immediately following the arising of spontaneous thought. We propose that brain regions that show antecedent recruitment may be preferentially involved in the initial inception of spontaneous thoughts, while those that show later recruitment may be preferentially involved in the subsequent elaboration and metacognitive processing of spontaneous thoughts. Our findings highlight the temporal dynamics of neural recruitment surrounding the emergence of spontaneous thoughts and may help account for some of spontaneous thought's peculiar qualities, including its wild diversity of content and its links to memory and attention.

1. Introduction

Where do thoughts come from? One of the most intriguing yet least understood aspects of the human mind is its tendency to spontaneously give rise to words, images, and emotions that flow effortlessly from one topic to another. There is a stunning ubiquity of such spontaneously arising mental content in people's lives: thoughts that occur without our deliberate control take up as much as one-third of our mental experience (Klinger and Cox 1987).

The last decade marked an upsurge of investigations into a number of closely related mental phenomena, often investigated using terms such as ‘mind-wandering’, ‘stimulus-independent thought’, or ‘task-unrelated thought’ (Christoff, 2012). Psychological research has focused on the conditions that facilitate these kinds of thought processes, showing that their frequency increases when task demands are low or when external sensory stimulation is weak (Smallwood and Schooler, 2006). In parallel, neuroscientific investigations have focused on identifying the brain regions that are consistently recruited during such conditions. The majority of investigations have placed particular emphasis on recruitment of the default mode network (for review, see Christoff, 2012), although a number of executive control network regions are recruited with equal consistency (Christoff et al., 2009a; Fox et al., 2015). While these investigations have greatly improved our understanding of which brain regions are engaged when spontaneous thought is ongoing, we still have virtually no knowledge of how these various brain regions contribute to the different components of a spontaneous thought experience and, in particular, which brain regions support the early inception of spontaneous thoughts (Smallwood, 2013).

The goal of the present study, therefore, was to investigate key brain regions associated with the arising of spontaneous thoughts. To do this, we set out to examine brain recruitment that occurs immediately *prior* to the onset of a spontaneous thought. The central difficulty in investigating this question lies in identifying the precise temporal onset of spontaneously arising mental content. There are currently no third-person behavioral measures that provide such information reliably, making it necessary for scientists to use first-person introspective reports from participants. Although most individuals can provide fairly reliable descriptions of the basic contents of their thoughts (Hurlburt and

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Schwitzgebel, 2007), their ability to report on the mental processes that give rise to thought content is generally considered to be poor (Nisbett and Wilson, 1977). This apparent lack of introspective ability, combined with the need for reliance on introspective measures, has created a methodological knot that has tied the hands of researchers interested in differentiating the neural systems associated with the early formation of spontaneous thoughts.

The ability to detect the arising of spontaneous thoughts, however, can vary across individuals (Seli et al., 2015) as well as within the same individual (Zedelius et al., 2015). This raises the possibility that the methodological difficulty described earlier can be tackled by employing participants with heightened introspective skills, a method known as neurophenomenology (Fazelpour and Thompson, 2015; Varela, 1996). In this approach, participants with introspective training give first-person reports about their mental processes that are then related to measures of neural activity (Lutz et al., 2002). One form of mental training that specifically focuses on observing the spontaneous arising of one's own thoughts is mindfulness practice (Lutz et al., 2008; Tang et al., 2015). Mindfulness training has been shown to enhance attention in numerous ways, including a greater ability to notice subtle or rapid events, such as increased line length discrimination at visual threshold during a vigilance task (MacLean et al., 2010; Sahdra et al., 2011; Zanesco et al., 2013) and improved second target detection during an attentional blink task (Slagter et al., 2007). Specifically, introspective ability appears to be enhanced through mindfulness training, as shown by increased metacognitive memory confidence judgments (Baird et al., 2014) and greater accuracy in emotional self-awareness relative to no training (Sze et al., 2010). Thus, we employed a group of highly experienced mindfulness practitioners, who tracked the arising of spontaneous thoughts during fMRI scanning, to capitalize on this potentially heightened introspective ability and more specifically examine the neural antecedents of spontaneous mental content as well as the full suite of neural recruitment before, during, and after spontaneous thought reports.

We hypothesized that the medial temporal lobe would show preferential recruitment during the initial generation of spontaneous thought as it is often recruited during rest (Buckner et al., 2008; Christoff et al., 2004; Stark and Squire, 2001) and has been associated with memory retrieval (Squire et al., 2004), future thinking (Addis et al., 2009), and mental simulation (Hassabis et al., 2007), which form a large portion of spontaneous thought content (Klinger, 2009; Klinger and Cox, 1987). We also hypothesized that the medial and lateral prefrontal cortices, also consistently recruited during rest (Christoff et al., 2009a; Fox et al., 2015), would show increased recruitment after the initial generation of spontaneous thought as they have been associated more with the evaluation and monitoring of self-generated thought content (Buckner et al., 2008; Dixon and Christoff, 2012; Dixon and Christoff, 2014; Dixon et al., 2014; Fox and Christoff, 2014; Miller and Cohen, 2001).

2. Materials and methods

2.1. Participants

Eighteen participants (8 male and 10 female; $M = 49.91$ years old, $SD = 11.17$, $range = 29.39–68.42$) took part in the experiment. The participants were long-term, expert mindfulness meditators with more than 3000 h of lifetime meditation experience and at least 1 h of daily practice in the Mahasi Vipassana tradition ($M = 8338.60$ h, $SD = 5989.98$, $range = 3174–23{,}700$). The number of hours reported did not include practice in other traditions (e.g., Zen meditation, Transcendental meditation, Goenka or body scanning meditation, Yoga, Tai Chi, Qi Gong). Eligibility screening consisted of the administration of a meditation experience questionnaire and a phone interview by S.P., a former Mahasi monk. The screening ensured consistency of the meditation technique across participants and attainment of extensive knowledge of and experience with the meditation technique through regular practice and attendance of several long-term intensive retreats.

The participants were recruited from Vipassana meditation communities in Vancouver (BC, Canada), Vancouver Island (BC, Canada), Boulder (CO, USA), San Francisco (CA, USA), and Seattle (WA, USA). All participants had normal or corrected-to-normal vision with no MRI contraindications and no current psychiatric medication use. Fourteen were right-handed and 4 were left-handed, but all used their right hand to respond during the experiment. From an original sample of 22 participants, three participants were excluded from the analyses due to excessive motion (2 with $>5°$ pitch rotation, and 1 with $>5°$ pitch rotation and >5 mm in the z-direction). One participant was excluded from the analyses due to technical problems with behavioral data recording. All protocols were approved by the University of British Columbia (UBC; Vancouver, BC, Canada) Clinical Research Ethics Board and the UBC MRI Research Center. All participants gave informed written consent prior to participating and received payment as compensation.

2.2. Procedure

One to two days prior to the actual scanning session, participants engaged in a practice session identical to the actual scanning procedure in a mock scanner environment in order to become acclimatized to the task, button pressing, and scanner noises. Participants alternated between 30 s blocks of monitoring thoughts that arose spontaneously (*thought* condition, Fig. 1A) and 30 s blocks of monitoring words that appeared onscreen (*word* condition, Fig. 1B). During both blocks, participants attended to the rising and falling of the abdomen (i.e., breathing). Participants reported with a first button press (index finger) to indicate when a thought arose or when a word appeared onscreen (see Stimuli), and with a second button press to indicate what type of thought or word it was (index finger = image or symbol, middle finger = narrative or inner speech, ring finger = emotion, pinky finger = body sensation). Each word stayed onscreen until the first button press. The first button press was followed by one asterisk (*) onscreen for 250 ms and the second button press was followed by two asterisks (**) onscreen for 250 ms to signal successful button presses. Each participant completed three 9-min task runs. Each run consisted of 8 *thought* blocks and 8 *word* blocks; each participant therefore completed 24 *thought* blocks and 24 *word* blocks in total. Blocks were separated by interstimulus intervals (ISIs) with jittered durations (randomly chosen from 250 ms, 500 ms, or 750 ms), with each ISI appearing an equal number of times.

The instructions were designed to be consistent with a typical mindfulness practice session (Sayadaw, 1985, 2002): the first and second button presses roughly corresponded to the standard steps of (*i*) noting the occurrence of thought and then (*ii*) labeling its content. In the *thought* condition, participants were instructed to report on the occurrence of mental events that took attention away from one's breathing, or became more prominent in attention than breathing. This enabled the assessment of mental content arising without being explicitly elicited by external cues in the environment. In the *word* condition, participants were instructed to briefly think about the definition of each word presented on the screen before responding. This enabled the assessment of mental content elicited by external cues in the environment.

The onsets and categories of words presented within each *word* block were selected in real-time by a computer algorithm that matched the timing onsets and categories of words to the timing onsets and categories of spontaneous thoughts reported in the immediately preceding *thought* block. Thus, each pair of *thought* and *word* blocks had the same number of events, and these events had the same content categories and appeared at the same time within the block.

2.3. Stimuli

The words presented during *word* monitoring blocks were randomly chosen from four lists that corresponded to the categories of thoughts routinely identified during mindfulness meditation (Sayadaw, 1985, 2002) and covered a large portion of spontaneous thought content

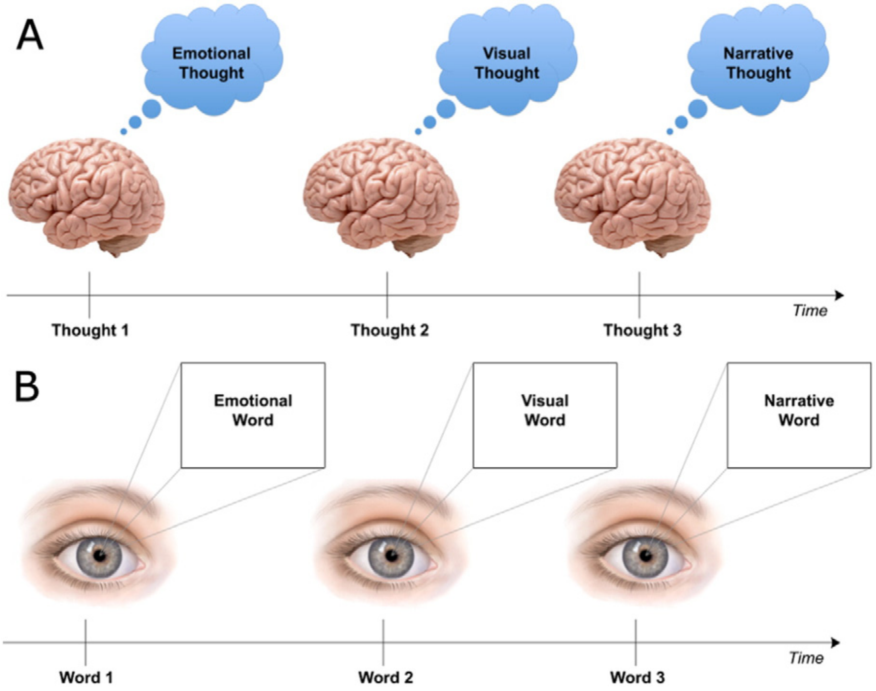

Fig. 1. Experimental procedure. Participants alternated between (A) spontaneous thought detection blocks (30 s) and (B) matched word detection blocks (30 s). Participants indicated with a first button press as soon as they noticed a thought spontaneously arising, which served as the experimental measure of the thought's onset, and with a second button press what category of thought it was, which allowed online matching of the subsequent word detection block. Each word block was constructed in real-time to correspond to the timing and categories of spontaneous thoughts reported during the immediately preceding thought block, allowing a closely matched comparison between neural recruitment associated with spontaneously arising and perceptually triggered mental content.

(Fox et al., 2013): (*i*) image or symbol, (*ii*) narrative or inner speech, (*iii*) emotion, or (*iv*) body sensation. Words in the image list consisted of 30 nouns (e.g., mountain, beach, rain, sun, pet) selected from the Medical Research Council (MRC) Psycholinguistics Database (Wilson, 1988), which had imageability, concreteness, and familiarity ratings of 500–700 (on scales of 100 = very low to 700 = very high) to ensure ease of visualization. Words in the narrative list consisted of 30 nouns (e.g., work, money, family, goals, health) selected from the Edinburgh Associative Thesaurus (EAT) (Kiss et al., 1973), which were associated with the types of current concerns that people tend to have and that are thought to be major determinants of spontaneous thought content (Klinger, 2009; Klinger and Cox, 1987). These included home and household matters; employment and finance; partner, family, and relatives; friends and acquaintances; love, intimacy, and sexual matters; self-changes; education and training; health and medical matters; spiritual matters; and hobbies, pastimes, and recreation (Klinger and Cox, 2004). Words in the emotion list consisted of 30 adjectives (e.g., calm, happy, sad, afraid, worried) also selected from the EAT that were associated with various emotions (e.g., happiness, sadness, anger, disgust, fear, surprise). Words in the body sensation list consisted of 30 nouns and adjectives similarly selected from the EAT that were associated with various body sensations (e.g., warmth, tickle, vibration, pressure, pain). Each word contained 3–10 letters and 1–3 syllables. The words and fixation cross appeared as gray text on a black background. The task and stimuli were implemented and presented using E-Prime 2.0 (Psychology Software Tools, Sharpsburg, PA, USA).

2.4. Data acquisition

Functional and structural MRI data were collected using a 3.0 Tesla Philips Intera MRI scanner (Best, Netherlands) with a standard head coil. Head movement was restricted using foam padding around the head. T2*-weighted functional images were acquired parallel to the anterior commissure/posterior commissure (AC/PC) line using a single-shot gradient echo-planar sequence (EPI; repetition time [*TR*] = 2 s, echo time [*TE*] = 30 ms, flip angle [*FA*] = 90°, field of view [*FOV*] = 240 × 240 × 143 mm, matrix size = 80 × 80, SENSE factor = 1.0). A total of 265 functional volumes were acquired for each task run, each including 36 interleaved axial slices (3 mm thick with 1 mm skip) covering the entire brain. Before functional imaging, an inversion recovery prepared T1-weighted structural volume was acquired in the same slice locations and orientation as the functional images using a fast spin-echo sequence (*TR* = 2 s, *TE* = 10 ms, *FA* = 90°, *FOV* = 224 × 224 × 143 mm, acquisition matrix size = 240 × 235, reconstructed matrix size = 480 × 480, inversion delay [*IR*] = 800 ms, spin-echo turbo factor = 5).

2.5. Data preprocessing

fMRI data for each participant were preprocessed and analyzed using SPM8 (Statistical Parametric Mapping, Wellcome Department of Imaging Neuroscience, London, UK). Slice timing correction was performed using sinc interpolation and resampling with the middle (18th) slice as a reference point. All functional volumes were realigned to the first volume to correct for between-scan motion. The structural volume was coregistered to the mean functional image and segmented to extract a gray matter image. The segmented structural volume was then spatially normalized to a gray matter image of the Montreal Neurological Institute (MNI) template and resliced to a voxel size of 2 × 2 × 2 mm. The derived spatial transformations were applied to the realigned functional volumes to bring them into standardized MNI space. Finally, the functional volumes were smoothed with an 8-mm full-width at half-maximum (FWHM) isotropic Gaussian kernel to compensate for residual between-subject variability after spatial normalization and to permit application of Gaussian random field theory for corrected statistical inference (Friston et al., 1994). To ensure that statistical analysis was performed for all brain regions, including those where the signal might have been low due to susceptibility artifacts, a mask was created by averaging and thresholding at >.80 the first preprocessed functional volume from all participants and was explicitly specified during model estimation at the individual level. To remove low-frequency drift in the blood oxygen-level dependent (BOLD) signal, the data were high-pass filtered using an upper cut-off period of 128 s. No global scaling was performed.

2.6. General linear model

Condition effects at each voxel were estimated according to the general linear model for the whole-brain analyses. The model included (*a*) the observed time series of intensity values, which represented the dependent variable; (*b*) covariates modeling session-specific effects (i.e., the six head movement parameters), later treated as confounds; and (*c*) regressor functions constructed by convolving condition-specific stick functions with a synthetic hemodynamic response function. The regressor functions were constructed to model each of the *thought* (t_{image}, $t_{narrative}$, $t_{emotion}$, and $t_{sensation}$), *word* (w_{image}, $w_{narrative}$, $w_{emotion}$, and $w_{sensation}$), and *button press* events and were compared using pairwise contrasts for each participant. Group random-effects analyses were then performed for each contrast. The resulting *T* maps were subsequently transformed to the unit normal *Z* distribution to create a statistical parametric map for each contrast. The threshold for significance was set at $Z > 2.576$ and $p < .05$ family-wise error (FWE) cluster corrected for multiple comparisons.

Onsets for the *thought* and *word* events were specified at 4 s prior to the corresponding first button press. A period of 6 s (3 TRs) yielded similar results as a period of 4 s but excluded more trials (i.e., those that did not occur 6 s or more after a previous event).

2.7. Time course extraction

Percent signal change time courses for brain regions showing greater activation during *thought* events compared to *word* events were extracted for each participant using the MarsBaR toolbox in SPM8 (MARSeille Boîte À Région d'Intérêt) (Brett et al., 2002). The extraction volumes were 4-mm radius spheres centered on local maxima from the group-level contrasts. Eight finite impulse response (FIR) functions were used, one for each peristimulus time point within a trial window of 16 s following the onset of a *thought* or *word* event (specified at 4 s before the first button press). This allowed the estimation of a region of interest's response over time without making assumptions about its shape and thus the assessment of activation differences across trial phases, compared to modeling the long duration of the hemodynamic response function (Dale, 1999; Henson and Friston, 2007; Ollinger et al., 2001).

2.8. Spatiotemporal partial least squares

Changes in neural recruitment over time during *thought* events compared to *word* events were assessed using spatiotemporal partial least squares. This whole-brain, multivariate technique identifies the temporal evolution of spatial patterns of activity correlated with different conditions across the length of an event and is not dependent on assumptions about the shape and duration of the hemodynamic response function (Lin et al., 2003; Lobaugh et al., 2001; McIntosh et al., 2004). The non-rotated task version of spatiotemporal Partial Least Squares (PLS) was used, which allows the specification of a priori non-orthogonal contrasts (instead of the rotated data-driven version that identifies orthogonal latent variables). One contrast was entered to examine differences in the pattern of neural recruitment across regions and over time between *thought* and *word* events (*thought* > *word*) within a trial window of 16 s (8 TRs) following the onset of a *thought* or *word* trial (specified at 4 s before the first button press). The statistical significance of the results at $p < .05$ was computed using permutation testing with 500 permutations. Correction for multiple comparisons was not necessary as the whole spatiotemporal pattern was tested in one analytical step instead of in a series of voxel-wise statistical tests. The reliability of the results was computed using bootstrap estimation of standard errors with 300 iterations. Reliable voxels were signified by bootstrap ratios greater than 2.576, which is approximately equal to a *Z*-score with $p < .01$.

3. Results

3.1. Frequency distribution and reaction times of reports

Participants reported an average of 67.33 thoughts ($SD = 35.02$) throughout all scanning sessions and an average of 2.81 thoughts ($SD = 1.21$) per *thought* block. However, only an average of 44.67 thoughts ($SD = 15.03$), or 73.80% of the thoughts reported, occurred 4 s or more after the previous thought report and were thus included in the analyses. Of the thoughts included, 18.66% ($M = 8.33$, $SD = 10.28$) were images, 37.31% ($M = 16.67$, $SD = 5.55$) were narrative, 12.94% ($M = 5.78$, $SD = 5.86$) were emotions, and 31.09% ($M = 13.89$, $SD = 8.80$) were body sensations. A two-way repeated measures ANOVA at the $\alpha = .05$ level indicated that the number of thought reports differed significantly across the four thought types [$F(3,51) = 7.01$, $p < .001$], but not across the three scanning sessions [$F(2,34) = 0.23$, $p > .05$] or their interaction [$F(6102) = 0.75$, $p > .05$]. Follow-up multiple paired *t*-tests with a Bonferroni correction ($\alpha = .05/6 = .0083$) revealed that there were significantly more narrative reports [$t(17) = 6.82$, $p < .001$] and body sensation reports [$t(17) = 4.39$, $p < .001$] than emotion reports. The participants' age in years and hours of meditation experience were not significantly correlated, at $\alpha = .05$, with the overall number of thoughts reported or with the different types of thoughts reported. In addition, participants responded with the first button press an average of 1145.28 ms ($SD = 403.71$ ms) after the presentation of a word. They categorized a word with the second button press an average of 971.96 ms ($SD = 352.21$ ms) after the first button press. They categorized a thought with the second button press an average of 707.75 ms ($SD = 358.16$ ms) after the first button press signaling the arising of a thought.

3.2. Overall neural recruitment during spontaneous thought reports

Spontaneous thought, in the general population, is associated with a consistent pattern of activation throughout the brain, including default mode network regions, medial temporal lobe structures, and executive control network areas (Fox et al., 2015). During spontaneous thought events, the mindfulness practitioners in the present study showed neural recruitment that closely mirrored this pattern, as revealed by a standard general linear model analysis that identified all brain regions where activation was greater in the time surrounding spontaneous thought reports compared to the time surrounding word detection reports (Fig. 2 and Table 1). These regions included bilateral temporopolar cortex (Brodmann area [BA] 38; peak $x, y, z = 32, 6, -32$ and $-44, -2, -44$; Fig. 2A); bilateral hippocampus (BA 28; $-26, -20, -22$ and $24, -14, -18$; Fig. 2B); bilateral parahippocampus (BA 36; $-16, -22, -22$ and $16, -36, -16$; Fig. 2C); medial prefrontal cortex (BA 10; $2, 52, 12$; Fig. 2D); bilateral mid-insula (BA 13; $-36, 6, -12$ and $46, 4, -2$; Fig. 2E); bilateral rostrolateral prefrontal cortex (BA 10; $-30, 56, 14$ and $18, 58, 22$; Fig. 2F); left dorsolateral prefrontal cortex (BA 9; $-28, 44, 28$; Fig. 2G); dorsal anterior cingulate cortex (BA 32; $0, 26, 26$; Fig. 2H); posterior cingulate cortex (BA 31; $-14, -46, 30$; Fig. 2J); and right inferior parietal lobule (BA 39; $44, -76, 36$; Fig. 2K). In all of these regions, the parameter estimates during the thought condition were positive relative to baseline, except in the inferior parietal lobule, where it did not differ significantly from baseline (Fig. 3). Entering the participants' number of reported thoughts, hours of meditation

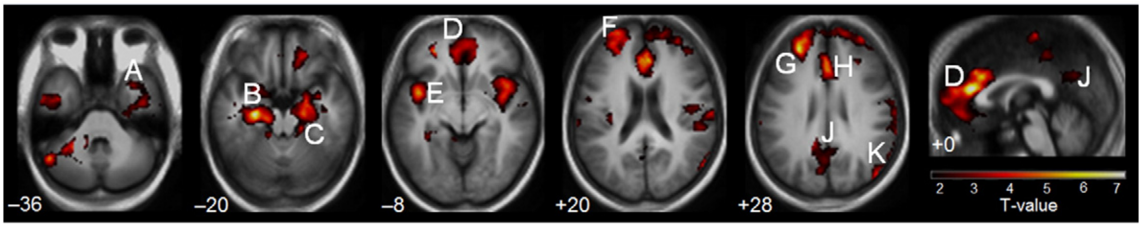

Fig. 2. Overall neural recruitment during spontaneous thought reports. Relative to matched word trials, spontaneous thought trials were associated with greater activation in (A) temporopolar cortex, (B) hippocampus, (C) parahippocampus, (D) medial prefrontal cortex, (E) mid-insula, (F) rostrolateral prefrontal cortex, (G) left dorsolateral prefrontal cortex, (H) dorsal anterior cingulate cortex, (J) posterior cingulate cortex, and (K) right inferior parietal lobule. Onsets for the spontaneous thought and matched word trials were specified at 4 s before the corresponding button press. All activations were significant at $p < .05$, family-wise error cluster-corrected for multiple comparisons. Results are displayed in neurological orientation, with the right hemisphere depicted on the right, on the average high-resolution structural image.

experience, and age in years as covariates in the analysis did not alter the significance of the results and yielded similar activation maps.

3.3. Neural recruitment prior to spontaneous thought reports

To specifically identify the neural antecedents of spontaneous thought, we computed the average time courses of activation in each of the brain regions identified in the standard general linear model analysis (Fig. 2 and Table 1). The spontaneous arising of thought was associated with activation in default mode network, medial temporal lobe, and paralimbic brain regions that preceded the onset of thought by several seconds. The specific brain regions where activation peaked *prior* to reports of spontaneous thought (Fig. 4) comprised the medial temporal lobe, including bilateral hippocampus (BA 28; −26, −20, −22 and 24, −14, −18; Fig. 4A,B) and bilateral parahippocampus (BA 36; −16, −22, −22 and 16, −36, −16; Fig. 4C,D), the posterior cingulate cortex (BA 31; −14, −46, 30; Fig. 4E), the right inferior parietal lobule (BA 39; 44, −76, 36; Fig. 4F), the rostral anterior cingulate cortex (BA 24; 0, 36, 14; Fig. 4G), and the right posterior insula (BA 13; 36, −20, 16; Fig. 4H).

Table 1
Activation peaks for *thought* events (*thought* > *word*).

Region	MNI coordinates						
	L/R/M	BA	*x*	*y*	*z*	Voxels	*Z* value
Frontal							
Rostral ACC	M	24	0	36	14	659	5.02
Dorsal ACC	M	32	0	26	26	178	4.25
Superior frontal gyrus (MPFC)	M	10	2	52	12	33	3.71
Middle frontal gyrus (RLPFC)	L	10	−30	56	14	81	3.90
Middle frontal gyrus (RLPFC)	R	10	18	58	22	357	3.46
Middle frontal gyrus (DLPFC)	L	9	−28	44	28	251	4.51
Mid-insula	L	13	−36	6	−12	55	3.28
Mid-insula	R	13	46	4	−2	505	4.86
Posterior insula	R	13	36	−20	16	32	3.50
Supplementary motor area	M	6	0	−26	66	165	3.14
Parietal							
Posterior cingulate cortex	M	31	−14	−46	30	55	3.15
Inferior parietal lobule	R	39	44	−76	36	30	4.08
Superior parietal lobule	L	5	−22	−38	58	31	2.86
Superior parietal lobule	R	5	20	−42	56	117	2.88
Postcentral gyrus	L	43	−50	−4	4	81	3.81
Postcentral gyrus	R	43	52	−10	14	33	4.21
Temporal							
Hippocampus	L	28	−26	−20	−22	33	4.74
Hippocampus	R	28	24	−14	−18	81	4.03
Parahippocampus	L	36	−16	−22	−22	33	3.75
Parahippocampus	R	36	16	−36	−16	184	4.13
Temporopolar cortex	L	38	−44	−2	−44	122	3.52
Temporopolar cortex	R	38	32	6	−32	61	3.52
Superior temporal gyrus	L	22	−54	−10	6	33	3.55
Superior temporal gyrus	R	22	60	−2	0	113	5.06
Subcortical							
Dentate of cerebellum	M	–	−14	−48	−34	47	3.34
Posterior cerebellum	L	–	−48	−62	−36	232	3.92

Note. All activations were significant at $p < .05$ FWE cluster corrected.

3.4. Neural recruitment during and following spontaneous thought reports

Time courses of activation in the brain regions identified in the standard general linear model analysis (Fig. 2 and Table 1) also revealed recruitment of additional areas simultaneous with and subsequent to spontaneous thought detection. The brain regions where activation peaked *during* reports of spontaneous thought (Fig. 5) comprised the medial prefrontal cortex (BA 10; 2, 52, 12; Fig. 5A), right rostrolateral prefrontal cortex (BA 10; 18, 58, 22; Fig. 5B), bilateral temporopolar cortex (BA 38; −44, −2, −44 and 32, 6, −32; Fig. 5C,D), and bilateral mid-insula (BA 13; −36, 6, −12 and 46, 4, −2; Fig. 5E,F). In addition, the brain regions where activation peaked *after* reports of spontaneous thought (Fig. 6) included the left dorsolateral prefrontal cortex (BA 9; −28, 44, 28; Fig. 6A), left rostrolateral prefrontal cortex (BA 10; −30, 56, 14; Fig. 6B), and dorsal anterior cingulate cortex (BA 32; 0, 26, 26; Fig. 6C).

3.5. Neural recruitment over time during spontaneous thought reports

The progression of neural recruitment during the time surrounding spontaneous thought reports, compared to the time surrounding word detection reports, was examined using non-rotated task spatiotemporal partial least squares, with the contrast being significant at $p < .001$. The positive saliences, or regions in which increases and decreases

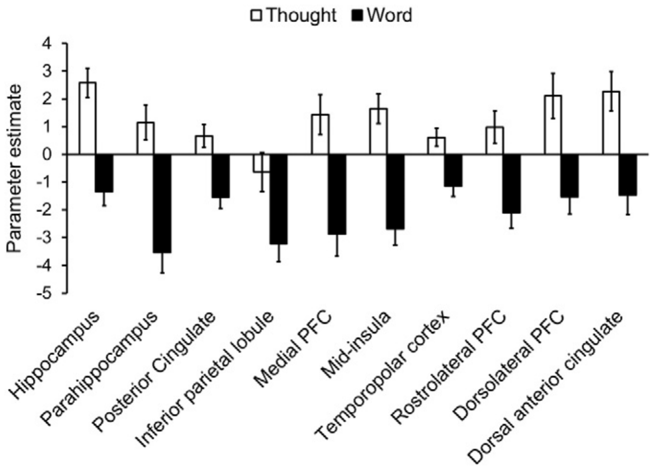

Fig. 3. Parameter estimates for activated brain regions. Histograms represent average parameter estimates for the thought and word conditions in 4-mm radius spheres centered on local maxima from the overall neural recruitment (Fig. 2 and Table 1). Error bars represent the standard error of the mean.

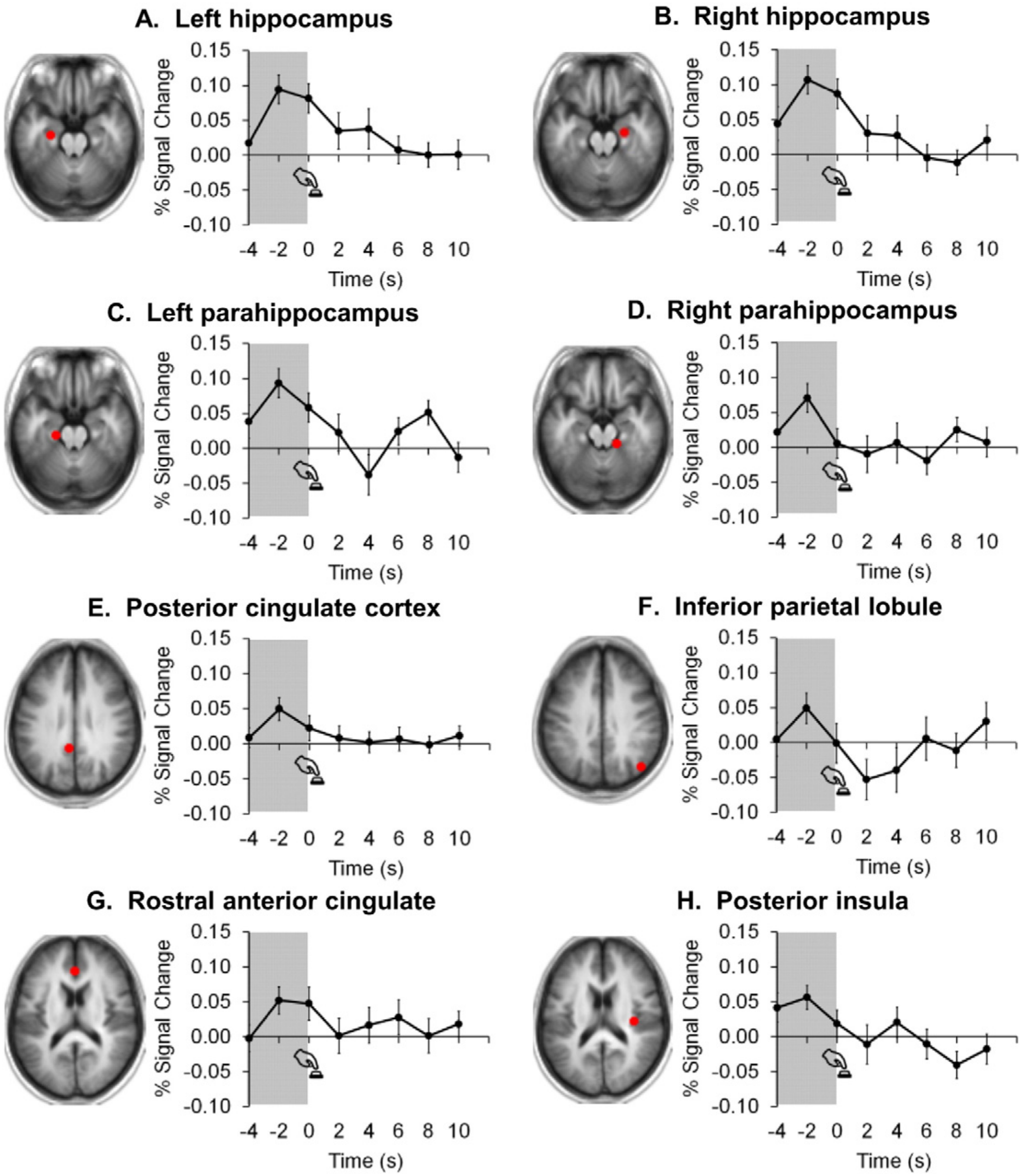

Fig. 4. Activation peaks occurring *prior to* spontaneous thought detection were observed in (A–D) medial temporal lobe, including hippocampus and parahippocampus, (E) posterior cingulate cortex, (F) right inferior parietal lobule, (G) rostral anterior cingulate cortex, and (H) right posterior insula. The graphs represent average percent signal change in 4-mm radius spheres centered on local maxima from the overall neural recruitment (Fig. 2 and Table 1). The gray bars indicate the 4-s time period before the reported spontaneous thought onset, while the hand icons mark the time point corresponding to the button press. The error bars represent the standard error of the mean.

in activation were associated with the positively weighted condition (i.e., *thought* trials), are shown in Fig. 7 and listed in Table 2. The left hippocampus (BA 28; −14, −36, 0; Fig. 7A), bilateral parahippocampus (BA 36; −20, −20, −22 and 14, −38, −6; Fig. 7B), and right inferior parietal lobule (BA 39/40; 50, −62, 46; Fig. 7C) were engaged *before* reports of spontaneous thoughts (TR 2). Meanwhile, the right temporopolar cortex (BA 38; 46, 2, −38; Fig. 7D), right posterior and mid-insula (BA 13; 48, −10, 4 and 38, 4, −10; Fig. 7E), medial prefrontal cortex (BA 11; −8, 38, −14; Fig. 7F), posterior cingulate cortex (BA 31; 0, −60, 26; Fig. 7G), left inferior parietal lobule (BA 39; −46, −74, 32), and left dorsolateral prefrontal cortex (BA 9; −22, 40, 44) were engaged *during* reports of spontaneous thoughts (TR 3). Finally, the right dorsolateral prefrontal cortex (BA 9; 28, 38, 30; Fig. 7J), bilateral rostrolateral prefrontal cortex (BA 10; −22, 58, 24 and 24, 54, 24), and dorsal anterior cingulate cortex (BA 24; −2, 18, 24; Fig. 7H) were engaged *after* reports of spontaneous thoughts (TR 4).

4. Discussion

Here we investigated the key neural regions associated with the early inception of spontaneous thoughts. By taking advantage of the introspective ability of mindfulness practitioners, the present study was able to examine the brain regions associated with the arising of spontaneous thought throughout the brain. Using this novel neurophenomenology-based approach (Fazelpour and Thompson, 2015; Lutz et al., 2002; Varela, 1996), we were able to observe subtle differences in timing among the many regions typically recruited by spontaneous thought (Fox et al., 2015). Only in some of these brain areas did neural activation peak *prior* to the spontaneous arising of a thought – most notably in the medial temporal lobe and inferior parietal lobule. How do these findings relate to previous research and what role might these neural antecedents play in the generation of spontaneous thought?

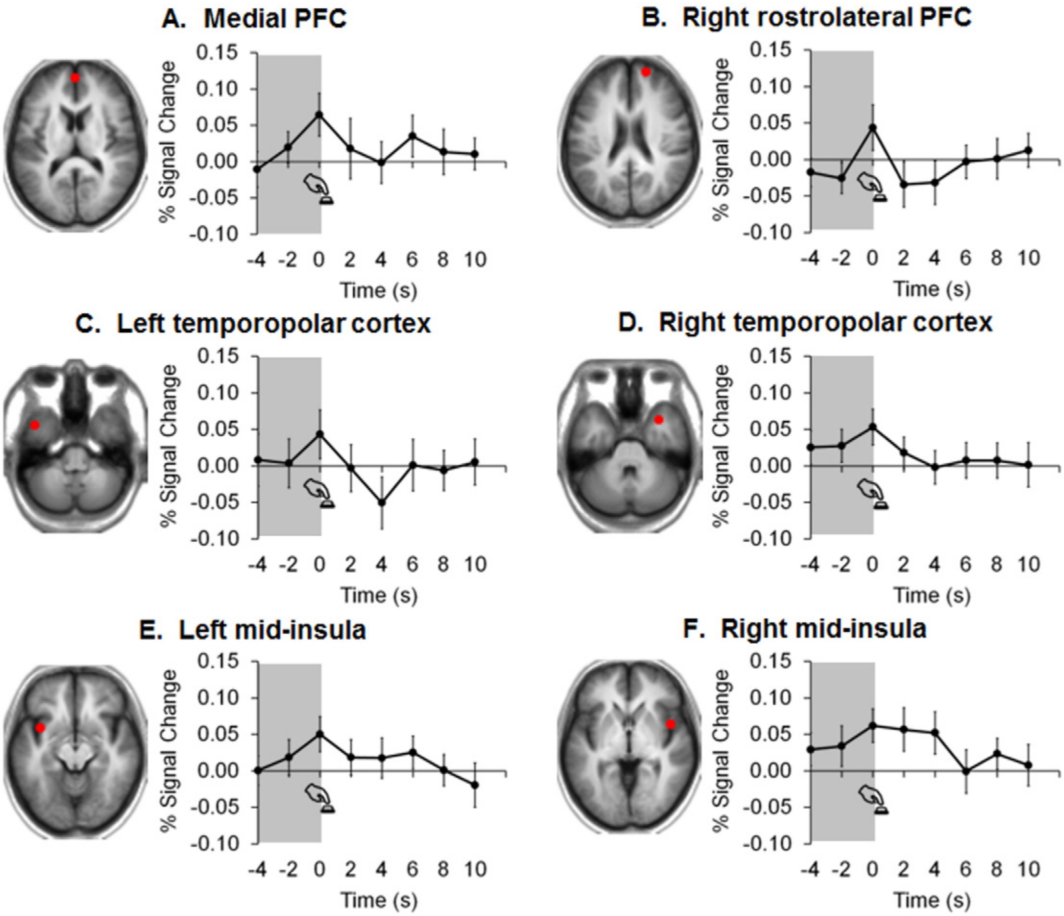

Fig. 5. Activation peaks occurring during spontaneous thought detection were observed in (A) medial prefrontal cortex, (B) right rostrolateral prefrontal cortex, (C,D) temporopolar cortex, and (E,F) mid-insula. The graphs represent average percent signal change in 4-mm radius spheres centered on local maxima from the overall neural recruitment (Fig. 2 and Table 1). The gray bars indicate the 4-s time period before the reported spontaneous thought onset, while the hand icons mark the time point corresponding to the button press. The error bars represent the standard error of the mean.

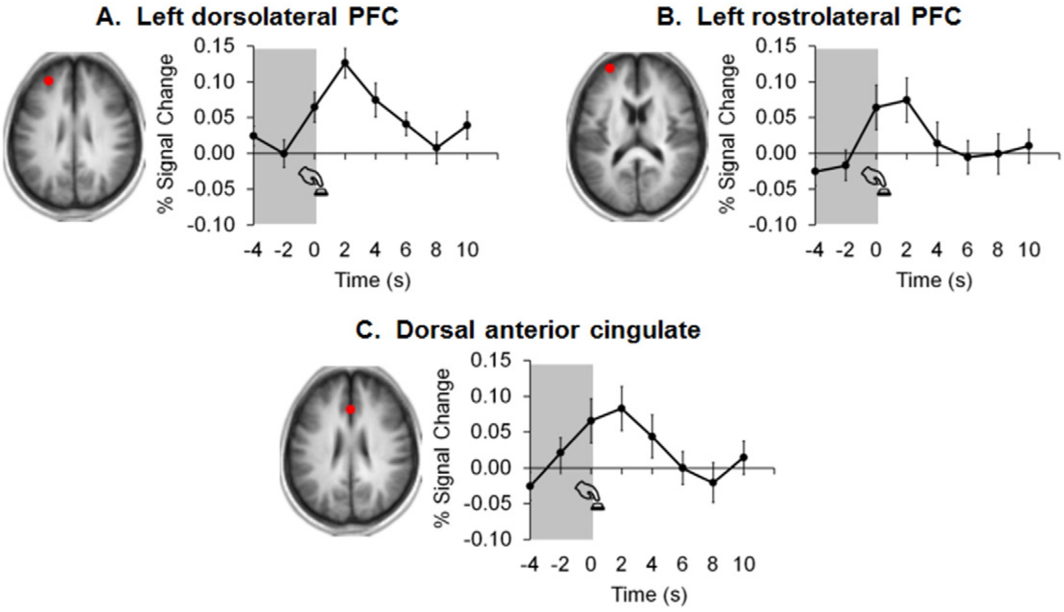

Fig. 6. Activation peaks occurring *subsequent* to spontaneous thought detection were observed in (A) left dorsolateral prefrontal cortex, (B) left rostrolateral prefrontal cortex, and (C) dorsal anterior cingulate. The graphs represent average percent signal change in 4-mm radius spheres centered on local maxima from the overall neural recruitment (Fig. 2 and Table 1). The gray bars indicate the 4-s time period before the reported spontaneous thought onset, while the hand icons mark the time point corresponding to the button press. The error bars represent the standard error of the mean.

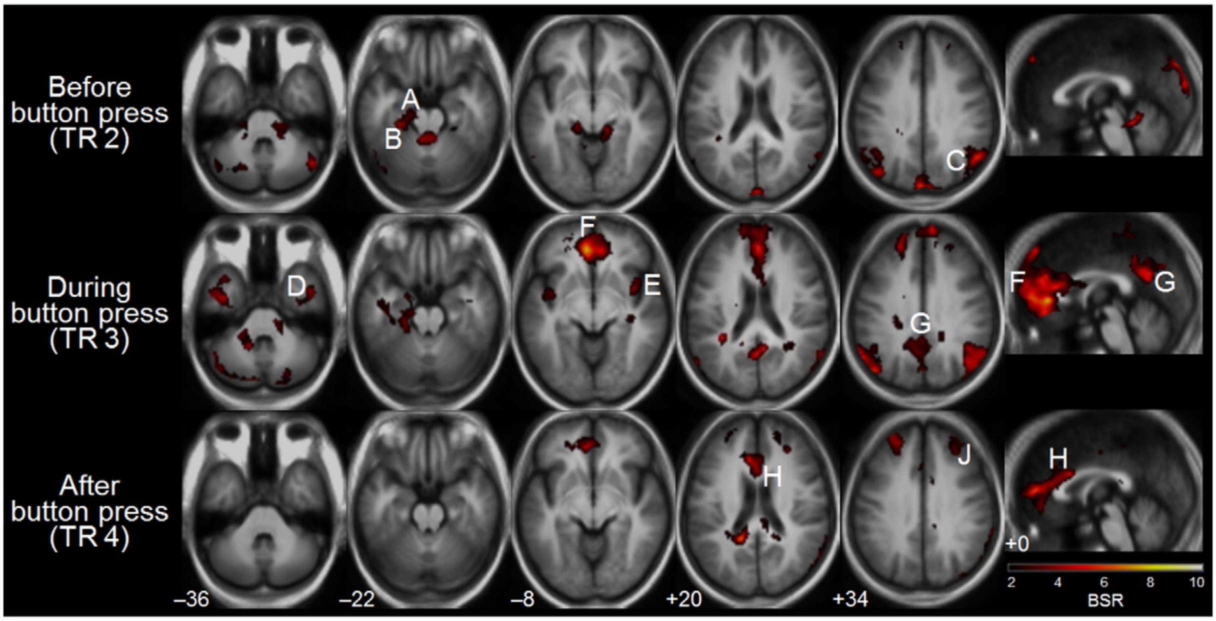

Fig. 7. Progression over time of brain activation associated with spontaneous thought reports, compared to word detection report (*thought* > *word*), based on spatiotemporal Partial Least Squares (PLS) analyses. During spontaneous thought trials, the (A) hippocampus, (B) parahippocampus, and (C) inferior parietal lobule were engaged before the button press (TR 2), while the (D) temporopolar cortex, (E) insula, (F) medial prefrontal cortex, and (G) posterior cingulate cortex were engaged during the button press (TR 3), and the (H) dorsal anterior cingulate cortex and (J) lateral prefrontal cortex were engaged after the button press (TR 4). Results are displayed in neurological orientation, with the right hemisphere depicted on the right, on the average high-resolution structural image and thresholded using a bootstrap ratio (BSR) of 2.576 (equivalent to $p < .01$) and a spatial extent of 50 voxels.

Table 2
Activation over time associated with *thought* events (*thought* > *word*), based on spatiotemporal Partial Least Squares (PLS) analysis.

Region	MNI coordinates						
	L/R/M	BA	*x*	*y*	*z*	BSR	TRs
Frontal							
Medial orbital gyrus (MPFC)	M	11	−8	38	−14	9.52	3*, 4
Dorsal ACC	M	24	−2	18	24	4.11	3, 4*
Middle frontal gyrus (DLPFC)	L	9	−22	40	44	6.68	2, 3*, 4
Middle frontal gyrus (DLPFC)	R	9	28	38	30	4.79	2, 3, 4*
Middle frontal gyrus (RLPFC)	L	10	−22	58	24	3.69	3, 4*
Middle frontal gyrus (RLPFC)	R	10	24	54	24	3.23	3, 4*
Mid-insula	R	13	38	4	−10	4.27	3*, 4
Posterior insula	R	13	48	−10	4	5.26	3*, 4
Supplementary motor area	M	6	4	32	62	3.68	2, 3*
Parietal							
Posterior cingulate cortex	M	31	0	−60	26	5.58	2, 3*,4
Inferior parietal lobule	L	39	−46	−74	32	6.63	2, 3*, 4
Inferior parietal lobule	R	39/40	50	−62	46	7.58	2*, 3, 4
Temporal							
Hippocampus	L	28	−14	−36	0	5.51	2*, 3
Parahippocampus	L	36	−20	−20	−22	3.23	2*, 3
Parahippocampus	R	36	14	−38	−6	4.57	2*, 3
Temporopolar cortex	R	38	46	2	−38	4.54	3*, 4
Superior temporal gyrus	L	22	−64	0	8	4.57	3*
Superior temporal gyrus	R	22	62	−6	8	5.08	3, 4*
Occipital							
Cuneus	M	19	4	−92	28	6.27	2*, 3
Subcortical							
Anterior cerebellum	R	–	28	−32	−30	4.74	2*, 3
Posterior cerebellum	L	–	−46	−64	−38	4.02	2, 3*
Posterior cerebellum	R	–	46	−66	−36	5.01	2*, 3

Note. For each cluster, the TRs of activation are noted, and the peak of activation (from which the bootstrap ratio and coordinates were taken) is indicated by an asterisk. All clusters had bootstrap ratios (BSR) greater than 2.576 (equivalent to $p < .01$) and had a spatial extent of at least 50 voxels.

Recruitment of the medial temporal lobe several seconds before reports of spontaneously arising thoughts is consistent with previous findings from single-cell recordings in humans showing that firing rates in medial temporal lobe neurons can peak up to several seconds before memories spontaneously come to mind (Burke et al., 2014; Gelbard-Sagiv et al., 2008), with only medial temporal lobe antecedent activity correlated with memory performance (Burke et al., 2014). Furthermore, electrical stimulation of medial temporal lobe structures has been found to evoke thought-like or dream-like experiences far more frequently than stimulation of other regions (Fish et al., 1993; Selimbeyoglu and Parvizi, 2010). However, in contrast to these single-cell findings from patients with epilepsy, the present results demonstrate a key role for the medial temporal lobe during the generation of spontaneous thought in a neurologically healthy sample.

The antecedent medial temporal lobe activation that we observed may reflect spontaneously occurring reactivation and recombination of memory traces – a process originally described during sleep but also more recently identified during waking rest (Gelbard-Sagiv et al., 2008). The medial temporal lobe is commonly associated with episodic memory retrieval (Squire et al., 2004), but has also been found to support thinking about the future (Schacter and Addis, 2009), imagining novel situations (Hassabis et al., 2007), and generating creative ideas (Ellamil et al., 2012). It is also consistently recruited in the absence of experimental tasks or during “rest” (Buckner et al., 2008; Christoff et al., 2004; Stark and Squire, 2001). Medial temporal lobe-driven spontaneous reactivation and recombination of memory traces may influence cortical activation patterns (O'Reilly et al., 2014), in the process giving rise to spontaneously retrieved old episodic memories or spontaneously generated novel mental simulations.

Memories or novel simulations are often said to “come to us” — a phrase reflecting the common subjective experience of mental content arising in a bottom-up fashion and capturing our attention reflexively in the process. The neural antecedents identified in the present study are consistent with this subjective experience. Bottom-up attentional orienting towards retrieved memory content has been closely linked to inferior parietal lobule recruitment (Cabeza et al., 2008). The activation of the inferior parietal lobule prior to reports of spontaneous thoughts suggests that reflexive attentional orienting towards spontaneously arising mental content may form an integral early part of the process of spontaneous thought generation. At the same time, the antecedent recruitment of paralimbic areas such as the posterior cingulate cortex, rostral anterior cingulate cortex, and posterior insula may reflect the bottom-up tuning of attention towards salient features in the internal mental stream, including spontaneously generated memories (Leech and Sharp, 2014), affective states (Lane et al., 1997), or body sensations (Craig, 2002).

Some of the neural antecedents observed in the present study – such as activations in the inferior parietal lobule and posterior cingulate cortex – fall clearly within the boundaries of the default mode network (Fig. S1). Other antecedent activations, however – such as, notably, the posterior insula – would be considered well beyond even a liberal boundary of this network (Fig. S1). This suggests that the early inception of spontaneous thought may not be exclusively linked to default mode network functions (for related arguments, see Christoff, 2012; Fox et al., 2015). However, while the present results show antecedent co-activation of brain regions both within and beyond the default mode network, the question of how these brain regions interact and support the early inception of spontaneous thought remains an important subject for further research.

While recruitment of the medial prefrontal cortex, temporopolar cortex, mid-insula, lateral prefrontal cortex, and dorsal anterior cingulate cortex are consistently associated with mind-wandering and related spontaneous thought processes (Fox et al., 2015), none of the antecedent activations identified in the present study were in these brain regions. This is consistent with the idea that these brain regions may be more involved in the subsequent elaboration or evaluation of spontaneous thought rather than its initial generation (Dixon et al., 2014; Fox and Christoff, 2014). The medial prefrontal cortex, temporopolar cortex, and mid-insula have been linked to the binding of emotional and physiological information to external stimuli as well as internal experiences (Craig, 2011; Ochsner and Gross, 2008; Olson et al., 2007). Their recruitment may therefore reflect the automatic affective appraisals of spontaneously generated hippocampal-neocortical firing patterns. Meanwhile, the lateral prefrontal cortex and dorsal anterior cingulate cortex are known to support metacognitive processing and higher-order abstract thought (Carter et al., 1999; Christoff et al., 2009b; Christoff et al., 2001; Fox and Christoff, 2014; Miller and Cohen, 2001). Their recruitment may thus be associated with the metacognitive processing of spontaneously arising mental content, such as their explicit evaluation, categorization, or monitoring. Spontaneous activations in medial temporal and paralimbic structures may serve as inputs to heteromodal association areas, in the process giving rise to internally directed cognition — similar to the way activations in primary and unimodal association regions serve as inputs to heteromodal association areas, in the process giving rise to externally directed cognition (Dixon et al., 2014). Our results are consistent with such a model, but to test this more precisely it would be necessary to examine the generation of spontaneous thoughts using modalities with higher temporal resolution such as electroencephalography (EEG) or human intracranial recordings.

To what extent do experienced mindfulness meditators differ from non-meditators in terms of the neural processes they recruit in association with spontaneously arising thoughts? The recruitment of medial temporal lobe, default mode, and executive control regions during spontaneous thought in the present study closely parallels the pattern of brain activation consistently associated with mind-wandering and spontaneous thought in prior work using non-meditators and conditions that do not require a high level of metacognitive awareness such as “rest” periods and thought probes during easy tasks (Fox et al., 2015). Furthermore, the present findings of medial temporal lobe recruitment preceding spontaneous thought reports in meditators is consistent with similar recruitment prior to spontaneously arising memories in non-meditators (Burke et al., 2014; Gelbard-Sagiv et al., 2008). Mindfulness training has previously been shown to influence the recruitment of default mode, executive control, and viscerosomatic structures, which may reflect their importance for monitoring processes during mindfulness practice (Bærentsen et al., 2010; Brefczynski-Lewis et al., 2007; Ives-Deliperi et al., 2011). However, the amount of meditation experience across participants in our study did not influence the pattern of brain recruitment during spontaneous thought: this pattern remained the same after the amount (i.e., hours) of meditation experience was entered as a covariate of no interest in the fMRI analysis. Thus, our overall findings suggest that the pattern of brain recruitment identified during spontaneous thought in the present study is not necessarily specific to mindfulness practitioners but may instead reflect more general neural processes supporting spontaneous thought.

A number of previous neurophenomenological studies have integrated first-person subjective reports with third-person neural measures. For example, Libet and colleagues (Libet, 1985; Libet et al., 1983) assessed neural recruitment prior to the volitional urge to act. In contrast, the present study assessed neural recruitment during the spontaneous arising of thoughts. Given that some thoughts are associated with the urge to act while others are not, the phenomenon examined here is orthogonal to that assessed by the Libet experiments. In addition, Hasenkamp and colleagues (Hasenkamp and Barsalou, 2012; Hasenkamp et al., 2012) examined neural recruitment around the time when the participant noticed becoming fully absorbed in a train of thought and compared different attentional states during meditation (i.e., mind wandering, awareness, shifting, and focusing). In contrast, the present study examined neural recruitment around the time when the participant detected the initial arising of an individual thought and compared differently generated mental content (i.e., spontaneously arising versus perceptually triggered). Thus, the present study made use of neurophenomenology to investigate the spontaneous onset of thoughts — a distinct aspect of thought that had remained unexamined so far.

Despite the relatively low temporal resolution of fMRI signal, the present results revealed consistent temporal differences in the dynamics of recruitment surrounding the spontaneous arising of thought. Further research will be necessary to determine the precise links between the timing of neural recruitment and the cognitive elements of early thought inception. More specifically, the present findings can be corroborated and further expanded by future investigations employing methods with higher temporal resolution such as magnetoencephalography (MEG) or large-scale human intracranial recordings (e.g., Burke et al., 2014), in combination with more refined phenomenological reporting techniques (e.g., Petitmengin and Lachaux, 2013). This combination of approaches and methodological developments is already beginning to set the stage for the systematic exploration of the neural basis of spontaneous thought — a phenomenon that until recently remained largely off-limits for scientific exploration, but is now well positioned to become part of the neuroscientific mainstream.

5. Conclusions

John Lennon famously sang, “Thoughts meander like a restless wind inside a letter box. They tumble blindly as they make their way across the universe.” What neural systems could give rise to such a wildly divergent stream of consciousness? The prominent hippocampal recruitment among the neural antecedents identified here suggests an intriguing possibility. In contrast to the connectivity of other cortical areas, where short-distance synapses to nearby neurons predominate and long-distance connections are rare, neurons within a large part of the hippocampus are equally likely to connect to nearby or distant neighbors (Buzsaki, 2006). This highly variable microcircuitry may facilitate the creation of arbitrary or unlikely connections between groups of neurons that otherwise encode distinct memories or experiences (Buzsaki, 2006). This capacity for novel connections at the synaptic level might be linked to the variability of spontaneous thought at the subjective level. Although the hippocampus is only one region among those identified here as neural antecedents of spontaneous thought, its role as an indexing system connecting many other brain areas (Teyler and Rudy, 2007) suggests that divergent patterns of hippocampal activation could lead to similarly divergent patterns of activation in other regions throughout the brain. While the specific neural systems underlying the restless nature of our minds remain a mystery, the present findings bring us one step closer to understanding the neural basis of our thoughts' universal meanderings.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2016.04.034.

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