Evidence for the Default Network’s Role in Spontaneous Cognition

Jessica R. Andrews-Hanna,1,3 Jay S. Reidler,1 Christine Huang,1 and Randy L. Buckner1,2,3,4

1Department of Psychology and Center for Brain Science, Harvard, University and 2Howard Hughes Medical Institute at Harvard University, Cambridge; 3Athinaoula A. Martins Center for Biomedical Imaging and 4Departments of Psychiatry and Radiology, Massachusetts General Hospital, Charlestown, Massachusetts

Submitted 10 September 2009; accepted in final form 4 May 2010

Andrews-Hanna JR, Reidler JS, Huang C, Buckner RL. Evidence for the default network’s role in spontaneous cognition. J Neurophysiol 104: 322–335, 2010. First published May 12, 2010; doi:10.1152/jn.00830.2009. A set of brain regions known as the default network increases its activity when focus on the external world is relaxed. During such moments, participants change their focus of external attention and engage in spontaneous cognitive processes including remembering the past and imaging the future. However, the functional contributions of the default network to shifts in external attention versus internal mentation have been difficult to disentangle because the two processes are correlated under typical circumstances. To address this issue, the present study manipulated factors that promote spontaneous cognition separately from those that change the scope of external attention. Results revealed that the default network increased its activity when spontaneous cognition was maximized but not when participants increased their attention to unpredictable foveal or peripheral stimuli. To examine the nature of participants’ spontaneous thoughts, a second experiment used self-report questionnaires to quantify spontaneous thoughts during extended fixation epochs. Thoughts about one’s personal past and future comprised a major focus of spontaneous cognition with considerable variability. Activity correlations between the medial temporal lobe and distributed cortical regions within the default network predicted a small, but significant, portion of the observed variability. Collectively, these results suggest that during passive states, activity within the default network reflects spontaneous, internally directed cognitive processes.

INTRODUCTION

People spend a great deal of time engaged in internally directed thought (Singer 1966). Spontaneous mental explorations, sometimes referred to as “mind-wandering,” punctuate the most demanding tasks and become frequent when people are at rest or performing monotonous activities. Contrary to earlier Freudian notions, spontaneous thought is dominated by typical life events and is minimally focused on fantasy (Singer and Antrobus 1963). Based on these observations, Singer (1966) and Klinger (1971) hypothesized that spontaneous cognition serves an adaptive function by helping us to mentally explore and prepare for upcoming situations.

Multiple lines of evidence suggest that a distributed cortical network, referred to as the “default network,” plays an important role in spontaneous cognition. The default network increases its activity during passive tasks when spontaneous thoughts are at their peak (Binder et al. 1999; Mazoyer et al. 2001; Shulman et al. 1997; also see Christoff et al. 2004), attenuates its activity when externally demanding tasks are made more difficult (Mazoyer et al. 2002; McKiernan et al. 2003, 2006), and is associated with stimulus-independent thoughts (Mason et al. 2007; McGuire et al. 1996; McKiernan et al. 2006; for reviews, see Buckner et al. 2008; Gusnard and Raichle 2001). Additionally, activity within the default network is linked to slowed response time and errors on externally directed tasks (Eichle et al. 2008; Polli et al. 2005; Weissman et al. 2006), presumably because such trials are associated with mind-wandering (Christoff et al. 2009). Lesions to the medial prefrontal cortex (MPFC) sometimes lead to reported loss of thought (e.g., Damasio and Van Hoesen 1983), and metabolic reductions in the MPFC and the posterior cingulate cortex (PCC) are characteristics of physiological states marked by loss of consciousness (reviewed in Baars et al. 2003).

The possibility that the default network is involved in internal mentation is controversial. A prominent alternative account of the default network is that it, or a subset of the regions that comprise the network, play a role in “the representation (monitoring) of the world around us” (Gusnard and Raichle 2001). In almost all situations where attention to the external environment is relaxed and spontaneous cognition increases, a concurrent shift in the focus of external attention occurs such that our awareness broadens, possibly reflecting the anticipation of unpredictable events (Gilbert et al. 2006, 2007).

Several lines of evidence lend credibility to the default network’s possible role in some aspect of external attention or monitoring. Shulman et al. (1997) noted in the first meta-analysis of the default network that modulation of the network was most pronounced when task blocks involved foveal stimuli. In addition, parietal lesions extending along the posterior midline can lead to simultanagnosia, a common feature of Balint’s syndrome where patients lack the ability to perceive multiple objects in their environment (Hécaen and de Aujariguerra 1954). However, Balint’s syndrome is often linked to posterior lateral lesions and the relationship between lesion loci and their corresponding functional deficits is unclear (for discussion, see Rizzo and Vecera 2002).

Support for the role of the MPFC and PCC in broad external attention comes from functional magnetic resonance imaging (fMRI) studies of attention to external stimuli. In particular, MPFC and PCC—nexus of connectivity within the default network (Andrews-Hanna et al. 2010; Buckner et al. 2008; Fransson and Marrelec 2008; see also Hagmann et al. 2008)—increase their activity during perceptual tasks in which targets appear randomly at one of multiple locations compared with a cued location (Hahn et al. 2007). Hahn and colleagues (2007) also found that activity within certain regions of the default network was correlated with trial-by-trial variability in performance, such that faster responses during peripheral target
detected were linked to activity increases. A similar finding was observed when participants performed a low-demanding foveal baseline task, leading to the suggestion that the default network supports stimulus-oriented thoughts, or “watchfulness” for upcoming stimuli (Gilbert et al. 2006, 2007). Note that these results contrast with those that demonstrate inverse relationships between default network activity and behavioral performance on externally directed tasks (e.g., Weissman et al. 2006).

Existing studies have thus linked activity within the default network to two opposing functions: 1) internal mentation and 2) attention to or monitoring of the external environment. Although the two hypotheses differ with respect to their emphases on external compared with internal processing modes, they have been difficult to disentangle because of the inherent challenge associated with measuring cognition during unconstrained states that lack a behavioral response. The main goal of the present studies was to adjudicate between these two plausible, but opposing, hypotheses about the functions of the default network.

In an initial study, we used fMRI to indirectly measure activity within the default network across three conditions that manipulated spontaneous cognition separately from the scope of external attention. Critically, stimuli were held constant in all three conditions. The subjects simply fixated on a central crosshair while expectations differentially modulated the direction and scope of their attention across the conditions. Results were consistent with a role of the default network in spontaneous cognition but not broad or focal attention to the external environment. In a second study, we probed the content of participants’ spontaneous thoughts and found that participants reported frequent thoughts about the past and future. Using a large sample of participants (n = 139), we demonstrated that the propensity for such thoughts was associated with functional coupling between the medial temporal lobe (MTL) and distributed cortical regions that are within the default network. Collectively, these results are most consistent with the role of the default network in spontaneous, internally directed cognition.

METHODS

Overview

The first objective of the present set of experiments was to distinguish between two prominent, but opposing, hypotheses implicating the default network in external attention or spontaneous cognition. The distinct hypotheses have been difficult to disentangle because the two variables often track each other and because of the inherent challenge associated with measuring spontaneous cognition during unconstrained states. Here we tested the two hypotheses by contrasting fMRI signal changes as an indirect measure of neural activity during fixation blocks that varied with respect to scope of external attention (broad and focal) and frequency of spontaneous thoughts as a measure of internal mentation. During conditions designed to encourage external attention, participants detected brief flickers occurring in either peripheral (broad) or central (focal) locations. In contrast, during a condition designed to encourage spontaneous cognition, participants passively fixated on a crosshair. To ensure that variables were manipulated as expected, an independent group of participants completed an identical paradigm in a mock MRI simulator. For these participants, randomly presented tones were placed throughout the tasks to gauge participants’ frequency of spontaneous thoughts.

Three different hypotheses about the expected results were entertained. If the default network plays a prominent role in external attention in general (i.e., watchfulness for upcoming stimuli; Gilbert et al. 2007), the contrast between the external attention conditions and the passive condition should isolate regions within the default network. If the default network plays a specific role in broad external attention, as suggested by a number of prior studies, the contrast between the broad and focal external attention conditions should elicit activity within the default network. If, on the other hand, the default network functions to support internal mentation, activity within the network should track reported measures of spontaneous cognition and should be weakest in the external attention conditions (both broad and focal). Of course an additional possibility is that distinct regions within the default network may enable broad attention and spontaneous cognition, respectively.

Our second objective was to explore the nature of participants’ spontaneous thoughts and to examine whether the individual variability underlying such thoughts was predicted by functional coupling between regions comprising the default network. Since prior studies have established that the MTL and distant cortical regions including the retrosplenial cortex (Rsp), posterior inferior parietal lobule (pIPL), and MPFC become engaged when participants remember their past and imagine their future, we investigated whether the tendency to experience spontaneous episodic thoughts about the past and future predicted functional coupling between the MTL and the default network. A significant relationship would strengthen support for the network’s role in certain forms of spontaneous cognition.

Participants

In all, 199 right-handed young adults participated in the study (22.2 yr, range: 18–35 yr, 97 male; Table 1). Participants were native English speakers recruited from Harvard University and the greater Boston community. Exclusion criteria included a history of psychiatric or neurological illness as well as use of psychoactive medications. Procedures were carried out according to the guidelines put forth by either the Harvard University Committee on the Use of Human Subjects in Research (experiment 1: behavioral) or the Review Board of Partners Healthcare at Massachusetts General Hospital (experiment 1: fMRI and experiment 2).

Task paradigms and questionnaires

Experiment 1 (Overview). To test between the two prominent hypotheses about the function of the default network, three conditions were explored that varied the direction and scope of attention by manipulating expectations: 1) broad attention, 2) focal attention, and 3) passive fixation. During critical task blocks used for analysis, stimuli were held constant and no responses were made in any

<table>
<thead>
<tr>
<th>TABLE 1. Participant demographics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Study</td>
</tr>
<tr>
<td>-------</td>
</tr>
<tr>
<td>Total*</td>
</tr>
<tr>
<td>Study 1</td>
</tr>
<tr>
<td>Mock MRI through sampling study</td>
</tr>
<tr>
<td>Functional MRI study</td>
</tr>
<tr>
<td>Study 2</td>
</tr>
</tbody>
</table>

*Within study 1, the participants who completed the thought sampling study were distinct from those who completed the functional MRI study (indicated by boldface entries). However, 19 participants comprising study 2 also volunteered for the functional MRI study comprising study 1; thus n = 199 represents the number of data sessions (there were 180 independent participants).
condition (Fig. 1). Only expectancies and ancillary processes linked to focus of attention and spontaneous cognition differed.

A block-designed paradigm was used where blocks of fixation across the three conditions alternated with baseline blocks consisting of an abstract/concrete semantic classification task on visually presented words. Note that the baseline here is different from most prior neuroimaging studies; the active task block serves as a common baseline for the three critical fixation conditions that provide the test of the hypotheses. Participants completed a total of six task runs, each comprised of six 30-s fixation blocks flanked by seven 20-s blocks of the baseline semantic classification task. Participants performed one condition at a time across two consecutive runs and condition order was counterbalanced across participants.

In the broad attention condition, participants were instructed to remain fixated on a central fixation crosshair for the duration of each fixation block and to concurrently press a button whenever a brief flicker was detected somewhere in the periphery of the visual display. A peripheral flicker was marked by a gray X that appeared for ~30 ms at one of three eccentricities (corresponding to visual angles: 1.4, 2.8, 4.2°) and eight angles (0, 45, 90, 135, 180, 225, 270, 315°), yielding 24 possible locations for each flicker. Importantly, unbeknown to the participants, flickers were omitted from four blocks and these blocks lacking flickers were the targets of analysis to compare across conditions. In the focal attention condition, participants were told that flickers would occur directly on top of the central fixation crosshair (marked by a gray X that appeared for 67 ms). Again, flickers were omitted from four unpredictable blocks. In the passive fixation condition, participants were instructed to fixate on the fixation crosshair but not to respond during these blocks because no flickers would occur.

To encourage top-down modulation of attention, participants were told that flickers would occur infrequently, were informed of the importance of detecting each flicker as fast as possible, and were discouraged from detecting false positives. Flickers appeared only briefly and were difficult to detect. Four lists that varied in the total number of blocks containing flickers (some lists included flickers in the abbreviated fixation block inserted to allow for intensity stabilization of the blood oxygenation level dependent [BOLD] signal), the total number of flickers per run (three to six), and the onset of the flickers within the run were created and counterbalanced across participants to ensure that the broad and focal conditions did not systematically differ in the onset of flickers. As mentioned earlier, four fixation blocks within each run were matched across conditions with respect to stimuli since flickers did not appear in these blocks. These blocks were the targets of analysis. Thus for the purpose of the fMRI analysis, only expectations and focus of external attention differed between conditions. The same onsets used for fixation blocks extracted from the focal attention runs were also extracted from the passive runs. Blocks in which false-positive key-press responses occurred were removed from analysis in all conditions.

**Experiment 1 (Behavioral Study).** An underlying assumption of the study was that the passive condition would encourage more spontaneous cognition than the broad or focal external attention conditions. To test this assumption, we conducted a separate behavioral thought sampling study during which an independent group of participants (n = 30, 24.5 yr, range: 18–35 yr, 17 male) completed the same six task runs while spontaneous thoughts were sampled throughout each run. Five tones within different fixation blocks were sounded during each run. Lists were created that varied the placement of the tones within the run and these lists were counterbalanced across subjects to ensure that the broad and focal conditions did not systematically differ in tone placement. Participants were asked to classify their thoughts whenever a tone sounded by stating aloud the word “thought” if they experienced a spontaneous thought unrelated to the task at hand immediately prior to the tone or “nothing” if a task-unrelated thought was not experienced. The specific instructions are listed below:

I Now, there is one additional component to this experiment. At random times while the fixation crosshair is on the screen, a brief tone will occur that sounds like a ring. Here is an example: [sample tone played]. When you hear the tone, we would like you to classify what you were thinking about immediately before the tone sounded. If your mind was wandering and you were thinking about something unrelated to the task at hand, please say the word “thought” out loud. For example, you may have been thinking about something that you did last night or something you should do on your way home. Or you may have been thinking how tired or hungry you are. If you were thinking about either of these types of things or about something else that was not related to the task at hand, please say the word “thought” out loud. You should not press anything.

2 On the other hand, if your mind was not wandering and you were thinking about the flickers, the fixation crosshair, or nothing at all, you should say the word “nothing” out loud. For example, you may have been wondering where or when the flicker is going to appear or thinking about the features of the fixation crosshair—for example, its color or size. Or you may have not been thinking about anything at all, meaning your mind was completely blank. What all these types of activities have in common is that they are not thoughts that are unrelated to the task. Therefore if you experience something that falls into this category, you should say the word “nothing” out loud. Again, you should not press anything.

3 Flickers will not occur during or immediately after a tone—therefore you should not rush through your response to the tone for the sole purpose of being able to detect flickers afterward. Instead, think carefully about your response before you say it because you will be allowed to state only one of the two options, either “thought” or “nothing.” At the same time, you should remember that your primary task in this experiment is to determine whether words are abstract or concrete and to detect the flickers.

An important aspect of the behavioral study was that participants performed the experiment while lying in a mock MRI simulator...
In this "tag on" study, a large number of participants (spontaneous thoughts. To obtain a large sample size, we added this were examined between distributed brain regions in addition to objective reports of spontaneous cognition for each condition. As in the behavioral study, we reasoned that by introducing a small number of tones to monitoring during the online thought probe study, they may have thoughts into explicit awareness and leaving fewer thoughts as un- 

correct techniques. Although the online thought sampling method re- 

quired less reliance on long-term memory compared with the retro- 

spective questionnaire, it is possible that the online method caused 

participants to monitor the nature of their thoughts, bringing more thoughts into explicit awareness and leaving fewer thoughts as un- 

aware (for discussion, see Smallwood and Schooler 2006). In addition, 

since participants may have experienced more thoughts relating to 

monitoring during the online thought probe study, they may have encountered difficulty determining whether these thoughts were task-unrelated. We reasoned that by introducing a small number of tones per run (n = 5) as well as emphasizing in the task instructions that the thought probe aspect of the study was secondary to the primary 

flicker/fixation task, participants would dedicate minimal time to 

monitoring their thoughts. Importantly, the retrospective thought sampling questionnaire was also given to the independent sample of 30 young adults who completed the experimental task in an MRI scanner (see following text).

Experiment 1 (fMRI Study). The fMRI study was conducted in an independent sample of participants matched on age and gender (n = 30, 21.7 yr, range: 18–31 yr, 17 male) using the identical experimental paradigm as outlined earlier, with the exception that the online thought probes were not present, nor were participants instructed to monitor the nature of their spontaneous thoughts so as not to interfere with performance on the primary task. As in the behavioral study, surprise postscanning questionnaires were distributed to gather subjective reports of spontaneous cognition for each condition.

Experiment 2. Low-frequency functional correlations (coupling) were examined between distributed brain regions in addition to spontaneous thoughts. To obtain a large sample size, we added this study to ongoing studies in our laboratory where time permitted. For this "tag on" study, a large number of participants (n = 139, 21.8 yr, range: 18–32 yr, 63 male) fixated on a crosshair for between two and 

four runs. The duration of each run varied between 4 min 20 s and 6 min 30 s depending on the context of the existing study.

In all cases, thought content was probed immediately after the participants exited the MRI scanner using a surprise questionnaire. The goal of the questionnaire was to estimate the content of spontaneous cognition using the best approach available. The approach has limitations including the ability of the participants to remember their thoughts and the possibility that they may not have conscious access to all aspects of their thought content. Nonetheless, motivated by past successes using self-report questionnaires (e.g., Andrews-Hanna et al. 2010; Kirchhoff and Buckner 2006; Mason et al. 2007), we used such an approach here recognizing these potential biases and limitations.

For the assessment, participants were asked to divide a blank circle to reflect the total amount of time they spent thinking about each of 14 a priori categories of thought during the fixation runs (see categories in Table 2). This approach encouraged the participants to make relative judgments about whether one category was represented more than another and also encouraged them to allocate the total time during fixation. The resulting pie chart percentages were measured with a protractor. Three versions of the questionnaire were randomly distributed to participants, each with a different order of categories. The nontemporal category was described as "thinking about something with no particular temporal domain (e.g., problem solving an idea; thinking about what the purpose of the experiment is)." If individuals chose the category “other” (represented in Table 2 as “uncategorized”) and were unable to categorize their response, they were further asked to write examples of such types of thoughts that could not be identified by the remaining categories. This allowed us to leave open the possibility that our categories were inadequate. The most frequent response for the uncategorized domain included “covertly singing.” The pie chart shown in Fig. 8 collapsed categories into the composites in bold in Table 2.

For purposes of the present experiment, total thoughts pertaining to the past and the future were calculated for each participant and were regressed against participants’ low-frequency functional correlation maps. See the following text for details.

MRI data acquisition parameters

Anatomical and functional data were acquired using a 3 Tesla Siemens Tim Trio scanner (Siemens, Erlangen, Germany) and a

<table>
<thead>
<tr>
<th>Category</th>
<th>Mean, %</th>
<th>SD</th>
</tr>
</thead>
<tbody>
<tr>
<td>Past</td>
<td>19.2</td>
<td>26.6</td>
</tr>
<tr>
<td>Earlier today</td>
<td>7.3</td>
<td>9.5</td>
</tr>
<tr>
<td>Yesterday to a week ago</td>
<td>9.1</td>
<td>9.8</td>
</tr>
<tr>
<td>Past year or several years</td>
<td>3.8</td>
<td>7.3</td>
</tr>
<tr>
<td>Future</td>
<td>28.7</td>
<td>32.1</td>
</tr>
<tr>
<td>Remainder of the day</td>
<td>12.7</td>
<td>13.1</td>
</tr>
<tr>
<td>Tomorrow to next week</td>
<td>11.5</td>
<td>10.8</td>
</tr>
<tr>
<td>Next year or several years</td>
<td>4.5</td>
<td>8.2</td>
</tr>
<tr>
<td>Nontemporal</td>
<td>15.4</td>
<td>16.0</td>
</tr>
<tr>
<td>Stimuli</td>
<td>10.3</td>
<td>14.0</td>
</tr>
<tr>
<td>Fixation crosshair</td>
<td>6.3</td>
<td>8.0</td>
</tr>
<tr>
<td>Additional stimuli</td>
<td>4.0</td>
<td>6.0</td>
</tr>
<tr>
<td>Mind Blank</td>
<td>5.0</td>
<td>10.2</td>
</tr>
<tr>
<td>Other</td>
<td>21.4</td>
<td>42.5</td>
</tr>
<tr>
<td>Counting</td>
<td>7.4</td>
<td>15.0</td>
</tr>
<tr>
<td>Focused meditation</td>
<td>5.6</td>
<td>9.3</td>
</tr>
<tr>
<td>Sleeping</td>
<td>3.3</td>
<td>6.6</td>
</tr>
<tr>
<td>Uncategorized</td>
<td>5.1</td>
<td>11.6</td>
</tr>
</tbody>
</table>

Listed in boldface are the composite measures used for Fig. 8. Below some composite measures are the categories comprising each composite.
12-channel phased-array head coil. Three-dimensional T1-weighted, high-resolution anatomical images were acquired using a magnetization-prepared rapid acquisition gradient echo (MP-RAGE) sequence (repetition time [TR] = 2,530 ms, time to echo [TE] = 3.39 ms, 1 × 1 × 1 mm voxel size). A gradient echo, echo-planar pulse sequence (TR = 2,500 ms, TE = 43 ms, 3 mm slice thickness, 36 axial oblique slices with a 0.5 mm gap aligned to the anterior commissure/posterior commissure plane) sensitive to BOLD contrast was used to acquire functional data across all experiments, except for one data set comprising experiment 2 (TR = 5,000 ms, TE = 30 ms, 2 mm slice thickness, 55 contiguous axial oblique slices). All participants wore MRI-compatible glasses (either corrective or noncorrective lens), were given ear plugs to dampen scanner noise, and responded to visual stimuli (created using Psychophysics Toolbox software; Brainard 1997), visible through an MRI-compatible mirror with a button box placed in their left hand.

**MRI data processing**

A combination of FSL (FMRIB, Oxford, UK) and SPM2 (Wellcome Department of Cognitive Neurology, London, UK) tools were used to prepare functional data for task and connectivity analysis. These steps included 1) removal of the first four frames of each run to eliminate signal variation caused by T1-stabilization (FSL), 2) correction for slice timing to remove differences in acquisition time across slices within each TR (SPM2), 3) motion correction within and across runs using a rigid-body motion correction algorithm that adjusts functional images based on movement calculated across three separate translations and three separate rotations (FSL), 4) registration of functional data to an EPI target template in the space of the Montreal Neurological Institute atlas (SPM2), 5) whole brain reslicing at 2-mm cubic voxels (SPM2), and 6) spatial smoothing using a 6-mm full-width half-maximum Gaussian kernel (SPM2).

**Experiment 1 (fMRI Study).** For fMRI analysis of block-designed task-related data, SPM2 was used to convolve a canonical hemodynamic response function and its temporal derivatives with a boxcar function lasting the length of the experimental task blocks (30 s). A high-pass filter was applied to remove low frequencies commonly associated with scanner drift or other properties unrelated to the tasks. The regressors of interest included the onsets of the four blocks from each condition in which no flickers appeared. The onsets of the remaining blocks were included in the general linear model but were not analyzed. Each subject’s fixed-effects contrasts were entered into a between-subject random-effects analysis using one-sample t-tests.

The 11 regions comprising the default network used for region of interest (ROI) analyses were defined in a separate study (Andrews-Hanna et al. 2010) and include the dorsal MPFC (dMPFC), anterior MPFC (aMPFC), ventral MPFC (vMPFC), PCC, Rsp, left pIPL (pIPL), left temporoparietal junction (TPJ), left lateral temporal cortex (LTC), left temporal pole (TempP), left parahippocampal cortex (PHC), and left hippocampal formation (HF). All 11 regions were combined into a single region representing the larger default network (shown in Fig. 4A). Additionally the activity within the dMPFC (Fig. 4B) and PCC (Fig. 4C) was examined separately.

**MRI correlation analyses (experiment 2)**

Functional correlation analyses procedures used in experiment 2 are based on those introduced by Biswal et al. (1995) and are described in detail in our previous studies (e.g., Van Dijk et al. 2010). A series of preprocessing steps were used to prepare the data for correlation analysis (Fox et al. 2005; Vincent et al. 2006). Data were first temporally filtered to retain only frequencies <0.08 Hz. Next, a series of “nuisance regressors” were created that captured physiological or other nonneural sources of variance. Regressors corresponding to the six translation/rotation parameters from the rigid-body motion correction captured variance related to the participants’ movement over the course of the runs. A regressor corresponding to the signal averaged within a white matter ROI and another regressor corresponding to the signal averaged within a ventricular ROI were also defined. The signal averaged over a whole brain mask was used to capture nonspecific sources of variance including respiration. Finally, the first temporal derivative was included for each regressor to capture temporal shifts in the BOLD signal. The regressors were simultaneously entered into a regression analysis with the voxelwise, whole brain BOLD signal across time. The residual, representing the voxelwise time series controlled for physiological or spurious nonneural sources of variance, was retained for correlation analysis.

Seed-based correlation analyses were accomplished in two ways. First, a linear regression was performed between the time series averaged across all voxels within a combined 8-mm-radius PHC (−28, −40, −12) and 8-mm-radius HF (−22, −20, −26) a priori ROI shown in Fig. 9 (seeds defined in Andrews-Hanna et al. 2010) and the time series within every other voxel in the brain. The regression yielded correlation maps for individual subjects reflecting the strength of correlation between the MTL seed and each brain voxel. These individual subject maps were then entered into a regression analysis with the subjects’ percentage of temporally oriented thoughts to examine which regions functionally coupled to the MTL predicted individual variability in the frequency of such thoughts (Fig. 9).

In addition to whole brain measures of functional correlation, we also used a seed-target approach by examining the correlation strength between all a priori regions comprising an “MTL subsystem” within the default network (for detailed descriptions of the MTL subsystem, see Andrews et al. 2010; Buckner et al. 2008). These regions included HF, PHC, vMPFC, Rsp, and pIPL and represented a subset of those analyzed in experiment 1. As mentioned earlier, the regions were defined in a previous study that demonstrated the role of the MTL and its functionally correlated cortical regions for episodic thought (for coordinates and details, see Andrews-Hanna et al. 2010). When computing correlations between these multiple a priori regions, the averaged sets of time series within each region were cross-correlated with each other. In all cases, correlations were converted to Fisher’s z correlation coefficients for statistical analyses because they are approximately normally distributed.

**RESULTS**

The default network is sensitive to changes in spontaneous cognition but not scope of external attention

**Behavioral results.** To confirm that the passive condition was characterized by increases in spontaneous cognition compared with the broad and focal external attention conditions, data from the behavioral thought sampling study were analyzed (similar to Binder et al. 1999). As predicted, participants experienced significantly more spontaneous thoughts when probed with tones during the passive condition (51.7 ± 6.1%) than during the broad (33.0 ± 5.5%) and focal (38.7 ± 6.3%) conditions (Fig. 2A; one-way repeated-measures ANOVA: F = 5.40, P < 0.01; passive vs. broad paired t-test: t = 3.25, P < 0.01; passive vs. focal paired t-test: t = 2.05, P < 0.05). No difference was observed between broad and focal conditions (broad vs. focal paired t-test, t = −1.07, P = 0.29). Postexperimental subjective mind-wandering reports for each condition mirrored the thought sampling results (Fig. 2B; one-way repeated-measures ANOVA: F = 11.1, P < 0.001; passive vs. broad paired t-test: t = 3.53, P < 0.01; passive vs. focal paired t-test: t = 3.56, P < 0.01; broad vs. focal paired t-test: t = −0.47, P = 0.65).

Participants detected a majority of the flickers, with no significant differences in accuracy and response time (RT) between the external attention conditions (broad accuracy:

---

J Neurophysiol • VOL. 104 • JULY 2010 • www.jn.org
also observed (broad vs. focal: mind-wandering more during the broad than focal condition was repeated-measures ANOVA: 3.7%, paired t-test: *P < 0.001; passive vs. focal paired t-test: t = 3.25, P < 0.01; passive vs. focal paired t-test: t = 3.82, P < 0.001). A nonsignificant trend toward mind-wandering more during the broad than focal condition was also observed (broad vs. focal: t = 1.88, P = 0.07). Across all conditions, participants again reported spontaneous thoughts that were personally significant (mean = 5.40 ± 0.24; scale from 1 to 7, where 1 = never and 7 = always) and moderately goal-oriented in nature (mean = 4.23 ± 0.31).

Participants detected a majority of the peripheral and central flickers, with no difference in accuracy between the two conditions (broad accuracy: 87.6 ± 3.1%; focal accuracy: 88.2 ± 3.6%; paired t-test: t = −0.15, P = 0.88). A trend toward longer RTs was observed in the broad condition (broad RT: 656 ± 25 ms) compared with the focal condition (focal RT: 605 ± 21 ms; paired t-test: t = 1.97, P = 0.06).

Regional fMRI results. Hypothesis-driven ROI analyses were performed using three a priori regions within the default network that were defined in a previous study (Andrews-Hanna et al. 2010) and overlap previous fMRI meta-analyses using our scanning and analysis procedures (e.g., Buckner et al. 2008, 2009). These ROIs included 1) a large composite region (mask) comprised of 11 identically sized midline and left-lateralized default network regions, 2) a region located in the aMPFC, and 3) a region located in the PCC. The aMPFC and PCC are considered “hubs” of the default network (Andrews-Hanna et al. 2010; Buckner et al. 2008) and have also been implicated in broad external attention in previous studies (see Hahn et al. 2007).

In support of the internal mentation hypothesis, activity within the default network ROI was significantly higher during the passive condition compared with that during the broad and focal conditions (Fig. 4A; one-way repeated-measures ANOVA: F = 46.2, P < 0.001; passive vs. broad paired t-test: t = 7.98, P < 0.001; passive vs. focal paired t-test: t = 9.22, P < 0.001). In contrast, we did not observe significant differences between the broad and focal conditions (broad vs. focal paired t-test: t = 1.54, P = 0.13). Similarly the aMPFC and PCC ROIs, paralleling the behavioral observations, exhibited increased activity during the passive condition with no difference between the broad and focal conditions (aMPFC: Fig. 4B; one-way repeated-measures ANOVA: F = 33.4, P < 0.001; passive vs. broad paired t-test: t = 7.14, P < 0.001; passive vs. focal paired t-test: t = 7.90, P < 0.001; broad vs. focal paired t-test: t = 0.89, P = 0.38; PCC: Fig. 4C; one-way repeated-measures ANOVA: F = 24.2, P < 0.001; passive vs. broad
paired $t$-test: $t = 6.34, P < 0.001$; passive vs. focal paired $t$-test: $t = 6.50, P < 0.001$; broad vs. focal paired $t$-test: $t = 0.59, P = 0.56$. Thus initial results are consistent with the idea that the default network supports spontaneous cognition.

**Temporal fMRI results.** Next, we examined the time course of activity for the three conditions (Fig. 5). Activity within the passive condition increased rapidly as contrasted with either of the external attention conditions. More detailed inspection revealed that activity within the default network increased for both the broad and focal attention conditions as the epochs elapsed in time, more so for the broad condition compared with the focal condition (Fig. 5A). With the consideration that both conditions were associated with mind-wandering, these results are consistent with the possibility that participants tended toward mind-wandering as time progressed, with a slightly greater tendency in the broad condition. Critically, the time courses revealed no difference between the broad and focal attention conditions during the first 15 s of the fixation blocks when task motivation was presumably greatest. During this initial time period, there was an increase in default network activity in the passive condition compared with that in either of the two external attention conditions. Here, there was no evidence of a difference between the broad and focal conditions even at the level of a trend. Similar observations were observed for the time course of activity within the aMPFC (Fig. 5B) and the PCC (Fig. 5C).

**Broad attention demonstrated effects distinct from the default network**

Next, whole brain exploratory analyses were conducted to directly examine the effects of broad external attention. Although previous ROI analyses did not reveal a role for the larger default network in broad attention, it is possible that smaller regions within the large ROI, or perhaps regions adjacent to those examined, support broad attention. As illustrated in Fig. 6, greater activity during the broad attention condition was observed in the dorsal and ventral aspects of the medial occipital cortex, including the putative human homolog of macaque area V6, the transverse occipital sulcus (TOS), collateral sulcus (CoS), parietotemporal sulcus (POS), as well as the posterior aspect of the precuneus (at or near area 7m). In contrast, a region near the lateral occipital area (LO) exhibited greater activity during the focal attention condition. Such findings correspond to those of previous studies examining differences in brain activity when viewing peripheral stimuli separately from focal stimuli (e.g., compare Fig. 6 in this study with Fig. 5 in Levy et al. 2004), but are inconsistent with studies highlighting the role of the default network in broad external attention (e.g., Hahn et al. 2007). Area V6 contains neurons with wide receptive fields (Pitzalis et al. 2006) and is contiguous with the posterior cingulate cortex. The image insets (top left in each panel) show the regions plotted in either transverse (A) or sagittal (B and C) views. Error bars reflect SE. ***$P < 0.001$. 

**FIG. 4.** Hypothesis-driven analyses reveal increased activity within the default network during the passive condition. Significantly increased fMRI blood oxygenation level-dependent (BOLD) signal (an indirect measure of activity) was observed during the passive condition compared with either the broad or focal attention conditions. BOLD signal is measured as percentage signal change compared with baseline. This pattern was observed in A, a large region of interest comprising multiple regions within the default network; as well as in B, the anterior medial prefrontal cortex; and in C, the posterior cingulate cortex. The image sections (top left in each panel) show the regions plotted in either transverse (A) or sagittal (B and C) views. Error bars reflect SE. ***$P < 0.001$. 

The whole brain analyses also yielded a result potentially relevant to reconciling past assertions that the default network is involved in some aspect of external attention. The default network is often loosely described as involving all of the precuneus, including regions along the dorsal extent of the midline that likely encroach on area 7m. Based on careful examination of macaque connectional anatomy and task activation in humans we have previously hypothesized that the region at or near the precuneus area 7m is likely not part of the default network (Buckner et al. 2008). Note that we use the term “at or near” because we cannot be certain of homology or areal boundaries in humans. Putative area 7m in humans, which is likely a component of the dorsal visual stream, is contiguous with regions of the posterior cingulate that receive widespread connections from distributed regions of cortex (for further discussion, see
Fig. 5. The time course of activity within the default network across conditions. The time course of the BOLD signal is plotted for the critical fixation epochs for each condition. BOLD signal is measured as percentage signal change compared with the abstract/concrete baseline task. The timing of each block is outlined below (C = cue). Dotted lines separate fixation blocks into 2 distinct 15 s epochs. In all regions, there was an increase in activity in the passive condition compared with either the broad or focal attention conditions. This difference emerged rapidly with the onset of the manipulation. What is also apparent is that the activity observed in the broad and focal conditions in Fig. 4 is largely accounted for by activity increases that occur late in the task epochs. This is most clear in A where the activity in the broad and focal conditions is absent in the first 15 s of the block. Error bars reflect SE.
processes, we conducted another fMRI study in which a large
percentage of the time (mean = 7.1%, SD = 2.5%) spontaneous thought during the epochs of passive fixation). The selected categories and corresponding percentages, however, varied across individuals (Table 2). Participants spent very little time thinking about the actual fixation stimulus (mean = 6.3%, SD = 8.0%) or any other stimuli in the study (mean = 4.0%, SD = 6.0%). Additionally, participants reported their mind being blank only a small percentage of the time (mean = 5.0%, SD = 10.2%). Stimulus-independent thoughts associated with active mental activity were reported the majority of time, with a preference toward thinking about the past (mean = 19.2%, SD = 26.6%) and the future (mean = 28.7%, SD = 32.1%; Fig. 8; Table 2). Consistent with previous behavioral studies examining the temporal trajectory of autobiographical thoughts (D’Argembeau and Van der Linden 2004, 2006; Spreng and Levine 2006), the past and immediate future were attributed the highest percentage. These results suggest that personal thoughts about the recent past and near future dominate the focus of spontaneous cognition in fMRI paradigms that elicit activity across the default network.

Thoughts about the past and future correlate with functional interactions between the medial temporal lobe and cortical regions within the default network

The medial temporal lobe contains structures necessary for autobiographical recall (Scoville and Milner 1957; Squire et al. 2004) and recent observations suggest a role in imagination and prospection (Buckner 2010; Hassabis et al. 2007; Klein et al. 2002; Schacter and Addis 2009). Stark and Squire (2001) noted that hippocampal activity during passive states renders

Spontaneous cognition is frequently directed toward the past and the future

The previous analyses support the hypothesis that the default network participates in spontaneous cognition and is not primarily modulated by attention to the external environment, even when unpredictable stimuli in the periphery were the targets. Although past observations suggest that individuals engage in "freely wandering past recollection, future plans, and other personal thoughts and experiences" (Andreasen et al. 1995) and construction of “alternative hypothetical behavioral patterns to be ready for what may happen” (Ingvar 1979) during passive states, a quantitative characterization of what individuals think about under typical fMRI rest state conditions is presently lacking.

To explore the content associated with such spontaneous processes, we conducted another fMRI study in which a large sample of participants classified the categories and frequency of their mental activity after fixating on a crosshair for an extended duration (between 10 and 30 min). Participants completed a quantitative questionnaire, attributing the percentage of total time they spent thinking about each of 14 a priori categories of thought on a blank pie chart (Table 2). Overall, participants reported experiencing a diverse array of thought content during the passive epochs (mean = 7.1%, SD = 2.5%; different forms of spontaneous thought during the epochs of passive fixation). The selected categories and corresponding percentages, however, varied across individuals (Table 2). Participants spent very little time thinking about the actual fixation stimulus (mean = 6.3%, SD = 8.0%) or any other stimuli in the study (mean = 4.0%, SD = 6.0%). Additionally, participants reported their mind being blank only a small percentage of the time (mean = 5.0%, SD = 10.2%). Stimulus-independent thoughts associated with active mental activity were reported the majority of the time, with a preference toward thinking about the past (mean = 19.2%, SD = 26.6%) and the future (mean = 28.7%, SD = 32.1%; Fig. 8; Table 2). Consistent with previous behavioral studies examining the temporal trajectory of autobiographical thoughts (D’Argembeau and Van der Linden 2004, 2006; Spreng and Levine 2006), the past and immediate future were attributed the highest percentage. These results suggest that personal thoughts about the recent past and near future dominate the focus of spontaneous cognition in fMRI paradigms that elicit activity across the default network.

Thoughts about the past and future correlate with functional interactions between the medial temporal lobe and cortical regions within the default network

The medial temporal lobe contains structures necessary for autobiographical recall (Scoville and Milner 1957; Squire et al. 2004) and recent observations suggest a role in imagination and prospection (Buckner 2010; Hassabis et al. 2007; Klein et al. 2002; Schacter and Addis 2009). Stark and Squire (2001) noted that hippocampal activity during passive states renders
Fixation a particularly poor experimental control condition for memory encoding tasks. Similarly, Christoff et al. (2004) reasoned that robust MTL activity during passive rest suggests that “long-term memory processes may form the core of spontaneous thought flow.” Furthermore, the MTL functionally correlates in a selective manner with components of the default network (Andrews-Hanna et al. 2010; Greicius et al. 2004; Kahn et al. 2008; Vincent et al. 2006) and tasks that require subjects to actively remember the past and envision the future show increased activity in the hippocampus and adjacent medial temporal structures as well as a number of core default network regions (Buckner et al. 2008; Schacter et al. 2007). Given the involvement of the MTL in the default network, we reasoned that the frequency with which participants engaged in temporally oriented thoughts would predict the nature of the interaction between the MTL and the default network.

To explore this relationship in the present experiment, we extracted individual functional correlation (fcMRI) maps with a seed region in the MTL in 139 participants. We then performed a whole brain regression of participants’ fcMRI maps with their respective measures of thoughts about the past and future. Individuals who reported a higher percentage of such thoughts exhibited increased functional correlations between the MTL and several regions that fall within the default network, including vMPFC, Rsp, and pIPL (Fig. 9). Functional correlation with the pIPL highlighted in our previous studies (Kahn et al. 2008; Vincent et al. 2006) exhibited the most robust relationship. We recently demonstrated that the pIPL, vMPFC, and Rsp tightly couple together, comprising an MTL-correlated subsystem within the default network that supports episodic memory retrieval and future prediction (Andrews-Hanna et al. 2010). Interpreted in this context, these results provide support for a functional contribution of the default network in spontaneous episodic thoughts. However, it should be noted that the results are somewhat limited by their correlational nature. For example, episodic thoughts may covary with other forms of cognition such as retrieval of semantic information or overall frequency of spontaneous thoughts (e.g., Binder et al. 1999, 2009).

To confirm the brain–behavior relationship between frequency of spontaneous thoughts and functional coupling within the default network, all pairwise z-transformed correlation coefficients between regions comprising the MTL subsystem (vMPFC, Rsp, pIPL, PHC, and HF: regions defined in Andrews-Hanna et al. 2010) were averaged into a composite measure of subsystem strength. This composite measure was then regressed against the percentage of time individuals reported experiencing spontaneous thoughts about the past and future. The predicted positive relationship was observed between MTL fcMRI and temporally oriented thoughts ($r = 0.18; P < 0.05$; two-tailed $t$-test; Fig. 10). Note that the amount of variance accounted for in the low-frequency spontaneous BOLD fluctuation is small. As Fig. 10 shows, five subjects reported no past or future oriented thoughts (falling on the $y$-axis line) and showed among the lowest levels of MTL functional correlations. The group correlation remained significant when these individuals were removed from analysis.

Spontaneous low-frequency fluctuations are present during sleep and anesthesia, suggesting that the major contribution is likely unrelated to the cognitive state of the participant and more likely constrained by invariant anatomical connectivity (for discussion, see Fox and Raichle 2007; Van Dijk et al. 2010). The observation that changes in task state can modulate the strength of default-network coupling (e.g., Buckner et al. 2009; Fransson 2006; J Sepulcre, H Liu, T Talukdar, I Martinoorena, BTT Yeo, and RL Buckner, unpublished data) suggests that a portion of intrinsic default-network activity is related to cognitive processes that fluctuate over short time-scales. The present results show that within the portion of spontaneous activity that is linked to awake, cognitive operations, a significant (but modest) amount of the variance across individuals is accounted for by participants’ tendencies to think about the past and future.

**Discussion**

Here we reveal multiple lines of evidence that implicate the brain’s default network in spontaneous cognition. We first used fMRI to dissociate two plausible cognitive processes occurring during passive states that have previously been linked to the default network. Results revealed robust activity increases in the default network when participants were engaged in a passive task that maximized spontaneous cognition, compared with tasks that maximized focal and broad external attention. Next, to explore individual variability in spontaneous cognition and the neural correlates of this individual variability, we examined the relationship between functional activity correlations within the default network and spontaneous thoughts. Episodic thoughts about the past and the future were associated with increased functional coupling between the MTL and specific cortical regions within the default network. Collectively, our results provide evidence that the default network
functions to support spontaneous cognition, particularly about significant personal past events and future goals.

**Internally guided thought involves spontaneous projection of oneself into alternative settings**

Our results suggest that humans use available moments to engage in spontaneous, internally directed thought. Spontaneous cognition (or “mind-wandering”) is a common and likely adaptive phenomenon (Klinger and Cox 1987; Singer and Antrobus 1963; Singer and McCraven 1961; for reviews see Buckner et al. 2008; Smallwood and Schooler 2006). We demonstrate here that even short epochs were sufficient to elicit prominent spontaneous cognition (>50% of time). Our results are consistent with prior reports using thought sampling techniques during blocks of passive fixation (Binder et al. 1999) and behavioral findings that note reciprocal relationships between attentional demands and spontaneous thoughts (Antrobus et al. 1966; McKiernan et al. 2006; Smallwood et al. 2008; Teasdale et al. 1995).

The content of participants’ spontaneous thought speaks to its possible function. Klinger (1971) proposed the “current concern hypothesis,” suggesting that humans mind-wander primarily about matters of self-importance. Here we show that during short epochs, a majority of thoughts were personally significant in nature and more than half were oriented toward a particular goal. One participant reported thinking about “events that happened during the weekend [and] what’s for dinner,” whereas another reported “what I’d do after leaving here—either go meet up with [my] significant other at his place or run home and get work done for tomorrow.” Still another wrote, “Well, I am moving in two days, so I find myself writing mental ‘to do’ lists and lists of things I had still to pack, and also just imagining life in a new apartment, new city, etc.” Consistent with these examples, quantitative analysis of the nature of participants’ thoughts during longer passive epochs revealed that participants spent a majority of their time thinking about their past and future, especially the recent past and immediate future. Pondering over our recent past may allow us to consolidate significant events, whereas envisioning our personal future enables us to entertain plausible future scenarios, “experiencing” them before they happen (Atance and O’Neill 2001; Gilbert and Wilson 2007). Broadly speaking, these likely adaptive phenomena deserve additional scientific attention.

**Activity increases within the default network are associated with spontaneous cognition**

Given that humans spend a great deal of time engaged in spontaneous cognition, we suspected the presence of a brain system to support it. Although passive states encourage spontaneous cognition, they may also encourage widely different cognitive processes, including exploratory monitoring of the external environment or enhanced watchfulness for upcoming stimuli. Such externally oriented processes have been previously linked to the default network (Gilbert et al. 2005, 2006, 2007).
Medial temporal lobe and functionally correlated regions are associated with spontaneous episodic thought

The present results provide support for the role of the MTL and a wider cortical brain system in spontaneous episodic thought. Results from functional correlation analyses reveal a positive relationship between temporally oriented thoughts and activity correlations between the MTL and other regions comprising the default network. These regions include bilateral vMPFC, pIPL, and Rsp, all corresponding to the MTL subsystem within the default network that may support memory retrieval and prospection (Andrews-Hanna et al. 2010; Buckner et al. 2008). Task activation paradigms reveal similar brain regions when participants recall their personal past and envision their possible future (e.g., Addis et al. 2007; Andrews-Hanna et al. 2010; Botzung et al. 2008; D’Argembeau et al. 2010; Okuda et al. 2003; Szpunar et al. 2007). Our results suggest that the MTL subsystem is used spontaneously, in a manner that relates to episodic thoughts about the past and the future. Combined with a number of behavioral demonstrations revealing similarities between the two temporal domains (Addis et al. 2008; D’Argembeau and Van der Linden 2006; Spreng and Levine 2006), these results are consistent with the notion that individuals draw on details from their past and flexibly recombine these details into novel future events.

Early work conducted by the psychologist Edward Tolman highlighted the flexible recombination of past events in the rat (Tolman and Gleitman 1949; Tolman et al. 1946). More recently, spontaneous activity patterns within the hippocampus have been dissociated from the rats’ immediate local cues, reminiscent of the findings in the present study. Consistent with the role of the MTL in memory and prediction, hippocampal activity patterns elicited during stopped periods reflect prior environmental input and, under certain conditions, correlate with the animal’s future choices, including errors in behavior (Buckner 2010; Diba and Buzsáki 2007; Foster and Wilson 2006; Johnson and Redish 2007; Lisman and Redish 2009; Pastalkova et al. 2008). An interesting speculation is that these activity patterns emitted spontaneously in the rodent may be a protoform of the more complex and controlled human skills such as creativity and innovation. These complex, yet flexible cognitive processes likely rely on continual interplay between the MTL and the cortical regions that have come to be known as the “default network.”

An interesting line for future research will be to examine the putative role of the default network in particular aspects of internal mentation (i.e., autobiographical memory and prospection) in relation to other more basic functions such as retrieval of semantic information (Binder et al. 2009), integration of imagery-based information into a coherent scene (Andrews-Hanna et al. 2010; Hassab is and Maguire 2007), or rapid retrieval of contextual associations (Bar 2007). Many such processes are likely at play during periods of rest and may represent the building blocks of more complex processes such as reminiscing and planning. Interpreted in this context, thoughts about the past and the future measured in experiment 2 may index participants’ tendency toward semantic retrieval or other such functions mentioned earlier, making the brain–behavior correlations difficult to interpret. Thus although the present results lend support to a link between the default network and spontaneous thoughts—especially about the past and the future—these thoughts may be a correlate of other cognitive processes. Again, a broad implication of the present results is a call for detailed and systematic study of spontaneous cognition and its adaptive functions.

Acknowledgments

We thank T. Hedden and R. Poulin for assistance with data collection; D. Schacter, M. Bar, I. Kahn, J. Vincent, F. Krienen, and three anonymous reviewers for helpful discussion; and A. Snyder for generously providing assistance in implementing the fcMRI processing tools.
GRANTS
This work was supported by National Institute on Aging Grant AG-021910 and the Howard Hughes Medical Institute.

DISCLOSURES
No conflicts of interest, financial or otherwise, are declared by the author(s).

REFERENCES


Fox MD, Raichle ME. Spontaneous fluctuations in brain activity observed with functional magnetic resonance imaging. Nat Rev Neurosci 8: 700–711, 2007.


