

Consistency and functional specialization in the default mode brain network

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The notion of a “default mode of brain function” has taken on certain relevance in human neuroimaging studies and in relation to a network of lateral parietal and midline cortical regions that show prominent activity fluctuations during passive imaging states, such as rest. In this study, we perform three fMRI experiments that demonstrate consistency and specialization in the default mode network. Correlated activity fluctuations of default mode network regions are identified during (i) eyes-closed spontaneous rest, (ii) activation by moral dilemma, and (iii) deactivation by Stroop task performance. Across these imaging states, striking uniformity is shown in the basic anatomy of the default mode network, but with both tasks clearly and differentially modulating this activity compared with spontaneous fluctuations of the network at rest. Against rest, moral dilemma is further shown to evoke regionally specific activity increases of hypothesized functional relevance. Mapping spontaneous and task-related brain activity will help to constrain the meaning of the default mode network. These findings are discussed in relation to recent debate on the topic of default modes of brain function.

activation | deactivation | default mode | functional MRI | spontaneous activity

The notion of a “default mode of brain function” has emerged as a compelling but controversial topic in neuroimaging research (1–4). At its core, it suggests the existence of an ongoing and anatomically organized mode of neuronal activity that is preferentially engaged in the brain and that is suspended only during specific goal-directed behaviors (3). In humans, this default mode system has been linked, in part, to the spontaneous thought processes or self-oriented mental activity that define the brain’s “resting state” (3, 5). To this end, the extent to which functional imaging studies of rest may help to further clarify the behavioral meaning of default mode activity, has been recently debated (1, 2, 4, 6).

The default mode network was originally identified in positron emission tomography (PET) studies and refers specifically to a set of cortical regions that show common activity decreases or deactivations when subjects perform cognitively demanding tasks (3). These regions include the posterior cingulate cortex and precuneus, the inferior parietal cortices, and dorsal and ventral areas of the medial frontal cortex (3, 7–9). The consistency of this observation, together with knowledge of the brain’s basic metabolic requirements at rest, lead to the proposal that this deactivation pattern may represent an organized mode of brain function whose primary role may be to support internally oriented mental processes in humans (3, 10). Importantly, ensuing studies with functional magnetic resonance imaging (fMRI) have both confirmed and extended original findings to show that the default mode network can be readily seen as deactivations in task-related fMRI experiments (11–14), can also be identified as a pattern of resting-state functional connectivity

(15–20), and may associate with specific profiles of spontaneous oscillations of electrical brain dynamics (21, 22).

Despite the robustness of the default mode network phenomenon in neuroimaging experiments, its precise meaning with respect to behavior is not well defined. From existing studies, the default mode network has been associated indirectly with the pattern of evoked activity that is observed with tasks involving self-judgments, autobiographical memory recall, moral dilemma, and prospective thinking, among others (5, 20, 23–25). In general terms, a common feature of these tasks is that they enhance subjects’ attention toward themselves—a presumed behavioral correlate of resting-state imaging conditions and the spontaneous thought processes, or “mind-wandering,” that accompany it (26). However, others have questioned this line of inference, arguing that the “cognitive nature at rest is at present almost entirely a matter of speculation” (ref. 2, p. 1079) and, instead, advocate the use of specific tasks to identify factors responsible for the consistency and variability within these findings.

This study sought to further constrain the meaning of default mode network function by jointly investigating its activity across three distinct fMRI contexts: task-related activation, task-related deactivation, and rest. We asked two broad but related questions: First, will the activity of default mode network regions show anatomical consistency across these distinct imaging contexts? If so, then the use of fMRI tasks to probe or “unpack” the behavioral meaning of the default mode network may prove viable, as recently proposed (2). Second, assuming some consistency exists, to what extent may tasks differentially activate default mode network regions, which have a characteristically high activity level at rest (3)? To approach this second question, we compared patterns of correlated blood oxygen level-dependent (BOLD) signal fluctuations of default mode network regions observed during a resting-state and moral dilemma experiment in the same subjects.

Results

Task Performance. Moral dilemma was chosen as the specific context to study “activation” of default mode network regions based on our own and others recent findings (25, 27, 28). Briefly, subjects ($n = 22$) responded to 24 moral dilemma and 24 memory control (non-moral dilemma) task vignettes that were presented

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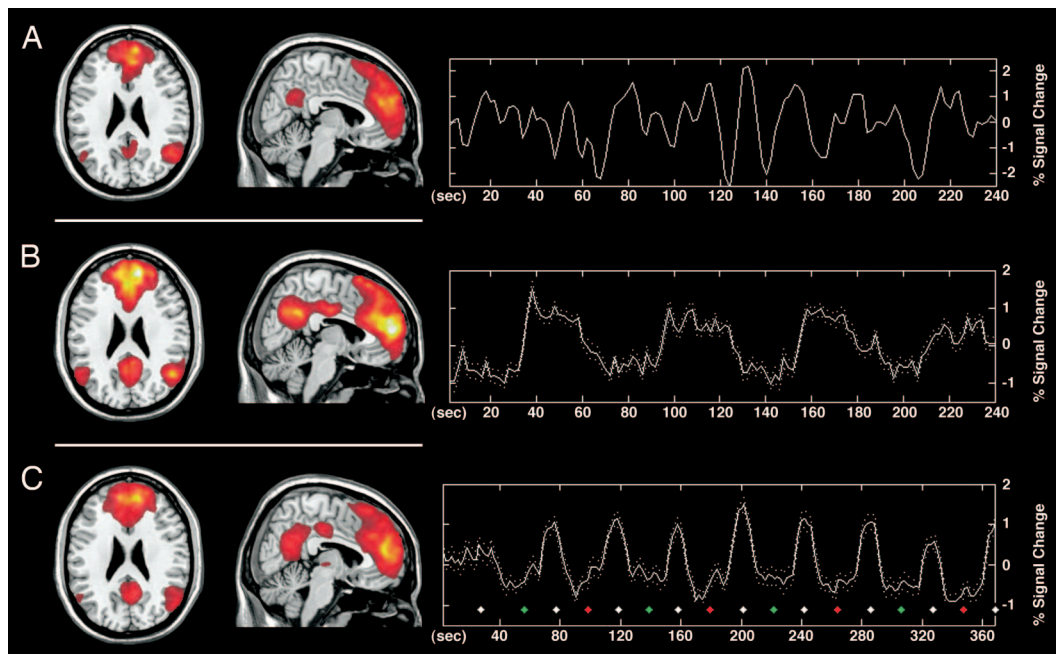


Fig. 1. Default mode network activities across the three imaging states. (A) Spontaneous activity in the default mode network during rest and the associated time course of a representative subject (z score range = 3.5 to 7). (B) Task-related activity of the default mode network during the moral dilemma experiment and the associated mean (solid line) and standard error (dotted line) time course estimated across all subjects (z score range = 3.5 to >8). (C) Task-related activity of the default mode network during the Stroop task experiment and the associated mean (solid line) and standard error (dotted line) time course estimated across all subjects (z score range = 3.5 to 7). Diamonds located below this time course correspond to the approximate middle point of each Stroop task block. White diamonds, rest-fixation periods; green diamonds, congruent trials; red diamonds, incongruent trials. Image display: left = right.

audio-visually in a block-design fMRI experiment [see full details in [supporting information \(SI\) Materials and Methods](#) and [SI Appendix](#)]. Performance-wise, subjects made correct responses to 95.3% of the control task vignettes (4.7% incorrect responses, including omissions). For the moral dilemma condition, the mean pattern of responses to each specific vignette is provided in [SI Appendix](#).

Consistent with the hypothesized role for emotion in moral judgment (28), subjects rated the moral dilemma vignettes as significantly higher in negative emotional intensity and lower in positive emotional intensity compared with the control vignettes in a postscanning interview (Fig. S1; $P < 0.001$).

To study “deactivation” of default mode network regions, a self-paced version of the Stroop color-word interference task was used (see [SI Materials and Methods](#)). Briefly, subjects responded to standard congruent and incongruent Stroop color-naming trials that were interleaved with rest-fixation periods in a block-design experiment. The analysis of response error and reaction time (RT) scores confirmed subjects’ attentional engagement during both of the task blocks (see results in [SI Materials and Methods](#)).

Identification of Default Mode Network Activity. fMRI-BOLD data were analyzed by using combined group independent component analysis (ICA) and statistical parametric mapping techniques (29). Group ICA was performed for each fMRI experiment separately, generating three sets of results that were investigated further with statistical comparisons. Full description of this analysis strategy is provided in [SI Materials and Methods](#).

For each experiment, we identified a statistically significant pattern of spatially correlated BOLD signal activity [an independent component (IC)] that reproduced the major anatomical features of the default mode network ($P_{FDR} < 0.05$). This was tested further and directly, using a spatial sorting analysis that estimated the spatial correlation of all IC patterns from a given

set of Group ICA results with an anatomical template of the default mode network created by using a Talairach and Tournoux (30) atlas labeling system (see [SI Materials and Methods](#)). In each case, the default mode network pattern that we identified from each Group ICA demonstrated the highest correlation to this anatomical template with respect to other estimated ICs (Pearson’s r range = 0.40 to 0.60).

Fig. 1 shows the default mode network patterns and their associated time courses that were identified in each of the fMRI experiments. For each of these observations, primary clusters of activity were located in the dorsal and polar medial frontal cortex, ventral posterior cingulate cortex, the inferior parietal and frontal cortices and lateral cerebellum. The corresponding anatomical coordinates of all regional activities and their associated statistical magnitudes and extents are provided in Table 1.

After the initial spatial identification of networks, a temporal sorting analysis was performed to determine the degree of “task-relatedness” of the moral dilemma and Stroop task default mode network patterns. For each set of ICA results, the associated time course for all ICs was correlated with an idealized reference function (task waveform) of the moral dilemma and Stroop experiments, respectively. In both cases, the identified default mode networks (Fig. 1 B and C) demonstrated the highest correlation to each corresponding task waveform of the relevant task periods.

As seen in Fig. 1B, the degree of task-relatedness of the default mode network activity pattern to the moral dilemma task was strong. This pattern was positively and most robustly correlated with the specific moral dilemma condition blocks (Pearson’s $r = 0.53$) relative to other estimated ICs. Similarly, the degree of task-relatedness of the default mode network pattern to the Stroop task was also high (Fig. 1C). This pattern was positively and most robustly correlated with the interleaved rest-fixation periods during Stroop task performance (Pearson’s $r = 0.53$) relative to other estimated ICs.

Table 1. Default mode network regions demonstrating significant activity in the fMRI resting-state, activation (moral dilemma) and deactivation (Stroop task) experiments

| Region | Resting state | | | | | Moral dilemma | | | | | Stroop deactivation | | | | | | |
|---------------------------|---------------|-----|-----|-------------|------|---------------------------|---------|-----|-----|------------|---------------------|---------------------------|---------|-----|-----|------------|------|
| | Anatomy* | | | Statistics† | | Region | Anatomy | | | Statistics | | Region | Anatomy | | | Statistics | |
| | x | y | z | CS | z | | x | y | z | CS | z | | x | y | z | CS | z |
| Medial frontal gyrus | -9 | 56 | 19 | 3,266 | 6.97 | Medial frontal gyrus | -9 | 50 | 17 | 5,242 | >8 | Medial frontal gyrus | -9 | 51 | 20 | 4,548 | 7.10 |
| Inferior parietal lobe | -48 | -54 | 25 | 344 | 6.02 | Posterior cingulate gyrus | 3 | -51 | 30 | 1,087 | 6.98 | Mid cingulate gyrus | -0 | -18 | 37 | 131 | 5.88 |
| Posterior cingulate gyrus | -3 | -54 | 30 | 126 | 4.82 | Inferior parietal lobe | -50 | -57 | 28 | 604 | 6.98 | Posterior cingulate gyrus | -6 | -51 | 27 | 639 | 5.43 |
| Inferior frontal gyrus | 45 | 25 | -19 | 71 | 4.75 | Inferior parietal lobe | 53 | -57 | 28 | 383 | 4.90 | Inferior parietal lobe | -53 | -63 | 28 | 346 | 5.29 |
| Cerebellum | -33 | -77 | -27 | 26 | 3.99 | Inferior frontal gyrus | 48 | 28 | -11 | 70 | 4.31 | Inferior frontal gyrus | 45 | 26 | -11 | 139 | 4.38 |
| Inferior temporal gyrus | -56 | -10 | -20 | 27 | 3.80 | Cerebellum | 24 | -74 | -29 | 79 | 4.22 | Inferior frontal gyrus | -39 | 23 | -14 | 151 | 4.26 |
| Inferior frontal gyrus | -40 | 31 | -13 | 13 | 3.41 | Inferior frontal gyrus | -45 | 25 | -16 | 72 | 4.13 | Cerebellum | -33 | -77 | -22 | 79 | 4.22 |
| Parahippocampal gyrus | -37 | -8 | -16 | 7 | 1.68 | Cerebellum | -31 | -71 | -30 | 40 | 4.04 | Parahippocampal gyrus | -32 | -5 | -23 | 12 | 1.88 |

CS, cluster size. Consistent with some (e.g., ref. 20) but not other (e.g., ref. 16) fMRI studies of the default mode network, activity in the parahippocampal region was also observed during the resting-state and Stroop task experiments, albeit at a subthreshold level ($P < 0.05$ uncorrected).

*Activity coordinates (x, y, z) are given in Talairach and Tournoux Atlas (30) space. Imaging coordinates were transformed from SPM-Montreal Neurological Institute (MNI) to Talairach space using the Brett transform implemented in GingerALE (www.brainmap.org).

†Magnitude and extent statistics correspond to a minimum threshold of $P_{FDR} < 0.05$ (range 0.05 to 0.0001).

Anatomical Comparison of Identified Networks. After the initial identification of default mode network activity patterns, our first aim was to assess the consistency of the spatial anatomy of the network across the three imaging contexts—activation, deactivation and rest. The primary intention of this analysis was to determine the extent to which the task-related activity patterns may reproduce the spontaneous anatomy of the network as characterized at rest. This was performed by calculating the percentage of common and unique voxel space in each activity map in a series of pairwise statistical comparisons (see *SI Materials and Methods*).

With reference to Fig. 2A, a spatial overlap of 97.3% was observed from the resting-state to dilemma task activity map, such that the dilemma map reproduced almost the entire voxel space of the default mode network represented at rest. The dilemma activity map was also 41.6% larger in additional voxel space compared with rest—an effect that was expressed predominantly in the anterior, mid, and posterior cingulate regions; right inferior parietal cortex; and dorsolateral frontal cortex.

With reference to Fig. 2B, a spatial overlap of 94.7% was observed from the resting-state to Stroop task activity map, such that the Stroop map also reproduced the original voxel space of the default mode network at rest. The Stroop task activity map was also found to be 48.5% larger in additional voxel space compared with rest—an effect that was expressed predominantly in the anterior, mid, and posterior cingulate cortex regions.

To extend the above approach, a group-level conjunction analysis was conducted to test the statistical consistency of default mode network regional activities across the three imaging states (see *SI Materials and Methods*). These results are presented in Fig. S2 and confirm a significant overlap in the correlated activity of major default mode network regions across all experiments (see also Table S1).

Functional Comparison of Identified Networks. Having confirmed a high degree of anatomical consistency of default mode network activity across the three experiments, our second aim was to investigate the extent to which the moral dilemma task may evoke specific changes (i.e., activity increases) in default mode network regions compared with their spontaneous activity at rest.

As a first approach, we performed a volume-of-interest (VOI) analysis that was designed to test the selectivity of changes in default mode network regions that had a common level of activity in both

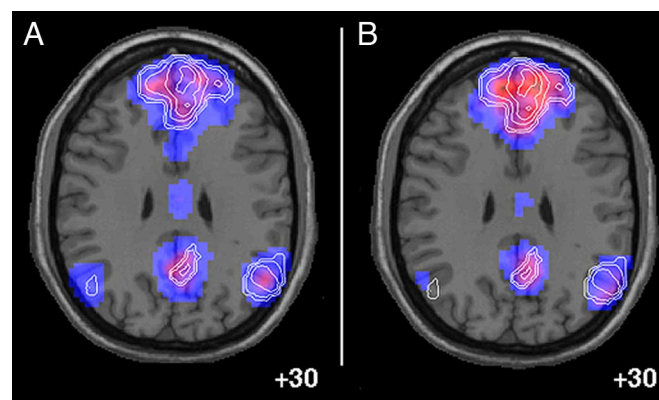


Fig. 2. Anatomical overlap of default mode network activities. (A) Representative axial slices showing the moral dilemma activation map (color) overlaid with the corresponding anatomy of the default mode network at rest (white contour lines). (B) Representative axial slices showing the Stroop task deactivation map (color) overlaid with the corresponding functional anatomy of the default mode network at rest (white contour lines). Image display: left = right.

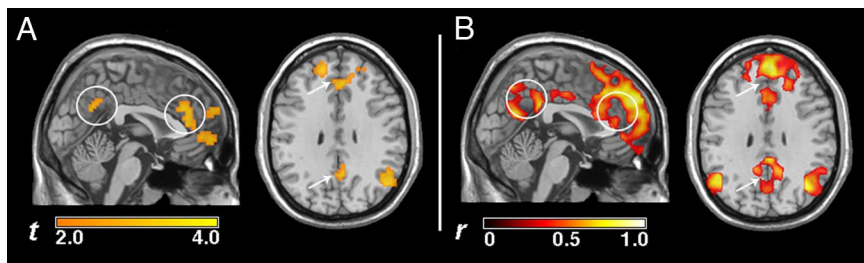


Fig. 3. Functional specialization in the default mode network. (A) Default mode network regions that showed relatively greater spatially correlated activity during the moral dilemma task compared with rest. (B) Default mode network regions whose spatially correlated activity at rest predicted their strength of correlated activity during the moral dilemma task. White circles and arrows indicate posterior and anterior cingulate cortex regions. Image display: left = right.

experimental states. VOI placements were determined by a conjunction analysis that identified regions having a consistent significant effect in both experiments ($P_{\text{FDR}} < 0.05$; see *SI Materials and Methods*). Fig. S3 shows the placement of all VOIs and regions whose activity was selectively increased during the moral dilemma task compared with rest. These regions included the medial frontal cortex/rostral anterior cingulate cortex, ventral posterior cingulate cortex, and bilateral inferior parietal cortices.

As a second approach, the specificity of regional differences in default mode network activity between the resting-state and moral dilemma experiments was further tested. This was done by performing a voxelwise mean difference analysis (paired samples t test) of the correlated activity maps that were identified in both experiments after scaling the activity range of each image (see *SI Materials and Methods*). Relative to rest, the strength of spatial correlations among specific default mode network regions was found to be greater during moral dilemma, but not vice versa. As shown in Fig. 3A, regions included the superior and polar medial frontal cortex, left inferior parietal cortex, ventral posterior cingulate cortex, and rostral anterior cingulate cortex (all P values < 0.005 , uncorrected; see Table S2).

Finally, we tested the extent to which spontaneous activity of default mode network regions may predict their corresponding task-evoked activity during the moral dilemma experiment. This was examined in a pairwise cross-correlation analysis of the z score activity maps identified from the resting-state and moral dilemma experiments. Fig. 3B shows the mean pattern of cross-correlations that were estimated within all default mode network regions. The highest cross-correlations were observed primarily in neocortical areas including the dorsal medial frontal cortex ($r > 0.90$) and inferior parietal cortices ($r > 0.80$). By comparison, the lowest cross-correlations were observed in two subregions of the cingulate system, the ventral posterior cingulate cortex and rostral anterior cingulate cortex ($r < 0.10$).

Discussion

Our results show that the basic anatomy of the default mode network was remarkably consistent from its resting-state organization to associated activity patterns during two distinct functional imaging tasks. This consistency emerged not as patterns of unmodulated or spontaneous activity that persisted throughout the tasks but as clear activity fluctuations that were dependent on each task's behavioral context. The nature of these fluctuations during moral dilemma lends credibility to the idea that default mode network function is, in part, associated with self-referential mental processes in humans.

Anatomical Consistency of the Default Mode Network. The first aim of this study was to test the consistency of default mode network observations made across the distinct functional imaging contexts of task-related activation, task-related deactivation, and rest. To date, such consistency has been inferred from specific analyses of task-related deactivation of brain regions, using PET

(3, 7, 9) and, to a lesser extent, from recent studies of resting-state functional connectivity (16, 31). As discussed by Raichle *et al.* (3) “whereas cortical increases in activity have been shown to be task specific and, therefore, vary in location depending on task demands, many decreases appear to be largely task independent, varying little in their location across a wide range of tasks” (p. 676). However, beyond this well studied deactivation phenomenon, the extent to which default mode network activity may be anatomically coherent in adult subjects across other imaging states has to our knowledge not been directly assessed.

Our current findings indeed confirm that a strong overlap exists in the basic functional anatomy of the default mode network when studied during rest, as a deactivation during cognitive task performance, and, additionally, as a functional activation during a moral dilemma paradigm. The consistency of this observation was highlighted by the fact that both task-related activity patterns identified here recapitulated almost entirely the resting-state organization of this network—in both cases sharing $\approx 95\%$ of its resting-state voxel space (Fig. 2). This finding appears to support recent work that has emphasized the intrinsic nature of default mode network activity in functional imaging studies, having now been observed in non-human primates (31, 32) and in studies of human subjects during sleep (33). However, what our findings also suggest is that full interpretation of the consistency of default mode network activity across different imaging contexts should be extended beyond the spatial-anatomical domain.

Functional Modulation of Default Mode Network Activity. Unlike some studies that have reported enduring spontaneous or resting-like activities of the default mode network under passive or non task-related imaging states, including sleep and anesthesia (11, 20, 31, 33), the default mode network patterns that we identified in association with moral dilemma and Stroop task performance were clearly and differentially modulated by each task. For the dilemma experiment, this was observed as a positive correlation between the network's time course and the specific moral dilemma condition blocks (Fig. 1B), whereas, for the Stroop task, this occurred as a positive correlation with the rest-fixation periods (Fig. 1C). At the level of brain function, this “on–off” modulation in each time course reflects, theoretically, patterns of both stronger and weaker spatial correlations of BOLD signal activity across time between the implicated default mode network regions.

To what extent do these on–off modulations during moral dilemma represent activation and/or functional connectivity of the default mode network? Similar to conventional activation mapping approaches, this type of modulated covariance in functional imaging studies may represent brain regional activities that are truly covariant (i.e., “functionally connected”) during the specific performance of a task, or those regions whose activities are more simply coactivated, but not functionally coupled, as a result of task performance (34). However, if these

activity fluctuations are characterized within a clearly and consistently defined functional network, as suggested by our results, then this type of modulated covariance may be best interpreted as a pattern of task-related functional connectivity among implicated regions.

Task-related functional connectivity of the default mode network may be particularly informative if demonstrated as a spatial decoherence between spontaneous and evoked BOLD signal activity changes. This phenomenon was investigated recently in a study of the visual cortex, where spatial decoherence defined a shift in the global pattern of spontaneous correlations of this system at rest (“coherence”), into specific patterns of stronger and weaker spatial correlations in parts of this system (“decoherence”) reflecting their functional specialization in response to different visual stimuli/task demands (35).

Consistent with the previous idea, we observed relative increases in the specificity and strength of spatial correlations of certain default mode network regions during the moral dilemma task compared to rest. Within this pattern of changes, some regions demonstrated especially high correlations with their spontaneous activity at rest, whereas others demonstrated almost no linear correlation at all (Fig. 3B). This result also appears to further inform functional specialization in the default mode network, distinguishing regions whose activity was common to the resting-state and moral dilemma experiments and those whose activity may have been more specific to the task condition.

Functional Specialization in the Default Mode Network. If the moral dilemma task does evoke functional specialization in the default mode network, which specific processes may this represent? In work by Greene and colleagues (27, 28) on the functional correlates of moral dilemma, these authors emphasized a specific role for emotion in the act of moral judgment and linked this to corresponding activations of anterior and posterior cingulate cortex regions. Notably, this activation was greatest in the context of personal versus impersonal moral dilemmas, relative to nondilemma conditions, and particularly when personal moral judgments were most difficult to make. We added to these findings by showing that equivalent activation of default mode network regions could be obtained during moral dilemma as well as a passive task condition where subjects received feedback about prior moral judgments (25). It was suggested that self-reference and emotion were relevant factors in sustaining/evoking activity of default mode network regions (see also ref. 5).

Existing imaging studies have highlighted, in particular, the rostral anterior cingulate cortex as one brain region that shows a prominent activation-deactivation duality depending on the relative emotional versus cognitive demands of imaging tasks (5, 36, 37). In the former case, activation of this region has been associated mostly with withdrawal related emotions, such as fear, sadness, and guilt (38), that may be augmented if experienced in an autobiographical context (39).

Ventral posterior cingulate cortex also demonstrates sensitivity to different forms of emotional stimulation in imaging studies, but is also responsive to nonemotive stimuli (24, 40). On the basis of such findings, it has been argued that emotional-related activity in this region might represent a general role in monitoring for the self-relevance of previously coded sensory events, and where emotional content itself is assigned and stored in subregions of the anterior cingulate cortex (40). This proposal is appealing, because it may potentially explain the known links between posterior cingulate function, spatial orientation and episodic memory, two important but distinct domains of self-referential processing (24, 40).

Unlike cingulate regions, activity in the dorsal medial frontal and inferior parietal cortices was highly correlated during the resting-state and moral dilemma experiments, suggesting some

commonality of function. Based on a recent meta-analysis of studies of self-referential imaging tasks, dorsal medial frontal cortex activity was discussed with reference to higher cognitive aspects of self-referential processing, such as reappraisal and evaluation of self-relevant stimuli (24). Such activity appears to generalize to a variety of imaging contexts, across different sensory domains, and irrespective of emotion.

The idea that emotional versus cognitive aspects of self-referential processing may be dissociated among default mode network regions has some empirical basis (5, 24, 25, 27, 28, 39–41) and offers a straightforward account of the current findings. Further work exploring differences between internally and externally evoked self-referential activity in the context of resting and task-related fMRI may be useful for expanding such accounts.

Cognitive Demand and Default Mode Network Activity. Considered in the development of our moral dilemma paradigm was the strict need to control the amount of cognitive effort that was demanded from subjects when performing the task in-scanner. Put simply, the task was designed to be maximally emotionally provocative and minimally cognitively demanding. The influence of cognitive demand in deactivating the default mode network is well known and may be appreciated even during the moral dilemma task itself, where the control condition, which involved simple memory recalls, may have also to some extent deactivated the network (Fig. 1B). However, more salient by comparison, was the pattern of deactivation that emerged during the performance of the Stroop task (Fig. 1C).

Task-induced deactivations of the default mode network have been typically reported from imaging contrasts of resting-state or low demand task conditions compared with periods of cognitively demanding task performance (e.g., refs. 11 and 12). In the case of a rest minus task comparison, the appearance of default mode network regions generally signifies their greater activity during rest (or less apparent activity during tasks) and hence are labeled as “deactivated.”

At first glance, our current results appear to indicate a biphasic response of this network to task performance, with both a true anticorrelated response (signal decrease) coinciding with the task blocks and a subsequent increase in signal after each of the performance blocks during rest (Fig. 1C). Thus, if one assumes a baseline as the initial pretask resting-state period (first 32 s), these observations appear to suggest that there was activation of the default mode network during the nontask rest-fixation periods. However, if one considers this initial pretask resting period as nonbaseline, then the observed fluctuations may be more suggestive of a classic deactivation effect. This may be the most accurate interpretation, because “first scan effects” have been identified from data-driven analyses of functional imaging data and as a presumed correlate of pretask arousal or anxiety (42).

Other Considerations. Although ICA methods have shown good utility in separating potential noise sources in task and resting-state fMRI studies, including aliased physiological signals associated with the cardiac (vascular pulsation) and respiratory (chest movement) cycles (15, 29, 43), we cannot entirely rule out the influence of these signals in this study without direct physiological monitoring. We were also unable to quantify the influence of slow variations in subjects’ breathing rate and volume (reflected as small variations in arterial CO₂) on the extracted BOLD signal measurements (44). Nevertheless, the consistency among the default mode network activity patterns reported here does reduce the concern about such artifacts, given that their influence may be expected to vary distinctly across the three imaging conditions.

Conclusions

We report a high degree of anatomical consistency between direct assessments of default mode network brain activity under fMRI activation, deactivation, and resting-state conditions. The moral dilemma paradigm, in particular, was illustrative in showing that a full expression of this network's activity could be obtained in a controlled experimental context that de-emphasized the influence of rest. The nature of this activity supports the idea that default mode network regions are, in part, functionally devoted to self-referential processes in humans.

Although much remains to be known about the physiological basis of spontaneous BOLD signal fluctuations (45), understanding their relationship with the common task-evoked activity patterns reported in fMRI studies appears to be of prime importance. Our findings add constructively to recent debate on the topic of "default modes of brain function" (2, 4) and suggest that these systems can be approached with the standard tools of imaging neuroscience, but with equal focus given to a role for spontaneous brain activity in shaping their functional organization.

Materials and Methods

Twenty-two healthy subjects (12 female; 10 male; mean age \pm SD = 26.0 \pm 3.5 years) were assessed with fMRI during (i) eyes-closed spontaneous rest; (ii) the performance of a novel moral dilemma paradigm; and (iii) the performance of a self-paced version of the Stroop task. Correlated spontaneous and task-related activity among default mode network regions was identified by using group independent component analysis (ICA), followed by specific further tests of the anatomical and functional consistency/specificity of these correlated BOLD signal activity maps within subjects.

For full description of this study's materials and methods, see *SI Materials and Methods* and *SI Appendix*.

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