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Performance-Related Activity in Medial Rostral Prefrontal Cortex (Area 10) During Low-Demand Tasks

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Neuroimaging studies have frequently observed relatively high activity in medial rostral prefrontal cortex (PFC) during rest or baseline conditions. Some accounts have attributed this high activity to the occurrence of unconstrained stimulus-independent and task-unrelated thought processes during baseline conditions. Here, the authors investigated the alternative possibility that medial rostral PFC supports attention toward the external environment during low-demand conditions. Participants performed a baseline simple reaction time (RT) task, along with 3 other tasks that differed in the requirement to attend to external stimuli versus stimulus-independent thought. Medial rostral PFC activation was observed in the baseline task and in a condition requiring strong engagement with external stimuli, relative to 2 conditions with a greater requirement for stimulus-independent thought. An important finding was that activity in this region was associated with faster RTs in the baseline task, ruling out an explanation in terms of task-unrelated thought processes during this condition. Thus, at least under certain circumstances, medial rostral PFC appears to support attention toward the external environment, facilitating performance in situations that do not require extensive processing of experimental stimuli.

Keywords: area 10, default mode, anterior prefrontal cortex, medial prefrontal cortex, simple reaction time

Periods of rest, in which participants are not instructed to perform any particular task, and simple baseline tasks such as passive fixation of visual stimuli have been associated with increased activity in certain brain regions relative to cognitive tasks requiring more extensive processing and manipulation of experimental stimuli. The location of these brain regions shows remarkable consistency across studies, despite the wide range of cognitive tasks investigated (involving such disparate domains as perceptual monitoring, visual attention, language, and memory). These regions have therefore been hypothesized to participate in a "default mode of brain function" (Raichle, MacLeod, Snyder, Powers, Gusnard, & Shulman, 2001), which is suspended during various attention-demanding, goal-directed activities. The structures implicated in this default mode are predominantly located along the medial wall, including the precuneus and posterior cingulate as well as a large expanse of medial rostral prefrontal cortex (PFC) encompassing Brodmann Areas (BAs) 8, 9, 10, and 11 (Binder, Frost, Hammeke, Bellgowan, Rao, & Cox, 1999; Greicius, Krasnow, Reiss, & Menon, 2003; Gusnard, Akbudak, Shulman, & Raichle, 2001; Gusnard & Raichle, 2001; Mazoyer et al., 2001; McKiernan, Kaufman, Kucera-Thompson, & Binder, 2003; Shulman et al., 1997).

Along with "low-demand tasks," defined here as those tasks with a minimal requirement to perform cognitive operations on experimental stimuli, neuroimaging studies have also implicated medial rostral PFC in a wide variety of tasks that may involve reflection on one's own mental states. Examples of such tasks are those involving "mentalizing" (i.e., attributing mental states to others; Frith & Frith, 2003; see also Bird, Castelli, Malik, Frith, & Husain, 2004); social cognition (Iacoboni et al., 2004); moral decision making (Greene, Sommerville, Nystrom, Darley, & Cohen, 2001); emotional decision making (Damasio et al., 2000; Lane, Fink, Chau, & Dolan, 1997); judging one's own character traits (Johnson, Baxter, Wilder, Pipe, Heiserman, & Prigatano, 2002); and evaluative judgments (Zysset, Huber, Ferstl, & von Cramon, 2002). Such neuroimaging findings have led researchers to suggest that medial rostral PFC plays a general role in self-referential mental processes (Gusnard et al., 2001) and that the occurrence of unconstrained self-referential thought processes during baseline conditions is responsible for the relatively high level of medial rostral PFC activity during such conditions (McKiernan et al., 2003; Wicker, Ruby, Royet, & Fonlupt, 2003).

According to this hypothesis, the activation that is observed in medial rostral PFC during baseline tasks is not related to any process that plays a functional role in accomplishing these tasks. Rather, this activation is attributed to thought processes that are *task unrelated*, which we define here as those cognitive processes that do not help participants accomplish the instructed task, and *stimulus independent*, which we define here as those cognitive processes that are decoupled from information currently available in the sensory environment (for further discussion of these terms, see Antrobus, 1968; Burgess, Simons, Dumontheil, & Gilbert,

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2005; Christoff, Ream, & Gabrieli, 2004; Giambra, 1995; Gilbert, Frith, & Burgess, 2005; McGuire, Paulescu, Frackowiak, & Frith, 1996; Smallwood, Obonsawin, & Heim, 2003; Teasdale et al., 1995). For example, McKiernan et al. (2003) suggested that "as task demands increase, processing resources are increasingly diverted from ongoing, internal processes occurring at 'rest' to areas that are involved in the task" (p. 403).

In the present study, we investigated an alternative explanation of medial rostral PFC activation in low-demand conditions. We suggest that medial rostral PFC may indeed play a functional role during baseline tasks by promoting attentional engagement with the external environment during low-demand conditions. This possibility is consistent with the results of several recent neuroimaging studies that have reported medial rostral PFC activation in tasks requiring strong attentional engagement with the external environment. For example, Small et al. (2003) found that activity in this region (along with activity in the posterior cingulate) was associated with the deployment of visual attention toward specific regions of space, in a spatial cueing paradigm (Posner, 1980). Janata et al. (2002) found that activity in medial rostral PFC varied systematically according to the musical key of a melody in an auditory vigilance task. Burgess, Scott, and Frith (2003) found that activity in medial rostral PFC was greater in a variety of tasks while participants performed those tasks alone, compared with when they performed those tasks while holding in mind a delayed intention. Recently, across three quite separate tasks, Gilbert, Frith, and Burgess (2005) consistently found greater activity in medial rostral PFC during task conditions that required participants to attend to externally presented information, compared with conditions in which they attended to internally generated information. Thus, contrary to the claim that medial rostral PFC is exclusively involved in stimulus-independent thought (e.g., Wicker et al., 2003), this region has been implicated in a variety of tasks involving attentional engagement with the external environment.

One potential way of clarifying the role of medial rostral PFC in baseline tasks is to investigate the relationship between activity in this region and fluctuations in behavioral performance. Insofar as this activity reflects task-unrelated and stimulus-independent processes, the occurrence of these processes (and hence the level of medial rostral PFC activity) should correlate on a trial-by-trial basis with worse performance (e.g., slower reaction times [RTs]) in the baseline task because participants will be distracted from the task. Alternatively, if medial rostral PFC activity reflects engagement with the external environment, activity should correlate positively with performance in baseline tasks (e.g., trials with faster RTs). Currently, researchers have little data with which to evaluate this question because previous studies investigating baseline conditions have tended to use tasks with no response requirements (e.g., rest, passive fixation). In other studies, researchers who have investigated the relationship between activity in medial PFC and behavioral performance (e.g., Bunge, Ochsner, Desmond, Glover, & Gabrieli, 2001; Laurienti et al., 2003) have typically investigated the relationship between individual differences in behavioral performance and individual differences in the blood oxygen level dependent (BOLD) signal (i.e., by investigating whether participants who show relatively large differences between two conditions in behavioral performance also show relatively large differences between those conditions in medial PFC BOLD signal). Such analyses may be difficult to interpret because the causes of between-subjects variation are likely to be complex. In the present study, we took an alternative approach: We investigated the relationship, in each participant, between trial-by-trial fluctuations in behavioral performance and trial-by-trial fluctuations in BOLD signal, within a single task (see also West & Alain, 2000, for a related approach).

To test for brain–behavior relationships in baseline conditions, we used a simple RT task as a baseline, in which participants simply pressed a response button every time the screen flashed (with the flashes occurring at unpredictable times). This simple RT task was appropriate for two reasons. First, similar to other baseline tasks such as passive fixation (Shulman et al., 1997), this task does not require any cognitive processing of stimuli, only the detection of their occurrence, and therefore fits our definition of low-demand tasks as those with minimal requirements to perform cognitive operations on experimental stimuli. Second, in this task the stimulus, response, and stimulus–response mapping were identical on every trial, so fluctuations in performance could be attributed to variation in the participant's psychological state (e.g., the degree of attention toward the external environment) rather than to variation in the difficulty of different types of trials.

In the present study, we also investigated three other conditions that differed in the requirement to attend to externally presented information versus internally generated information. We reasoned that if activity in medial rostral PFC reflects the occurrence of stimulus-independent thoughts, this activity should be relatively high in conditions in which participants are instructed to ignore stimuli, compared with conditions in which participants are instructed to turn their attention toward external stimuli. Furthermore, if activity in medial rostral PFC reflects the occurrence of task-unrelated thoughts, this activity should correlate with slower RTs in the baseline task because it will reflect distraction from the task at hand. However, if activity in this region reflects engagement with the external environment during baseline conditions, this activity should be high in those conditions requiring attention to externally presented information and should correlate with faster RTs in the baseline task.

Additionally, in the present study we sought to clarify the results from our previous study (Gilbert et al., 2005) in which we investigated the neural bases of stimulus-oriented thought versus stimulus-independent thought. In this previous study, participants performed three tasks, each of which they could accomplish either by using externally presented information (i.e., stimulus-oriented thought) or by doing the same task "in their heads." Consistently across the three tasks, we found that medial rostral PFC activity was greater in the conditions involving stimulus-oriented thought (vs. stimulus-independent thought). However, these two types of conditions differed in two potentially dissociable ways. First, the stimulus-oriented conditions, unlike the stimulus-independent conditions, required participants to process sensory information. Second, the stimulus-independent conditions, unlike the stimulus-oriented conditions, required participants to generate the task-relevant information themselves because it was not available to them perceptually. To dissociate these two factors, in the present study we included an additional condition that required participants to generate task-relevant information themselves and also to process incoming sensory information. By comparing this condition with a stimulus-oriented condition, requiring strong engagement with the external environment but no self-generation of information, and with a stimulus-independent condition, requiring the self-generation of information but no processing of incoming sensory information, we were able to investigate these two factors independent of one another.

Method

Participants

Participants included 14 healthy right-handed individuals, aged 22–36 years (M = 26; 9 women, 5 men). All participants provided written informed consent before taking part.

Tasks

Two tasks (numbers and letters) were performed in separate scanning sessions. Each task consisted of four separate conditions. In all conditions, stimuli appeared in a central viewing area approximately 1.5° wide and 3° tall. A continuously updated stream of stimuli passed through this viewing area, moving smoothly from the bottom to the top in a manner similar to that of movie credits. At any one time, up to three stimuli were visible (see Figure 1). Throughout all conditions, we degraded the stimuli by superimposing 200 small squares over the stimulus-viewing area, the positions of which constantly changed with each screen refresh (refresh rate = 60 Hz).

Baseline condition. Stimuli consisted of repeated presentations of the number 0 (numbers task) or the letter A (letters task). At unpredictable times, the entire screen was illuminated for 100 ms. Participants were asked to press a button with their index finger as soon as this illumination occurred. The time from one target to the next was sampled from a uniform distribution, ranging from 67% to 133% of the mean interstimulus interval (see below).

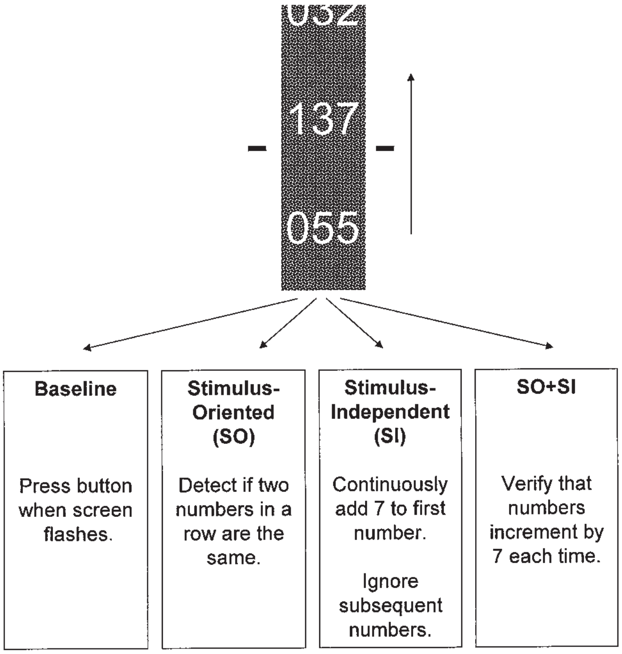

Figure 1. Schematic illustration of the stimulus display and the various experimental conditions in the numbers task. The stimuli scrolled smoothly and continuously and the stimulus display area was large enough that up to three stimuli could be seen at any one time. Throughout all conditions, stimuli were degraded with a constantly changing snow pattern, thus increasing the requirement to pay close attention to the external environment when the stimuli were task relevant.

Stimulus-oriented condition. Stimuli were randomly selected numbers (range = 0–299; numbers task) or randomly selected letters of the alphabet (letters task). Successive stimuli always differed from one another except for the final stimulus of the block, which repeated the previous stimulus. This final stimulus was the last one to make its way from the bottom to the top of the viewing area; additional stimuli were presented subsequently, but the block was terminated before these stimuli reached the top of the screen. In both tasks, participants were instructed to press a button with their index finger each time a stimulus passed the horizontal marks at the center of the viewing area and to press the button with their middle finger when a repeated stimulus appeared. Thus, this condition involved engagement with the external environment but little requirement to engage in internal processing of the presented stimuli, because participants needed only to process the stimuli in a "shallow" manner (i.e., making same vs. different judgments) and successive stimuli were always visible on the screen.

Stimulus-independent condition. Stimuli were identical to those presented in the stimulus-oriented condition. In the numbers task, participants were instructed to note the first number to be presented in the block and ignore all subsequent stimuli. Participants mentally counted upward in increments of 7 from this initial number, pressing a button with their index finger each time they thought of a new number. In the letters task, participants mentally generated a sequence of letters, moving through the alphabet from the first letter they saw and skipping two letters each time (i.e., if the first letter was A, participants would generate the sequence "A . . . D . . . G . . . J . . . etc."). Again, participants pressed a button with their index finger each time they thought of a new letter. Once they reached the end of the alphabet, participants were instructed to continue from the beginning. Throughout the block, even when the visually presented information was not task relevant, participants were instructed to maintain fixation in the stimulus presentation area. At the end of each block, participants used the keypad to input the number or letter they were thinking of at the time the block ended (using an interface that allowed participants to enter any number between 0 and 999 or any letter of the alphabet). This condition required participants to withdraw attention from the external environment because the stimuli served as distracters.

Stimulus-oriented + stimulus-independent (SO + SI) condition. In this condition, participants performed the same task as in the stimulus-independent condition. However, the stimuli now conformed to the sequence that participants were instructed to imagine (e.g., in the numbers task, successive numbers were presented in increments of 7), apart from the final stimulus in each block. In the numbers task, this final stimulus differed from the true continuation of the sequence by −2, −1, +1, or +2 on 80% of the trials and by −10 or +10 on the remaining 20%. In the letters task, the final stimulus was either one letter ahead in the alphabet of the true continuation of the sequence or one letter behind. Participants were instructed to monitor the externally presented sequence of items, pressing a button with their index finger each time a valid continuation of the sequence passed the horizontal marks in the center of the viewing area. When a target item was presented that did not conform to the sequence, participants pressed the button with their middle finger instead. Thus, participants were required to generate a sequence of numbers or letters internally (as in the stimulus-independent condition) and also to monitor the external environment (as in the stimulus-oriented condition).

Participants practiced the tasks outside the scanner before the first session. During this practice session, each participant's mean interresponse interval in the stimulus-independent condition was recorded (separately for each of the two tasks); this interval was subsequently used as the stimulus presentation rate in all four conditions. Thus, the mean interval between responses in the condition in which participants were free to respond at their own pace was used as the stimulus presentation rate in the other conditions. This stimulus presentation rate was continually updated throughout the scanning sessions in accordance with the mean response rate during the stimulus-independent condition. In this way, the stimulus presentation rate and response rate were matched across the four conditions. Stimuli were projected onto a mirror in direct view of the reclining participant, who responded by pressing buttons on a response pad with his or her right hand. The two tasks were performed in separate scans, each lasting approximately 12.5 min, with the order counterbalanced across participants. In each session, participants performed each of the four conditions five times, once with each of the following durations: 10 s, 17 s, 24 s, 31 s, and 38 s. The order of conditions and durations was randomized, with the constraint that the same condition was never performed twice in a row. Thus, even though the target events in the stimulus-oriented and SO + SI conditions always occurred at the end of the block, participants were unable to predict exactly when this would be. Each block was preceded by a screen that displayed instructions for that block for 7.5 s. At the end of each block, the screen was cleared and instructions for the next block were presented after a delay of 1 s. At the end of the stimulus-independent blocks, participants were given 16 s to input the letter or number they were thinking of at the end of the block before instructions for the next block appeared.

During scans, participants' eye movements were monitored with an infrared eye tracker (Applied Science Laboratories, Waltham, MA) with remote optics (Model 504, sampling rate = 60 Hz); the eye tracker was custom adapted for use in the scanner. Because of technical problems, eye-tracking data were available for only 5 of the 14 participants.

Functional MRI (fMRI) Acquisition

A 3T Siemens Allegra head-only system was used to acquire T1-weighted structural images and T2*-weighted echoplanar images (EPI; 64 × 64; 3-mm × 3-mm pixels; echo time [TE]: 30 ms) with BOLD contrast. Each volume comprised 48 axial slices (2 mm thick, separated by 1 mm), covering the whole brain. Each of the two functional scans comprised 239 volumes. Volumes were acquired continuously with an effective repetition time (TR) of 3.12 s per volume. The first five volumes in each session were discarded to allow for T1 equilibration effects. Following the functional scans, a 12-min structural scan was performed.

Data Analysis

fMRI data were analyzed using Statistical Parametric Mapping 2 (SPM2) software (http://www.fil.ion.ucl.ac.uk/spm/software/spm2). Volumes were realigned, corrected for different slice acquisition times, normalized into 2-mm cubic voxels using a standard EPI template based on the Montreal Neurological Institute reference brain in Talairach space and smoothed with an isotropic 8-mm full-width half-maximum Gaussian kernel. The volumes acquired during the two sessions were treated as separate time series. For each series, the variance in BOLD signal was decomposed with a set of regressors in a general linear model. In each session, each of the four conditions was modeled separately with a boxcar regressor convolved with a canonical hemodynamic response function, encompassing the time from the presentation of the second stimulus until the end of the block. In this way, the four conditions were modeled in an identical manner. Additional regressors represented (a) the presentation of instructions (jointly for all conditions), (b) the periods after stimulus-independent blocks in which participants inputted the letter or number they were thinking of at the end of the block, and (c) the presentation of targets in the stimulus-oriented and SO + SI conditions. These regressors, together with regressors representing residual movement–related artifacts and the mean over scans, made up the full model for each session. The data and model were high-pass filtered to a cutoff of 1/128 Hz.

Parameter estimates for each regressor were calculated from the least mean squares fit of the model to the data. Effects of interest were assessed in a random effects analysis as follows. Eight contrasts were performed, each contrast individually assessing the variance explained by the regressors representing each of the four conditions in the two tasks. We entered these contrasts into a repeated-measures analysis of variance (ANOVA) using nonsphericity correction (Friston et al., 2002). Appropriate contrasts for effects of interest were conducted at the second level, separately for the two tasks. Statistical parametric maps (SPMs) of the minimum t statistic across these two orthogonalized contrasts were generated; these SPMs were converted into SPMs of the Z statistic in a conjunction analysis (Friston, Holmes, Price, Büchel, & Worsley, 1999) via associated p values. Thus, it is unlikely that the activations reported below are due to processes specific to one or the other task because they were observed in both. Contrasts were thresholded at $p < .05$, corrected for multiple comparisons across the whole brain volume (except where stated).

Brain–Behavior Relationships

To assess brain–behavior relationships in the baseline condition, we analyzed fMRI data as above, with the following changes. The general linear model for each session consisted of one regressor constructed by convolving a series of delta functions, representing the presentation of each target in the baseline condition, with a canonical hemodynamic response function. A second regressor represented the parametric modulation of this regressor by log(RT)[1], where RTs faster than 100 ms or slower than 1,000 ms were replaced with the mean. Thus, the regressor represented the RT for each trial, relative to the other RTs of that participant in that session. Along with regressors representing movement-related artifacts and the mean over scans, these two regressors made up the full model for each session. We assessed effects of interest by forming contrasts separately for the two regressors representing the modulation of target-related activity by RT (one for each task) and entering these into a repeated-measures ANOVA (with nonsphericity correction). We then performed a conjunction analysis by calculating an SPM of the minimum t statistic across these two contrasts and converting this into an SPM of the Z statistic via associated p values.

Results

Behavioral Data

The mean interstimulus interval (i.e., time between successive stimuli passing through the center of the stimulus display area) was 1.41 s in the letters task and 1.98 s in the numbers task, $F(1, 13) = 9$, $p = .01$. Neither the mean interstimulus interval nor the mean interresponse interval differed significantly between conditions (stimulus-oriented, stimulus-independent, SO + SI, and baseline), and there were no Task (letters vs. numbers) × Condition interactions (all Fs[1, 13] < 3, *ns*). Thus, both stimulus presentation rates and response rates were successfully matched across the four conditions. We analyzed eye-movement data (available for 5 of the 14 participants) by calculating the proportion of time spent fixating within the stimulus presentation area in the stimulus-oriented, stimulus-independent, and SO + SI conditions. In the letters task, the proportion of time spent fixating the stimulus presentation area was 95%, 97%, and 93% in these three conditions, respectively. The corresponding figures for the numbers task were 91%, 84%, and 87%, respectively. These figures did not differ significantly between tasks or among conditions, nor was there a reliable Task × Condition interaction, $F(1, 4) < 3$, *ns*. Thus, although data were available only for a small sample of the group, the results

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[1] RT distributions are generally positively skewed (Luce, 1986). To maximize the power of this analysis, log(RT) was therefore chosen as a regressor so that relatively slow RTs did not account for a disproportionately large amount of the variance among trials.

suggest that participants were able to maintain fixation well during the stimulus-independent condition (even though they were instructed to ignore the visual display) and that the proportion of time that participants spent fixating on the central stimulus presentation area did not differ reliably among conditions or between tasks.

Full behavioral data for each of the four conditions in the two tasks are presented in Table 1. Participants were able to carry out the tasks adequately in all conditions. In the stimulus-oriented and SO + SI conditions, each participant was presented with five targets in the letters task and five targets in the numbers task (one in each block). The mean number of nontargets was 79 in the letters task and 60 in the numbers task. We used the proportion of hits and correct rejections to calculate d' scores, which we analyzed in a 2 (task: letters vs. numbers) × 2 (condition: stimulus-oriented vs. SO + SI) repeated-measures ANOVA. Accuracy was lower in the SO + SI condition than in the stimulus-oriented condition, $F(1, 13) = 62$, $p < .01$. There was no main effect of task, $F(1, 13) = 3$, *ns*, but there was a significant Task × Condition interaction, $F(1, 13) = 32$, $p < .01$, because the difference in accuracy between the two conditions was greater in the letters task than in the numbers task. Accuracy in the stimulus-independent condition was calculated by counting the number of responses made by each participant in each block. We used these data to generate the correct target stimulus that should have been reported at the end of the block, if participants had correctly maintained an internal representation of the sequence of numbers or letters throughout the block. Any response within one step of the target (e.g., ±7 in the numbers task) was counted as correct. There were no significant differences between the two tasks in the behavioral data for the baseline or stimulus-independent conditions, $t(13) < 0.9$, *ns*.

Neuroimaging Data

First we investigated regions showing relatively high activity during the baseline condition by comparing this condition with the mean of the other three conditions (see Table 2, Figure 2). This comparison revealed activity in regions including medial rostral PFC and posterior cingulate/precuneus, in common with previous investigations of rest or baseline conditions (e.g., Binder et al., 1999; Greicius et al., 2003; Mazoyer et al., 2001; McKiernan et al., 2003; Shulman et al., 1997; Raichle et al., 2001). Additionally, there was extensive medial occipital activation, which may have been caused by the additional visual stimulation in the baseline condition (i.e., intermittent illumination of the screen) that did not occur in the other three conditions.

Next, we contrasted activity in the stimulus-independent and stimulus-oriented conditions (see Figure 3, Table 3). The contrast of stimulus-independent > stimulus-oriented revealed activity in the bilateral SMA/cingulate gyrus, left insula, left premotor cortex, and left inferior parietal lobule. The reverse contrast (stimulus-oriented > stimulus-independent) revealed activity in bilateral medial prefrontal cortex (primarily BA 10, but also BA 9 and BA 11), posterior cingulate, lateral occipito-temporal cortex (in the region of the fusiform gyrus), temporal pole, and cerebellum. Thus, activity in medial rostral PFC, which was higher in the baseline condition than the mean of the other conditions, was also associated with a condition requiring attention to the external environment, compared with a condition requiring stimulus-independent thought alone.

Crucially, the analysis of voxels showing a significant relationship between BOLD signal and trial-by-trial fluctuations in baseline RT identified only one significant activation, which overlapped with the medial rostral PFC region identified in the stimulus-oriented > stimulus-independent contrast (2, 62, 4; BA 10; $z_{\max} = 5.00$; extent: 2 voxels; $p < .05$, corrected). The correlation was negative—that is, greater activity in this region was associated with trials that had faster RTs. This finding rules out an explanation of medial rostral PFC activity during the baseline condition in terms of task-unrelated thoughts (i.e., distraction from the baseline task) because greater activity occurred on trials with better performance (see Figure 4).[2] The overlap between the voxels showing this brain–behavior relationship in the baseline condition and the voxels activated by the stimulus-oriented > stimulus-independent contrast is remarkable, because the two contrasts were based on separate sets of data (i.e., separate functional scans collected in different experimental conditions) and different types of analyses (i.e., parametric analysis of brain–behavior correlations in the baseline condition compared with a subtraction between the stimulus-oriented and stimulus-independent conditions).

Table 1
Behavioral Results

Condition	Numbers task *M*	Numbers task *SD*	Letters task *M*	Letters task *SD*
Baseline				
Mean RT	322	47.0	306	52.0
Stimulus-independent				
% correct	77	25.8	84	19.5
Stimulus-oriented				
% false alarms	1	1.46	0	0.45
% hits	97	8.23	99	5.35
d'	3.47	0.44	3.77	0.24
SO + SI				
% false alarms	1	1.46	3	2.88
% hits	87	8.23	66	17.1
d'	3.10	0.74	2.30	0.41

Note. RT = reaction time. SO + SI = stimulus-oriented + stimulus-independent. RTs are available only for the baseline condition because it was the only condition that required speeded responses.

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[2] In a further analysis, we specified two parametric regressors, representing (a) the response–stimulus interval following each stimulus (i.e., the time from the response to that stimulus until the presentation of the following stimulus) and (b) RT (specified in a linear manner, rather than log-transformed, so that both regressors represented linear effects). Even after controlling for the variance accounted for by response–stimulus interval, we noted that the regressor representing RT still had a negative correlation with activity in medial rostral PFC (4, 60, 4; BA 10; $z_{\max} = 3.46$; extent: 15 voxels; $p < .001$, uncorrected). Thus, the association between medial rostral PFC activity and faster RTs could not have been caused simply by faster responses being followed by a longer interval until the next stimulus.

Table 2
Significant Clusters of Activation ($p < .05$, Corrected) in the Contrast of Baseline Condition With Mean of Other Three Conditions

Region	BA	Hemisphere	x	y	z	$Z_{\max}$	Voxels
Medial frontal cortex	10	L	−20	62	14	5.0	5
	8	R	2	56	44	4.9	3
	9/10/24/32	B	−4	44	12	6.6	1,126
	8	L	−6	34	54	6.1	170
	11	B	2	34	−14	5.0	24
	24	R	6	24	2	5.2	13
Lateral frontal cortex	47	R	42	36	−14	5.9	49
	11/47	R	26	34	−14	5.2	10
	47	L	−42	30	−12	6.7	217
	8	L	−30	28	44	5.0	5
Striatum	—	R	12	20	0	5.0	7
Temporal pole	38	R	32	18	−36	5.2	7
Caudate nucleus	—	L	−4	16	−2	4.9	4
Lateral temporal cortex	21/22	L	−58	−6	−10	6.5	1,132
	20/21/22/38	R	54	−26	22	7.6	3,217
	21/22	R	70	−32	4	5.0	8
	22	L	−40	−34	18	6.1	131
Thalamus	—	B	4	−12	8	5.1	12
Central sulcus	3	L	−38	−16	40	5.0	8
Lateral occipito-temporal cortex	37	L	−42	−42	−18	5.2	13
	39	L	−58	−52	26	7.5	1,590
Posterior cingulate/precuneus	23/31	B	−8	−44	38	6.6	1,331
Lateral occipital cortex	19	R	52	−74	8	4.9	5
Cerebellum	—	R	28	−82	−34	5.3	13
Medial occipito-temporal cortex	17/18/27	B	−10	−90	8	>8	13,376

Note. Brodmann areas (BAs) are approximate. L = left, R = right, B = bilateral. Coordinates refer to the Montreal Neurological Institute reference brain. Slashes in BA column indicate either that multiple BAs were activated or that the location of an activation was ambiguous between two or more BAs. Dashes in BA column indicate that the activation was in a region with no corresponding Brodmann number.

Comparisons With the SO + SI Condition

The SO + SI condition involved aspects of both the stimulus-oriented and stimulus-independent conditions. Participants were required to process incoming sensory information (as in the stimulus-oriented condition) and also generate information internally (as in the stimulus-independent condition). Thus, by comparing activity in the SO + SI condition with the stimulus-oriented condition, we were able to isolate activity related to the requirement to generate information internally, controlling for the requirement to process externally presented information (which was present in both conditions). This contrast revealed activity in right insula and left inferior parietal lobule (see Table 4). At a more liberal threshold of $p < .001$, uncorrected, all of the regions activated in the stimulus-independent > stimulus-oriented contrast were also activated in this contrast. Moreover, none of these regions differed in activity between the stimulus-independent and SO + SI conditions, even at an extremely liberal threshold of $p < .05$, uncorrected. Thus, in the present tasks, the regions involved in generating and processing internally represented sequence information were similar, regardless of whether participants additionally processed externally presented information (as in the SO + SI condition) or ignored such information (as in the stimulus-independent condition).

Next, we contrasted the SO + SI condition with the stimulus-independent condition. This allowed us to isolate activity related to

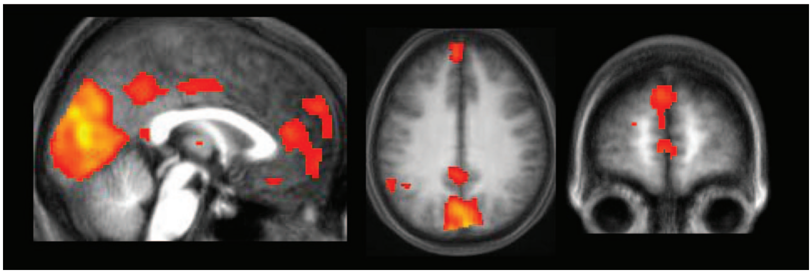

Figure 2. Regions showing greater activation in the baseline condition than the mean of the other three conditions ($p < .05$, corrected), plotted on slices of the mean normalized structural image ($x = 0$, $y = 60$, $z = 34$). Images follow neurological convention (left–right, not flipped).

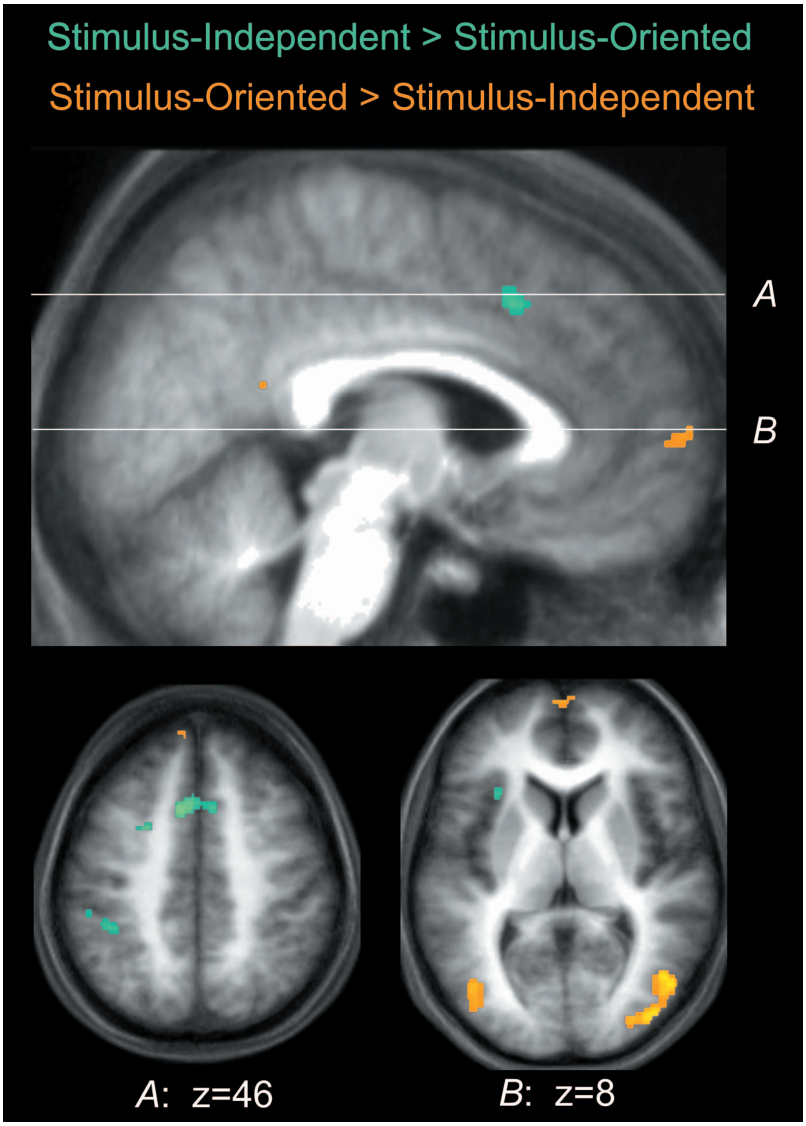

Figure 3. Areas of activation in contrasts between the stimulus-independent and stimulus-oriented conditions ($p < .05$, corrected), plotted on a sagittal slice ($x = 4$) of the mean normalized structural image of the 14 participants and two axial slices (A and B). Images follow neurological convention (left–right, not flipped).

the requirement to process externally presented information, controlling for the requirement to generate information internally. The contrast revealed bilateral activity in lateral occipital areas (similar to those activated in the stimulus-oriented > stimulus-independent contrast), as well as in the left cerebellum (see Table 4). In the right hemisphere, this large cluster of occipital activity extended superiorly into superior parietal cortex (BA 7). The reverse contrast (stimulus-independent > SO + SI) revealed activity in medial frontal cortex (BA 6) and medial occipital cortex (BA 18).

Notably, the contrast of SO + SI > stimulus-independent did not lead to activation in medial rostral PFC, despite the activation of this region in the contrast of stimulus-oriented > stimulus-independent. This remained true even at a threshold of $p < .05$, uncorrected. Thus, medial rostral PFC activity was not associated with simply any condition requiring attention to externally presented information. Rather, activity in this region was associated specifically with the low-demand conditions that involved attention toward the external environment but that did not require participants to generate information internally. This conclusion can be illustrated by contrasting activity in the stimulus-oriented condition with activity in the SO + SI condition (see Figure 5, Table 4). Both conditions required participants to attend to the stimuli presented to them. However, the stimulus-oriented condition (which required participants simply to remain vigilant to the sequence of stimuli and did not require participants to pay attention to any internally generated information) was associated with substantial activation in bilateral medial rostral PFC, posterior cingulate, and temporal pole, along with right temporo-occipito-parietal junction and left cerebellum.

Table 3

Significant Clusters of Activation in Contrasts Between the Stimulus-Independent and Stimulus-Oriented Conditions ($p < .05$, Corrected)

Region	BA	Hemisphere	x	y	z	$Z_{\max}$	Voxels
Stimulus-Independent > Stimulus-Oriented							
Insula	13	L	−34	18	12	5.2	15
SMA/cingulate gyrus	6/32	B	−8	14	46	6.3	173
Premotor cortex	6	L	−24	6	44	5.6	38
Inferior parietal lobule	40	L	−52	−32	48	4.9	5
	40	L	−44	−42	50	5.2	40
Precuneus	—	L	−30	−62	46	5.0	4
Stimulus-Oriented > Stimulus-Independent							
Medial frontal cortex	10	L	−10	68	16	4.8	1
	10	L	−6	64	22	5.1	7
	10	B	0	62	4	5.3	41
	9	L	−6	60	36	5.3	51
	10/11	B	0	48	−16	4.9	8
	11	L	−6	32	−12	5.4	60
	32	R	6	32	−12	4.9	2
	11	B	0	30	−26	5.0	2
Temporal pole	38	R	42	18	−38	5.0	9
	38	L	−28	12	−36	4.9	1
Cerebellum	—	R	38	−44	−24	5.5	32
	—	L	−38	−52	−20	5.1	4
	—	L	−38	−62	−16	4.9	1
Posterior cingulate	23	B	−2	−50	22	5.0	12
Occipital cortex	18/19/37	R	46	−74	−10	7.5	1,238
	18/19	L	−42	−78	−4	6.8	659
	18/19	L	−30	−88	18	5.4	86

Note. Brodmann areas (BAs) are approximate. SMA = supplementary motor area, L = left, B = bilateral, R = right. Coordinates refer to the Montreal Neurological Institute reference brain. Dashes in BA column indicate that the activation was in a region with no corresponding Brodmann number.

Task Difficulty

Previous studies have suggested that activity in medial rostral PFC is inversely related to task difficulty (McKiernan et al., 2003). Because medial rostral PFC activation in the present study was greater in the low-demand baseline and stimulus-oriented conditions than in the more demanding stimulus-independent and SO + SI conditions, the question arises of how closely this activation mirrors the relative difficulty of these conditions. Therefore, we investigated signal change across the various conditions in medial rostral PFC (10-mm radius sphere, centered on the peak voxel identified in the analysis of brain–behavior correlations: 2, 62, 4). Additionally, we reanalyzed the data collected by Gilbert et al. (2005) to investigate signal change in the same region. The results of these two analyses established a double dissociation between BOLD signal and task difficulty, as indexed by behavioral performance (i.e., RT and accuracy).

In the first analysis, we investigated differences between the stimulus-oriented and SO + SI conditions in the present study. The difference in performance between these two conditions was much greater in the letters task than in the numbers task (see the *Behavioral Data* section). Thus, if signal change in medial rostral PFC simply reflected task difficulty, we would predict that the difference in BOLD signal between the stimulus-oriented and SO + SI conditions would be larger in the letters than in the numbers task. However, this was clearly not the case; if anything, the difference in BOLD signal between the two tasks was in the opposite direction (see Figure 6, panel A). To statistically verify this dissociation between BOLD signal and behavioral data, we first normalized the two types of data so that they were in comparable units. All behavioral data points (i.e., the 28 data points corresponding to the data from the letters task and the numbers task for each participant) were transformed in a linear manner into z scores so that the mean of these 28 data points was 0 and the standard deviation was 1. A similar transformation was performed on the BOLD data. Thus, both sets of data had the same mean and standard deviation. These z scores were then entered into a 2 (task: letters vs. numbers) × 2 (dependent variable: behavioral vs. BOLD) repeated-measures ANOVA[3]. This resulted in a significant Task × Dependent Variable interaction, $F(1, 13) = 17$, $p < .01$.

In the second analysis, we reanalyzed the data collected by Gilbert et al. (2005), in which participants performed three tasks that could be accomplished on the basis of either externally presented information or internally generated information. In all three tasks, medial rostral PFC was more active during phases of tasks in which participants attended to externally presented information than during conditions in which they attended to internally generated information. In one of the tasks (Task 2), there was no

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[3] In this analysis (and all other analyses with Dependent Variable as a factor), the factors were arranged so that a significant interaction represents deviation from an inverse relationship between BOLD signal and task difficulty.

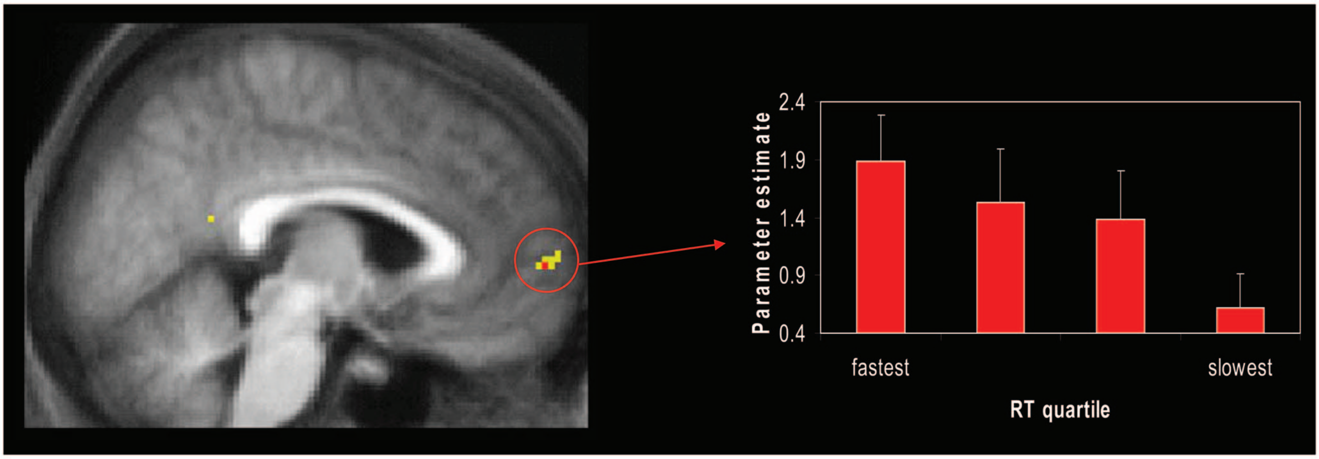

Figure 4. Left panel: Voxels showing a significant correlation between BOLD activity and faster reaction times (RTs) in the baseline task (plotted in red; $p < .05$, corrected), and voxels showing significantly greater activity in the stimulus-oriented condition than in the stimulus-independent condition (plotted in yellow; $p < .05$, corrected), plotted on a sagittal slice of the mean normalized structural image ($x = 4$). Right panel: In a separate analysis, the four quartiles of the baseline RT distribution were modeled separately for each participant. The resulting parameter estimates show that greater activation was associated with trials that had faster RTs. Error bars indicate standard errors.

significant difference in either error rates or RTs between the stimulus-oriented and stimulus-independent conditions. RTs were 33 ms faster and error rates were 0.9% higher in the stimulus-independent condition than in the stimulus-oriented condition, $F(1, 11) < 1.05$, $p > .30$, for RTs and for error rates. However, BOLD signal in medial rostral PFC was significantly higher in this task during the stimulus-oriented condition than during the stimulus-independent condition, $t(11) = 4.2$, $p < .01$; see Figure 6, panel B. Thus, it is possible to observe differences in medial rostral PFC activity between conditions requiring attention to externally presented information and conditions requiring information to be generated internally, even in the absence of behavioral differences

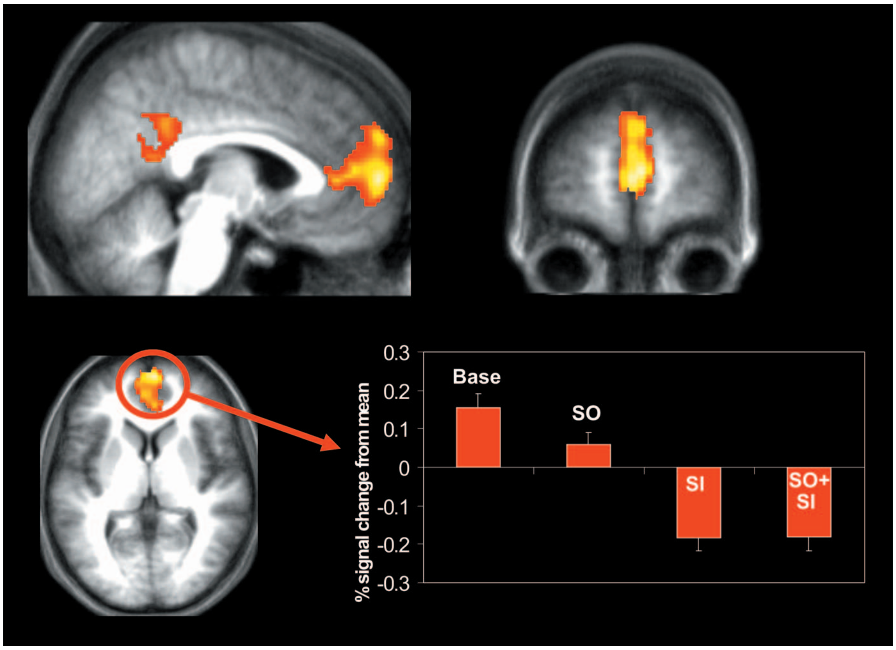

Figure 5. Regions of activity in the contrast of stimulus-oriented > SO + SI, plotted on the mean normalized structural image ($p < .05$, corrected; $x = 4$, $y = 60$, $z = 6$), and percent signal change (compared with mean) associated with the baseline (Base) conditions, stimulus-oriented (SO) conditions, stimulus-independent (SI) conditions, and SO + SI conditions in medial BA 10 (2, 62, 4). Images follow neurological convention (left–right, not flipped). Error bars indicate standard errors.

Table 4
Significant Clusters of Activation in Contrasts Between the SO + SI, Stimulus-Oriented, and Stimulus-Independent Conditions ($p < .05$, Corrected)

Region	BA	Hemisphere	x	y	z	$Z_{\max}$	Voxels
SO + SI > stimulus-oriented							
Insula	13	R	32	22	−2	5.0	7
Inferior parietal lobule	40	L	−46	−38	50	6.4	180
SO + SI > stimulus-independent							
Lateral occipital cortex	18/19/37	L	−42	−76	−2	7.8	949
	18/19	L	−24	−76	28	6.1	83
Occipital/parietal cortex	18/19/37/7	R	46	−76	−4	7.5	1,598
Cerebellum	—	L	−2	−78	−34	5.3	22
Stimulus-oriented > SO + SI							
Medial frontal cortex	9/10/32	B	−2	46	10	7.2	1,450
	8	R	14	50	46	5.3	18
	8	L	−14	40	50	5.5	81
	8	R	14	36	54	5.1	4
Temporal pole	38/28	R	50	12	−30	5.6	113
Cerebellum	—	L	−30	8	−44	5.1	8
Posterior cingulate	31/23	B	−4	−44	34	6.8	682
Temporo-occipito-parietal junction	39	R	56	−64	28	5.6	49
Stimulus-independent > SO + SI							
Medial frontal cortex	6	R	6	18	54	4.9	3
Medial occipital cortex	18	B	−2	−86	24	5.9	81

Note. Brodmann areas (BAs) are approximate. SO + SI = stimulus-oriented + stimulus-independent, R = right, L = left, B = bilateral. Coordinates refer to the Montreal Neurological Institute reference brain. Dashes in BA column indicate that the activation was in a region with no corresponding Brodmann number.

between these conditions. After normalizing the data in the same manner as above, we found that there was a significant Condition (stimulus-independent vs. stimulus-oriented) × Dependent Variable (behavioral vs. BOLD) interaction, $F(1, 11) = 18$, $p < .01$, using RT as the behavioral measure. Results were similar when error rate was used as the behavioral measure, $F(1, 11) = 7.0$, $p < .03$. In the other two tasks investigated by Gilbert et al. (2005), RTs were slower and error rates were higher in the stimulus-independent conditions, but these differences in behavioral data between the stimulus-independent conditions and stimulus-oriented conditions did not correlate with BOLD signal in medial rostral PFC (see Gilbert et al., 2005). Finally, we repeated the two analyses described above, looking at signal change in just the peak voxel identified in the analysis of brain–behavior correlations (2, 62, 4). The results of these repeated analyses were similar to those found in the original analyses; all significant results remained significant, and all nonsignificant results remained nonsignificant.

In summary, data from the present study show that it is possible to observe significant variation in behavioral performance in the absence of reliable variation in medial rostral PFC BOLD signal. Gilbert et al. (2005) showed that it is possible to observe significant variation in BOLD signal in the same medial rostral PFC region without observing any reliable variation in behavioral performance. We therefore conclude from this double dissociation that BOLD signal in medial rostral PFC does not simply reflect "task difficulty," as measured by RT and error rate (see Gilbert et al., 2005, for further evidence supporting this conclusion).

Discussion

In the present study, we replicated the finding that relatively high medial rostral PFC activity may be associated with low-demand conditions (for further examples, see Mazoyer et al., 2001; McKiernan et al., 2003; Shulman et al., 1997). However, the results provide additional constraints for theorizing about the causes of "deactivation" during high-demand tasks.

Self-Generated Thought in Low-Demand Conditions?

Some authors (e.g., McKiernan et al., 2003; Wicker et al., 2003) have suggested that medial rostral PFC activity in low-demand conditions reflects the occurrence of self-generated thought processes such as "mind wandering," which are (a) task unrelated (i.e., they do not help to accomplish the instructed task), and (b) stimulus independent (i.e., they are decoupled from information currently available in the sensory environment). However, the present data are inconsistent with this account. If medial rostral PFC activity reflects the occurrence of task-unrelated processes, then greater levels of activity (and hence a greater amount of task-unrelated cognition) should be accompanied by worse behavioral performance because participants will be distracted from the task. In fact, we observed the reverse pattern of data. Activity in medial rostral PFC was functionally related to performance in the baseline task because greater activity was associated with faster RTs. Therefore, this activity cannot be attributed to the occurrence of task-unrelated processes.

We also found that performance of simple tasks requiring participants to pay attention to the external environment but not

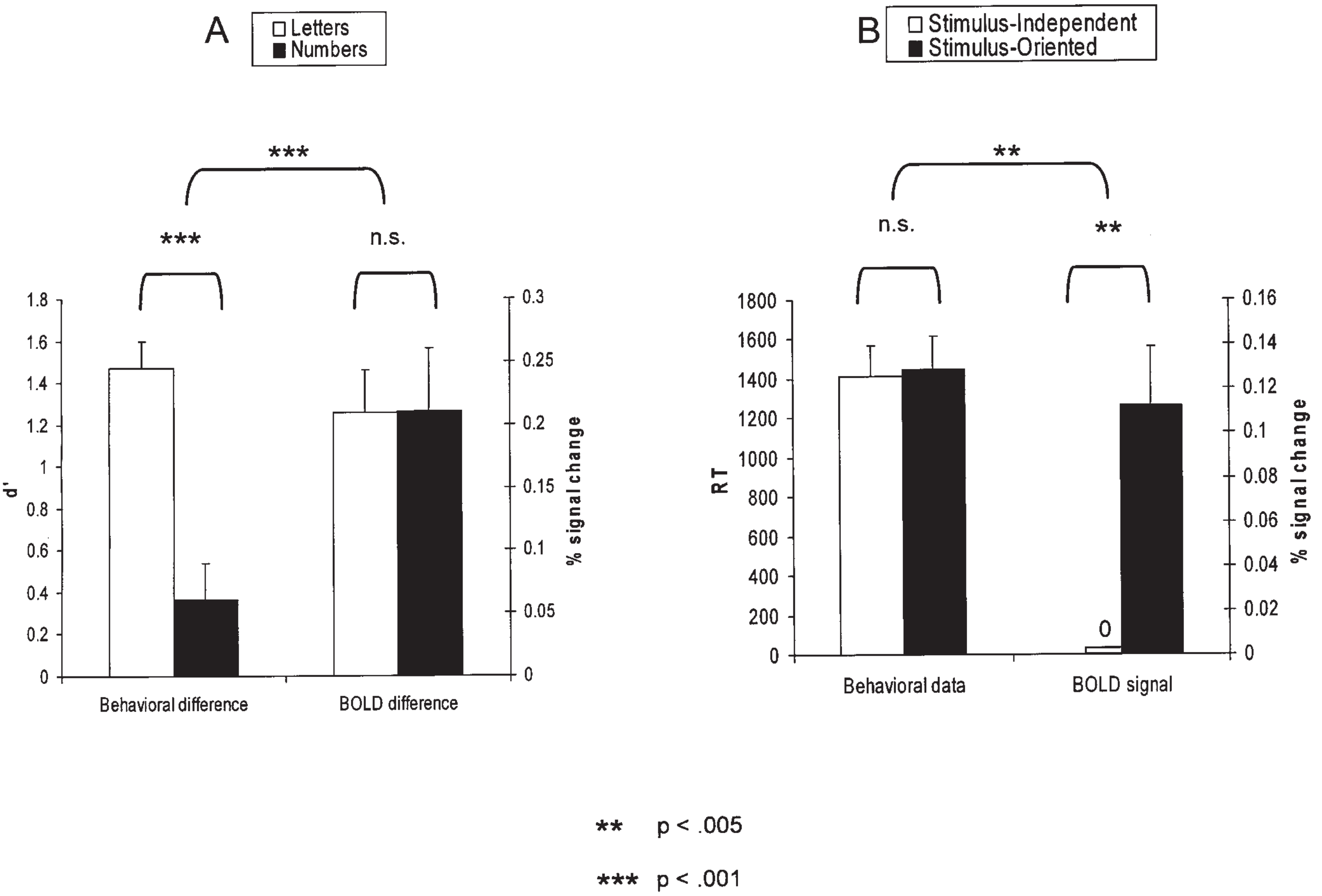

Figure 6. Double dissociation between BOLD signal in medial rostral PFC and task difficulty. Panel A: Difference in *d′* (left vertical axis) and BOLD signal (right vertical axis) between stimulus-oriented and SO + SI conditions, plotted separately for the letters and numbers tasks. The two tasks differ reliably in behavioral data but not in associated BOLD signal. Error bars indicate standard errors. Panel B: RT (left vertical axis) and BOLD signal (right vertical axis), plotted separately for stimulus-independent and stimulus-oriented conditions in Task 2 of Gilbert et al. (2005). The two conditions differ reliably in BOLD signal but not in behavioral data. In this study, the two conditions simply alternated and were modeled with a single regressor, yielding just one parameter estimate to represent the difference between conditions. Thus, the BOLD signal for the stimulus-independent condition constitutes a statistical baseline, with a value of zero.

requiring them to generate any information internally was associated with strong activity in medial rostral PFC (along with posterior cingulate, temporal pole, temporo-occipito-parietal junction, and cerebellum), compared with conditions requiring participants to generate information internally. In other words, medial rostral PFC activity was associated with the state of simply remaining alert toward external stimuli, as opposed to generating information internally. This finding is inconsistent with an account of medial rostral PFC activity solely in terms of stimulus-independent processes (see Gilbert et al., 2005, for further evidence). Therefore, we suggest that in the present study, medial rostral PFC played a role in maintaining attention toward the external environment during low-demand tasks, rather than being active when participants were distracted from those tasks by task-unrelated, stimulus-independent thought.

It is somewhat counterintuitive that the simple baseline condition, which involved minimal stimulus processing, was associated with an increased BOLD signal in many brain regions, compared with conditions involving more extensive stimulus processing or manipulation of internally represented information. This observation suggests that the state of simply remaining alert to the external environment without engaging in complex internal processing of stimuli is in some way special, leading to increased activity in certain brain regions. However, this neurophysiological observation is paralleled by the behavioral literature on RT. Although it is well established that RT may decrease as the number of choices decreases (Hick, 1952), responses are particularly fast in situations involving only a single stimulus and a single response (e.g., Leonard, 1958). In such situations, the correct response may be chosen without evaluating the stimulus. Frith and Done (1986) have therefore proposed that performance in simple RT tasks may use a special “fast route” for responding in situations without stimulus or response uncertainty. The current results support this model and suggest that medial rostral PFC may play a role in facilitating this route for action. These results are in good agreement with recent neuropsychological evidence indicating that medial frontal lesions may be associated with poor performance in simple RT tasks (Stuss et al., 2005; Stuss, Binns, Murphy, & Alexander, 2002). The present results are also consistent with a recent meta-analysis of neuroimaging studies, showing that activations in medial rostral PFC tend to be associated with conditions with relatively fast RTs (Gilbert, Spengler, Simons, Frith, & Burgess, in press-a).

Implications for Theoretical Accounts of Rostral PFC Function

The proposal that medial rostral PFC may be involved in attention toward the external environment is consistent with the "gateway" hypothesis of rostral PFC function (Burgess, Gilbert, Okuda, & Simons, in press; Burgess, Simons, Dumontheil, & Gilbert, 2005; Gilbert et al., 2005; Simons, Gilbert, Owen, Fletcher, & Burgess, 2005; Simons, Owen, Fletcher, & Burgess, 2005; for related accounts, see Christoff & Gabrieli, 2000; Christoff, Ream, Geddes, & Gabrieli, 2003). According to this hypothesis, rostral PFC activity is not associated exclusively with internally or externally oriented cognitive processes; rather, it is associated with situations that require deliberate biasing of the attentional balance between current sensory input and internally generated thought.

Low-demand baseline tasks may involve this attentional biasing precisely because they encourage task-unrelated, stimulus-independent thought while still requiring participants to maintain watchfulness toward external stimuli. Previous studies have shown that highly monotonous tasks (e.g., Antrobus, 1968) or tasks with a high degree of automaticity (e.g., Teasdale et al., 1995) are associated with an elevated level of task-unrelated, stimulus-independent thought. Thus, performance of tasks with these characteristics (such as the baseline condition in the present study) will benefit particularly from deliberate biasing of attention toward externally presented information in order to overcome the tendency toward task-unrelated, stimulus-independent thought. In contrast, tasks with less of a tendency to encourage self-generated thought will not be so dependent on this form of attentional biasing.

A similar argument may be applied to the state of rest. Neuroimaging studies that have investigated rest may be compared with earlier studies of sensory deprivation, which often used similar experimental conditions. For instance, in a study by Zuckerman, Albright, Marks, and Miller (1962), participants "were in total darkness and wore earphones connected through an intercom system to a microphone in the adjoining room. When the experimenter was not using this microphone to . . . communicate with [them], . . . 'white noise,' came through it" (p. 2). This perceptual isolation lasted for 7 hr. Zuckerman et al. suggested that "subjects were more oriented toward 'external' stimuli in the earlier part of isolation but became increasingly preoccupied with internal stimuli . . . toward the end. It is as if the subjects give up trying to get something from the external world . . . and shift their attention to internal events" (p. 13). We propose that the medial rostral PFC activity that is frequently observed during neuroimaging studies of rest (which, of course, have a duration of well under 7 hr) may correspond with the psychological process of "trying to get something from the external world" (p. 13). Thus, even when participants are not explicitly instructed to attend to events in the external environment (e.g., during rest), they may nevertheless attempt to do so.[4]

This account has some similarity with the "default mode" hypothesis, which attributes activity in medial rostral PFC (along with other areas, including posterior cingulate) during rest and baseline conditions to a process whereby "[i]nformation broadly arising in the external and internal milieu is gathered and evaluated" (Raichle et al., 2001, p. 682). The present results are broadly consistent with this hypothesis. However, although Raichle et al. suggested that activity in medial rostral PFC is attenuated by "attention-demanding, goal-directed activities," the present results extend this hypothesis by showing that it is not necessarily the "goal-directedness" of a task that determines activity in this region. In the present study, there is no reason to suppose that the baseline and stimulus-oriented conditions were less goal directed than the SO + SI and stimulus-independent conditions. Thus, it does not seem that any goal-directed task will lead to deactivation of the medial rostral PFC. Rather, we propose that this region plays a specific role in particular types of goal-directed tasks (e.g., deliberately biasing attention toward externally presented information) that it may also play during the state of conscious rest. One consequence of this view is that although medial rostral PFC activity may well be associated with easier tasks in some circumstances, this need not always be the case. The present results, along with the results of Gilbert et al. (2005), support this view by demonstrating a double dissociation between task difficulty (as measured by behavioral performance) and BOLD signal in medial rostral PFC.

The hypothesis that rostral PFC plays a role in modulating the attentional balance between stimulus-oriented and stimulus-independent thought (rather than being exclusively involved in one or the other type of process) would also apply to neuroimaging studies that have investigated mentalizing and other self-referential processes (see Frith & Frith, 2003). In such studies, participants were presented with stimuli but needed to interpret them with reference to unobservable (i.e., internally represented) mental states. This interplay between stimulus-oriented and stimulus-independent thought may explain the recruitment of rostral PFC. Thus, the present framework provides the outlines of an account that could explain the role of rostral PFC in a wide range of processes, from simple vigilance toward the external environment (as in the present study) to complex evaluative processing (as in studies that have investigated mentalizing). However, there are many remaining questions that require investigation by future studies, concerning the precise operating dynamics of this system (such as the relationship between lateral and medial subregions of rostral PFC; for discussion, see Burgess, Scott, & Frith, 2003; Burgess et al., 2005; Gilbert et al., 2005; Gilbert et al., in press-a; Gilbert et al., in press-b; Simons, Gilbert et al., 2005; Simons, Owen et al., 2005).

The Roles of Posterior Brain Regions

The present study also identified a network of other regions involved in the experimental tasks. First, attention to externally presented letters and numbers was associated with activity in

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[4] It is not clear whether a rest condition would have led to greater medial rostral PFC activation in the present study than the baseline condition. However, a study by Christoff et al. (2004), which contrasted a low-demand two-choice RT task with a rest condition, failed to observe any difference between the two conditions in medial PFC (although rest condition was associated with activation in other regions). This finding suggests that low-demand tasks may lead to levels of activation in medial rostral PFC that are comparable to those during the state of rest.

bilateral lateral occipito-temporal regions, extending into superior parietal cortex in the right hemisphere. Second, generating well-learned sequential information (i.e., sequences of numbers, or letters of the alphabet) was associated with activity in a network of insula, inferior parietal, and premotor regions. These findings are consistent with earlier studies implicating similar regions of lateral occipital cortex in the processing of visual alphanumeric stimuli (e.g., Eger, Sterzer, Russ, Giraud, & Kleinschmidt, 2003; Flowers et al., 2004) and similar parietal and premotor regions in the processing of sequentially organized information (e.g., Schubotz & von Cramon, 2002). It is interesting that the stimulus-independent condition (requiring visual stimuli to be ignored) was associated with activity in visual cortex (BA 18), compared with the SO + SI condition, which required participants to attend to visual information. One possible explanation of this finding is that the stimulus-independent condition required participants to engage in visual imagery, which has been associated with activity in nearby medial occipital areas (Kosslyn et al., 1999). An alternative explanation might be that participants paid greater attention to the low-level visual features of the display (e.g., the snow pattern used to degrade the stimuli) when they had to ignore the alphanumeric characters that were presented in the stimulus-independent condition.

Along with medial rostral PFC, the posterior cingulate was another region that was more active in the present study in conditions that did not require stimulus-independent thought. Medial rostral PFC and posterior cingulate are often coactivated in neuroimaging studies, including our earlier study of stimulus-oriented versus stimulus-independent thought (Gilbert et al., 2005; for further examples, see also Greicius et al., 2003; Johnson et al., 2002; Raichle et al., 2001; Small et al., 2003). However, one potential difference between the roles of these two regions is that the posterior cingulate may play a greater role in tasks that involve orienting of attention toward particular regions of space (Hopfinger, Buonocore, & Mangun, 2000; Olson, Musil, & Goldberg, 1996), whereas medial rostral PFC may be more involved in nonspatial orienting of attention toward the external environment. For instance, Mesulam, Nobre, Kim, Parrish, and Gitelman (2001) found that activity in posterior cingulate, but not in medial PFC, correlated with RT reductions in a spatial cueing task. In contrast, the results from the present study (along with previous studies by Mazoyer et al., 2002, and Naito et al., 2000) suggest that faster RTs in nonspatial vigilance tasks are associated with activity in medial rostral PFC regions but not in posterior cingulate regions.

Conclusion

The present results corroborate previous findings that medial rostral PFC activity may be associated with low-demand conditions (e.g., Mazoyer et al., 2001; McKiernan et al., 2003; Shulman et al., 1997). However, this activity was functionally related to performance in these conditions and was dissociable from behavioral measures of task difficulty. Therefore, we conclude that medial rostral PFC plays a role in maintaining attention toward the external environment during low-demand conditions, rather than simply being responsible for task-unrelated and stimulus-independent thought processes. In other words, although such processes may be more common during low-demand conditions (Antrobus, 1968; Giambra, 1995; Teasdale et al., 1995), their occurrence does not provide a sufficient explanation of activity in medial rostral PFC.

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