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Recruitment of lateral rostral prefrontal cortex in spontaneous and task-related thoughts

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Short title: U-shaped function of RPFc recruitment

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Abstract

Behavioural and neuroimaging studies suggest that spontaneous and task-related thought processes share common cognitive mechanisms and neural bases. Lateral rostral prefrontal cortex (RPFC) is a brain region that has been implicated both in spontaneous thought and in high level cognitive control processes, such as goal/sub-goal integration and the manipulation of self-generated thoughts. We therefore propose that the recruitment of lateral RPFC may follow a U-shaped function of cognitive demand: relatively high in low-demand situations conducive to the emergence of spontaneous thought, and in high-demand situations depending on processes supported by this brain region. We used functional magnetic resonance imaging to investigate brain activity while healthy subjects performed two tasks, each with three levels of cognitive demands, in a block-design. The frequency of task-unrelated thoughts, measured by questionnaire, was highest in the low cognitive demand condition. Low and high cognitive demand conditions were each compared to the intermediate level. Lateral RPFC and superior parietal cortex were recruited in both comparisons, with additional activations specific to each contrast. These results suggest that RPFC is involved both when (I) task demands are low and the mind wanders, and (II) the task requires goal/sub-goal integration and manipulation of self-generated thoughts.

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Introduction

Neuroanatomical and neurophysiological studies have suggested that the prefrontal cortex (PFC) is a heterogeneous brain region, composed of several structurally different subregions, with specific connections to other parts of the brain and specialized functions (e.g. see Hoshi, 2006; Cavada, Compañy, Tejedor, Cruz-Rizzolo, & Reinoso-Suárez, 2000; and Petrides, 2005 for reviews). Recently a number of theories have attempted to account for the particular role played by rostral prefrontal cortex (also called frontopolar cortex, and approximating Brodmann area 10) in human cognition (Koechlin, Basso, Pietrini, Panzer, & Grafman, 1999; Christoff & Gabrieli, 2000; Burgess, Simons, Dumontheil, & Gilbert, 2005; Ramnani & Owen, 2004; Braver & Bongiolatti, 2002; Raichle, MacLeod, Snyder, Powers, Gusnard, & Shulman, 2001; Pollmann, 2001; 2004).

One hurdle in the study of rostral PFC (RPFPC) is the tendency for this region to show relatively high levels of activity at rest or in "low demand" conditions. The demands of a task can be defined in terms of the complexity of the instructions to be followed, the number of errors subjects make, the slowness of reaction times and the subjects' perception of the difficulty of the task. Christoff and colleagues (Christoff & Gabrieli, 2000; Christoff, Ream, & Gabrieli, 2004) detail a number of studies which found lateral RPFPC activations when comparing a cognitively demanding task to a less demanding one, but did not find these activations when comparing it to a much easier task, or to rest (e.g. Buckner, Raichle, Miezin, & Petersen, 1996; Owen, Herrod, Menon, Clark, Downey, Carpenter, et al., 1999). This issue stresses the importance of the consideration of the baseline tasks used in functional magnetic resonance (fMRI) studies of RPFPC (see also McKiernan, Kaufman, Kucerra-Thompson, & Binder, 2003; Morcom & Fletcher, 2007). Indeed, the recruitment of RPFPC in experimental conditions could be masked when contrasted with baseline conditions that are much easier than the experimental conditions.

This study aimed to explore the role played by RPFPC in conditions of varying cognitive demands. Christoff et al. (2004) recently investigated the generation of spontaneous thoughts by comparing

a resting condition to a task with low cognitive demand, where subjects had to press a key with their left or right finger in response to a left or right arrow presented on the screen. Although the trials occurred at fixed intervals of two seconds, the importance of responding quickly (<500ms after stimulus onset) was stressed to the subjects in order to make the arrows task continuously engaging. The results showed increased blood oxygen dependent (BOLD) signal during rest compared to the arrows task in the left middle frontal gyrus (BA10/46), right inferior parietal lobe (BA40), as well other posterior and temporal regions.

Christoff et al. (2004) present these results in the wider framework of the literature of spontaneous thought processes, which suggests that spontaneous thoughts consistently increase with decreasing task demands (Antrobus, 1968; Filler & Giambra, 1973; Teasdale, Proctor, Lloyd, & Baddeley, 1993) and that the generation of spontaneous thought, or mind wandering, depends on central executive processes (see Smallwood & Schooler, 2006 and Christoff et al., 2004 for reviews). For example Teasdale and colleagues have demonstrated that continuous task demands on central executive resources interfere with the production of spontaneous thoughts (Teasdale et al., 1993; Teasdale, Dritschel, Taylor, Proctor, Lloyd, Nimmo-Smith, et al., 1995).

Christoff et al. (2004) suggest that lateral RPFc supports part of those central executive processes that are thought to be involved both in spontaneous thoughts and in tasks with high cognitive demands. What are the tasks that recruit lateral RPFc? Neuroimaging studies have repeatedly found this region to show increased BOLD signal in a very large number of paradigms (see Burgess et al., 2005; Ramnani & Owen, 2004; Christoff & Gabrieli, 2000 and Gilbert, Spengler, Simons, Steele, Lawrie, Frith, et al., 2006b for reviews). Efforts to synthesize these data have led to the propositions that lateral RPFc supports: processes of branching or goal/sub-goal management and monitoring (Koechlin et al., 1999; Koechlin & Summerfield, 2007; Braver & Bongiolatti, 2002); contextual control of task rules (Badre & D'Esposito, 2007); integration of sub-goals solutions (Ramnani & Owen, 2004); integration and segregation in working memory (Braver & Bongiolatti, 2002; De Pisapia, Slomski, & Braver, 2007); source or context memory retrieval

(e.g. Velanova, Jacoby, Wheeler, McAvoy, Petersen, & Buckner, 2003; Simons, Gilbert, Owen, Fletcher, & Burgess, 2005; Ranganath, Johnson, & D'Esposito, 2000; Rugg, Fletcher, Chua, & Dolan, 1999); prospective memory (Burgess, Quayle, & Frith, 2001; Burgess, Scott & Frith, 2003; den Ouden, Frith, Frith, & Blakemore, 2005; Simons, Scholvinck, Gilbert, Frith, & Burgess, 2006); monitoring and manipulation of self-generated information (Christoff & Gabrieli, 2000; Smith, Keramatian, & Christoff, 2007); relational processing (Wendelken, Nakhabenko, Donohue, Carter & Bunge, 2008); reallocation of attention (Pollmann, 2001; 2004); switching between attending to information derived from the environment or self-generated information (Gilbert, Frith, & Burgess, 2005); or attending to self-generated information (Burgess et al., 2005; Burgess, Dumontheil & Gilbert 2007a; Burgess, Gilbert, & Dumontheil 2007b). These theories of lateral RPFPC function do not make specific claims about hemispheric differences as there is little experimental support for any lateralisation of the observed activations (e.g. Gilbert et al., 2006b; Koechlin et al., 1999; Wendelken et al., 2008).

It is important to note here that medial, rather than lateral RPFPC has also previously been suggested to support mind wandering (see McGuire, Paulesu, Frackowiak, & Frith, 1996; Gusnard, Akbudak, Shulman, & Raichle, 2001; Mason, Norton, Van Horn, Wegner, Grafton, & Macrae, 2007a). However, Gilbert, Simons, Frith & Burgess (2006a) demonstrated that BOLD signal in medial RPFPC was stronger during trials where participants responded faster, which does not support an involvement of this region in mind wandering, as this would supposedly be reflected by stronger activations associated to slower reaction times (see Gilbert, Dumontheil, Simons, Frith, & Burgess, 2007a and Mason, Norton, Van Horn, Wegner, Grafton, & Macrae, 2007b for discussion).

On the basis of the literature presented above, it is proposed that lateral RPFPC recruitment is a U-shaped curve function of task demands (see Figure 1). On one hand, lateral RPFPC is suggested to be recruited both (I) when the task demands are low: during rest or simple reaction time tasks, when minimal processing of the stimuli is necessary, accuracy is high and reaction times fast, and (II) when the tasks demands are high: when each trial requires a number of processing steps, for

example when information from different parts of the stimulus needs to be integrated with previously obtained information, or when the task requires the manipulation of self-generated thoughts or the integration of sub-goal solutions, and accuracy is low and/or reaction times slow. On the other hand it is suggested that lateral RPFc recruitment is limited when the task demands are intermediate, e.g. when the subjects perform a task requiring some manipulation of perceptually-derived information, for example during a categorisation task, when participants need to make a choice of response in function of the properties of the stimulus.

(Figure 1 about here)

In order to test this hypothesis within a single experiment, three conditions were designed, corresponding to: low, intermediate, and high task demands. To investigate the hypothesis that lateral RPFc functioning is independent of material type, the three conditions were presented to the subjects in two different sets of tasks, using numbers or arrows stimuli (see Braver, Barch, Gray, Molfese, & Snyder, 2001; Burgess et al., 2001; Gilbert et al., 2005; Simons et al., 2006; for similar approaches).

Condition 1 required the detection of the presentation of the stimuli, but did not require any processing or categorisation of the stimuli, and was hypothesized to favour the occurrence of spontaneous thoughts processes. Condition 2 was comparable to that used as a baseline by Christoff et al. (2004), with a choice between two responses dependent on the characteristics of the presented stimuli (number magnitude or spatial location). This condition was considered to be sufficiently demanding to limit mind wandering, without requiring the manipulation of task-related self-generated thoughts. Condition 3 required the maintenance and manipulation of self-generated information in a 1-back manner. This condition was thus considered to involve the manipulation of items in working memory and goal/sub-goal processing, as well as attending to and manipulating self-generated information. The tasks were quite closely matched in error rates and reaction times for each condition. In addition, a questionnaire was completed by the

participants, after the brain scanning, to provide a measure of task-unrelated thoughts frequency and perceived difficulty of each task in the three different conditions.

The hypothesis of this study was that lateral RPFc would be more recruited in situations that encourage mind wandering and during the attending towards and manipulating of task-related self-generated information than in situations requiring continuous attention to the stimulus and manipulation of perceptually-derived information. These results would provide support for the Gateway hypothesis (Burgess et al., 2005, 2007a, 2007b) and Christoff & Gabrieli's (2000) proposal of rostrocaudal hierarchical organization of the human PFC. Thus, it was predicted that the BOLD signal in lateral RPFc regions would follow a U-shaped curve with higher BOLD signal in conditions 1 and 3 (low and high task demands) than in condition 2 (intermediate demands). However, as RPFc has already been shown to be subdivided in possibly functionally different subregions (Burgess et al., 2007b; Gilbert et al., 2005; 2006b; Gilbert, Williamson, Dumontheil, Simons, Frith, & Burgess, 2007b; Koechlin, Corrado, Pietrini, & Grafman, 2000), the possibility of activations specific to mind wandering and to the integration of goals/sub-goals was also investigated.

Methods

Task Stimuli

Two tasks ("Arrows", "Numbers") were administered in three conditions. Stimulus presentation was programmed with the Cogent2000 software of the physics group of the Wellcome Trust Centre for Neuroimaging, 12 Queen Square, London, UK.

In the Arrows task, stimuli were composed of a white horizontal line in the middle of the screen ("midline"), and two white arrows, whose positions changed from trial to trial (see Figure 2 for an example of stimulus and instructions). The visual angle for these stimuli was H: 17° x W: 26°. In the lowest cognitive demand condition 1, the instruction was to press alternately the right and left keys as soon as a stimulus appeared on the screen. In condition 2, subjects were asked to judge whether the intersection of the lines indicated by the arrows was higher or lower on the screen than the midline. They pressed the right key when the intersection was above the midline, and the left when it was below. In condition 3, goal/sub-goal integration and the manipulation of self-generated thoughts was necessary, as subjects were asked to compare the current position of the imagined intersection with the position of the intersection on the previous trial. If the present intersection was above the previous intersection, the right key was pressed, the left key if it was below. In a fourth condition, not discussed in this paper, the participants compared the position of a pair of arrows (fixed relative to each other) in the previous and current stimulus.

(Figure 2 about here)

In the Numbers task, stimuli were two numbers ranging from 1 to 5 presented in white in the centre of the display (see Figure 2 for an example of stimulus and instructions). The visual angle for these stimuli was H: 2° x W: 6°. In the low cognitive demand condition 1, the instruction was to press alternately the right and left keys as soon as a stimulus appeared, similarly to condition 1 of the Arrows task. In condition 2 participants were asked to press the key on the side of the bigger number (i.e. left or right). In the goal/sub-goal integration and manipulation of self-generated thoughts condition 3, they were asked to calculate the sum of the two numbers

presented on the screen and compare it to the sum of the two previous numbers. If the sum was bigger than the previous sum, the right key was pressed, if it was smaller, the left key was pressed. In a fourth condition, not discussed in this paper, the participants compared the magnitude of the current left (or right, counterbalanced across subjects) number to the previous left number.

Subjects and procedure

Sixteen right-handed volunteers with normal or corrected-to-normal vision took part in the experiment (six males, ten females, mean age 24.9 years, range 18-33). Ethics approval was granted by the local research ethics committee, and informed written consent was obtained.

Subjects were trained for approximately 15 minutes prior to scanning; the training for each task and condition was performed in turn and ended when subjects made fewer than two errors out 20 consecutive trials on the task, with no reaction time longer than three seconds. The experiment was divided in two sessions, with each condition encountered twice in each session. The conditions of each task were grouped; their order was counter-balanced across the four repeats and across subjects. The Arrows and Numbers tasks alternated during the experiment (ABAB-ABAB); half of the subjects started with the Arrows task and the other half with the Numbers task. Each condition block lasted 30 seconds and was preceded by seven seconds of instruction and two seconds of blank screen. The fourth condition was performed in a similar manner, but discussion of this condition is beyond the scope of the present article. Each of the two sessions lasted 11 minutes, with a short break between them.

Stimuli were projected onto a screen, viewable via a mirror in direct view of the reclining subject at a distance of approximately 50 cm. Subjects responded by pressing buttons on a response pad with the index and middle finger of their right hand. There was no other source of illumination. All tasks were self-paced, with the delay before the next stimulus uniformly randomised between 300

and 700 ms in condition 1 (to avoid a completely automatic rhythm of response and increase the vigilance demands) and fixed at 300 ms in conditions 2 and 3.

After the brain scanning, subjects completed a questionnaire, which asked them to rate how difficult they found each task and condition, and how often two types of task-unrelated thoughts occurred to them. A paragraph, inspired from McGuire et al. (1996), explained: "During the experiment you may have had thoughts which were irrelevant to the task you were doing. For instance, some of these thoughts might have been about what was happening around you (e.g. noticing the sound of the scanner), and others might have been quite unrelated (e.g. daydreaming, thinking about what you will be doing later in the day etc.)." Participants were then asked to estimate how often these two types of thoughts occurred to them in each part of the experiment (environmentally triggered task-unrelated thoughts: envTUT, self-oriented task-unrelated thoughts: selfTUT). Questions were answered using a 7 points Likert scale. The order of the questions was counterbalanced.

Imaging Acquisition and Data Analysis

A 3T Siemens Allegra head-only system was used to acquire both T1-weighted structural images and T2*-weighted echoplanar (EPI) images (64x64; 3x3 mm pixels; echo time (TE), 30 ms) with BOLD contrast. Each volume comprised 34 axial slices (2 mm thick, separated by 1.7 mm), covering the whole brain. Functional scans were acquired during two sessions, each comprising 297 volumes acquired continuously with an effective repetition time (TR) of 2.21 s per volume. The first seven volumes in each session were discarded to allow for T1 equilibration effects. fMRI data were analyzed using SPM2 software (<http://www.fil.ion.ucl.ac.uk/spm/spm2.html>). Volumes were realigned (using 4th-degree-B-spline interpolation), corrected for differences in slice acquisition times, normalised into 3mm cubic voxels using a standard EPI template based on the Montreal Neurological Institute (MNI) reference brain in Talairach space, and spatially 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 the BOLD

signal was decomposed with a set of ten regressors in a general linear model (Friston, Holmes, Poline, Grasby, Williams, Frackowiak, et al., 1995): eight boxcar regressors representing each of the conditions of the two tasks; and two regressors representing the presentation of instructions, and error trials (jointly for all conditions in both cases). All regressors were convolved with a canonical hemodynamic response function and, together with regressors representing residual movement-related artefacts and the mean over scans, comprised the full model for each session. The data and model were high-pass filtered to a cut-off 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 by a random effects analysis as follows. Six contrasts were performed, individually assessing the variance explained by the regressors representing each of the three conditions in the two tasks. These contrasts were entered into a repeated-measures ANOVA, using non-sphericity correction (Friston, Glaser, Henson, Kiebel, Phillips, et al., 2002). Appropriate contrasts for effects of interest were conducted at the second level, separately for the two tasks, and combined using the global conjunction analysis implemented in SPM2. This method ensures that the evidence for consistent effects across the two tasks is significant (Worsley and Friston, 2000). Contrasts between conditions were conducted across the whole brain volume with a criterion for significance of five or more contiguous voxels surviving a threshold of $p < 0.001$ (uncorrected for multiple comparisons). (For similar criteria see Henson, Shallice, & Dolan, 1999; Zysset, Huber, Samson, Ferstl, & von Cramon, 2003; Christoff, Prabhakaran, Dorfman, Zhao, Kroger, Holyoak, et al., 2001; Badre & D'Esposito, 2007). The resulting statistical parametric maps (SPMs) were converted into SPMs of the Z statistic via associated p-values. Significant regions were localized using approximate Brodmann areas estimated from the Talairach and Tournoux (1988) atlas, after adjusting coordinates to allow for difference from the MNI templates (Brett, Johnsrude and Owen, 2002).

Behavioural analyses were performed on accuracy and reaction time data. The first trials of all blocks were discarded from the analyses, as they were not meaningful in condition 3, which

followed a 1-back task design (subjects were told to press a key as soon as they were ready to move on to the second trial). Mean accuracy and reaction times of correctly responded trials were analysed using 2 (Task: Arrows/Numbers) x 3 (Condition: 1/2/3) repeated measures ANOVAs. Follow-up paired t-tests were performed with Bonferroni correction. Questionnaire data were analysed in the same way.

Results

Behavioural results

Mean reaction time (RT) and accuracy of the 16 participants in the different conditions in each task are displayed in Table 1. Reaction times of correctly responded trials were analysed in a 2 (Task) x 3 (Condition) repeated measures ANOVA. Both main effects were significant: a main effect of task, $F(1,15)=16.45$, $MSE=6965$, $p=.001$, indicated that reaction times were slower in the Arrows than the Numbers task; and a main effect of condition, $F(2,30)=214.39$, $MSE=26707$, $p<.001$ (Greenhouse-Geisser correction (GG): $\epsilon=.601$). Follow-up paired t-tests demonstrated that pairwise comparisons between the three conditions, averaging across tasks, were all significant, $t(15)> 11.18$, $p<.001$, with slower reaction times in condition 2 than condition 1, and in condition 3 than condition 2. These paired t-tests were also significant when looking at each task separately (all $p<.001$). The task by condition interaction was also statistically significant, $F(2,30)=4.26$, $p=.048$ (GG: $\epsilon=.601$), and follow-up paired t-tests indicated that reaction times were slower in the Arrows than the Numbers task in condition 1, $t(15)=2.85$, $p=.012$, and condition 2, $t(15)=9.45$, $p<.001$, but not in condition 3, $t(15)=0.83$.

(Table 1 about here)

Accuracy was analysed in the same way and the results were similar. There was a significant main effect of task, $F(1,15)=7.25$, $MSE=12.48$, $p=.017$, indicating that participants made more errors in the Arrows task than the Numbers task, as well as a significant main effect of condition, $F(2,30)=48.02$, $MSE=11.75$, $p<.001$. Follow up paired t-tests indicated that all condition differed significantly from each other when averaging across tasks, $t(15)>3.72$, $p<.007$; participants committed more errors in condition 3 than condition 2 and condition 2 than condition 1. These paired t-tests were also significant when looking at each task separately (all $p<.006$). The task by condition interaction was not significant $F(2,30)=3.40$, $MSE=12.63$ (GG: $\epsilon=.633$).

Analysis of questionnaire data.

Data were Z transformed on a subject-by-subject basis to remove individual response bias. Two (Task) x 3 (Condition) repeated measures ANOVA were performed on self reported task difficulty, on the frequency of environmentally triggered task-unrelated thoughts (envTUT), and on the frequency of self-oriented task-unrelated thoughts (selfTUT) (see Figure 3). Subjects found the Arrows task more difficult than the Numbers task, $F(1,15)=7.00$, $MSE=.396$, $p=.018$, but task was not found to affect the reported frequencies of envTUT, $F(1,15)=3.93$, $MSE=.529$, or selfTUT, $F(1,15)=.014$, $MSE=.559$. However, a significant effect of condition was found in all three cases: task difficulty, $F(2,30)=156.68$, $MSE=.204$, $p<.001$; envTUT, $F(2,30)=6.42$, $MSE=1.44$, $p=.013$ (GG, $\epsilon=.684$); selfTUT, $F(2,30)=16.31$, $MSE=1.22$, $p<.001$ (GG: $\epsilon=.704$). Follow-up paired t-tests were performed for each measure on the three conditions, averaged across tasks. Task difficulty was significantly different in all pairwise comparisons, $t(15)>7.00$, $p<.001$: reported task difficulty was higher in condition 3 than in conditions 1 and 2, and higher in condition 2 than condition 1. Self-reported frequency of envTUT was higher in condition 1 than condition 3, $t(15)=2.81$, $p=.039$, and self-reported frequency of selfTUT was significantly greater in condition 1 than in condition 2 $t(15)=3.78$, $p=.005$, and than in condition 3, $t(15)=4.49$, $p=.001$. Task by condition interactions were not significant: task difficulty, $F(2,30)=.26$, $MSE=.558$; envTUT, $F(2,30)=.73$, $MSE=.159$; selfTUT, $F(2,30)=2.42$, $MSE=.693$.

(Figure 3 about here)

To summarise, condition 1 was found to be the easiest condition and was associated with the greatest frequency of envTUT and selfTUT, or mind wandering, while condition 3 was found to be the most difficult and was associated with the least selfTUT. Condition 2 was found to have intermediary levels on these self-report measures.

Imaging results

To test the U-shape function hypothesis, the two conditions of interest (low and high task demands) were first contrasted, separately in each task, with condition 2, which served as a baseline. Lateral RPFC activations were observed in all four contrasts (see Figure 4), although overall these contrasts showed greater changes in BOLD signal in the arrows task than the numbers task. Conjunction analyses between the Arrows and Numbers tasks were then used to investigate the effects common to the two tasks.

(Figure 4 about here)

The hypothesis of a U-shape function of lateral RPFC recruitment depending on task demands was tested statistically by looking for regions where BOLD signal was greater in condition 1 (low demand, mind wandering condition) than condition 2 (baseline) as well as greater in condition 3 (goal/sub-goal integration, manipulation of self-generated thoughts) than condition 2. To perform this analysis, an inclusive masking of the contrasts 1-2 and 3-2 at the threshold $p < .001$ uncorrected for multiple comparisons was performed. This revealed two common areas of activations in the left hemisphere in lateral RPFC/dorsolateral PFC and parietal cortex (see Table 2A and Figure 5). Lowering the threshold of this contrast revealed similar regions in the right hemisphere, arguing against laterality differences.

(Table 2 about here)

Additional contrasts were performed to test for activations specific to conditions 1 or 3 in the comparison of interest. The contrast 1-3 inclusively masked by the contrast 1-2 ($p < 0.001$ uncorrected) revealed brain areas where the BOLD signal was greater in condition 1 than 3 and greater in condition 1 than 2; these were bilateral temporal (BA21, 22, 28, 38), right insula, bilateral inferior parietal lobule and right inferior middle frontal gyrus (BA47/10/11) regions (see Table 2B and Figure 5). Conversely, the contrast 3-1 inclusively masked by the contrast 3-2

($p < 0.001$ uncorrected) revealed brain areas where the BOLD signal was greater in condition 3 than 1 and greater in condition 3 than 2; fewer regions were found, and included superior parts of the left inferior parietal lobule and of the middle frontal gyrus (BA10/46), as well as the precuneus (see Table 2C and Figure 5).

(Figure 5 about here)

Common activation for the contrasts 3-2 and 1-2 were found in both the lateral RPFC and the inferior parietal lobules. The results also indicated the presence, in these two regions, of loci of activation more specifically recruited in condition 1 or condition 3, i.e. in a low demand condition with increased mind wandering, or when attending to and manipulating self-generated thoughts is necessary to perform the task. Percentage signal changes were extracted for the three main lateral RPFC voxels found in the statistical contrasts presented above (Table 2) and were plotted for each task to illustrate the different patterns of activation observed in lateral RPFC (Figure 5).

The aim of this study was to design two tasks with conditions similarly varying in their demands on functions possibly supported by RPFC. Our assumption of similar patterns of activity in this region in the contrasts presented above was investigated by testing for interaction effects between condition and task in this region. Only one significant interaction was observed in the prefrontal cortex and indicated that BOLD signal was greater in condition 1 than condition 2 in the Arrows task while lower in condition 1 than condition 2 in the Numbers task in right RPFC ([30 60 -9], $Z=4.31$, 107 voxels, BA10/11), as well as in medial and right BA8, left BA9 and right BA32.

Discussion

This study aimed to compare the recruitment of lateral RPFc in conditions with different levels of cognitive demands. Condition 1 made only low cognitive demands, which was predicted to lead to frequent task-unrelated thoughts. Condition 3 made high cognitive demands, requiring subjects to manipulate self-generated thoughts, and manage goal and sub-goals for each trial. These two conditions were compared to a baseline task with intermediary cognitive demands, involving a choice between two responses according to the properties of the stimuli (condition 2). This baseline task was chosen to avoid using a weakly constrained rest condition, and was thought to lead to minimal task unrelated thoughts and minimal management of goal/sub-goals and manipulation of self-generated thoughts. These three conditions were designed in two tasks, using arrows and numbers stimuli.

The behavioural results show that these two tasks were relatively well matched. Accuracy differed between the tasks overall, with an average of 1.9% more errors made in the Arrows task than the Numbers task, but there was no task by condition interaction. Reaction times differed significantly between the tasks in conditions 1 and 2, with responses on average faster by 31 and 138 ms, respectively, in the Numbers task compared to the Arrows task. Task difficulty, measured with self-reports, did not differ between the tasks, and showed a pattern consistent with the speed and accuracy results, with condition 1 being the easiest and condition 3 the most difficult, with an intermediary level for condition 2.

Self-report measures were also obtained on two types of task unrelated thoughts (TUT): those relating to the environment, and those relating to the self. As predicted, TUT frequencies showed differences between the three conditions, with selfTUT most frequent in the low cognitive demands condition 1, which supports the hypothesis that this condition should lead to mind wandering. The pattern of mind wandering frequencies across the conditions supports the previously mentioned findings of reduction of spontaneous thoughts when task demands increase (Antrobus, 1968; Filler & Giambra, 1973; Teasdale et al., 1993). A similar pattern to that

observed for the selfTUT was observed for envTUT, but only the difference between the condition 1 and 3 reached statistical significance.

In this study, RPFc recruitment was assumed to be independent from the type of stimuli used in the tasks. The results generally supported this hypothesis and only one interaction between task and conditions 1 and 2 was found to be affecting lateral RPFc. The difference in reaction times between the Arrows and Numbers task was greater in condition 2 than in condition 1. It is possible that this reaction time difference in the contrast 1-2 could be the origin of the observed neuroimaging interaction effect. Overall a similar set of regions were recruited in the contrasts 1-2 and 3-2 in both Arrows and Numbers task, suggesting that the two tasks were indeed recruiting a similar network, involving inferior parietal cortex and lateral PFC, as was predicted on the basis of the experimental design of the conditions.

Conjunction analyses across the two tasks focused on the low and high cognitive demand conditions 1 and 3, in comparison to the baseline condition 2. As predicted on the basis of the mind wandering/task-unrelated thoughts literature, a common network was found to be activated both in the low demand condition with a high frequency of TUT and the high demand condition, with minimal frequency of TUT. This network consisted mainly of the left inferior parietal lobule (BA40) and lateral RPFc (BA10/46/9) (see activations in red on Figure 5). Lowering the statistical threshold revealed similar activations in the right hemisphere.

Activations specific to either condition 1 or condition 3 in comparison to the baseline condition 2 were also found. A ventral network of regions was specifically recruited in the low demand condition 1, while a more dorsal network of regions was recruited in condition 3. BOLD signal changes specific to condition 1 were observed in the bilateral superior and middle temporal gyri, bilateral parietal lobe (BA40), right middle frontal gyrus (BA47, BA10, BA11) and right insula. BOLD signal changes specific to condition 3 were observed in the more dorsal part of the left and right inferior parietal lobules (BA40), as well as in the left precuneus (BA7), left inferior frontal

gyrus (BA9) and left RPFC (BA10/46). These results suggest a possible specialisation of left RPFC in the manipulation or attending towards task-related self-generated thoughts. However, the current study provides little evidence of strong hemispheric dissociations in lateral RPFC. This is consistent with the neuroimaging literature (Gilbert et al., 2006b; Koechlin et al., 1999; Wendelken et al., 2008).

The dorsal brain regions showing increased activations specific to condition 3 include a fronto-parietal network that supports the trial-by-trial control and implementation of task-sets (Dosenbach, Visscher, Palmer, Miezin, Wenger, et al., 2006; Dosenbach, Fair, Miezin, Cohen, Wenger, et al., 2007; Dosenbach, Fair, Cohen, Schlaggar, & Petersen 2008). The recruitment of this network is thus compatible with the suggestion that lateral RPFC supports task-related attending towards or manipulation of self-generated thoughts in condition 3. A more ventral network of regions including the insula, inferior parietal lobule (BA40) and superior temporal gyri showed specific activations in condition 1. These results replicate findings of increases activity in similar brain regions in rest compared to a task with low cognitive demand, where subjects had to press a key with their left or right finger in response to a left or right arrow presented on the screen (Christoff et al., 2004). In both paradigms, increased BOLD signal in the temporal lobes could reflect long-term memory processes involved in spontaneous thought flow (Christoff et al., 2004). Tentatively, one could suggest that dorsal lateral RPFC interacts more strongly with a dorsal fronto-parietal task-control system during the manipulation of task-relevant self-generated thoughts, while ventral lateral RPFC regions may interact specifically with temporal and inferior parietal cortices during spontaneous task-unrelated thoughts. Research into context-related connectivity between RPFC and other brain regions would provide stronger evidence for this distinction.

The BOLD signal increase in lateral RPFC in condition 3 occurs in a condition where participants have to keep in mind some self-generated information, i.e. representations not directly derived from the stimulus, while processing a new stimulus, and then compare the two pieces of self-

generated information to each other to select the appropriate response. This condition made the following demands: switching between attending towards perceptually-derived information and self-generated information (Gateway Hypothesis, Burgess et al., 2006), integration of goal/sub-goals (Braver & Bongiolatti 2002), branching (Koechlin et al. 1999), and manipulating self-generated information in working memory (Christoff & Gabrieli, 2000), processes that have been suggested to be supported by lateral RPFc. The lateral RPFc activations, and inferior parietal lobule activations, which were observed in condition 3 are thus consistent with these theories of lateral RPFc function.

The case of the BOLD signal increases in lateral RPFc in condition 1, relative to condition 2, is more complex. Condition 1 was designed as a condition where subjects needed to perform a very simple task, pressing a key when a stimulus appeared on the screen. Only very limited processing of the stimulus was required as the detection of a change on the screen was sufficient to do the task. On the basis of previous studies of task-unrelated thoughts and mind wandering, it was predicted that because this task made only low cognitive demands on the subjects, it would be associated with a higher frequency of task-unrelated thoughts. Participants indeed reported higher frequencies of task-unrelated thoughts in condition 1 compared to conditions 2 and 3. Two particular accounts of lateral RPFc function were considered. Christoff and colleagues (Christoff & Gabrieli, 2000; Christoff, Prabhakaran, Dorfman, Zhao, Kroger, Holyoak, et al., 2001; Christoff et al., 2004; Christoff, Ream, Geddes, & Gabrieli, 2003) propose that lateral RPFc is involved in the manipulation of either task-related or task-unrelated self-generated thoughts. Burgess and colleagues (Burgess et al., 2005; 2007b; Gilbert et al., 2005) suggest that lateral RPFc is involved in the orienting of attention towards either perceptually-derived or self-generated thoughts. On the basis of these two accounts, it was predicted that a similar network of regions, including lateral RPFc, would be activated in conditions 1 and 3, compared to the baseline condition 2, reflecting the processes of attending towards and manipulating self-generated thoughts in both tasks. The results support this hypothesis and are discussed further below.

First, it is necessary to address the fact that in the literature medial, rather than lateral RPFc, has been implicated in mind wandering (Mason et al., 2007a, Raichle et al., 2001, McGuire et al., 1996). This issue has been discussed by Gilbert et al. (2006a, 2007a). In this particular study, a strong case can be made from the fact that although condition 1 was less demanding (as measured by accuracy, reaction times, and self-reports of task difficulty) and was associated with a higher frequency of task-unrelated thoughts (as measured by self-reports of mind wandering) than condition 2, no BOLD signal changes were observed in medial RPFc when comparing condition 1 to condition 2.

Second, it is important to discuss whether the BOLD signal increases observed in condition 1 compared to condition 2 are indeed supporting task unrelated thoughts. In the current study, mind wandering was only measured using a questionnaire at the end of the experiment. Being based on self-report, and thus on subjects' awareness of their mind wandering, it is only a measure of retrospective report of awareness of mind wandering (Smallwood & Schooler, 2006). This issue has been discussed by Gilbert et al. (2007a) in relation to a recent study, which proposed that the default mode network (Raichle et al., 2001), in particular the medial RPFc and posterior cingulate cortex, supports mind wandering (Mason et al., 2007a). Gilbert et al. (2007a) suggest that stronger support of associations with mind wandering or task focusing could be obtained by investigating correlations of BOLD signal changes in the regions of interest with behavioural data, such as reaction times. In particular, a region proposed to be involved in mind wandering should show increase BOLD signal with slower reaction times, thought to be markers of a reduction of attending to the task. A possible correlation between reaction times and lateral RPFc BOLD signal changes was investigated in condition 1 in this study but reached significant statistical criterion only in the most ventral peak of activation [51 42 -12],.

What other possibilities could explain lateral RPFc activations in condition 1? Another interpretation could relate to the requirement of vigilance in condition 1. Indeed, as Gilbert et al. (2007a) note, the likelihood of mind wandering may provoke increased effort to remain alert

towards the environment. Few studies of vigilance have been run, and thus it is difficult to rule out this interpretation. Coull, Frith, Frackowiak, & Grasby (1996) found that the regions which responded specifically to sustained attention were: left inferior parietal cortex, left middle frontal gyrus, left orbital frontal gyrus, and thalamus. However, the lateral RPFc activations found by Coull and colleagues were much more dorsal than those found in the current study, in particular those found to be specific to condition 1 (BA47/10).

Another possible interpretation of the results of this study is that the lateral RPFc activity observed in condition 1 reflects the process of trying to inhibit task-unrelated thoughts and mind wandering. This would correspond, as in condition 3, to a task-related, or goal-directed, manipulation of self-generated thoughts, as subjects attempt to inhibit their mind wandering to achieve a better performance on the task. This interpretation can be put in relation to the findings by Navie and colleagues of increased sensitivity to distraction in conditions of high working memory load (de Fockert, Rees, Frith, & Lavie 2001; Lavie & de Fockert, 2005), which suggest that the prefrontal cortex regions recruited during working memory tasks are necessary to reduce interference from irrelevant perceptually-derived information. In the current study, we may have shown evidence for the involvement of lateral PFC regions, in particular the lateral RPFc, in reducing interference from irrelevant self-generated, rather than perceptually-derived information, when the conditions lead to an increase in mind wandering.

Further studies investigating lateral RPFc activations in low cognitive demand tasks could use methods that have been developed for the study of mind wandering (Smallwood & Schooler, 2006), in particular with variations of stimulus frequency (e.g. Antrobus, 1968; Giambra, 1995; Smallwood, O'Connor, Sudberry, Haskell, & Ballantyne, 2004), and the use of probes to evaluate mind wandering. This would provide the possibility to correlate brain activations and behaviour in more details. The current results, however, do provide new information regarding lateral RPFc function. For the first time, BOLD signal increases were observed in this region when comparing a low cognitive demand task (as opposed to rest or fixation) compared to a 2-choice reaction time

task. It will be necessary for theories of RPFPC functions to account for this observation of BOLD signal increases in lateral RPFPC in conditions of low cognitive demands.

To conclude, this study indicates that the rostral PFC is a region where BOLD signal increases both in low cognitive demand conditions (as well as rest, see Christoff et al. 2004) and high cognitive demand conditions, compared to intermediary levels. BOLD signal in lateral RPFPC thus follows a U-curve function, where the Y axis is lateral RPFPC BOLD signal and the X axis represents cognitive demands of the task (see Figure 1). Moreover, this study provides support for a possible specialization of the rostral PFC at the two ends of this spectrum, with the specific recruitment of an inferior rostral PFC region in low cognitive demand tasks, associated to mind wandering, or to the inhibition of mind wandering, and the specific recruitment of a left lateral rostral PFC region in the manipulation of task-related self-generated thoughts.

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Figure legends

Figure 1: Proposed U-curve function of recruitment of lateral RPFPC in tasks with varying task demands. Task demands increase from left to right, from minimal processing of stimuli to attention-grabbing stimulus processing tasks, and onto tasks requiring the manipulation of information that have been self-generated and are not perceptually available.

Figure 2: Examples of stimuli, and summary instructions of each condition of the Arrows (left) and Numbers (right) tasks. Note: for the Arrows task, the dashed lines and circle representing the imagined intersection of the arrows are shown merely for explanatory purposes and were not displayed during the experiment.

Figure 3: Mean Z-score (+SE) of participants' self-reports of task difficulty, environmentally triggered task-unrelated thoughts (envTUT) and self-related task-unrelated thoughts (selfTUT) for each task (Arrows or Numbers) and conditions. Condition 1: mind wandering, condition 2: baseline, condition 3: manipulation of task-related self-generated information.

Figure 4: Rendering of the activations observed when comparing conditions 1 and 3 to the baseline condition 2 in each task separately ($p < 0.001$ uncorrected). Condition 1: mind wandering, condition 2: baseline, condition 3: manipulation of task-related self-generated information.

Figure 5: A, B, C: Brain rendering of the activations observed in the conjunction of contrasts 3-2 and 1-2 (red), and of the activations specific to condition 1 (contrast 1-3 masked by 1-2, green), and those specific to condition 2 (contrast 3-1 masked by 3-2, blue). A: front view, B: right lateral view, C: left lateral view. **D:** Percentage signal change ($n=16$, mean and SE) of the differences between conditions 1 and 2, and conditions 3 and 2 in each task (a: Arrows task, n: Numbers task) in RPFPC peaks of activations: in the conjunction between contrasts 1-2 and 3-2 (red), in the contrast 1-3 masked by 1-2 (green) and in the contrast 3-1 masked by 3-2 (blue). Condition 1: mind wandering, condition 2: baseline, condition 3: manipulation of task-related self-generated information.

Table 1

Mean and standard deviation of reaction time and accuracy in each condition and each task (n=16). Condition 1: mind wandering, condition 2: baseline, condition 3: manipulation of self-generated information.

	Condition 1	Condition 2	Condition 3
Arrows Task			
RT (ms)	376 ± 120	722 ± 128	1035 ± 252
Accuracy (%)	98.8 ± 2.7	95.7 ± 2.0	88.8 ± 5.8
Numbers Task			
RT (ms)	345 ± 128	584 ± 112	996 ± 212
Accuracy (%)	99.1 ± 1.9	97.2 ± 1.4	92.7 ± 4.4

Table 2

Regions of BOLD signal change observed in: A: inclusive masking of global conjunction (across tasks) of contrasts 1-2 and 3-2; B: Global conjunction 1-3 inclusively masked by 1-2, C: Global conjunction 3-1 inclusively masked by 3-2 (main contrast and masks at $p < 0.001$ uncorrected, ≥ 5 voxels).

Lobe	Region	x,y,z MNI	BA	cluster	Z	p(FWE)
A: Common activations						
Parietal	Inferior Parietal Lobule	-51 -51 45	40	12	4.67	
Frontal	Middle frontal gyrus	-48 45 6	46/10	6	4.23	
B: Activations specific to condition 1						
Temporal	Superior temporal gyrus	-48 -6 3	22	12	7.81	<0.001
		60 6 -6	2/38	97	7.22	<0.001
		57 15 -9	8/22		5.99	<0.001
		57 6 6	22		5.9	<0.001
		-57 9 -6	22/28	7	5.78	<0.001
	Middle temporal gyrus	63 -51 3	21/22	19	6.16	<0.001
		66 -42 -3	21/22		5.62	<0.001
		42 -12 -12	21	9	5.96	<0.001
Parietal	Inferior parietal Lobule	66 -30 27	40	138	7.03	<0.001
	Supramarginal gyrus	57 -51 33	40		6.33	<0.001
	Inferior parietal Lobule	57 -36 21	40		5.19	<0.01
	Inferior parietal Lobule	-63 -39 30	40	15	5.99	<0.001
	Supramarginal gyrus	-57 -60 36	40	7	5.56	<0.001
Frontal	Middle frontal gyrus	48 42 -3	47/10	54	6.28	<0.001
		39 39 -12	11/47		6.1	<0.001
		51 42 -12	47/11		5.98	<0.001
Insula		45 3 0	13	11	5.93	<0.001
		39 3 6	13		5.12	<0.01
C: Activations specific to condition 3						
Parietal	Supramarginal Gyrus	-39 -48 36	40	38	4.59	
	Inferior Parietal Lobule	-45 -45 42	40		4.42	
		-48 -45 54	40		3.96	
		36 -51 36	40	6	3.46	
	Precuneus	-6 -72 48	7	8	3.83	
Frontal	Inferior Frontal Gyrus	-42 3 36	9	6	4.36	
	Middle Frontal Gyrus	-39 51 15	10/46	5	3.43	

Figure 1

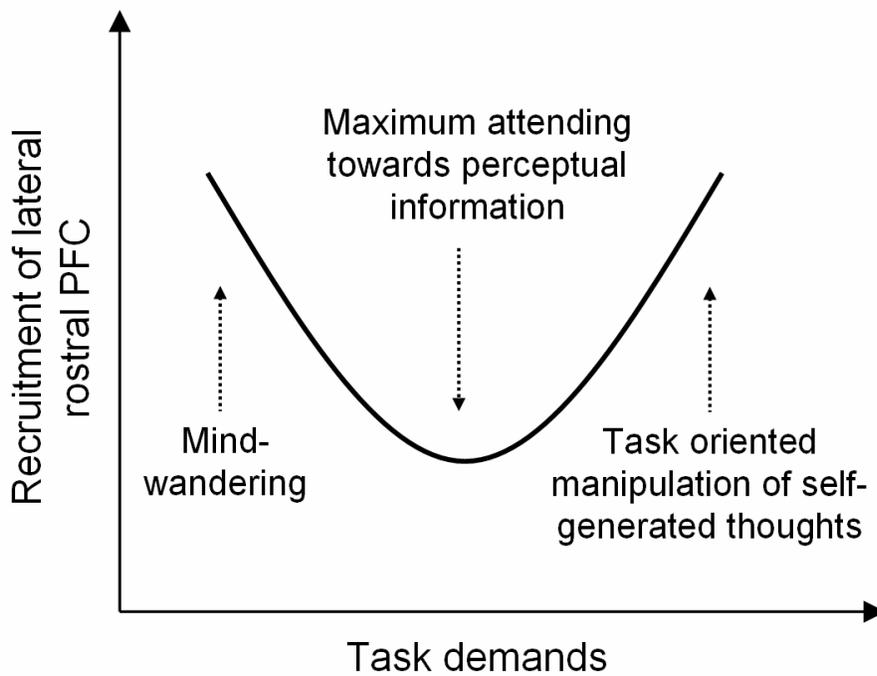


Figure 2

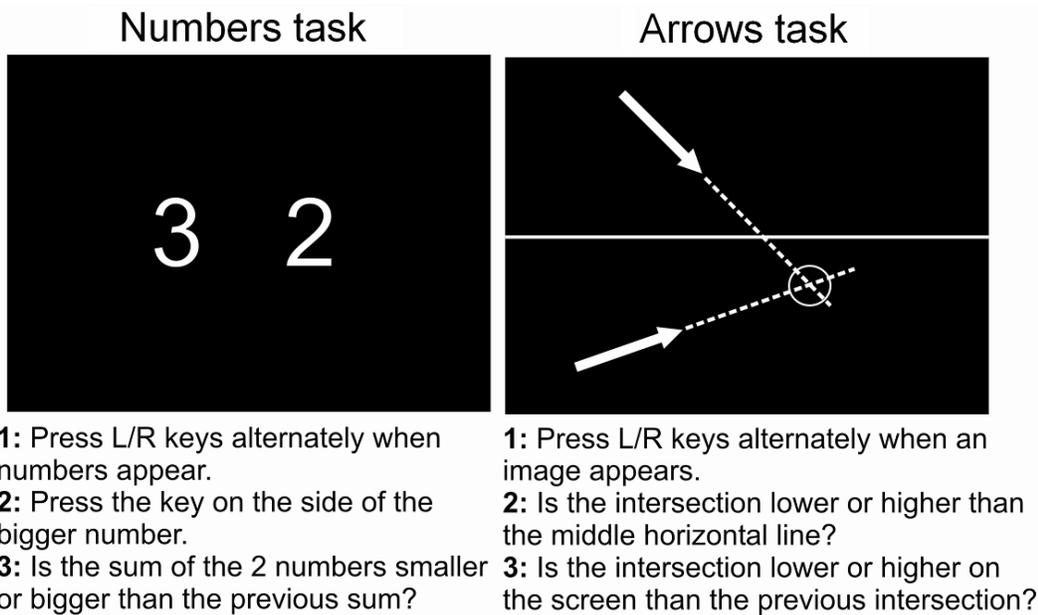


Figure 3

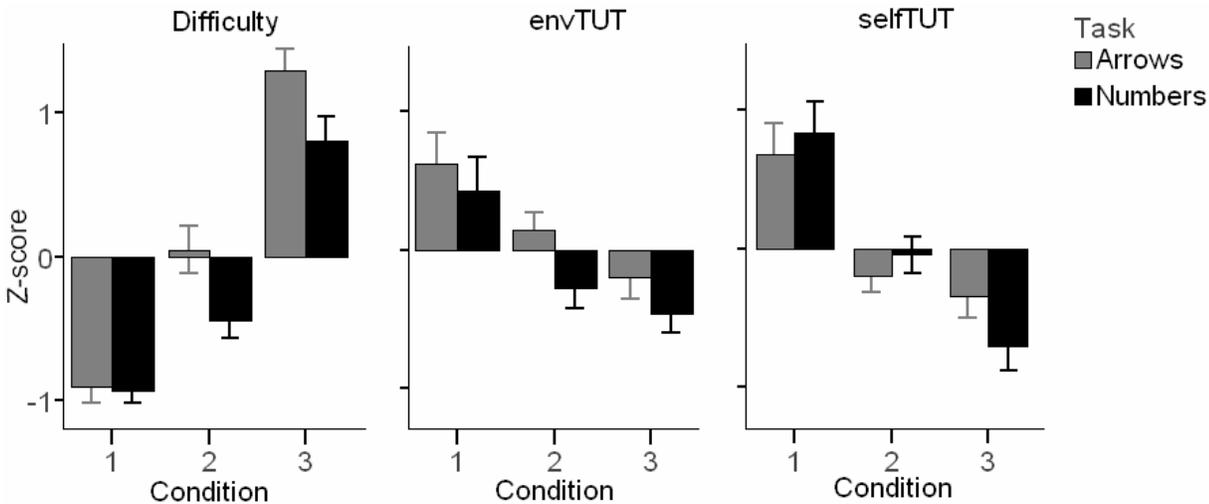


Figure 4

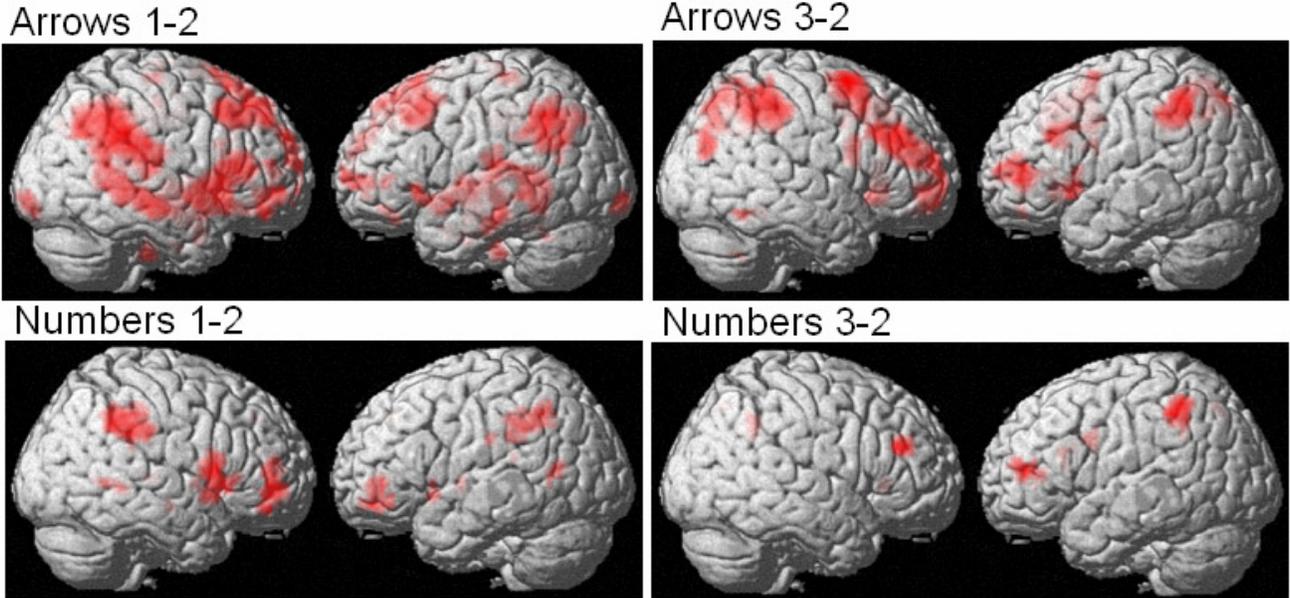


Figure 5

