Cerebral Cortex August 2009;19:1929–1936
doi:10.1093/cercor/bhn222
Advance Access publication December 1, 2008

The Representation of Abstract Task Rules in the Human Prefrontal Cortex

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We have previously reported sustained activation in the ventral prefrontal cortex while participants prepared to perform 1 of 2 tasks as instructed. But there are studies that have reported activation reflecting task rules elsewhere in prefrontal cortex, and this is true in particular when it was left to the participants to decide which rule to obey. The aim of the present experiment was to use functional magnetic resonance imaging (fMRI) to find whether there was activation in common, irrespective of the way that the task rules were established. On each trial, we presented a word after a variable delay, and participants had to decide either whether the word was abstract or concrete or whether it had 2 syllables. The participants either decided before the delay which task they would perform or were instructed by written cues. Comparing the self-generated with the instructed trials, there was early task set activation during the delay in the middle frontal gyrus. On the other hand, a conjunction analysis revealed sustained activation in the ventral prefrontal and polar cortex for both conditions. We argue that the ventral prefrontal cortex is specialized for handling conditional rules regardless of how the task rules were established.

Keywords: decision making, fMRI, free selection, prefrontal cortex, task set

Introduction

In the laboratory, the task rules are provided by the instructions given before testing. These can either be concrete, for example, when shown stimulus A press button 1, or abstract, for example, when shown a novel word press button 1 if it is in upper case and button 2 if it is in lower case. Here the rule applies whatever the word presented. The rules can either be cued or uncued. In the first case, a word or symbol appears that specifies the rule, whereas in the second, a switch between rules can occur without warning, as on the Wisconsin Card Sorting Task.

We have previously looked for the representation of abstract task rules by scanning participants while they prepared to perform 1 of 2 tasks. The current rule was specified by a word presented at the beginning of a trial. We reported sustained activation in the anterior ventral prefrontal cortex (Sakai and Passingham 2003, 2006) and suggested that this reflected task set, that is preparation to perform a specific task operation. Bunge et al. (2003) also found similar activation in the ventral prefrontal cortex, whereas the participants were maintaining a matching or nonmatching rule.

But there are studies, both on human participants and nonhuman primates, which have reported activation reflecting task rules elsewhere in prefrontal cortex. This is true in particular when the task rules have not been cued. So, for example, Forstmann et al. (2005) compared cases where the task for the next trial was either specified by an instructing cue or by a transition cue simply instructing “stay” or “switch.” They reported activation in the rostral cingulate cortex and middle frontal gyrus when the participants had to retrieve the task rule, which occurred after switch instructions. A special case of uncued retrieval allows the participant to decide on the rule, sometimes called the “free selection” task. Again there is activation in the rostral cingulate cortex and middle frontal gyrus when the participants spontaneously retrieve the rule, varying the rules in a semirandom fashion across the trials (Forstmann et al. 2006, 2008; Rowe et al. 2008). That this activation can represent the specific rule was shown by Haynes et al. (2007) who used a multivariate analysis to distinguish which task the participants intended to perform.

There is a more direct way to prove that task set activation can code for a specific rule. This is to record from cells in monkeys while they are preparing to perform a particular task. Wallis et al. (2001) taught monkeys 2 rules, either to respond if a picture matched a previous one (matching rule) or to respond if it did not match (nonmatching rule). They recorded from cells after a cue was given that told the monkey which rule held for that trial, found many cells that coded for the rule, and did so irrespective of the specific task items that were presented. These cells were found not only in the ventral prefrontal cortex but also in the dorsal prefrontal cortex. And it does not matter if the rule concerns the identity of the items or their spatial location: Cells that fire differently according to the current rule can be found in both the ventral and dorsal prefrontal cortex (White and Wise 1999).

The advantage of functional brain imaging is that, unlike single unit recording, it is a whole-brain method. This means that one can identify activation reflecting task rules wherever it is. Another advantage is that with human participants one can easily compare different way of setting up task rules and look for areas that are activated in common; however, the rule is established. Rules can be learned by trial and error as in the case of monkeys (Mansouri et al. 2006); they can be indicated by switch or stay cues (Forstmann et al. 2005); they can be self-generated (Rowe et al. 2008); or finally, they can be verbally instructed (Sakai and Passingham 2006). The present experiment specifically compares self-generated with verbally instructed rule so as to see whether there is sustained activation in common. We supposed that, because the tasks were the same, however the rules were established, there might be a common area in which there was sustained activation and that it might be activation in this area that influenced activation in task-specific areas. Sakai and Passingham (2006) showed that, when the rules were provided by instructions, it was sustained activation in the ventrolateral prefrontal cortex that influenced the performance of the tasks.

We looked for this common representation by analyzing sustained activation before the task items are presented. To do this, we introduced a variable delay of 2–10 s between the setting up of the rule and the presentation of the task items. This allowed us to identify sustained activation and to follow the course of that activation during the delay. This was not possible from the previous experiments comparing freely selected with externally instructed rules by Forstmann et al. (2006) and Rowe et al. (2008) because in their experiments the delay was very brief. In our own experiments (Sakai and Passingham 2006; Haynes et al. 2007), we have reported sustained activation in several prefrontal regions, but the design did not allow us to look for common activation, however, the rules are established. Our reason for concentrating on sustained activation is that we have shown in previous studies (Sakai and Passingham 2006; Haynes et al. 2007) that in experiments of this type, sustained activation reflects the intention to perform a specific task. The finding of significant sustained activation also rules out the possibility that it simply reflects reading the instructing word.

We used 2 task rules. The first was to judge whether a word was abstract or concrete (semantic rule) and the second to judge whether it was 2 syllables or not (phonological rule). The task items were single nouns. Advantages of introducing a variable delay before presentation of the task items are that it forces the participants to prepare for the task instantly and that one can distinguish activation at the end of the delay when the participants make their judgment on the word.

Methods

We scanned 13 healthy, right-handed volunteers. There were 4 males and 9 females. They had a mean age of 23.6 (range 20–35 years). All gave written consent to participate in the study. All were native English speakers. The study was approved by the joint ethic committee of the London Institute of Neurology and University College London Hospital, United Kingdom.

Behavioral Task

The participants were required to make phonological or semantic judgments on a visually presented word as in Sakai and Passingham (2006). There were 3 experimental conditions (Fig. 1). In the first 2, task instructions were presented followed by a variable delay. For the phonological condition, the instruction “Two Syllables” appeared on the screen, and the task was to judge whether the word that was presented after the delay had 2 syllables or not. For the semantic condition, the instruction “Abstract” appeared, and the task was to judge whether the word had an abstract meaning or not. We refer to these trial types as Instr Phon and Instr Sem. In a third condition, the word “Decide” appeared, and this told the participants to freely decide which of the 2 tasks to perform after the delay. On some trials, they decided to perform the phonological task and on others to perform the semantic task. We refer to these trial types as Self Phon and Self Sem.

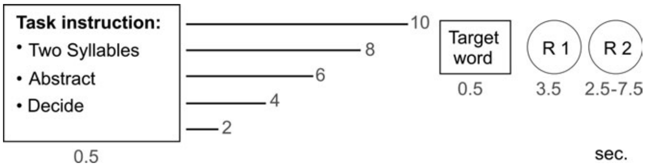

Figure 1. The self-generated and instructed tasks. The instruction was followed by a varying delay (2–10 s). The task word appeared for 500 ms after which the participants responded (R1). They then made a second response (R2) reporting which task they had performed.

After an instruction delay of 2, 4, 6, 8, or 10 s, a target word was presented for 500 ms. The variable delays were equally often presented. The words were nouns with written frequency over 30, chosen from the Medical Research Council Psycholinguistic Database http://www.psy.uwa.edu.au/mrcdatabase/uwa_mrc.htm. Half of the words had 2 syllables, and the other half had 1 or 3 syllables. Half of the words had a concrete rating below 300, and the other half had a concrete rating above 550. In our previous study (Sakai and Passingham 2006), this selection criterion was successful in equating the reaction time between the phonological and semantic tasks. On presentation of a word at the end of the delay, the participants were asked to make a response as quickly as possible. They pressed a button with their right index finger to indicate a yes-response and with their right middle finger to indicate a no-response. A new target word was presented for each trial. The 3 types of task instructions were given in pseudorandom order.

Before the scanning, the participants performed a practice session of 90 words for 15 min. During the scanning session, the total number of trials for each task was 50 for the 2 instructed tasks and 100 for the self-generated task. In total, 200 trials were given using different words divided into 5 sessions. Participants were asked to decide roughly evenly between the 2 tasks over the course of the experiment. After the response to the task word, a second response was required where the participants reported which of the 2 tasks they performed (Fig. 1). In this way, we registered which task they had decided to perform during the self-generated trials, on a trial by trial basis. Also for the second response participants pressed a button with their right index finger or right middle finger. The interval between the second response and the task instruction for the next trial was varied between 6 and 10 s in a step of 2 s.

It was essential that on the self-generated trials the participants made their decision as quickly as possible so that we could be sure that any sustained activation genuinely reflected the maintenance of the rule. This was achieved, in part, by having a variable and unpredictable delay, with some delays as short as 2 s. After the 5 sessions constituting the fMRI data set, we therefore ran a sixth session where the participants read the instruction Decide and reported with a button press when they had decided what task to perform. On other trials, they read Abstract or Two Syllables and pressed a button to report when they had understood the instruction. In this way, we obtained a measure on how fast subjects made their decisions. Apart from introducing this response, the sixth session was identical to the other sessions. No scans were taken during this sixth session.

Functional Resonance Imaging

Imaging was performed using a 3 Tesla scanner (Allegra; Siemens, Erlangen, Germany). Contrasts for the blood oxygen level–dependent (BOLD) signal were acquired by T_2^*-weighted echo planar imaging. The time repetition (TR) was 2.34 s and the time echo (TE) 40 ms, with whole-brain acquisition. The in-plane resolution was 3 mm in a 64 × 64 matrix. There were 36 slices of 2-mm thickness, with an interslice gap of 1 mm. High-resolution structural T_1-weighted were also acquired for all subjects (TR 7.92 s; TE 2.4 ms; voxel size of 1 × 1 × 1.5 mm; 108 slices).

Data Analysis

We used SPM5 (http://www.fil.ion.ucl.ac.uk/spm) for image processing and analysis. The first 5 volumes were discarded to allow for T_1 equilibration. The remaining volumes were realigned to the first image and normalized with the unwrap algorithm to the Montreal Neurological Institute (Montreal, Canada) reference brain using a 12-parameter affine transformation along with nonlinear transformations using cosine basis functions. The images were resampled into 2-mm cubic voxels and spatially smoothed with a Gaussian kernel (8-mm full width at half maximum). Statistical parametric maps of t-statistics were calculated for condition-specific effects within a general linear model. For each of 4 trial types (Instr Sem, Instr Phon, Self Sem, and Self Phon), sustained activation was modeled as epochs with onsets time locked to the presentation of the instruction and with a duration matched to the length of the delay. The model also included the following covariates: 1) covariates for transient activation on presentation of the instructing word at the beginning of the trial, separately for free and instructed trials; 2) covariates for transient activation in response to presentation of the word stimuli, separately for each condition; and 3) a covariate for transient activation in response to the second button response, in common for all the conditions. Error trials were modeled separately and defined as conditions of no interest.

All epochs and events were convolved with a canonical hemodynamic response function. The data were high pass filtered with a frequency cutoff at 128 s. Images of parameter estimates for the contrast of interest were created for each subject (first-level analysis) and were entered into a second-level analysis using a 1-sample *t*-test across the 13 participants. We first thresholded the images such that the false discovery rate (FDR) was 0.05 for each map, whole brain corrected at the voxel level (Genovese et al. 2002). Because of a priori hypotheses about activations in the middle frontal gyrus and the rostral cingulate cortex, we also used regions of interest (ROIs) for the dorsal prefrontal cortex and the rostral cingulate cortex, derived from the results of the previous study by Rowe et al. (2008). We report results for the regions of interest at a significance level of family wise error correction (FWE). $P < 0.05$ corrected. The interest of the present study was in those prefrontal areas that have been described in previous studies on abstract rules, and so we report here activations for the frontal lobe only.

Sustained Activation

We first looked for sustained activations that differed between conditions and for sustained activations that were in common. Thus, we compared self-generated trials and instructed trials, that is (Self set vs. Instr set) and (Instr set vs. Self set). To investigate common activation, irrespective of how whether the rules were cued or not, we performed a global null conjunction analysis (Friston et al. 2005).

We then plotted the time course of these activations. The time series of the BOLD signals at the peak of activation was realigned to the onset of the trial. A time bin corresponded to 1TR (2.34 s). The signals within each bin were then averaged across trials for all the participants. This was done separately for trials with different length of the delay and separately for the 2 conditions of interest, “Instructed” and “Self generated” trials.

Activations Aligned to Presentation of Target Word

Then, we analyzed the activation aligned to presentation of the target word, that is the task activation. We compared Phonological with Semantic trials (Instr phon task + Self phon task vs. Instr sem task + Self sem task) and Semantic versus Phonological trials (Instr sem task + Self sem task vs. Instr phon task + Self phon task). We also performed a global null conjunction analysis to identify task activations in common for semantic and phonological judgments.

Results

Behavioral Results

All subjects performed the task with high accuracy. The mean error rate for the self-generated trials was 6.2 ± 0.7% and 4.1 ± 0.8% for the instructed trials. Error trials were subsequently excluded from the imaging analysis. When participants made decisions on the task word, their response time was slightly longer ($P < 0.053$, 2-tailed, 1-sample *t*-test) when they themselves had decided upon the task (1557 ± 40 ms), as compared with following the instructions (1496 ± 35 ms) (Fig. 2*A*).

As explained in the methods, it was important to establish that sustained activation that we found was not due to late decisions made by the participants on the self-generated trials. The average time that participants took to make up their minds on self-generated trials was 1181 ± 128 ms, compared with 979 ± 62 ms for reading the instructions on the externally instructed trials (Fig. 2*B*). In total, the participants decided to perform the phonological task 681 times and the semantic task 680 times.

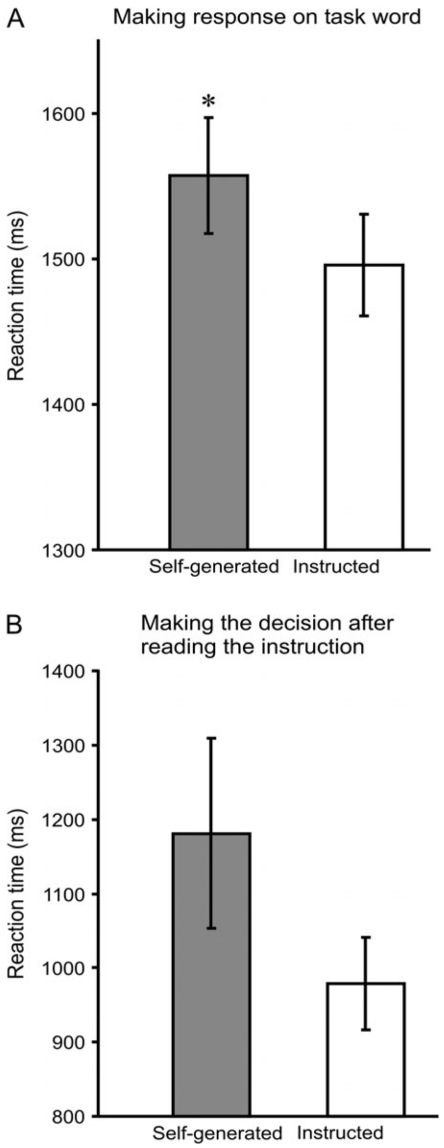

Figure 2. (*A*) Time to make a decision about the target word in the self-generated and instructed conditions. (*B*) Time to decide on the task (self-generated) or to process the task instruction in session 6.

Sustained Activation

Self-Generated versus Instructed

First we tested for sustained activation that was greater in the self-generated condition than in the externally instructed condition. There was no sustained activation that survived the threshold of FDR $P < 0.05$ corrected. As explained in the Methods, we used regions of interest from the comparison of self-generated trials with externally instructed trials from the paper by Rowe et al. (2008). The peaks for the ROIs were at (2, 36, and 34) for the rostral cingulate cortex and at (–44, 34, and 34) for the middle frontal gyrus, and the radius was 8 mm. We tested these for both the left and right hemispheres.

We found significant sustained activation in the left middle frontal gyrus ($t = 3.43$, $P < 0.05$, corrected for small volume). This activation lay within area 46 (Rajkowska and Goldman-Rakic 1995). At uncorrected levels ($P < 0.001$), there was a peak for sustained activation nearby at the coordinate (–54, 26, and 30). The test for sustained activation in the rostral cingulate cortex did not reach significance, though inspection of Figure 4 suggests that there was sustained activation early in the delay. Instead, there was significant transient activation in the rostral cingulate cortex, that is, the paracingulate cortex (2, 24, 42) at the time of presentation of the instructing word (Decide vs. Abstract or Two syllables) ($t = 4.60$, FDR $P < 0.01$). Because the vector modeling the transient activation of the presentation of the instruction and the vector modeling the sustained activation are correlated, we cannot completely rule out the possibility that there is sustained activation in the paracingulate area. But with the present model we fail to pick this up.

Figure 3 shows the plots for self-generated (left) and instructed trials (right) versus baseline for the middle frontal gyrus and paracingulate cortex. The data are aligned to the time of presentation of the instructing word. The timescale on the *x*-axis has been adjusted to take into account the lag in the BOLD signal. This means that “0” represents the time at which

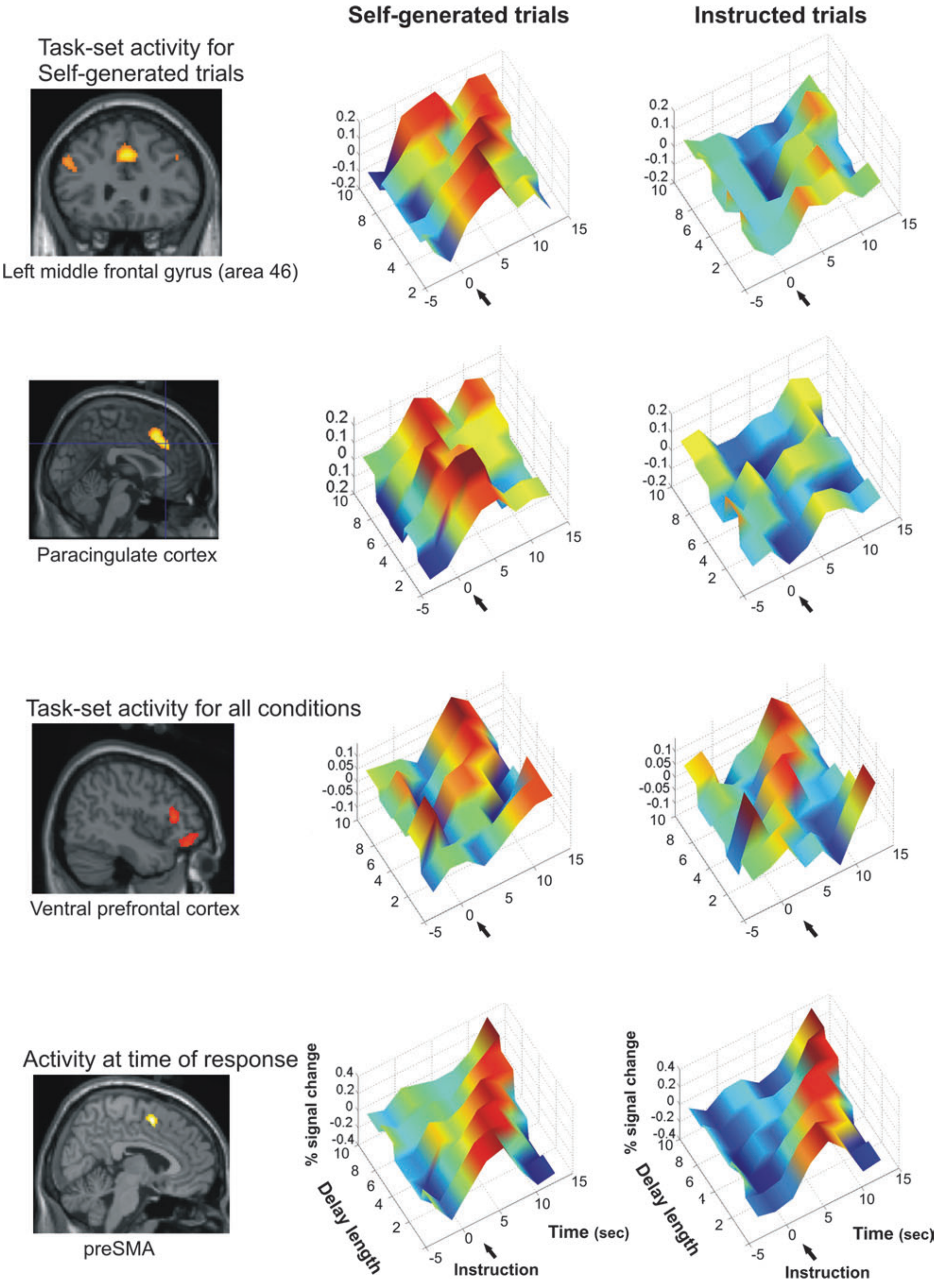

Figure 3. All the plots in Figure 3 show the adjusted data for the BOLD signal (vertical axis), aligned to the time of presentation of the instructing word. Time is shown along the axis in the foreground. The numbers on the *x*-axis are adjusted to take into account a delay in the peak of the BOLD signal of 5 s. In other words, 0 (arrow) corresponds to 5 s after the instructing word. The data for the different delay lengths are shown along the left-hand receding axis, with the longest delay at the back and the shortest delay at the front.

transient activation at the time of the word Decide would be expected to peak. The *y*-axis shows the data for the different delay lengths.

Figure 4 plots the data for self-generated trials (top) and instructed trials (bottom) for the longest delay, that is 10 s.

Instructed versus Self-Generated

We then tested for sustained activation that was greater in the externally instructed condition than in the self-generated condition. There was no significant peak for this comparison at FDR $P < 0.05$ corrected and no peak that reached

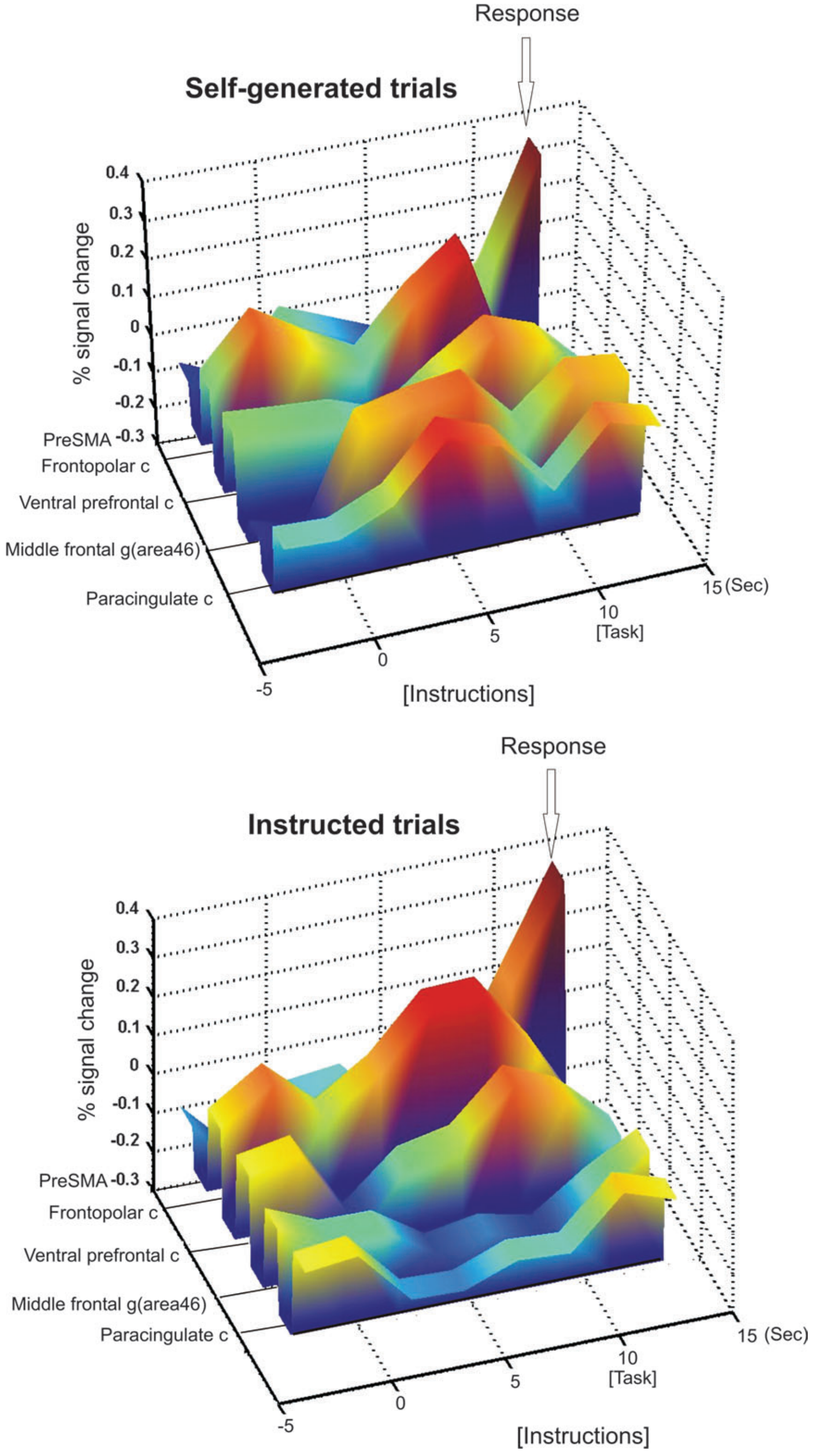

Figure 4. As in the plots in Figure 3, this figure shows the adjusted data for the BOLD signal (vertical axis), aligned to the time of presentation of the instructing word. Data are plotted for the longest delay only (10 s). Time is shown along the axis in the foreground. The numbers on the *x*-axis are adjusted to take into account a delay in the peak of the BOLD signal of 5 s. In other words, 0 corresponds to 5 s after the instructing word. The receding axis on the left indicates the 5 areas from which the data were taken. The data for the right-hand side of the BOLD signal for the preSMA are not shown in this figure. c = cortex, g = gyurs.

significance even when we lowered the significance level to $P < 0.01$ uncorrected.

Sustained Activation in Common for Both Self-Generated and Instructed

We tested for sustained activation that was in common for both self-generated and instructed trials. At a significance level of FDR $P < 0.05$, there were peaks in the ventral prefrontal cortex and frontal polar cortex. These are presented in Table 1.

Figure 3 shows the plots for sustained activation for the ventral prefrontal cortex for self-generated and instructed trials.

It will be seen from Figure 4 that on self-generated trials the sustained activation for the middle frontal gyrus occurs early in the delay and that it peaked well before the peak for the sustained activation in the ventral prefrontal cortex for self-generated and instructed trials combined. The figure also shows the transient activation for the presupplementary motor cortex at the time of the button press. It will be seen that the sustained activation in the ventral prefrontal cortex peaked before the button press.

Figure 5 shows that the sustained activation in common fills the ventral prefrontal cortex and does not extend into the middle frontal gyrus above the inferior frontal sulcus.

Table 1

Peaks of sustained activation in common, irrespective of whether the task rules were self-generated or verbally instructed

Area	Coordinates	Z (voxel level)	*P* (FDR corrected)
Left (L) polar cortex	−10, 68, 18	3.54	0.05
Right (R) polar cortex	12, 70, 18	3.34	0.05
L ventral prefrontal cortex	−52, 42, 2	5.25	0.001
L ventral prefrontal cortex	−36, 34, −12	5.58	0.001
R ventral prefrontal cortex	46, 48, −8	3.77	0.001
R ventral prefrontal cortex	46, 28, 12	4.28	0.001
R ventral prefrontal cortex	50, 26, 20	3.99	0.01
R lateral orbital cortex	46, 42, −18	3.99	0.01
R orbital cortex	26, 34, −20	3.42	0.05

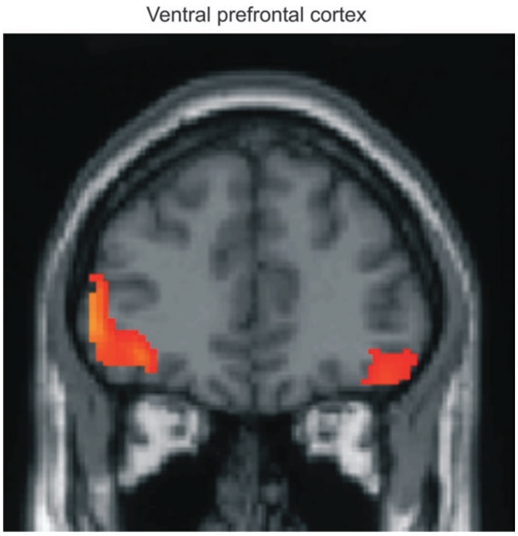

Figure 5. Areas of sustained activation in common, irrespective of whether the rules were self-generated or verbally instructed.

Activations Aligned to the Presentation of the Target Word

Comparing the phonological with the semantic task, there were significant activations in the premotor cortex bilaterally (–28, –12, and 64; 32, –16, and 52). Comparing the semantic task with the phonological task, there was a significant activation in the left inferior frontal gyrus (–56, 30, and 12).

We also performed a conjunction analysis to look for activations in common when the participants made decisions about the words. At a significance level of FDR 0.01 (corrected), there were activations in both the left (–36, 12, 26) and right (48, 16, 30) inferior frontal sulci and also in the left ventral prefrontal cortex (–54, 20, –2). There were no significant activations in the middle frontal gyrus.

Discussion

Our aim was to search for sustained activation representing the task rules and to see whether there was a common representation irrespective of the way in which the task rules were established. We did this by comparing self-generated task rules and rules that were specified by the instructions. The contrast between these reveals activations that depend on the way in which the task rule is established. The conjunction of the activations for these 2 conditions reveals the common representation.

When the self-generated task was compared with the externally instructed task, there was sustained activation in the middle frontal gyrus, that is within the dorsal prefrontal cortex. It lay within area 46 as judged from the probability map published by Rajkowska and Goldman-Rakic (1995). There was also a significant difference in activation between the 2 conditions in the cingulate cortex as in the studies by Forstmann et al. (2006) and Rowe et al. (2008). However, the peak was associated with the transient activation aligned to the instructing word. Generating task rules requires the ability to evaluate alternatives. We suggest that the anterior cingulate cortex is involved in this process. First, in a previous study, we compared self-generated and externally instructed responses and showed that activation in the anterior cingulate cortex was specific to self-generated responses, whereas activation in area 46 related to the difficulty in selecting a response (Lau et al. 2004). Second, removal of the tissue in the anterior cingulate sulcus impairs the ability to make use of switch or stay cues concerning actions (Kennerley et al. 2006) or task rules (Buckley MJ, Mansouri FA, Mahboubi M, Hoda H, Browning GF, Kwok SC, Phillips A, Tanaka K, unpublished data).

Though there was sustained activation in the dorsal prefrontal cortex (area 46) for the self-generated task, there was no such activation for the externally instructed task (Fig. 3). The formal demonstration that this was so comes from the conjunction analysis for sustained activation. Here there was sustained activation in the ventral prefrontal cortex bilaterally and in the polar cortex (Table 1). It will be seen from Figure 5 that the activation is extensive, including not only the ventral prefrontal convexity but also the lateral orbital cortex. These are both cytoarchitechtonic area 47 (Petrides and Pandya 2002). The activations were also extensive in the study by Bunge et al. (2003) for externally instructed task rules. However, there was no sustained activation in common in the dorsal prefrontal cortex. So as to find out whether this was simply due to lack of sensitivity, we lowered the significance level to $P < 0.01$ uncorrected, and though there was activation in the inferior frontal sulcus, it did not extend to the middle frontal gyrus.

Figure 4 illustrates the sustained activation in the dorsal prefrontal cortex (area 46) for the self-generated task and the sustained activation in common in the ventral prefrontal cortex. The figure suggests that the sustained activation in the ventral prefrontal cortex peaked later in the delay. One should be cautious in interpreting differences in peaks as evidence of temporal order. Such differences could occur as an artifact of differing shapes for the BOLD response due to differences in neurovascular coupling. But the differences suggested by Figure 4 are of the order of 3 s, and this makes that explanation less likely. Furthermore, the activation in the dorsal prefrontal cortex tended to decrease with delay. We therefore suggest that the final common path involves the ventral prefrontal and polar cortex. Other studies have suggested a role for the polar cortex in "prospective memory" (Burgess et al. 2000, 2007; Gilbert et al. 2006).

It could be that the ventral prefrontal cortex was activated because the tasks that our participants performed were verbal tasks. Performance of both tasks themselves led to activation in the ventral prefrontal cortex, as in the earlier study of semantic and phonological processing by Devlin et al. (2003). But, as mentioned above, Bunge et al. (2003) have also reported that when task rules are externally instructed the delay-related activation is in the ventral prefrontal cortex, even though the task rules were visual matching and nonmatching. Monkeys with ventral prefrontal lesions are very impaired at learning the visual matching rule (Rushworth et al. 1997; Bussey et al. 2001), whereas monkeys with dorsal prefrontal lesions that included area 46 are not (Passingham 1975; Mishkin and Manning 1978). Monkeys with ventral prefrontal lesions are also poor at learning conditional rules (Bussey et al. 2001) and abstract response rules (Bussey et al. 2001; Baxter MG, Gaffan D, Kyriazis DA, Mitchell AS, unpublished data).

In an earlier study (Sakai and Passingham 2006), we showed that task set activation in the ventral prefrontal cortex correlated in a task-specific manner with the activation in the premotor cortex when the participants performed the phonological task and with the activation in the left inferior frontal gyrus when they performed the semantic task. Because the sustained activation was recorded before the task items were presented, we have suggested that this activation is involved in setting up the task that is appropriate for that trial (Sakai and Passingham 2006). If this is the case, interfering with the activation should disrupt performance of the task rules. Rowe et al. (2007) reported that after prefrontal resections in patients there was a decrease in the covariance between activation in task-specific regions. However, the lesions were large, invading the white matter, and 3 of the lesions included the dorsal, ventral, and polar frontal cortex.

Buckley MJ, Mansouri FA, Mahboubi M, Hoda H, Browning GF, Kwok SC, Phillips A, Tanaka K (unpublished data) made more specific cortical lesions in monkeys. The animals had been taught to match by shape on one block of trials and by color on another, with the switch being cued by the failure to obtain the expected reward (Mansouri et al. 2006). Monkeys with ventral prefrontal lesions were unable to relearn either of the matching rules. Monkeys with dorsal lesions that included area 46 and the polar cortex could learn the rules, but if there was a longer than usual intertrial interval, they failed to retain this rule Buckley MJ, Mansouri FA, Mahboubi M, Hoda H, Browning GF, Kwok SC, Phillips A, Tanaka K (unpublished data). The same effect was not found for monkeys with lesions in the cingulate sulcus, and this is consistent with the fact that we failed to find evidence of significant sustained activation in the paracingulate cortex.

Conclusion

When a participant has generated a task rule, it must be kept in memory and protected from distraction until the time when the task items are presented. We suggest that the dorsal prefrontal cortex is involved in this process. Once the task rule has been generated and maintained, it must then influence later performance of the task. Our data indicate that, however the rule was established, the final common pathway involves the ventral prefrontal and polar cortex.

Funding

Wellcome Trust (05/Q0512/50).

Notes

We are grateful to Hakwan Lau for help with the experimental design, to James Rowe for advice on the analysis, and to Sam Gilbert for valuable comments on the manuscript. *Conflict of Interest*: None declared.

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