Involvement of right dorsolateral prefrontal cortex in ill-structured design cognition: An fMRI study

How to cite:

For guidance on citations see FAQs.

© 2009 Elsevier B.V.

Version: Accepted Manuscript

Link(s) to article on publisher’s website:
http://dx.doi.org/doi:10.1016/j.brainres.2009.11.045

Copyright and Moral Rights for the articles on this site are retained by the individual authors and/or other copyright owners. For more information on Open Research Online's data policy on reuse of materials please consult the policies page.
Involvement of right dorsolateral prefrontal cortex in ill-structured design cognition: An fMRI study

Sam J. Gilbert, Theodore Zamenopoulos, Katerina Alexiou, Jeff H. Johnson

PII: S0006-8993(09)02499-8
Reference: BRES 39847

To appear in: Brain Research

Received date: 20 July 2009
Revised date: 14 October 2009
Accepted date: 19 November 2009

Please cite this article as: Sam J. Gilbert, Theodore Zamenopoulos, Katerina Alexiou, Jeff H. Johnson, Involvement of right dorsolateral prefrontal cortex in ill-structured design cognition: An fMRI study, Brain Research (2009), doi 10.1016/j.brainres.2009.11.045

This is a PDF file of an unedited manuscript that has been accepted for publication. As a service to our customers we are providing this early version of the manuscript. The manuscript will undergo copyediting, typesetting, and review of the resulting proof before it is published in its final form. Please note that during the production process errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.
Involvement of right dorsolateral prefrontal cortex in ill-structured design cognition: An fMRI study

Sam J. Gilbert¹, Theodore Zamenopoulos², Katerina Alexiou², Jeff H. Johnson²

¹Institute of Cognitive Neuroscience and Department of Psychology, University College London, 17 Queen Square, London, WC1N 3AR, UK

²Design Group, Department of Design, Development, Environment and Materials, The Open University, Milton Keynes, MK7 6AA, UK

Total pages: 34
Tables: 4
Figures: 4

Address correspondence to:
Sam Gilbert
Institute of Cognitive Neuroscience
17 Queen Square
London WC1N 3AR
UK
Email: sam.gilbert@ucl.ac.uk
Tel: +44 (0)20 7679 1149
Fax: +44 (0)20 7813 2835
Abstract

In ill-structured tasks, the problem to be solved is poorly specified and there is no unique correct solution. Most evidence on brain mechanisms involved in dealing with such tasks comes from neuropsychology. Here, we developed an ill-structured design task suitable for testing in a functional neuroimaging environment, and compared it with a matched well-structured problem-solving task using fMRI. Consistent with prior neuropsychological results, the design task was associated with greater activity in right dorsolateral prefrontal cortex, compared with problem solving. This differential activity was specific to the problem studying phase rather than performance. Furthermore, the design and problem-solving tasks differed not only in overall levels of brain activity but also in patterns of functional interactions between brain regions. These results provide new evidence on the role of right dorsolateral prefrontal cortex in ill-structured situations, such as those involved in design cognition. Additionally, these results confirm the suitability of functional neuroimaging for studying such situations.
1. Introduction

One characteristic shared across many tasks sensitive to prefrontal cortex (PFC) function is the need to select responses in the absence of, or in conflict with, established stimulus-response links (Miller and Cohen, 2001; Norman and Shallice, 1986). However, this characteristic describes a very large range of situations. Amongst these situations, an important distinction may be drawn between well-structured and ill-structured tasks. In a well-structured task, the goal state, set of appropriate responses, and criteria by which to evaluate whether the goal has been achieved are clearly specified. By contrast, ill-structured tasks are more subjective. They may be interpreted in more than one way and lack a unique solution. Seeing as ill-structured tasks typically lack well-defined criteria for evaluating whether the goal has been met, these tasks are typically “open ended” in the sense that it may not be obvious at what point the task has been completed (Burgess et al., 2006; Goel and Grafman, 2000; Reitman, 1964).

The great majority of tasks used in studies of PFC function, especially those using neuroimaging techniques, are well-structured (though see Goel and Vartanian, 2005; Vartanian and Goel, 2005). For example conflict tasks such as
the Stroop (MacLeod, 1991), flanker (Eriksen and Eriksen, 1974), and antisaccade tasks (Munoz and Everling, 2004) may require inhibition of prepotent responses but nevertheless the set of potential stimuli, responses, and applicable stimulus-response mappings are known to the participant in advance. Similarly, studies of task switching (Monsell, 2003) are typically well-structured because the appropriate task is well-specified and clearly cued on each trial.

Experimental investigations of ill-structured tasks have more commonly been found in the neuropsychological literature. For example, Shallice and Burgess (1991) developed two tasks, the Multiple Errands Test and Six Elements Test, both of which were performed poorly by patients with frontal lobe damage, even in the context of good performance on traditional tests of frontal lobe function such as the Stroop task, Wisconsin card sorting test (Grant and Berg, 1948), and Tower of London test (Shallice, 1982). In the Multiple Errands Test, participants are taken to a shopping centre and given a list of items to purchase, information to discover (e.g., what was the coldest place in Britain yesterday?) and rules to follow (e.g., no shop can be entered other than to buy something). In the Six Element Test, participants are given three subtasks and told that they must attempt at least part of each task, even though they cannot be completed in the allocated time. This test therefore requires participants to switch voluntarily between subtasks, without being directly cued to do so.
The Multiple Errands Test and Six Element Test are relatively ill-structured, in the sense that participants’ behaviour is not strongly constrained by their environment. Instead, participants must organise their own behaviour in a self-initiated manner and there is no unique correct solution to the tasks (e.g. the items could be purchased in several different orders in the Multiple Errands Test, and there is no specific correct time to switch between subtasks in the Six Element Test). Of course, everyday life presents many situations that lack a unique correct way of behaving. This observation is congruent with reports of patients with frontal lobe lesions, who experienced behavioural disorganisation in everyday life with such severity that they were unable to return to work at their previous level, yet performed well on classical tests of frontal lobe functions (Eslinger and Damasio, 1985; Mesulam, 1986). Ill-structured tasks such as the Multiple Errands Test or Six Elements Test (Shallice and Burgess, 1991), and related tests (Levine et al., 1998; Manly et al., 2002), may be more sensitive to cognitive deficits in such patients (Burgess et al., in press).

Further evidence for a role of the frontal lobes in dealing with ill-structured situations comes from a study by Goel and Grafman (2000). Goel and Grafman studied an architect with a right PFC lesion on an architectural planning task, involving designing a new office space. Despite good performance on a range of
other tests (Stroop test, Wisconsin Card Sorting Test, Tower of London, verbal fluency), the patient performed poorly on the design task, compared with an age- and education-matched control participant (also an architect). Goel and Grafman (2000) argue that these results suggest that the patient had a selective difficulty with ill-structured representations. This manifested itself in a particular deficit with problem structuring, i.e. organising and structuring the problem space in advance of generating specific solutions.

In the present study, we seek to investigate ill-structured design cognition, following on from the results of Goel and Grafman (2000), using functional magnetic resonance imaging (fMRI). As noted above, ill-structured tasks have rarely been studied using neuroimaging techniques. This can probably be traced to a simple reason: there is relatively little experimental control over participants’ behaviour in most ill-structured tasks, because such tasks require participants to structure their behaviour themselves.

The lack of experimental control in ill-structured tasks creates at least two methodological problems. First, it is difficult to find a suitable well-structured control condition, matched to an ill-structured task in terms of basic input/output operations, because there may be relatively little control over the
sensorimotor processing involved in the ill-structured task. This is more of a problem for neuroimaging techniques than neuropsychological approaches. Differences between an experimental and control task in peripheral factors such as visual stimulation may yield potentially confounding differences in activation between the two conditions in a neuroimaging study. But in a neuropsychological study, it may suffice merely to show impaired performance of an ill-structured task in the context of good performance of other tasks (e.g. visual processing tasks) without needing to match the various tasks precisely for factors such as visual stimulation (Burgess, 1997). In order to mitigate this potential problem, we made efforts in the present study to match an ill-structured task with a well-structured control condition as closely as possible on visual input and motor output.

A second methodological problem caused by the lack of experimental control over ill-structured tasks is that such tasks may potentially involve a wide range of cognitive processes. With little experimental control over the time at which particular processes are engaged, it is difficult to link brain activity with specific processes. In order to address this difficulty, we split our tasks into study and performance phases, so that we could investigate whether differences between ill-structured and well-structured conditions were associated with initial problem structuring and solution generation, or with executing solutions.
Despite the difficulties outlined above, the use of fMRI complements neuropsychological approaches to the study of ill-structured cognition by presenting at least three advantages. First, fMRI offers much greater spatial resolution than neuropsychological approaches. We are therefore able to identify brain regions involved in ill-structured design cognition with greater spatial precision than neuropsychological approaches. In this study, we particularly focus on 1) right dorsolateral PFC, seeing as this was the region damaged in the architect studied by Goel and Grafman (2000), and 2) rostral PFC (approximating Brodmann Area 10), seeing as this region has been suggested to play an important role in dealing with ill-structured situations (Burgess et al., in press).

Second, fMRI permits the investigation of brain activity that distinguishes experimental conditions even in the absence of overt concurrent behaviour. For example, this allows us to investigate brain activity while participants study ill-structured or well-structured problems, even in the absence of behaviour.

Finally, fMRI permits the investigation of effective connectivity, i.e. the interactions between brain regions that may differ as a function of task context. This allows us to investigate not only the brain regions showing differences in activity between experimental conditions, but also the way in which experimental conditions differ in interactions between distinct brain regions. Such changes in effective connectivity may play an important role in supporting
competent behaviour (e.g. Rowe et al., 2005).

In the present study, participants performed a series of Design and Problem Solving tasks, which differed only in the instructions provided on each trial. Indeed participants were not informed beforehand that there would be two types of task. Each task was split into a Study phase, where participants studied the instructions for that task and planned their solutions, and a Performance phase, where they could execute their solutions. The tasks involved positioning and rotating a set of items using trackball, depending on the instructions provided on each trial. In the Problem Solving tasks, a criterion was provided for deciding the termination of the task, as well as a definition of legal moves. Although a particular Problem Solving task might require creative thinking and hypothesis formation or inductive reasoning, the problems themselves were well defined, the legal moves were known, and the solutions were unique (i.e. there was a unique set of equivalent solutions). In the Design tasks, there was no predetermined final state or criterion for deciding the termination of the task (i.e. the tasks were open ended). There was therefore no unique correct (or incorrect) solution; participants were required to structure the problems themselves and set their own evaluation criteria. Thus, despite involving similar stimulus materials and requiring similar motor output, the Problem Solving tasks were well-structured whereas the Design tasks were ill-structured. This distinction between
Problem Solving and Design tasks is common in design literature (e.g. Buchanan, 1992; Goel, 1995). See figures 1-2 for examples of the tasks used.

[Figure 1 about here]

[Figure 2 about here]

2. Results

Post-task interview

Participants were asked, “Could you identify the existence of different kinds of tasks? What do you think the difference was?” Transcripts of representative responses are provided in Table 1. All but three participants identified that there were two groups of tasks. These participants all used words to the effect that instructions for the Design tasks were less prescriptive, involved more opportunity for interpretation and/or were more subjective, with the exception of participant 10, who used words that are arguably consistent with this
description. These observations fit well with the distinction between ill-structured and well-structured tasks that was targeted in our experimental design in the sense that ill-structured tasks require participants to structure the problem themselves (rather than receiving detailed, specific instructions) and set their own subjective evaluation criteria.

[Table 1 about here]

Behavioural results

Videos of participants’ behaviour in each performance phase were analysed, and the following behavioural measures were recorded: 1) time until first movement of the trackball; 2) time until first object was clicked; 3) total number of clicks (excluding clicking on the same object twice in a row); 4) total number of revisits, i.e. returns to objects that had already been clicked previously. None of these measures differed significantly between Design and Problem Solving tasks, suggesting that the two types of task were well matched on initiation time following the study phase, and total movement complexity. Additionally, 5) the time until the final object was clicked was recorded. This was significantly longer for the Design than the Problem Solving tasks, showing that participants were
slower to execute their solutions for Design tasks. These results are summarised in Table 2.

[Table 2 about here]

fMRI results

Direct comparisons between the Problem Solving and Design tasks (collapsing over study and performance phases) failed to find any significant differences, after correcting for multiple comparisons. We therefore searched for differences between the tasks using regions of interest defined by orthogonal contrasts (Kriegeskorte et al., 2009). First we made direct comparisons between the study and performance phases, collapsing over the Problem Solving and Design tasks (Table 3). The study phase was associated with greater activity in a predominantly right-lateralized network including right occipital cortex, right lateral temporal cortex, right intraparietal sulcus, right lateral PFC and bilateral ventromedial PFC. The performance phase was associated with widespread bilateral activation in motor and premotor cortices, inferior parietal cortex, medial occipital cortex, cerebellum, and thalamus.
To identify regions differentially activated by the Problem Solving and Design tasks, we compared the two tasks at each region of interest defined by the main effect of study versus performance phases. For these comparisons, we only investigated the relevant phase, e.g. for regions of interest defined by the study > perform contrast, we examined the difference between Design study and Problem Solving study conditions. We examined activity in 12-mm radius spheres centered on each region of interest, family-wise error corrected for multiple comparisons across the search volume. Of the regions identified in the study > perform contrast, only right dorsolateral PFC showed a significant difference between the Design study and Problem Solving study conditions. This region was more active for the Design than the Problem Solving study phases (50, 30, 34; BA 9/46; Z=3.4; p_{corrected} < .05), but did not show a significant difference in activity between the Design and Problem Solving performance phases. Furthermore this region showed a significant Task (Design / Problem Solving) x Phase (Study / Performance) interaction (50, 26, 34; BA 9/46; Z=3.6; p_{corrected} < .05). This suggests that engagement of right dorsolateral PFC during Design versus Problem Solving tasks was specific to the study phases. Of the regions identified by the perform > study contrast, only right thalamus showed a
significant difference between the Design perform and Problem perform conditions (10, -22, 14; Z=3.5; \( p_{\text{corrected}} < .05 \)). This region was also more active for the Design than Problem Solving tasks but did not show a significant Task x Phase interaction.

Signal change in right dorsolateral PFC for the contrast between study phases of the two tasks, calculated separately for each participant, did not correlate with the behavioural difference between the two tasks in the time until the final object was clicked (\( r=-0.01, \ p=0.97 \)). Similarly, the difference in right thalamus activation between performance phases of the two tasks was unrelated with this behavioural measure (\( r=-0.24, \ p=0.36 \)).

[Figure 3 about here]

In order to illustrate these results, Figure 3A displays the contrast of study versus performance phases, separately for Problem Solving and Design tasks. It can be seen that an overlapping network was activated in the two types of task. However, only Design tasks significantly activated right dorsolateral PFC in this contrast. Ventromedial PFC and intraparietal sulcus appear to be activated only in the Problem Solving tasks. However, only right dorsolateral PFC showed a
significant difference between Design and Problem Solving tasks. In the reverse contrast of performance versus study, presented separately for Problem Solving and Design tasks, a largely overlapping network appears to be activated in both types of task (Figure 3B).

PPI analysis

Because the only significant difference between Design study and Problem Solving study conditions was in right dorsolateral PFC, our a priori region of interest, we went on to investigate whether this region showed functional connectivity with other brain regions that differed between the two conditions. We investigated functional connectivity using a seed co-ordinate of 48,22,26, the region defined by the contrast of study versus perform phases (orthogonal to the Design / Problem Solving distinction). The PPI analysis did not reveal any regions showing significantly different connectivity with our seed region at a corrected threshold. However, an exploratory analysis at an uncorrected threshold of p < .001 with 5 voxel minimum extent revealed widespread activation for the positive contrast (i.e. greater functional connectivity with right dorsolateral PFC during Design study compared with Problem Solving study phases). A total of 26 clusters were activated in this contrast, yielding a set-level
probability of \( p<.001 \) (Friston et al., 1996). This reveals that there was significantly greater activity associated with this contrast than would be expected by chance. Seeing as the voxel-level analysis did not reveal any significant activations at a corrected threshold, results from specific regions are preliminary. However, the most prominent activation for this contrast was a region of medial parietal cortex / precuneus (-12, -40, 40; BA 31; \( Z_{\text{max}}=4.94 \), 122 voxels, cluster extent: \( p < .05 \) FWE corrected). Additional activation was observed in left lateral frontal pole (-30, 58, 6; BA 10; \( Z_{\text{max}}=3.30 \); 7 voxels), a region of particular theoretical interest because it has previously been suggested to play an important role in dealing with ill-structured situations (Burgess et al., in press). These regions are listed in Table 4 and illustrated in Figure 4.

[Table 4 about here]

[Figure 4 about here]

3. Discussion

In this study we compared an ill-structured Design task with a well-structured Problem Solving task, each divided into study and performance phases. Direct
comparison between the study and performance phases revealed a predominantly right-lateralized set of brain regions showing greater activity during the initial study phase than during the subsequent task execution phase. Amongst these regions, right dorsolateral PFC was unique in showing significantly greater activation during Design tasks than Problem Solving tasks. This result is congruent with neuropsychological data from Goel and Grafman (2000), and confirms the suitability of fMRI for studying brain regions involved in ill-structured, open-ended tasks.

Although methodological problems can make it difficult to study ill-structured tasks with functional neuroimaging, techniques such as fMRI present certain advantages over the neuropsychological approaches that they complement. First, of course, fMRI offers far greater spatial resolution than the single case approach adopted by Goel and Grafman (2000), whose patient had a large lesion affecting much of the right frontal lobe. The critical region in the present study was in right dorsolateral PFC, corresponding approximately to Brodmann Area 9/46 (see Figure 3).

As well as offering greater spatial resolution than neuropsychological approaches, fMRI can be used to identify with greater precision the time at which particular
brain regions are activated in particular cognitive tasks, even in the absence of overt behaviour. In the present study, right dorsolateral PFC was identified as playing an important role in the study phase, when participants were first presented with task instructions, rather than the performance phase where they actually executed their plans. This would be consistent with the proposal by Goel and Grafman (2000) that right PFC plays a particularly important role in preliminary problem structuring, where participants must generate information missing from the problem scenario and define the problem space. The requirement for substantial preliminary problem structuring may be considered to be a crucial difference between the Design and Problem Solving tasks in the present study. Indeed, within design theory it has been proposed that a fundamental characteristic of design cognition is the requirement to define the problem as well as the solution (Dorst and Cross, 2001; for further discussion of the present tasks from the perspective of design studies see Alexiou et al., in press).

An additional advantage of fMRI over neuropsychological approaches is that one can assess effective connectivity in order to investigate interactions between distinct brain regions. The PPI analysis in the present study revealed that right dorsolateral PFC, as well as exhibiting greater signal during the study phases of the Design versus Problem Solving tasks, also showed increased coupling with
other brain regions during Design tasks. Although these results are preliminary, seeing as they did not meet a corrected statistical threshold, two brain regions showing increased coupling with right dorsolateral PFC were of particular theoretical interest. The region showing the strongest modulation of coupling with right dorsolateral PFC, depending on problem type, was the precuneus. This area has previously been suggested to support visual imagery (Fletcher et al., 1995). We might therefore speculate that during the study phases of Design tasks, where participants had to generate potential solutions without yet interacting with the visual display, participants engaged strongly in visual imagery, mediated by interactions between right dorsolateral PFC and precuneus. A second region showing greater coupling with right dorsolateral PFC during the study phases of Design than Problem Solving tasks was left frontal pole (BA 10). This region has been particularly implicated in dealing with ill-structured situations (Burgess et al., in press), and with attending to self-generated, internally-represented information (Burgess et al., 2007; Christoff et al., 2003; Gilbert et al., 2005). The Design tasks in the present study might therefore be expected to engage this region.

Along with the advantages of fMRI over neuropsychological approaches outlined above, there are a number of disadvantages. For example neuropsychological approaches are more appropriate for drawing conclusions
about the causal role of a brain region than correlational techniques such as fMRI. Furthermore, fMRI requires careful matching of experimental against control conditions, otherwise differences in activation may result from confounding factors. Ill-structured tasks tend to be hard to assess by quantitative criteria, because the appropriate criteria against which to judge solutions are, by definition, not well specified. This would apply to the tasks in the present study, which did not generate behavioural data in terms of correct or incorrect task performance, unlike typical neuroimaging studies. A question that therefore arises is whether the Design and Problem Solving tasks may have differed simply in “task difficulty”, in the sense that both types of task involved the same processes, but Design tasks simply invoked those processes to a greater degree than Problem Solving tasks. This seems unlikely for three reasons. First, initiation time (i.e. the time until the first movement of the trackball or object clicked in the performance phase) was matched between the two tasks (Table 2). Thus the study phases of the two types of task gave rise to matched initiation times in the subsequent performance phases. Second, although the time until the last object was clicked was greater for Design than Problem Solving tasks, this difference was unrelated to right dorsolateral PFC signal change between the two types of task. Thus, insofar as the time taken to perform the two types of task represents their “difficulty”, this does not account for differences in right dorsolateral PFC activity. Third, if the two types of task had simply differed according to some global factor of “difficulty”, it would be a coincidence that out of all regions
identified in the study > perform contrast (pooled across Design and Problem Solving tasks), the only region to show a significant difference between the two types of task was the one predicted from prior evidence (Goel and Grafman, 2000).

In conclusion, the present results suggest 1) that a crucial area for dealing with ill-structured problems is right dorsolateral PFC (BA 9/46), 2) that this region is particularly involved in early stages of problem structuring and solution generation rather than solution execution, and 3) that this region may play a role in ill-structured situations via changes in its effective connectivity with other brain regions. Furthermore, these results indicate that ill-structured tasks may be fruitfully examined using fMRI as well as neuropsychological approaches. At present, we are far from a computational description of the processes supported by right dorsolateral PFC in ill-structured situations. Future studies will be required to investigate in greater detail the processes supported by this region in such situations, for example problem structuring, the requirement to set evaluation criteria, or hypothesis generation. Although the role of right dorsolateral PFC need not be limited to supporting just one of these, interesting recent data suggests that different brain structures may be involved in dealing with these different properties of ill-structured tasks (Goel and Vartanian, 2005; Vartanian and Goel, 2005). Finally, an open question for further studies is
whether the role of right dorsolateral PFC is specific to visuospatial planning, or extends to additional domains.

4. Experimental procedures

Participants

There were 18 participants (11 female, 7 male), aged 27-60 (mean: 37). All participants had some experience with design; 10 had formal training in a design discipline (architecture, multimedia or graphic design, interior design, product design, art etc). All provided written informed consent before participating. Data from one participant were discarded due to data quality problems. The study was conducted with ethical approval granted by the Ethics Committee of the Open University and in accordance with guidelines of the British Psychological Society and the UK Data Protection Act 1998.

Tasks and procedure

Problem Solving and Design tasks were matched as closely as possible. In both
tasks, participants were first presented with a study phase in which they saw a collection of items next to a blank space. They were also presented with a series of instructions (see Figures 1-2 for examples). The study phase lasted for 30s. Following the study phase, a performance phase of 50s commenced. The phase was indicated by an instruction at the top of the screen saying ‘Study the task’ or ‘Perform the task’. During the performance phase, participants used a trackball device to position and rotate the items according to the instructions. Participants could also click an ‘End’ button to indicate that they had completed the task.

Participants performed a total of eight Problem Solving and eight Design tasks. Each set of items was encountered once in the context of a Problem Solving task and once in the context of a Design task. Half of the sets of items were encountered first as a Problem Solving task and the other half were encountered first as a Design task. The assignment of items to orders (Problem Solving first or Design first) was counterbalanced between participants. After each task, there was a 15 second rest period, in which participants viewed a fixation cross, until the next task. The tasks were presented in two blocks of eight; within each block participants alternated between Problem Solving and Design tasks. Following scanning, all participants underwent a semi-structured interview to determine their views of the experiment.
Scanning procedures

A 1.5T Siemens TIM Avanto scanner was used to acquire both T1-weighted structural images and T2*-weighted echoplanar (EPI) images [64 x 64; 3 x 3mm pixels; echo time (TE), 40 ms] with BOLD contrast. Each volume comprised 35 axial slices (3.3mm thick, oriented approximately to the AC-PC plane), covering the whole brain apart from ventral aspects of the cerebellum. Functional scans were acquired in two sessions, each comprising 314 volumes (approximately 13 minutes). Volumes were acquired continuously with an effective repetition time (TR) of 2.5s per volume. The first four volumes in each session were discarded to allow for T1 equilibration effects. Following the functional scans, a 6 minute T1-weighted structural scan was performed.

Data analysis

fMRI data were analyzed using SPM5 software (http://www.fil.ion.ucl.ac.uk/spm/software/spm5/). The volumes were realigned, corrected for different slice acquisition times, normalized into 2mm cubic voxels using the Montreal Neurological Institute (MNI) reference brain using 4th-degree B-spline interpolation, and smoothed with an isotropic 8mm
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 regressors in a general linear model (Friston et al., 1995). Separate boxcar regressors coded for sustained activity in the four conditions: Problem Solving study, Problem Solving perform, Design study, and Design perform. These regressors, together with the regressors representing residual movement-related artifacts 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 least mean squares fit of the model to the data. Effects of interest were assessed in a random effects analysis as follows. Contrast images representing each of the four conditions of interest were entered into a repeated-measures analysis of variance (ANOVA) using non-sphericity correction (Friston et al., 2002). Appropriate contrasts for effects of interest were conducted at the second level, thresholded at p < 0.05 family-wise error corrected for multiple comparisons across the whole brain volume (except where stated).

PPI analysis
PPI (psychophysiological interaction) analysis assesses the hypothesis that activity in one brain region can be explained by an interaction between the presence of a cognitive process and activity in another part of the brain (Friston et al., 1997). We used PPI analysis to compare functional connectivity between right dorsolateral PFC and the rest of the brain, during Design study and Problem Solving study phases. In this analysis, we created a volume of interest for each participant, in the form of a sphere of radius 12mm centered on right dorsolateral PFC (using the co-ordinate 48,22,26 based on the main effect of study versus performance phases, collapsed across the two types of problem). We then created a separate model for each subject with separate regressors for movement parameters along with 1) the timecourse data from this VOI; 2) the psychological variable (with Design study phases coded as 1, Problem Solving study phases coded as -1, and all other conditions coded as 0); and 3) the interaction between the two. We then assessed the interaction term in a random effects analysis using a one-sample t-test.

Acknowledgements

SJG is supported by a Royal Society University Research Fellowship.
References


Rowe, J.B., Stephan, K.E., Friston, K., Frackowiak, R.S., Passingham, R.E., 2005. The prefrontal cortex shows context-specific changes in effective connectivity to motor or visual cortex during the selection of action or colour. Cereb Cortex. 15, 85-95.
Table 1 Transcripts of representative comments from each participant’s post-task interview on the difference between the two types of task.

<table>
<thead>
<tr>
<th>Participant number</th>
<th>Design</th>
<th>Problem Solving</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>&quot;less logical, more free style or design&quot;, &quot;do your best&quot;</td>
<td>&quot;more logical, giving instructions to do stuff&quot;</td>
</tr>
<tr>
<td>2</td>
<td>&quot;left a bit more freedom for me to match them&quot;</td>
<td>&quot;instructed me very strictly what to do&quot;</td>
</tr>
<tr>
<td>3</td>
<td>no difference</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>&quot;you had to think more options, more implications, you had to make a judgement on it&quot;</td>
<td>&quot;more prescribed, telling you where things had to go, more straightforward&quot;</td>
</tr>
<tr>
<td>5</td>
<td>&quot;related to what looks nicest, or how you would portray it, how would I like it&quot;</td>
<td>&quot;you didn’t really have to think for your self, but just do what you were told&quot;</td>
</tr>
<tr>
<td>6</td>
<td>&quot;it was more your interpretation of the brief, more trial and error&quot;</td>
<td>&quot;specified what you needed to do, without any getting to think about design&quot;</td>
</tr>
<tr>
<td>7</td>
<td>&quot;creative, take control of what you are doing&quot;</td>
<td>&quot;understand the rules and obey the rules&quot;</td>
</tr>
<tr>
<td>8</td>
<td>no difference</td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>&quot;requiring you to design, included that you have to like it, it must be nice for you&quot;</td>
<td>&quot;just requiring you to allocating space in precise orders&quot;</td>
</tr>
<tr>
<td>10</td>
<td>&quot;you needed to go to a second level of design&quot;</td>
<td>&quot;more instinctive&quot;</td>
</tr>
<tr>
<td>11</td>
<td>&quot;more subjective, you can’t say there was a correct or wrong answer&quot;, &quot;open to interpretation&quot;</td>
<td>&quot;there were right or wrong&quot;, &quot;clear instructions as to what were to place things&quot;</td>
</tr>
<tr>
<td>12</td>
<td>&quot;open-ended&quot;</td>
<td>&quot;definite instructions, you are just trying to make sure you are conforming&quot;, &quot;more logic&quot;</td>
</tr>
<tr>
<td>13</td>
<td>&quot;more general, make something that is aesthetically pleasing, more open-ended&quot;</td>
<td>&quot;quite prescriptive, not leaving any freedom&quot;</td>
</tr>
<tr>
<td>14</td>
<td>&quot;more subjective&quot;</td>
<td>&quot;more objective&quot;</td>
</tr>
<tr>
<td>15</td>
<td>no difference</td>
<td></td>
</tr>
<tr>
<td>16</td>
<td>&quot;your input is more substantial, there is a description of what you should achieve, but you have to sort it out how you do it&quot;</td>
<td>&quot;you are given specific instructions and you just have to follow them&quot;</td>
</tr>
<tr>
<td>17</td>
<td>&quot;make qualitative judgements about things&quot;</td>
<td>&quot;straightforward, there was a finite answer&quot;</td>
</tr>
</tbody>
</table>
Table 2  Behavioural results: means for five different measures calculated separately for Problem Solving and Design tasks (standard deviations in parentheses), t statistic for comparisons and associated p values.

<table>
<thead>
<tr>
<th></th>
<th>Time to first movement / s</th>
<th>Time to first click / s</th>
<th>Number of clicks</th>
<th>Number of revisits</th>
<th>Time to last click / s</th>
</tr>
</thead>
<tbody>
<tr>
<td>Problem Solving</td>
<td>0.43 (0.18)</td>
<td>2.72 (0.76)</td>
<td>6.44 (0.99)</td>
<td>1.27 (0.99)</td>
<td>31.8 (5.6)</td>
</tr>
<tr>
<td>Design</td>
<td>0.44 (0.19)</td>
<td>2.92 (0.93)</td>
<td>6.36 (1.05)</td>
<td>1.25 (0.85)</td>
<td>36.0 (4.7)</td>
</tr>
<tr>
<td>t(16)</td>
<td>0.54</td>
<td>1.56</td>
<td>0.39</td>
<td>0.14</td>
<td>3.41</td>
</tr>
<tr>
<td>p</td>
<td>0.60</td>
<td>0.14</td>
<td>0.70</td>
<td>0.89</td>
<td>0.004</td>
</tr>
</tbody>
</table>
Table 3 Direct comparison between the study and performance phases, collapsing over Design and Problem Solving tasks, thresholded at p < .05 FWE corrected for multiple comparisons across whole brain volume. BA=Brodmann Area. Brodmann areas are approximate.

<table>
<thead>
<tr>
<th>Region</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>BA</th>
<th>Z_{max}</th>
<th>N voxels</th>
</tr>
</thead>
<tbody>
<tr>
<td>Study &gt; Perform</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ventromedial prefrontal cortex</td>
<td>-8</td>
<td>48</td>
<td>-16</td>
<td>11</td>
<td>5.55</td>
<td>50</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>46</td>
<td>-16</td>
<td>11</td>
<td>4.97</td>
<td>3</td>
</tr>
<tr>
<td>Dorsolateral prefrontal cortex</td>
<td>48</td>
<td>22</td>
<td>-26</td>
<td>9/46</td>
<td>5.33</td>
<td>40</td>
</tr>
<tr>
<td>Premotor cortex</td>
<td>46</td>
<td>8</td>
<td>52</td>
<td>6</td>
<td>5.88</td>
<td>110</td>
</tr>
<tr>
<td>Lateral temporal cortex</td>
<td>60</td>
<td>-32</td>
<td>0</td>
<td>21</td>
<td>6.75</td>
<td>576</td>
</tr>
<tr>
<td>Lateral parietal cortex</td>
<td>50</td>
<td>-54</td>
<td>52</td>
<td>40</td>
<td>5.31</td>
<td>49</td>
</tr>
<tr>
<td>Medial occipital cortex</td>
<td>14</td>
<td>-100</td>
<td>10</td>
<td>18</td>
<td>6.42</td>
<td>109</td>
</tr>
<tr>
<td>Perform &gt; Study</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lateral frontal cortex</td>
<td>-50</td>
<td>8</td>
<td>2</td>
<td>44</td>
<td>5.43</td>
<td>105</td>
</tr>
<tr>
<td></td>
<td>-54</td>
<td>6</td>
<td>22</td>
<td>44</td>
<td>4.86</td>
<td>8</td>
</tr>
<tr>
<td>Supplementary Motor Area</td>
<td>2</td>
<td>-8</td>
<td>52</td>
<td>6</td>
<td>&gt;8</td>
<td>1585</td>
</tr>
<tr>
<td>Thalamus</td>
<td>-8</td>
<td>-20</td>
<td>8</td>
<td>-</td>
<td>5.36</td>
<td>35</td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>-22</td>
<td>8</td>
<td>-</td>
<td>5.60</td>
<td>37</td>
</tr>
<tr>
<td>Motor / premotor cortex</td>
<td>30</td>
<td>-22</td>
<td>64</td>
<td>4/6</td>
<td>&gt;8</td>
<td>4591</td>
</tr>
<tr>
<td>Inferior parietal cortex</td>
<td>-60</td>
<td>-22</td>
<td>22</td>
<td>40</td>
<td>7.78</td>
<td>2208</td>
</tr>
<tr>
<td>Medial parietal cortex</td>
<td>-10</td>
<td>-26</td>
<td>44</td>
<td>31</td>
<td>5.83</td>
<td>64</td>
</tr>
<tr>
<td>Cerebellum</td>
<td>-12</td>
<td>-54</td>
<td>-18</td>
<td>-</td>
<td>&gt;8</td>
<td>4206</td>
</tr>
<tr>
<td>Lateral occipital cortex</td>
<td>46</td>
<td>-66</td>
<td>6</td>
<td>19</td>
<td>7.30</td>
<td>640</td>
</tr>
<tr>
<td>Medial occipital cortex</td>
<td>-14</td>
<td>-80</td>
<td>42</td>
<td>19</td>
<td>5.71</td>
<td>158</td>
</tr>
</tbody>
</table>
Table 4  Results of PPI analysis: regions showing significantly greater coupling with right dorsolateral PFC during study phases of the Design versus Problem Solving task (p < .001, minimum extent 5 voxels). BA = Brodmann Area. Brodmann Areas are approximate.

<table>
<thead>
<tr>
<th>Region</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>BA</th>
<th>Zmax</th>
<th>N voxels</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lateral frontal cortex</td>
<td>-30</td>
<td>58</td>
<td>6</td>
<td>10</td>
<td>3.30</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>50</td>
<td>36</td>
<td>24</td>
<td>46</td>
<td>3.52</td>
<td>14</td>
</tr>
<tr>
<td>Anterior insula</td>
<td>34</td>
<td>20</td>
<td>-4</td>
<td>-</td>
<td>3.90</td>
<td>12</td>
</tr>
<tr>
<td>Lateral frontal cortex</td>
<td>58</td>
<td>10</td>
<td>16</td>
<td>44</td>
<td>3.98</td>
<td>9</td>
</tr>
<tr>
<td>Amygdala</td>
<td>30</td>
<td>6</td>
<td>-18</td>
<td>-</td>
<td>3.66</td>
<td>5</td>
</tr>
<tr>
<td>Lateral temporal cortex</td>
<td>-50</td>
<td>-2</td>
<td>-28</td>
<td>21</td>
<td>4.21</td>
<td>15</td>
</tr>
<tr>
<td></td>
<td>-46</td>
<td>-6</td>
<td>-18</td>
<td>21</td>
<td>4.11</td>
<td>53</td>
</tr>
<tr>
<td>Premotor cortex</td>
<td>-14</td>
<td>-8</td>
<td>58</td>
<td>6</td>
<td>3.62</td>
<td>18</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>-10</td>
<td>60</td>
<td>6</td>
<td>3.67</td>
<td>40</td>
</tr>
<tr>
<td>Lateral temporal cortex</td>
<td>-66</td>
<td>-20</td>
<td>-10</td>
<td>21</td>
<td>3.67</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>-54</td>
<td>-20</td>
<td>8</td>
<td>42</td>
<td>3.20</td>
<td>5</td>
</tr>
<tr>
<td>Lateral parietal cortex</td>
<td>40</td>
<td>-22</td>
<td>32</td>
<td>40</td>
<td>3.45</td>
<td>10</td>
</tr>
<tr>
<td>Midbrain</td>
<td>-4</td>
<td>-22</td>
<td>-12</td>
<td>-</td>
<td>3.24</td>
<td>5</td>
</tr>
<tr>
<td>Lateral temporal cortex</td>
<td>54</td>
<td>-24</td>
<td>-22</td>
<td>20</td>
<td>3.80</td>
<td>22</td>
</tr>
<tr>
<td>Lateral parietal cortex</td>
<td>-56</td>
<td>-24</td>
<td>50</td>
<td>40</td>
<td>3.25</td>
<td>6</td>
</tr>
<tr>
<td>Fusiform cortex</td>
<td>36</td>
<td>-32</td>
<td>-24</td>
<td>36</td>
<td>3.53</td>
<td>5</td>
</tr>
<tr>
<td>Lateral temporal cortex</td>
<td>-62</td>
<td>-32</td>
<td>4</td>
<td>22</td>
<td>3.30</td>
<td>18</td>
</tr>
<tr>
<td>Fusiform cortex</td>
<td>-18</td>
<td>-36</td>
<td>-12</td>
<td>36</td>
<td>3.39</td>
<td>5</td>
</tr>
<tr>
<td>Medial parietal cortex</td>
<td>-12</td>
<td>-40</td>
<td>40</td>
<td>31</td>
<td>4.94</td>
<td>122</td>
</tr>
<tr>
<td>Lateral parietal cortex</td>
<td>-46</td>
<td>-40</td>
<td>40</td>
<td>40</td>
<td>3.80</td>
<td>16</td>
</tr>
<tr>
<td>Fusiform cortex</td>
<td>38</td>
<td>-42</td>
<td>-14</td>
<td>37</td>
<td>3.81</td>
<td>51</td>
</tr>
<tr>
<td>Medial parietal cortex</td>
<td>2</td>
<td>-42</td>
<td>50</td>
<td>7</td>
<td>3.34</td>
<td>9</td>
</tr>
<tr>
<td>Superior parietal cortex</td>
<td>28</td>
<td>-44</td>
<td>66</td>
<td>7</td>
<td>3.47</td>
<td>86</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>-50</td>
<td>68</td>
<td>7</td>
<td>3.37</td>
<td>6</td>
</tr>
<tr>
<td>Cerebellum</td>
<td>10</td>
<td>-58</td>
<td>-16</td>
<td>-</td>
<td>3.63</td>
<td>21</td>
</tr>
<tr>
<td>Superior parietal cortex</td>
<td>36</td>
<td>-60</td>
<td>58</td>
<td>7</td>
<td>3.72</td>
<td>8</td>
</tr>
</tbody>
</table>
Figure captions

*Figure 1.* Example of a Problem Solving task.

*Figure 2.* Example of a Design task.

*Figure 3.* Three-dimensional rendering of regions showing significant differences in signal between the study and performance phases, plotted separately for the Problem Solving (red) and Design (green) tasks. Overlap is shown in yellow. Results were thresholded at $p < .05$ FWE corrected for multiple comparisons across the whole brain volume. The region of right dorsolateral prefrontal cortex (DLPFC) showing greater activity for Design study than Problem Solving study phases is illustrated in panel A.

*Figure 4.* Two regions showing significantly greater effective connectivity with right dorsolateral prefrontal cortex during Design versus Problem Solving tasks. Results from the PPI analysis are thresholded at $p < .001$ uncorrected, minimum extent 5 voxels, for illustrative purposes, and plotted on a template T1-weighted structural scan. Left illustration shows a sagittal slice at x=-10; right illustration shows a coronal slice at y=58.
STUDY THE TASK

Organise the tables and chairs in the conference room so that:
- The two tables face each other
- The long table is parallel to the screen
- The participants can see each other
- One participant cannot see the screen
- All the furniture is used
STUDY THE TASK

Organise the tables and chairs in the conference room so that:
- The room is spacious
- The room enables collaboration
- The participants can see each other
- All participants can see the screen
- You may use any furniture you like
A: Study > Perform

B: Perform > Study

Right DLPFC

- Red: Design
- Green: Problem Solving
- Yellow: Overlap
Medial parietal cortex / precuneus

Left frontal pole