

The role of the prefrontal cortex in higher cognitive functions

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Abstract

The higher cognitive functions, working memory, mental imagery and willed action, are all intimately associated with consciousness. The common process underlying all these functions is that information is “held in mind” for a period of time. This information, which may be about stimuli or responses, can be derived from the past or generated for the future. Brain imaging studies show that “holding something in mind” is associated with activity in an extended system which involves both prefrontal cortex and more posterior areas whose location is determined by the nature of the information being held in mind. Automatic actions and perceptions which do not involve consciousness are associated with activity in the relevant posterior areas, but not in the prefrontal cortex. These studies demonstrate that activity occurs in the same posterior area whether the associated information comes from the outside world or is internally generated. This raises the problem of how we know whether our experience derives from mental imagery or from something happening in the outside world. There is evidence that patients with schizophrenia have precisely this problem since they perceive their own thoughts and even sub-vocal speech as coming from outside (hallucinations). Recent brain imaging studies suggest that there is a disconnection between prefrontal and posterior areas in these patients which could explain their characteristic misperceptions.

Keywords: Higher cognitive function; Prefrontal cortex; Working memory; Mental imagery; Brain imaging

1. Higher cognitive functions

Much of the literature in cognitive psychology is devoted to finding a rationale for making the distinction between higher and lower cognitive functions. Low order cognitive processes are said to be automatic or routine, while higher order processes always contain a novel element and require controlled, strategic or executive processes [32]. A parallel account of this distinction is that of modular and non-modular systems [6]. These accounts distinguish low order processes that are obligatory and automatic from high order processes that are under conscious or voluntary control. It is clear that the distinction cannot be made solely in terms of the complexity of the computations required. Understanding speech and reading are both difficult problems in computational terms, but both tasks can be carried out routinely and with little effort. Speech recognition is thus an example of a complex skill for which appropriate specialised “hard ware” has evolved within the brain [28]. Reading, in contrast, is a skill which develops within the span of a few years in the life time of each individual when first going to school. This serves to emphasize the fact that almost any difficult

task can become an easy one (in the sense of automatic) with sufficient practice, even though the complexity of the task remains the same. Perhaps the best distinction between high level and low level cognition is in terms of the subjective degree of “mental effort” required for any particular task.

Another important and parallel distinction is that, only for tasks requiring high level cognition, do we have to think about what we are doing. In other words high level cognition is associated with phenomenological consciousness. While phenomenal consciousness seems always to be associated with high level cognitive processes, no one has yet produced a satisfactory account of whether phenomenological consciousness is a necessary component of such processes [2].

2. Holding things in mind

Humans have a highly developed faculty to hold representations of things in mind. This holding in mind (or active memory) can occur in the absence of perceptual input and can be maintained over extended time periods [13]. This ability enables us to bridge temporal discontinuities between perception and action. The process is thought

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to be critical for behavioural flexibility, the internal monitoring of behavioural responses and the on-going guidance of action. In cognitive terms, active memory involves at least two components: (i) a general system for “holding in mind” material (the central executive), and (ii) the process or code that is to be held in mind which can be in any modality (the slave system) [1]. Neurophysiological accounts modelled on this cognitive approach emphasize interactions between DLPFC (the central executive) and task specific posterior areas (the slave systems) [15]. These models have been derived principally from studies in non-human primates. Thus, for example, when holding in mind a position in space the frontal and parietal lobes are involved. Brain imaging experiments permit us to identify the neural components of active memory in humans who are capable of holding in mind and manipulating many types of material including complex and abstract concepts.

To study the brain regions involved purely in “the maintenance of a representation” we measured neural activity during the delay period of a spatial delayed response (DR). The tasks used were formally similar to those used in studies of non-human primates. The task required subjects to fixate on a central cross prior to the scan. A stimulus, an open circle 1 cm in diameter, was displayed for 200 ms approximately 5 s before the scanning window. Throughout the delay period of 45 s subjects were required to fixate the cross and hold in mind the position of the circle. Responses were made subsequent to the scan and involved pointing to the location of the stimulus (see Fig. 1). The control condition required subjects to fixate a

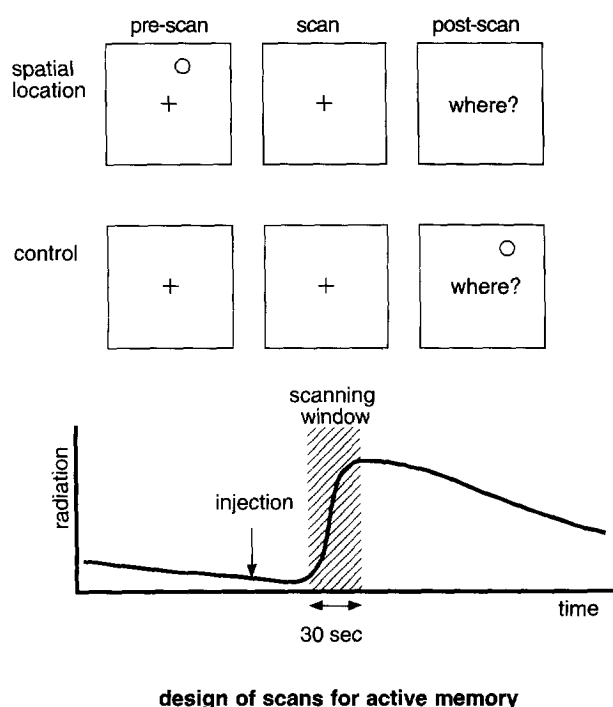


Fig. 1. Illustration of experimental and control tasks for the study of active memory for spatial location showing the relation between the task protocol and the scanning head curve.

Table 1

Common activations for active memory, imagining movements and mental manipulation

	Left		Right			
<i>Active memory for spatial location</i>						
DLPFC	-32	26	36	28	38	24
Anterior cingulate				0	6	44
Lateral PMC	-18	-6	60	20	-4	52
Inferior parietal	-36	-38	40	34	-44	44
Occipital cortex	-24	-82	20	32	-76	16
<i>Imagining hand movements</i>						
DLPFC	-	-	-	-	-	-
Anterior cingulate				0	2	48
Lateral PMC	-16	-10	64	-	-	-
Inferior parietal	-28	-44	40	34	-50	44
Occipital cortex	-	-	-	-	-	-
<i>Mental manipulation (Tower of London)</i>						
DLPFC	-42	26	32	36	28	32
Anterior cingulate				4	12	44
Lateral PMC	-30	-4	60	22	-4	60
Inferior parietal	-30	-44	32	26	-68	36
Occipital cortex	-24	-82	0	28	-84	16

Significant activations are listed in terms of Talairach coordinates.

central cross throughout the 45 s scanning period and subsequently to touch the centre of a circular target which appeared at a pseudo-random location. The crucial element of this study was that stimuli were presented and responses made, outside the scanning window in each condition. The sole requirement during the scan was the active representation of spatial location.

A widespread pattern of cortical activation was observed (see Table 1), including bilateral dorsolateral prefrontal cortex (DLPFC). Representation of spatial location was associated with activation of medial and lateral parietal cortices and also extrastriate visual cortex. Activations were also observed in regions that are associated with motor preparation and response, including anterior cingulate and lateral premotor cortex. This activity probably reflected a readiness to move the hand to a particular position in space. The overall findings from this study are remarkably consistent with the extensive animal literature using delayed response tasks.

In a second experiment with essentially the same design subjects were asked to remember the shape of a rectangle (delayed matching; DM). The frontal activations observed in this task were the same as in the previous study. However, the locations of the co-activated posterior brain regions were dependent on the nature of the representation. In the DR task the predominant co-activation involved the posterior medial and lateral parietal cortex. In the DM task parietal activation was again observed but in addition there was focus in the inferior temporal cortex. These findings are again consistent with observations in primate studies which have indicated relative functional specialisation in the parietal cortex for spatial representations and inferior

temporal cortex for object representations. The data strongly suggest that the nature or content of a maintained representation is less dependent on prefrontal activation, but is conditional on which particular regions are co-activated with the DLPFC. Analogous observations in primates indicate that working memory is a function of sustained activity, not only in DLPFC, but in the relevant distributed neural system [7].

The results of this experiment are largely confirmatory of animal studies. However, there are now data from related tasks which cannot be performed with animals. Furthermore very similar patterns of brain activity can be found with tasks which would not normally be classified as involving memory. For example, Stephan et al. asked volunteers to imagine making a series of hand movements (in order to move a joystick in 4 different directions) [35]. Brain activity associated with this task was contrasted with what occurred when actually making the movements and with preparing to make a movement. Imagining making the movements was associated with activity in parietal cortex and premotor cortex in locations strikingly similar to those found in the active memory task for spatial location (see Table 1). In cognitive terms the two tasks are similar in that volunteers have to hold in mind movements in particular directions. However, the critical difference is that in the memory task it was an external stimulus which had indicated the direction of movement to be held in mind, whereas in the imagination task the direction of movement was self-generated. The implication of these results is that the brain uses identical mechanisms and systems for handling representations of movement and spatial location irrespective of whether these are given externally or self-generated.

In the study by Stephan et al. [35] there was no activity in frontal cortex when imagining movements was compared with the control task. This is because the control task, preparing to make a movement, was also associated with frontal activity. In a very similar study by Cabalos-Bauman and colleagues (personal communication) frontal activity was observed in the motor imagery task when this was compared with rest.

In the early, exploratory brain imaging studies it was often observed that there was more frontal activity associated with imagining doing something than actually doing it [18]. We agree with the conclusion that frontal activity is a critical component of motor imagery. This, we believe, is because in order to imagine something we have to “hold it in mind”, while there are many things we can do in reality without holding the action in mind. William James [19] called these *ideo-motor acts*. “Where ever movement follows unhesitatingly and immediately the notion of it in the mind. We are then aware of nothing between the conception and the execution.” Examples come from studies of learning. Passingham and his colleagues (personal communication) have shown that, in the early stages of learning (when we have to think about what we are doing), there is

considerable frontal activity. Once a task has become routine (after much practice) we no longer have to think about what we are doing and frontal activation is no longer apparent (relative to rest). However, if we are asked to think about what we are doing in this routine task, then the frontal activity reappears (interestingly the performance gets slightly worse). Of necessity, in order to imagine doing even the most routine of tasks, we have to have to hold in mind what we are doing. Thus it seems likely that all imagery will be associated with frontal activity.

3. Manipulating things held in mind

Active memory enables a person to hold something in mind over an extended time period. Over and above simply holding something in mind humans have a highly developed facility to manipulate things held in mind. This ability to manipulate representations within an active memory system is captured by the concept of working memory [1]. Manipulating things in mind is critically important when we engage in certain cognitive acts such as conceptualising and planning. Planning involves complex cognitive operations that require a number of subprocesses [22]. Firstly, to implement a plan it is necessary to have a goal. Secondly, it is necessary to prepare and implement responses aimed at achieving a series of sub-goals while holding the end goal in mind. Finally it is necessary to monitor and verify each response in relation to the sub-goals and the final goal. For effective planning these separate subcomponents must be integrated into a functional whole, an integration often attributed to the workings of a central monitor or central executive system [32]. Planning is also a prototypical conscious act and conscious awareness has been identified with the phenomenal experience of the contents and operations of this central processor [37].

One approach to the study of planning with functional imaging is to use a task that requires self-organised responding. The Tower of London provides a well validated example of such a task [31]. In essence this task requires subjects to rearrange, in the minimum number of moves, a set of three coloured balls arranged on pegs to attain a final configuration that matches a prespecified goal state (Fig. 2). To solve the problem the complete sequence of moves required must be planned and prepared in advance of making an actual response.

We used a computerised version of the task wherein subjects solved each problem using only “mental” transformations of the initial position, before executing a single response to indicate the minimum number of moves needed to solve the problem [26]. In the context of the study subjects were presented with sequences of problems lasting 4–6 min. Concealed within these sequences were runs of easy problems (2- and 3-move solutions) and difficult problems (4- and 5-move solutions) which were presented

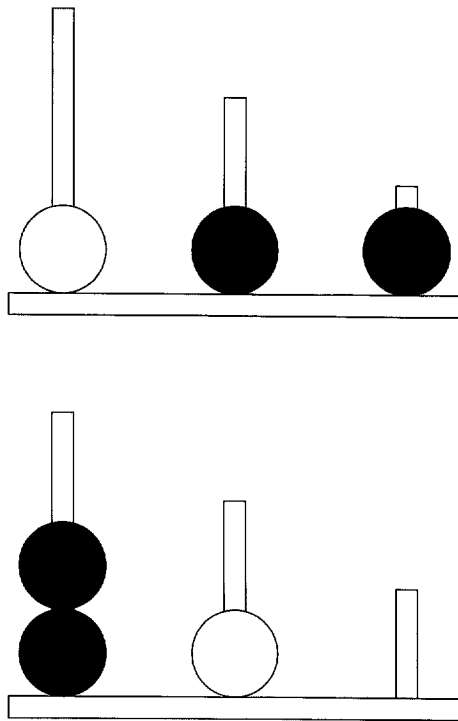


Fig. 2. The Tower of London task [31] consists of a board with three pegs and three balls of different colours. The pegs will hold three, two or one balls respectively. The upper figure illustrates the starting position and the lower figure the finishing position. This transition must be achieved by moving one ball at a time. The example shown requires five moves.

during the acquisition phase of the scan. Each subject was scanned 6 times (three scans each with the easy and difficult conditions) and 6 times while performing a control task in which the visual display and motor response were matched with the experimental tasks.

During the planning component of the task activations were observed in a number of cortical areas that included the prefrontal, cingulate, premotor and parietal and occipital cortices (see Table 1). These activations bore close correspondence to areas that were activated during our visuo-spatial working memory tasks, the one exception being an area of rostral prefrontal cortex that was uniquely activated in the planning task. Enhanced neural activity in both this rostral prefrontal area and the visuo-spatial working memory system was associated with increased task difficulty. This suggests that the rostral prefrontal area might be involved in the executive components of planning such as response selection and evaluation.

Manipulating something held in mind would thus seem to activate not only frontal regions but also posterior brain regions. As planning involves holding a representation of both the end goal and intermediate stages of the problem in mind there must necessarily be an engagement of an active memory system. From our study of active memory, and given the visuo-spatial nature of the Tower task, it is reasonable to identify activations in the DLPFC, posterior parietal and extrastriate visual cortices with this system.

The attention to action implicit in implementing the intermediate stage solutions can be identified with activation in the inferior frontal, premotor and anterior cingulate cortices. The activation of the rostral prefrontal cortex, which was engaged to a greater extent in the more difficult problems, suggests that this region may implement executive processes concerned with the selection and evaluation of sequences of moves. Consistent with this latter suggestion are findings that activation of the rostralateral frontal cortex together with DLPFC has been observed in "random" movement generation and motor sequence learning paradigms [4,21]. Activation of this rostral area has also been observed during retrieval of material from episodic memory [16,33,36]. This probably results from the need to evaluate and monitor responses, processes also required for performance of the Tower task. Anterior prefrontal lesions that characteristically lead to impaired performance in the Tower of London task almost invariably encompass this rostral area [26,31].

4. How do we choose what to do?

Planning has affiliations with the concept of action. The concept of action can encompass moving a limb, uttering a sentence or performing a manipulation on a mental image. Action and planning are also closely tied to a concept of agency. Not all actions involve a sense of agency. Examples of this latter type of action are those responsive to external cues both in terms of timing and goal. Self-generated actions are usually accompanied by a sense of agency and are determined principally by internal, as opposed to external, context [14]. William James suggested that this sense of agency arises when we are aware of choosing between several possible courses of action [19]. If one course of action dominates then we have little sense of choice (or agency) and action can be said to be stimulus or context driven. The necessity for choice is particularly likely to arise in novel situations where we have inadequate information for choosing one action rather than another, or situations in which different actions are roughly equal in the likelihood of achieving a desired outcome (the tyranny of choice). In line with the conceptual framework we have adopted for this essay, we are concerned in this section with the ability to hold in mind several alternative actions in order to choose which one to initiate.

We have carried out a series of studies in which volunteers were explicitly required to choose for themselves which of several responses to make. In one study subjects had to choose for themselves which of two fingers to move [9]. This was contrasted with a condition in which they simply moved whichever of the two fingers was touched. During self-generated movement there was activity in DLPFC bilaterally and in anterior cingulate cortex. Similar results were obtained when volunteers had to choose be-

tween four possible joy-stick movements and this was compared with moving the stick in the same direction every time [4]. Once again activity was observed in DLPFC and anterior cingulate cortex when the movements were self-generated. In these studies subject chose which movement to make, but, because the tasks were paced, not when to make the movements. In another experiment, volunteers made the same movement every time, but chose for themselves when to make the movement [20]. Again, in this condition there was activity in DLPFC and anterior cingulate cortex.

The tasks discussed above are sometimes described as generation tasks, since the volunteer has to generate the movement sequence for himself. There have also been many studies of word generation. There are two basic forms of these tasks; generating many words in a particular category (e.g. words beginning with F) or generating one word that goes with a cue word (e.g. generating verbs for nouns, cake – eat) [10,29]. These tasks are rather different from the motor tasks we have already discussed. In the motor tasks the volunteer keeps in mind all the possible responses and chooses one of them. In the word generation tasks the volunteer has, somehow, to summon into his mind a possible response from within a rather tightly specified category. Although the tasks have this different quality the pattern of activity associated with word generation is very similar to that seen in the movement generation tasks. The main activity is again seen in DLPFC especially on the left and, in addition, there is activity in the anterior cingulate cortex (Table 2).

Activation of DLPFC is also seen in episodic memory tasks. However, there is a striking difference in the frontal activity associated with acquisition and retrieval [33,36]. Acquisition tends to be associated with left frontal activity while retrieval is associated with right frontal activity. Presumably this difference reflects the different kinds of processes typically involved in acquisition and retrieval. Such processes should also be involved in tasks that do not directly concern memory. On the basis of the results discussed in this section we might speculate that left frontal activity is associated with the generation of items (bringing things into mind). For example, in order to remember word pairs it is useful to generate ‘‘mediators’’, that is concepts that link the two words. In contrast, right

frontal activation might be associated with checking items already held in mind.

5. An extended system for consciousness

One of our aims in this essay has been to show that the content of consciousness is determined by the location of the associated brain activity and that this activity is in the same location during direct perception or action as when we hold the same perception or action ‘‘in mind’’ during imagery or the mental manipulation of information. If this assumption is correct, it raises the question of how we distinguish between a direct perception, a memory or an act of imagination. If these states are to be distinguishable then they must be associated with different patterns of brain activity. We propose that this distinction critically depends upon frontal activity and, in particular, on the relationship between frontal activity and the activity in the location that determines the contents of consciousness. The major difference between a direct perception and a mental image is that the nature of the direct perception is determined by events in the outside world. A mental image, in contrast, is determined from within and is the result of our own actions. Changes in perception have two sources. The first is caused by events and agents in the outside world that are outside our control. These changes are essentially unpredictable. The second results from our own actions (hearing the sound of our own voice, etc.). These changes are essentially predictable.

The well established mechanisms of corollary discharge and reafference copy provide one way in which the degree of predictability can be signalled [17,34]. The signals which lead to precisely determined movements of limbs or larynx can also be used to modify the response of perceptual areas to the perceptual results of these movements. Eye movements provide the most dramatic case. Each time we move our eyes there is, in consequence, a rapid movement of our image of the world across the retina. It has been known for a long time that during rapid eye movements there is saccadic suppression. During the rapid movement of the eye the image is effectively switched off. Paus et al. have performed an elegantly simple experiment to show the pattern of brain activity associated with this phenomenon [27]. Volunteers lay in the dark and moved their eyes at different rates across a series of scans. Activity in the frontal eye fields was positively correlated with the rate of eye movements. However, in visual cortex and visual association areas the activity was negatively correlated with rate of eye movements. This result implies that each eye movement was accompanied with reduced activity in visual areas and provides a physiological basis for saccadic suppression.

Similar observations have been made in the auditory system by recording neural activity from implanted electrodes. In the squirrel monkey cells have been found in the

Table 2
Common activations for word generation and movement generation [9]

<i>Word generation</i>			
DLPFC	– 43	29	20
Anterior cingulate	4	23	36
<i>Movement generation</i>			
DLPFC	– 35	39	21
Anterior cingulate	– 3	16	34

Significant activations are listed in terms of Talairach coordinates.

temporal cortex which respond to the vocalisations of other monkeys, but not when the monkey itself vocalises [25]. Creutzfeld et al., using implanted electrodes in patients undergoing neurosurgery, have found areas of temporal cortex in which activity is reduced when patients vocalise [3]. This mechanism by which the sensory effects of our own actions can be anticipated is likely to be intimately bound up with our sense of agency. In other words we know we are in control of our actions because we can precisely predict their effects. We know almost nothing as yet about how we detect agency in the outside world, although this must be a very important ability in most mammals [30]. It is likely that the mechanism for the detection of agency in others will be related to the mechanisms by which we are aware of our own agency.

Our proposal is that this modulation of perceptual areas by activity stemming from areas concerned with action generates difference in the overall patterns of activity which serves to identify the source of perceptions (internal or external). In principle, the same mechanism could be used to distinguish whether active representations derive from direct perception, memory or imagination. In these cases the critical interactions are likely to be with prefrontal rather than premotor areas. We have reviewed studies of active memory, of motor imagery and of the manipulation of mental images, all of which have shown activation in both prefrontal areas and sensory and/or motor association areas specific to the content of the mental image. However, there are other studies in which the relationship between frontal and posterior areas seems to be reciprocal.

6. Decreased activity associated with willed action

In the word generation task described above volunteers had to summon into mind words beginning with a certain letter [9,10]. In this task the representation of the word to be spoken becomes active in the absence of any presentation of that word to the senses. This task is associated with marked activation of left DLPFC and anterior cingulate. In the control task volunteers simply repeated the word that they heard. In this case there is an active representation of the word to be spoken which derives directly from the senses. In comparison with this control task there is reduced activity bilaterally in superior temporal cortex during word generation [9,10]. We have interpreted this result, which has been replicated many times, as evidence that the prefrontal cortex modulates temporal cortex during the intrinsic generation of words. We obtained a similar result with finger movements. When volunteers generated finger movements (contrasted with copying them) there was increased activity in prefrontal cortex and reduced activity in the region of the angular gyrus where lesions are associated with finger agnosia [9]. Friston et al. have suggested a mechanism in which successful activation of a representa-

tion from sensory input (extrinsic, bottom up) would require general activation of the network in which that representation was stored, while successful activation from an intrinsic source (top down) would require a general reduction of activity in the same network [8]. However, the point we want to make here is that the difference in the level of activation also provides an indication of the source of the activation, i.e., whether it was extrinsic or intrinsic. We suggest that, just as ‘‘corollary discharge’’ can label sensations as a result from intrinsic actions, so the fronto-temporal interactions observed in word generation label inner representations as resulting from intrinsic actions. We anticipate that similar interactions will be identified which are associated with episodic memory and mental imagery.

7. Disconnections in the extended system

In the major psychosis many of the key symptoms involve a loss of the feeling of agency or the false perception of agency in the outside world. For example patients with schizophrenia sometimes report that alien forces are controlling their actions (delusions of control) or that alien thoughts are being inserted in their minds (thought insertion). Auditory hallucinations are a particular common feature of schizophrenia. There is increasing evidence that these experiences can be associated with the patients’ own sub-vocal speech or inner speech. For example, brain imaging studies have shown that activity in Broca’s area and left temporal cortex is occurring during hallucinations [23]. All these observations suggest that schizophrenic patients are experiencing intrinsically generated activity as if it were extrinsically generated. A number of theories have been put forward essentially along the lines that patients with schizophrenia confuse memories and self-generated images with direct sensory perceptions [11]. We can now begin to think about how these descriptions at the psychological level can be translated into underlying physiology. On the basis of our discussion in the previous section we would predict that, during the experience of schizophrenic symptoms, something is going wrong with the interaction between prefrontal cortex and posterior brain areas concerned with the content of the experience. The first direct evidence of such disconnections comes from studies of word generation in schizophrenia. When performing this task patients showed as much activation in DLPFC as controls. However, there was a striking failure to show the normal pattern of reduced activity in superior temporal cortex on the left. This abnormality was observed both in chronic patients and in drug-free patients in the acute phase of the illness [5,12]. We have yet to show whether this kind of disconnection can be directly related to the experience of symptoms such as auditory hallucinations. Preliminary studies of patients who are prone to hallucinate during remission suggest that they show abnor-

mal patterns of brain activity when trying to imagine the sound of someone else's voice [24]. The location of this abnormal activity is in the supplementary motor area and left superior temporal cortex. These areas are very likely to be part of the system involved in the generation and perception of speech.

8. Conclusion

Higher cognitive functions are intimately related to consciousness and depend upon interactions between prefrontal cortex and more posterior brain regions. The contents of consciousness is dependent on the precise location of these posterior activations. Our experience of the source of our consciousness depends on the nature of the interaction between the prefrontal cortex and the posterior areas. Psychotic experiences occur when these interactions go awry.

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