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Prefrontal attention and multiple reference frames during working memory in primates

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The prefrontal cortex (PFC) is responsible for executive functions, including planning, goal setting, problem solving, inhibitory control, monitoring, and action adjusting. Executive functions also include selective attention and the flexibility or switching of attention; therefore, attention is an executive function in which the PFC participates. Working memory (WM), which is the temporary maintenance and processing of particular information, is usually considered to be a basic neural mechanism underlying the executive functions. This review systematically discusses the relationship between the prefrontal WM and attention and emphasizes two forms of prefrontal attention. The first form occurs in the dlPFC, which encodes the location of objects with respect to the position of the head, thereby providing a frame of reference from which the focus of attention can be centered. The second occurs in the inferior convexity of the prefrontal cortex (IFC), which encodes the different attributes (shape, texture, color) of objects to enable the ability to focus on one or to switch attention between sensory attributes of objects.

prefrontal cortex, attention, working memory, inferior convexity, multi-reference frames

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The prefrontal cortex (PFC) is located rostral to the motor and premotor cortices. It is also called the frontal association cortex or the frontal granular cortex in reference to its functional and structural attributes, respectively. The primate prefrontal cortex has been the focus of a host of studies over the past century. In primates, lesions in the frontal lobe produce deficits in delayed response that have been related to the impairment of interest and, hence, sustained attention and working memory (WM) (Figure 1).

The prefrontal cortex is responsible for executive functions, including planning, goal setting, problem solving, inhibitory control, monitoring, and action adjusting. Executive functions also include selective attention and the flexibility or switching of attention; therefore, attention is an executive function in which the PFC participates. WM, which is the temporary maintenance and processing of particular information, is usually a basic neural mechanism underlying executive functions.

It is well known that covertly directing the spatial attention to a particular location enhances the sensory processing of the stimuli within the current focus of attention. In spatial WM and attention tasks, subjects are typically asked to pay attention to or temporarily maintain in their memory a spatial location, such as “left” or “right”. However, these spatial relational terms are ambiguous because they can be defined by different frames of reference. For example, “left” could mean the left of the body, but it could also mean the left of an object. Humans interpret spaces differently depending on the functions they serve. Attention can be flexibly and strategically assigned to a reference frame depending on the contingencies of the task. Previous research has suggested that the coding of a single spatial location can involve different reference frames, which are in turn associated with different brain circuits. In the study of prefrontal

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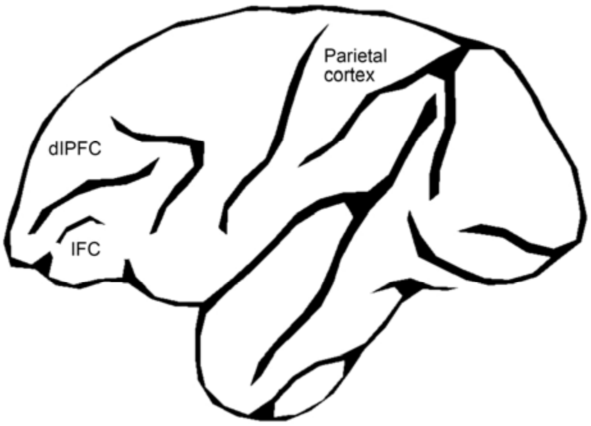

Figure 1 The monkey brain and the locations of dlPFC, IFC and parietal cortex.

information processing, the particular prefrontal spatial coordinate system cannot be ignored.

For a systematic approach, it is important to review several of the cognitive functions of the PFC and to understand the relationship between them. Therefore, this review discusses the relationship between the prefrontal WM and attention and further emphasizes two forms of prefrontal attention: egocentric information processing, which is closely related to the spatial deployment of attention and relies on the dorsolateral prefrontal cortex (dlPFC), and object-centered attention, which requires the IFC.

1 The relationship between WM and attention

1.1 Deficits in DR tasks after PFC lesions

In this context, it is instructive to consider the history of the studies involving the PFC. Frontal lobectomy or, more impressively, the limited resection of the dlPFC of monkeys produces profound deficits in the delayed response (DR) task performance [1–4]. Jacobsen [5] was the first to show the deficits in the DR task performance resulting from dlPFC damage and interpreted these deficits to mean that the dlPFC damage impaired spatial memory (Figure 2).

However, no consensus has been reached in the interpretation of these experiments. For example, Malmo [6,7] provided evidence that the deficit observed by Jacobsen [5] was an attention disorder and not a loss of spatial memory. Malmo's experiment was conventional in some respects. For example, monkeys performed a DR task that required the memory of the spatial location of a target object over a 10-s delay. The testing room was illuminated during the delay interval in the first condition and was dark during the delay in the second condition; this was an unconventional manipulation and was the critical test to show the validity of the two competing hypotheses of dlPFC function in memory or in attention. The results of this study were clear: the monkeys with damage to the dlPFC were impaired when the delay periods were illuminated but not when it was dark during the delay. Malmo argued that the dlPFC damage led to the susceptibility to the interfering effects of the extraneous stimuli during the delay period. According to Malmo, the primary deficit was distractibility (i.e., an inability to maintain attention on a stimulus and its location) rather than a loss of the memory for the spatial location.

The Malmo study [6] has the following three minor flaws: (1) the study was limited to 2 monkeys; (2) the monkeys were different species (one female rhesus macaque and one male mangabey); and (3) the mangabey was tested both pre- and postoperatively, whereas the rhesus was tested only postoperatively. However, despite these differences, both animals responded similarly. They were able to perform the DR task normally (81% and 94% correct) when the delay period was dark, but they both performed at the level of chance (46% and 50% correct) in the illuminated condition.

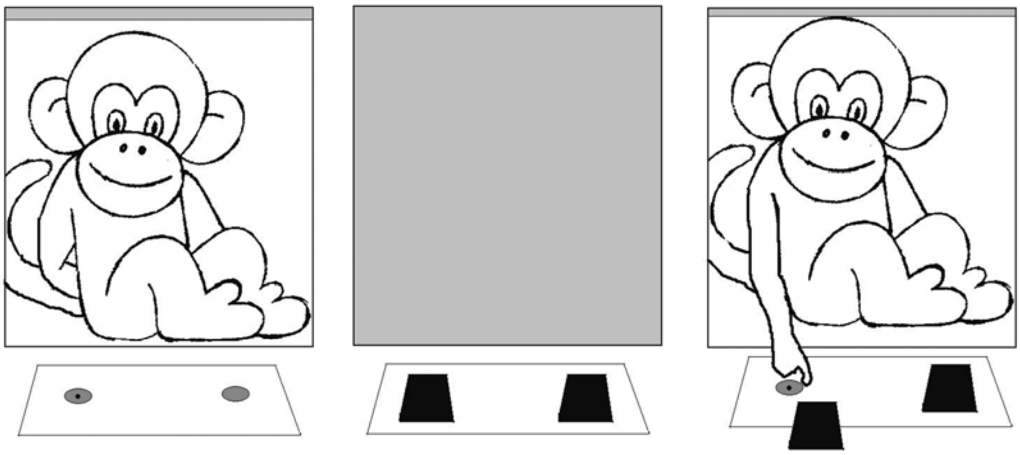

Figure 2 The diagram of the delayed response task. In the delayed response task, the monkey watches an experimenter place a food morsel in one of two wells (left); both wells are then covered. Subsequently, a screen is lowered for an interval of a few seconds to several minutes (the delay) (middle). When the screen is raised, the monkey gets only one chance to uncover the well containing food and receive the reward (right).

The substantial impairments observed in both monkeys in the illuminated condition are consistent with a study regarding the loss of attentional function in humans with prefrontal damage [7]. The loss of spatially directed attention in humans with prefrontal damage has not been explained by the primate studies interpreted within the framework of spatial working memory. In fact, it is very uncommon for studies to consider the possibility that the delay-related neuronal activity is related to attention; all the emphasis has been placed on WM. Despite this lack of consideration, it is possible to reconcile the attention/memory dichotomy by fully adopting Baddeley's concept [8] of WM. Baddeley defines WM to be a series of components in which attention plays an integral role. Specifically, Baddeley [8] invokes the notion of a central executive component, which is thought to consist of a controller system related to attention that coordinates the operation of cognitive modules (e.g., visuospatial scratchpad, phonological loop). Many studies [9–12] have provided compelling evidence for a role of the dlPFC in attention.

1.2 Neuropsychological studies of dlPFC patients: Disorders of attention

In their review of the relationship between the dlPFC and attentional processes, Stuss and Benson [7] conclude that "it can be hypothesized that the ultimate control of the attentional system being the domain of the frontal lobes". Disorders of attention are so common following frontal lobe damage that a chapter of their book, *The Frontal Lobes*, is devoted to attention. Clinical attention disorders are generally described as the impairment of directed concentration over a defined period of time. Some patients with frontal lobe damage have difficulty attending to important stimuli, some are easily distracted, and some are abnormally fixated on a particular behavior. Stuss and Benson [7] emphasize the resemblance between schizophrenia and frontal lobe injury: "the most striking impairment occurs on tasks requiring planning and on sustaining behavior during distraction".

According to Chao and Knight [13,14], prefrontal damage results in increased distractibility in an auditory WM task. They reported that normal subjects respond to auditory stimuli with a characteristic evoked potential called the sustained focal negativity (SFN). The SFN is associated with performance effort and sustained attention; increasing the demands of the task results in an enhancement of the frontal negativity, whereas the absence of attention abolishes the SFN potential. Chao and Knight concluded that damage to the PFC affects the ability to ignore irrelevant inputs and the ability to focus attention on significant stimulus attributes.

The research in primates is consistent with the studies of Chao and Knight in several ways. First, the data from Malmo [6] showed that the deficit in the delayed response task is due to increased distractibility. Second, the notion of an egocentric attentional system in the dlPFC is consistent with the view that the PFC acts to suppress irrelevant signals [14]. Third, the hypothesis that the IFC provides an object-centered attentional mechanism that allows the subjects to select a within-object stimulus dimension for the use in a current behavioral task is consistent with the impairments in the intra- and extra-dimensional shifts seen in the Wisconsin Card Sorting Test [15–17]. Finally, the enhancement of the SFN evoked potential in humans described by Chao and Knight [13,14] appears to be closely related to the neuronal enhancement observed in behaving monkeys.

A recent study [18] found that irregularly presented auditory or visual distracters disrupt the auditory or visual WM task performance and the underlying neuronal activity in monkeys. Distractions of the same sensory modality as the memorandum were more likely to impair WM performance and interfere with memory-related neuronal activity than the information that was of a different sensory modality. This study also showed that neurons not involved in the memory processing under less demanding conditions may become engaged in WM processing under more demanding conditions. The study demonstrates that WM performance and the underlying neuronal activity are vulnerable to irregular distracters and suggests that the PFC has mechanisms that help to compensate for the disruptive effects of the external distracters.

The relationship between working memory and selective attention has traditionally been discussed as operating in one direction: attention filters incoming information, allowing only relevant information into short-term processing stores. But it is not a whole story. In fact working memory and attention interact in a way that enables us to focus on relevant items and maintain current goals. The influence of working memory on attention has been noted in several studies. It is generally agreed that the PFC plays a critical role in attention and working memory, which activation is positively correlated with the load of object WM [19]. Attention broadly participate in manipulation and updating of contents in working memory, and the temporary information preservation and manipulation in working memory are also essential components to attention, for example, some studies [20] showed that forming a visual image of a target will facilitate the visual search, in another words, the act of preparing to search might consist, not in some mental operation specific to search per se, but merely in forming a mental image of the target to be searched for. Anatomically studies indicate that mediate working memory and selective attention show a striking degree of overlap in neural substrates [21]. Thus the temporary maintenance of information and its processing are important neural components of attention. It is obvious that attention may not work without these components. Therefore, WM must be a very important neural mechanism for attention. Thus some scholars suggested that the working memory is a very important neural mechanism for understanding attention and attention would not work well without working memory [22,23]. These discussions would benefit the study of the information processing in PFC.

2 The dlPFC provides an egocentric frame of reference and the lFC provides an object-centered attentional mechanism

2.1 Multiple reference frames in prefrontal attention

Here, the concept of functional dissociation will be discussed by proposing that the lFC and dlPFC provide the substrates for two types of attentional mechanisms. Specifically, the lFC provides an object-centered attentional mechanism, whereas the dlPFC provides an egocentric frame of reference.

First, the egocentric coding of space by the dlPFC is closely related to the spatial deployment of attention. Thus, to remember where an object is located with respect to the body, it is essential to be able to attend to that part of space and to move the eyes and limbs to that region. There is overwhelming evidence from studies of brain-damaged patients and functional imaging studies that the prefrontal and parietal cortices contribute to the ability to search for a target in visual space, and damage to these regions contributes to the neglect of visual space [24–26].

Second, the lFC contributes to object-centered attention. Object-centered attention is defined as the ability to select between the different attributes (shape, texture, color) of an individual stimulus and then to use this information in problem solving. In fact, it can be said that the hallmark of frontal lobe deficits is the inability to perform the Wisconsin Card Sorting Test [16]. Patients with prefrontal lobe defects are unable to identify the appropriate dimensions of a stimulus that are relevant for a behavioral task and, in particular, to use and switch between the stimulus dimensions [16]. In addition to the impairment of object-centered attention (the selection of stimulus attributes), there are substantial data showing that prefrontal damage impairs the ability to attend to a stimulus in a sustained fashion [27] and that patients with prefrontal lobe defects are susceptible to proactive interference [28].

As mentioned above, many studies have suggested that the information processing in the lFC and dlPFC are different. The dlPFC is related to spatial information processes [1–4]. In contrast, the lFC is specialized for object-related information processes, and the information about their location is secondary [29].

Consistent with the view that the dlPFC and lFC are functionally different, studies by Wilson et al. [30] have suggested that there is a functional dissociation between the lFC and dlPFC in primates. Specifically, the lFC is specialized for the processing of complex pictures, whereas the dorsolateral sector of the PFC is specialized for the analysis of the spatial location of objects in pictures. The inferior temporal (IT) cortex is involved in the integrity of identification, recognition and memory of complex pictures [4]. The IT projects to the lFC [31], which further strengthens the case for the functional dissociations between the lFC and dlPFC. These dissociations have also been found in the human frontal cortex. For example, Courtney et al. [32] studied the functional activation of the human PFC in spatial and non-spatial processing tasks and reported a dorsolateral focus for spatial tasks but an inferior lateral focus for the non-spatial tasks.

2.2 Egocentric encoding in the dlPFC

A recent study [33] has provided further evidence of the functional differences between the lFC and dlPFC, and these data support the dichotomy of the object and spatial processing separately embedded in the two sectors of the prefrontal cortex. The authors of this study developed two variants of the Match to Sample (MTS) WM task in which monkeys had to remember either the spatial (the location—left or right—of a sample stimulus) or configural information about two circles.

Ma et al. [33] found that only the spatial MTS task was impaired, and the configural MTS task was not in the monkeys with dlPFC damage. This experiment supports the general view that the dlPFC is specialized for processing spatial information [30] and particularly for encoding cue locations [34,35]. Additionally, it suggests that the dlPFC sectors are not functionally important for the performance of tasks that require the object-centered spatial relationships to be attended and remembered.

In summary, damage to the dlPFC produces severe impairments in the spatial delayed response task, and this brain region has been proposed to be the site of spatial memory. This concept has had a profound influence on the functional studies of the frontal lobe, and the concept of spatial memory has been understood to mean the location of an object. However, it is a simplification to say that the dlPFC contributes to the processing of spatial information because the concept of space is not simple. By studying the processing of spatial information of the PFC, Ma et al. [34,35] provided evidence that the dlPFC provides an egocentric mechanism that represents the location of an object with respect to the observer's head.

2.3 Object-centered encoding in the lFC

Wilson et al. [30] noted strong similarities between the neurons in the lFC and IT. For example, the neurons in both structures prefer complex visual stimuli and are most responsive to stimuli presented on the fovea. These similarities do not address the question of the function of the two areas. Although there is strong evidence that the IT mediates the recognition of objects, there is no convincing evidence that the lFC contributes to object recognition. Damage to the IFC in monkeys or humans does not produce deficits in the recognition of objects.

What does the IFC contribute to the visual object-oriented behavior? We propose that it contributes object-centered attention, which is defined as the ability to select between the different attributes (shape, texture, color) of an individual stimulus and then to use this information in problem solving. Several behavioral deficits that result from prefrontal damage support this object-centered attentional hypothesis. The first is the inability to perform the Wisconsin Card Sorting Test [16]. Patients with prefrontal lobe defects are unable to identify the appropriate dimensions (the shape, number, color, etc.) of the stimuli that are relevant for the behavioral task. Specifically, they are unable to use this information or switch between the stimulus dimensions. A second impairment is the inability to shift the attention from one perceptual aspect of a complex stimulus to another dimension. This skill is required, for example, in the intradimensional-extradimensional task. The performance in this type of task is impaired in both monkeys and humans with prefrontal lobe defects [15,17]. A third impairment is the loss of the third of the three attentional mechanisms mediated by PFC [36], which maintains the selection of the defined schema (the task contingencies) so that consistent target selections are made and the responses to the competing targets are inhibited. This function strongly resembles Mishkin et al.'s [37] proposal for the functional role of the monkey IFC. These phenomena provide evidence for the underlying hypothesis that the role of the IFC is to identify the correct dimension of a complex multi-dimensional stimulus and then to use this information to guide behavior.

Of the many theoretical and empirical studies in support of object-based processes [38–40], we refer to the representative study of Fink et al. [41]. In this study, the authors showed that a task requiring the ability to judge the center of a square activates the lingual gyrus in the human ventral occipitotemporal cortex. They also showed that a task requiring the ability to judge the center of a horizontal line activates the right parietal cortex. The study by Fink et al. provides a functional and anatomical dissociation between an object-centered process (judging the center of an object) and a spatial process (judging the midline of a body). Their study is particularly persuasive because their subjects used stimulus-centered coordinates and not egocentric coordinates when judging the center of the square objects. Fink et al. [41] also noted that their data are consistent with those of neuropsychological studies showing that neglect patients who show a severe impairment in marking the center of horizontal lines can accurately mark the center of squares. They also observed that "as a stimulus becomes a better, more 'object-like' gestalt, the ventral visuoperceptive route assumes more responsibility for assessing position within the object". According to Wilson et al. [30], the IFC is a rostral extension of the ventral object-oriented processing pathway. In addition to the Fink et al. study, neurophysiological, psychological, and brain imaging studies support the operation of object-centered processes [42,43].

2.4 The representation of egocentric space in the parietal and premotor cortices

The dlPFC is one of a series of anatomically connected brain structures that are involved in the mediation of an egocentric spatial frame of reference. There is a great deal of evidence showing that certain sectors of the parietal cortices and the ventral premotor cortex represent the spatial world within an egocentric, head or body-part representation. Many studies of brain-damaged humans indicate that the parietal cortex represents the spatial world in egocentric coordinates (for a review, see Andersen et al. [44]). Although the majority of evidence indicates that the parietal cortex plays a role in determining where an object is located, there are data to suggest that the parietal cortex also interacts with the ventral object recognition pathway. First, neurophysiological studies have shown that neurons in the anterior inferior parietal cortex are stimulus-selective for shape and orientation when they are the target for a hand movement [45,46]. Second, some authors (e.g., Humphreys [47]) have noted that the inferior parietal lobe may actually form part of a ventral or overlapping ventral-dorsal processing area that deals with aspects of object coding. Accordingly, lesions to this area affect object recognition. Alternatively, the parietal areas may be recruited when the attention needs to be switched from one part of an object to another or when the spatial relations between the parts are important for identification.

The pathways from the striate and prestriate cortices of the visual system innervate the parietal cortex with strong projections to areas 7a and VIP. The neurons in area 7a have large visual receptive fields that encode the locations of visual stimuli on the retina. These visual receptive fields move as the eye moves [44]; thus, the representation of visual space is "retinocentric" as is the case for the striate and prestriate cortical regions. A retinocentric code is entirely different from an egocentric representation of visual space.

The VIP and 7b areas are the recipients of the information from area 7a. The VIP area has different properties than those of 7a. Many VIP neurons are bimodal, and some visual receptive fields in the VIP move with the eye, whereas some do not.

The ventral premotor cortex has been the subject of previous research. Therefore, it is worthwhile to briefly review the properties of the premotor cortex, which is the recipient of the pathways from the VIP and 7b areas. The ventral premotor cortex (PMv) is involved in the visual guidance of movement [48]. Approximately 40% of the neurons in the PMv are bimodal cells that respond to both visual and tactile stimuli. Most of the visual receptive fields are confined to the space near the tactile receptive fields. That is, most of the bimodal neurons with a tactile receptive field on the arm have a visual receptive field around that tactile receptive field (termed "arm+visual" cells), and most of the bimodal neurons with a tactile receptive field on the face have a visual receptive field around that tactile receptive field (termed "face+visual" cells). One interesting characteristic of these "arm+visual" and "face+visual" cells is that when the eye moves, the visual receptive fields do not move but remain anchored to the tactile receptive fields. These neurons therefore encode the space near the body in "body-part-centered" coordinates, rather than in retinal coordinates [48].

Thus, the PMv neurons reflect a form of egocentric coding of the visual space in which the face and arms are the primary effectors, whereas the primary effectors in the dlPFC are the head and eyes. In effect, there is a rostral-caudal distribution of body-part function within the dlPFC and PM cortex that is congruent with the proposal that the dlPFC neurons represent the spatial world in egocentric coordinates, whereas the PMv neurons represent the spatial world in face- and arm-centered coordinates.

3 Conclusions

In daily life our brain is constantly exposed to a huge amount of sensory information. The ability to capture and hold key information is critical for goal-directed behavior. This cognitive ability to lead future goal-directed behavior is always described as executive functions which is crucial for PFC [49,50]. To perform executive functions, a WM to temporarily keep and manipulate information in brain will be required. Meanwhile, to temporarily store and manipulate information in working memory, attention ability to focus on target and ignore distraction will be required. The most well known process-oriented definition of attention comes from William James [51], who defined attention as involving "withdrawal from some things in order to deal effectively with others". In addition, due to limited brain processing capacities selective attention is a key mechanism to select and structure information according to our goal, so that the brain could effectively cope with environment. Actually, working memory and attention, these two core components of cognitive processing, both are critical for goal-driven cognitive processing, and are rely on each other. Attention filters incoming information, allowing only relevant information into short-term processing stores while WM is a very important neural mechanism for attention as well.

The PFC is functionally divided into two major sectors: the dlPFC which encodes the location of objects with respect to the position of the head and provides a frame of reference in which a spotlight of attention can be deployed; and the IFC encodes the different attributes (shape, texture, color) of objects and enables the viewer to focus and switch attention between one of the several sensory attributes of objects.

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