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Humans

A P Shimamura, University of California, Berkeley, CA, USA

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The frontal lobes comprise roughly a third of the human cerebral cortex. Through evolution this brain region has increased disproportionately, and as a result of this expansion it has been viewed as the basis for human intellect and thought. Studies of individuals with brain injury have suggested that frontal lobe damage affects many aspects of cognition, including attention, memory, language, problem solving, emotion, and decision making. Yet, its role as the seat of human reasoning and thought became suspect, as findings indicated that frontal lobe damage did not grossly affect measures of general intelligence. Now, there is general consensus that the frontal lobes – or more specifically the anterior portion of the frontal lobes identified as the prefrontal cortex (PFC) – contributes to the regulation or control of mental processing.

The PFC can be parcelled into five general regions – the dorsolateral (dlPFC), ventrolateral (vlPFC), posterior (pPFC), anterior (aPFC), and ventromedial (vmPFC) prefrontal regions. These first four regions are spatially located as north, south, east, and west regions within the PFC when the left hemisphere is viewed from the side (i.e., laterally). The fifth region, vmPFC, refers to the lowest and medial (i.e., inner) portions of the PFC. These regions are intricately connected to regions outside the PFC (i.e., in the posterior cortex) and also have interconnections among themselves. These regions are distinct both in terms of anatomical and functional characteristics. In particular, functional neuroimaging techniques, such as functional magnetic resonance imaging (fMRI) and positron emission tomography (PET), have been successful in demonstrating that these brain regions play different roles in the control of cognitive (and emotional) processes. With respect to memory, the dlPFC, vlPFC, and aPFC have been most associated with control processes associated with encoding, organizing, and retrieving memory.

Consider the following question: What did you eat for dinner 3 days ago? It is unlikely that you were able to answer this question immediately. However, with some time and searching through your memory, you may have been able to retrieve the information. Most of us would begin by trying to figure out the day of the week. “Let see, today is Wednesday, three days ago would be Tuesday, Monday, Sunday…yes Sunday, what was I doing on Sunday….” If you ultimately retrieved the information – or even if you tried but were unsuccessful – you likely engaged in a variety of mental processes, particularly those involved in selecting, maintaining, organizing, and ultimately retrieving the desired memory. These processes enabled you to guide and control your mental path toward successful retrieval. In psychological terms, these functions enabled executive control, a process that is critically dependent on the PFC. By analogy, the PFC is your brain’s chief executive – it functions to select information, monitor its use, disregard irrelevant information, make decisions, and initiate actions. Without it, your memory – just like a poorly run business – is disorganized, inefficient, and more susceptible to disruptions.

Stimulus Overload and Working Memory

One reason for the necessity of executive control is that we cannot possibly hold in mind everything that we know or perceive. Indeed, it would be an inordinate load on our cognitive system if we even attempted to consider everything that we experienced at any given moment. Because of this stimulus overload, we need to select certain information to be analyzed. Other information is filtered or ignored. For instance, at this moment you are reading and presumably paying attention to this sentence. Yet, pause briefly and pay attention to other sensory information. Perhaps, you can now hear surrounding noises such as a fan or people talking. You can direct your attention to other things, such as the rhythmic changes of pressure on your chest as you breathe. Clearly, at any given moment we experience a multitude of sensations. Not only can we select aspects from the environment, we can select and consider a plethora of memories. It almost seems incredible that in the midst of this information overload, we are able to select, maintain, and control what to bring into our realm of consciousness. The term working memory is used to describe the information that we choose to keep in mind at any given moment. Working memory is transient, and executive control is the dynamic process by which information is selected, maintained, updated, and organized in working memory.

Patients with damage to the PFC (more specifically damage to dlPFC and vlPFC) exhibit a syndrome in which executive control is severely impaired. These patients have problems in paying attention, holding things in mind, organizing thoughts, and retrieving memories. They experience particular problems when
confronted with multiple sensations or choices and must decide which ones to select and which ones to disregard. One particular problem concerns their ability to hold information in mind. A simple task to test this ability is the digit span test, in which individuals are asked to report a string of digits immediately after presentation. Most individuals can hold about six or seven digits in mind, just as we might when we have to hold a phone number in mind before placing a call. Patients with PFC damage have reduced digit span—they have difficulty keeping information in mind. This deficit pervades many domains, including the ability to maintain locations, colors, or sounds in mind.

Neuroimaging studies have confirmed the role of the PFC in working memory. When individuals must hold or maintain information in mind for a brief delay, prefrontal activity is increased. Interestingly, different prefrontal regions appear to be responsible for maintaining different kinds of information. For example, increased activity in left vlPFC is observed when individuals are asked to hold names of objects in mind, whereas increased activity in right vlPFC is observed when individuals are asked to keep spatial locations in mind. In many instances, these prefrontal activations are linked to activations in posterior regions of the brain, suggesting that the holding of information in working memory involves a brain circuit that includes the information to be activated (presumed to be stored in posterior cortex) and the executive control process that keeps the information active (presumed to be established by PFC).

In addition to its role in maintaining information in mind, the PFC is also involved in updating and manipulating information in working memory. In many everyday situations, it is necessary to rearrange or update information in mind. In laboratory studies, this aspect of working memory has been investigated by asking individuals to reorganize information, such as putting a random string of letters in alphabetical order. Another manipulation task is called the self-ordered pointing task in which individuals are presented with an array of stimuli (e.g., eight objects) and asked to point to one of the stimuli. On subsequent trials, the same objects are shown in different positions, and individuals are asked to point to a different object on each presentation. This task not only requires the holding of objects in mind but also remembering which objects have already been selected. Thus, after each presentation, the contents in working memory must be updated or reorganized to include another item. Patients with PFC damage have difficulty performing this task. Also, neuroimaging studies suggest that the dlPFC is particularly active during such manipulations of information in working memory compared to conditions in which only the maintenance of information is required. Taken together, findings suggest that the mere maintenance or holding of information involves the vlPFC, whereas the manipulation of that information additionally recruits the dlPFC.

Encoding Memories

Executive control is also critical for efficient learning—that is, the encoding of new memories. For example, how would you learn the following series of words: peach, bus, shirt, car, apple, socks, train, shoe, pear? Perhaps, you continually repeated the words in your mind. Alternatively, you may have noticed that the words could be grouped into three meaningful categories: vehicles, fruits, and clothing. In fact, when learning such word lists, many people organize words during encoding and then report the words by grouping all of the words in each category—such as reporting the vehicles first, then fruits and clothing. This kind of organizational strategy would involve maintaining, manipulating, and updating items while they are being presented. Thus, efficient encoding of memories would depend critically upon the kind of executive control processes involved in working memory tasks, such as digit span and the self-ordered pointing task.

Patients with frontal lobe lesions exhibit poor organizational strategies during learning. They fail to elaborate information, such as grouping information into meaningful categories. Moreover, long-lasting memory formation requires the integration of the new information with existing knowledge. This interchange between new and existing information is called elaborative encoding and depends upon the PFC for efficient analysis. Neuroimaging studies corroborate the role of the PFC in elaborative encoding. For example, the left vlPFC has been shown to be particularly active when individuals are asked to consider the meaning of items, such as determining whether a word is concrete (e.g., dollar) or abstract (e.g., freedom) compared to conditions in which they determine superficial features, such as the number of vowels in a word.

The extent of PFC activity during encoding can predict the success of later retrieval. In neuroimaging studies, activations during the initial encoding of items were analyzed separately on the basis of whether the items were later remembered or forgotten. Remembered items were associated with greater prefrontal activity (generally in left vlPFC) during encoding compared to forgotten items. That is, if you recruited PFC during the encoding of an item, you increased your chances of later remembering that item. These findings further support the notion that
efficient encoding depends upon prefrontal activation during learning. The method of backsorting brain activations during learning in terms of whether items are subsequently remembered or forgotten offers a useful means by which to relate efficient encoding strategies to long-lasting memory retrieval.

Another aspect of executive control is related to the suppression of distracting or irrelevant information. In such situations, multiple activations of information place heavy demands on updating and manipulating information in working memory. Proactive interference is the term used to describe instances when earlier information impedes or interferes with the encoding of new information. For example, in memory tests individuals are asked to learn word associates, such as dog–boxer, which are then tested by presenting the first word in a pair and asking for the second word, such as thief–? Proactive interference is assessed by presenting a second learning phase involving the same cues but different responses (e.g., thief–bandit). Patients with PFC damage exhibit particular impairment when they try to recall the second set of responses. That is, they exhibit heightened proactive interference due to the learning of the first set of associates. Evidence for interference is demonstrated by the fact that these patients make many intrusion errors—that is, they use words from the first set during testing of the second set. These problems can be explained by a lack of inhibiting or suppressing the activation of related but now irrelevant information. With respect to executive control, the mitigation of proactive interference requires selecting and updating relevant information. The importance of the PFC in inhibitory control of distracting information has also been demonstrated in fMRI analyses using similar learning paradigms. For example, when individuals are asked to learn word associates such as dog–boxer then later dog–Labrador, they exhibit increased left dIPFC activity when attempting to learn the second related word pair.

**Selecting Semantic Memory**

A hallmark feature of PFC damage is a problem in searching through memory and selecting specific information. This deficit can be demonstrated in the verbal fluency task, in which individuals are given a minute to retrieve words from a specific semantic category (e.g., ‘animals’) or retrieve words that begin with a specific letter (e.g., ‘A’). This task requires a search through semantic memory—that is, our database of memory for facts and knowledge. Similar to tasks involving the manipulation of working memory or the encoding of new information, efficient retrieval involves the development of strategies to control what words are generated. For example, after trying to come up with just any animal, it would be useful to consider subcategories of animals, such as pets, farm animals, or reptiles. Such strategies are efficient because they facilitate the selection of different words and prevent the report of words already generated. Patients with PFC damage have difficulty controlling their memory searches on this task. They report only 10–12 animal names in a minute, whereas most individuals would be able to retrieve twice as many animal names. Moreover, patients with PFC damage tend to repeat words over and over, as if they have difficult in suppressing the activation of words that were already selected.

The verbal fluency task appears to be a rather easy one, though it is important to appreciate the role of executive control in selecting and updating such information. Not only is it necessary to generate and select information, it is also necessary to monitor responses so that one avoids repeating the same word. Thus after each response all prior responses must be kept in mind so that they will not be repeated. As such, this task has some similarities with the self-ordered pointing task and tasks associated with proactive interference, in which prior information interferes with current performance. In these tasks, it is necessary to monitor and control the activation of previously relevant but currently irrelevant information.

In neuroimaging studies, vIPFC is particularly active during the generation and selection of semantic knowledge. One often-used task to assess retrieval from semantic memory is the verb generation task, in which individuals are presented a noun cue (e.g., ‘nail!’ and asked to generate an associated verb (e.g., ‘pound’). As in the verbal fluency task, verb generation requires a search and selection process through one’s semantic database. Also, it is necessary to control competing or interfering items during retrieval. In fact, vIPFC activity increases to the extent that there are many competing responses from which to choose. Such regulation of semantic retrieval extends to other linguistic tasks, such as making decisions about the conceptual relatedness between items or interpreting difficult or ambiguous sentences.

The retrieval of general factual knowledge can be assessed by tests of remote public events (e.g., “Who shot John Lennon?” [answer: Chapman]). In one study, patients with PFC lesions and control subjects were asked to recall public events or faces of famous people. These tests assessed recent to very remote semantic knowledge. Thus, exposure to these events and people occurred well before the onset of neurological damage. As such, it can be presumed that deficits in performance are due to problems in retrieval rather than encoding. Patients with PFC damage exhibited
recall impairment that was similar across all time periods tested. However, the patients were not impaired on tests of recognition memory, in which they selected the correct answers from several choices. The disproportionate impairment on tests of recall compared to recognition memory suggests that the PFC is involved in controlling the search through semantic memory rather than impairment in the knowledge itself. That is, selecting, updating, and manipulating information in working memory play a significant role in strategic retrieval of information, such as recalling a public event or a famous face. Such retrievals require searching through semantic knowledge, generating relevant information, and disregarding irrelevant information. Recognition memory can be based on a familiarity judgment. That is, on recognition tests it is simply necessary to determine which choice seems most closely related or familiar.

Another example of the distinction between impaired in control of semantic memory and damage to semantic memory itself can be demonstrated in other analyses of recognition versus recall. Consider again the verbal fluency task, in which patients are asked to generate animal names. This task requires recall of information, and patients with PFC damage are impaired. Yet, these patients exhibit intact semantic knowledge of animals when asked to make recognition judgments of animal characteristics. In one study, patients were shown three animal names, such as dog, cow, and pig, and asked to determine which two animals go together. They were told that there were no correct answers and to simply make decisions based on which two go together. The patients exhibited intact semantic memory ability in that they based their decisions on appropriate subcategories of animals, such as associating farm animals (e.g., indicating that cow and pig go together in the example above). In such studies, executive control is minimized by having individuals make simple choice decisions rather than searching, updating, and organizing self-generated retrievals.

Retrieving Autobiographical Memories

Another aspect of memory that requires extensive executive control is the retrieval of autobiographical memory – that is, recollecting an event or experience from the past. The opening exercise of remembering what you had for dinner 3 days ago is an example of retrieving autobiographical memory. Closely related to this form of memory is the notion of source recollection, in which individuals are asked to recollect specific time and place features of an event, such as when an event occurred or who was present during an event. Remembering such information requires executive control in that it is likely that you will have to make a guided analysis to reconstruct an autobiographical memory.

Neuropsychological studies have also demonstrated a prominent role of the PFC in mediating aspects of autobiographical retrieval. Although patients with PFC damage do not exhibit severe amnesia, they are impaired when asked to recollect past experiences. As in the retrieval of semantic knowledge, patients with PFC damage exhibit a particular impairment of recall compared to recognition memory. With respect to source recollection, patients with PFC damage exhibit particular impairment in remembering details of a learning event, such as where and when some information was presented. Such findings are consistent with disorders in memory for the temporal order of events, a common disorder in patients with PFC damage.

In neuroimaging studies, the dIPFC and aPFC are particularly involved in retrieval of autobiographical memory. Studies of autobiographical memory have assessed brain activity during the reminiscence of life experiences, reexperiencing spatial locations in virtual realities, and recognizing photographs taken by oneself or others. Such retrieval tasks have implicated both right and left PFC along with a host of other brain regions, including parietal cortex, medial temporal cortex, and retrosplenial cortex. Similarly, studies of source recollection have shown similar brain activations. In such studies, individuals are asked to recollect features of a learning event, such as the color a stimulus, its spatial location, or its temporal order. In studies of source recollection, left PFC appears to be more active than right PFC.

To the extent that the PFC is involved in the control of autobiographical retrieval – rather than in the actual storage of such information – it is necessary to demonstrate that this kind of retrieval places particular demands on executive control. That is, it must be demonstrated that the selecting, maintaining, updating, and organizing of memory is particularly important for retrieval of details about one’s past experiences. This issue was addressed with a task that facilitated executive control in patients with PFC damage. Individuals were presented objects and were asked to perform an action with each one (e.g., bounce the ball). This manipulation was presumed to increase sensorimotor activation during encoding and thereby increase the distinctiveness of stimuli. Memory for the temporal order of items was assessed by presenting pairs of objects and asking individuals to determine which of the two was presented more recently. Performance by patients with PFC damage did not differ from performance by control subjects on this test. However, the patients exhibited significant impairment on a control task in which they were
presented the objects but did not manipulate them. This benefit appeared to be rather selective to patients with PFC damage because performance by amnesic patients with temporal lobe lesions was not facilitated by the manipulation condition.

A Board of Executives

How can one interpret the role of the PFC in memory processes? As described here, the PFC monitors and controls information processing thus enabling executive or ‘top-down’ control. Top-down control refers to the manner in which thoughts and knowledge control lower levels of analysis. In one view of top-down processing, called metacognitive control, basic processes – such as object recognition, speech analysis, and semantic memory access – are defined as ‘object-level’ processes, which are controlled by ‘meta-level’ processes. Meta-level processes monitor object-level processes, and – as a result of this monitoring – initiate control (see Figure 1). The PFC fits well in this model as it can serve as the meta-level processor to basic processors. It is presumed that top-down control is implemented by reciprocal neural pathways between PFC and posterior regions. Control occurs as a result of selecting and maintaining task-relevant activity (activation) and by filtering irrelevant activity (inhibition).

As suggested by findings presented above, different PFC regions serve different control functions, such as selecting information from the environment, maintaining information in working memory, accessing semantic knowledge, and retrieval. Thus, rather than one executive controller, there appear to be numerous controllers that monitor and control different aspects of information processing. By analogy, one could view the brain as having a board of executives, with each one assigned to a specific function. Executives interact with each other, though each one is responsible for monitoring and controlling a particular part of a business. It is known that different PFC regions are connected to distinct regions in the posterior cortex. By way of these reciprocal interconnections, PFC has the capability of influencing many object-level processes in posterior cortex.

Physiological evidence exists for the role of the PFC in metacognitive control of neural activity. Studies using electroencephalogram (EEG) scalp recordings assess neural activity in response to stimulus presentations. Patients with PFC lesions exhibit abnormal increases in neural response in posterior cortex. Thus, as a result of PFC damage, bottom-up neural signals are disinhibited due to a failure to modulate or control posterior cortical activity. In PET and fMRI studies of normal individuals, increased activity in the dIPFC is often correlated with decreased activity in posterior cortical regions, as if PFC can not only select posterior activity, but it can also suppress irrelevant activity.

In summary, the frontal lobes play a significant role in human memory. Rather than being the storehouse of semantic knowledge or autobiographical memories, the PFC monitors and controls processes associated with accessing, encoding, and retrieving memories. PFC initiates and channels information so that it can be held in working memory and efficiently manipulated or updated. PFC facilitates encoding and organization during learning, and access and recall during retrieval. Without it, thoughts are disorganized, and memories are poorly learned and retrieved. Executive control, top-down processing, and metacognitive control are terms used to describe how PFC monitors and controls information processing. In the service of memory processes, PFC is critical for efficient access to and retrieving from our storehouse of knowledge, as well as adding new knowledge to it. It is as critical for memory as an efficient librarian is for a library.

See also: Cognition: An Overview of Neuroimaging Techniques; Episodic Memory; Executive Function and Higher-Order Cognition: Neuroimaging; Frontal Lobe Syndrome; Memory Representation; Memory Consolidation: Systems; Memory Disorders; Prefrontal Cortex: Structure and Anatomy; Recognition Memory; Semantic Memory; Short Term and Working Memory.

Figure 1  Metacognitive model of executive control. Monitoring of object-level processes is achieved by bottom-up pathways from posterior cortex to PFC. Meta-level processors in the PFC initiate control by top-down pathways to object-level processes. Control of memory is enabled in this model by the role of the PFC in selecting, maintaining, accessing, and retrieving object-level processes for efficient learning and memory.

Further Reading


