REVIEW: NEUROSCIENCE

Storage and Executive Processes in the Frontal Lobes

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The human frontal cortex helps mediate working memory, a system that is used for temporary storage and manipulation of information and that is involved in many higher cognitive functions. Working memory includes two components: short-term storage (on the order of seconds) and executive processes that operate on the contents of storage. Recently, these two components have been investigated in functional neuroimaging studies. Studies of storage indicate that different frontal regions are activated for different kinds of information: storage for verbal materials activates Broca's area and left-hemisphere supplementary and premotor areas; storage of spatial information activates the right-hemisphere premotor cortex; and storage of object information activates other areas of the prefrontal cortex. Two of the fundamental executive processes are selective attention and task management. Both processes activate the anterior cingulate and dorsolateral prefrontal cortex.

The frontal cortex comprises a third of the human brain; it is the structure that enables us to engage in higher cognitive functions such as planning and problem solving (*1*). What are the processes that serve as the building blocks of these higher cognitive functions, and how are these implemented in frontal cortex?

Recent discussions of this issue have focused on working memory, a system used for temporary storage and manipulation of information. The system is divided into two general components: short-term storage and a set of "executive processes." Short-term storage involves active maintenance of a limited amount of information for a matter of seconds; it is a necessary component of many higher cognitive functions (*2*) and is mediated in part by the prefrontal cortex (PFC) (*3*). Executive processes are implemented by PFC as well (*4*). Although executive processes often operate on the contents of short-term storage, the two components of working memory can be dissociated: there are neurological patients who have intact short-term storage but defective executive processes and vice versa (*5*).

We review here neuroimaging studies of these two components of working memory. We consider experiments that have used positron emission tomography (PET) or functional magnetic resonance imaging (fMRI) to image participants while they engage in cognitive tasks that are designed to reveal processes of interest, such as tasks that isolate short-term storage of verbal material. We concentrate on studies in which participants performed an experimental and a control task while being scanned and in which the control task has typically been chosen so that it differs from the experimental task only in a process of interest; a comparison of the experimental and control tasks thus reveals activations due to the process of interest (*6*). These paradigms contrast with standard neuropsychological tasks that may have diagnostic value for patients with frontal cortical lesions but that do not reveal individual cognitive processes.

Storage Processes and the Frontal Lobes

Many neuroimaging studies are founded on Baddeley's (*7*) model of working memory. In part, it posits separate storage buffers for verbal and visual-spatial information. Baddeley further argued that verbal storage can be decomposed into a phonological buffer for short-term maintenance of phonological information and a subvocal rehearsal process that refreshes the contents of the buffer. We examine evidence about each aspect of this model as it relates to frontal cortex.

Verbal storage. Some evidence about storage mechanisms comes from experiments with the item-recognition task (*8*) (Fig. 1A). In most of these studies, a small set of target letters was presented simultaneously, followed by an unfilled delay interval of several seconds, followed by a single-letter probe; the participant's task was to decide whether the probe matched any of the target letters. Compared with a control task, the item-rec-

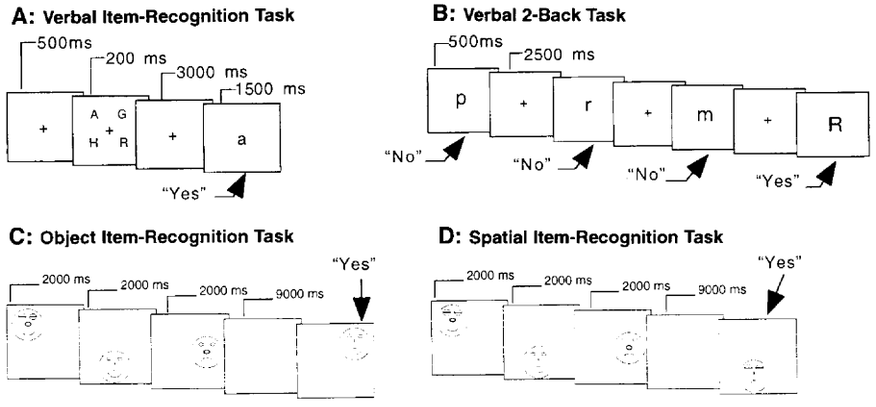

Fig. 1. Schematic representations of four tasks used to study working memory. (**A**) Verbal item-recognition task, which taps mainly short-term storage for verbal information. A trial includes (i) fixation point, (ii) four uppercase letters, (iii) blank delay interval, and (iv) a lowercase probe letter. The participant's task is to decide whether the probe names one of four target letters. (**B**) Verbal 2-back task, which presumably involves executive processes (temporal coding) as well as storage of verbal material. Each letter is followed by a blank delay interval, and the participant's task is to decide whether each letter has the same name as the one that occurred two back in the sequence. (**C**) Object item-recognition task, which taps short-term storage for object information. A trial includes (i) a sequence of three target faces, (ii) a blank delay interval, and (iii) a probe face. The participant's task is to decide whether the probe face is the same as any of the target faces. (**D**) Spatial item-recognition task, which taps short-term storage for spatial information. A trial includes the same events as in the object task, but the participant's task is to decide whether the probe face is in the same location as any of the target faces.

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ognition task results in activations in left posterior parietal cortex [Brodmann's area (BA) 40] and three frontal sites[Broca's area (BA 44) and left supplementary motor and premotor areas (BA 6)]. (The latter three areas, along with other important frontal areas and divisions, are presented schematically in Fig. 2.) Given that these frontal areas are known to be involved in the preparation of speech (*9*) and that participants rehearse the targets silently during the delay, the frontal speech areas likely mediate subvocal rehearsal of the targets. As evidence for this claim, the activation in Broca's area closely matches that obtained in an explicitly phonological task, rhyme judgments (*10*). [Evidence from neurological patients suggests that the posterior parietal region mediates a storage buffer (*11, 12*).]

Further evidence for localizing rehearsal in the frontal speech areas comes from a PET study that used a "2-back" task (*13*) (see Fig. 1B). Participants viewed a sequence of single letters separated by 2.5 s each; for each letter they had to decide whether it was identical in name to the letter that appeared two items back in the sequence. The experiment used two different controls. In one, participants saw a sequence of letters but simply had to decide whether each letter matched a single target letter. Subtracting this control from the 2-back condition yielded many of the areas of activation that have been obtained in item-recognition tasks, including the left frontal speech regions and the parietal area. The second control required participants to rehearse each letter silently. Subtracting this rehearsal control from the 2-back task should have removed much of the rehearsal circuitry since rehearsal is needed in both tasks; indeed, in this subtraction, neither Broca's area nor the premotor area remained active. Hence, this experiment isolated a frontal rehearsal circuit.

Several other PET and fMRI studies have used 2-back and 3-back tasks. All have found activation in Broca's area and the premotor cortex (*14, 15*). In addition, two studies have used a free-recall paradigm to study short-term storage, and they also found activation in frontal speech regions (*16*). Thus, frontal regions that no doubt evolved for the purpose of spoken language appear to be recruited to keep verbal information active in working memory.

Figure 3 summarizes the relevant results; Fig. 3A shows data from item-recognition tasks, which require mainly storage, whereas Fig. 3B shows data from *n*-back tasks and free-recall tasks, which presumably require executive processes as well as storage. In Fig. 3A, in the sagittal view, the activations cluster posteriorly in the frontal lobes—running from the premotor and supplementary motor area (SMA) ventrally to Broca's area; this is the rehearsal circuit. In the coronal and axial views of Fig. 3A, the activation foci show a left lateral tendency; indeed, the mean x coordinate is significantly less than zero [$t(31) = -2.9$; $P < 0.01$], indicating a center of mass in the left hemisphere. The lateralization pattern changes when nonstorage processes are added to the task. In the axial and coronal projections of Fig. 3B, the activation foci were bilateral, not left-lateralized. Furthermore, in addition to the clusters in premotor and SMA, Broca's, and posterior parietal lobe, these tasks also produce a cluster in dorsolateral prefrontal cortex (DLPFC), as shown in the sagittal view of Fig. 3B. In fact, the mean y coordinate of frontal activations ($y > 0.25$) in Fig. 3B is significantly anterior to that in Fig. 3A [$t(79,52) = 4.18$; $P < 0.001$]. These activations therefore reflect the distinction between tasks requiring mainly storage and those requiring additional processing.

Spatial and object storage. Research on nonverbal working memory has been influenced by physiological work with nonhuman primates (*3*). Single-cell recordings made while monkeys engage in spatial-storage tasks have found "spatial memory" cells in DLPFC (which is usually taken to include BA 46 and 9). These cells selectively fire during a delay period and are position specific. Recordings made while monkeys engage in object-storage tasks have found delay-sensitive "object memory" cells in a more ventral region of PFC that are object specific (*17*). The implications of these findings are that (i) spatial and object working memory have different neural bases, and (ii) at least part of the circuitry for these two types of memory is in PFC, with spatial information being represented more dorsally than object information (*18*).

Neuroimaging evidence supports a distinction between human spatial and object working memory as well (*19–21*). In one paradigm used to demonstrate the distinction, three target faces were presented sequentially in three different locations, followed by a probe face in a variable location. In the object working-memory task (see Fig. 1C), participants decided whether the probe matched any of the three targets in identity; in the spatial task (see Fig. 1D), they decided whether the probe matched any of the targets in position. The object task activated regions in the right DLPFC whereas the spatial task activated a region in the right premotor cortex. Follow-up studies have shown that the region in DLPFC remains active during a delay period in the object task, whereas the premotor area remains active during a delay in the spatial task, thus strengthening the case that the two areas mediate separate kinds of storage (*22, 23*).

Figure 4 summarizes the relevant results. The sagittal and coronal projections reveal a dorsal-ventral difference between spatial and object working-memory tasks, respectively, particularly in posterior cortex. For posterior cortex ($y > -25$), the average z coordinate of the spatial-memory

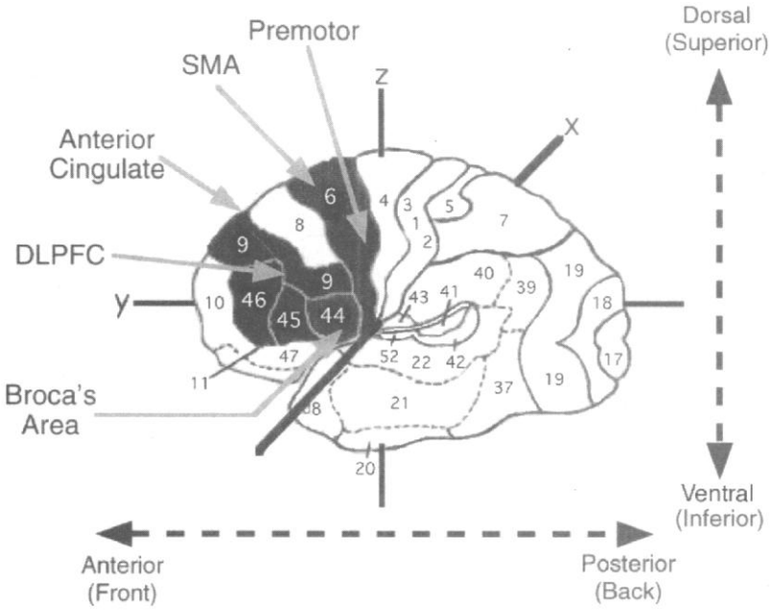

Fig. 2. Schematic of the left lateral cortex, displaying major prefrontal areas (numbers correspond to Brodmann areas). The areas of greatest interest are shaded, and they include Broca's area, DLPFC, the anterior cingulate (not visible in the schematic, as it lies on the medial side of the cortex), SMA, and premotor. Also shown are the x, y, and z dimensions, which are used to report the coordinates of activations (where the three dimensions intersect, all coordinates are zero). In addition, anterior-posterior and dorsal-ventral directions, which are used in anatomical descriptions, are indicated.

activation foci was significantly greater (more dorsal) than that of object-memory activation foci [$t(41,45) = 9.87$; $P < 0.001$]. The anterior cortex ($y > -25$) also shows a significant dorsal-ventral difference [$t(37,47) = 3.24$; $P < 0.004$]. Specifically, spatial working-memory activations seem to cluster primarily in the premotor area, whereas object working-memory activations spread from premotor to DLPFC.

Although the dorsal-ventral difference is in line with the results from monkeys, there are two findings from spatial tasks that differ from the results obtained with monkeys: the presence of activation in premotor cortex and the failure to consistently find activation in DLPFC. The first finding has considerable support, as spatial tasks routinely activate the right premotor area (*24*). Perhaps the true functional homologue of DLPFC in monkeys is the premotor region in humans (*25*), or perhaps the major site of spatial working-memory in monkeys is more posterior than was originally believed (*18*). The issue remains unresolved.

Can the activations obtained in the spatial tasks be divided into storage and rehearsal functions, parallel to verbal working memory? One possibility is that the right premotor activation is a reflection of spatial rehearsal. By this account, spatial rehearsal involves covertly shifting attention from location to location, and doing so requires recruitment of an attentional circuit, including premotor cortex (*26*). Support for this account comes from the fact that neuroimaging results from studies of spatial working memory and spatial attention show overlap in activation in a right premotor site (*27*).

Implications. The research reviewed and the meta-analyses presented in Figs. 3 and 4 are relevant to two major proposals about the organization of PFC. One is that PFC is organized by the modality of the information stored; for example, spatial information is represented more dorsally than object information (*17*). The second proposal is that PFC is organized by process, with ventrolateral regions (BA 45 and 47) mediating operations needed to sustain storage and dorsolateral regions (BA 46 and 9) implementing the active manipulation of information held in storage [see references in (*28*)]. Our review provides support for both organizational principles. Relevant to the first, we have noted that verbal storage tasks activate left-hemisphere speech areas, spatial storage activates the right premotor cortex, and object storage activates more ventral regions of PFC (as shown in Fig. 4). Relevant to the second, verbal tasks that require only storage lead primarily to activations that typically do not extend into DLPFC, whereas verbal tasks that require executive processes as well as storage lead to activations that include DLPFC (Fig. 3) (*28*).

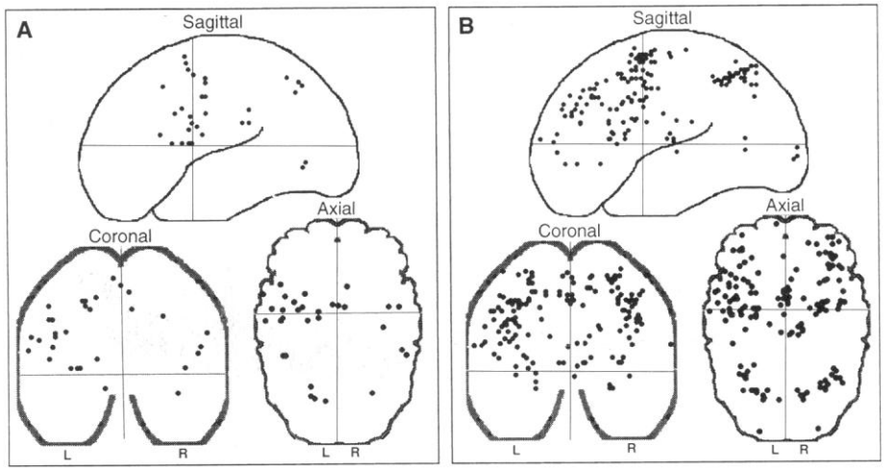

Fig. 3. Neuroimaging results for verbal working memory are summarized by sets of three projections, with each containing points and axes conforming to standard Talairach space (*40*). Each projection collapses one plane of view for each activation focus—that is, the sagittal view collapses across the *x* plane as though one were looking through the brain from the side; the coronal view collapses across the *y* plane as though one were looking through the brain from the front or back; and the axial view collapses across the *z* plane as though one were looking through the brain from the top. Included in the summary are published ^{15}O PET or fMRI studies of verbal working memory that reported coordinates of activation and had a memory load of six or fewer items. (Cerebellar activation foci, not shown, were predominantly in the right hemisphere, which is consistent with the crossed connections of cerebellum and cerebrum.) (**A**) Activation foci from studies that involve mainly storage. Awh *et al.* (*13*), item recognition; Jonides *et al.* (*15*), 0- and 1-back; Jonides *et al.* (*33*), item recognition; Paulesu *et al.* (*10*), item recognition. (**B**) Activation foci from studies that require executive processing as well as storage. Awh *et al.* (*13*), 2-back; Braver *et al.* (*15*), 2- and 3-back; Cohen *et al.* (*14*), 2-back; Cohen *et al.* (*15*), 2- and 3-back; D'Esposito *et al.* (*28*), 2-back; Fiez *et al.* (*16*), free recall; Jonides *et al.* (*15*), 2- and 3-back; Jonides *et al.* (*16*), free recall; Schumacher *et al.* (*15*), 3-back; Smith *et al.* (*15*), 3-back.

Executive Processes and Frontal Cortex

Most researchers concur that executive processes are mediated by PFC and are involved in the regulation of processes operating on the contents of working memory. Although there is lack of consensus about a taxonomy of executive processes, there is some agreement that they include (i) focusing attention on relevant information and processes and inhibiting irrelevant ones ("attention and inhibition"); (ii) scheduling processes in complex tasks, which requires the switching of focused attention between tasks ("task management"); (iii) planning a sequence of subtasks to accomplish some goal ("planning"); (iv) updating and checking the contents of working memory to determine the next step in a sequential task ("monitoring"); and (v) coding representations in working memory for time and place of appearance ("coding"). Tasks manifesting each of these executive processes are known to be selectively impaired in patients with prefrontal damage (*4*). Of the five executive processes noted, the first two appear to be the most elementary and the most interrelated; for these reasons, we focus on attention and inhibition and task management.

Attention and inhibition. A paradigmatic case of attention and inhibition is the Stroop test (*29*). Participants are presented a set of color names printed in different colors and asked to report the print colors; performance is poorer when the print color differs from the color name than when it is the same (it takes longer to say blue to the word red printed in blue than to the word blue printed in blue). The effect arises because two processes are in conflict: a prepotent one that automatically names the word and a weaker but task-relevant process that names the print color. Successful performance requires focusing attention on the task-relevant process and inhibiting the task-irrelevant one (*30*). More generally, the executive process of attention and inhibition is recruited whenever two processes are in conflict.

PET studies of the Stroop test show substantial variation in regions of activation, although one broad region is the anterior one-third of cingulate cortex (*31*). Activations in the anterior cingulate have been obtained in other experiments that induce a conflict between processes or response tendencies as well (*32*). These studies suggest that the anterior cingulate may be involved in the resolution of cognitive conflict.

If executive processes are indeed distinct from short-term storage, it should be possible to add attention and inhibition to a short-term storage task. Two recent studies have attempted to do this by introducing conflict into the verbal

item-recognition task (again, see Fig. 1A) (*33, 34*). These studies included trials in which distractor probes—probes that were not in the memory set—were familiar, thereby putting into competition a decision based on familiarity and one based on the target items being coded as "current targets." Conflict led to activation in the left lateral prefrontal cortex, however, not the anterior cingulate.

Why are different areas of activation found in studies of attention and inhibition? One possibility is that the anterior-cingulate region mediates the inhibition of preprogrammed responses. Incorrect responses may often be preprogrammed in tasks such as Stroop's but not in the item-recognition task; hence, only the former would recruit the cingulate region. By contrast, the frontal site activated in studies of item-recognition may reflect operation of attention and inhibition earlier in the processing sequence. This interpretation is consistent with an fMRI study in which participants were led to prepare a response to an expected probe but on occasional trials had to respond differently to an unexpected probe and hence had to inhibit the prepared response (*35*). Statistical techniques were used to isolate trials that should have involved response inhibition; analyses of these trials revealed activations in the anterior cingulate, not in prefrontal cortex (*36, 37*).

Task management. A canonical case of task management arises when participants are presented with dual tasks. For example, they might be presented a series of numbers and have to add three to the first number, subtract three from the second, and so on through successive trials (*38*). Both tasks require some nonautomatic or "controlled" processes, and a critical aspect of task management is switching from one controlled process to another.

An fMRI study has examined dual-task performance (*39*). In one task, participants had to decide whether each word presented in a series named an instance of the category Vegetable; in the other task, participants had to decide whether two visual displays differed only by a matter of rotation; in the dual-task condition, participants performed the categorization and rotation tasks concurrently. Only the dual-task condition activated frontal areas, including DLPFC (BA 46) and the anterior cingulate. The frontal areas overlap those found in attention and inhibition tasks, but in this case the anterior cingulate does not dominate the picture. The commonality of results should be expected if a critical component of scheduling is management of the same attentional process that is involved in attention and inhibition tasks.

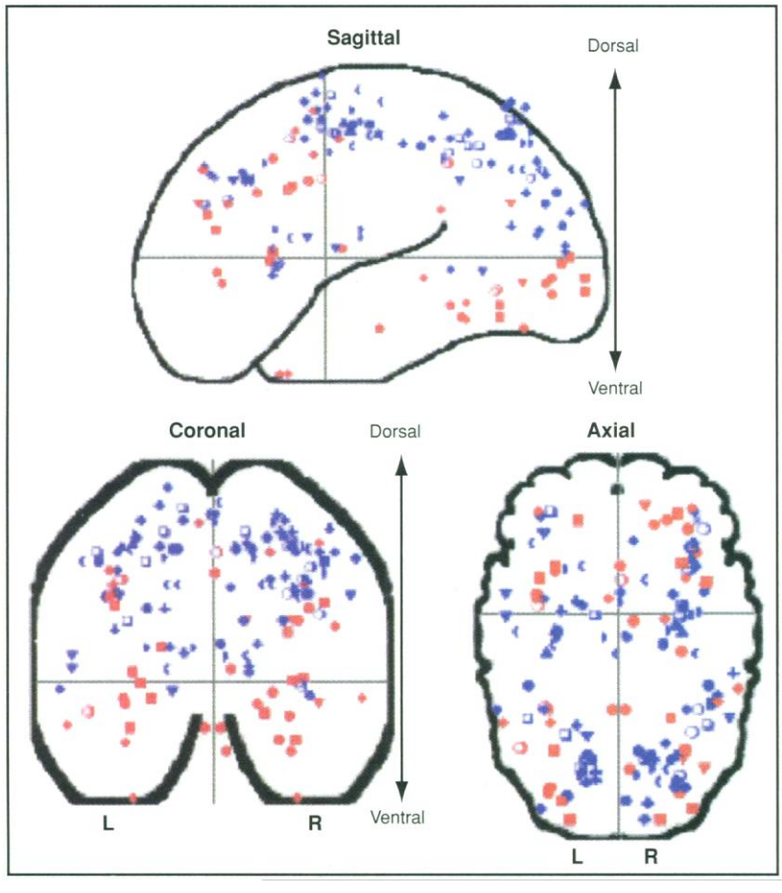

Fig. 4. Neuroimaging results for spatial (blue) and object (red) working memory are summarized on three projections, with each containing points and axes conforming to standard Talairach space (*40*) (see Fig. 3 legend). Included in the summary are published ^{15}O PET or fMRI studies of spatial or object working memory that reported coordinates of activation. Courtney *et al.* (*19*) (●): item recognition (faces), item recognition (locations); Courtney *et al.* (*22*) (■): item recognition (faces); Courtney *et al.* (*23*) (▲): item recognition (faces), item recognition (locations); D'Esposito *et al.* (*28*) (◗): 2-back (locations); Faillenot *et al.* (*21*) (▼): item recognition (objects), item recognition (orientation); Jonides *et al.* (*24*) (▮): item recognition (locations); McCarthy *et al.* (*19*) (✳): item recognition (locations); Owen *et al.* (*20*) (◆): item recognition (locations), spatial span; Owen *et al.* (*21*) (✙): *n*-back (locations), *n*-back (objects); Smith *et al.* (*19*) (❑): item recognition (locations), item recognition (objects); Smith *et al.* (*15*) (○): 2-back (locations); Sweeney *et al.* (*41*) (❰): memory guided saccades (locations).

Concluding Remarks

Neuroimaging studies of humans show that storage and executive processes are major functions of the frontal cortex. The distinction between short-term storage and executive processes appears to be a major organizational principle of PFC. With regard to storage, the PFC areas most consistently activated show modality specificity (verbal versus spatial versus object information), and generally they appear to mediate rehearsal processes, at least for verbal and spatial information. Neuroimaging analyses of executive processes are quite recent, and they have yet to lead to clear dissociations between processes. Perhaps the highest priority, then, is to turn further attention to executive processes and their implementation in frontal cortex.

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