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) (figure 27.1a). 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-recognition task results in activations in left posterior parietal cortex (Brodman’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 figure 27.2). 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 figure 27.1b). 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 27.3 summarizes the relevant results; figure 27.3a shows data from item-recognition tasks, which require mainly storage, whereas figure 27.3b shows data from n-back tasks and free-recall tasks, which presumably require executive processes as well as storage. In figure 27.3a, in the sagittal view, the activations cluster posteriorly in the frontal lobes—running from the pre-motor and supplementary motor area (SMA) ventrally to Broca’s area; this is the rehearsal circuit. In the coronal and axial views of figure 27.3a, 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 figure 27.3b, the activation foci were bilateral, not left-lateralized. Furthermore, in addition to the clusters in pre-motor and SMA, Broca’s, and posterior parietal lobe, these tasks also produce a cluster in dorso-lateral prefrontal cortex (DLPFC), as shown in the sagittal view of figure 27.3b. In fact, the mean y coordinate of frontal activations ($y > 0.25$) in figure 27.3b is significantly anterior to that in figure 27.3a ($t(79, 52) = 4.18; P < 0.001$). These activations therefore reflect the distinction between tasks requiring mainly storage and those requiring additional processing.
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.
Spatial and Object Storage

Research on nonverbal working memory has been influenced by physiological work with non-human 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 figure 27.1c), participants decided whether the probe matched any of the three targets in identity; in the spatial task (see figure 27.1d), 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 27.4 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 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 figures 27.3 and 27.4 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,
Figure 27.4
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 figure 27.3 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).
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 figure 27.4). 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 (figure 27.3) (28).

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 figure 27.1a) (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 ante-
rior cingulate.

Why are different areas of activation found
in studies of attention and inhibition? One pos-
sibility is that the anterior-cingulate region
mediates the inhibition of preprogrammed re-
sponses. Incorrect responses may often be pre-
programmed 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 acti-
vations in the anterior cingulate, not in pre-
frontal 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” pro-
cesses, and a critical aspect of task management
is switching from one controlled process to
another.

An fMRI study has examined dual-task per-
formance (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
communality 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.

Concluding Remarks

Neuroimaging studies of humans show that
storage and executive processes are major func-
tions of the frontal cortex. The distinction be-
tween 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 spe-
cificity (verbal versus spatial versus object infor-
mation), and generally they appear to mediate
rehearsal processes, at least for verbal and spa-
tial information. Neuroimaging analyses of ex-
ecutive processes are quite recent, and they have
yet to lead to clear dissociations between pro-
cesses. Perhaps the highest priority, then, is to
turn further attention to executive processes and
their implementation in frontal cortex.

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References and Notes

1. A. R. Luria, Higher Cortical Functions in Man
97, 404 (1990).


12. None of the cited item-recognition studies found activation in DLPFC. However, a recent item-recognition experiment found DLPFC activation with a memory load of six items compared with three items, which suggests a role for DLPFC with larger memory loads (B. Rypma, V. Prabhakaran, J. E. Desmond, *Neuroimage* 9, 2 (1999). Follow-up work suggests that the role of DLPFC in this task is to mediate executive processes during encoding of the larger loads (M. D’Esposito, personal communication).


18. There is currently some controversy about the degree of separation of object and spatial regions in PFC in nonhuman primates. Recent findings indicate that dorsal or ventral regions can contain neurons that process either spatial or object information or both (S. C. Rao, G. Rainer, E. K. Miller, *Science* 276, 821 (1997); G. Rainer, W. F. Asaad, E. K. Miller, *Proc. Natl. Acad. Sci. U.S.A.* 95, 15008 (1998)). However, even these studies find some neural segregation—a sizable proportion of neurons tested by Rainer et al. are selective only for location, and these neurons predominate in posterior locations.


28. Two other recent meta-analyses of neuroimaging studies of working memory also found evidence that PFC is organized by storage versus executive processes (M. D’Esposito et al., *Cogn. Brain Res.* 7, 1 (1998); A. M. Owen, *Eur. J. Neurosci.* 9, 1329 (1997)). However, neither of these meta-analyses found evidence that PFC was organized by modality. There are at least two reasons for this discrepancy from the present analyses. Neither of the previous meta-analyses focused on ver-
bal storage or included recent fMRI studies that isolate delay-period activity and that provide relatively strong evidence for a difference between spatial and object storage (22, 23).

36. The anterior cingulate is also activated in tasks that do not involve response inhibition, indicating that the cingulate serves multiple functions. (R. D. Badgaiyan and M. I. Posner, Neuroimage 7, 255 (1998); P. J. Whalen et al., Biol. Psychiatry 44, 1219 (1998)).
37. Attention and inhibition may also be involved in self-ordering tasks, such as the following: on each series of trials, a set of forms is presented in random positions, and participants must point to a form they have not selected on a previous trial in that series. This task activates the anterior cingulate and DLPFC, similar to tasks that involve attention and inhibition (M. Petrides, B. Alivisatos, A. C. Evans, Proc. Natl. Acad. Sci. U.S.A. 90, 873 (1993)). Some researchers have proposed that self-ordering tasks reflect the executive process of monitoring, but alternatively they may involve an appreciable working memory load and some inhibition, either of which may cause the frontal activations.