

Todd S. Braver and Hannes Ruge

Introduction

For humans, the most prized of all our mental faculties is likely our capability for directing our thoughts and actions in accordance with internal goals, and for flexibly readjusting these goals when necessary. The term “executive function” is typically used to describe these regulatory and goal-directed components of cognition. However, the term itself, with its implicit reference to a hidden homunculus, indicates the difficulty of understanding how such executive functions might arise in the brain. Thus, a fundamental challenge for cognitive neuroscience is to determine the underlying representations, computations, and neural specializations that enable cognition and action to appear coordinated, purposeful, and self-regulatory. Cognitive neuroscience investigations of executive functions have accelerated in an amazingly rapid fashion within the last decade, due in large part to the development of sophisticated neuroimaging methods for noninvasively monitoring human brain activity. Indeed, a striking example of this accelerating growth is the observation that studies of executive processes are currently one of the largest components of the cognitive neuroimaging literature, yet in the previous edition of this book (published in 2001) there was no chapter devoted to executive function as a distinct area.

Although neuroimaging contributions to executive control research have only been very recent, there has been a long tradition of study in this area within neuropsychology, behavioral neuroscience, and cognitive science. Neuropsychological research has focused attention on the critical role of the frontal lobes in self-regulatory behavior, starting from the earliest case studies of individuals such as Phineas Gage (e.g., Harlow, 1848; Macmillan, 2000), to the more focused and systematic reports of Luria (1966). Starting with the seminal work of Milner (1963),

experimental neuropsychology investigations have been instrumental in developing task paradigms that provide sensitive and objective probes for assessing executive function and its relationship to underlying brain areas. For example, studies with the Wisconsin Card Sort Task (WCST) indicated that frontal patients were more likely than other brain-damaged groups to show "perseverative" type behavior, staying with an old card-sorting rule even after repeated feedback that the rule was no longer correct. In addition, the experimental neuropsychology literature has contributed a number of other tasks for studying executive functions developed in the context of work with brain-damaged populations. These include tests of verbal fluency, planning (the Tower of London), attention switching (Trail Making), inhibition (go-no go), and sustained/selective attention (continuous performance test).

In parallel with the human neuropsychological research, behavioral neuroscience studies have provided strong confirmation and elaboration of the importance of the prefrontal cortex (PFC) in executive control. Early studies demonstrated fairly convincingly that frontal lesions markedly increased distractibility in delayed-response tasks (which require holding a reward-eliciting behavior in check for a short period of time following presentation of an environmental cue) by impairing the ability to maintain goal-relevant information or context in mind even when such information is no longer perceptually available (e.g., Jacobsen, 1935). Later electrophysiological studies in awake behaving monkeys showed that during such delayed-response tasks, prefrontal neurons showed stimulus-specific increases in activity that were sustained throughout the delay interval and correlated with correct performance (Fuster, 1989; Goldman-Rakic, 1987). These studies have been of critical importance for establishing the role of PFC in active maintenance functions, and in specifying the representational and dynamic properties of this brain region. More recent work has emphasized how these properties of PFC might subservise cognitive control functions by representing rule-like information, enabling the learning of temporal associations between stimuli and response, filtering perceptual information in accordance with task goals, and exerting a top-down bias on action and perceptual systems (E. K. Miller & Cohen, 2001).

These types of neuropsychological and neurophysiological findings influenced the development of general theoretical models of cognition, starting with early work on planning (G. A. Miller et al., 1960) and progressing to more recent computational cognitive architectures (Anderson, 1983; Meyer & Kieras, 1997; Newell, 1990). In these models, a central role was given to a working memory structure where goal-related representations could be temporarily activated to bias sequences of thought and action. Ideas regarding the top-down biasing effects of goal information on action selection were more firmly crystallized in the supervisory attentional system (SAS) theory of Norman and Shallice (1986), which specified a control mechanism

selectively invoked when automatic stimulus-response sequences are inappropriate or inadequate for completing actions in a goal-compatible fashion.

The SAS theory explicitly suggested that this control structure was located in the frontal lobes, and further specified the types of tasks situations most dependent upon frontal integrity: (a) when the task requires that a habitual response be suppressed; (b) when the task is novel and unpracticed; (c) when the task is dangerous or technically difficult; (d) when planning is required; and (e) when errors need to be monitored or corrected. Consequently, the SAS model has been very influential in guiding modern cognitive neuroscience investigations regarding the decomposition of different executive functions, as described below. Similarly, the SAS account has influenced more neuroscience-based theoretical models of control. For example, the models of Cohen and colleagues show how active maintenance of goal-like representations can occur in PFC via local recurrent connectivity, and how simple feedback connections allow these PFC representations to serve as a top-down bias on local competitive interactions within direct task pathways, thus achieving a simple form of control in cognitive tasks such as the Stroop (Cohen et al., 1996; Cohen et al., 1990).

Notions of executive function have also strongly influenced more domain-specific cognitive theories, in particular theories of memory. The classic information-processing theory of Atkinson and Shiffrin (1971) suggested that control processes play a significant role in how information gets into and out of the short-term and long-term stores, via modulation of encoding, rehearsal, decision, and retrieval strategies. This basic idea has been elaborated in more recent theories postulating that PFC may serve as this control interface, "working with memory" by strategically filtering retrieved content (Moscovitch, 1992; Shimamura, 1995, 2000).

Baddeley, in his influential model of working memory (WM), reinterpreted the Atkinson and Shiffrin view of short-term memory by suggesting that (a) short-term storage occurs in qualitatively distinct buffers for verbal (the phonological loop) and visuospatial (the visuospatial scratch pad) information, and (b) that these buffers serve as a "mental blackboard" for complex cognition (Baddeley, 1986). Critically, the Baddeley model cast a specific role for a "central executive" that appropriately utilized the stored information in the service of task-related processing. Baddeley's structurally based account provided a strong impetus for cognitive neuroscience-based research programs aimed at dissociating storage and control functions within WM in terms of their underlying neural substrates (D'Esposito et al., 1998; Smith & Jonides, 1999).

Nevertheless, a limitation of the Baddeley model, repeatedly acknowledged by Baddeley himself, is that the theory did not clearly specify what constituted an executive function within WM. Thus, it has not been clear whether the central

executive referred to a single, monolithic mechanism or to a collection of distinct subprocesses subserved by multiple separate mechanisms. This major gap in theorizing regarding executive control has begun to be remedied (Baddeley, 1996). However, there is still no consensus as to exactly what are the functions that should be termed "executive," and how many distinct functions there are (Miyake et al., 2000).

The lack of conceptual clarity regarding the components of executive control is especially noticeable when surveying the large and ever-growing neuroimaging literature in this domain. Thus, there is some ambiguity as to how to structure a review of the literature in a chapter such as this one. In the following section, we have decided to organize the literature into categories according to what seem to be natural groupings of studies and tasks, rather than arguing for strict conceptual divisions.

Functional Neuroimaging Studies of Executive Functions

Given the vastness of the literature, it is beyond the scope of this chapter to provide an exhaustive review of all neuroimaging studies of executive function. Rather, in this section we hope to provide a road map or overview of the existing literature, pointing out the emerging trends and themes in different subareas, and thus provide a starting point for further study. Likewise, because of the very nature of executive functions, neuroimaging studies in this domain have a strong overlap with many others, especially WM, episodic memory, attention, and emotion. Since these other domains are the focus of different chapters, we will restrict our coverage to studies that are explicitly targeted toward examining the interaction of executive control with domain-specific processes. Finally, given the focus in the literature on the frontal lobes as the critical neural substrate of executive control, we will pay special attention to PFC-relevant findings. However, it should go without saying that a full understanding of executive function will likely involve a network of multiple interacting brain systems, of which the PFC is just one component.

Below, we review seven distinct categories of executive function that have been examined in the neuroimaging literature. These categories are summarized in table 10.1, which provides an organizing structure regarding the nomenclature we have adopted for each category and the associated task paradigms discussed.

Strategic Control of Memory

As mentioned above, much of the attention given to executive functions in cognitive psychology and neuroscience has emerged from the memory literature. Thus, many of the earliest neuroimaging studies focusing on executive control functions and PFC occurred in the context of examining WM and episodic memory tasks. Moreover,

Table 10.1
Executive functions and associated tasks

Category	Tasks Reviewed
Strategic control of memory	source memory, prospective memory, recency memory, tip-of-the-tongue (TOT), divided-attention encoding, manipulation and updating in WM, "recent negative" Sternberg, n-back (+lures)
Stimulus-response interference	Stroop, Eriksen, Simon
Response inhibition	go nogo, stop signal, antisaccade
Underdetermined responding	verb generation, random number generation, manual "free selection" tasks
Performance monitoring	WCST, error-processing tasks, reward/penalty feedback tasks
Task management	task switching, dual-task coordination, psychological refractory period (PRP)
Higher cognition	Tower of London (ToL), Raven's Progressive Matrices (RPM), logical reasoning tasks, integration tasks

in recent years there has been a growing appreciation of the notion that many putative WM or episodic memory tasks actually more strongly tap into executive processes (for review, see Fletcher & Henson, 2001). Thus, in the n-back, a now standard WM task in the neuroimaging literature, the activation of lateral PFC regions is thought by many investigators to reflect executive operations on stored information rather than active maintenance processes per se (Smith & Jonides, 1999; Veltman et al., 2003). Likewise, the activation of anterior PFC regions (BA 10) that is so commonly observed in episodic retrieval tasks, is now thought to reflect control operations acting to structure how retrieval occurs, via engagement of a sustained retrieval mode (Duzel et al., 2001; Lepage et al., 2000; Velanova et al., 2003) or through transient activation of postretrieval monitoring and decision processes (Ranganath et al., 2000).

Neuroimaging studies of memory have also broadened considerably, and now a significant subset of these studies are explicitly focused on elucidating the role of control processes within different memory domains. In particular, there are now neuroimaging studies focused on memory tasks that are thought to predominantly tap into the strategic control of mnemonic processes, such as recency memory (determining which of two items was more recently encountered), source memory (determining the specific context, such as where or when an item was encountered), and prospective memory (retrieving previously encoded action goals at a specific time or when a specific event occurs).

These studies have confirmed the basic assumption that PFC is engaged to subservise such strategic processes, but have also provided more detailed information. For example, source memory tasks appear to engage anterior PFC regions,

suggesting a specific role for a retrieval mode or postretrieval processes establishing recollection (e.g., Dobbins et al., 2003). Similar observations have been made regarding prospective memory (Burgess et al., 2003). In contrast, recency memory may involve only dorsolateral PFC regions, particularly within the right hemisphere (Dobbins et al., 2003; Konishi et al., 2002). Another interesting study examined executive control in semantic memory, focusing on the so-called tip-of-the-tongue (TOT) phenomenon, when facts that are familiar and known cannot be appropriately retrieved. In this study (Maril et al., 2001), TOT events were associated with a distinct pattern of brain activity, involving activation within dorsolateral PFC and anterior cingulate cortex (ACC), that was interpreted as a sign of the cognitive conflict elicited in such situations, and the need to resolve it (see "Stimulus-Response Interference" and "Performance Monitoring," below).

Other memory studies have focused on how changes in the encoding context influence the demands on control processes. For example, dividing attention during intentional encoding (typically by adding a secondary task requirement) reduces the activity within lateral PFC regions, and also impairs memory performance (Iidaka et al., 2000; Kensinger et al., 2003). This suggests that PFC control processes are an important component of how encoding occurs. For verbal stimuli, PFC-mediated control may be especially critical for enabling elaborative phonological and semantic processing, which have a strong impact on encoding and later memory. This idea has been suggested by findings in which item-level activity in lateral PFC (particularly in the left hemisphere) during encoding tasks involving elaborative phonological or semantic processing is correlated with later memory performance (Wagner et al., 1998). Interestingly, these left frontal regions may be involved not only in controlling how each item is encoded but also in instantiating and updating the relevant task or instructional context when needed (see "Task Management," below).

In a study by Reynolds et al. (2004) testing this hypothesis, trial-by-trial switching of encoding contexts (i.e., two different semantic classification tasks) led to increased activity in left lateral PFC, but this activity appeared to reduce the activation available to support elaborative item-level processes that are associated with successful encoding. Thus, a consensus appears to be emerging that left lateral PFC, particularly in inferior regions, is critical for enabling controlled access to task-relevant phonological and semantic representations of verbal stimuli, especially in situations where such task-relevant representations are not automatically evoked by the stimulus (Fletcher et al., 2000; Thompson-Schill et al., 1997; Wagner et al., 2001). Moreover, there has been quite a bit of research consistent with the idea that left inferior PFC is subdivided into posterior and anterior portions that are selectively involved in controlling access to phonological and semantic representations, respectively (e.g., Poldrack et al., 1999).

Within the domain of WM, much attention has been directed toward the role of executive processes in “manipulating” actively maintained information in accordance with task demands. Thus, in studies conducted by D’Esposito and colleagues, verbal WM conditions involving manipulation (e.g., alphabetic reordering of verbal materials) appear to engage dorsolateral PFC regions more than tasks involving simple maintenance (e.g., Postle et al., 1999). Similar results have been observed in studies examining manipulation in spatial WM (e.g., vertical flipping of stored spatial locations; Glahn et al., 2002). However, it has been notoriously difficult to demonstrate this dissociation in an unambiguous fashion, especially when considering confounds such as task difficulty (e.g., Veltman et al., 2003). This may be partly due to the problems of defining exactly what constitutes manipulation, in mechanistic terms, and of determining whether generic manipulation processes exist (rather than having special-purpose mechanisms devoted to different types of manipulation).

A similar issue examined in the literature is whether WM updating—deactivating previously stored information to enable new information to gain access to storage—represents a unique executive process specialized brain region (Collette & Van der Linden, 2002). One way this issue has been investigated is through a focus on the dynamics of brain activity, since active maintenance processes are likely to be sustained throughout the storage interval, while updating processes should be engaged only transiently. A study of the *n*-back task supported this dissociation, with dorsolateral PFC regions showing sustained activity and WM load-sensitive activity, while inferior PFC regions showed transient activity (Cohen et al., 1997). Similarly, a study comparing the *n*-back task and the WCST task found that these same inferior PFC regions were also transiently engaged in the WCST when the card-sorting rule had to be updated (Konishi et al., 1999).

Other work has suggested that the inferior PFC activity may not reflect updating *per se*, but a more generic inhibitory process operating on WM contents. A task paradigm that has been gaining rapid popularity for investigating this issue is the “recent negative” variant of the Sternberg item recognition task (e.g., Jonides et al., 1998). In this task, recognition probes on some trials are “recent negatives,” which indicate an item that was not part of the memory set maintained in WM for the current trial, but was part of the memory set from the previous trial. On “recent negative” trials, successful responding requires both a strong WM trace of the current trial memory set and inhibition of the misleading familiarity cues evoked by the probe. In a series of neuroimaging studies of with the “recent negative” Sternberg task, Jonides and colleagues observed that “recent negative” trials were selectively associated with activation in the left inferior PFC region associated with updating in the *n*-back task (Brodmann’s area 45), with activation occurring following probe onset (Jonides et al., 2002). This result seems to suggest that “recent negative” probes elicit transient inhibitory (or interference resolution; see

“Stimulus-Response Interference,” below) processes to allow WM content to compete more effectively with probe-evoked (but misleading) familiarity traces. However, a study by Bunge et al. (2001) found that “recent negative” effects were associated with increased activity in the same (wider set of) brain regions showing sensitivity to WM load. This finding suggests a more complex interpretation of the relationship between WM maintenance and probe-related interference.

More recent studies of the n-back task may also support the notion that interference resolution is an important component of task performance. In a study by Gray et al. (2003), analyses focused on “lure” trials, in which the item was a nontarget because it was not an n-back repeat, but was a repetition of a recently presented item (e.g., a 2-back repeat in a 3-back task). These items were assumed to require the same types of inhibitory or interference resolution processes as “recent negative” trials in the Sternberg task. It was found that transient activation on lure trials in the same lateral inferior PFC regions (among others) was selectively associated with performance on these trials—and, moreover, with individual differences in fluid intelligence. Thus, high-ability individuals may be more likely to be able to resolve lure-trial interference by transiently engaging specific PFC mechanisms that combat this interference.

Stimulus-Response Interference

A second category of neuroimaging studies on executive functions derives from the cognitive literature on attention control. In particular, a major focus of this literature is on the mechanisms of selective attention: keeping attention focused on task-relevant stimulus-and-response information in the face of irrelevant and distracting stimulus-and-response features. Neuroimaging methods provide a means of determining what neural mechanisms are critical for selective attention control, and in particular how instances of stimulus-response interference can be resolved when encountered. The paradigmatic example of stimulus-response interference in a selective attention task is the Stroop task, probably the most familiar and well-used task in all of experimental psychology. Thus it is not surprising that since the mid-1990s, the Stroop task has also become one of the most frequently studied neuroimaging tasks, with over 100 papers published at the time of writing this chapter. Many of these studies have used the Stroop task to probe brain function changes in different populations (e.g., schizophrenics; Carter et al., 1997).

However, the critical issue regarding the Stroop task that captures the interest of cognitive neuroscientists studying executive function is what neural control processes become engaged to suppress interference arising from incongruent word-name information. This question has been examined in numerous ways, across various neuroimaging studies, by (1) comparing incongruent trials or task blocks

against *neutral* trial or block controls (e.g., Banich et al., 2000); (2) comparing incongruent trials or blocks against congruent trial or block controls (e.g., Carter et al., 2000); (3) manipulating the frequency of different trial types (e.g., congruent vs. incongruent; Leung et al., 2000); (4) comparing different forms of incongruent stimuli (e.g., those which directly conflict with the response vs. those which conflict only at a semantic level; Milham et al., 2003); (5) comparing different types of relevant and irrelevant stimulus dimensions (e.g., COLOR-word, PICTURE-word; Milham et al., 2001) or response modalities (e.g., verbal vs. manual; Barch et al., 2001); and (6) by comparing the effects of practice (e.g., Bush et al., 1998).

In general, across all of these studies a few common themes have emerged. First, the lateral PFC and anterior cingulate cortex are reliably more active under conditions involving high interference relative than conditions involving low interference. Further, the activity level in lateral PFC has been found to be positively associated with successful performance (e.g., MacDonald et al., 2000). However, many other brain regions have also been implicated, such as the posterior parietal cortex and extrastriate cortex (Carter et al., 1995; Pardo et al., 1990). These types of findings have led to the development of further questions, regarding the various subprocesses associated with interference suppression. For example, an important issue in the attention literature revolves around the distinction between the source of attention control and the site at which attention control modulates ongoing processing. It has been postulated by some authors that the lateral PFC serves as the source of Stroop attentional control, whereas extrastriate cortical regions serve as the site of attentional modulation (Carter et al., 1995). Yet a further question remains as to whether the processes occurring at the site of attentional modulation reflect attention-based enhancement of the task-relevant dimension or attention-based suppression of the irrelevant dimension.

A study by Banich et al. (2000) investigated this issue by altering, in various conditions, either the information contained in the task-relevant dimension (color, location) or the information contained in the irrelevant dimension (word, picture). They observed that holding the relevant dimension constant while manipulating the irrelevant dimension led to modulations of activity within parietal and extrastriate cortex. Conversely, manipulating the relevant dimension while holding the irrelevant one constant modulated activity within the lateral PFC and precuneus. This result seems to suggest that the PFC and precuneus form a network involved in attention-based enhancement, whereas the parietal and extrastriate cortex may form a network for attention-based inhibition. Further studies will be needed to determine more conclusively whether these regions form functionally connected networks, with one serving as the source and the other the site of attentional modulation (e.g., by focusing on the temporal dynamics of activity, as in Corbetta et al., 2000).

The Stroop task is not the only paradigm used to examine stimulus-response interference. In fact, many task situations have “Strooplike” characteristics arising from a form of stimulus-response interference. Relevant examples include the Eriksen flanker and Simon tasks. Moreover, theoretical analyses have suggested that these tasks and others can be taxonomized according to how such interference arises (Kornblum et al., 1990). In the Simon paradigm, interference arises when the irrelevant spatial location of an object conflicts with the response required for the object, if the response also has a spatial component to it (e.g., making a left-hand response to the shape of an object located in the right side of a display). In the Eriksen task, interference arises when irrelevant flanking stimuli conflict on some dimension with the features of a task-relevant central stimulus. The similarities and differences among these paradigms have captured the interest of neuroimaging researchers studying attention control. Thus, a number of imaging studies have begun to focus on other Strooplike tasks, such as the Eriksen and Simon tasks—and, moreover, have begun to compare brain activation patterns across tasks, to better understand their underlying commonalities and differences (e.g., Peterson et al., 2002). In terms of commonalities across tasks, a generally reliable finding in this literature is that interference conditions are associated with increases in lateral PFC activity, along with other related brain areas such as the ACC.

One interesting examination of cross-task differences has been in examining different types of interference present within the Flanker task. In particular, in this task, interference between flanking stimuli and the response (stimulus-response or S-R interference) can be dissociated from interference between the central and flanking stimuli (stimulus-stimulus, or S-S interference, which occurs when the two stimuli differ but are both associated with the same response). A study by Van Veen et al. (2001) directly examined brain activity across these two types of interference, and found that only S-R interference was associated with ACC activity, even though both types affected behavioral performance. In contrast, left inferior PFC showed increased activity to both types of interference (though activity was greater for S-R). No region showed selective activation to S-S interference. Other studies have confirmed the selective engagement of ACC in S-R interference in both the Stroop (e.g., Milham et al., 2001) and “recent negative” Sternberg tasks (Nelson et al., 2003). Such results are consistent with a general action-monitoring function ascribed to the ACC in various theories (Ridderinkhof et al., 2004). (See “Performance Monitoring,” below).

Response Inhibition

A third category of executive function examined in neuroimaging studies is that of response inhibition. A common observation in the clinical and neuropsychological

literatures is that many types of disorders appear to involve impairments in the ability to withhold strong response tendencies that are contextually or socially inappropriate. Thus, individuals exhibiting a "disinhibition" syndrome (frequently due to traumatic brain injury) often cannot stop themselves from making inappropriate social actions (e.g., making offensive comments in conversation). Likewise, disorders such as ADHD seem to be associated with a strong tendency to act impulsively or without normal restraints on behavior. Classically, neuropsychologists have studied failures of inhibition via well-known tasks such as Luria's tapping task or the go-no go paradigm. These and other tasks from the experimental literature have also been examined in neuroimaging studies. In these studies, the central question of interest is, What neural processes become engaged when inappropriate actions must be suppressed, and how are these inhibitory processes affected by various task factors?

The go-nogo has become a favorite tool for investigating these questions in neuroimaging studies, because the stimuli and responses can be very simple and frequently repeated. The basic paradigm involves a class of stimuli to which the participant is to respond as quickly as possible (go), and another class that, when presented, requires a withholding of the response (nogo). With the advent of event-related imaging techniques it is very simple to analyze brain activation on go and nogo trials separately, and to examine activation differences between successful and unsuccessful inhibition. Across a number of studies the most common theme reported is that the pattern of brain activity associated with inhibition (e.g., nogo > go trials) is right-hemisphere-dominant with distinct foci within prefrontal and parietal cortex, along with additional reliable activity in the ACC (e.g., Garavan et al., 1999; Konishi, Nakajima, Uchida, Sekihara et al., 1998). However, this typical pattern does not seem to be absolute; many studies have observed a bilateral pattern of activity, at least in dorsolateral and inferior PFC regions (e.g., Durston et al., 2002; Menon et al., 2001).

A secondary issue that has been frequently examined is how activity in these regions is affected by manipulations of the relative frequency of go vs. nogo trials. Interestingly, activation in nogo-sensitive PFC and ACC regions was greatest under conditions when nogo frequency was the lowest (Braver et al., 2001), or following a sequence of go trials (e.g., Durston et al., 2003). Under these conditions, inhibitory processes might be thought to be the most challenged, since inhibitory events are rare, and thus potentially surprising. Some investigators have argued from these results that response frequency is the primary factor driving nogo activity rather than inhibition per se, whereas others have shown that even when frequency is controlled, the same brain regions are active. For example, Braver et al. (2001) found that the ACC, right dorsolateral PFC, and right inferior PFC were equally active for both low-frequency nogo trials and low-frequency go trials. Yet Liddle

et al. (2001) kept go and nogo trials at equal frequency but found these same regions were more strongly activated on nogo trials. A potential resolution of the issue may involve whether and how participants prioritize go and nogo responses (i.e., which category is more salient or more strongly in the focus of attention). Future studies will need to investigate this question more directly.

A related paradigm for studying response inhibition is the stop-signal task (Logan, 1994). An attractive feature of this task is that it provides a method for estimating the time required to stop a response, as well as a means of manipulating the tendency for inhibitory failure, through the timing of when the stop signal occurs. Thus, under these conditions it has been examined whether activity in any brain region adequately predicts inhibitory success or failure (Garavan et al., 2002; Rubia et al., 2003). Rubia et al. found that right inferior PFC was significantly more active on successful stop-signal trials, further suggesting that this region plays a central role in the inhibition process. A similar result was observed in a study by Hester et al. (2004) in a go/nogo task which also showed that lateral PFC regions increased activity when a preceding cue predicted future inhibitory demands. Finally, a focused neuropsychological investigation found that right inferior PFC damage was selectively associated with inhibitory deficits in the stop-signal task, with the extent of tissue damage correlated with the magnitude of inhibitory deficit (Aron et al., 2003).

A final class of inhibitory task that has been widely used is the anti-saccade (Guitton et al., 1985). This task differs from the other two in that it typically involves a distinct response modality (eye movements instead of hand movements). The key requirement of the task is that following the onset of a briefly presented peripheral cue, the subject must make a saccade to a location 180 degrees opposite from the cue. Such a saccade strongly conflicts with the innate and prepotent tendency to move the eyes directly to the location of the cue (known as a pro-saccade). Thus, inhibitory processes are thought to be engaged to override the automatic response tendency, such that oculomotor control systems can be utilized in a voluntary and task-driven manner. Although similar to the other inhibitory paradigms, the anti-saccade offers the opportunity to study inhibitory processes within the context of a motor system whose neuroanatomy and neurophysiology have been extensively examined and characterized in primates. For example, it is well understood that the frontal and supplementary eye fields (FEF and SEF) play key roles in voluntary saccade generation, through interactions with posterior parietal (LIP) and subcortical systems such as the superior colliculus (Dorris et al., 1997).

Human neuroimaging studies of the anti-saccade task have thus standardly focused attention on the role of the FEF and SEF in suppressing reflexive eye movement (e.g., Sweeney et al., 1996). Event-related fMRI studies have offered the opportunity to examine and dissociate preparatory activity during anti-saccade

trials from response-related activity (Curtis & D'Esposito, 2003; DeSouza et al., 2003). For example, a study by Curtis and D'Esposito (2003) provided more specific evidence that increased activity in the FEF and SEF is critical for appropriate oculomotor preparation, by demonstrating that activity levels in these areas are related to anti-saccade success. Interestingly, however, these results actually suggest that the FEF and SEF regions involved in anti-saccade responses appear to be the same ones that subserve normal memory-guided saccades in the absence of inhibition. Thus, appropriate anti-saccade behavior appears to be due to the preparatory engagement of systems required for the facilitation of saccades in a planned direction rather than the engagement of specific regions needed to inhibit incorrect response tendencies. Indeed, this may be a general principle of cognitive control, in which top-down frontal signals enhance activation in task-relevant perceptual and motor pathways rather than directly suppressing irrelevant information (e.g., Desimone & Duncan, 1995).

Underdetermined Responding

A hallmark of executive control is the ability to respond freely on the basis of an endogenously generated decision, goal, or intention. This captures the sense that much of our behavior is truly voluntary or willed. This characteristic of executive control is best seen in situations where responses to be generated are only weakly determined by the current environment and context. Such underdetermined response situations contrast with others in which the available responses are strongly constrained by the properties of the eliciting stimulus (i.e., its "affordance")—which we typically refer to as stimulus-response associations—or by the specific task to be performed (i.e., given the task context, there is only one correct response). Thus, to examine underdetermined responding, it is necessary to devise conditions in which multiple actions may be equally appropriate to a given stimulus or at a given moment in time. The assumption then is that under these conditions, an endogenous control mechanism is engaged to select a specific response on the basis of some internal criteria, even if those criteria reflect the (abstract) goal of randomness.

A large number of neuroimaging studies have attempted to examine the neural mechanisms underlying underdetermined responding (or "willed action" or "free selection"). These studies have been examined in both manual responding and language production. Studies of language production have a long history, beginning with the first verb generation tasks studied by Petersen and colleagues (1989). In the verb generation paradigm, participants are required to verbally generate an appropriate action to a visually presented noun (e.g., say "BAKE" if the word "CAKE" is presented). Similar paradigms involve fluency tasks, such as thinking of words beginning with a particular letter or in a particular semantic category (e.g.,

Frith et al., 1991) and stem completion tasks (Buckner et al., 1995). A common finding across all of these tasks is activation in medial frontal regions such as the anterior cingulate and pre-SMA, and in left lateral PFC.

Other studies have directly examined the effect of selection in these tasks by examining differences in brain activation related to changes in generative constraints, such as the number of response options possible on a given trial (Barch et al., 2000; Desmond et al., 1998; Thompson-Schill et al., 1997). For example, in an event-related fMRI study of the verb generation task, Barch et al. (2000) examined activation on trials where the noun was associated with many possible verbs in comparison with trials in which there were few possible associates. Activity in left inferior frontal cortex (BA 44) and ACC was greater when there were many possible associates (low-constraint nouns), and thus a higher demand on selection. Additionally, the ACC also showed greater activity on trials in which the participant produced a verb that was only weakly associated with the noun, and this effect was enhanced for nouns for which there was a strongly associated verb (that was not selected). Interestingly, the left inferior frontal cortex was not sensitive to these latter effects. This finding and others (e.g., Wagner et al., 2001), suggest that the left inferior frontal cortex may be engaged primarily to provide goal-based facilitation of semantic or lexical retrieval when stimulus cues are insufficient by themselves (as discussed in "Strategic Control of Memory," above). Conversely, the ACC may have served to detect the high degree of response conflict or stimulus-response interference evoked by the target noun (see "Stimulus-Response Interference," above, and "Performance Monitoring," below).

Probably the most extreme form of verbal underdetermined response task is the random-number generation paradigm (Baddeley et al., 1998). There have been many variants of this task studied over the years (Jahanshahi & Dirnberger, 1999; Petrides et al., 1993), but all require participants to verbally generate, at a relatively quick rate, a nonrepetitive, nonstereotyped sequence of digits. These studies have all tended to observe the same pattern of dorsolateral PFC activity associated with generation, as well as that activity patterns show sensitivity to counting rate (Daniels et al., 2003). The pattern of results suggests that dorsolateral PFC may serve as a response controller, monitoring for and suppressing tendencies to respond according to habitual patterns. Support for this hypothesis has come from studies using transcranial magnetic stimulation (TMS) techniques to temporarily deactivate the PFC (Jahanshahi & Dirnberger, 1999; Jahanshahi et al., 1998). During TMS stimulation occurring over the dorsolateral PFC, the tendency for participants to generate stereotyped sequences increased. Interestingly, the pattern has been observed only during left hemisphere stimulation, with right hemisphere stimulation producing no behavioral changes.

The initiation, selection, and generation of “willed actions” has been studied with tasks requiring manual responses. Most of these tasks require participants to move a joystick in one of multiple directions or to press one of multiple responses, according to a pattern of their own choosing (e.g., Frith et al., 1991). The pattern of results appears to be similar to that observed in verbal generation tasks, with both dorsolateral PFC, and medial frontal cortex, including the ACC and SMA, being reliably engaged. However, in this domain, more recent work has enabled further functional dissociation of these two regions. For example, in a study conducted by Lau et al. (2004), dorsolateral PFC activity was found to be equivalent in a random selection task and in cued-selection task with a high number of potential targets. In contrast, a region of pre-SMA was found to be engaged only by random selection, and activation in the region was significantly correlated with reaction time latency. Lau et al. suggested that pre-SMA might be specifically involved in the endogenous generation of potential response options, while the dorsolateral PFC might be involved in selecting one of these options for execution.

Performance Monitoring

An important feature of many task situations is the need to dynamically monitor and adjust one’s own behavior in order to optimally achieve task goals. Performance monitoring and adjustment seem to rely upon a number of component executive processes: (a) sensitivity to either environmental or internal cues that indicate performance success or failure; (b) maintenance and integration of such cues over time, to assess and confirm subtle trends; and (c) translation of performance information into an adaptive adjustment of cognitive or response strategy. Since the mid-1990s there has been a rapidly accelerating pace of neuroimaging research geared toward understanding the neural mechanisms underlying performance monitoring.

The relationship of performance monitoring to executive control has been classically studied within the neuropsychological literature through examination of the Wisconsin Card Sort Task (WCST). Although this task is multicomponent in nature, the greatest demands on executive function may center around the requirement to adjust an internal task set or decision rule, based upon somewhat ambiguous feedback information. The perseverative errors reliably observed by patients with PFC damage and other patient groups with executive control impairments appear to involve a failure to appropriately process or utilize such feedback signals to adjust cognitive strategy. Neuroimaging studies of the WCST have long confirmed the role of PFC in global performance (e.g., Berman et al., 1995), but more recently have also focused attention on the feedback processing components of the task itself. For example, Konishi and colleagues (Konishi, Nakajima, Uchida, Kameyama, et al.,

1998) used event-related fMRI to isolate activation on trials with negative feedback. This analysis revealed selective activation in bilateral regions of inferior PFC (BA 45).

A similar study by Monchi et al. (2001) also observed feedback-related activation in lateral PFC that included both inferior and dorsolateral regions, along with activation in the ACC. Another study by Konishi and colleagues (2003) attempted to dissociate the affective component of negative feedback (i.e., signaling an inappropriate response) from the informational content (i.e., signaling the need to adjust the task set). They found that the medial frontal lobe was associated primarily with the affective component of feedback, whereas right-lateralized inferior (BA 47) and dorsolateral PFC regions (BA 9/45/46) were associated with the informational component.

A somewhat different theme in the investigation of performance monitoring processes emerged in the early 1990s from studies in the ERP literature. In particular, this research identified a specific ERP (event-related potential) component, known as the ERN (error-related negativity), that was elicited following commission of an error in simple cognitive tasks. The ERN was first observed in tasks where no explicit feedback was provided to participants, but the task was simple enough (and speeded, to produce a high error rate) that errors were likely detected internally with high reliability (Falkenstein et al., 1990; Gehring et al., 1993). Later studies also detected the presence of an ERN-like component linked to explicit (i.e., external) error feedback, under conditions where internal error detection was much more difficult (Miltner et al., 1997). These studies suggested that the source of the ERN was in the medial frontal cortex, around the location of the ACC (Dehaene et al., 1994). Thus, an interpretation of the results was that the ACC served as a neural system invoked to detect and respond to error-related information through corrections in behavior, such as slowing of responses (a performance pattern frequently observed following errors; e.g., Laming, 1979).

The error-related research on the ERN has been subsequently confirmed with fMRI, with event-related imaging studies clearly indicating increased ACC activity during error commission (e.g., Kiehl et al., 2000). Interestingly, at the same time these neuroimaging findings were coming out, a somewhat different theory was emerging which suggested that the ACC played a more general performance-monitoring function that involved the detection of conflict during the course of response generation, even under conditions where the eventual response was correct (Botvinick et al., 1999; Carter et al., 1998). The conflict-monitoring theory suggested that error detection was a special case of conflict, and provided a computational account that appeared to integrate many disparate results (such as explaining why the same pattern of ACC activity is commonly observed across response inhibition, stimulus-response interference, and underdetermined response tasks). Importantly,

a component of this theory specifies the relationship between conflict detection and subsequent performance adjustment by postulating that ACC activity feeds into control mechanisms, such as those in lateral PFC, that implement a change in task goals, response speed, or attentional bias (Botvinick et al., 2001).

The conflict-monitoring and error detection hypotheses of ACC function have together spawned a large and growing literature not only from ERP and fMRI methods, but also involving ACC or frontal lesion patients (e.g. Gehring & Knight, 2000; Swick & Turken, 2002). A number of studies have sought to test whether error-related signals in ACC might be anatomically distinct from those associated with conflict (e.g., Garavan et al., 2003; Ullsperger & von Cramon, 2001). Other studies have focused on whether explicit error feedback also produces activity within the same ACC regions (e.g., Holroyd et al., 2004). Still other studies have focused on the relationship between errors and subsequent changes in cognitive control or behavioral performance (Garavan et al., 2002). The literature is rapidly evolving, and a growing theme is that the ACC and related medial frontal areas may play a generalized performance-monitoring function, of integrating both internal and external cues regarding performance, that could be used to adjust response selection strategies (Ridderinkhof et al., 2004).

A final theme in the neuroimaging literature on performance monitoring has been to focus on feedback-related brain activity within the context of gambling or decision-making tasks involving monetary rewards and penalties (e.g., Elliott et al., 2000). One prominent finding in this literature is the involvement of the orbitofrontal cortex (OFC) under conditions involving trial-by-trial monetary feedback information. This has led to a general idea that the OFC may be important for keeping track of the valence of such feedback (Krawczyk, 2002; Rolls, 2000).

A study by O'Doherty and colleagues (2001) examined this hypothesis, using event-related fMRI to compare the neural response on reward vs. penalty feedback trials. Distinct OFC regions were engaged by positive and negative monetary feedback, with medial regions showing more responsivity to rewards and lateral regions showing greater sensitivity to punishments. Moreover, the magnitude of activity in each of these regions was correlated with the magnitude of reward and penalty. A follow-up study by O'Doherty, Dayan, et al. (2003) provided evidence that activity in these regions does not merely track reinforcement values over time, but may also signal whether such information will be used to bias changes in behavioral choices. Thus, activity levels in the medial and lateral OFC was greater for trials in which reward or punishment did not lead to a change in behavior, relative to trials in which a behavioral switch occurred. The dorsal ACC (a similar region to that activated in conflict and error studies) was found to be selectively active under conditions in which penalties were associated with a subsequent shift in behavioral choice.

Other studies employing similar task designs have suggested that a region at the intersection of the anterior insula and caudolateral OFC might be involved in linking penalties or reduction in reward with a switch in behavioral choice (e.g., Cools et al., 2002). Interestingly, a recent study has suggested that activity in dorsal ACC and in lateral OFC could be doubly dissociated on the basis of whether feedback information was given after a response that was freely selected or made according to an externally specified instruction (Walton et al., 2004). The task was a response-switching paradigm in which one of three stimulus-response mapping rules was in place at any time. Participants were intermittently given a cue to switch response rules, but were not told which rule was now appropriate, and had to determine this through feedback information. In one condition, following a switch cue, participants had to freely select the next response and evaluate the subsequent feedback, while in another condition participants had to make a prespecified (by the experimenter) response before evaluating the feedback. ACC activity was selectively associated with feedback monitoring under free-choice conditions, whereas OFC activity was linked to feedback-monitoring when the response was prespecified. This result was interpreted as suggesting that ACC monitors the feedback relationship between freely generated actions and their associated outcomes, whereas OFC tracks the outcome of externally guided actions in order to adjust internal representations of stimulus-reward associations.

Task Management

A central notion of many theories of executive control is that individuals are able to internally represent "task sets" or "task rules" (a set of goals and constraints for behavior within a task context) that collectively provide a regulating force on information processing and action selection (Bunge, 2004). These task-set representations (and the processes that act on them) are postulated to be distinct from the task-specific representations and processes themselves, and thus serve a managerial function in coordinating task flow. Theorists have suggested that the best approach for tapping into these task management processes is by studying performance in multitask environments (Monsell & Driver, 2000). Under these conditions, cross-task interference is thought to be a central limiting factor in performance, and thus control processes may be invoked to minimize or resolve this interference. Two types of experimental paradigms have emerged in the behavioral literature for studying these processes: task-switching and dual-task coordination. Neuroimaging researchers have adapted both of these paradigms to understand the neural mechanisms underlying task management.

Task-switching paradigms require rapid switching among two (or sometimes more) tasks, in either a predictable but uncued, or random and cued, sequence. The

central finding is that performance suffers on trials where the task switches relative to when it repeats (e.g., Allport et al., 1994; Meiran, 1996). This finding has been classically interpreted as suggesting that a distinct process is required to accomplish the “switch” or reconfiguration of internal task representations. Although this original interpretation has become much more complex, it has served as the theoretical basis for a quickly growing neuroimaging literature. Thus, a number of studies have compared activity in task-switch trials relative to task-repeat trials, using event-related fMRI (e.g., Dove et al., 2000; Sohn et al., 2000). Although, as is typical in the executive control literature, many of these studies were focused on the role of lateral PFC, the results have been somewhat ambiguous.

Studies using less sensitive blocked designs have suggested PFC activity is increased during task-switching blocks (e.g., Dreher et al., 2002). However, event-related fMRI studies do not typically find switch-selective activity in lateral PFC—that is, the same regions are also activated on task-repeat trials (e.g., Kimberg et al., 2000). Moreover, the studies that have reported switch-related lateral PFC increases observe this pattern only under specific (and potentially contradictory) conditions, such as when advance preparatory cues are provided (e.g., Sohn et al., 2000) or when insufficient preparatory time is given (e.g., Ruge et al., 2005). Instead, the most reliable region for observing switch-related activity seems to be the superior parietal cortex (for review, see Wager et al., 2004).

Lateral PFC, particularly posterior PFC regions (e.g., the inferior frontal junction, BA 44/6), does seem to play an important role in task-switching environments, but the activity appears to index more general processes associated with cued task preparation or interference resolution that may not be specific to task switches (Brass & von Cramon, 2002; Derrfuss et al., 2004). For example, PFC activity is greater (a) when task sequences are random rather than predictable (Dreher et al., 2002); (b) following an explicit preparatory cue (Braver et al., 2003); (c) when a previously suppressed task set has to be activated again (Dreher & Berman, 2002); and (d) when the task-set representation increases in complexity, i.e., task rules are more complicated (Bunge et al., 2003). Interestingly, anterior (BA 10) rather than dorsolateral regions of PFC were found to show sustained activation during task-switch blocks relative to single-task blocks, and this activity was associated with the “mixing cost” (the performance effect due specifically to performing in multitask relative to single-task environments) (Braver et al., 2003). The activity in this region was interpreted as potentially reflecting a high-order subgoal monitoring or preparatory attentional process that detects cues indicating a switch in task.

An interesting issue that has not been fully explored in this literature is the exact distinction between task switching and other forms of attention switching, such as switching between: response mappings (e.g., Dove et al., 2000), different perceptual features (e.g., Rushworth et al., 2002), different perceptual dimensions (e.g., Pollman,

2001), or the focus of attention within working memory (e.g., Garavan et al., 2000). Do these other situations activate the same brain areas as task-switching studies? One meta-analysis (Wager et al., 2004) suggests that the commonalities across different types of switching tasks are greater than the differences, with the parietal cortex showing the most reliable effects of all switching conditions.

Studies involving dual-task paradigms differ from those involving task-switching in that multiple tasks are presented, and have to be performed, within an overlapping time interval. Thus, dual-task performance requires the coordination, scheduling, and segregation of task representations rather than simply rapid updating (Baddeley, 1996). Neuroimaging researchers have sought to determine the brain regions selectively engaged under dual-task conditions, under the assumption that such regions might serve as the central "task coordinator" that enables successful performance. In the first study to make this claim, D'Esposito suggested that dorsolateral PFC was selectively activated by requirements to perform a spatial and a semantic task concurrently, and that the activation could not be purely due to the increase in task difficulty itself (D'Esposito et al., 1995). However, later studies provided more equivocal results, with PFC and other regions showing increased dual-task activity but in the same location as regions activated during single-task conditions (e.g., Bunge et al., 2000). Thus, these studies argued against the presence of "dual-task-specific" brain areas. Yet other dual-task studies have drawn conclusions more similar to the early D'Esposito work (e.g., Szameitat et al., 2002). Still, no definitive demonstration of selective dual-task-related activity has been presented at this time.

A different set of questions has been addressed by other researchers in this domain: How, why, and under what conditions do two tasks interfere with one another when performed simultaneously? One idea, investigated by Klingberg and colleagues, is that two tasks will interfere with one another if they both engage the same region of cortex (Klingberg & Roland, 1997). Thus, under dual-task conditions, the activation level in certain task-related brain regions has been found to be less than the sum of activity occurring in each of the single-task conditions (i.e., a subadditive interaction; see "Interactive Effects" under "Issues," below; Just et al., 2001). Such findings suggest some kind of constraint on task-related activation, due to inhibitory processes or limited processing capacity, or a combination of the two.

Other studies have focused on finding out the processing stage at which interference occurs. These studies have examined the temporal characteristics of task overlap, relying on a phenomenon known as the psychological refractory period (PRP) effect (Pashler, 1994; Welford, 1952). The PRP effect is a slowing of reaction time when a second task is presented while the first task is still in a particular stage of completion, but not if it has already passed that stage. Thus, PRP tasks standardly

manipulate temporal overlap between the two tasks by varying the SOA (stimulus onset asynchrony) for the second task relative to the first. Neuroimaging studies examining the PRP effect have suggested that inferior PFC, typically right-lateralized, shows increased activity during short SOAs (when temporal overlap between the tasks is high), but not during long SOAs (when task overlap is low; e.g., Herath et al., 2001). This activity has been interpreted as reflecting the presence of cross-task interference (and the need to resolve it) either at the response selection stage (Herath et al., 2001) or during perceptual attention (Jiang & Kanwisher, 2003). It will be important for future studies to investigate the relationship between these forms of cross-task interference resolution process, and the simpler forms of stimulus-response interference resolution processes discussed above (under "Stimulus-Response Interference").

Higher Cognition

There are certain mental processes that seem to represent the pinnacle of human cognitive skills and achievement, and that most strongly set our species apart from others. These mental processes, which include planning, novel problem-solving, and abstract reasoning, have long been the subject of intense research interest because they are typically thought to reflect the essence of intelligence and higher cognition. Likewise, these higher cognitive skills may be the ones that most strongly require the engagement of executive processes, to ensure that complex chains of thought can be appropriately directed toward highly abstract behavioral goals. Within the neuroimaging literature growing attention has been given to the underlying cognitive and neural processes associated with the higher cognitive domains of planning, problem solving, and reasoning. Two research strategies have emerged for investigations within this domain. One approach has been to directly utilize or adapt classic experimental tasks drawn from the neuropsychological or intelligence testing literature, such as Raven's Progressive Matrices, the Tower of Hanoi/London, analogy problems, and logical reasoning tasks (e.g., syllogisms). A second approach has been to develop new experimental paradigms (or novel variants of existing tasks) that attempt to get at the essential cognitive elements of the standard tasks within a more simplified framework, such that critical task factors can be isolated and manipulated more selectively.

The most popular of the classic experimental tasks studied in higher-cognitive neuroimaging studies is the Tower of London (ToL) planning task, adapted from the well-known Tower of Hanoi problem in cognitive psychology. An attractive feature of the ToL is that it enables the presentation of multiple planning problems that can be incrementally graded in complexity and difficulty. A number of studies

have directly examined the effect of difficulty manipulations on brain activity (e.g., Baker et al., 1996; Fincham et al., 2002). These studies have tended to find that increased planning complexity is associated with corresponding increases in a widespread network including parietal, prefrontal, and medial frontal regions. This network is highly overlapping with that observed in a range of visuospatial WM tasks. However, Baker et al. (1996) established that in a direct comparison of the two types of tasks (ToL vs. visual WM), the ToL was associated with selectively increased activity in anterior PFC regions (BA 10). Other studies have tended to confirm this pattern (e.g., van den Heuvel et al., 2003). Conversely, a study by Beauchamp found that increased practice with ToL problems led to automatization in task performance that was associated with decreased activity in dorsolateral and anterior PFC but an increase in activity within basal ganglia regions (Beauchamp et al., 2003).

A similar pattern of findings has been observed in studies with a different problem-solving task—Raven's Progressive Matrices—that has been employed experimentally as a probe of general fluid (i.e., knowledge-independent) intelligence. As with the ToL, neuroimaging studies with Raven's task have varied problem complexity to examine the effect of this manipulation on brain activity (e.g., Prabhakaran et al., 1997). This work has suggested that the most difficult Raven's problems, which demand integrating relationships among various stimulus dimensions (e.g., shape, texture, etc.), selectively engage anterior PFC regions. The pattern has been found to remain selective even when controlling for effects due to task difficulty (Kroger et al., 2002) or changes in performance (i.e., slower response latencies; Christoff et al., 2001).

A third type of higher-cognitive task studied in the neuroimaging literature is logical reasoning. Many of these types of studies have been carried out by Goel and colleagues (Goel, in press). A number of different types of logic problems have been examined, including inductive vs. deductive and transitive inference. As might be expected, a wide variety of logic problems all commonly activate lateral PFC regions (e.g., Knauff et al., 2003). Some studies have attempted to specifically dissociate the executive mechanisms that support different reasoning processes. For example, a common distinction in the reasoning literature is between judging logical validity and judging plausibility. Deductive arguments attempt to demonstrate logical validity or necessity, while inductive arguments attempt only to demonstrate plausibility. In two imaging studies directly comparing matched inductive and deductive reasoning tasks (Goel & Dolan, 2004; Goel et al., 1997), left inferior PFC (BA 44) was more strongly activated in the deductive condition, whereas left dorsolateral PFC (BA 9) was more strongly engaged by induction. The results were interpreted as suggesting that deductive reasoning makes strong demands on verbal working memory and the phonological loop, whereas inductive reasoning requires the

evaluation of propositions against background knowledge, and thus may engage specific executive monitoring processes.

A review of the neuroimaging literature on higher cognitive tasks conducted by Christoff & Gabrieli (2000) argued that many of these tasks tend to activate anterior or polar regions of PFC (BA 10). Likewise, these authors have suggested that a common cognitive component of these types of tasks is that they require internally generated (i.e., abstract) monitoring or evaluation representations (Christoff et al., 2003). For example, in the Tower of London task, one has to internally generate several possible moves and then evaluate which of these is most promising in terms of progress toward a goal. Thus, Christoff and Gabrieli postulated that frontopolar PFC might be selectively engaged to carry out these monitoring or evaluation functions in a wide variety of cognitive task contexts, including episodic retrieval (see "Strategic Control of Memory," above). The ideas proposed by Christoff and Gabrieli were very similar to an account put forward by Koechlin et al. (1999) in a study reported at around the same time. Koechlin et al. provided results that demonstrated the selective activation of frontopolar cortex (lateral BA 10) under conditions requiring cognitive "branching." This term was invoked to describe the process of maintaining information in working memory while performing a second task, such that the two sources of information can be evaluated or integrated. Koechlin et al., like Christoff and Gabrieli, claimed that branching operations form a core component of many higher cognitive tasks.

The development of specific functional hypotheses regarding the role of anterior PFC in higher cognition has led to an increased and more focused interest in both "branching" or integration-type computations and how they engage anterior PFC (Ramnani & Owen, 2004). A number of studies have now investigated integration effects within working memory, demonstrating that such requirements also tend to engage anterior PFC regions (e.g., Badre & Wagner, 2004; Braver & Bongiolatti, 2002; Prabhakaran et al., 2000). For example, in Prabhakaran et al. (2000), anterior PFC was selectively engaged by conditions requiring participants to integrate the location and identity of spatially arranged letters in working memory, in comparison with conditions requiring the same numbers of letters and locations to be maintained (but letters and locations were segregated). Similarly, Braver & Bongiolatti demonstrated that right frontopolar cortex was engaged by the requirement to integrate the contents of working memory with the results of a subgoal task (semantic classification), but not by a matched working memory or semantic classification task performed in isolation (Braver & Bongiolatti, 2002). Finally, related work has also shown that anterior PFC regions are also engaged by integration effects within analogical reasoning (Bunge et al., 2004). In this study, judging whether two word pairs were related along the same semantic dimension (i.e., analogous) engaged left anterior PFC, whereas just judging semantic relatedness of a single word pair did

not lead to increased activation. Taken together, these findings suggest that anterior PFC involvement might be a critical feature of many higher cognitive tasks, since such tasks often require the integration of abstract sources of information within working memory.

Issues

As the above review indicates, the neuroimaging literature on executive function is vibrant, vital, and rapidly expanding. Indeed, it is fair to say that we may look back at the first decade of the twenty-first century as a “golden age” in executive function research. However, the rapidity with which new studies have emerged over the last few years makes it very difficult to keep pace with, and adequately summarize, the progress of the field. Nevertheless, it is clear that a few themes and trends have emerged in the last few years regarding the neural basis of specific control functions (see figure 10.1, plate 17):

- Task conditions involving the preparatory cuing of attention or the use of attentional control to resolve interference tend to activate posterior and inferior regions of lateral PFC.
- Task conditions requiring the temporary suppression of ongoing responses tend to activate right inferior PFC regions.
- Task conditions requiring rapid shifting of attention to different dimensions or reconfiguration of task sets reliably engage the superior parietal cortex.
- Task conditions involving the free selection of potential response alternatives engage superior medial frontal areas near the SMA.
- Task conditions involving the processing of internal or external feedback related to the outcome of generated actions reliably engage the ACC and nearby medial frontal areas
- Task conditions that require the tracking of changing stimulus-reinforcement contingencies elicit activation in the OFC.
- Complex cognitive activities (such as planning, analogy verification, and controlled episodic retrieval) that involve the evaluation or integration of abstract dimensions maintained in working memory tend to engage the anteriormost regions of PFC (BA 10).

Despite the excitement stemming from these new discoveries regarding the neural substrates of executive control, a reader of this review might find it difficult to not be discouraged by the diverse set of tasks and studies that appear to engage a common set of brain regions, such as the lateral PFC and ACC. Indeed, a fair

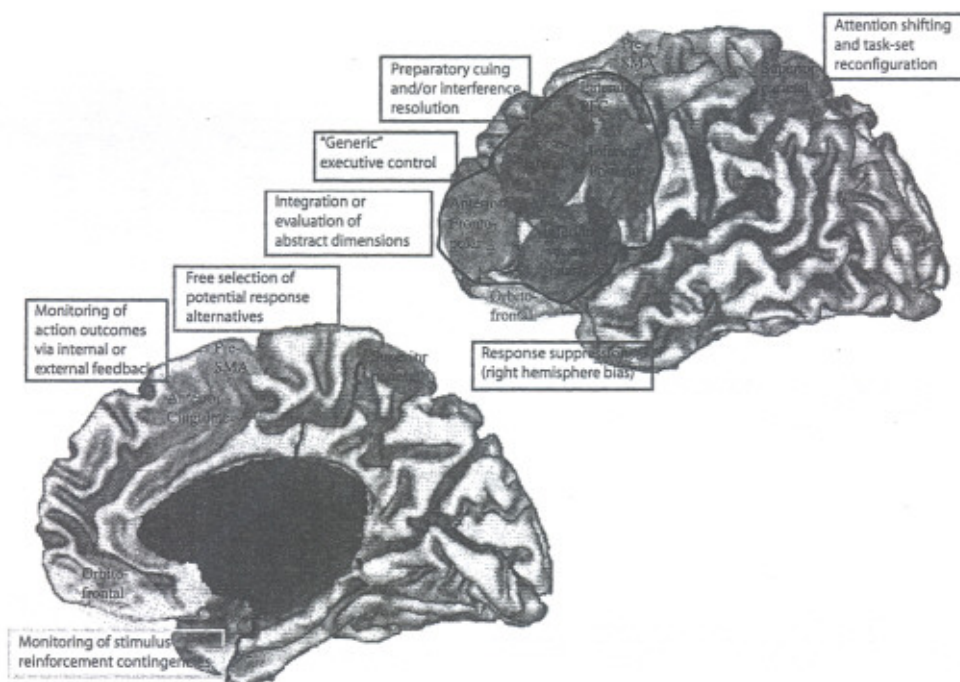


Figure 10.1

Anatomical designations of brain areas that are part of the network for executive control and the task conditions or factors that reliably activate them. Shown are lateral (upper) and medial (lower) brain surfaces. Color codes represent different brain regions discussed in the review and the corresponding task conditions or factors that appear to activate them. Lateral PFC region (outlined in black) is subdivided into inferior/posterior, inferior/ventrolateral, dorsolateral, and anterior/frontopolar regions. See plate 17 for color version.

summary of the neuroimaging literature is that lateral PFC, and dorsolateral regions in particular, will be engaged during the performance of any task that requires the invocation of executive control. Thus, on the basis of such a literature survey one might reasonably conclude that the lateral PFC and similar regions, such as the ACC, serve as neural substrates of a monolithic and mysterious “central executive” that is ubiquitously engaged whenever a task requires the invocation of executive control. In fact, similar conclusions have been drawn by a number of investigators (Dehaene et al., 1998; Duncan & Owen, 2000). While such interpretations do seem reasonable, given the bulk of the literature, they nevertheless feel somewhat unsatisfying to the cognitive neuroscientist seeking to decompose executive functions into their most basic elements and fundamental components.

What, exactly, is the lateral PFC doing that gives it such importance in executive control? In particular, a fundamental challenge for the field seems to be to

determine the particular processing mechanisms, representational specializations, and organizing properties of this brain area that give rise to its involvement in such a wide range of control processes and tasks. Likewise, even if certain specific regions within and outside of lateral PFC are coming into greater focus in terms of their particular roles in executive control, a better understanding needs to emerge regarding the "division of labor" among distinct control process, and how such processes interact to produce coordinated behavior in complex cognitive tasks. In the text that follows, we provide our own opinions, recommendations, and illustrative examples about how best to make further progress in this domain.

Processes vs. Tasks

A common approach utilized in neuroimaging studies of executive control is to directly import tasks developed in the neuropsychological or cognitive literature to examine particular executive processes (e.g., Stroop and interference, go-no go and inhibition, Tower of London and planning). In this approach, patterns of brain activity evoked during task performance (relative to a control condition) serve as a window into the neural systems subserving such processes. However, a truism from cognitive psychology is that no task is "process pure," which indicates that classical subtractive design approaches (e.g., Posner et al., 1988) will be insufficiently selective for isolating control processes of interest in executive function research.

Within cognitive psychology, a standard research strategy is to develop an underlying process model, based upon detailed task analysis, that specifies how the process of interest will be engaged in various tasks and be affected by various task variables. This translates into an experimental approach in which complex, multifactor, or parametric designs are utilized to provide a range of control conditions. Likewise, multiple, convergent experiments are conducted to confirm predictions regarding a complete pattern of behavior. Thus, we would argue that a similar approach is the one most likely to be successful in neuroimaging studies attempting to isolate and identify neural substrates of specific executive processes. Indeed, it is heartening to see that such approaches are starting to be the norm rather than the exception within the literature. For example, Banich and colleagues have provided an extended neuroimaging analysis of the Stroop task across multiple studies that has revealed how various task factors influence interference detection and resolution processes within lateral PFC, ACC, and interacting posterior brain regions (Banich et al., 2001).

A similar type of process-oriented research strategy might be to understand the commonalities and differences in neural activity across superficially distinct tasks that may nevertheless all engage the same underlying control functions, albeit in potentially different ways. For example, Braver et al. (2001) demonstrated that a

common network of brain regions, including the ACC, were equivalently activated by low-frequency events across three different tasks—oddball, go/nogo, and two-alternative forced choice—suggesting that low-frequency responding may involve specific control functions regardless of task context.

In addition, such approaches might reveal hidden factors that are linked to the activation of control-associated brain regions across tasks but tend to be overlooked by researchers. Thus, in the Braver et al. study, there was a suggestive hint that the right-lateralized PFC activity typically associated with response inhibition (as in the go/nogo), might be more strongly linked to the frequency of inhibitory events rather than to the demands on inhibition per se. Thus, response frequency (or a related construct, such as the violation of a local sequential pattern; e.g., Huettel et al., 2002) might be an important factor influencing right lateral PFC that could be more thoroughly explored across a wider range of task contexts. It is likely that there are other types of similar critical, but “undiscovered,” task variables which may modulate control processes in multiple task contexts.

Double Dissociations

Currently, the strongest evidence within neuroimaging for establishing the presence of regional brain specialization in cognitive function is the double dissociation (Smith et al., 1995). Importantly, firm conclusions regarding the presence of a double dissociation can be drawn only when it is successfully demonstrated that the dissociation pattern is statistically reliable. The most rigorous statistical criterion is the presence of a full region \times condition crossover interaction (or more complex variants), whereby condition A is significantly greater than condition B in Region 1, while in Region 2 condition B is significantly greater than condition A. Thus, although it is seemingly obvious, we would recommend that more effort be extended toward the establishment of double dissociation among control-related brain regions before drawing inferences regarding functional specialization. Moreover, we would suggest that further emphasis be given to pairs of regions for which double dissociations have already been established as a focus of further systematic research efforts. Thankfully, there have been a number of such dissociations demonstrated in the literature (many of which we have discussed above), and these have led to important advances in our conceptual understanding of the neural organization of executive control. For example, in MacDonald et al. (2000) a double dissociation between lateral PFC and ACC was clearly demonstrated in a task-switching variant of the Stroop. In this study ACC was found to be selectively engaged by the detection of response conflict (i.e., the presentation of an incongruent trial), whereas the lateral PFC was selectively engaged by the demand for preparatory attentional control (i.e., the presentation of a task cue specifying an upcoming color-naming trial).

Interactive Effects of Task Factors

A definitional characteristic of executive processes is that they are not an embedded component of task-specific processing networks, but serve to modulate the flow of processing within such networks, in accordance with behavioral goals. Consequently, it is likely that the presence of specific executive processes will be best revealed not through direct manipulation of experimental factors affecting task-specific processes, but instead by determining how such factors interact with other factors that influence the demand on such control processes. In other words, it is likely that executive control processes are going to be most sensitive to the interaction of two or more task factors rather than to single factors. This may be especially true when considering processes that are involved in integrating diverse sets of information. For example, Ramnani & Owen (2004) argued that anterior PFC regions will be engaged only by the coordination of multiple subtasks, and thus should be revealed in terms of a superadditive interaction of factors affecting the difficulty of completing each task. Likewise, Gray et al. (2002) postulated that if lateral PFC was selectively involved in the integration of affective states and cognitive task goals, then this brain region should show a mood state \times cognitive task interaction, but no main effect of either mood or task itself (i.e., a full crossover or subadditive interaction). Such a pattern was observed in bilateral anterior PFC (BA 46/10). These results suggest that studies of executive control should utilize factorial designs wherever possible, and in particular in experimental contexts where theoretical significance can be attributed to the interaction effect in terms of its relevance for executive control.

Brain-Behavior Relationships

Although it is seemingly obvious, inferences regarding the control functions thought to be subserved by specific brain regions can be most strongly tested by linking activity in these regions to behavior. In particular, one would ideally observe a selective relationship between the activity level in the putative neural control region and performance in task components thought to be most dependent on the specific control function subserved by the region. Of course in standard neuroimaging studies the kinds of relationships that can be established are purely correlational rather than causal. Nevertheless, even correlational relationships, if specific enough, can greatly strengthen inferences regarding causality. Thus, as is occurring with greater frequency in the literature, testing for activity-performance correlations in putative neural control regions should form an essential part of the neuroimaging analysis procedure.

The types of correlations that can be examined might be both between individuals and within individuals. For example, MacDonald et al. (2000) found a negative between-subject correlation between cue-related preparatory activity in lateral PFC and the size of the Stroop interference effect. This suggested that individuals who more strongly activated PFC prior to a Stroop stimulus showed a greater ability to combat the interfering effects of stimulus incongruence. In contrast, Braver et al. (2003) found a within-subject negative correlation between cue-related lateral PFC activity and the magnitude of task-switching reaction time costs. This indicated that trials with small switch costs were associated with greater preparatory PFC activity. Thus, both trial-related and subject-related variability in task performance appear to be linked to corresponding variations in lateral PFC activity following the presentation of preparatory attention cues.

Individual Differences

An issue closely linked to the one just discussed is that executive control processes may be highly variable across individuals. In particular, there may be many different routes or strategies available for achieving executive control during cognitive task performance. Such control-related variability may be an intrinsic or stable characteristic of individuals, and linked to constructs such as domain-specific cognitive skills, domain-general cognitive capabilities, or dispositional traits. Thus, it may become increasingly important to consider these sources of individual difference when interpreting the results of neuroimaging studies. As an example, Gray and colleagues observed that activation of lateral PFC and ACC during performance of the n-back WM task was negatively correlated with trait levels of dispositional extraversion (Gray & Braver, 2002; Gray et al., 2005). This finding was interpreted as suggesting that extraverted individuals exhibited greater neural efficiency (mediated by personality-linked changes in dopamine function) that enabled successful performance even with reduced control-related brain activity (Braver et al., in press). The important take-home point is that without measuring and controlling for such sources of individual variation, misleading interpretations of neuroimaging data may occur.

Consideration of Affective-Motivational Variables

Related to the previous point, it is worth pointing out the emerging relationship between imaging studies of emotion and those of executive control. There have now been imaging studies of working memory that have examined the role not only of personality and emotion on working memory, as discussed above (Gray & Braver,

2002; Gray et al., 2002), but also of the impact of reward and motivational manipulations on brain activity (Pochon et al., 2002; Taylor et al., 2004). All of these studies have shown that critical neural systems of executive control (e.g., lateral PFC and ACC) are also influenced by affective-motivational variables. Indeed, it is rapidly becoming appreciated that there may be a tight relationship between the neural systems involved in executive control and those involved in emotion processing and regulation. This view has been strengthened by studies in the emotion literature which have demonstrated that exerting self-control over emotional reactions to events or reward feedback recruits lateral PFC and ACC, along with more "traditional" emotion-related brain systems such as the striatum, orbitofrontal cortex, and amygdala (e.g., Beauregard et al., 2001; Ochsner et al., 2002). Although studies of this type are in their infancy, the second decade of the twenty-first century will likely see an accelerating pace of research examining the intersection of emotion and cognition. For example, imaging studies are beginning to compare the relationship between emotional conflict or interference and the more traditional stimulus-response interference examined in Strooplike tasks (Compton et al., 2003). Additional systematic investigations of this type are needed. More generally, we encourage investigators conducting neuroimaging studies of executive control to more closely consider affective-motivational processes when interpreting the results of their studies. In particular, we suspect that successful theories of the neural mechanisms of executive control will provide an account in which the specialized contributions of specific brain systems are described in terms of integrated cognitive and affective components.

Temporal Dynamics of Neural Activity

The primate neurophysiology literature has strongly suggested that a critical characteristic of PFC neurons is their ability to sustain changes in activity levels over extended temporal intervals and distractor stimuli (Miller et al., 1996). This finding serves as the core evidence regarding the involvement of PFC in the active maintenance functions of WM. Nevertheless, in human neuroimaging studies, it is controversial whether PFC activity truly represents active maintenance processes, and under what conditions such processes occur (e.g., Postle et al., 1999; Sakai et al., 2002). Thus, in some WM studies, PFC activity is transient rather than sustained, and occurs at the time of response selection rather than active maintenance (Rowe et al., 2000). Indeed, for some theorists, the role of PFC in executive functions rather than WM per se is defined by the transient engagement of this region when control demands temporarily increase (Smith & Jonides, 1999).

In our own work, we have been developing a theoretical framework which suggests that the temporal dynamics and types of control functions subserved by PFC

regions might be highly variable (Braver et al., in press). In particular, we have suggested the dual mechanisms of control (DMC) account, whereby control processes can be either proactive (i.e., anticipatory and sustained) or reactive (i.e., demand-driven and transient), depending on both situational and individual factors. As an example, we have observed that in the Stroop task, when the expectancy for Stroop interference is low (mostly congruent trials), activity in lateral PFC and ACC transiently increases during performance of interference trials (Braver & Hoyer, 2003). Conversely, when interference expectancy is high (mostly incongruent trials), lateral PFC activity is observed that is sustained across trials (i.e., present during intertrial intervals) and not modulated by the presence of interference. We interpreted this result as suggesting that interference expectancy can modulate the temporal dynamics of PFC activity and, moreover, that the type of executive control is implemented during task performance. Based on this framework, we suggest that executive control studies should focus on the temporal dynamics of activity within critical brain areas such as the PFC and, in particular, examine both transient and sustained types of effects. Moreover, careful attention needs to be paid to the potentially subtle task factors (and individual difference characteristics of the studied sample) that might influence whether executive control is occurring in a reactive or proactive manner.

Connectivity Approaches

Executive control almost certainly involves the widespread interaction and coordination of processing from multiple neural systems. Moreover, it is likely that critical mechanisms of control will be revealed not only through changes in activation of individual brain regions but also in how one brain region influences the activation of another. Analyses of cross-regional interactions in brain activation, typically referred to as “functional and effective connectivity,” can be studied through a number of different approaches, from simple correlation to more complex and specialized techniques, such as structural equation modeling, partial least squares, dynamic causal modeling, and independent components analysis (Nyberg & McIntosh, 2001; Penny et al., 2004).

Although the application of such techniques is still not widespread within neuroimaging studies of executive control, it is growing, and will likely have a strong influence on the future direction of the field. Connectivity approaches are likely to be most critical in understanding how changes in executive control function, both across individuals (e.g., group or individual difference effects) and across time within individuals (e.g., strategy or learning effects), are reflected in changed information flow through critical nodes of the brain control network. Indeed, the utilization of functional connectivity analyses has already provided intriguing findings

related to these questions in related areas, such as the relationship between PFC and posterior and subcortical brain regions in working memory (Glabus et al., 2003), episodic memory (Grady et al., 2003), and attention tasks (Rowe et al., 2002). We hope that investigators will incorporate such connectivity approaches more regularly into studies of executive function.

Model-Based Neuroimaging

A final suggestion we would like to make is that neuroimaging studies of executive control are likely to be most informative when designed with explicit reference to an existing theoretical or computational model. Models provide a basis from which to make strong predictions and inferences regarding the nature of specific control mechanisms. In particular, models can specify the conditions under which specific control processes might be engaged, how these will interact with other processes, and, most important, how they should influence behavior. There are now a number of examples in which different types of formal or computational models have been used to design and interpret neuroimaging studies of executive control. Some of the models are based on high-level symbolic or production system frameworks (Anderson et al., 2003; Newman et al., 2003), others on neural network architectures (Botvinick et al., 2001; Holroyd & Coles, 2002), and still others on mathematical formalisms (O'Doherty et al., 2003).

An important component of such work is that it drives a tighter integration between the accumulation of neuroimaging results and the development and refinements of specific executive control theories. For example, in Jones et al (2002), simulations with a computational model of the ACC conflict monitoring theory led to predictions regarding trial-by-trial fluctuations in ACC activity that were tested (and confirmed) in a reanalysis of previously published neuroimaging data. Likewise, Brown and Braver (2005) recently developed a novel computational model of ACC function in which ACC serves as a prediction-learning system regarding the likelihood of error commission in specific contexts. This model was used to derive counterintuitive predictions regarding ACC activity that were tested and confirmed in a subsequent imaging study.

Models can also be used to test predictions regarding how different neural mechanisms of executive control interact to influence behavior during cognitive task performance. Thus, Kerns et al. (2004) conducted an fMRI study of the Stroop to test a prediction of the conflict-monitoring theory regarding how fluctuations in ACC activity produce subsequent shifts in lateral PFC activity, and also corresponding changes in behavioral performance. Similarly, computational models can provide a formal mathematical basis from which to understand how large-scale activity might propagate in a distributed neural control network (Deco et al., 2004; Horwitz et al.,

2000). In short, it is our firm belief that formal theoretical models will be essential for making substantial progress in understanding how large-scale interactions in a distributed network of specialized neural mechanisms can give rise to the emergent phenomena of executive control. Thus, we hope that the synergistic linkage of modeling and imaging will enable the next decade to become a true "golden age" in the cognitive neuroscience of executive control.

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