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Neural Mechanisms of Cognitive Control in Cued Task-Switching: Rules, Representations, and Preparation

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A hallmark of human cognition is its flexibility. We are able to pursue multiple goals or tasks simultaneously, but can also prioritize these in accord with both our internal states and the continually changing nature of the external environment. Moreover, we are able to switch rapidly from one primary task to another, which can have a dramatic effect on the way in which we interact with the environment, even when that environment remains constant (Norman and Shallice, 1986; Miller and Cohen, 2001). This ability suggests that task-related information must be actively represented in a way that can bias perception and action.

The task-switching paradigm has become one of the most widely used tools for studying cognitive flexibility and the nature of task-related representations (Monsell, 2003). Typically, experiments are set up in such a way that participants are exposed to multivalent target stimuli that imply multiple behavioral opportunities (e.g., a letter-digit target pair affording either vowel-consonant or odd-even classification). However, only a single option is to be selected at a given moment, depending on which task is currently set to a higher priority. Task priority is typically specified by the experimenter, either through a pre-experimentally defined sequence (e.g., AABB . . .) or through an explicit task cue that varies randomly from trial to trial. Thus, in the sense that appropriate behavior is made *conditional* on (experimentally defined) changing task priorities, task-switching implies a form of high-level, *rule-guided* control. Rule-guided control provides a means of selecting relevant perceptual dimensions and response parameters based on signals relating to task priority. Moreover, such control is critical for preventing behavior from being erratically driven in a bottom-up fashion by the most salient, but not necessarily most appropriate, stimulus affordances.

In this chapter, we specifically focus on the cognitive and neural mechanisms that subserve the different types of *preparatory* task control that can be

engaged in such multitasking situations. Numerous previous studies have sought to specify the preparatory mechanisms involved when a specific task can be prioritized in preparation for processing task-ambiguous target stimuli (for a review, see Monsell, 2003), often based on explicit task cues indicating the currently relevant task (e.g., Sudevan and Taylor, 1987; Meiran, 1996; Brass and von Cramon, 2002). Surprisingly little (if anything) is known about the reverse preparatory condition, in which it is possible to consider the multiple behavioral opportunities afforded by task-ambiguous target stimuli before a final task decision can be made based on an unambiguous task cue (for exceptions in the behavioral literature, see Shaffer, 1965, 1966; Gotler and Meiran, 2003). To close this gap in the literature, we have recently begun to systematically compare the mechanisms of preparatory control involved in these two situations in a series of behavioral and brain imaging studies.

As described later, this seemingly straightforward comparison of two preparatory conditions (that we term "advance-cue" versus "advance-target") during multitasking has proven highly informative, but also reveals a number of tricky theoretical issues regarding the nature of the underlying functional and neural architecture of task control. Specifically, we examine three key issues in this chapter. (1) We examine whether cue-based task prioritization should be conceptualized as a distinct function in terms of both cognitive architecture and brain localization, or if not, what kind of alternative theoretical views are possible. (2) We argue that a comprehensive account of task control must consider the distinction between *attentional* control mechanisms guiding action selection based on perceptual stimulus representations versus *intentional* control mechanisms guiding action selection based on action goal representations. (3) We discuss the possibility that top-down control might not be limited to the biasing of action selection processes, but that certain phenomena can be better explained by assuming an additional control point at the interface between action selection and concrete motor planning—especially when behavior relies on novel and arbitrary task rules. Finally, we begin an attempt to determine the extent to which the two preparatory mechanisms can be considered "voluntary."

Our theoretical views of these issues draw heavily on the results of behavioral and imaging studies of task-switching that we have recently conducted (Ruge and Braver, in preparation; Ruge et al., submitted). We describe these findings briefly, and discuss their theoretical implications in relation to a broad range of other empirical and conceptual approaches. In particular, we hope to convey a novel perspective on task-switching phenomena that we believe opens up important new future directions for research and understanding.

SELECTIVE REVIEW OF THE TASK-SWITCHING LITERATURE

Before we turn to the theoretical issues mentioned earlier, we set the stage by briefly summarizing one of the most frequently discussed issues in the extant task-switching literature. As the label "task-switching" suggests, most studies

have been interested in the processes that enable task priority *changes* from one trial to the next (Monsell, 2003; Wager et al., 2004). One key assumption, probably inspired by early neuropsychological observations of so-called "perseverative behavior" (Milner, 1963; Stuss and Benson, 1984), is that there is a default tendency to repeat the previously performed task, and that this tendency has to be overcome if a different task must be implemented. Indeed, behavioral task-switching studies have consistently shown that task-switch trials are more demanding than task-repeat trials, as indicated by behavioral switch costs (i.e., performance differences between the two types of trials). However, the theoretical interpretation of this observation remains a focus of heated debate.

One account suggests that, after a task priority change, implementation of the new task can occur only after an active reconfiguration of relevant processing routines, akin to a mental "gear shift" (Meiran, 1996; Monsell, 2003). If this were true, the implementation of a new task should benefit from additional time for preparatory "task set" reconfiguration, resulting in a reduction of switch costs. Many studies have used the *cued* task-switching procedure, in which a random task cue indicates which of (typically) two alternative tasks to prioritize in each trial. This procedure allows for a well-controlled examination of task preparation effects, by presenting the cue at various time intervals before a task-ambiguous target stimulus. Typically, switch costs are reduced when the preparatory (cue-target) interval is longer. This finding is consistent with the idea that task set reconfiguration can be at least partially completed before target stimuli are presented (Rogers and Monsell, 1995; Meiran, 1996).

In contrast, this finding is often believed to be less compatible with an alternative explanation of switch costs, here referred to as the "competition-resolution account" (e.g., Allport and Wylie, 2000). According to this view, a new task set is not established during the preparatory interval. Rather, the new task set is believed to emerge during the course of task implementation (i.e., during target processing) as the result of the successful resolution of competing processing tendencies associated with: (1) the current task cue, and (2) the current stimulus affordances, which are biased toward the more recently performed task (this bias facilitates performance in repeat trials, but interferes with performance in switch trials). However, a number of authors have recently pointed out that the preparation-related reduction of switch costs is, in fact, equally consistent with the competition-resolution account as it is with the reconfiguration account. Under the competition-resolution account, a prior task cue confers a temporal advantage to the processing tendencies associated with the cue, which provides protection against the activation of misleading processing tendencies triggered by subsequently presented targets (Goschke, 2000; Gilbert and Shallice, 2002; Yeung and Monsell, 2003).

A potentially more conclusive approach for distinguishing between these two theoretical accounts is to isolate and selectively analyze neural activity occurring during the preparation interval (Ruge et al., 2005; Badre and Wagner,

2006). According to the reconfiguration account, preparatory activation should be increased in switch trials compared with repeat trials, reflecting the additional effort to reconfigure the task set. In contrast, the competition-resolution account would predict equal preparatory activation levels for switch and repeat trials, because target-induced competition is absent at this point. The pattern of results across studies and methods is, however, rather inconsistent. In support of the competition-resolution account, event-related functional magnetic resonance imaging (fMRI) studies of cued task-switching usually do not report reliable preparatory activation differences between switch and repeat trials. Moreover, when the cue-target interval is short (which should produce stronger target-induced interference, according to the competition-resolution account), blood-oxygen level–dependent (BOLD) activation is typically increased for switch trials versus repeat trials (Dove et al., 2000; Brass and von Cramon, 2004; Ruge et al., 2005; Badre and Wagner, 2006). In contrast, and in support of the task set reconfiguration account, event-related electroencephalogram (EEG) studies do consistently report preparatory activation differences between switch and repeat trials (Rushworth et al., 2002; Kieffaber and Hetrick, 2005; Nicholson et al., 2005). These discrepancies between the types of methods have not yet been resolved, and may require more systematic comparison of fMRI and EEG studies.

In particular, four key issues still need to be addressed: (1) There may be systematic procedural differences in the studies conducted across the two methods (e.g., different lengths of the cue-target interval or the response-cue interval). (2) The fMRI and EEG studies may be picking up on different aspects of neural activation (e.g., synchronous or oscillatory effects between brain regions that affect EEG more than fMRI). (3) Event-related potential activation may be more strongly dominated by repetition priming effects that occur at the time of the cue. Such repetition effects are typically confounded with task-switch effects (see Logan and Bundesen, 2004), and might originate and propagate from brain regions typically ignored in fMRI studies of executive control, such as occipital cortex. (4) An fMRI study may be less sensitive when effects occur in a temporally variable manner. For example, Braver et al. (2003) showed that, in a subset of trials presumably associated with the highest degree of task preparation (because reaction times were the fastest), a switch-related enhancement of preparatory BOLD activation was, in fact, observed in posterior parietal cortex. The reason might be that only in these trials were preparatory processes implemented quickly and reliably during the preparation interval.

NEW PERSPECTIVES

In this chapter, our goal is to step back from this debate and examine a number of alternative approaches and conceptualizations that might be important for characterizing cue-based and target-based processes in task-switching. First, regarding cue-based processes, we start from the assumption that performance

during multitasking conditions requires determination of the current task priority before task implementation, regardless of whether a *new* task needs to be implemented in a given trial, and whether task switches involve task set reconfiguration processes (see Rubinstein et al., 2001). In other words, presentation of a task cue provides a clear signal regarding which task has highest priority, regardless of whether that task also had high priority in a previous trial. Thus, instead of focusing on the potential functional differences between switch and repeat trials, our aim is to scrutinize in more detail the nature of cue-based task prioritization as a common feature of both trial types. Second, we adopt a perspective on target-based processes that goes beyond the dichotomy between cue-based top-down control (i.e., strictly facilitative) and target-induced bottom-up processes (i.e., primarily interfering). Instead, we characterize target-based preparatory processes in terms of their potentially active role in generating task-related opportunities implied by the current stimulus affordances. Figure 12–1 depicts the experimental setup we used and the methodological issues one faces when preparatory BOLD activation is to be isolated.

Task Prioritization

How can we operationalize the functional characteristics of task prioritization? One approach is to ask under what circumstances prioritization is *necessary*. Prioritization is obviously required in situations in which stimuli afford multiple tasks (multivalent stimuli). One straightforward experimental manipulation, therefore, is to compare multivalent stimuli with univalent stimuli, which afford only a single task and thus do not require task prioritization (Rubin and Meiran, 2005; Rubin et al., submitted). Similarly, one could compare mixed-task blocks with single-task blocks, again, assuming that task prioritization becomes unnecessary when the same single task is implemented over and over again (Braver et al., 2003; Rubin and Meiran, 2005; Rubin et al., submitted).

However, one potential caveat to both approaches is that, even in apparently unambiguous situations, participants might still need to prioritize, because even with only one available task, there is always the possibility of not carrying it out (except in the case of highly automatized behaviors that tend to be initiated in an obligatory and ballistic fashion). Indeed, a study by Rubin et al. (submitted) showed that, although prefrontal and parietal areas exhibited enhanced event-related activation for mixed-task block trials as well as for multivalent target stimuli, the same areas were still substantially activated above baseline for single-task block trials and for univalent stimuli. However, results obtained by Braver et al. (2003) suggest that mixed-task blocks and single-task blocks might not differ so much in terms of the transient processes engaged on a trial-by-trial basis, but that task-mixing is accompanied by a specific sustained processing mode maintained across an entire experimental block.

Alternatively, instead of studying the circumstances under which task prioritization is *necessary*, one can manipulate the conditions under which it is
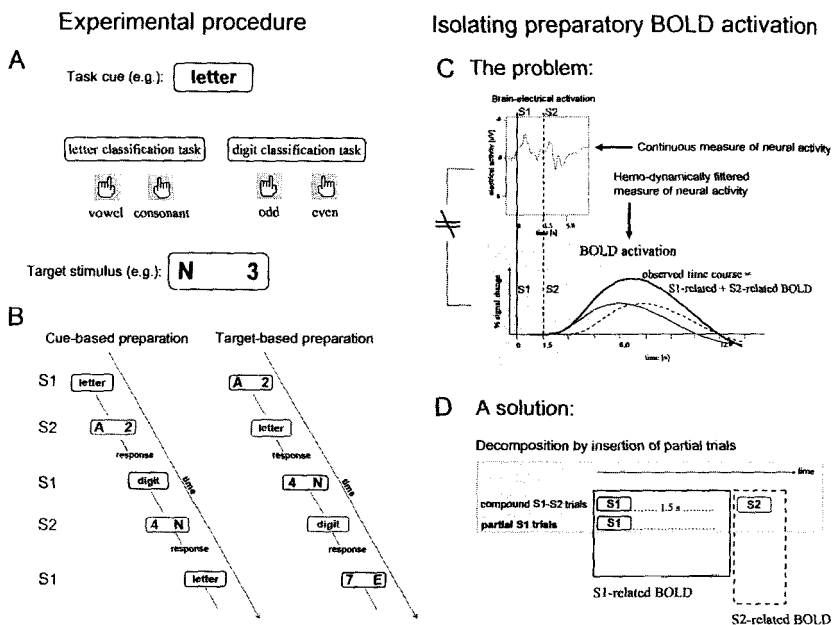
Experimental procedure   **Isolating preparatory BOLD activation**

A

Task cue (e.g.): [**letter**]

C The problem:

[letter classification task]   [digit classification task]

🤚   🖐   🤚   🖐

vowel consonant   odd   even

Target stimulus (e.g.): [**N   3**]

B

Cue-based preparation   Target-based preparation

S1 [letter]   [A   2]

S2 [A   2]   [letter]

response   response

S1 [digit]   [4   N]

S2 [4   N]   [digit]

response   response

S1 [letter]   [7   E]

D A solution:

Decomposition by insertion of partial trials

Figure 12–1 The basic task design that was used in our own studies presented in this chapter (*A* and *B*). The analysis of functional magnetic resonance imaging data collected in such S1-S2 designs needs to take into account temporal overlap between event-related blood-oxygen level–dependent (BOLD) responses associated with consecutive S1 and S2 events appearing in a fixed order (*C* and *D*). *A*. Participants were made familiar pre-experimentally with the task rules for letter classification and digit classification. In each trial, a task cue (e.g., letter) indicated which task to implement in the presence of a task-ambiguous target stimulus (e.g., "N 3"). *B*. The order of the cue and target presentation was varied across two blocked conditions, either cue-target or target-cue. The main goal was to compare preparatory BOLD activation associated with advance cues versus advance targets. *C*. Unlike brain electrical event-related responses, which directly reflect the time course of neural activity associated with consecutive events, the BOLD response reflects a hemodynamically filtered measure of the underlying neural activity that causes massive signal overlap. *D*. To reconstruct the BOLD components associated with S1 and S2 events occurring within a single trial, we used a deconvolution technique based on the insertion of partial S1-only trials (Ollinger et al., 2001; Serences, 2004).

possible. Generally speaking, priority information needs to be available, and in the cued task-switching paradigm, it is the task cue that is supposed to convey it.[1] In contrast—and this constitutes the key experimental innovation we introduced—advance task-ambiguous target stimuli demand a priority decision, but do not (by definition) provide the kind of priority information from which task selection could occur. Thus, we hypothesized that brain areas involved in task prioritization should be activated by advance task cues, but not by advance-target stimuli (Fig. 12–2).
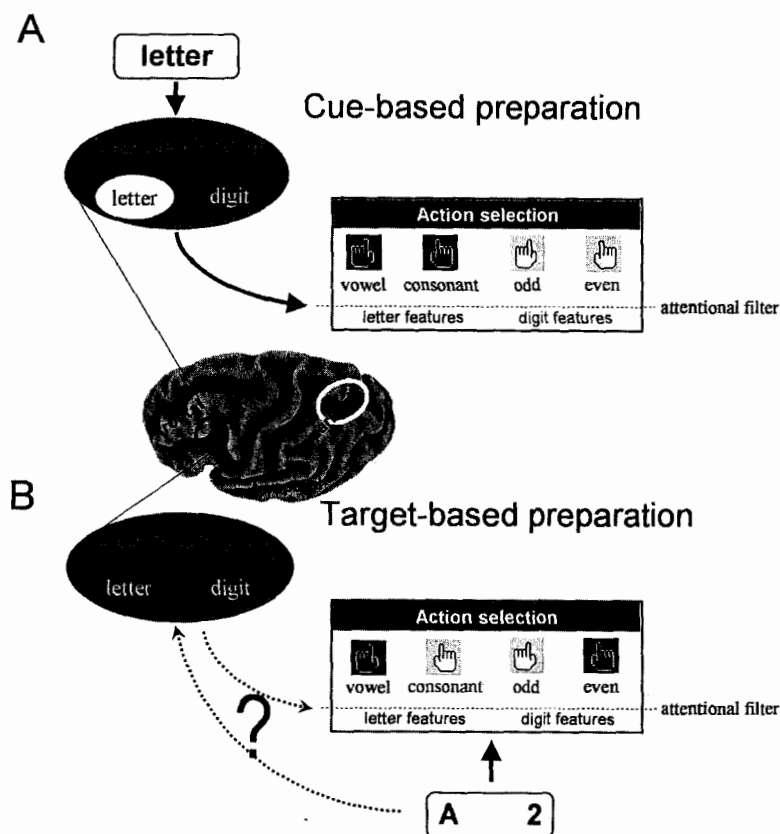
Figure 12-2 Hypotheses regarding the involvement of a putative task prioritization mechanism localized within posterior lateral prefrontal cortex. A. Presentation of advance task cues is supposed to enable task prioritization based on a prefrontal representation of abstract task demands that can bias lower-level action selection processes so that they will operate preferentially on target input that matches the currently task-relevant perceptual dimension. B. According to our initial hypothesis, target stimuli would not engage the prioritization mechanism because they are, by definition, task-ambiguous and thus do not convey information that would significantly affect a priority decision.

Hierarchical Model

In fact, such a prediction is very much in line with rather traditional, but still popular and highly intuitive, hierarchical models of executive control that postulate that regions within lateral prefrontal cortex (PFC): (1) represent task demands or task goals in a relatively abstract form, and (2) sit at the top of a task-processing hierarchy by providing the top-down information needed to resolve competing processing tendencies developing in parallel on lower

hierarchy levels in other parts of the brain, such as posterior parietal cortex (e.g., Norman and Shallice, 1986; Cohen et al., 1990). A number of previous studies have been conducted in an effort to isolate cue-related preparatory activation, but these studies did not include a direct comparison with target-based preparation. In such studies, one frontal cortex region in particular has been most consistently identified in paradigms with advance task cues, namely, the posterior part of inferior frontal sulcus (Brass and von Cramon, 2002; Bunge et al., 2003; Sakai and Passingham, 2003; Ruge et al., 2005). The same region, sometimes referred to as "inferior frontal junction" (IFJ) [Derrfuss et al., 2005], also exhibits elevated activation under high task-interference conditions, suggesting that its functional role is not restricted to cue-based task preparation per se. More generally, it appears to process task information in such a way as to exert top-down task control when required. See Figure 12–3 (see color insert) for the results of a recent meta-analysis (Koechlin et al., 2003; Derrfuss et al., 2005; Ruge et al., 2005).

Although these observations are consistent with a cue-specific task prioritization function of IFJ, it remains to be answered whether advance task cues are necessary or merely sufficient to engage the presumed high-level task representations. If lateral PFC areas, such as IFJ, were also activated by advance targets, thus demonstrating that advance task cues are not a *necessary* condition, the standard hierarchical model would be called into question. Indeed, when we conducted the direct comparison of cue-related and target-related preparatory activation (Ruge et al., submitted), we found results that called into question the original interpretation that IFJ implements a cue-specific task prioritization mechanism. Specifically, we found that neither IFJ nor any other
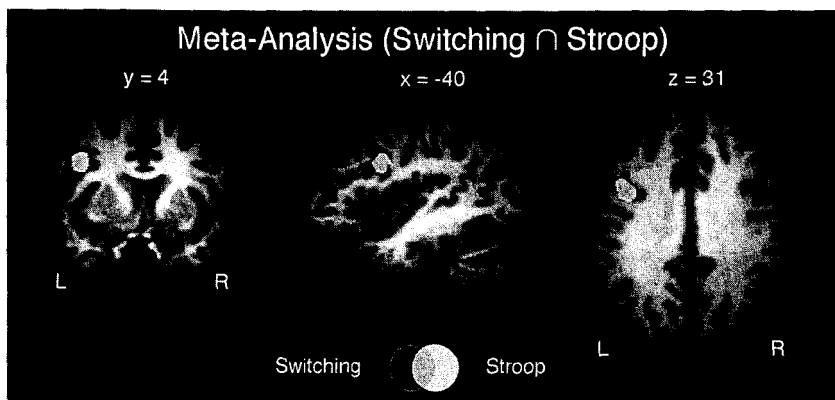

Figure 12–3 Meta-analysis conducted by Derrfuss et al. (2005), demonstrating the involvement of inferior frontal junction across different studies that commonly shared a strong demand for top-down task control.
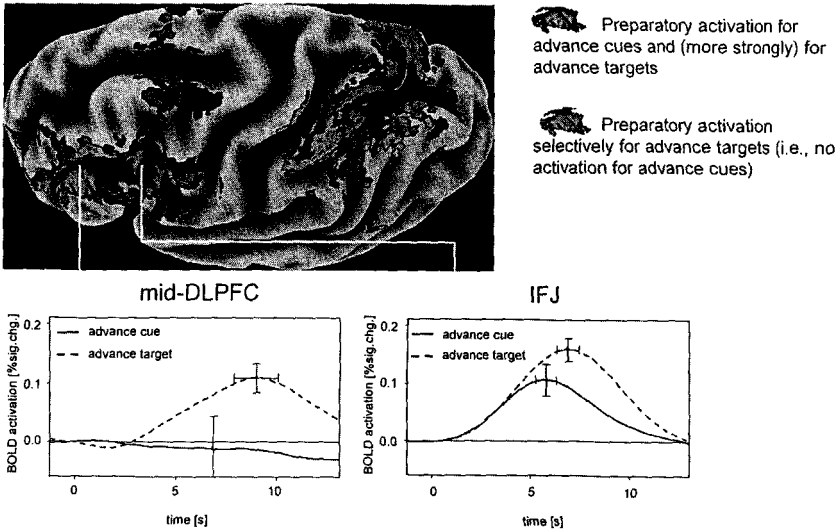
Figure 12-4 Two different patterns of preparatory brain activation associated with advance task cues, advance-target stimuli, or both. Remarkably, neither IFJ nor any other region was selectively (or even more strongly) activated for advance task cues. Conversely, a number of areas, such as mid-dorsolateral prefrontal cortex, were selectively activated by advance targets. mid-DLPFC, mid-dorsolateral prefrontal cortex; IFJ, inferior frontal junction.

brain region was selectively activated for advance cues. Instead, all regions that were activated by advance cues (including IFJ) were equally or even more strongly activated for advance-target stimuli (Fig. 12–4; see color insert). This surprising result seems to prompt a reconceptualization of the standard hierarchical account of task prioritization. Next, we provide two possible explanations that attempt such a reconceptualization.

Nonhierarchical Model I: Cumulative Prioritization

A good starting point is the computational model by Gilbert and Shallice (2002) depicted in Figure 12–5. One important difference between this model and related previous computational models (e.g., Cohen et al., 1990) is that task-ambiguous target stimulus input can fully activate the processing pathways for both tasks (word-reading and color-naming) in parallel up to the level of abstract task demands. In this sense, the model can be considered nonhierarchical,[2] and it seems to be suited to accommodate our brain activation results.

According to such an interpretation, abstract task demands (assumed to be represented within IFJ) are activated directly and equally well by both cues and
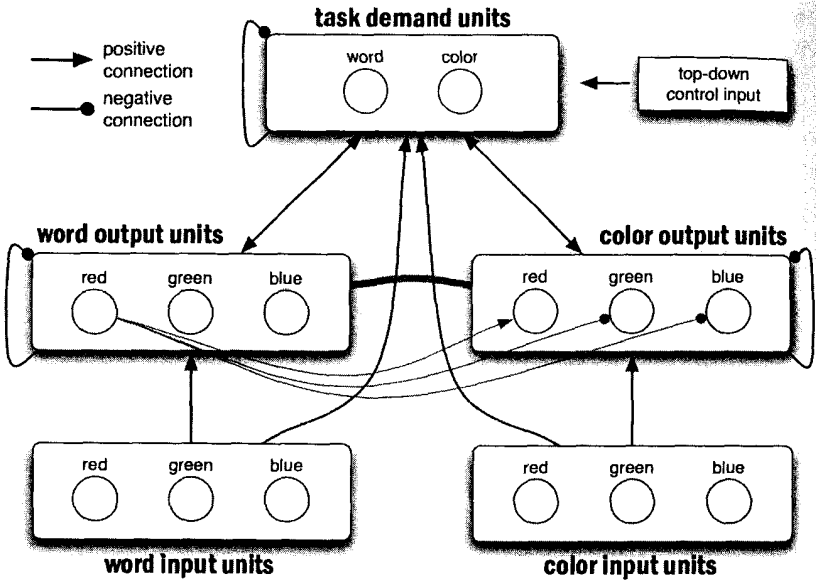
Figure 12-5 Computational task-switching model by Gilbert and Shallice (2002), in a modified graphical representation. The novel contribution of this model is that target stimulus input is allowed to activate abstract task demand units (word-reading and color-naming), thereby activating its own task-related processing pathways.

targets, with cue-associated task information being relayed via the task demand layer in exactly the same fashion as target information. From this perspective, there is no true functional difference between a situation in which multiple task demands are activated in parallel by multivalent targets and a situation in which a single task demand is activated by an unambiguous task cue. Accordingly, task prioritization is not a distinct functional (and neuroanatomical) entity specifically associated with task cues, but instead, it emerges cumulatively, with the representation of task demands settling into a unique and stable state as soon as sufficient evidence has been accumulated for a single task. This happens immediately after an advance task cue, but it requires additional information when the representation of task demands remains in an undecided state after advance multivalent targets. Thus, according to this alternative "cumulative prioritization" account, task control is a continuously evolving process, with no privileged route of access to task demand representations.

Interpreted in this way, our imaging results can also potentially arbitrate a debate within the behavioral task-switching literature concerning the processing level at which stimulus-induced task competition occurs (Hübner et al., 2004). Although there is now ample evidence that target stimuli are not merely passive objects of top-down cue-based control biasing (e.g., Allport and

Wylie, 2000; Waszak et al., 2003; Yeung and Monsell, 2003), it has been unclear whether targets activate task-related processing pathways at the level of abstract task demands (presumably represented within lateral PFC), or instead, at the lower level of specific stimulus-response (S-R) associations (presumably represented within posterior parietal cortex). Under the assumption that IFJ represents abstract task demands, our results clearly favor the former interpretation.

Nonhierarchical Model II: Compound Cue-Target-Response Mappings

The cumulative prioritization model is a nonhierarchical account of task control, in the sense that it abandons the idea of a *cue-specific* task prioritization module. However, it still assumes a control hierarchy in the sense that higher-order abstract task demands are used to modulate the activation strength of lower-order representations: the actual S-R mapping rules. Alternatively, it is possible to entirely abandon the idea that a representation of abstract task demands is involved in task control. Instead, IFJ could directly code the actual task rules by integrating task cues and target categories into compound S-R mappings using conjunctions, such as, "if the cue indicates letter AND the target is a vowel, then press the right button OR if the cue indicates letter AND the target is a consonant, then press the left button." From this perspective, IFJ is activated by both advance cues and advance targets because they both provide information that can be used to partially instantiate the same compound mapping rule. This view of IFJ-mediated task control is reminiscent of Logan and Bundesen's (2003, 2004) account of cue-repetition effects, which led them to the conclusion that "... the explicit task cuing procedure is not a viable method for investigating executive control." (Logan and Bundesen, 2004, p. 839). An alternative, and in our view, more adequate conceptualization would be that the employment of compound mapping rules in cued task-switching genuinely constitutes an "executive control" function. The reasoning is that the tasks are typically novel and only weakly practiced. Therefore, compound S-R mappings may have to be computed in an online, possibly verbally coded fashion (Goschke, 2000), within working memory. Maintaining compound S-R mappings in working memory (when necessary) might be critical because the components of the conjunction might be presented in a temporally separated fashion and thereby might require a mechanism capable of cross-temporal integration to complete the conjunction. Indeed, these conjunctive working memory representations may be the instantiation of what is meant by the term "rule-like" when describing the mechanisms of task control (Bunge, 2004).

Target-Specific Preparatory Processes

Regardless of which of these models one prefers, they share one common feature. In these models, control over action selection is assumed to be exerted

via "attentional" mechanisms that guide the transformation from perceptual stimulus representations into response options according to pre-experimentally instructed S-R mapping rules. Furthermore, both cue-based and target-based preparatory mechanisms are presumed to share this attentional (i.e., S-R) pathway. Yet, we would like to suggest that this model, as intuitive as it may be, is not complete. Instead, we argue that a more comprehensive account of *target-based* preparatory control must take into consideration two additional levels of processing.

First, a viable model must incorporate an *intentional* control path, where behavioral options are selected in accordance with potentially obtainable action goals suggested by the current state of the environment (Meiran, 2000b; Waszak et al., 2005). Importantly, we make a clear distinction between "intention," referring to the encoding of action goals (i.e., the anticipated action effects), and "volition," referring to the actual commitment to implement a planned action based on cost-benefit considerations.

Second, such a model needs to take into account the fact that the generation of future behavioral options based on abstract mapping rules (S-R or goal-response associations)—hereafter referred to as "action selection"—is not identical to the planning of concrete motor responses based thereon. We will argue that the interface between abstract action selection and concrete motor planning is controlled by an additional rule type related to the consideration of subjective cost-benefit tradeoffs.

Intentional Control of Action Selection

Within the task-switching context, Meiran (2000a, b) was the first to propose that concrete target stimuli might not only activate action selection processes based on perceptual stimulus representations, but also trigger additional action selection processes based on representations of action goals, which are themselves supposed to be independent of cue-based control biases. This conclusion was derived from the observation that cue-based preparation reduces subsequent target-induced competition on a perceptual level, but fails when competition among action goals is present.

Additional support for these conclusions comes from brain imaging studies. One study compared task-switching conditions in which the competing tasks comprised overlapping goal-response associations (referred to as "response meanings" in that study) against a control condition in which there was no overlap. The overlap condition was associated with increased activity in mid-dorsolateral PFC (mid-DLPFC), suggesting that this might be the prefrontal region that contributes to intention-based conflict resolution (Brass et al., 2003). Yet another task-switching study that specifically focused on cue-based preparation did *not* observe activity in mid-DLPFC (Ruge et al., 2005). This pattern of results suggests that intentional control is only weakly (if at all) engaged during cue-based preparation, again supporting the earlier performance-based conclusions.

To summarize the findings so far, there is evidence that intentional processes are associated with concrete target stimuli (but not task cues), and that specifically, mid-DLPFC is implicated in intentional control. Still missing in this picture is evidence showing that target-based intentional processes can be engaged in preparation. If this were true, we would expect preparatory activation in mid-DLPFC after advance-target stimuli. Our recent study (Ruge et al., submitted) replicated the absence of mid-DLPFC activity during the preparatory period for the advance-cue condition. At the same time, we found, as hypothesized, that preparation after advance targets was associated with robust activity in this brain area. Moreover, as shown in Figure 12–4, the comparison of cue-related and target-related preparatory activation reveals that the distinct neuronal signatures of attentional control (preparatory activation for both advance cues and advance targets) versus intentional control (preparatory activation selectively for advance targets) are not limited to IFJ and mid-DLPFC, respectively. Rather, the same two activation patterns are found in a number of other brain regions (parietal cortex along IPS, dorsal premotor cortex, and medial frontal cortex), thereby forming two widely distributed, but segregated control networks.

Although the empirical results, both behavioral and imaging, do quite convincingly converge onto a dual-path (attention-intention) model, it still seems important to discuss the somewhat unusual notion that intentional control can be externally triggered by target stimuli. In fact, a popular view in the literature is that intentional control becomes relevant specifically when action selection is *not* fully determined by the current stimulus input, but instead needs to be based on *internally* generated future action goals (e.g., Frith et al., 1991; Jahanshahi and Dirnberger, 1999).[3] Yet, from a general theoretical standpoint, we do not see any good reason why intentional processes should not also be triggered externally (i.e., activated by the appearance of stimuli that are associated with particular action goals). For instance, to give a real-world example, the fasten-your-seat-belt alarm ringing in your car suggests the action goal of silencing it (by fastening your seat belt).[4]

Based on the notion that intention is associated with the "internal" generation of action goals, many studies of intentional control have used free selection tasks. The respective brain imaging studies have typically identified mid-DPLFC as one key brain region (besides medial frontal cortex) involved in the internal intention generation process (e.g., Frith et al., 1991; Jahanshahi and Dirnberger, 1999). Mid-DLPFC is exactly the region we reported to be involved in externally triggered target-based intentional control. This suggests that this brain region might be engaged during both internally guided and externally guided intention. Indeed, a recent fMRI study conducted by Lau et al. (2004) *directly* compared the two situations and found that mid-DLPFC is engaged, regardless of whether action selection is externally or internally guided. In contrast, it was medial frontal cortex that seemed to be specifically associated with internal action selection.

The perspective of externally guided intention becomes particularly clear in the light of the "mirror neuron" literature (Rizzolatti and Craighero, 2004; Arbib, 2005). The central notion of this work is that there exists a special class of neurons that codes actions according to their anticipated observable effects (i.e., action goals) [see also Hommel et al., 2001]. This interpretation is based on the intriguing finding that such neurons are active not only when an action is about to be performed, but also when the same action is observed being performed by another individual (i.e., when the effects of another person's actions are perceived). This data pattern demonstrates that intention (i.e., activation of action goals) can easily be triggered *externally* by adequate stimulus input. Brain imaging studies seeking to identify the human equivalent of the monkey mirror neuron system have revealed a set of brain areas that overlap remarkably well with the brain regions we have found to be selectively engaged during target-based preparation, including the anterior part of intraparietal sulcus, and Broca's area (BA 44), which is supposed to be the human homolog of the monkey's mirror neuron area F5 within ventral premotor cortex (e.g., Buccino et al., 2001; Grezes et al., 2003; Manthey et al., 2003; Hamilton and Grafton, 2006; for a review, see Rizzolatti and Craighero, 2004). Mid-DLPFC does not seem to be as consistently implicated in human activation studies. However, cortical connectivity studies in monkeys suggest that mid-DLPFC has a strong projection to the anterior intra-parietal sulcus (aIPS), and also, to a lesser degree, with ventral premotor area F5 (Rizzolatti and Luppino, 2001).

Action Selection Versus Motor Planning

So far, our discussion of target-based preparation has dealt with the distinction between attentional and intentional action selection processes that generate response options based on either abstract S-R rules or abstract goal-response rules, respectively. In this section, we argue that the examination of target-based preparation is also useful for elucidating the putative role of mechanisms that regulate the transfer from an "action selection" stage into a final "motor planning" stage. The conceptual distinction between these two processing levels becomes especially useful in task situations for which motoric response codes are *not* automatically activated via associative shortcuts that are either pre-experimentally overlearned (e.g., word-reading in the Stroop task) or otherwise predisposed, for instance, by their spatial compatibility (e.g., Simon task). When, instead, novel and relatively unpracticed tasks are involved, we postulate that the transfer from action selection into motor planning processes is under a more flexible control regime.

The idea is that action selection processes first generate abstract behavioral options that may or may not be translated into concrete motor plans. Such flexibility in motor planning is of particular relevance in the context of multivalent advance-target stimuli that can present in one of two opposing types. On one hand, advance targets can be *congruent* (i.e., different tasks require the same response; for example, the target "A 7," if both vowels and odd digits

require a left-button response). In this case, it would be of great use to engage in advance motor planning to prepare a single motor response, which could then be executed right away, as soon as the subsequent cue gives the "go" signal. On the other hand, for *incongruent* advance targets (i.e., different tasks require different responses, such as "A 8" in the example discussed earlier), such advance motor planning would have costs as well as benefits because the preparation of motor plans would lead to competition between mutually incompatible responses that could create interference before and during response execution. Thus, in contrast to congruent trials, for incongruent trials, the cost of the extra effort required for preparation of motor responses may outweigh the potential benefits to be gained in response time (Fig. 12–6).

The presence of such a cost-benefit tradeoff related to motor planning makes it clear that different preparation strategies are possible. It is therefore of interest to determine how actual participants decide to optimize the interface between action selection and motor planning. A first strategy would be always to defer the start of motor planning until the cue is presented to effectively prevent interference in case of incongruent targets, yet, at the cost of
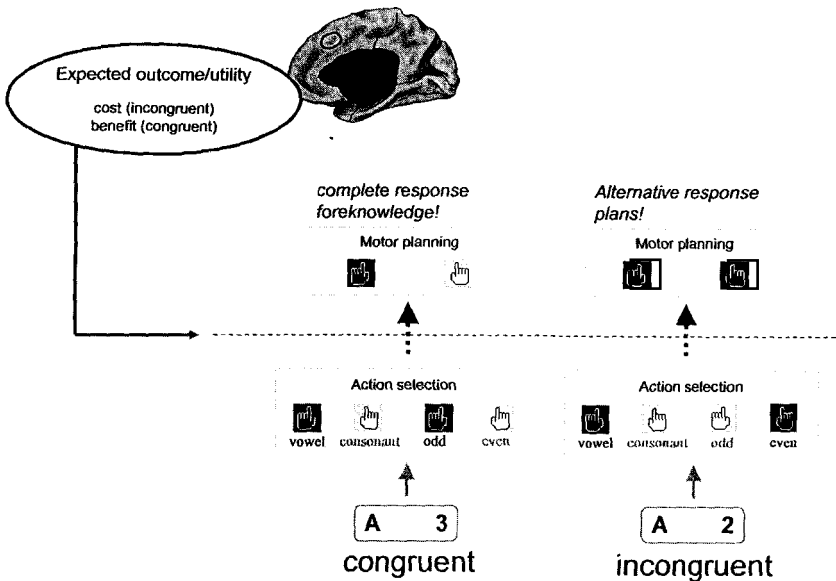

congruent   **incongruent**

Figure 12-6 Model assumptions about the involvement of strategic control at the interface between action selection and motor planning processes. The core assumption is that this interface is regulated by the subjective evaluation of expected utility (implemented by medial frontal cortex) associated with preparation based on congruent versus incongruent advance-target stimuli.

suboptimal preparedness in case of congruent targets. A second strategy would be always to start motor planning right away after advance-target presentation, to be optimally prepared in case of congruent targets, yet, at the cost of risking motor interference in case of incongruent targets. Of course, a third, mixture strategy is also possible, in which the decision to engage in preparatory motor planning occurs flexibly on a trial-by-trial basis, depending on whether the current target is recognized as congruent or incongruent.

We examined this issue in our recent study of advance-target preparation (Ruge et al., submitted). We found evidence that different individuals seemed to adopt different strategies (Fig. 12–7). This interpretation is most strikingly evidenced by the observation that one group of participants ("congruency-sensitive") exhibited a large speeding up in reaction time for advance congruent targets compared with incongruent targets. Yet, in the other group of participants ("congruency-insensitive"), performance in congruent and incongruent targets was almost identical, in terms of reaction time. We also examined brain activation patterns as a function of this behavioral group difference, and observed a complex pattern (Fig. 12–7). We found that group differences in preparatory brain activity were observed in all advance-target trials, not just congruent ones. This suggests that participants were not adopting the mixture strategy of engaging in preparatory motor planning on a trial-by-trial basis, depending on whether the current target is congruent (engage) or incongruent (do not engage). Instead, we observed that the congruency-sensitive group had increased preparatory activity in medial frontal regions (along with other regions) compared with the congruency-insensitive group, even in incongruent trials.

These results suggest that participants in the congruency-sensitive group adopted a global strategy (i.e., maintained across all individual trials) to generally engage in advance motor planning, irrespective of the status of congruency. This interpretation was also supported by the observation that, during the final response planning and execution phase after the cue, brain activation in the congruency-sensitive group was reduced for congruent targets and increased for incongruent targets in posterior parietal cortex and dorsal premotor cortex—notably, in the caudal part that has been postulated to represent more concrete motor codes, as opposed to the more abstract, "cognitive" representation of motor plans represented in the rostral portion (Picard and Strick, 2001). This activity pattern is exactly what would be expected of the congruency-sensitive participants if they: (1) benefited in congruent trials from an already prepared single motor response ready for execution (less planning effort, reduced activation), and (2) faced a disadvantage in incongruent trials because of the concurrently prepared competing motor response (more effort to eliminate erroneous response tendencies, enhanced activation).

To conclude, these results tentatively suggest that the interface between action selection and motor planning processes is under voluntary control—for two reasons: (1) Motor planning seems to be an *optional* strategy adopted by only a subset of participants, instead of being the inevitable result of
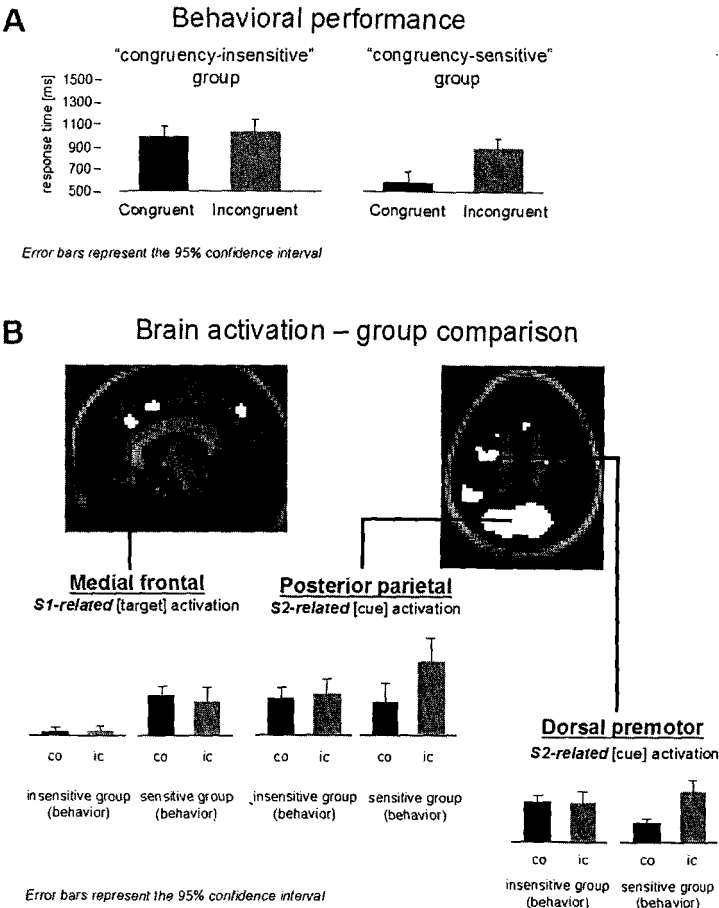
A   **Behavioral performance**

Error bars represent the 95% confidence interval

B   **Brain activation – group comparison**

Medial frontal   **Posterior parietal**
S1-related [target] activation   *S2-related* [cue] activation

Dorsal premotor
S2-related [cue] activation

Error bars represent the 95% confidence interval

Figure 12–7 *A.* Comparison of behavioral performance (response times) for congruent and incongruent advance targets. A distributional analysis of congruency effects suggested a subdivision into two groups of subjects, either showing a strong speed-up for advance congruent targets or showing no difference between congruent and incongruent advance targets. *B.* Three different patterns of brain activation that followed the group difference, defined according to the presence or absence of a behavioral congruency effect. co, congruent; ic, incongruent.

automatic priming processes taking place in each and every participant. (2) This presumed strategy difference was accompanied by selective medial frontal cortex activation for the congruency-sensitive group. As noted earlier, medial frontal cortex is a brain region that has long been associated with the initiation and perpetuation of voluntary motor behavior (Barris and Schuman, 1953; Paus, 2001; Rushworth et al., 2004). In the next and final section, we elaborate on the idea that only some components of task preparation might be volitional.

Voluntary Control?

A putative hallmark of executive control is its presumed voluntary nature. Although volition is certainly the most fascinating aspect of higher-order brain function, it is also an enigmatic and elusive one. As we have mentioned earlier, in the context of free selection tasks, we draw a clear conceptual line between intention and volition. On one hand, the notion of intention is used to refer to the activation of action goals (i.e., anticipated action effects) and action selection processes based thereon (e.g., Hommel et al., 2001). On the other hand, the notion of volition is used to refer to the actual initiation and perpetuation of behavior based on the assessment of expected subjective outcome or utility in terms of cost-benefit tradeoffs (e.g., Rushworth et al., 2004). Thus, we distinguish between anticipated action *effects* and action *outcomes*. We use the term "effect" to refer to an expected perceptual or conceptual state produced by an action, and the term "outcome" to refer to the subjective value (in terms of reward components) associated with that expected state. Thus, volitional processes may be more directly motivational (i.e., "hot"), whereas intentional processes are more coldly cognitive.

Maybe the most intuitive observable property of voluntary control is its optional engagement. Based on this criterion, we suggested in the preceding section that target-based preparation involves a volitional component operating at the interface between action selection and motor planning processes. However, a potential weakness of this conclusion is that it relies on a post hoc interpretation of naturally occurring interindividual differences. It would therefore be desirable to employ procedures that enable tighter experimental control over volitional processes. A number of reasonable experimental approaches have been suggested in the context of cue-based preparation, two of which we discuss in more detail below.

Measuring Volition I: Optional Engagement of Preparatory Processes

The first experimental approach to measuring volition is based on the presumption that participants are, in principle, free *not* to use the task cue.[5] In this case, they would exhibit "utilization behavior" (Lhermitte, 1983; Shallice et al., 1989) driven by the currently most salient stimulus affordances. DeJong (2000) followed this line of reasoning to explain the often limited effectiveness of cue-based preparation by postulating that participants would occasionally fail to initiate cue-based preparation. Based on a distributional analysis of within-subject response times, DeJong demonstrated that participants are optimally prepared in a subset of trials (i.e., show no switch costs), but completely unprepared (i.e., show switch costs equivalent to having no preparation time) in another subset of trials. The all-or-none character of task preparation suggests that it is optional, and therefore under voluntary engagement. If, instead, preparation was achieved via automatic cue-based priming processes, the degree of preparedness (measured via the amount of residual switch cost) should have followed a unimodal distribution across trials.

Measuring Volition II: Conscious Accessibility of Preparatory Processing

The second experimental approach to measuring volition was pursued by Meiran et al. (2002), who allowed participants to have full control over their level of preparedness by self-determining how long to process an advance cue. Thus, preparation time was self-paced, and target stimuli appeared on the screen only after a readiness response was given. The rationale for this procedure was the assumption that voluntary control operates in a *conscious* mode. Participants should therefore be able to estimate their own state of preparedness. Based on this assumption, one can make inferences based on the relationship between preparation time and target response time. To derive precise predictions for this relationship, we need to apply somewhat complex reasoning. First of all, in a perfect world, self-pacing would allow each participant to be optimally prepared in every trial, resulting in zero variability of the actual state of preparedness, which would also imply a zero correlation between preparation time and response time.

Assuming a more realistic model, subjective estimates of the true state of preparedness should be subject to both interindividual and intraindividual variability. *Interindividually,* different participants might systematically adopt different criteria for when they feel sufficiently well prepared. This implies that more liberal (i.e., impulsive) participants would indicate their readiness sooner, leaving them less well prepared. Conversely, more conservative participants would indicate their readiness later, which leaves them better prepared. Thus, a negative correlation between average preparation time and average response time would be expected (i.e., participants with *slower* average readiness response times would tend to have a more conservative criterion and thus better preparedness, which would lead them to have to *faster* average response times).

Similarly, as a source of *intraindividual* variability, participants would be assumed to exhibit a certain estimation error around their subjective criterion, which implies that, in some trials, they underestimate their preparedness (thus indicating their readiness later than necessary, thereby being better prepared), whereas in other trials, they overestimate it (thus indicating their readiness too early, thereby being less well prepared). In effect, as for the correlation across participants, a negative relationship between trial-by-trial preparation times and response times would be expected (e.g., slower preparation times within individuals would occur in trials with better preparedness than at criterion, which should lead to faster response times).

Surprisingly, and in direct contradiction to the conclusions derived from DeJong's distributional analysis, Meiran et al. (2002) did not find the predicted negative relationship between preparation time and response time (even though there was substantial inter- and intraindividual variability).[6] Thus, they arrived at the conclusion that the internal state of preparedness is not consciously accessible; therefore, participants are unable to come up with a reasonable estimate.

Voluntary Control during Cue-Based and Target-Based Preparation

We recently attempted to replicate and extend the results of Meiran et al. (2002) by comparing preparation time effects in advance-cue as well as advance-target conditions (Ruge and Braver, in preparation). In the advance-cue condition, we also did not find negative correlations between preparation time and response time. However, in the advance-target condition, we observed strong negative correlations both inter- and intraindividually (Fig. 12–8).

Our results, therefore, suggest that target-based preparation is consciously accessible, whereas cue-based preparation may not be. Thus, if conscious accessibility is taken as a criterion for the engagement of voluntary control, target-based preparation would meet this criterion. This conclusion is also in line with our earlier interpretation of interindividual differences regarding congruency-related effects in performance and brain activation. In that study, even under standard conditions of a fixed-duration preparatory interval, we attributed the effects of individual differences to the optional character of voluntarily initiated motor planning processes during target-based preparation (discussed earlier). A second finding from the self-paced study is also important in supporting the brain imaging results. We found that the negative correlation between preparation time and response time was present in both congruent and incongruent target trials. This confirms our earlier conclusion that the initiation of motor planning processes is the result of a global strategy applied in all trials, rather than a mixture strategy applied only after determining whether a target stimulus is congruent or incongruent. Nevertheless, the shallower slope of the regression line in the incongruent condition supports the hypothesis that preparation was somewhat less effective in this condition, presumably due to induced response competition effects induced by motor planning.

Two Modes of Voluntary Control

The results described earlier, obtained across a variety of studies, can be summarized as follows. If voluntary control is defined by its optional engagement, then both cue-based and target-based preparation should be classified as voluntary. In contrast, under the assumption that voluntarily controlled processes are consciously accessible, our recent self-pacing results suggest that cue-based preparation should not be categorized as voluntary. To explain this discrepancy, we tentatively suggest a distinction between two modes of voluntary control: a "semiautomatic" mode, employed during cue-based preparation, and a "fully controlled" mode, employed during target-based preparation. Which of these two modes is active in a given situation depends on whether participants are merely consciously aware of the initiation of preparatory processes (as might occur for advance cues) or whether they are also consciously monitoring the unfolding of preparatory information processing after its initial activation (as might occur for advance targets). Accordingly, we
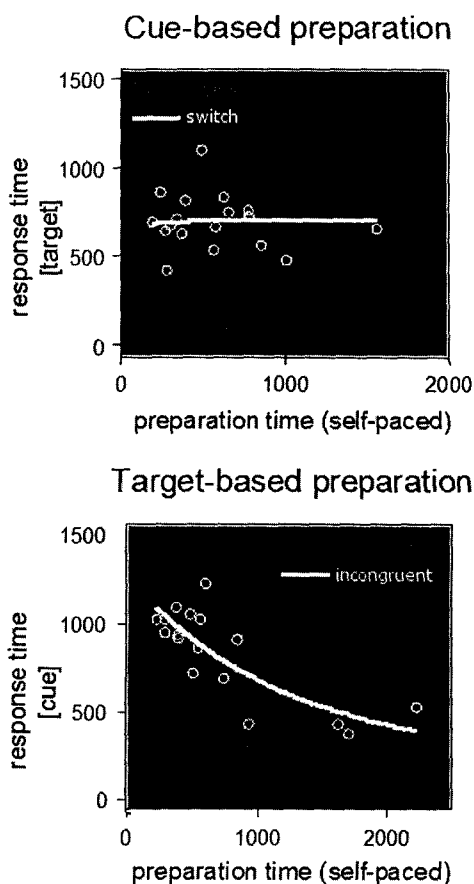
Cue-based preparation

Target-based preparation

Figure 12–8 Relationship between self-paced preparation time and response times (across subjects). For the advance-cue condition, there was no noticeable relationship— either when the advance cue implied a task switch (Spearman rho $= -0.08$) or when it implied a task repetition (Spearman rho $= -0.09$). For the advance-target condition, instead, there was a strong negative relationship (longer preparation times, faster response times) for both advance congruent targets (Spearman rho $= -071$, $p < 0.002$) and advance incongruent targets (Spearman rho $= -0.67$, $p < 0.004$).

suggest that self-paced preparation time can provide a reasonable measure of voluntary processes only in the fully controlled mode.

Fully Controlled Mode during Target-Based Preparation

How can we explain why only target-based preparation (more specifically, the advance motor planning component), but not cue-based preparation, is

consciously monitored under the proposed regime of fully engaged voluntary control? A possible answer to this question is that target-based motor planning is only a small step shy of actual response execution and is therefore associated with a high risk of erroneous behavior. In contrast, cue-based preparatory processes are relatively far removed from the final execution of motor responses (at least in the way in which these cue-based processes have been operationalized in the laboratory).

Such reasoning naturally relates to theoretical concepts developed in the context of error processing and performance monitoring that point to the central role played by medial frontal cortex (Ridderinkhof et al., 2004). Not surprisingly, this is the same region whose activation pattern we found to be reflective of whether a given participant was engaging in target-based preparatory motor planning (discussed earlier). The specific contribution of medial frontal cortex in the context of target-based preparation seems to be to compute and represent the expected outcome or utility in terms of benefits (speeding response time) and costs (extra effort, potential response competition in incongruent trials), when engaging in concrete preparatory motor planning. Depending on subjective evaluation criteria, which we postulate to be computed in medial frontal cortex, an individual may or may not feel motivated to engage in advance motor planning.

Semiautomatic Control Mode during Cue-Based Preparation

What is the reasoning behind the notion of semiautomatic voluntary control operating during cue-based preparation? The rationale is that the preparatory benefit associated with advance task cues may rely on processes that subconsciously operate on task-related representations. Yet, whether such processes can unfold may depend on the status of a voluntarily controlled initiating signal. Thus, in the self-paced situation, participants would be able to consciously indicate whether they started active preparation, but they would be unable to give a reasonable estimate of the progress they make during the unfolding of this process. As such, preparation in the cue-based condition should be considered semiautomatic, because only the initiation, and not the unfolding and duration, of preparatory processes is under voluntary control.

A computational model that we designed recently helps to clarify the role of a voluntary gating signal in cue-based task preparation (Reynolds et al., 2006). In this modeling study, the success of cue-based preparation relies on an optional all-or-none (dopaminergic) gating signal that controls whether task information conveyed by advance cues would gain access to a PFC-based representation of abstract task demands. Importantly, the gating signal need only occur briefly, as long as it coincides with the presentation of the cue. This gating signal then initiates the encoding and activation of cue-related task information into PFC. As a consequence of this activation, the current task demand representation settles into a self-maintained stable activity pattern that persists across time. Thus, it could be that only the initial gating mechanism operates consciously, whereas the actual preparation of the subsequent task

might rely on the subconscious maintenance of a PFC representation. This PFC representation may, in turn, also subconsciously bias task-appropriate S-R transformation processes in posterior cortical regions (e.g., posterior parietal cortex).[7]

CONCLUSIONS

In our recent studies, the comparison of cue-based and target-based preparatory conditions have proven highly potent in generating a wealth of interesting, and often unexpected, empirical phenomena and novel theoretical insights. Consequently, the conceptualization of rule-based control evolved and expanded throughout this chapter, often leading to questions about what seemed intuitive from the standard perspective of cue-based (preparatory) task control.

We started from a highly intuitive, strictly hierarchical model that assumes that high-level task prioritization rules are employed to disambiguate action selection processes that occur at a lower level of the task hierarchy, and that are activated by task-ambiguous target stimuli. One of the key assumptions of such a model is that task prioritization rules (represented within lateral PFC) would become engaged to fulfill their function of task disambiguation only under conditions in which unambiguous task decisions are possible (i.e., after advance task cues, but not after advance-target stimuli). The failure to find brain regions (particularly IFJ area) exhibiting cue-specific preparatory activation does not confirm this initial hypothesis, and prompts a re-evaluation of the nature of PFC representations underlying task control. Two fundamentally different models seem possible, one of which retains a notion of semi-hierarchical task rules, whereas the other implies a nonhierarchical representational scheme. In particular, a critical question regarding the function of IFJ is whether this region exerts "attentional" control based on representations of either (1) abstract templates of task-relevant stimulus dimensions employed to activate and configure lower-level S-R transformation processes or (2) compound S-R mapping rules composed of conjunctions between stimulus categories and task cues. Further research will be needed to adjudicate between these two possibilities (see Ruge et al., submitted, for a more detailed argument in favor of the compound mapping account).

Beyond shedding some new light on the functional characteristics of brain areas commonly found to be involved in cue-based attentional control, the use and comparison of the advance-target condition also demonstrated the relevance of preparatory processes occurring via an additional "intentional" control path originating from dorsolateral PFC regions specifically engaged when action selection can be based on concrete action goals. Similar to the discussion about the representational code underlying attentional control, it remains unclear whether intentional control is based on representations of (1) abstract templates of task-relevant action goals employed for activating and configuring lower-level goal-response transformation processes or (2) the actual goal-response mapping rules.

Finally, we started to explore the question of whether there is a meaningful distinction between different forms of preparation in terms of the extent to which they involve strategic or voluntary control. Although, once again, seemingly counterintuitive, our results and those of others suggest that it is not cue-based preparation, but instead, target-based preparation that is more dominantly guided by volitional strategy. More specifically, it seems that subjective estimates of cost-benefit tradeoffs represent another type of rule that guides the task preparation process. These representations appear to be housed within medial frontal cortex, and help to determine whether concrete motor planning processes will be engaged during preparation. A future challenge will be to design experiments that more systematically manipulate and dissociate the factors that determine subjective cost-benefit tradeoffs, along with the attentional and intentional control processes that enable effective task preparation.

NOTES

1. Task prioritization can also be based on subjective task preferences (e.g., Forstmann et al., 2006) or memorized task sequences, as is the case in the alternating-runs paradigm (e.g., Rogers and Monsell, 1995).

2. Despite its nonhierarchical nature, the model seems to contain a "hidden" hierarchy (which is not explicitly modeled) by assuming that cue-associated task information is mediated via a privileged route that provides "top-down control input" into lower-level task demand units to disambiguate competing activation there. Again, the lack of cue-selective prefrontal activation in our study argues against such a conceptualization.

3. In contrast to the distinction we made earlier, in this context, the terms "intention" and "volition" are typically used synonymously.

4. In many experimental settings, it is difficult to determine whether an observable motor response was planned under the influence of attentional control (stimulus-response associations), intentional control (goal-response associations), or both. For instance, both the stimulus-response rule "if the alarm rings, fasten your seat belt" and the goal-response rule "to silence the alarm [the goal], fasten your seat belt" do imply the same response on hearing the alarm. Thus, just from observing the overt response (fastening the seat belt), it is not possible to infer the type of rule it was based on.

5. A conceptually different approach was pursued by Forstmann et al. (2006), who allowed subjects to freely choose which task to implement next.

6. Instead, readiness response time and target response time were positively correlated. According to Meiran et al. (2002), this somewhat paradoxical pattern suggests that readiness response time, rather than reflecting an estimate of the internal state of preparedness, merely reflects random fluctuations of the currently adopted speed-accuracy criterion. This criterion then "spills over" into the subsequent period of target processing, thus implicating that a relatively fast (slow) readiness response is likely to be followed also by a relatively fast (slow) target response.

7. Although such an interpretation might seem unintuitive for prefrontal cortex functioning, it would not be the first example of prefrontal cortex operating in an un-

conscious mode. For instance, it has been demonstrated that mid-dorsolateral prefrontal cortex can acquire novel action selection rules without subjects being able to report these rules (Berns et al., 1997).

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