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In memory of my father

Peter Forstmann

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'...the seat of the soul and the control of voluntary movement – in fact of neuron functions in general are to be sought in the heart. The brain is an organ of minor importance, perhaps necessary to cool the blood.'

Aristotle (384-322 B. C.)

1 Introduction

A fundamental ability in human cognition is the ability to change and adapt our behavior in accordance with changing environmental demands and internal goals (Miller & Cohen, 2001). For this ability, cognitive control is required. Research on cognitive control aims at providing answers to seemingly simple yet very fundamental questions: How can we do what we want instead of what our environment wants us to do?

In the 19th century, a few authors have addressed this question with their ideo-motor theories (Harless, 1861; James, 1890). The ideo-motor principle states that an action is initiated by the anticipation of its effects (see, e.g. Stock & Stock, 2004). A central construct in this theory is the "will". It was proposed that the will should enable us to imagine a movement and then perform it. This was possible by making use of the idea of a 'mental cue' (for a broader overview, see Prinz, 1987). A mental

cue refers to an association between a mental state and the motor activities necessary to bring that state of affairs into being. Hence, a mental cue can activate and control motor activities. The simple assumption drawn from this idea was that the mind can control the body.

Taking this assumption one step further, one might ask whether the mind can control the mind. Or, in other words, can the mind control itself? To answer this question, several authors proposed that there must be some kind of homunculus or 'signal person' (Rogers & Monsell, 1995), pushing and pulling levers in our heads (see also Monsell & Driver, 2000). This should enable us to configure the system in a way so that we can adapt our behavior in accordance with internal goals. However, with respect to system theories, one might argue that the term 'will' was simply substituted by the term 'controller' or 'executive' (see, e.g., Baddeley & Hitch, 1974; Norman & Shallice, 1986). The crucial problem with these terms is that they can be regarded as placeholders for what is still failed to be understood (Baddeley, 1986).

Fortunately, the recent years have brought changes in both methodological procedures and theoretical accounts. This opened up the possibility of new connections between separate fields of research on cognitive control. The 'homunculitis' bemoaned by Monsell and Driver (2000) is in the process of giving way to a more distributed view that conceives of cognitive control as a multifaceted construct (cf., Hommel, Ridderinkhof & Theeuwes, 2002). In contrast to traditional unitary views on cognitive control, recent approaches have emphasized a complex interplay between several subprocesses (e.g., Miller & Cohen, 2001; Smith & Jonides, 1999). Thus, only a concert of many processes may be what creates the emergent property of being 'the controller' or 'executive'.

In this view, my thesis aims to contribute to the understanding of control processes by investigating subprocesses relevant for task switching. The crucial feature is to bring different perspectives, namely a cognitive and neuroscientific point of view, together.

Outline of the Present Thesis

The thesis evolved from a cooperation project between the Department of Cognitive Neurology of the Max Planck Institute in Leipzig and the Department of Psychology of the Max Planck Institute in Munich (now having merged to a single institute, the Max Planck Institute for Human Cognitive and Brain Sciences located in Leipzig). The aim of the work was to investigate endogenous control processes in task switching. Behavioral and neural correlates are used to address two major research questions: 1. What happens if an external cue is not directly indicating the task? 2. What happens if participants are not explicitly told what to do but can voluntarily select a task by their own? To answer the first question, a novel variant of the task-switching paradigm, the so-called 'transition-cueing paradigm' was developed (Chapter 3) and tested in several behavioral experiments. Two out of five experiments are described in more detail (Chapter 5). In addition, a functional magnetic resonance imaging (fMRI) version of this newly developed paradigm was investigated (fMRI Experiment 1; Chapter 5). To answer the second question, fMRI Experiment 2 was conducted. Here, an extension of classical cueing versions was introduced to investigate the voluntary selection of task sets (Chapter 6).

In the General Discussion (Chapter 7), one section will focus on the integration of behavioral and neural measures obtained in the experiments reported in Chapter 5. In a second section, the results of both fMRI Experiment 1 and 2 are brought into a broader context to account for a functional-anatomical framework of endogenous control in task switching.

2 Theoretical Background

2.1 Cognitive Control

There is extensive literature on cognitive control processes required for the ability to coordinate thoughts or actions in relation with internal goals (see, e.g., Koechlin et al., 2003; Miller & Cohen, 2001). One of the main characteristics of the flexibility of human agents is their capability to perform actions according to their intentions. More specifically, these actions can be characterized as internally-driven rather than externally- or stimulus-driven. The basis of such intention-based actions is their goal-directedness (see, e.g. Jahanshahi & Haggard, 1998). It is widely acknowledged that the prefrontal cortex (PFC) plays a major role for goal-directed behavior (Miller & Cohen, 2001). For goal-directed behavior, several subprocesses are required, e.g. the selection of an appropriate action, conflict monitoring, planning, and decision making. So far, there are different theoretical approaches to explain how these subprocesses are controlled and coordinated during the performance of complex cognitive tasks (for an overview, see Monsell, 1996, 2000). However, it has been argued that the field still lacks a compelling theory of cognitive control, i.e. a theory of '… general-purpose control mechanisms that modulate the

operation of various cognitive subprocesses and thereby regulate the dynamics of human cognition' (Miyake et al., 2001; p. 50). There is an extensive debate about the unity or diversity of cognitive control. Early theoretical frameworks like the multi-component model of working memory by Baddeley (1986) or the Supervisory Attentional System (SAS) introduced as an attentional control model by Norman and Shallice (1986) both argue for a unifying concept. Note, that both system theories have experienced some progress in the recent years in specifying the nature of control mechanisms (Baddeley, 2002; Shallice, 2002). This is in line with the view of a nonunitary nature of frontal lobe or cognitive functioning and is corroborated by neuropsychological observations and experimental data from healthy participants (Stuss & Knight, 2000). Following the latter approach, however, one has to face the so-called 'impurity' problem. Because cognitive control processes necessarily manifest themselves by operating on other cognitive processes, a cognitive task might implicate other cognitive processes that are not directly relevant to the target cognitive function (see also Jacoby, 1991). Thus, also the prevalent account that conceives of control as a multifaceted construct faces limitations. These limitations will certainly remain a challenge for the years to come.

2.2 The Task-Switching Paradigm

A commonly used tool to investigate cognitive control processes in experimental psychology is the so-called task-switching paradigm. The educational psychologist Arthur Jersild is widely believed to have published the first systematic study on task switching (Jersild, 1927). He compared the time required to perform a single task (e.g. task A or task B) on a pure list of items (e.g., AAA... or BBB...) with the time required to alternate two different tasks within a mixed list (e.g., ABAB...). The tasks introduced in one experiment were the subtraction or the addition of numbers from a list of two-digit numbers. His results revealed prolonged

reaction times when participants had to alternate between the two tasks (mixed blocks) compared to the repetition of the task (pure blocks). These prolonged reaction times have been termed 'shift costs'. However, a crucial problem with this method was a confound between two cognitive processes. In mixed blocks the participants had to alternate between the tasks as well as maintain two tasks simultaneously in working memory. This increased the memory load along with the requirement to keep track of which task is currently relevant, is leading to so-called 'mixed-list costs' (Fagot, 1994). Due to these problems, half a century later several new procedures were introduced which not only used mixed lists but lists where the performance on individual repeat and switch trials can be measured. With these procedures, switch and repeat trials could be contrasted within one block leading to 'uncontaminated' shift costs.

2.2.1 Endogenous and Exogenous Control Processes in Task Switching

One of the most intriguing questions in the life of a 'task switcher' concerns the basis of shift costs. Intuitively, it appears plausible that shift costs reflect, to some degree, cognitive control processes needed to adjust to the new task context. However, the theoretical challenge is to decompose the empirically observed shift costs into subcomponents and to relate them to specific cognitive processes. For example, Meiran, Chorev, and Sapir (2000) suggested that there is a stimulus-related component and a response-related component. In general, some authors interpret these costs as reflecting endogenous or top-down controlled processes (e.g., Arrington, Altmann & Carr, 2003; Logan & Gordon, 2001; Mayr & Kliegl, 2000; Rogers & Monsell, 1995; Rubinstein, Meyer & Evans, 2001). Others believe that shift costs reflect exogenous or bottom-up controlled processes (Allport, Styles & Hsieh, 1994; Allport & Wylie, 2000; Logan & Bundesen, 2003, 2004; Schuch & Koch, 2003, 2004). In this context, two-process models have been proposed. Generally, they

assume endogenously controlled processes to be related to the retrieval of the task goal (e.g., 'goal setting', Fagot, 1994; 'goal shifting', Rubinstein, Meyer & Evans, 2001; 'advance reconfiguration', Rogers & Monsell, 1995; 'cue-based preparation', Koch & Allport, in press; 'retrieval of task rules', Mayr & Kliegl, 2003). In addition, there are exogenously controlled processes, which come into play when participants actually perform the task. The latter processes have been interpreted as 'task readiness' (Fagot, 1994), 'stimulus-cued completion of reconfiguration' (Rogers & Monsell, 1995), 'rule activation' (Rubinstein, Meyer & Evans, 2001), 'response set' (Meiran, Chorev & Sapir, 2000; Schuch & Koch, 2003), or, more generally, as an 'application stage' (Mayr & Kliegl, 2003).

The present thesis will elaborate on the two-stage models from Mayr and Kliegl (2000) as well as Rubinstein, Meyer and Evans (2001). More specifically, the present thesis set out to further elucidate the role of the first stage, namely the goal setting/shifting stage (see Fig. 2.1).

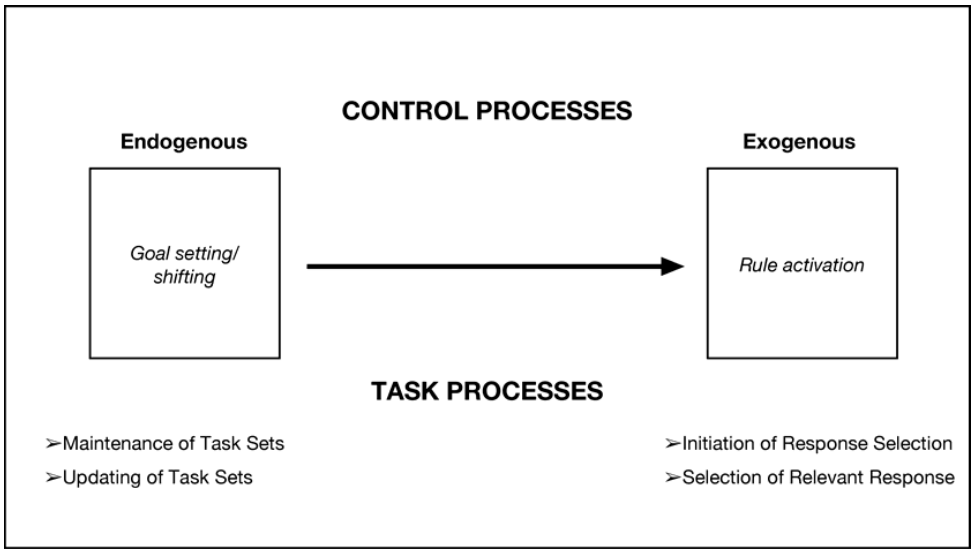

Figure 2.1: Two-stage model of task switching with distinct executive control and task processes (adapted from Rubinstein, Meyer and Evans, JEP:HPP, 2001).

In Rubinstein´s et al. model, a distinction between endogenous, i.e. goal-directed, processes and exogenous, i.e. stimulus-based, control processes is introduced (see also Mayr & Kliegl, 2000; Rogers & Monsell, 1995). According to these control processes, task processes are assigned. The *goal-shifting stage* keeps track of current and future tasks and, in case of a task switch, involves an updating of the contents in working memory through production rules. Most importantly, in this model working memory processes and task switching are tightly intermingled. In a very similar vein, Mayr and Kliegl (2000) propose that memory retrieval constitutes a large share, if not all, of what participants can do to prepare for a task set before the stimulus arrives. An important function of working memory is the temporary storage of information during ongoing processing until it becomes relevant again. Comparably, in task switching usually two task sets have to be maintained within working memory. In this view, because the updating of information in working memory is generally not required on repetitions, repetitions of tasks are faster than alternations.

The *rule activation stage* is triggered exogenously by the stimulus and takes place during an interval between the end of stimulus identification and the beginning of response selection for the current task, after goal shifting has finished (Rubinstein, Meyer, & Evans, 2001, p. 771). Two functions, namely the selection of the current task's response and disabling the rules for selecting the prior task's response, are essential for the rule activation.

2.2.2 Summary

There are different lines of evidence to explain the behavioral effects of task switching. Both endogenous and exogenous control processes are held responsible to cause shift costs. So far, it seems conceivable that an interplay of both endogenous as well as exogenous control processes is needed to account for the wealth of data. Some authors have suggested to

conceptualize the interplay as a continuum between endogenous and exogenous processes (see, e.g. Goschke, 2000). This might be a good compromise, yet one leaving open to what extent the different procedures of the task-switching paradigm require either one of these processes.

2.3 Task-Switching Procedures

2.3.1 The Alternating-Runs Procedure

This procedure was first introduced by Rogers and Monsell (1995) who used two different tasks. These were presented in a predictable sequence of alternating tasks or runs (e.g., AABBAABB..., where A denotes one task and B denotes the other). Thereby, it is possible to compare performance on each task in trial N as a function of whether the same task was carried out in trial N-1 (repeat trials; e.g., AA or BB) against performance when the tasks on trials N-1 and N differed (switch trials; e.g., AB or BA). With this design, the maintenance as well as the alternation between the two task sets is held constant throughout the experimental blocks. Furthermore, it allows to vary the time between the given response and the presentation of the next stimulus, the so-called response-stimulus interval (RSI).

Within the alternating-runs procedure, different versions were investigated. Rogers and Monsell (1995) provided visual cues (in this case, the location in which the stimuli appeared) to indicate the currently required task. Other versions abandoned external visual cues to guide behavior (see, e.g., Kray & Lindenberger, 2000) so that participants had to recollect the N-1 task in order to retrieve the now relevant task set in working memory. Other approaches manipulated the length of the predictable task sequences in separate trials (e.g., ABA; Allport, Styles & Hsieh, 1994; Mayr & Keele, 2000a).

In sum, the alternating-runs procedure provides a tool to measure the effect on the magnitude of shift costs when manipulating the RSI.

Furthermore, this can be done without confounding the maintenance of two tasks while alternating between these two.

2.3.2 The Explicit Task-Cueing Procedure

The manipulation of the RSI is an experimental feature which allows the investigation of processes relevant for the alternation of tasks. However, one disadvantage of the alternating-runs procedure is that participants may begin to prepare for the required task in trial N before they have completed their response in trial N-1. This complicates the exact measure and evaluation of the preparation time (Meiran, 1996).

In the explicit task-cueing procedure, participants have to perform different tasks indicated by explicit task cues (e.g., Meiran, 1996; Sudevan & Taylor, 1987). These are presented in random order with a task cue preceding the target stimulus. This offers the opportunity to manipulate the so-called cue-target interval (CTI) and allows to determine the point in time when task preparation may occur (see also Meiran 2000a). Moreover, the response-cue interval (RCI) can be manipulated and the functional decay of the previous task set can be controlled. There are various versions of the explicit task-cueing procedure which differ with respect to the cue types. For example, Goschke (2000) used semantic cues, whereas others used spatial (e.g., Meiran, 1996, 2000a), arbitrary (e.g., Mayr & Kliegl, 2003), or probability cues (Dreisbach, Haider & Kluwe, 2002).

The explicit task-cueing procedure has the advantage of permitting an experimenter to manipulate separately the cue-target interval and the response-cue interval. Thus, task preparation and task decay can be dissociated. The manipulation of the CTI is of special interest for functional magnetic resonance imaging studies which will be thoroughly discussed in Chapter 3.

2.3.3 Summary

Table 2.1 summarises the core features of both the alternating-runs and the explicit task-cueing paradigm.

Table 2.1: Core features of the alternating-runs and explicit task-cueing procedures

	Task-Switching Procedures	
Features	Alternating Runs	Explicit Task-Cueing
Cue	usually no	yes
Task Sequence	predictable	unpredictable
Response-Stimulus Interval (RSI)	manipulable	manipulable
Cue-Target Interval (CTI)	non-manipulable	manipulable
Response-Cue Interval (RCI)	non-manipulable	manipulable

2.4 Neuroimaging Results of the Task-Switching Paradigm

2.4.1 The Alternating-Runs Procedure

There are only a few neuroimaging studies examining the alternating-runs procedure. These revealed a very heterogeneous data pattern. One of the first neuroimaging studies of task switching was conducted by Meyer et al. (unpublished data). In this PET study, participants performed 'pure' blocks of trials in which only a single task was carried out (e.g. color

discrimination task or shape discrimination task) or switch blocks in which the task alternated predictably. Several regions were more active in the switch blocks than in the 'pure' blocks, including the lateral prefrontal cortex (LPFC), posterior parietal cortex (PPC), anterior cingulate cortex (ACC), and premotor cortex. Interestingly, the LFPC activation was in a more anterior direction, namely along the inferior frontal sulcus (IFS), compared to the activation found in the studies using explicit task cues. This might be due to the requirement to keep two tasks in working memory which is not relevant in pure blocks (see, e.g., Fletcher & Henson, 2001).

Sohn et al. (2000) conducted an event-related fMRI study examining the alternating-runs procedure. In this study, half of the blocks were so-called 'foreknowledge' conditions, so that information about task repetition or task switch was available. A right lateralized prefrontal activation around the IFS among parietal and subcortical activations was found for the foreknowledge condition compared to the unpredictable condition. Dreher et al. (2002) also examined preparation-related activation by contrasting blocks in which trials alternated in a predictable manner against blocks in which the task switched randomly. Interestingly, the data revealed that the anterior medial prefrontal cortex and the left frontopolar cortex (FPFC) were related to the endogenous preparation of the task set, being activated when knowing which task was going to occur. The lateral PFC was involved with cognitive control processes in relation to external events. These findings suggest that regions more anterior situated in the prefrontal cortex come into play when the need for endogenous control is increased (Dreher et al., 2002).

2.4.2 The Explicit Task-Cueing Procedure

Several neuroimaging studies used the explicit task-cueing procedure (Brass & von Cramon, 2002, 2004; Derrfuss, Brass & von Cramon, 2004; Dove et al., 2000; Kimberg et al., 2000; Luks et al., 2002; Ruge et al.,

2005). The initial studies were focusing on the anatomical locus of shift costs (e.g., Dove et al., 2000; Pollmann et al., 2000) whereas many other researchers were interested in preparation-related activation (e.g., Brass and von Cramon, 2002, 2004; Derrfuss, Brass & von Cramon, 2004; Luks et al., 2000; Ruge et al., 2005; Sakai & Passingham, 2003).

Dove et al. (2000) and Pollmann et al. (2000) used event-related fMRI to examine the neural basis of shift costs. On each trial they presented a red or green '+' or '-' to indicate the response mapping. The arithmetic symbols were assigned to either the right or left response button depending on the colors. The colors indicated to repeat or switch the response mapping of the previous task. It is important to note that Dove et al. (2000) presented more repeat trials than switch trials. Furthermore, cue (color) and target (arithmetic symbol) appeared simultaneously so that task preparation and task execution were not separable. The results revealed a fronto-parietal network associated with a task switch compared to a task repetition.

Brass and von Cramon (2002, 2004) and Ruge et al. (2005) examined preparation-related activation. In these studies the interval between cue and target was manipulated in order to dissociate the preparation-related activation from response-related activation. The results revealed that a frontal network involving an area in the vicinity of the inferior part of the left precentral sulcus and the inferior frontal sulcus, the so called inferior frontal junction area, IFJ, and the pre-supplementary motor area (pre-SMA) are crucial components in task preparation. Moreover, Derrfuss et al. (2004) investigated an overlap of three different cognitive control tasks, task-switching, Stroop color-word task, and verbal N-back task. In this study they could corroborate the essential role of the IFJ for the updating of task sets.

The fMRI results with the explicit task-cueing paradigm reveal a crucial role for the posterior part of the lateral prefrontal cortex (LPFC) for the updating of task sets. Furthermore, studies which failed to find stronger frontal activations for the contrast of switch and repeat trials with a long

CTI used an equal likelihood of switch and repetition trials (Brass & von Cramon, 2002, 2004; Ruge et al., 2005). It is suggested that the necessity and demand of exerted cognitive control might be equivalent for both trial types (for further discussion see Ruge, 2004; Ruge et al., 2005).

2.4.3 Summary

There are several neuroimaging studies which either used the explicit task-cueing version, in which the task set is externally induced through a direct task cue, or followed the alternating-runs logic, where the task set is not directly triggered by an external cue. The neural data pattern with the cueing procedure revealed a consistent frontal network including the IFJ and the pre-SMA. However, with the alternating-runs procedure, the data pattern is rather heterogeneous, revealing activations in more anterior PFC regions compared to studies using the explicit task-cueing procedure.

3 Experimental Approach

Several previous studies on task switching followed the initializing work from Rogers and Monsell (1995). Most notable are the behavioral studies by Kray and Lindenberger (2000) and Koch (2003) who conducted a modified alternating-runs version without using external cues. In general, it is an important feature to abandon external cues, as one might argue that external cues minimize the need for 'endogenous control processes' (see, e.g., Logan & Bundesen, 2003, 2004). This might be due to the direct association between the external task cue and a task set. Thus, one might argue that previous task-switching procedures reveal limitations with respect to the investigation of endogenous control processes. More precisely, in most task-switching paradigms, cues are used which directly indicate the relevant task. Furthermore, in these paradigms, participants cannot choose the task by their own and are explicitly instructed which task to perform. Both the manipulation of the directness of the cue-task association and the opportunity to voluntarily select a task set are thought to play an important role for the investigation of endogenous control in task switching.

The experiments presented in this thesis were designed to investigate endogenous control processes in task switching. Two central questions were asked:

1. What happens if the external cue does not directly indicate the relevant task set (Chapter 5)?
2. What happens if participants are not explicitly told what to do but can voluntarily select the task set by their own (Chapter 6)?

To answer these questions, several prerequisites had to be fulfilled. With respect to the first question, a new task-switching procedure had to be developed. This paradigm should allow to manipulate the cue-task association thereby circumventing several shortcomings of previous task-switching procedures. Moreover, it should be possible with this paradigm to investigate behavioral and neural correlates of the memory-based internal generation of task sets.

With respect to the second question, an extension of classical cueing procedures was necessary. Hence, a new variable, the 'degrees of freedom (DF) in choice' variable was introduced. Thus, purely internally driven processes like the voluntary selection of task sets could be investigated.

3.1 Development of a Novel Paradigm

3.1.1 The Transition-Cueing Paradigm

The rationale behind introducing transition cues was to devise a synthesis of both the alternating-runs and the explicit-cueing paradigm in order to obtain a contrast between relatively more internally generated and relatively more directly cued task sets. Therefore, two different types of external cues were used (see Fig. 3.1).

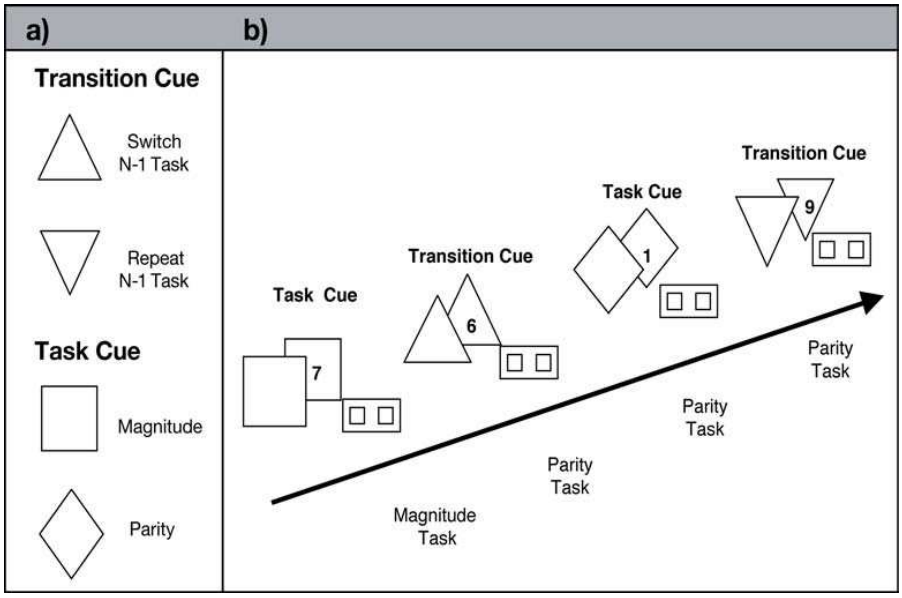

Figure 3.1: Transition-cueing paradigm: a) Two different cue types (transition cue and task cue). The transition cue indicates whether the N-1 task should be repeated or switched whereas the task cue is directly associated with either task A or task B. b) The two cue types were presented in pseudo-randomized order.

The *transition cue* reveals an indirect association between cue and task. That is, this cue type informs the participants about repeating or switching the task but not about the task identity (see, e.g., Rushworth et al., 2002). The characteristic feature of the alternating-runs paradigm, namely the need to relatively stronger *internally* generate the task set, because of the lack of a strong direct task set information, could be realized with the transition cue type. Concurrently, it was possible to use unpredictable task sequences comparable to the task cueing procedure. Contrary to that, the *task cue* is comprised of a direct association between cue and task, thus being identical to the task cues used in cueing versions of previously adopted task-switching studies (see, e.g., Brass & von Cramon, 2002; Koch, 2003). Participants had to shift between two numerical judgement tasks either deciding whether a given digit is greater or smaller than 5 (magnitude task) or whether it is odd or even (parity task). Each of the two

task cues was directly associated with either the magnitude task or the parity task, respectively, whereas transition cues instructed a switch or repeat of the task, thereby requiring the participants to infer the now relevant task identity.

The transition cue offers several methodological advantages compared to previously adopted task-switching procedures. One is concerned with the opportunity to investigate the internal generation of task sets while using an external cue type. Most importantly, this allows to determine the point in time when the internal generation process occurs (see Meiran, 2000b for a discussion). A second advantage is the opportunity to adopt a design in which transition cues can be mixed with task cues, hence allowing an event-related fMRI analysis of an mixed design.

3.1.2 Empirical Section I: Hypotheses

Behavioral Hypotheses

With the manipulation of the directness of the cue-task association we aimed at investigating the memory-based retrieval of task sets as potentially underlying process of endogenous control. Transition cues presumably afford a higher memory-based retrieval demand compared to task cues. Therefore, we assume that transition cues lead to higher reaction times and shift costs compared to task cues. This is based on the assumption that the N-1 task set and the transition cue rule have to be integrated in working memory to internally generate the now relevant task set. Finally, we expect to find a preparation effect for both cue types as well as a cue-specific preparation effect for the performance on transition cues. The latter finding would provide evidence for participants to access the task representations within working memory.

Neural Hypotheses

For fMRI Experiment 1, our main focus was on the contrast between both cue types (transition cues vs. task cues). Contrary to the behavioral experiments, the CTI was held constant for 800 ms to provide sufficient time for preparation.

1. For the contrast between cue types, we expected to find relatively stronger activations for the transition cues compared to the task cues in a fronto-parietal network also found in studies using explicit task cues. This would provide evidence that the performance on transition cues is comparable to the performance on task cues, however, requiring the relevant processes to a higher degree.
2. We expected to find an activation shift in anterior direction for the frontolateral and frontomedian cortex. In a previous task-switching study following the alternating-runs logic, Dreher et al. (2002) could show that the anterior medial prefrontal cortex and the left frontopolar cortex were more related to endogenous control processes, being activated when knowledge about which task was available, while the lateral PFC was more involved with cognitive control processes in relation to external events. These findings suggest that regions more situated anteriorly in the prefrontal cortex come into play when the need for endogenous control is increased (Dreher et al., 2002).

3.2 Extension of Explicit Task-Cueing Procedures

3.2.1 The Voluntary Selection of Task Sets

A second goal of this thesis was to investigate the voluntary selection of task sets with a modified and extended cueing procedure (see also Empirical Section II). The idea stems partly from the results of fMRI Experiment 1. Here we could show that the posterior frontomedian cortex (pFMC) plays a crucial role for the internal generation of task sets.

However, one might argue that even with transition cues, participants are always unequivocally told which task to perform and cannot deliberately select the task set by their own.

Thus, the question remained, what would happen if the participant was not explicitly told what to do. Previous task-switching procedures have in common that participants were explicitly told what to do and could not deliberately decide which task to perform. This leads to the question whether previously adopted task-switching procedures are optimally suited to investigate endogenous control processes.

In fact, in a recent behavioral study by Arrington and Logan (2004), a task-switching procedure was adopted in which participants could voluntarily choose and perform one of two tasks. The results revealed higher reaction times with a voluntary task switch which was interpreted to reflect endogenous rather than exogenous processes. This suggests that the voluntary selection of task sets might be a viable procedure to investigate active processes.

There is currently only one fMRI study reported in the literature which investigated voluntary selection processes with a response-switching paradigm. This study was conducted by Walton and colleagues (2004) who investigated the voluntary selection of response sets. Contrary to a task set, a response set refers to the association between only one stimulus dimension, e.g., shape, with different responses, e.g., press left when circle, press right when square. Participants had to shift or repeat the response set while in some cases they could voluntarily choose the response set by their own. The results revealed that the midcingulate cortex (MCC) is crucial for the free selection of responses. However, up to now it is unclear which cortical regions subserve the voluntary selection of task sets. Furthermore, it remains open whether activity in these cortical regions might be modulated by the number of choices. It is conceivable that a higher number in choices leads to a higher effort in selecting a task set. This might be due to more task sets concurrently activated in high choice conditions compared to low choice conditions.

The aim of fMRI Experiment 2 was to investigate the voluntary selection of task sets with a modified task-cueing paradigm. The number of tasks to choose from was varied between a forced condition (no-choice) and two voluntary conditions (2 or 3 choices). Participants always had to switch between task sets. That is, the task that was chosen on the present trial was never a valid option for choice on the next trial. To achieve this constraint, four simple discrimination tasks were introduced. A trial always started with a cue indicating which task(s) could potentially be chosen. After selecting a task, a target stimulus was presented requiring participants to respond according to their preceding task selection. Finally, a probe stimulus appeared and participants should now indicate with a second response which task they had actually selected and responded to with their first response.

3.2.2 Empirical Section II: Hypotheses

Two hypotheses were formulated in the present study.

1. We expected to find activation within the MCC for the contrast between the choice conditions versus the no-choice condition. This would provide further evidence for the MCC to play a crucial role in voluntary selection processes on a more abstract level than the mere selection of movements or response sets.
2. The activations from the main contrast of choice were expected to be higher for the condition with three choices compared to the condition with two choices. We presumed that with three task sets, a higher effort is needed to activate a task set above threshold. This finding would speak in favor of an effort-related selection process.

4 Functional Magnetic Resonance Imaging

Functional Magnetic Resonance Imaging (fMRI) provides a powerful tool to investigate the functional organization of the human brain. Over the last years, starting with first reports by Ogawa et al. (1990, 1993), there has been an ever growing interest in this method. One reason is its non-invasiveness. A second reason is an unsurpassed spatial resolution compared to other neuroimaging modalities such as Electroencephalography (EEG) and Positron Emission Tomography (PET). Thus, with the advent of fMRI as a tool for mapping brain activity, the neuroscience field has experienced a boost due to the possibility to study human brain function in a non-invasive manner. How brain activity can be detected in magnetic resonance images and the physiological basis of fMRI are further described below.

4.1 Physical Parameters

Magnetic resonance (MR) arises from the interaction of atomic nuclei, which have a magnetic moment, with an applied magnetic field. In the case of brain measurements, the MR signal originates from the hydrogen

nuclei in water, which are the only dipoles with a concentration to support measurements at high spatial resolution.

The hydrogen nuclei achieve an organized low-energy state when exposed to a static magnetic field B_0. This B_0 field is present in an MR scanner and causes the magnetic moment of the hydrogen nuclei to align parallel or antiparallel to the B_0 field.

With the application of a radio frequency (RF) pulse, the nuclei are excited away from their resting state into a higher-energy state. This excitation pulse is only effective at a resonance frequency known as the Larmor frequency which is specific to each nucleus. The essential information about the nearby tissue is derived from the rate at which the atomic nuclei return to the lower-energy state following the excitation. This relaxation can be described in two dimensions. These are the longitudinal re-growth *(T1)* and the transverse relaxation *(T2/T2*)* which exhibit two exponential processes with time constants. The *T1* constant measures the longitudinal re-growth and thus the relaxation in the direction of the B_0 magnetic field. The *T*2 constant measures the transverse relaxation time of the nucleus in the x-y plane which is perpendicular to the B_0 field. It is important to note that the transverse relaxation time is essential for functional magnetic resonance imaging. Finally, to get spatial information of the atomic nuclei, it is possible to vary the magnetic B_0 field by superimposing a magnetic field gradient which codes for the spatial properties of these nuclei. With a gradient superimposed on the magnetic B_0 field, it is possible to select a slice for imaging by applying the proper excitation pulse. Thus, the nuclei within a slice are excited and therefore contribute to the signal. However, to derive a signal in three-dimensional space, two more gradients are required. One is used to alter the precession frequency of the nuclei, whereas the other one is used for phase encoding. In the end, a signal is received which codes for information of one slice which is characterized by particular frequencies and by a particular phase. To reconstruct an image from the signal emitted by the precessing nuclei this phase and frequency information can be used.

4.2 Physiological Parameters

In principle, fMRI studies are set out to localize cognitive processes in the brain in a non-invasive manner. This localization can be based on the so-called blood oxygenation level-dependent (BOLD) contrast mechanism (Ogawa & Lee, 1990; Ogawa et al., 1990). Ogawa and colleagues could show that the oxygenation of blood is a highly interesting marker due to its contrast properties.

The neurons in the brain consume oxygen. The oxygen is attached to hemoglobin molecules in the blood and the flow of blood continuously provides new oxygen to the neurons. Thus, an increase of neuronal activity subsequently leads to an increase in the demand of oxygen. To meet this demand, an increased flow of blood is regionally supplied to the population of active neurons. The mechanisms underlying this very local regulation of blood flow are not yet fully understood. What is important, however, is that an excess of oxygen is supplied to the active neurons, leading to an increased concentration of oxygenated blood in the capillaries surrounding the active brain area.

The concentration of oxygenated blood can be measured due to the changing magnetic properties of hemoglobin. Hemoglobin is either referred to as oxyhemoglobin, i.e. carrying oxygen, or as deoxyhemoglobin, i.e. carrying no oxygen. Depending on whether it carries oxygen or not, it is either diamagnetic or paramagnetic, respectively. Paramagnetic deoxyhemoglobin leads to inhomogenities in the local magnetic field which diminish the transverse relaxation time $T2$, leading in turn to a decrease in signal intensity. During experimental stimulation more oxyhemoglobin is present during stimulation period compared to non-stimulation. In fact, the additional requirement of more oxyhemoglobin leads to an overcompensation which in turn increases the MR signal during the stimulation period. It is the difference in oxygenation concentration between a baseline state and an active state that

can be measured with a MR scanner due to the different magnetic properties of oxygenated blood and deoxygenated blood.

4.3 Analysis of Functional Imaging Data

In general, fMRI results in digital images displaying local changes in blood oxygenation, i.e., hemodynamic measures over time. The result of an fMRI study is a time sequence of images taken at predefined time-intervals. The time sequence is extracted for each voxel, i.e. volume element. The voxels of fMRI studies typically measure a spatial in-plane resolution of 3 x 3 mm in a matrix of 64 x 64 or 128 x 128 voxels, and a stack of 10 to 40 slices are generally acquired. Around 100 to 200 such image volumes are then repeatedly collected during the examination with a sampling period usually between 1 and 5 seconds. For a detailed description of the scanning parameters used in fMRI Experiments 1 and 2 see also Sections 5.4.1 and 6.1.1.

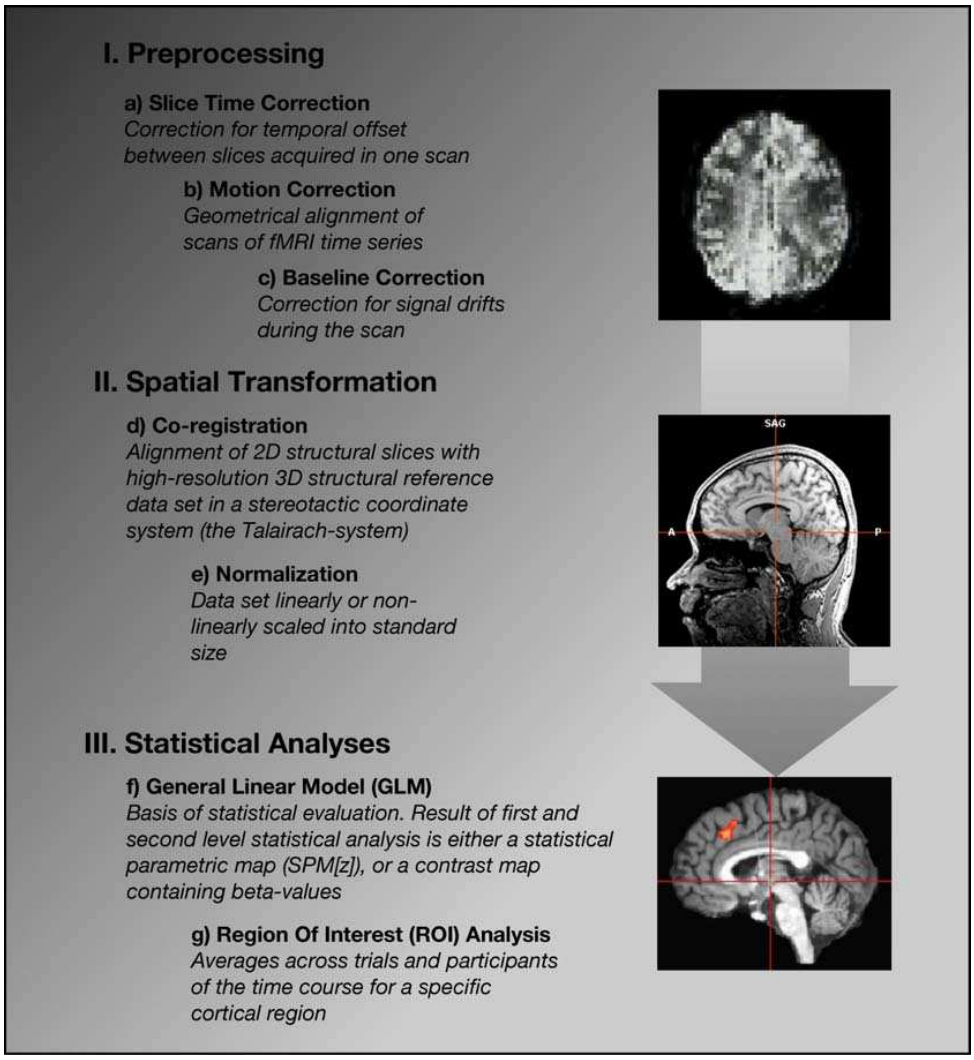

Figure 4.1: Analysis of functional imaging data: Each analyzing step (roman numbered from I-III) comprises several substeps (alphanumeric from a-g; see also Lohmann et al., 2001).

To summarize the analysis of functional imaging data, a flowchart with the different analysis steps is shown (see Fig. 4.1). For the analysis of the present functional data, the in-house software LIPSIA (Leipzig Image

Processing and Statistical Inference Algorithms) was used (Lohmann et al., 2001).

Several preprocessing steps are required prior to statistical evaluation of the measured data, in order to improve the data quality and remove artefacts. Artefacts are caused by motion and low frequency drifts which are due to physiological reasons, e.g. blood pulsation, respiration, or technical reasons, e.g. lower signal intensities at the beginning of a scan compared to the end.

Usually, image volumes have to be preprocessed so that they are geometrically aligned with each other and conform to a standard anatomical space, e.g., the Talairach stereotaxic space (Talairach & Tournoux, 1988). In order to compare image volumes of single participants and subsequently perform a group analysis, fMRI data of all participants have to be rotated and scaled such that the data sets are geometrically aligned with each other. In the experimental session 2D structural slices are acquired using a MDEFT (Modified Driven Equilibrium Fourier Transform) sequence. In a separate session 3D high resolution T1-weighted images have to be acquired for each subject. The 2D structural slices are then co-registered and linearly or non-linearly (Thirion, 1998) scaled with the 3D structural reference data set in the stereotaxic Talairach coordinate system.

In a last step, the statistical analysis is performed. This is based on the general linear model (GLM) to obtain Statistical Parametric Maps (SPM) or contrast maps containing beta-values. The beta-values provide an estimated measure of the signal change in the BOLD time course in relation to the stimulation. For multi-session analysis, the estimated model parameters for the specified conditions are tested by using a t-statistic. The resulting t-values are transformed into Z-scores resulting in an individual SPM[z] (Lohmann et al., 2001). The Z-score indicate whether the specified conditions significantly differ from each other on a voxel-wise basis. In a subsequent step, it is also possible to test for differences between groups. Thus contrast images of each group are tested by using a

two-sample t-test. To minimize the probability of false positives (type I error), exclusively voxels with a z-score greater than 3.09 ($p<0.001$, uncorrected) and with an adequate volume size are considered as activated voxels (Forman et al., 1995). Finally, to obtain information about the time course of pre-specified anatomical loci, regions of interest (ROI) analyses can be performed. It is possible to derive time courses from the preprocessed or modelled data so as to perform an average across trials and participants. Subsequently, this data can be submitted to statistical analysis.

5 Empirical Section I

5.1 Behavioral Experiment 1

The aim of the first behavioral experiment was twofold: on the one hand, the study set out to replicate the results commonly found with task cues. This is a shift-specific preparation effect, i.e. reduced shift costs with prolonged preparation time. This would indicate the ability to reconfigure the system prior to stimulus presentation. On the other hand, it was the aim to show that with the transition cue, additional processes become relevant. This should be reflected in a larger preparation benefit for the transition cues compared to the task cues. It was expected to find larger shift costs for the transition cues compared to the task cues, because with indirect cue-task associations the task set has to be generated internally which is especially relevant in switch trials. In the present experiment, a pseudo-randomized version with two cue types (task cues vs. transition cues) was used. Furthermore, two different preparation intervals were introduced in order to investigate preparation-related processes.

5.1.1 Methods

Participants

Fourteen participants (6 females, mean age = 25.57, SD = 2.89) were tested in a 1h session. Five participants were recruited and tested at the Max Planck Institute for Human Cognitive and Brain Sciences, Department for Psychology, in Munich, and the remaining participants were recruited and tested at the Max Planck Institute for Human Cognitive and Brain Sciences, Department for Cognitive Neurology, in Leipzig. Participants received 8 Euro/h for participation. All participants were right-handed as assessed with the Edinburgh Handedness Inventory (Oldfield, 1971). All participants reported normal visual acuity.

Stimuli and Tasks

Visual stimuli were the digits 1 to 9, excluding 5. Their height was approximately 0.8 cm. They were centrally presented inside in one of four geometrical figures (see Fig. 3.1): a square, a diamond, a triangle on its tip, and a triangle on its base. The figures measured 3.8 x 3.8 cm on a computer screen (15") connected to an IBM-compatible PC. Participants were placed in front of the screen with an approximate distance of 1 m. Thus, stimuli were foveally presented with a visual angle of 2.1°. Stimulus presentation and response registration were synchronized with the vertical refresh rate of the screen. Participants had to perform a two-choice reaction task deciding whether the digit was odd or even, or whether it was smaller or greater than 5. Stimulus order was random. Responses were made by pressing either the left or right button of an external response panel. Response keys measured 1.7 x 1.7 cm and were separated by 3.3 cm.

Procedure

Prior to the experimental procedure, participants were familiarized with the two cue types and the relevant cognitive operations to be performed. Furthermore, the stimulus-response mapping was introduced, which was counter-balanced across participants. Participants were then informed that stimuli would be individually presented in the centre of the cue (i.e., the corresponding geometrical figure). Three practice blocks (two blocks with only one of the cue types and one block with both cue types) each consisting of 16 trials preceded the experimental trials. The first trial of each block consisted of a semantic cue (there was either 'Grösse' [magnitude] or 'Parität' [parity] written in the centre of the screen), so that the second trial was not constrained to task cues only. Participants were given a schema of the S-R mappings for each task. This schema was placed beneath the screen. Visual error feedback was given for 500 ms on the bottom part of the screen, when participants pressed the wrong key. The experiment consisted of 20 blocks of 16 trials each (n = 320 trials). In this experiment, we used a constant trial duration of 5500 ms[1].

Design

The design was 2 (cue type) x 2 (trial type) x 2 (CTI) factorial. Cue type (task cue vs. transition cue), trial type (repeat vs. switch), and CTI (100 ms vs. 1000 ms) were all within-subjects variables that were pseudo-randomized, while the combinations of the factors were counter-balanced within blocks of trials. Significance level for statistical analyses was set to $\alpha = 0.05$.

[1] This was done to allow a comparison of the results with the results obtained in a functional imaging experiment.

5.1.2 Results

Reaction Time Analysis: The first trial of each block was not analyzed, because it was associated with a semantic cue. Reaction times (RTs) were determined for each participant as a function of cue type, trial type, and CTI. For RT analysis, we discarded incorrect trials, those following them, as well as RTs above 3000 ms and below 300 ms (outliers: less than 1% on both sides). For the remaining RTs, we determined the mean for each participant as a function of cue type, trial type, and CTI. Table 5.1 shows these data averaged across participants.

Table 5.1: Mean RT (in ms) in Experiment 1 as a function of trial type (switch vs. repeat), cue-target interval (CTI, short vs. long), and cue type (transition cue vs. .task cue).

	Trial Type		
Cue Type	Repeat	Switch	Shift Costs
Transition Cue			
CTI = 100 ms	1543	1706	163
CTI = 1000 ms	900	1129	229
Cue-specific preparation	643	577	
Task Cue			
CTI = 100 ms	1207	1321	114
CTI = 1000 ms	740	870	130
Cue-specific preparation	467	451	

These data were submitted to an analysis of variance (ANOVA) with the independent variables cue type (task cue vs. transition cue), trial type (switch vs. repeat), and CTI (short vs. long). The results revealed a significant main effect of cue type $F(1, 13) = 60.07$, $p < .001$, indicating that RTs for the transition cue type are higher than for the task cue type (1319 ms vs. 1034 ms). Also, the main effect of trial type was significant $F(1, 13) = 49.87$, $p < .001$, indicating that RTs in switch trials were higher than for repeat trials (1256 ms vs. 1097 ms). Finally, the main effect of CTI was significant $F(1, 13) = 662.96$, $p < .001$. This indicated higher RTs with the short CTI (1444 ms) than with the long CTI (909 ms). There were

two significant interactions. First, cue type interacted with trial type $F(1, 13) = 12.34$, $p < .01$, revealing larger shift costs for the transition cues (196 ms) than for the task cues (122 ms). Second, cue type interacted with CTI $F(1, 13) = 43.52$, $p < .001$, indicating a larger cue-specific preparation effect for the transition cues (610 ms) than for the task cues (504 ms). The shift-specific preparation effect $F(1, 13) = .12$; $p = .27$, as well as the three-way interaction $F(1, 13) = .89$; $p = .36$, were not significant.

Error Rates: The overall accuracy was 95.7 %. Error rates were submitted to the same analyses as RTs. The ANOVA revealed a significant main effect for cue type $F(1, 13) = 7.40$, $p < .05$, indicating more errors with transition cues (5.5%) than with task cues (3.2%). No further effects reached significance (Fs < 1).

5.1.3 Discussion

The goal of Experiment 1 was to investigate the role of memory-based task set retrieval with a new variant of the task-switching paradigm. This was done by comparing performance for two different cue types, namely transition cues with task cues. The results revealed higher RTs with transition cues than with task cues. Furthermore, shift costs as well as the cue-specific preparation effect were larger with transition cues than with task cues. These new findings are in line with the hypotheses and are discussed in more detail in Section 5.3.

Furthermore, both cue types led to a very substantial, general preparation effect with a prolonged cueing interval. However, this preparation effect was nearly equivalent for both repeat and shift trials, which is contrary to many other studies using the cueing version (e.g., Meiran, 1996). Usually, a shift cost reduction with a prolonged preparation interval is found in studies with a manipulation of the cueing interval at least in within-subject designs (see, e.g., Altmann, 2004; Koch, 2001) and is interpreted as evidence for a strategic reconfiguration mechanism in anticipation of the stimulus (Rogers & Monsell, 1995; Meiran, 1996).

There are several explanations for the missing shift-specific task preparation effect. One is provided by the length of the response-cue interval (RCI) which is about twice as long (about 2500 ms) as compared to other cueing studies (see, e.g., Meiran, 2000). This may have induced passive dissipation of the previous task set compared to cueing versions with shorter RCIs (see Allport, Styles & Hsieh, 1994, for a discussion). Thus, priming effects of the previous task set may have played a less critical role in the present experiment at least for the performance on task cues (cf. Allport & Wylie, 1999; Allport & Wylie, 2000). However, a recently published study by Koch et al. (2003a) casts doubt on this explanation. The study by Koch et al. (2003a) investigated performance in a spatial cueing paradigm with an RCI that was comparable to the RCI in the present study, but there were clear shift-specific preparation effects in that study. Interestingly, the spatial cueing version used by Koch et al. (2003a) was the same as the one investigated by Meiran (2000) with a short RCI. The comparison of both studies revealed an equivalent data pattern concerning the shift-specific preparation effect. This equivalence of preparation effects across studies advises a subordinate role of the length of the RCI for the explanation of the missing shift-specific preparation effect in the present experiment.

In fact, there is a more plausible explanation with respect to the missing shift-specific preparation effect in the present experiment. This may be caused by a potential carry-over effect between both cue types. Thus, participants did not only have to shift between different task sets but also between varying degrees of directness of the association between cue and task. Since a randomized task-sequence was used, participants could not predict whether a direct task cue or an indirect transition cue would appear. Hence, participants did not know whether a direct cue-task association or an indirect cue-task association would be present in the upcoming trial. This lack of pre-knowledge required the participants to maintain the N-1 task set between given response and appearance of the next cue. However, in task-cueing procedures it is usually not necessary for participants to retain the previous task set for performing on the present

trial. As a consequence, this could have introduced a particularly large retrieval burden that might have prevented the recruitment of shift-specific preparatory processes (see, e.g., Baddeley, 2003).

To exclude the potential for carry-over effects between both cue types and to replicate the main effects as well as the interaction between cue type and trial type, Experiment 1 was replicated with Experiment 2 now using a between-subjects manipulation of the cue type. One group of participants performed the tasks exclusively on the basis of task cues, while another group of participants performed the tasks on the basis of transition cues. The aim of using this design was to investigate whether the randomized presentation of both cue types can account for the missing shift-specific preparation effect. Two expectations were formulated for Experiment 2: First, we expected to replicate the RT data pattern of Experiment 1 and second, we expected to find a shift-specific preparation effect.

5.2 Behavioral Experiment 2

Experiment 2 was designed to be comparable to Experiment 1. However, in this experiment both cue types were treated as a between-subjects variable. This is, a factor 'group' was introduced separating both cue types into a task cue group and a transition cue group. This was done in order to circumvent long-term interference effects between both cue types.

5.2.1 Methods

Participants

Thirty-two participants (13 female, mean age = 23.8 years, SD = 2.34) were tested in a 1h session. Sixteen participants were randomly assigned to each of two independent groups: 'task cue group' and 'transition cue group'. All participants were recruited and tested at the Max Planck

Institute for Human Cognitive and Brain Sciences, Department for Cognitive Neurology, in Leipzig. They received 8 Euro/h for participation. All participants were right handed as assessed with the Edinburgh Handedness Inventory (Oldfield, 1971). All participants reported normal visual acuity.

Stimuli, Task, Procedure and Design

Stimuli and tasks were identical to those of Experiment 1. The participants of the 'task cue group' performed 20 blocks of 16 trials with only the task cue. The participants of the 'transition cue group' performed 20 blocks of 16 trials but with the transition cue. The trial duration was equivalent to that of Experiment 1.

The experiment started with three practice blocks. At the beginning of each block, a semantic cue was presented. This was especially important for the 'transition cue group' in order for participants to know which task to start with. The independent variables were trial type (repeat vs. switch) and CTI (100 ms vs. 1000 ms) as within-subject variables and group ('task cue group' vs. 'transition cue group') as between-subject variable.

5.2.2 Results

Reaction Time Analysis: RT data were submitted to an ANOVA with the independent within-subject variables trial type (repeat vs. switch), CTI (100 ms or 1000 ms), and the between-subject variable group (task cue group vs. transition cue group). The first trial of each block was not analyzed because it was associated with a semantic cue. For RT analysis, we discarded incorrect trials, those following them, as well RTs above 3000 ms and below 300 ms (outliers: less than 1% on both sides). Table 5.2 depicts the RT data as a function of trial type and CTI for the 'task cue group' and for the 'transition cue group'.

Table 5.2: Mean RT (in ms) in Experiment 2 as a function of trial type (switch vs. repeat), cue-target interval (CTI, short vs. long), and group (task cue vs. transition cue).

	Trial Type		
Group	Repeat	Switch	Shift Costs
Transition Cue Group			
CTI = 100 ms	1232	1547	315
CTI = 1000 ms	781	1034	253
Cue-specific preparation	451	513	
Task Cue Group			
CTI = 100 ms	907	1081	174
CTI = 1000 ms	685	759	74
Cue-specific preparation	222	322	

The RT data analysis revealed a significant main effect of trial type $F(2, 30) = 173.32$, $p < .001$, showing that RTs for switch trials were higher than for repeat trials (1105 ms vs. 901 ms). Also, the main effect of CTI was significant $F(2, 30) = 419.70$, $p < .001$, indicating that RTs in the short CTI were higher than in the long CTI (1192 ms vs. 814 ms). Finally, the main effect of group was significant $F(2, 30) = 13.35$, $p < .001$, indicating that RTs in the 'transition cue group' were generally higher than in the 'task cue group' (1148 ms vs. 858 ms).

There were also significant interactions. CTI interacted with group $F(2, 30) = 32.48$, $p < .001$, indicating a larger cue-specific preparation effect for the 'transition cue group' (482 ms) than for the 'task cue group' (272 ms). Also, group interacted with trial type, revealing higher shift costs for the 'transition cue group' (284 ms) compared to the 'task cue group' (124 ms). The three-way interaction between group, CTI and trial type was not significant (Fs < 1).

Importantly, Experiment 2 was conducted to test whether we observed a shift-specific preparation effect when the cue-type manipulation was between-subject rather than within-subject as in Experiment 1. In fact, we found that CTI interacted with trial type $F(2, 30) = 20.11$, $p < .01$. This

interaction indicates a shift-specific preparation effect where shift costs are higher in the short CTI (245 ms) compared to the long CTI (164 ms).

Error Rates: The overall accuracy was 95.9%. Error rates were submitted to the same analysis as RTs. The ANOVA revealed a significant effect of CTI $F(2, 30) = 8.81$, $p < .01$, indicating more errors with the short CTI (4.7%) than with the long CTI (3.4%). Furthermore, the main effect for trial type was significant $F(2, 30) = 17.12$, $p < .001$. Participants made more errors in switch trials (5.1%) compared to repeat trials (3.1%). Neither the group main effect nor an interaction between group, CTI, and trial type were significant (Fs < 1).

5.2.3 Discussion

The results of Experiment 2 first replicated the basic finding of Experiment 1, namely that the performance on transition cues leads to higher shift costs and a larger cue-specific preparation effect compared with the performance on task cues. The overall RT level was lower in the present experiment than in Experiment 1, indicating that participants were faster when attending to only one cue type within a block rather than shifting between the two cue types as in Experiment 1. However, the main effects for cue type, trial type and CTI as well as the interactions between cue type and CTI and cue type and trial type were observed. Finally, the shift-specific preparation effect was found for both cue groups, whereas this effect was not observable in Experiment 1. We therefore attribute the lack of shift-specific preparation in Experiment 1 to the mixing of cue types, which presumably increased the retrieval burden within working memory.

5.3 General Discussion of Behavioral Experiments

The behavioral experiments aimed at investigating the role of memory-based retrieval in task-switching by manipulating the directness of the association between cue and task. To do this, a new variant of the task-switching paradigm called the *transition-cueing paradigm* was developed. This paradigm can best be characterized as a synthesis of the cueing paradigm (Meiran, 1996; Sudevan & Taylor, 1987) and the alternating-runs paradigm (Rogers & Monsell, 1995). Thus, introducing the transition cue type allowed us to investigate cue-locked task set retrieval without directly indicating the relevant task set.

The present findings replicate the results of previous studies insofar as the unpredictable switching between two simple cognitive tasks results in large shift costs (see, e.g., Monsell, 2003 for a review). Furthermore, the long CTI resulted in a strong preparation effect for both cue types in Experiment 1 and in Experiment 2. Finally, Experiment 2 revealed a significant reduction of shift costs with a prolonged preparation interval for both cue groups. That is, not only the data of the 'task cue group' in Experiment 2 but also that of the 'transition cue group' revealed a significant reduction of shift costs with prolonged preparation time. Thus, the ability to prepare the cognitive system for an upcoming task shift seems to be possible with direct as well as indirect external cues.

The core feature of the transition-cueing paradigm is the manipulation of the directness of the cue-task association. The results of both experiments revealed a reliable main effect for the transition cue. That is, the performance on transition cues led to substantially higher RTs as compared to the performance on task cues. At first glance, it seems to be obvious that acting on the transition cue is more 'difficult' than acting on the task cue, since participants had to constantly recollect the N-1 task set. Therefore, one might argue that it is merely the act of maintaining the previous task set in working memory that accounts for cue-specific effects.

However, in Experiment 1, both cue types were presented in a randomized task-sequence. Here, the retention of the preceding task set was obligatory for the performance on both the task cue as well as the transition cue, because participants could not anticipate which cue type would be presented on the next trial. Hence, if memory load alone was responsible for the main effect of cue type, we would expect to find no difference between task cues and transition cues in Experiment 1. Nevertheless, we found an RT difference of 285 ms. To account for this effect as well as higher shift costs associated with transition cues, which were replicated in Experiment 2, we refer to the retrieval demand and not the maintenance of memory load which differs between both cue types. With the transition cue, participants have to retrieve the N-1 task set, whereas this is not relevant for the task cue. Proceeding with a task analysis for the performance on transition cues, we suggest that an integration process becomes relevant to produce a task name for the current trial. And finally, the current stimulus has to be interpreted in terms of that task name to select a response. In the sequence of these processes there is a locus of additional shift costs. This is the integration of information to internally generate the now relevant task set. This process could take the N-1 task information as input, along with the current transition cue, and if the transition cue is 'repeat', simply use the N-1 task for the current trial, whereas if the transition cue is 'switch', conduct an additional retrieval to produce the other task name and use that for the current trial.

It should be noted that the stimulus compound account proposed by Logan and Bundesen (2003) does not provide an explanation for the integration and additional retrieval of the relevant task set. However, the present findings might be reconciled with this account, if the interpretation of the task analysis consisted of a retrieval of the correct response, cued jointly by task name and target stimulus. Thus, the stimulus compound account would need an extension, if this account was to explain that one part of the 'compound' can apparently reside in memory and thus does not

necessarily have to be present in the environment (see also Mayr & Kliegl, 2003).

The retrieval of the previous task set is also of importance for the strong preparation effect with transition cues compared to task cues. It is assumed that with the short CTI, participants are not able to retrieve and integrate the contextual information needed to internally generate the correct task set during the CTI. As a consequence, the benefit of the prolonged preparation interval is stronger for transition cues than for task cues. Hence, it is assumed that this memory-based retrieval step with the subsequent integration of different sources of information within working memory can be accomplished with more preparation time, while leading to prolonged RTs in the short interval.

In sum, the present findings provide evidence for memory-based retrieval processes with indirect cue-task associations compared to direct cue-task associations. Furthermore, the integration of cue- and task-related information in working memory seems most likely to be the locus of shift costs with indirect cue-task associations.

5.4 FMRI Experiment 1

FMRI Experiment 1 was designed to investigate the neural basis of the internally generated processes which are linked to indirect cue-task associations. Two behavioral experiments revealed that the performance on transition cues leads to higher RTs as well as higher shift costs compared to the performance on task cues. However, shift-specific preparation effects were only observed for a between-subjects design. Since these designs are accompanied with several major problems using fMRI (e.g. greater sample size, large interindividual variance, etc.), the CTI manipulation was abandoned for the present experiment.

The major focus in the fMRI experiment was the contrast of indirectly and directly cued task sets in a task-switching context (see also Forstmann

et al., 2005). Hence, the essential experimental manipulation pertained to the variation of the association between cue and task in a within-subjects design.

5.4.1 Methods

Participants

Sixteen healthy volunteers were recruited and tested at the Max Planck Institute for Human Cognitive and Brain Sciences, Department for Cognitive Neurology, in Leipzig. We obtained written consent from all sixteen participants prior to the scanning session. All participants had normal or corrected-to-normal vision. No subject had a history of neurological, major medical, or psychiatric disorder. The data of two participants were excluded from the analysis due to nausea of one participant during the scanning procedure and technical problems with the headphones in the other case. The remaining fourteen participants were 6 females and 8 males (mean age = 23.6, SD = 2.81) who were all right handed as assessed by the Edinburgh Inventory (Oldfield, 1971). They received 8 Euro/h for participation.

Stimuli, Task, Procedure and Design

Stimuli and tasks were identical to those of the behavioral Experiment 1 and 2 (see Fig. 3.1). Cue and stimulus order were random. The crucial difference to the behavioral Experiments pertained to the length of the CTI which was held constant (800 ms).

Prior to the experimental procedure in the scanner, participants were familiarized with the two cue types and the relevant cognitive operations to be performed. Furthermore, the stimulus-response mapping was introduced which was counter-balanced across participants. Participants were then informed that stimuli would be individually presented in the centre of the cue (i.e., the corresponding geometrical figure). Also, two

pure blocks with only one of the cue types and three mixed blocks with both cue types each consisting of 16 trials preceded the experimental blocks in the scanner. The pre-experimental procedure lasted for about 15 min before participants were placed in the scanner.

The timing of the sequence of trials was triggered from the MRI control every 6 seconds. Image acquisition started with a variable oversampling interval of 0, 500, 1000, or 1500 ms to obtain an interpolated temporal resolution of 500 ms (Miezin et al., 2000). Then, a fixation cross was presented for 50 ms followed by one of the four cues, which were always presented for 800 ms (constant CTI). While the cue remained on the screen, the digit was presented in the centre of the cue. Cue and digit together remained on the screen until a response was made or the response time interval of 3000 ms was exceeded. Responses were made with the right index or middle finger by pressing either the left key, if a digit was smaller than 5 or odd, or the right key, if a digit was larger than 5 or even.

The experiment consisted of two blocks with 160 experimental trials each, resulting in approximately 80 trials for the combinations of the two factors cue type (transition cue vs. task cue) and trial type (switch vs. repeat). Trials were presented in a pseudo-randomized order to equal the number of switch and repetition trials and the transition probabilities of the different conditions and cue types. We also included 40 null events, which were pseudo-randomly interspersed. The null events were included to compensate the overlap of the BOLD response between adjacent trials. The experiment lasted for about 50 min. Stimuli were displayed using VisuaStim (Magnetic Resonance Technologies, Northridge, USA), consisting of two small TFT-monitors placed directly in front of the eyes, simulating a distance to a normal computer screen of about 100 cm with a resolution of 1024 x 768 and a refresh rate of 60 Hz. A TR[1] of 2 seconds was used, resulting in 540 time steps for each block. Every block started out with two dummy trials which were excluded from further analysis.

[1] Repetition Time **(TR)** The time interval between successive excitation pulses, usually expressed in seconds.

MRI Scanning Procedure

The experiment was carried out on a 3T scanner (Medspec 30/100, Bruker, Ettlingen). 20 axial slices were acquired (19.2 cm FOV[2], 64 by 64 matrix, 4 mm thickness, 1 mm spacing) parallel to the AC-PC plane and covering the whole brain. Slice gaps were interpolated to generate output data with a spatial resolution of 3 x 3 x 3 mm. We used a single shot, gradient recalled EPI[3] sequence (TR 2 s, TE[4] 30 ms, 90^{o} flip-angle). Prior to the functional runs, corresponding 20 anatomical MDEFT-slices and 20 EPI-T1 slices were acquired.

5.4.2 Data Analysis

Preprocessing of fMRI Data

The analysis of the fMRI data was performed using the LIPSIA software package (Lohmann et al., 2001). The functional data were first corrected for movement artefacts. Further, the temporal offset between the slices acquired in one scan was corrected using a sinc-interpolation algorithm. Data were filtered using a spatial Gaussian filter with sigma = 0.6. A temporal highpass filter with a cut-off frequency of 1/100 Hz was used for baseline correction of the signal. All functional data sets were individually registered into stereotaxic Talairach space using the participants` individual high-resolution reference image. These 3D reference data sets were acquired during a previous scanning session. The 2D anatomical MDEFT slices, geometrically aligned with the functional slices, were used to compute a transformation matrix containing 6 degrees of freedom (3

[2] Field of View **(FOV)** The total extent of an image along a spatial dimension.
[3] Echo Planar Imaging **(EPI)** A technique that allows collection of an entire two-dimensional image by changing spatial gradients rapidly following a single electromagnetic pulse from a transmitter coil.
[4] Echo Time **(TE)** The time interval between an excitation pulse and data acquisition, usually expressed in milliseconds.

rotational, 3 translational) that registered the anatomical slices with the 3D reference image. These transformation matrices were normalized to the standard Talairach brain size (Talairach & Tournoux, 1988) by linear scaling, and finally applied to the individual functional data.

Statistical Evaluation

For the computation of whole-brain contrasts, we used the General Linear Model for serially autocorrelated observations (Friston et al., 1995). The design matrix for event-related analysis was created using a model of a synthetic BOLD function (Friston et al., 1998). Event onsets were synchronized with the presentation of the cue. Only correct trials were included in the analysis. The model equation, including the observation data, the design matrix, and the error term, was convolved with a Gaussian kernel with a dispersion of 4 s FWHM to deal with the temporal autocorrelation (Worsley & Friston, 1995). In the following, contrast maps, i.e. estimates of the raw-score differences between specified conditions, were generated for each participant. A one-sample Student's t-test of contrast maps across participants (random-effects-model considering participants as a random variable) was computed to indicate whether observed differences between specified conditions were significantly different from zero. Subsequently, t-values were transformed into Z-scores. To protect against false positive activations, only regions with a Z-score higher than 3.09 ($p < 0.001$, uncorrected) and with a volume greater than 450 mm^3 (10 adjacent voxels) are reported (Forman et al., 1995).

Furthermore, we were interested in obtaining regions of interest (ROI) x cue type interactions between three frontolateral and two frontomedian regions of interest for both cue types in order to test for a functional gradient in anterior direction for the transition cue. The underlying signal time courses were obtained for the most activated voxel of the frontopolar PFC (FPFC), the mid-part of the left middle frontal gyrus (mid-MFG), and the IFJ on the frontolateral side for each participant. On the frontomedian

side, we obtained the signal time course for the most activated voxel in BA 8 and for a mean coordinate in the pre-SMA/SMA (x = 1, y = 5, z = 53). While the latter coordinate was derived from the study of Brass and von Cramon (2002), all other ROIs were determined from the random effects analysis of the main contrast between both cue types (see Table 5.3). On the lateral prefrontal cortex, the coordinate of the mid-MFG and the coordinate of the FPFC were chosen, because it has been argued by several authors that these areas are important for the relational integration of information in working memory (D'Esposito et al., 1999; Fletcher & Henson, 2001; Koechlin et al., 1999). On the medial side, BA 8 has been argued to be important for uncertainty in decision making (see, e.g., Volz, Schubotz & von Cramon, 2003). The more posteriorly situated ROIs on the lateral and medial PFC, i.e. IFJ and pre-SMA, belong to a cortical network commonly found with explicit task cues (see, e.g., Brass & von Cramon, 2002; Ruge et al., 2005).

To compute the signal change of the hemodynamic response, we determined the most activated voxel of the relevant contrast in the mean Z-map. We then extracted the time course of the signal underlying this voxel for each participant from the preprocessed data. The percent signal change was calculated in relation to the mean signal intensity across all timesteps for this voxel. For each condition the signal change was averaged for 12 seconds beginning with the presentation of the cue at the start of a trial. We then subtracted the time course of the null event from the time course of the relevant conditions to compensate for the overlap of the BOLD response (Burock et al, 1998). The logic behind this is that null events are (at least on average) embedded within the same past and future trial conditions as a regular event, and thus have the same preceding and succeeding average BOLD signal. By subtracting the null event from the relevant condition, one assumes that the brain area, i.e. voxel, exhibits no activation for the null event so that the remaining BOLD signal is solely caused by the experimental manipulation. The largest value of the signal was searched in the time window between 4 to 8 seconds. This value was then averaged across participants. Finally, the maximum signals of three

lateral and two medial ROIs were submitted separately to an ANOVA. For the ROI analysis, effects were considered significant at α=0.05.

For the visualization of a functional-anatomical gradient in the posterior-anterior direction, we masked the estimated beta-values, i.e. measure of the signal change in the BOLD response, of each difference of cue type and null event separately with the Z-map resulting from the main contrast (transition cue versus task cue) with a Z-score higher than 3.1 ($p <$ 0.001, uncorrected). This assured us that only voxels being significantly activated in the random effects analysis for the main contrast of cue type were chosen, except for the coordinate in the pre-SMA which was derived from the study from Brass and von Cramon (2002).

5.4.3 Results

Reaction Time Analysis: The behavioral results (Fig. 5.1a and 5.1b) revealed a significant main effect for the cue type $F(1,13) = 56.6$; $p < .001$, indicating that RTs for the transition cue were higher than for the task cue (1124 ms vs. 907 ms). In addition, the main effect for trial type was significant $F(1,13) = 25.38$; $p < .001$, indicating that RTs in switch trials were higher than in non-switch trials (1060 ms vs. 971 ms). The interaction of cue type and trial type was significant $F(1,13) = 6.00$; $p <$ .05, indicating higher shift costs for the transition cue in switch trials compared to the task cues (138 ms vs. 40 ms).

Error Rates: The overall accuracy was 94.7%. Error rates were submitted to the same analysis as RTs. The ANOVA revealed a significant main effect for cue type $F(1, 13) = 31.08$; $p < .01$, showing higher error rates for the transition cues (8 %) compared to the task cues (3 %). No further main effect or interaction reached significance (Fs < 1).

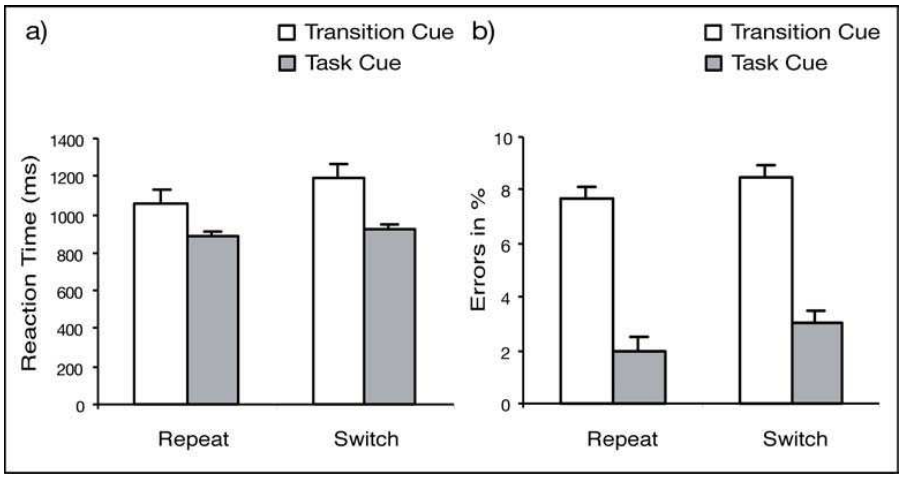

Figure 5.1: a) Mean RT in ms as a function of cue type (transition cue vs. task cue) and trial type (switch vs. repeat). b) Mean error rates in % as a function of cue type (transition cue vs. task cue) and trial type (switch vs. repeat).

Neuroimaging Data

The first question we addressed in the analysis of the fMRI data was whether brain activation associated with the internal generation of task sets would significantly differ from directly cued task sets. The random effects analysis for the main contrast of transition cues versus task cues revealed several activation foci along the left inferior frontal sulcus (Fig. 5.2 and Table 5.3). There was an activation in the mid-part of the left middle frontal gyrus (mid-MFG) which extended in posterior and anterior direction of the middle frontal gyrus (posterior MFG and anterior MFG) and reached the IFJ. Furthermore, bilateral activation was found in the posterior part of the inferior frontal gyrus, namely at the tip of Boca's area (BA 44). The frontopolar PFC (FPFC) as well as the ventral premotor cortex revealed exclusive activation in the right hemisphere. Medially, activation was found in the dorsal part of BA 8 extending into the pre-SMA. In the following sections we will refer to this activation as medial BA 8. Furthermore, the anterior insula was activated bilaterally. The parietal lobe revealed activation along the ascending branch of the intraparietal sulcus (IPS), in the supramarginal gyrus (SMG) bilaterally,

and in the superior parietal lobule (SPL) of the right hemisphere. Finally, the right thalamus was significantly activated.

A further analysis was conducted to test for frontal areas subserving the (re)-configuration of task sets, namely areas elicited in switch trials. Therefore, we calculated the main effect of trial type (switch vs. repeat) thereby applying the defined threshold criteria derived from the main effect of cue type. The results revealed no significant prefrontal activation for the main effect of trial type. However, we obtained parietal and subcortical activations which will not be further addressed, because we were only interested in frontal activations. The results of the whole brain interaction between cue type and trial type revealed also no prefrontal activation. Hence, in all subsequently following analyses, we focused on activations obtained from the whole brain contrast between both cue types.

The second question of this study was concerned with a functional gradient in posterior-anterior direction for the transition cue compared to the task cue. Therefore, we calculated ROI x cue type interactions for three lateral prefrontal ROIs (FPFC, mid-MFG and IFJ) and both cue types (transition cue vs. task cue; see also Fig. 5.3) as well as two frontomedian ROIs (BA 8 and pre-SMA) and both cue types, respectively. The results revealed a significant interaction between the frontolateral ROIs and cue type $F(2,12) = 7.36$; $p < .01$. In post-hoc analyses, we then calculated the percent signal change difference between transition cues and task cues for each lateral ROI and adopted three two-sided Student's t tests with effects to be considered significant at an alpha of 0.05. The results revealed a significant difference between mid-MFG and IFJ $t(13) = 3.79$, $p = 0.002$, indicating a larger cue type effect for the mid-MFG compared to the IFJ. All other lateral ROI x cue type effects were not significant (Fs > 1). For the frontomedian wall, the ROI x cue type interaction was significant $F(1,13) = 9.11$; $p < .01$, indicating a larger percent signal change difference in BA 8 compared to the percent signal change in the pre-SMA for the transition cue compared to the task cue. In Figure 5.3, the activation shift on the lateral PFC along the left inferior frontal sulcus and medial PFC is shown by the estimated beta-values for each cue type which

are higher than 0.2. Note that the mean coordinate in the pre-SMA derived from the study of Brass and von Cramon (2002) revealed no difference between both cue types for the estimated beta-values, which is consistent with the ROI analysis.

Table 5.3: Anatomical location and Talairach coordinates for the comparison of transition cues and task cues with Z > 3.09 (p = 0.001, uncorrected). Activated areas lie more than 1 cm apart. Activations with a minimum volume size of 450 mm^3 (10 adjacent voxels) are shown.

	Left Hemisphere				Right Hemisphere			
Anatomical Area	x	y	z	Zmax	x	y	z	Zmax
Frontal								
FPFC					29	47	15	4.1
IFG	-52	14	9	4.1				
Posterior MFG	-44	8	41	4.1				
Mid-MFG	-44	23	27	4.0				
Anterior MFG	-43	35	6	4.0				
IFJ	-35	-4	32	3.9				
Anterior insula	-29	17	-3	3.9	35	20	0	4.7
Premotor cortex					32	5	50	3.8
Frontomedian cortex (BA 8)	-5	17	50	3.7				
Parietal								
IPS	-37	-52	38	4.5	35	-46	38	4.2
SMG	-46	-46	44	4.5	43	-43	47	3.9
SPL					8	-70	47	4.2
Subcortical								
Thalamus					11	-10	6	3.7

Abbr.: FPFC = frontopolar prefrontal cortex, IFG = inferior frontal gyrus, MFG = middle frontal gyrus, IFJ = inferior frontal junction, IPS = intraparietal sulcus, SMG = supramarginal gyrus, SPL = superior parietal lobule.

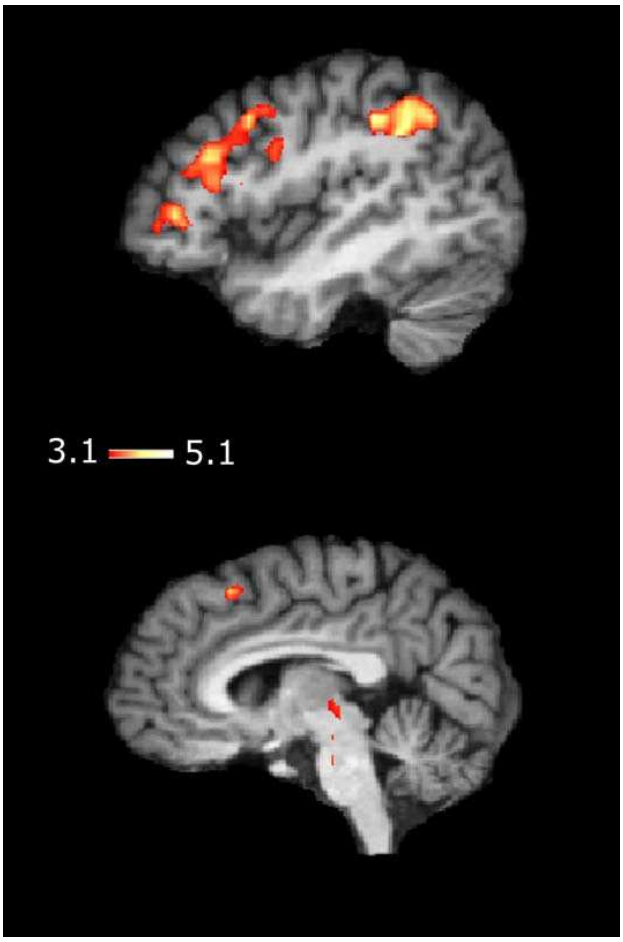

Figure 5.2: Activation map averaged across all 14 participants (Z-threshold at Z = 3.09) mapped onto the mean brain of all participants. Shown is the sagittal view of the left lateral cortex (x = -43) and the frontomedian cortex (x = -5) for the mean contrast of transition cues versus task cues. Red labels indicate positive Z-values.

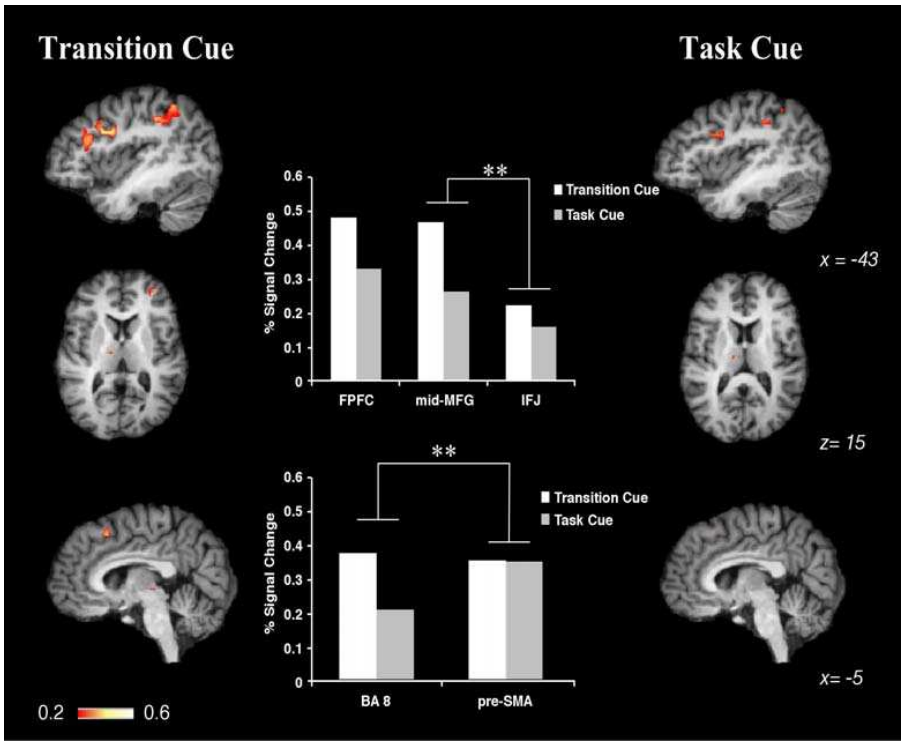

Figure 5.3: Separately masked estimated beta-values for each random effects analysis of cue type and null event (i.e., transition cue vs. null event and task cue vs. null event) with the random effects analysis of the main contrast (transition cue vs. task cue) with a Z-score higher than 3.09 ($p < 0.001$, uncorrected). Only voxels being significantly activated and with a beta-value higher than 0.2 are displayed. Red labels indicate beta-values ranging from 0.2 – 0.6. Diagrams report the averaged percent signal change for both cue types (transition cue and task cue) for three frontolateral ROIs (FPFC x: 29, y: 47, z: 15; mid-MFG x: -44, y: 23, z: 27; IFJ x: -35, y: -4, z: 32) and two frontomedian ROIs (BA 8 x: -5, y: 17, z: 50; pre-SMA x: 1; y: 5; z: 53). Asterisks (*) indicate the significant ROI x cue type interaction between two left lateral ROIs (mid-MFG and IFJ) and two frontomedian ROIs (BA 8 and pre-SMA) with the two cue types, respectively.

5.4.4 Discussion

FMRI Experiment 1 set out to investigate brain regions subserving the internal generation of task sets by contrasting transition cues which exhibit and indirect cue-task association with task cues which exhibit a direct cue-task association.

Several frontolateral activations and one frontomedian activation were found to be more strongly activated for the transition cue compared to the task cue. When comparing these results with previous findings from task-cueing paradigms, it becomes evident that the pattern of the frontal activations usually found with task cues shifted in an anterior direction (see, e.g., Brass & von Cramon, 2002, 2004; Ruge et al., 2005) on both the frontolateral cortex as well as the frontomedian wall. ROI x cue type interactions corroborated this finding.

The contrast between switch and repetition trials as well as for the interaction between cue type and trial type revealed no frontal activations. This finding is in accordance with a number of recent studies which failed to find stronger frontal activations for the contrast of switch and repeat trials with a long CTI (Brass & von Cramon, 2002, 2004; Ruge et al., 2005). They argued that the necessity and demand of exerted cognitive control might be equivalent for both trial types. This is especially the case for an experimental context in which there is an equal likelihood of switch and repetition trials. Therefore, the contrast between trial types may not be a suitable indicator of cognitive control processes (Brass & von Cramon, 2002, 2004).

The Role of the Lateral Prefrontal Cortex for Internally Generated and Directly Cued Task Sets

In the present study, several frontolateral activations were obtained for the transition cue compared to the task cue. Among them is the left inferior frontal junction area (IFJ), the left mid-MFG extending along the upper bank of the inferior frontal sulcus, and the right frontopolar cortex (FPFC),

which have been observed in a number of task-switching studies using both predictable task sequences or direct task cues (Brass & von Cramon, 2002, 2004; Dreher et al., 2002; Luks, 2002; Ruge et al., 2005; Sohn et al., 2001).

Several studies implicate that the IFJ area is relevant for context-related updating of general task representations, which has mainly emerged from task-switching studies using direct task cues (Brass & von Cramon, 2002, 2004; Dove et al., 2000; Sylvester et al., 2003) and Wisconsin Card Sorting studies (Konishi et al., 2002; Monchi et al., 2001; Nagahama et al., 2001).

Activations along the IFS, especially the mid-MFG, have been shown by a variety of tasks where a high degree of cognitive control was required in order to 'monitor', 'maintain', and 'integrate' information over a period of time (D´Esposito et al., 1999; Fletcher & Henson, 2001; Frith & Dolan, 1996; Owen et al., 1999). With the transition cue, different sources of contextual information (N-1 task set) and the present cue information have to be integrated. Therefore, we suggest that the left frontolateral activations reflect the integration of information within working memory.

Additionally, the right FPFC revealed higher activation for the transition cue compared to the task cue. The FPFC is said to be associated with a process that has been termed 'relational integration' (see also Christoff et al., 2001). In general, relational integration refers to planning processes characterized by a requirement to consider multiple relations simultaneously (Robin & Holyoak, 1995). Thus, the FPFC comes into play in complex tasks where a number of related dimensions, or sources of variation, have to be brought together in order to come to a solution. Interestingly, Christoff and Gabrieli (2000) proposed that the right FPFC may be selectively involved in active processing, such as manipulation or evaluation, performed upon self-generated information. In a similar vein, the mid-MFG is interpreted to play a crucial role in integrating different sources of information. However, one might speculate that a higher

relational complexity of tasks leads to an additional recruitment of frontopolar areas (see also Christoff & Gabrieli, 2000).

The Role of the Medial-Frontal Wall for Internally Generated and Directly Cued Task Sets

The comparison of activations of both cue types revealed an activation peak in the medial BA 8 for the transition cues. Contrary to that, previous task-switching studies showed that the pre-SMA/SMA is involved in cue-related processing (Brass & von Cramon, 2002; Dove et al., 2000; Luks et al., 2002; Rushworth et al., 2002). Furthermore, the pre-SMA is assumed to be important for the internal generation and preparation of motor activity (Lee et al., 1999; Picard & Strick, 1996; Picard & Strick, 2003). Regarding the present findings, it is conceivable that a functional gradient from the pre-SMA into the rostrally situated BA 8 is elicited by the indirect cue-task associations in which the external transition cue information does not determine the relevant task set. Evidence for the account of a functional gradient in anterior direction was also revealed by a ROI x cue type interaction of the medial BA 8 and a coordinate in the pre-SMA. Here we could show that the medial BA 8 compared to the pre-SMA plays a dominant role for the transition cue compared to the task cue.

However, it is necessary to specify the subprocesses relevant in indirect cue-task associations. Besides the memory aspect which requires the participants to integrate information over a period of time, it is necessary to internally generate the now relevant task set representation due to the indirect cue-task association. We presume that the medial BA 8 is subserving this internally driven process. This is further corroborated by studies investigating the internal generation of synonyms (Nyberg et al., 2003), uncertainty in decision making (Volz, Schubotz & von Cramon, 2003) as well as during rule application (Goel & Dolan, 2000), serial event prediction in increasingly complex stimulus trains (Schubotz & von Cramon, 2002), and response competition (Ullsperger & von Cramon, 2004).

Finally we suggest that the medial BA 8 is important for the internal generation of task sets which becomes relevant for solving environmental ambiguity. This is in accordance with the view that less determined action contexts require a higher demand of endogenous control compared to directly cued task sets.

Other Frontolateral Activations Revealed by the Transition Cue

Besides the activations along the dorsal bank of the inferior frontal sulcus, we also obtained left-sided activation in the posterior part of the inferior frontal gyrus, namely the tip of Broca (BA 44). There is broad evidence for BA 44 to be involved in phonological rehearsal processes (see, e.g., Fletcher & Henson, 2001). It seems conceivable that the present activation might reflect the phonological rehearsal of the contextual information facilitating the coordination process within working memory.

5.4.5 Conclusion

In fMRI Experiment 1, the newly developed transition-cueing paradigm was investigated. Two cue types, the transition cue and the task cue, were contrasted to reveal neural correlates of endogenous control processes. The results revealed higher activations for the transition cue compared to the task cue in several frontal, parietal, and subcortical areas. This is in line with findings of studies using solely explicit task cues. Moreover, the results revealed a functional gradient in posterior-anterior direction along both the left frontolateral and frontomedian cortex when comparing an indirect with a direct cue-task association. ROI x cue type interactions showed that the mid-MFG and the medial BA 8 play an essential role when the action context is less determined. We suggest that the activation in the mid-MFG subserves the integration of external information and internally represented information in working memory revealing a higher demand of cognitive control compared to directly cued task set representations. The activation in the medial BA 8 is associated with the

requirement to internally generate the task set representation, reflecting an act of endogenous control.

6 Empirical Section II

The prospect of functional MRI Experiment 2 was to go one step ahead in investigating endogenous control processes. In fact, one might argue that with indirect cue-task associations, the relevant task set is still determined by the experimental context. That is, participants are still explicitly instructed which task to perform on. Therefore, one interesting question is: What happens, if participants are not explicitly told what to do but can voluntarily choose the task by their own? FMRI Experiment 2 was designed to investigate processes that are relevant when participants can select the task set by their own (Forstmann et al., 2006).

6.1 fMRI Experiment 2

6.1.1 Methods

Participants

Twenty-three healthy volunteers were recruited and tested at the Max Planck Institute for Human Cognitive and Brain Sciences, Department for Cognitive Neurology, in Leipzig. We obtained written consent from all 23 participants prior to the scanning session. All participants had normal or corrected-to-normal vision. No subject had a history of neurological, major

medical, or psychiatric disorder. The data of one subject was excluded from the analysis due to high error rates (> 10% error). The remaining 22 participants were 12 females and 10 males (mean age = 24.2 years, SD = 2.76) who were all right handed as assessed by the Edinburgh Inventory (Oldfield, 1971). Participants received 8 Euro/h for participation.

Stimuli and Tasks

Four cues each associated with one of four simple discrimination tasks, i.e. color, orientation, size, and line task, were introduced. The cues were foveally presented in a 2x2 grid at the beginning of each trial with a visual angle of 2.8° (see Fig. 6.1). Each quadrant of the grid contained a semantic abbreviation for one of the four tasks, i.e. 'FAR' for 'Farbe' which corresponds to color, 'SPI' for 'Spitze' which corresponds to tip, 'GRÖ' for 'Grösse' which corresponds to size, and 'LIN' for 'Linie' which corresponds to line. The locations of the cues were balanced across participants. There were 16 possible 'cue location mappings' which were randomly assigned to the participants so that each mapping was presented at least once. In order to instruct the participants which task set could be chosen, the quadrants were either presented in a bold frame, indicating that this task could be chosen, or not, indicating that this task is not available for choice. After a constant cue-target interval the target was presented. This target was multivalent, i.e. the target contained one value of each discrimination task. There were 16 possible values of a target. Corresponding to their choice of task, participants had to respond to the target with either the index or the middle finger of the right hand.

In order to check for accuracy and to give valid feedback, the four semantic abbreviations of the four tasks were presented again. This time, they were horizontally aligned in pseudo-randomized order. Pressing a spatially compatible key with their left hand, participants should now indicate which task they had actually chosen and responded to with their first response. In the following, the horizontally aligned cues are referred to as the probe stimuli. The randomization of the probe stimuli assured us that participants did not prepare for the second response during the

decision time. Finally, a feedback for wrong, miss, or correct responses was presented.

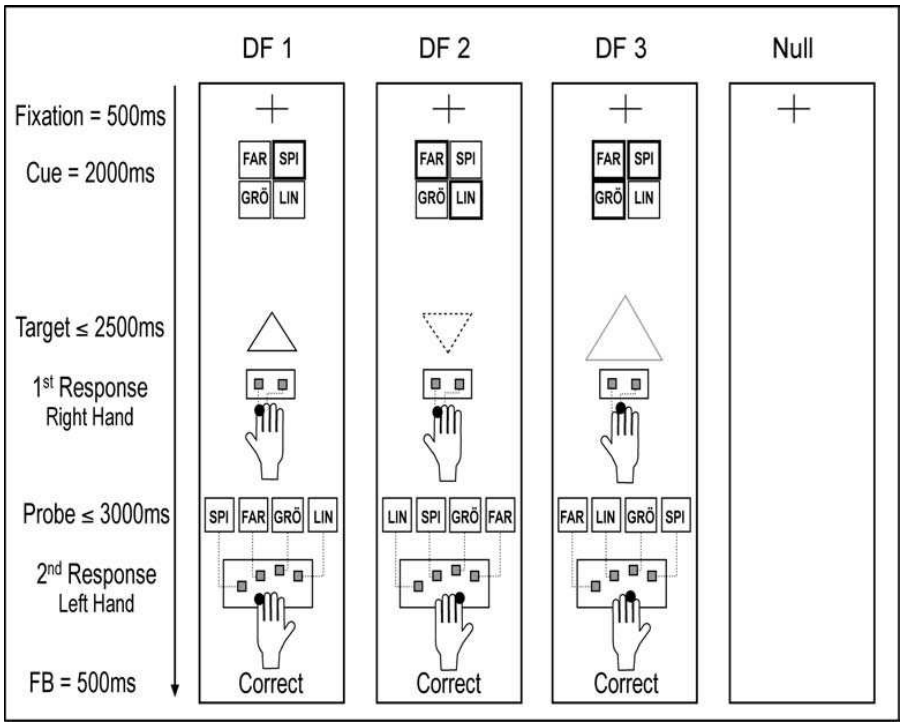

Figure 6.1: Schematic drawing of the different conditions. Degrees of freedom in choice were varied between forced condition (DF 1) and choice conditions (DF 2 and DF 3). These were indicated by bold lines. Tasks were instructed by German abbreviations in the 2x2 grid with 'FAR' (color),'SPI' (tip),'GRÖ' (size), and 'LIN' (line). Target and probe stimulus were presented until a response was given or an interval of 2500 ms or 3000 ms was exceeded, respectively.

Abbr.: FB = Feedback

Scanning Procedure

The design consisted of one independent variable, the 'degrees of freedom in choice', shortly referred to as degrees of freedom (DF), which varied from 1 to 3. The timing of the sequence of trials was triggered from the

magnetic resonance imaging (MRI) control every 10 seconds. Image acquisition started with a variable oversampling interval of 0, 500, 1000, or 1500 ms to obtain an interpolated temporal resolution of 500 ms. Then, a fixation cross was presented for 50 ms followed by the 2x2 grid, which was always presented for 2000 ms. Thus, the cue-target interval was held constant. Then the target was presented until a response was made with the right hand or until the response interval exceeded 2500 ms. After the first response was given, the probe stimuli were presented. These remained on the screen until the second response was made with the left hand or until the response interval exceeded 3000 ms. Finally, feedback was presented for 500 ms. One trial lasted for 10 s.

The experiment consisted of two blocks with 180 experimental trials each, resulting in approximately 13 trials of the combination of the task and the degrees of freedom (1-3 DF). There were 14 different combinations of tasks and DF (DF 1 = 4 combinations; DF 2 = 6 combinations; DF 3 = 4 combinations). Even though we could not introduce pre-randomized task sequences due to the manipulation of free choice, we defined subsets of each combination of tasks and the DF. Trials were pseudo-randomly chosen from each subset. This assured us that each combination was presented with approximately equal frequency. Furthermore, it is important to note that the subsequent trial of the DF 3 condition was not constrained to the one task which was not valid for choice.

We also included 40 null events, which were pseudo-randomly interspersed. The null events were included to compensate the overlap of the BOLD response between adjacent trials. The experiment lasted for about 60 min. Every block started out with two dummy trials which were excluded from further analysis.

MRI Scanning Procedure

The experiment was carried out on a 3T scanner (Siemens, Erlangen, Germany). 20 axial slices were acquired (19.2 cm field of view, 64 x 64

matrix, 4 mm thickness, 1 mm spacing) parallel to the AC-PC plane and covering the whole brain. Slice gaps were interpolated to generate output data with a spatial resolution of 3 x 3 x 3 mm. We used a single shot, gradient recalled EPI sequence (TR 2000 ms, TE 30 ms, 90^{O} flip-angle). Prior to the functional runs, corresponding 20 anatomical MDEFT slices and 20 EPI-T1 slices were acquired. Stimuli were displayed using VisuaStim (Magnetic Resonance Technologies, Northridge, USA), consisting of two small TFT-monitors placed directly in front of the eyes, simulating a distance to a normal computer screen of about 100 cm with a resolution of 1024 x 768 and a refresh rate of 60 Hz.

6.1.2 Data Analysis

Preprocessing and Statistical Evaluation of fMRI Data

The preprocessing and statistical evaluation of fMRI Experiment 2 was comparable to that of fMRI Experiment 1 (see also Section 5.4.2). Design-specific differences of the statistical analysis pertained to the onsets for the event-related analysis. These were set to the presentation of the 2x2 grid at the beginning of each trial. Moreover, only cortical areas with a Z-score higher than 3.1 ($p < 0.001$, uncorrected) and with a volume greater than 180 mm^3 (5 adjacent voxel) are reported. Finally, the computation of the signal change of the hemodynamic response was equivalent for fMRI Experiment 1 and 2, however, here the onset was again set to the presentation of the 2x2 grid at the start of a trial.

6.1.3 Results

Reaction Time Analysis: For the analyses of error rates and reaction times (RTs), two-tailed Student's t tests for the relevant comparisons were used. Error rates and reaction times are displayed in Figure 6.2.

The RTs for the target response revealed a significant effect for the degrees of freedom (DF) 2 condition vs. the DF 1 condition (867 ms vs. 829 ms), $t(21) = 4.1$; $p < .001$, and the DF 3 condition vs. the DF 1 condition (881 ms vs. 829 ms), $t(21) = 3.2$; $p < .001$, indicating higher RTs for the conditions in which participants could voluntarily choose a task compared to the no-choice condition (DF 2 $\cup$ DF 3 = 874 ms vs. DF 1 = 829 ms). There was no significant difference between choice conditions (DF 3 vs. DF 2), $t(21) = 1.18$; $p > .25$. Since participants were instructed that the response to the probe stimuli was unspeeded and only relevant for giving valid feedback, the RTs were not analyzed.

Error Rates: The overall accuracy was 96.47%. The error rates revealed no significant effects (ts < 1) between conditions.

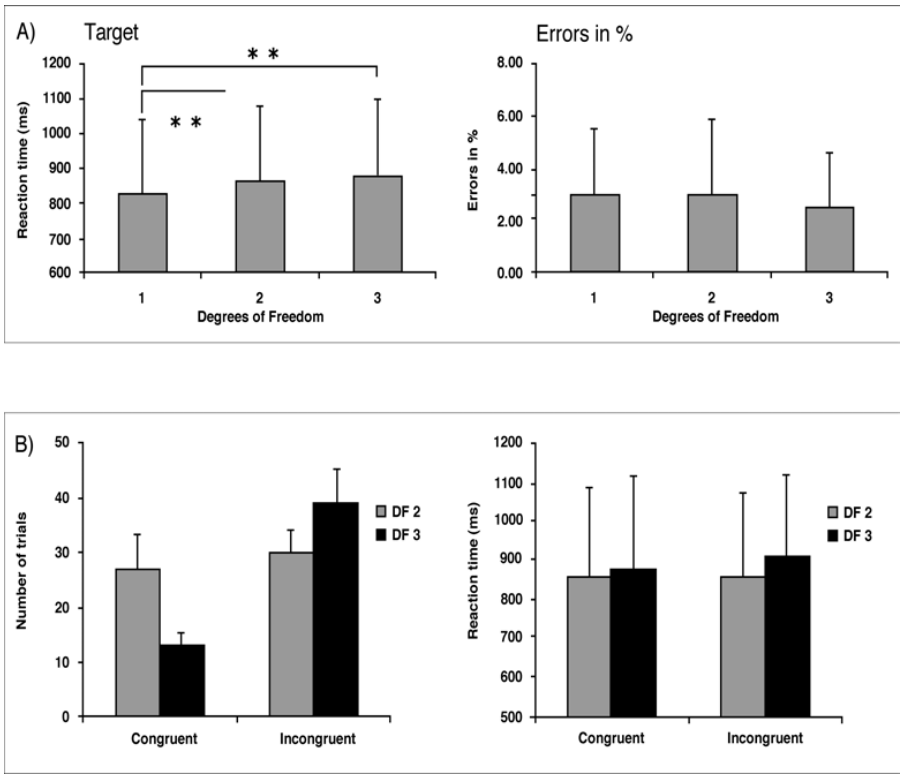

Figure 6.2: A) Mean reaction time of the target response, and percent errors as a function of degrees of freedom in choice (DF 1, DF 2, DF 3). B) Number of congruent and incongruent trials, and mean reaction time of congruent and incongruent trials as a function of the degrees of freedom (DF 2 and DF 3). Note that both incongruency cases of the DF 3 condition are averaged.

Selection Strategies

Since we tried to equalize the frequency of task types in combination with the degrees of freedom, it is important to note that the interpretation of specific selection strategies is highly constrained (see also method section). Furthermore, participants always had to switch between task sets so that the task set that was chosen on the present trial was never valid for choice on the next trial.

However, to test for the potential occurrence of specific selection strategies, several post-hoc analyses were performed. The dependent

measure was the number of trials that were chosen for each particular task. The independent variables were a) the task type to account for a preference in 'task selection' and b) the cue location to account for a preference in 'location selection'. Both analyses revealed no significant effect (*t*s < 1).

Neuroimaging Data

Whole Brain Analysis

The first question we addressed in the analyses of the fMRI data was whether choice conditions would significantly differ from the condition in which no-choice was required. The random effects analysis for the main contrast of choice conditions (DF 2 ∪ DF 3) versus the no-choice condition (DF 1) revealed activation in the anterior midcingulate cortex (aMCC) of the left hemisphere. Furthermore, there was an activation in the superior parietal lobule (SPL) and the posterior part of the intraparietal sulcus (pIPS) in the right hemisphere (see Fig. 6.3 and Table 6.1).

Table 6.1: Main contrast of choice (DF 2 ∪ DF 3 vs. DF 1). Anatomical location and Talairach coordinates with Z > 3.09 (p = 0.001, uncorrected). Activated areas lie more than 0.5 cm apart. Activations with a minimum volume size of 180 mm^3 are shown.

	Left Hemisphere				Right Hemisphere			
Anatomical Area	x	y	z	Zmax	x	y	z	Zmax
Frontal								
aMCC	-5	23	38	3.7				
Parietal								
pIPS					31	-73	35	3.7
SPL					8	-70	46	3.9

Abbr.: aMCC = anterior midcingulate cortex, SPL = superior parietal lobule, pIPS = posterior intraparietal sulcus.

Selection-Specific Analysis

Selection-specific analyses were calculated for regions of interest extracted from the whole brain contrast of choice conditions (DF 2 ∪ DF 3) versus the no-choice condition (DF 1; see Fig. 6.3, right panel). For the analyses of the percent signal change differences between conditions, two-tailed Student's t tests were calculated. Most importantly, the results revealed no significant percent signal change difference between choice conditions (DF 3 vs. DF 2) for the aMCC. Moreover, a significant percent signal change difference for the aMCC was found for both the DF 2 condition versus the DF 1 condition, $t(21) = 4.13$; $p < .001$, and for the DF 3 condition versus the DF 1 condition, $t(21) = 4.23$; $p < .001$, indicating a higher percent signal change in choice conditions compared to the no-choice condition.

A comparable data pattern was also found for the pIPS and the SPL. Again, no significant percent signal change difference was obtained between the choice conditions (DF 3 vs. DF 2). A significant percent signal change difference for the pIPS was found for the DF 2 condition versus the DF 1 condition $t(21) = 4.88$; $p < .001$, and for the DF 3 condition versus the DF 1 condition $t(21) = 5.57$; $p < .001$, indicating a higher percent signal change difference for the choice conditions compared to the no-choice condition. Finally, the SPL revealed a significant percent signal change difference for the DF 2 condition versus the DF 1 condition $t(21) = 4.85$; $p < .001$, and the DF 3 condition compared to the DF 1 condition $t(21) = 3.98$; $p < .001$, indicating a higher percent signal change difference for the choice conditions compared to the no-choice condition.

Congrueny of S-R Mappings

As is shown in Figure 6.4, the activation located in the aMCC might also be referred to as a region called the rostral cingulate zone (RCZ; see, e.g., Picard & Strick, 1996). Because the RCZ has been argued to play a crucial role in conflict monitoring (see, e.g., Botvinick et al., 1999), we were

interested in whether incongruent stimulus-response mappings in the DF 2 and DF 3 conditions might have elicited the present data pattern. In choice conditions, it is possible that the stimulus dimensions which are mapped onto different responses (incongruent trials) elicit higher response conflict compared to stimulus dimensions which are mapped onto the same response (congruent trials). In particular, one might argue that the S-R mappings of valid tasks in choice conditions are automatically co-activated by the bold cue in the 2x2 grid. This would lead to a higher response competition for the valid S-R mappings compared to the S-R mappings of all tasks. However, with the present design, it was not possible to control for S-R congruency beforehand. Furthermore, the present design does not allow to test congruency for all S-R mappings, i.e. for all four tasks independently of the degrees of freedom, because of too few trials for all conditions.

We conducted a post-hoc analysis to test for the influence of congruency effects only for the choice conditions (see Fig. 6.3). Thus, congruency for the choice conditions was defined for a given trial with respect to the valid tasks in that particular trial. In a first step, we defined trials as congruent or incongruent for the DF 2 condition and the DF 3 condition, respectively. In the DF 2 condition, the number of incongruent trials and congruent trials was approximately equalized. Note, however, that there are two different cases of incongruent trials for the DF 3 condition. That is, the chosen S-R mapping could either be incongruent with one or two of the other relevant S-R mappings. Both cases of incongruency were averaged for further analyses. This led to an unequal distribution of incongruent and congruent trials in the DF 3 condition (incongruent = 73.3%; congruent = 26.7%), so that a non-parametric Wilcoxon test for two paired samples was computed. Finally, we computed a ROI analysis with the peak activated voxel in the aMCC for congruent and incongruent trials for the DF 2 condition and the DF 3 condition.

The results revealed no main effect for congruency or the degrees of freedom for both the reaction times and the percent signal change. This

was also the case for the interaction between congruency and the degrees of freedom for both RTs and the percent signal change. In sum, the results indicate that congruency of valid S-R mappings is unlikely to explain the present data pattern.

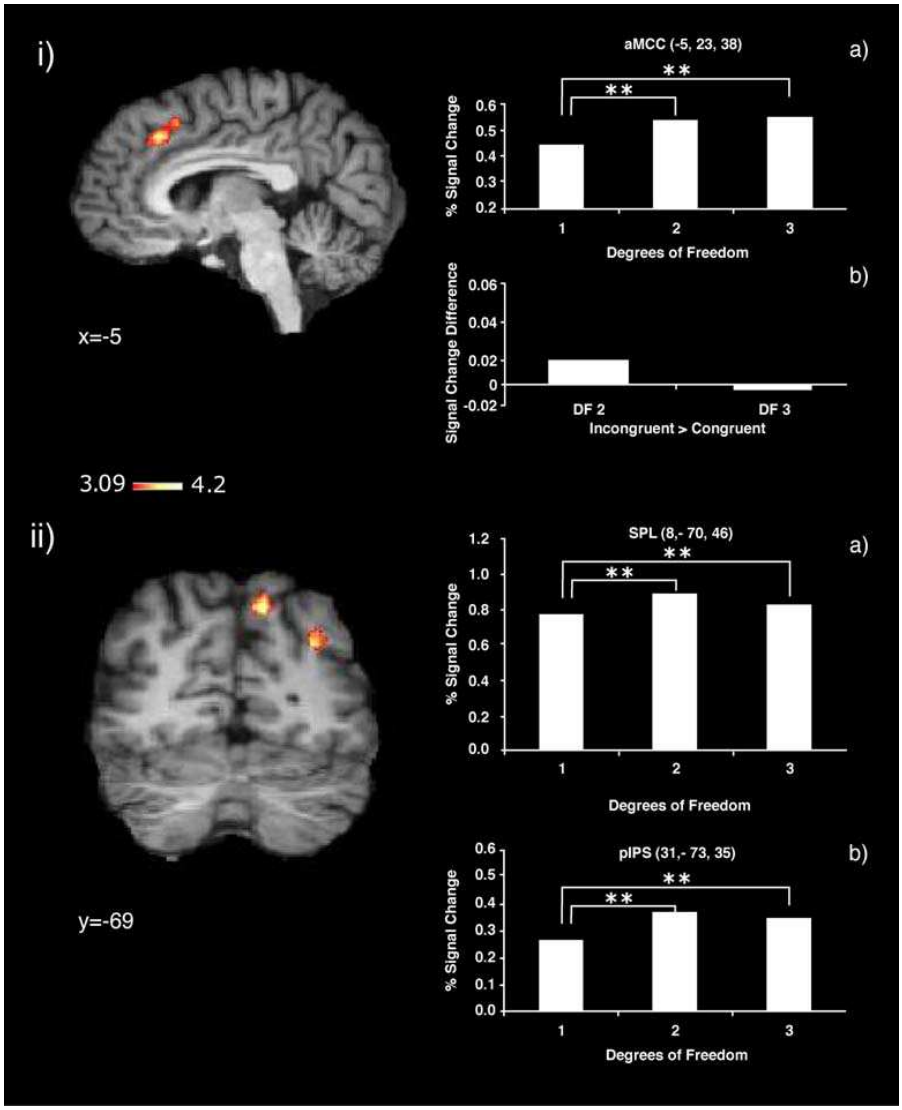

Figure 6.3: Main contrast of choice (DF 2 ∪ DF 3 > DF 1). Activation map averaged over 22 participants (Z-threshold at Z = 3.09, uncorrected) mapped onto an individual brain from the inhouse database. Red labels indicate positive Z-values. ***i)*** *Sagittal plane showing activity in the left aMCC (-5, 23, 38);* ***ia)*** *the corresponding percent signal change for DF 1-3;* ***ib)*** *percent signal change difference for the DF 2 and DF 3 condition for incongruent versus congruent trials;* ***ii)*** *Coronal plane showing activation in the right SPL (8, -70, 46) and the right pIPS (31, -73, 35);* ***iia)*** *corresponding percent signal change for the SPL for DF 1-3;* ***iib)*** *corresponding percent signal change in the right pIPS for the DF 1-3.*

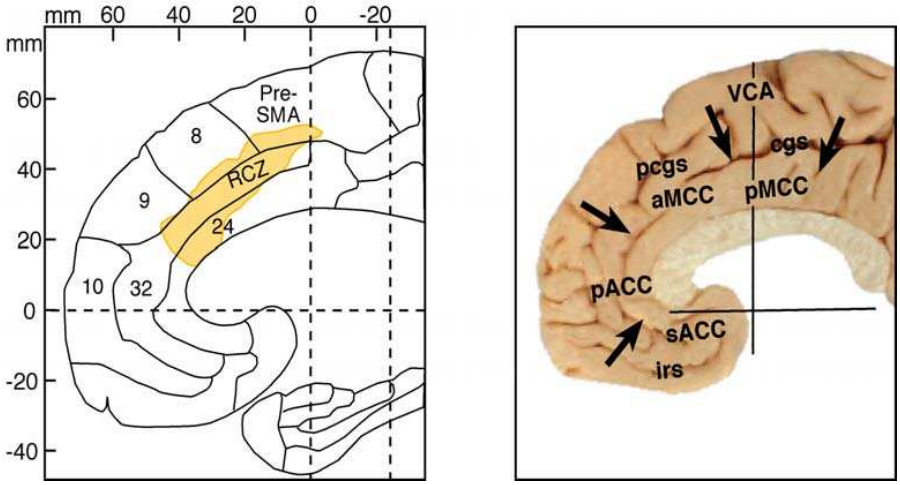

Figure 6.4: Sagittal view of the frontomedian cortex: a) Schematic drawing of the frontomedian cortex (adapted from Ridderinkhof et al., 2005). The yellow area denotes the rostral cingulate zone (RCZ). Numbers denote Brodmann areas. b) Anatomical slice adapted from Vogt (Nat Rev Neurosci, 2005). aMCC = anterior midcingulate cortex, pACC = pregenual anterior cingulate cortex, sACC = subgenual anterior cingulate cortex, pMCC = posterior midcingulate cortex, VCA = vertical plane at the anterior commissure, cgs = cingulate sulcus, irs = inferior rostral sulcus, pcgs = paracingulate sulcus.

6.1.4 Discussion

The present study aimed at investigating neural correlates of the voluntary selection of task sets. Previous task-switching studies used external task cues which were directly or indirectly indicating the relevant task set (see, e.g., Brass & von Cramon, 2002, 2004; Forstmann et al., 2005; Rushworth et al., 2002), or they relied on predictable task sequences (Dreher et al., 2002; Sohn et al., 2000). Here we investigated brain regions subserving the voluntary task-set selection by manipulating the 'degrees of freedom in choice'. That is, participants could voluntarily choose between two or three task sets. Furthermore, we were interested in whether brain regions obtained from the whole-brain contrast of choice would be sensitive to selection-specific differences between choice conditions.

The results of the contrast of the choice conditions versus the no-choice condition (DF 2 ∪ DF 3 versus DF 1) revealed a fronto-parietal network associated with the voluntary selection of task sets. An activation was found in the left anterior midcingulate cortex (aMCC) in a region corresponding to the rostral cingulate zone (RCZ; see, e.g., Picard & Strick, 1996). Furthermore, activation was found in the right superior parietal lobule (SPL) and the right posterior intraparietal sulcus (pIPS). Subsequent selection-specific ROI analyses revealed activation differences between choice conditions and the no-choice condition in these cortical regions (DF 3 vs. DF 1; DF 2 vs. DF 1). However, no activation difference between choice conditions (DF 3 vs. DF 2) was obtained.

Finally, because the MCC is said to play a crucial role in processing conflict, we were interested in whether incongruent S-R mappings might have elicited the present data pattern. Moreover, the results indicate that congruency between S-R mappings cannot account for the observed data pattern.

The Voluntary Selection of Task Sets

The MCC has been shown to subserve various cognitive processes (see also Ridderinkhof et al., 2004; Rushworth et al., 2004; Ullsperger & von Cramon, 2004) like the resolution of response conflict (Botvinick et al., 1999; Carter et al., 1998), or the detection of errors (Coles, Scheffers, Holroyd, 2001; Falkenstein et al., 2000; Ullsperger & von Cramon, 2001). Moreover, it has recently been shown that the MCC is involved in decision making processes, too (see, e.g., Lau et al., 2004; Walton, Devlin & Rushworth, 2004). In these studies, MCC activation was found in conditions where participants could voluntarily select a movement or response set.

We found activation in the aMCC for the conditions in which participants could voluntarily select a task set. This result corroborates the

findings of a recent study by Walton and colleagues (2004) using a response-switching paradigm (see also Rushworth et al., 2002). In their study, participants could voluntarily select one of two response sets which was compared with a no-choice condition. The results revealed an activation in the MCC for the choice condition compared to the no-choice condition. This activation is very similar to the coordinate found in the present study (Walton, Devlin & Rushworth: -6, 22, 36; present study: -5, 23, 38).

We were interested in whether the activation within the aMCC might be modulated by the number of degrees of freedom. In fact, we hypothesized that a higher number in degrees of freedom would lead to a significantly higher percent signal change. We presumed that with three task sets, a higher effort is needed to activate a task set above threshold. However, the present data indicate that there is no selection-specific difference between choice conditions. This finding is consistent with the idea that the activation within the aMCC reflects an all-or-none process which, however, has so far only been investigated for a maximum of three possible choices. In the context of the present study, we propose that this process can be best characterized as the voluntary selection of task sets.

However, one might ask what these findings imply in the light of recent meta-analyses which reveal that the MCC plays a crucial role in performance monitoring processes (see Ridderinkhof et al., 2004; Rushworth et al., 2004; Ullsperger & von Cramon, 2004)? In fact, there are two major theories associated with the RCZ. These are the error detection model (Coles, Scheffers & Holroyd, 2001; Falkenstein et al., 2000) and the conflict monitoring theory (Botvinick et al., 1999; Carter et al., 1998; Van Veen & Carter, 2002). While the error detection model proposes a specific error detection system, the response conflict hypothesis denies the necessity of a specific error detection system in favor of a more general unitary system evaluating response conflict (see, e.g., Ullsperger & von Cramon, 2001).

Several authors proposed that the error detection system is activated when a comparison between representations of the appropriate (correct, intended) and the actual response yields a mismatch (e.g., Coles, Scheffers & Holroyd, 2001; Falkenstein et al., 2000; Gehring et al., 1993). As a consequence of the comparison process, errors are detected. With respect to the present data, higher error rates should have been obtained for the choice conditions compared to the no-choice condition. However, the analysis of the error rates revealed no significant effects.

With respect to the conflict monitoring theory, one might argue that response conflict is higher in choice conditions compared to the no-choice condition because more than one task set and hence S-R mapping might be activated. This can be tested by investigating the congruency between stimulus-response (S-R) mappings for the DF 2 and DF 3 condition. However, in doing so, different stimulus dimensions, e.g., color or size, have to be associated with different responses, e.g., press left when red and small; press right when green and big. Note that with the response-switching or S-R reversal paradigms, it is not possible to test for S-R congruency, since there is only one stimulus set for which the S-R mapping is sometimes reversed.

With the present design, it was possible to distinguish between incongruent and congruent trials for both choice conditions. However, in contrast to the response conflict theory, which assumes long-lasting congruency effects between all S-R mappings, the present analysis allows to control for task-dependent response conflict on the present trial. Hence, if task-dependent response conflict could account for the present data, one would have expected that the incongruent trials lead to higher activation within the aMCC compared to congruent trials. Concerning the S-R congruency analysis of the present data, no difference for choice conditions between incongruent and congruent trials for the peak activated voxel in the RCZ was found.

A tentative explanation for the present findings might be that the possibility of voluntarily selecting between different alternatives is

accompanied with a higher degree of uncertainty. We presume that uncertainty arises from the lack of a specific goal to drive the choice. In this sense, uncertainty refers to a lack of perceived subjective controllability of the situation which is caused by a missing selection criterion (see, e.g., Jungermann, Pfister & Fischer, 1998; Volz, Schubotz & von Cramon, 2004). In fact, one might argue that the requirement to choose, without any valence in choosing, may set up a special form of decision-making conflict. Contrary to the response-conflict theory, the decision-making conflict refers to the competition between different task sets. However, it seems conceivable that a higher number of choices would lead to a higher conflict. Thus, a selection-specific difference between the DF 3 versus the DF 2 condition for the activation within the RCZ would have been expected. However, no selection-specific difference between choice conditions was obtained.

In sum, activation in the RCZ seems to be related to the voluntary selection of task sets in an all-or-none manner. However, with respect to the present study, this assumption is only valid for choice conditions with maximally three options in choice. At the same time, selecting between different alternatives might be accompanied with a higher degree of uncertainty due to the lack of explicit instructions on which task to select.

The Visual Attentional Selection of Task Sets

The whole-brain contrast of choice conditions versus the no-choice condition revealed an activation in the posterior part of the intraparietal sulcus (pIPS) and the superior parietal lobule (SPL). That is, the DF 2 condition and the DF 3 condition both revealed a higher percent signal change difference compared to the DF 1 condition. Furthermore, no significant difference between choice conditions was found.

In general, activations in the intraparietal sulcus (IPS) and the SPL are reported by a number of studies investigating task-related control with the task-switching paradigm (Brass & von Cramon, 2002, 2004; Derrfuss, Brass & von Cramon, 2004; Forstmann et al., 2005; Ruge et al., 2005;

Wylie, Javitt & Foxe, 2003). Furthermore, these areas have been consistently activated in various tasks involving spatially directed attention (Corbetta et al., 2000; Corbetta & Shulman, 2002; Fink et al., 1997). A common feature among the visuospatial tasks in the experiments revealing comparable posterior parietal activations is that participants were asked to direct their attention covertly to peripheral target locations in order to detect or discriminate a stimulus (Fink et al., 1997; Kastner et al., 1999; Nobre et al., 1997).

With respect to visual attentional selection processes in the pIPS, Rushworth et al. (2001) adopted two different procedures of the task-switching paradigm and revealed evidence for a complementary role in pIPS and the adjacently situated anterior intraparietal sulcus (AIP) for visual attention and visuomotor transformation, respectively. The activation in pIPS was reported for a visual switch paradigm, where participants made an attentional shift between stimuli on the basis of either color or shape, whereas manual responses were only rarely required at the time of attentional switching.

Evidence for the SPL to be involved in attentional shifting comes from Yantis et al. (2002). In their study, participants covertly shifted attention between two peripheral spatial locations. The results revealed that both the SPL and the pIPS are associated with a discrete signal to shift spatial attention.

The activation found in pIPS and SPL might subserve the attentional selection of the task set. It is conceivable that they provide a biasing signal for the visual cortex that affects on-going processing to favor an attended location. With respect to the 2x2 grid at the beginning of each trial, it might be possible that a higher degree of visual attention was required for the selection of a specific task set in choice conditions.

As yet, both processes seem to be equally required in choice conditions independent of the number of degrees of freedom in choice. A tentative explanation might be that it is more efficient for the system to adopt to the

category ‘choice vs. no-choice’ than ‘different weights of alternatives in choice conditions’.

6.1.5 Conclusion

The presented study aimed at investigating the voluntary selection of task sets with a modified task-switching paradigm. A second question was concerned with the number of task sets to choose from. The results revealed activations in a fronto-parietal network subserving the voluntary selection of task sets in an all-or-none manner. Activation in the RCZ is interpreted to reflect the voluntary selection of task sets, whereas activations in the posterior parietal cortex are presumed to subserve visual attentional selection processes.

7 General Discussion

The experiments presented in this thesis were designed to investigate behavioral and neural correlates of endogenous control processes in task switching. The first aim was to devise a new cueing procedure, the transition-cueing paradigm, to manipulate the cue-task association. This was done to investigate the memory-based internal generation of task sets. Two behavioral experiments revealed results comparable to classical cueing versions of the task-switching paradigm. Most interestingly, we found prolonged reaction times and higher shift costs for transition cues compared to task cues. This was taken as evidence for the requirement to internally generate the task set due to indirect cue-task association. In a subsequent fMRI experiment, this behavioral finding could be replicated. The comparison of transition cues versus task cues revealed higher activations in frontolateral as well as posterior frontomedian regions. The frontolateral activations are assumed to reflect the integration of information within working memory, and the activation in the frontomedian cortex seems to reflect the internal generation of task sets. Furthermore, regions of interest analyses indicate an important role for several regions along the left IFS and the posterior frontomedian wall. This is suggested to reflect a functional gradient in posterior-anterior direction which is linked to the relative degree of required endogenous control.

The second aim of this thesis was to investigate neural correlates involved in the voluntary selection of task sets. In this context, we asked whether there are differences between choice and no-choice conditions. The results revealed activations within the anterior midcingulate cortex and the posterior parietal cortex for the choice conditions compared to the no-choice condition. No selection-specific differences between three and two choices could be found.

The General Discussion will focus on two remaining aspects of the presented data. The crucial findings of behavioral and imaging data of Empirical Section I will be integrated. Subsequently, endogenous control processes as revealed by fMRI Experiment 1 and 2 will be discussed in the light of recent theoretical frameworks about the functional architecture of the human PFC.

7.1 Integrating Behavioral and Neural Measures

In cognitive neuroscience, it is common practice to infer the psychological structure of cognition from conjoint measures of behavior, e.g. reaction times, and brain activation, e.g. BOLD. This approach is especially interesting when developing a new experimental procedure as described in Empirical Section I. Furthermore, functional imaging can provide valuable insights into cognitive subprocesses which are otherwise not dissociable and detectable upon the reaction time data alone. This is especially interesting for experimental manipulations such as the cue-task association, because here several subprocesses are necessary to perform on indirect compared to direct associations.

In two behavioral experiments, a synthesis of two different procedures of the task-switching paradigm, called the transition-cueing paradigm, was tested. This allowed to investigate cue-locked task set retrieval without directly indicating the relevant task set. The results replicated the results of previous task-switching studies insofar as the unpredictable switching between two simple cognitive tasks resulted in large shift costs. Moreover,

the long CTI resulted in a strong preparation effect for both cue types in both experiments. Finally, in the second experiment a shift-specific preparation effect was found for both cue groups indicating the ability to reconfigure the cognitive system in advance for an upcoming task shift for both direct and indirect cue-task associations (Rogers & Monsell, 1995).

In general, the results obtained with the present studies using transition cues and task cues in one experimental session can be compared to studies using explicit task cues only. Thus, the findings support the idea that performance with transition cues can be compared to that with direct task cues. However, the crucial question of these experiments pertained to the investigation of the directness of the cue-task association. Transition cues indicate the upcoming task with reference to the preceding task. Thus, to activate the upcoming task set, participants need to maintain the identity of the preceding task in memory and integrate this information with the meaning of the current cue in order to determine the required task. It is evident that this kind of sequentially defined task cue differs markedly from the traditionally used task cues that directly indicate the task (see also Forstmann, Brass & Koch, 2006a). Direct task cues may lead to automatic activation of the associated task set (see also Koch, 2003; Koch & Allport, in press), whereas such direct stimulus-based automatic task-set activation is not possible when using transition cues. Interestingly, the behavioral results revealed prolonged RTs and higher shift costs for transition cues compared to task cues. This finding was interpreted to reflect the additional need to integrate different sources of information in working memory to internally generate the now relevant task set with indirect cue-task associations compared to direct cue-task associations.

In a subsequent fMRI experiment, we were interested in the neural correlates of the memory-based internal generation of task sets. Therefore, a highly comparable design to Behavioral Experiment 1 was chosen. Thus, the crucial manipulation pertained again to the comparison of both cue types. The fMRI results revealed higher activations in several frontal, parietal and subcortical areas for the transition cues compared to the task cues. Interestingly, a very similar network of activations was obtained in

studies using explicit task cues only (Brass & von Cramon, 2002; Ruge et al., 2005). Thus, it might be conceivable that the performance on both cue types is subserved by a comparable neural circuit which is activated more strongly for the performance on transition cues than on task cues. What does this finding reveal about the necessity to internally generate the task set with indirect cue-task associations indicated by the results of both behavioral experiments? A tentative explanation of the findings could be that transition cues do not require an additional generation process, but rather, a longer engagement of the same processes required for the performance on task cues. Evidence for such an explanation can be derived from the behavioral data pattern where the transition cues revealed prolonged RTs compared to the task cues. Hence, one might argue that systematic differences in response latencies between conditions contribute to the activation pattern in that they simply reflect a higher engagement rather than a novel process (see, e.g. Christoff et al., 2001; D´Esposito et al., 1997).

However, there are two arguments which make this explanation unlikely. Evidence for an additional process is, on the one hand, revealed by higher shift costs for transition cues compared to task cues reliably found in both behavioral experiments. Even though transition cues may require a higher memory-based retrieval demand compared to task cues, the higher shift costs for the former cue type cannot be explained by higher working-memory engagement. It is rather suggested that in switch trials, participants have to internally generate the now relevant task set due to the indirect cue-task association which is reflected in relatively higher shift costs for transition cues compared to task cues.

A second line of evidence for the assumption of an additional process required for the performance on transition cues comes from the neural data pattern. Even though a comparable cortical network was found for the transition cues compared to task cues, it is important to note that there are also differences in the localization of activations between studies using explicit task cues and fMRI Experiment 1 (see, e.g. Brass et al., 2005). The differences pertain to the extension of frontal activations on both the

frontolateral and frontomedian cortex in posterior-anterior direction. More specifically, the results revealed activations along the IFS as well as the posterior frontomedian wall (BA 8 bordering the pre-SMA) for the transition cues compared to the task cues.

Areas along the IFS, especially in the mid-MFG, have been associated with integration processes in working memory (see, e.g. Duncan & Owen, 2000; Fletcher & Henson, 2001). Moreover, activation within BA 8 has been shown in studies investigating the internal generation of synonyms (Nyberg et al., 2003), and uncertainty in decision making (Volz, Schubotz & von Cramon, 2004).

Thus, a tentative explanation for the present findings might be that the memory-based internal generation is subserved by both the frontolateral and frontomedian cortex. The former is believed to subserve the integration of information whereas the latter subserves the internal generation of task sets. Hence, both working-memory and the internal generation of task sets might reflect two sides of the same coin. In sum, both the behavioral and neural data of Empirical Section I provide evidence for sequential subprocesses relevant for the performance in less determined action contexts.

7.2 A Functional-Anatomical Framework of Endogenous Control Processes in Task Switching

Several neuroimaging studies on cognitive control used the explicit task-cueing procedure in which a cue is directly associated with a task (Brass & von Cramon, 2002, 2004; Derrfuss, Brass & von Cramon, 2004; Dove et al., 2000; Kimberg et al., 2000; Luks et al., 2002; Ruge et al., 2004). However, what happens if the external cue is not directly indicating the relevant task set?

The results of the fMRI experiment of Empricial Section I revealed extended activations along the IFS for the transition cue compared to the task cue. In fact, when comparing the present results with previous findings from task-cueing paradigms, it becomes evident that the pattern of the frontal activations usually found with task cues shifted in an anterior direction (see, e.g. Brass & von Cramon, 2002, 2004; Ruge et al., 2005). This finding was corroborated for both the frontolateral and the frontomedian wall.

Recently, several authors proposed a functional-anatomical gradient in the lateral PFC along a posterior-anterior dimension (Braver, Reynolds & Donaldson, 2003; Buckner, 2003; Christoff & Gabrieli, 2000; Dreher et al., 2002; Koechlin, Ody & Kouneiher, 2003). Evidence for a cytoarchitectonic gradient relies inter alia on studies conducted by Sanides (1962). However, the functional characterization of such a gradient remained open. Braver and colleagues (2003) suggested that the PFC might be organized according to the temporal duration of actively maintained representations, with the most anteriorly regions being recruited under conditions where active memory needs to be sustained.

Regarding the task-switching literature, Dreher et al. (2002) proposed a posterior-anterior axis as the task becomes more endogenously guided. In their study, anterior PFC activity was associated with improved performance under conditions where sustained endogenous preparation for task-switching could be achieved, i.e. when task switches were predictable across the block.

In Empricial Section I, the ROI x cue type interactions for the three frontolateral ROIs revealed a dominant role of the more anterior situated mid-MFG compared to the IFJ area for the integration of information in working memory compared to the directly cued task sets.

The results of fMRI Experiment 1 also revealed a dominant role of the anteriorly situated ROI in the posterior frontomedian wall (BA 8/pre-SMA) for the performance on the transition cues compared to the performance on task cues. This finding was interpreted to reflect the

internal generation of the task set due to the indirect cue-task association. In fact, previous task-switching studies revealed that the pre-SMA/SMA is involved in cue-related processing (see, e.g., Brass & von Cramon, 2002; Dove et al., 2000; Luks et al., 2002; Rushworth et al., 2002). Moreover, the pre-SMA is assumed to be important for the internal generation and preparation of motor activity (Lee, Chang, & Roh, 1999; Picard & Strick, 1996, 2003). With respect to the findings from fMRI Experiment 1, it is conceivable that a functional gradient from the pre-SMA into the rostrally situated BA 8 is elicited by the indirect cue-task association in which the external transition cue information does not determine the relevant task set. More specifically, the data provide evidence that in less determined action contexts a higher demand of endogenous control is required compared to directly cued task sets. A tentative explanation for a functional characterization of this posterior-anterior gradient in the PFC may be the complexity of relational integration of information in time (see, e.g., Koechlin et al., 2003). This is compatible with the view that in less determined action contexts, additional internally-guided subprocesses need to be carried out to establish goal-directed behavior.

However, what happens if the cue does not unequivocally instruct the participant what to do? One might argue that with indirect cue-task associations, the relevant task set is still determined by the experimental context. This was the reason for conducting fMRI Experiment 2, i.e. to investigate voluntarily initiated processes in task switching by letting participants choose the task by their own. Most importantly, this experimental manipulation reveals a higher ecological validity compared to previous task-switching studies in that many real life situations require the selection among different alternatives.

When participants could voluntarily select a task set, prefrontal activation was only found in the aMCC (see also Forstmann et al., 2006). This finding is in line with the results of recent fMRI studies investigating the voluntary selection of response sets (Walton, Devlin & Rushworth, 2005) and movements (Lau et al., 2004). Moreover, the results of fMRI Experiment 2 revealed no selection-specific difference between 3 and 2

choices. Thus, the activation in the aMCC might reflect the voluntary selection of task sets in an all-or-none manner.

In general, there is empirical evidence for an involvement of the MCC in willful acts (see, e.g., Frith et al., 1991; Zhu, 2004). Moreover, abnormal volition is encountered in e.g. depression, organic dementia, schizophrenia, and akinetic mutism (Zhu, 2004). Such disorders are characterized by inactivity, lack of ambitions, and a reduced motor and verbal output. In a recent study, Williams and colleagues (2004) reported on patients with obsessive compulsive disorder after surgical cingulotomy for the ablation of the dorsal portion of the midcingulate cortex but sparing the cingulate bundle. The results revealed that the dorsal portion of the MCC seems to play an essential role in the linkage of reward-related information with alternative actions. In fact, there is broad evidence for the MCC to play a crucial role for reward-based decision-making processes (see, e.g., Rushworth et al., 2004; Schall, Stuphorn & Brown, 2002). With respect to our fMRI Experiment 2, an activation was found in the anterior portion of the MCC although no reward was associated with voluntarily selecting a specific task set. A simple, yet straightforward answer is that the activation in the MCC reflects a 'willful' act in choosing between tasks without any explicit valence in making this choice. Thus, 'willful' acting and the anticipation of reward do not coincide in the present experiment compared to classical decision-making paradigms.

In conclusion, regarding former cueing versions, there might not only be a distinction in posterior-anterior direction along the frontolateral and posterior frontomedian cortex but also a lateral-medial distinction. The latter distinction refers to processes which are either externally determined by explicit environmental information like the updating of task representations (Brass et al., 2005), or internally initiated processes. As has been argued in the present thesis, these processes can either reflect the internal generation or the voluntary selection of task sets. Moreover, the assumption that internally initiated processes may be located in the frontomedian cortex is also corroborated by several studies where participants have to generate an action under limited or no constraints

(review by Posner & DiGirolamo, 1998; Carter, Botvinick & Cohen, 1999; Cunnington et al., 2002). In the end, there might be two distinctions, one in posterior-anterior direction (Koechlin, Ody & Kouneiher, 2003) and the other in lateral-medial direction, to account for the functional architecture of the human PFC.

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Dissertationsbezogene bibliographische Daten

Birte U. Forstmann

Behavioral and Neural Correlates of Endogenous Control Processes in Task Switching

University of Leipzig, Doctoral thesis

107 pages, 138 references, 9 figures, 5 tables

Abstract

The aim of the present work was to investigate endogenous control processes in task switching. Behavioral and neural correlates were used to address two major research questions: 1. What happens if an external cue is not directly indicating the task? 2. What happens if participants are not explicitly told what to do but can voluntarily select the task by their own? To answer the first question, a new variant of the task-switching paradigm, the so-called 'transition-cueing paradigm' was developed and tested in several behavioral experiments. The core feature of this procedure are transition cues which are indirectly associated with a task so that participants have to internally generate the relevant task set. In addition, a functional magnetic resonance imaging (fMRI) version of this newly developed paradigm was investigated. The contrast between transition cues and task cues revealed that more anteriorly located regions in the prefrontal cortex (PFC) come into play when a higher demand of endogenous control is required.

To answer the second question, an extension of classical cueing procedures was elaborated. The crucial manipulation pertained to the voluntary selection of task sets. The number of task to choose from was varied between a specified condition and two voluntary conditions. The fMRI results revealed that a region in the posterior frontomedian cortex,

the anterior midcingulate cortex, is most important for the selection of task sets in an all-or-none manner. Furthermore, activations were also found in the posterior parietal cortex which might subserve visual attentional selection processes.

The present thesis incorporates different lines of empirical evidence in investigating endogenous control processes in task switching. Thus, behavioral results with the newly developed transition-cueing paradigm could be replicated with fMRI Experiment 1. Moreover, fMRI Experiment 1 corroborated a recently published cascade model of a posterior-anterior gradient to account for the functional architecture of the human PFC (Koechlin et al., 2003). With respect to fMRI Experiment 2, it is argued that this model can be extended in lateral-medial direction to account for externally determined and voluntarily initiated processes, respectively. Taken together, there might be two different distinctions, one in posterior-anterior direction and the other in lateral-medial direction, to account for the functional architecture of the human PFC.

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