The many faces of preparatory control in task switching: reviewing a decade of fMRI research

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Short Title: Preparatory control in task switching

Keywords: Task Preparation; Proactive Control; Cognitive Flexibility; Reconfiguration; Task Set; Action Set; Attentional Set; Set Shifting; Goal Representation; Task Demand

Abstract

A large body of behavioural research has employed the cued task switching paradigm to characterize the nature of trial-by-trial preparatory adjustments that enable fluent task implementation when demands on cognitive flexibility are high. This paper reviews the comparably small but growing number of fMRI studies on the same topic, mostly focusing on the central hypothesis that preparatory adjustments should be indicated by enhanced prefrontal and parietal BOLD activation in task switch as compared to task repeat trials under conditions that enable advance task preparation. The evaluation of this straight-forward hypothesis reveals surprisingly heterogeneous results regarding both, the precise localization and the mere existence of switch-specific preparatory activation. Explanations for these inconsistencies are considered on two levels. First, we discuss methodological issues regarding (i) the possible impact of different fMRI-specific experimental design modifications and (ii) statistical uncertainty in the context of massively multivariate imaging data. Second, we discuss explanations related to the multi-dimensional nature of task preparation itself: Differences in the precise localization of switch-related preparatory activation might be related to distinctions between (i) attention-related vs. action-related aspects of task preparation on the one hand and (ii) hierarchical control via abstract goal representations on the other. Furthermore, we suggest that different preparatory modes can be adopted based either on advance goal activation or on the advance reconfiguration of action sets or attentional sets. Importantly, while either mode can result in a reduction of behavioural switch cost, only the latter two are associated with enhanced switch-related BOLD activation in prepared trial conditions.

Introduction

Cognitive control has been broadly defined as the ability to *flexibly* use and change rules on the basis of *advance information* or feedback from previous performance (Kok, Ridderinkhof, & Ullsperger, 2006). Just about ten years ago, many brain imagers interested in cognitive control processes shared an expectation that the *task switching paradigm* would offer a simple and well-controlled experimental approach to uncover a distinct set of brain regions that constitute the neuro-anatomical basis of some key aspects of cognitive flexibility. Moreover, a special interest emerged into the neural basis of *advance task preparation*, a process which is often regarded as one of the defining elements of cognitive control (e.g., Meiran, 2010). The importance of advance preparation was indicated by early performance data which showed that advance preparation can reduce behavioural switch cost as compared to unprepared trial conditions. This suggests that advance task preparation enables switching to a new task set before an imperative stimulus requires the concrete implementation of the prepared task rather than other equally possible tasks (for reviews focusing on behavioral results, see Kiesel et al., 2010; Meiran, 2010; Monsell, 2003b; Vandierendonck, Liefooghe, & Verbruggen, 2010). These findings indicate that the human brain is equipped with a powerful control mechanism that operates via *proactive adjustment* instead of solely relying on *reactive adjustment* of task control (cf., Braver, Gray, & Burgess, 2007; Meiran, 1996; Rogers & Monsell, 1995). Note that the term "adjustment" is used as a placeholder for processes that enable the fluent implementation of the currently relevant task. Later in this review we will elaborate in greater depth on the range of processes that constitute switch-related preparatory adjustment as suggested by the pattern of preparatory BOLD activation under different study conditions.

Principally, an advantage of the use of brain imaging techniques like fMRI is that it can provide measures of proactive adjustment processes itself rather than their impact on subsequent overt behaviour as indicated by the reduction of behavioural switch cost. Switch-related preparatory BOLD activation patterns are characterized by the *amplitude* of preparation-related BOLD activation in task switch and task repeat trials and by the neuro-anatomical *localization* of such activation. We will discuss the theoretical implications of different types of preparatory switch-related amplitude patterns (switch only, switch > repeat, switch = repeat) for explaining the reduction of behavioural switch cost in prepared trial conditions. We will also discuss implications of the specific localisation of such switch-related activation patterns. Generally, switch-related activation patterns that are consistent across different study designs would indicate the operation of core preparatory processes common to different types of task switching, whereas variation in the amplitude of such modulations and/or their localization as a function of particular study design would suggest dissociable sub-components of preparatory processes.

As this review will show, fMRI activation patterns vary considerably across different task switching protocols and so it is still premature to define clear BOLD activation signatures associated with reliably dissociable components of preparatory task control. Broadly, existing studies show that the precise functional anatomical expression of preparatory control processes is dependent upon a number of modulatory variables, many of which

remain to be clearly defined. Some of the variability of BOLD activation patterns between fMRI studies can be attributed to the multidimensional nature of the process itself. However, some of the inconsistency might also be related to fMRI-specific methodological constraints. Accordingly, one central objective of this paper is to critically assess the strengths and limitations of inferences that can be derived from different types of fMRI designs and analyses that aim to disentangle BOLD response components associated with cue-driven proactive control processes as compared to target-driven reactive control processes (Section 1). Keeping in mind these methodological challenges, we attempt to answer three key research questions regarding the signature of preparatory switch-related BOLD activation in cued task switching and its implications regarding the nature of task preparation.

Key question 1: Is there evidence that some brain areas are exclusively activated proactively on switch trials but not on repeat trials (Section 2)?

If yes, this would indicate the operation of an exclusive switch-only process that is not required when the previous task repeats and that might be, at least partly, responsible for the reduction of behavioral switch cost in prepared trial conditions. Furthermore, it is important to establish what potential modulatory variables (e.g., the degree of task practice or the relative proportion of switch and repeat trials) might determine whether a preparatory process engages exclusively in switch trials, or, put differently, disengages in repeat trials. Depending on such modulatory variables, brain regions that would otherwise be associated with switch-only preparatory processes might instead fall into the scope of the following key question 2.

Key question 2: Is there evidence that some brain areas show greater preparatory activation on switch trials than on repeat trials (Section 3)?

Notwithstanding any evidence for switch-only preparatory processes as addressed by question 1, the identification of brain areas exhibiting just *relatively* stronger activation for switch as compared to repeat trials would be sufficient to infer the operation of proactive adjustment processes which mediate the reduction of behavioral switch cost in prepared trial conditions. Furthermore, it is important to establish what variables determine the precise localization of switch-related activation in prepared trial conditions and the relative strength of amplitude enhancements for switch versus repeat trials, or indeed, whether any switch-related amplitude enhancements can be detected at all.

Key question 3: Is there evidence for separable brain areas exhibiting switch-related activation in prepared vs. unprepared trial conditions (Section 4)?

If yes, this would suggest a functional-anatomical segregation of proactive switch-related adjustment processes (i.e. mostly cue-driven in prepared trials) and re-active adjustment processes (i.e. mostly target-driven in unprepared trials). If not, these two control modes might simply reflect temporal differences in the engagement of a

common switch-related adjustment process.

Inclusions criteria for task switching studies considered in this review

Importantly, this paper is not a meta-analysis or even a comprehensive review of all fMRI task switching studies. Instead, we attempt to provide an in-depth review of existing fMRI studies specifically addressing the neuro-cognitive basis of *preparatory* processes in *cued* task switching. This present approach complements a previous, highly condensed review, which provided an integrative account of results across different data modalities, including behavioural performance, event-related brain-electrical potentials (ERPs), and fMRI (Karayanidis et al., 2010). The reader is referred to a number of recent behavioral review papers that provide detailed analyses of behavioral studies and conceptual issues of task switching (Kiesel et al., 2010; Meiran, 2010; Monsell, 2003b; Vandierendonck et al., 2010).

This review will focus on those fMRI studies that seem to be best suited to address the three questions raised above. First, since this review deals with preparatory processes, we only included studies that incorporate and separately analyze at least one "prepared trial condition", that is, preparation intervals > 500 ms (roughly 30-50% of all fMRI task switching studies). Second, we only included studies that employ randomly *cued* task switching procedures – using either "task cues" directly indicating the relevant task or "transition cues" indicating whether to continue with the previous task or to switch to the alternative task. These cued task switching studies represent the vast majority of fMRI studies on prepared task switching. Studies using predictable task sequences (i.e., memory-based instead of randomly cued) (Kimberg, Aguirre, & D'Esposito, 2000; Sohn, Ursu, Anderson, Stenger, & Carter, 2000) and variants of the Wisconsin Card Sorting Test (e.g., Monchi, Petrides, Petre, Worsley, & Dagher, 2001) were excluded due to relatively weak experimental control over the timing of preparatory processes. Third, we restricted our analysis to studies investigating switching between different *stimulus-response (S-R) mappings*, that is, studies in which participants have to switch between two different S-R rules defined on the same or distinct categories of stimuli (e.g., classifying a number as odd/even vs. </> 5; or classifying a number as odd/even and a letter as vowel/consonant). We also included task switching studies which require the reversal of S-R mapping (e.g., task A: circle – left hand; triangle – right hand vs. task B: circle – right hand; triangle – left hand). Common to these task switching procedures is that a switch trial requires disengagement from the previous S-R mapping and re-engagement of the alternative S-R mapping. "Attentional set shifting" studies which require switching between stimulus features or dimensions, but involve only a single constant S-R mapping throughout the entire experiment are not included in this review, except where necessary to highlight important similarities and differences with task switching studies (for an earlier meta-analysis including all types paradigms, see Wager, Jonides, & Reading, 2004).

Section 1 will highlight the relevant fMRI-methodological issues and will be followed by Sections 2-4 addressing each of the three key research questions listed above. For each question, we will first provide a broad overview of the main findings and interpretations

from relevant studies, largely ignoring study-specific issues. These more distinct contributions of individual studies, together with a critical assessment of contradictory results will be addressed subsequently within each section, highlighting promising future research directions. Finally, Section 5 will provide an overall summary of key conclusions and future directions.

1. General fMRI-methodological issues

In the behavioral research domain, many variants of the task switching paradigm have been established in order to measure indices associated with different underlying cognitive processes (e.g., Meiran, Chorev, & Sapir, 2000). The comparison of single task blocks with blocks of mixed task trials (mixed task blocks) provides a measure of the global cost ("general switch cost") of alternating between tasks irrespective of any differential local processes associated with repeating or switching task within the mixed task sequence. This global switch effect can be readily captured by blocked fMRI designs (Dreher, Koechlin, Ali, & Grafman, 2002). However, event-related fMRI designs are necessary to capture the constituent components of this effect. One such component – expressed by the behavioral "switch cost" – provides a more specific measure of the local cost of alternating between tasks by comparing switch trials and repeat trials within the same mixed task block. The other component – expressed in behavioral "mixing cost" – provides a measure of the additional demands of implementing a task in random sequence with a competing task by comparing repeat trials in mixed task blocks with physically identical repeat trials in single task blocks (Rubin & Meiran, 2005)[1].

From an fMRI-methodological perspective, the task switching paradigm is a perfect example of the usefulness of event-related design and analysis. Straightforward rapid event-related designs can be implemented to determine *relative* BOLD response differences between switch and repeat trials when the separation of preparatory and target-related BOLD activation components is *not* of interest (Henson & Friston, 2007). In this case, the original behavioral task switching designs can simply be adopted without considerable modifications. Importantly though, for other more specific research questions, fMRI design issues become more complicated and require considerable modifications of the original task switching designs, as discussed below.

1.1 Measuring trial-related BOLD activation against baseline

To compare BOLD response estimates of switch and repeat trials against an inter-trial interval (ITI) baseline, it is necessary to modify the typical task-switching procedure by including a *variable* ITI. This may be required when the aim of the study is to determine whether a brain region is selectively active for switch trials or for both switch and repeat

[1] So-called mixed block/event-related designs can be used to distinguish sustained BOLD activation maintained across a mixed task block from transient event-related BOLD activation for repeat and switch trials occurring within this block of mixed trials (Braver, Reynolds, & Donaldson, 2003).

trials. The optimal ITI distribution depends on several, partly antagonistic considerations related to the detectability and the estimation accuracy of the BOLD response (Birn, Cox, & Bandettini, 2002; Hagberg, Zito, Patria, & Sanes, 2001). However, irrespective of the specific ITI distribution, the introduction of variable ITIs might vary the level of task set carryover from one trial to the next. This would in turn impact on the extent to which passively decaying task set activation from the preceding trial would disadvantage the subsequent repeat trial or advantage the subsequent switch trial. Indeed, behavioral data suggest that the impact of passive task set decay processes on task switching performance depends on the response-cue interval (RCI), particularly when the RCI is randomly varied (Meiran et al., 2000). Shifting from a fixed to a variable ITI can also have an effect on expectancy. The ability to accurately predict cue onset will affect the readiness to process the cue and the task-related information it conveys. In simple and choice RT paradigms, it has been shown that preparatory activities other than anticipatory responses may begin before the onset of the cue, especially in designs with short foreperiods (Niemi & Naatanen, 1981). While the effects of ITI/RCI jittering have not been examined systematically in any fMRI task switching study, evidence from ERP studies suggests that RCI jittering may change the effectiveness of preparatory control in task-switching[2]. So, switch-related BOLD activation obtained under modified ITI distributions cannot be assumed to be directly comparable to results from studies using short and constant ITIs, as is typically the case in behavioral and ERP task switching studies.

1.2 Segregating preparation-related and target-related BOLD activation components

A second considerable modification of the original task switching designs is required for the functional imaging of *preparatory processes* in task switching. The length of the cue-target-interval (CTI) is certainly a critically important variable when investigating preparatory processes. Behavioral data suggest that 'short' preparatory intervals (i.e. <300 ms) result in unprepared or incompletely prepared states. By contrast, 'long' preparation intervals (i.e. 500-2000 ms) result in prepared states, with an 'optimal' interval around 600 ms (Monsell & Mizon, 2006; Nicholson et al., 2005). Intervals longer than 2000 ms have been shown to result in an increase in RT, error rate, and switch cost (Monsell & Mizon, 2006; Nicholson et al., 2005), presumably due to the aversive nature of maintaining the prepared state or because of the introduction of additional memory-related processes.

Clearly, the optimum range of long CTIs for implementing 'prepared' task-switching conditions in behavioral and ERP studies is simply too fast to be directly implemented in the fMRI environment without considerable design modifications. This is especially true when attempting to isolate preparatory BOLD activation from subsequent target-driven BOLD activation (Sections 1.2.1 – 1.2.4). An alternative approach for examining BOLD correlates of

[2] Indirect evidence that jittered RCI may affect switch-related preparatory processing can be obtained by comparing results across different task switching studies using ERPs. In cued paradigms with RCI jittering, the amplitude of the switch-positivity is much reduced, ranging between 0.3-1.5 μV (Jamadar et al. (2010b) [0.3 μV]; Jamadar, Hughes et al. (2010) [~1.5 μV]; Jamadar et al. (2010a) [~0.8 μV]), as compared to non-jittered paradigms where the amplitude generally ranges from 2-5 μV (Nicholson et al. (2005) [2.5-5μV]; Kieffaber & Hetrick (2005) [~4 μV]; Karayanidis et al. (2009) [~3 μV]; Astle et al. (2008) [~3 μV]; Goffaux et al. (2006) [~2 μV]).

preparatory processes which does not require fMRI-related design modifications relies on the direct contrast of prepared and unprepared trial conditions (Sections 1.3 and 4). However, this approach comes at the expense of not being able to explicitly disentangle preparation-related and target-related BOLD components.

-- insert Figure 1 here --

The separation of preparation-related and target-related BOLD components represents a general fMRI-analytical problem due to the temporal overlap of successive BOLD responses across at least 20 seconds[3]. That is, due to the sluggishness of an event-related BOLD response, the modulation of BOLD activation in a given voxel cannot be easily attributed to a particular time point or an associated distinct event within a cue-target trial (see Figure 1). Thus, without taking additional measures, the event-related analysis of fMRI data yields one single *trial*-related BOLD response estimate for a given voxel that integrates all the different potential BOLD sub-components associated with the successive within-trial events, including the cue, the delay, delay termination, the target, and the response (cf., Jennings & van der Molen, 2005). A range of different approaches have been designed to disentangle within-trial BOLD sub-components, including the use of long constant CTIs, jittering of CTIs, and partial trials designs.

1.2.1 Constant long CTI design

A first approach that has been used in cued task switching as well as other paradigms is to use a constant, but "sufficiently long" CTI of, say, 5 seconds at the very least (e.g., Barber & Carter, 2005, who used a CTI of 7.5 seconds). Based on this simple design two distinct activation patterns can be interpreted unambiguously. First, a CTI >5 seconds gives sufficient time for cue-related activation to reach its maximum before a possible target-related BOLD component can start contributing considerably to the overall trial-related BOLD signal[4]. Thus, BOLD activation measured until target onset can clearly be attributed to preparation (more precisely, this holds for activation until approximately 1 second after target presentation, considering that a BOLD response typically starts rising with a short delay). Second, BOLD activation that starts to rise from a flat baseline after target onset is clearly *not* related to preparation, but can instead only reflect target-related processes. Importantly, only in this case can target-related BOLD activation be determined without being contaminated by preceding preparation-related BOLD activation. As soon as there is above-baseline activation prior to target onset, target-related activation cannot be isolated from preceding preparation-related activation. A second serious problem is that preparatory activation can only be determined unambiguously in case of transient cue-related activation elicited early within the CTI. Delay-related activation evolving later during the CTI (i.e., closer

[3] This *temporal* component overlap problem in fMRI is different from the ERP-related *spatial* component overlap problem (i.e., a voltage difference observed in a given time point cannot be unambiguously linked to a specific neural generator or to a generic ERP component).

[4] This is a very liberal lower CTI limit. To completely separate successive BOLD components associated with cue and target, the CTI should be at least 20 seconds (Bandettini & Cox, 2000; Goghari & MacDonald, 2008). However, no existing fMRI task switching study has implemented such long CTIs.

to target onset) will be largely indistinguishable from target-related BOLD activation. Finally, as elaborated in Section 1.2.4, the use of such untypically long CTIs might have unintended "psychological" side effects in terms of altered preparatory strategy of participants.

1.2.2 Jittered CTI design

A second approach attempts to de-correlate cue-related, delay-related and target-related BOLD activation by introducing a variable cue-target interval and including a delay-related GLM regressor convolved with the length of the delay (Bunge, Kahn, Wallis, Miller, & Wagner, 2003; Curtis & D'Esposito, 2003; Sakai & Passingham, 2003). Importantly, the jittered-CTI approach only works properly when a delay-related regressor is explicitly included within the model. Otherwise, an undistorted estimation of separate cue-related and target-related BOLD activation components rests on the unverifiable assumption that trial-related activation in a given voxel is independent of the length of the CTI, that is, when no delay-related activation is present (Serences, 2004). Furthermore, to be able to adequately capture delay-related activation, a rather wide range of CTIs might be preferable in order to increase delay-related variance (e.g., CTIs ranging between 2 and 12 seconds). As far as BOLD de-composition is concerned, the jittered CTI design – if properly implemented – is certainly preferable to the constant-long CTI design. However, as elaborated in Section 1.2.4, CTI jittering – as the use of single constant CTI – might come with its own set of problems with regard to "psychological" side effects in terms of altered preparatory strategy of participants.

1.2.3 The partial-trial design

A third approach uses the so-called partial-trial design which attempts to de-correlate cue-related and target-related BOLD components by including partial 'cue-only' trials intermixed with full 'cue plus target' trials (Brass & von Cramon, 2002; Ollinger, Shulman, & Corbetta, 2001; Ruge, Goschke, & Braver, 2009; Serences, 2004). More complex versions of the partial trial design attempt to additionally determine the contributions of delay-related and target-omission-related BOLD activation (Ruge, Goschke, et al., 2009). The main advantage of the basic partial trial design as compared to both the constant-long CTI design and the jittered CTI design is that a typical, non-jittered CTI can be used (e.g., 1000 ms). The main drawback of partial trial designs is that the omission of the target stimulus in cue-only trials might itself elicit a BOLD response that cannot easily (if at all) be distinguished from genuine preparation-related BOLD activation (for an extensive discussion of this issue, see Ruge, Goschke, et al., 2009). Also, like CTI jittering, the occasional omission of the target stimulus might affect the participants' preparatory strategy or unintentionally introduce sequence effects in the data (see Jamadar, Michie, et al., 2010b).

1.2.4 Altered preparatory processes in task switching through design modifications?

Notwithstanding their intended purpose to disentangle preparation-related and target-related BOLD components, the above design modifications might inadvertently alter the very preparatory processes they are designed to measure. Such altered process characteristics are conceivable for all fMRI design approaches discussed above, be it due to prolonged CTIs as is the case in constant-long or jittered CTI designs, CTI jittering itself, or target omission in

partial trial designs. Thus, preparation-related BOLD activation obtained in these designs might index partly different preparatory processes than those indexed by the standard cued task switching designs typically used in behavioral and EEG studies. Moreover, preparation-related BOLD activation might indicate partly different preparatory processes across the different fMRI designs (cf., Goghari & MacDonald, 2008; Serences, 2004).

Functional MRI design modifications might affect preparatory processes on two levels: General process alterations would affect both switch and repeat trials similarly whereas task-switching-specific process alterations would affect switch and repeat trials differently. Unfortunately, there has been little systematic work that might provide hints as to the severity of such processes alterations specifically in task switching.[5] Notably, results from a recent study looking at event-related brain-electrical potentials (ERP) suggest that CTI jittering may *differentially* affect neural (here: ERP) vs. behavioral indices of preparation in cued task switching (Karayanidis, Heathcote, Provost, Sanday, & Jamadar, September 2008). Specifically, this study examined preparation-related ERPs in blocked vs. randomly jittered CTI groups with 150, 600 and 1000ms CTI[6]. Behaviorally, randomized CTI negatively affected indicators of both general and switch-related processes including slowed RT to long CTIs and increased response criterion to short CTIs and no reduction in switch cost with increasing CTI. By contrast, cue-locked ERPs showed *no* difference between blocked and randomized CTI in switch-related preparation (i.e., no difference in the amplitude of the cue-locked switch-related positivity which is an ERP correlate of switch-related preparation; see Karayanidis et al., 2010) but a generally smaller cue-locked positivity for both switch and repeat trials in the randomized CTI group. This latter ERP finding is suggestive of an overall reduction in preparation for randomized CTIs and is consistent with the well-established finding of higher RT with random relative to constant foreperiods, an effect typically attributed to reduced expectancy and preparation for the target, readiness to respond to the target stimulus, and/or maintenance of preparatory state (Niemi & Naatanen, 1981). More importantly, these results show that CTI jittering had dissociable effects on ERP components and behavior. While CTI jittering did not affect preparatory switch-positivity in the cue-locked ERP, it eliminated the preparation-related reduction in behavioral switch cost (but see Monsell & Mizon, 2006). This cross-modal dissociation nicely demonstrates that different data modalities might tap into different preparation processes (see Section 3.1.3, for another such example with regard to the impact of target omission on switching-related

[5] Goghari & MacDonald (2008) compared a jittered CTI/ITI design to a slow interval design and a partial trial design in a protocol similar to cued task switching, using Stroop-like stimuli. They analyzed how these different fMRI designs affected performance and BOLD activation on a general level of preparation (i.e. irrespective of trial type) and regarding cue type (word-reading vs. color-naming), but unfortunately not regarding task switching (task repeat vs. task switch). While the jittered design showed a faster RT relative to the other two designs, this effect did not interact with cue type (word-reading vs. color-naming). The fMRI data suggested that the different designs were differentially sensitive to activity in different brain regions, rather than implicating general changes in signal-noise ratio. All three designs activated similar regions during the preparation interval. Note that a design implementing 'traditional' design parameters (i.e., not changed to accommodate fMRI scanning parameters) was not included for comparison.

[6] Note, however, that these CTIs are considerably shorter than the range of CTIs typical used in the jittered-CTI fMRI design. Thus, it remains to be established that the effects obtained in this ERP study can be generalized to longer CTI ranges.

processes in the subsequent trial). Moreover, it highlights an important caveat against the strategy to evaluate the adequacy of fMRI/ERP design modifications based on changes (or absence of changes) in behavioral outcomes (e.g., Koch et al., 2003; Ruge, Muller, & Braver, 2010).

1.3 Examining preparatory processes without explicitly isolating preparatory BOLD activation components

Notably, most cued task switching studies that examined prepared trial conditions did *not* implement one of the above fMRI designs. Instead, many studies implemented prepared trial conditions with a constant long CTI > 0.5 seconds and << 5 seconds. In contrast to the fMRI designs discussed in the preceding Section 1.2, these studies cannot explicitly disentangle preparation-related and target-related BOLD components within a cue-target trial. Instead, the compound trial-related BOLD response that includes both preparation-related and target-related BOLD components needs to be related to additional sources of information that may help determine whether this compound activation is more likely associated with proactive or reactive processes in task switching. One approach examines cross-modal relationships between this compound BOLD response and either behavioral or ERP indices of preparatory and target-related processes (see Section 1.3.1 below). Another approach directly contrasts the compound BOLD response elicited in prepared trial conditions with the BOLD response elicited in unprepared trial conditions with a CTI << 500 ms (see Section 1.3.2 below). Although both these approaches offer less direct evidence than designs that explicitly disentangle BOLD components associated with proactive and reactive adjustment processes, they have the distinct advantage that they do not require fMRI-specific design modifications that might unintentionally alter the preparatory processes of interest (see Section 1.2.4 above).

1.3.1 Cross-modal correlational approaches

A first cross-modal correlational approach relates switch-related compound BOLD activation in prepared trial conditions with the corresponding behavioural residual switch cost (Braver et al., 2003; Jamadar, Michie, et al., 2010a). Depending on the direction of this relationship, the compound BOLD effect is either more likely associated with proactive adjustment processes or with reactive adjustment processes (for a concrete example, see Key Question 2; Section 3). Following a similar line of reasoning, switch-related compound BOLD activation in prepared trial conditions can be correlated with cue-locked and target-locked ERP components to arrive at more specific conclusions regarding the likely temporal locus of the observed BOLD activation (Jamadar, Hughes, et al., 2010). However, it is important to note that the inferences drawn from such cross-modal correlational approaches about the temporal locus of the observed compound BOLD response are indirect. As in all correlational analyses, a significant positive relationship between the compound BOLD response and cue-locked ERP activation might be mediated by a third variable (e.g., target-related outcome of preparation) rather than a cue-related process per se. Additionally, the absence of a relationship between these measures must also be interpreted with caution, as ERPs and

fMRI BOLD activation capture different types of neuronal activity. It is highly probable that not all ERP activity will be visible in the BOLD activation signal and correspondingly, not all BOLD activation signal will be captured in ERP activity.

1.3.2 Directly contrasting BOLD responses across prepared and unprepared trial conditions

Some studies directly compare the brain activation correlates of proactive vs. reactive control adjustment processes by contrasting switch-related compound BOLD activation for prepared trials (e.g., trials with a long CTI>500ms where the cue provides full information about the upcoming task) and unprepared trials (i.e., trials with CTI<<500ms or where the cue provides no information about the upcoming task). This contrast yields a number of valuable conclusions, based on two basic assumptions (for a similar rationale in the context of modelling behavioral performance data, see Meiran, Kessler, & Adi-Japha, 2008). First, in unprepared trials switch-related BOLD activation indicates pure reactive control adjustments, simply because there is no time for proactive adjustments. Second, in prepared trials, switch-related compound BOLD activation indicates a mixture of potential proactive switch-related adjustments during the CTI and potential residual reactive adjustments after target presentation (cf., Rogers & Monsell, 1995). Based on these assumptions, three relevant activation patterns can be distinguished. First, a brain region that shows larger switch-related activation for prepared as compared to unprepared trial conditions is more likely to be associated with proactive switch-related adjustment processes (i.e., more time for proactive control). Second, a brain region that shows larger switch-related activation for *unprepared* as compared to prepared trial conditions is more likely to be associated with reactive adjustment processes (i.e., less time for proactive control must be compensated by increased reactive control effort). Third, a region that exhibits similar switch-related activation for *both* prepared and unprepared trials is likely to be associated with control processes that are common to both proactive and reactive adjustment and are flexibly activated either before or after target onset depending on the time available for preparation. In other words, the longer the CTI, the more proactive adjustment is possible and therefore less reactive adjustment is necessary when the target appears. Conversely, for shorter CTI, less proactive adjustment is possible and therefore more reactive control is necessary when the target appears[7]. This analytical rationale will be used to evaluate Key Question 3 (see Section 4 below).

1.4 Methodological issues: concluding remarks

None of the techniques described above comes without justified criticism. Thus, as applies more generally in all empirical sciences, the results of individual studies using certain design and analysis procedures should not be over-interpreted and the design-specific constraints should always be taken into consideration. It is also important to note that these differences

[7] Such an activation pattern might alternatively indicate the operation of a task adjustment process that is inserted strictly serially between cue and target processing (i.e., even with CTI = 0 the adjustment process needs to be completed before target processing can be initiated). Such a process is therefore assumed to be exactly the same in prepared and unprepared trials. Yet, such a strictly serial process model which has often been associated with the task set reconfiguration metaphor is rather unrealistic (Kiesel et al., 2010).

in design and methodology can provide invaluable information regarding specific effects that remain highly replicable regardless of paradigm specifications. However, it is also clear that more research is needed to determine the precise way in which different variables alter the nature of preparatory processes involved in task switching

2. Key Question 1: Is there evidence that some brain areas are exclusively activated on switch trials but not on repeat trials?

In contrast to the highly heterogeneous pattern of results concerning the other two key questions, the quest for brain regions exhibiting preparatory BOLD activation exclusively in switch trials yields a rather consistent picture. We are not aware of studies that have unambiguously confirmed the existence of switch-*only preparatory* BOLD activation, that is, brain areas significantly activated in switch trials that are not reliably activated in repetition trials when contrasting each condition against the inter-trial interval baseline (for an exception, see below). The studies that report enhanced BOLD activation for switch relative to repeat trials in prepared trial conditions and also separately analyzed switch and repeat trials against baseline typically report above-baseline activation for repeat trials as well (Barber & Carter, 2005; Braver et al., 2003; Crone, Wendelken, Donohue, & Bunge, 2006; Shi, Zhou, Muller, & Schubert, 2010). Additionally, as discussed below (Key Questions 2 and 3), many studies report above-baseline activation in prepared repeat trials in the absence of significantly enhanced activation in switch trials (Brass & von Cramon, 2002, 2004; Bunge et al., 2003; Cavina-Pratesi et al., 2006; Luks, Simpson, Feiwell, & Miller, 2002; Ruge et al., 2005). Together, this consistent absence of switch-only BOLD activation in cued task-switching suggests that switch trials rely on the recruitment of the same basic neural regions and thus likely the same preparatory processes that are involved in repeat trials. This conclusion is consistent with the conclusion drawn from many behavioural studies (e.g., Gilbert & Shallice, 2002; Kiesel et al., 2010; Koch & Allport, 2006).

To our knowledge, the only exception to this pattern (i.e., no switch-only preparatory BOLD activation) is a recent study by Chiu & Yantis (2009) which does report switch-only preparatory BOLD activation in the medial SPL in a conjunction analysis of spatial vs. categorisation switching. Importantly though, this study used a special protocol in which the inter-trial-interval baseline was made up of a series of rapidly presented distracter stimuli. This is not comparable to the typical "empty" inter-trial-interval baseline used by the other event-related task switching studies. Thus, the hemodynamic response during baseline in the relevant brain areas might have been higher than usual, obscuring a relatively weak repeat-related activation[8].

[8]There are two studies that report switch-specific BOLD activation elicited by the target stimulus (i.e., not during the preparation interval). Barber & Carter (2005) found switch-only *target*-related activation in an inferior parietal cortex region. Another study employing a predictable (i.e., not randomly cued) task switching procedure reports switch-only target-related BOLD activation in the pSPL (Kimberg et al., 2000).

2.1 Open questions and promising directions

2.1.1 Relative proportion of intermixed switch and repetition trials and its impact for task automatization

A possible caveat to the conclusion that there is no strong evidence for switch-*only* BOLD activation is that many of the above studies used relatively high proportions of switch trials of at least 50 % (e.g., Braver et al., 2003; Crone et al., 2006; Ruge et al., 2005). Thus, one might argue that these studies lack switch-only activation because repeat trials are treated similarly to switch trials under such circumstances (cf., Monsell & Mizon, 2006; Monsell, Sumner, & Waters, 2003). For instance, when the relative proportion of switch and repeat trials is 1:1, a task repetition relative to trial N-1 will have been a task switch relative to trial N-2 on roughly half the trials. Thus, memory traces of the N-2 task might still be sufficiently strong to necessitate proactive control processes in repeat trials that are supported by the same brain areas that are also engaged proactively in switch trials. An interesting follow-up question is whether such brain regions might become increasingly disengaged in task repeat trials when switch and repeat trials are made more dissimilar by increasing the relative proportion of repeat trials (at the extreme end this would be repeat-only, that is, single task blocks). A possible hypothesis is that a higher proportion of repeat trials would increase, on average, the extent of short-term task automatization across longer sequences of repeat trials. Another approach to examine the impact of short-term task automatization would be to compare different lengths of repeat and switch sequences within blocks of intermixed repeat and switch trials (e.g., RR, RRR, RRRR compared to SS, SSS, SSSS; see Wilkinson, Halligan, Marshall, Buchel, & Dolan, 2001). A study by Slagter et al. (2006) found that increasing the relative proportion of repetitions (25%, 50%, 100%) resulted in a decrease in preparatory activation for repeat trials in all areas that also showed switch-related activation (i.e., PreSMA, PMC, and pSPL). Yet even in the 100% repetition condition, these areas still showed significant preparatory activation. Note that this activation pattern was restricted to non-PFC areas, and that there was little evidence for any PFC involvement in this study, possibly due to the use of low-level *attentional attribute* switching. We are not aware of similar studies investigating the influence of repetition frequency using higher-level switching tasks that are more likely to *include* PFC involvement. With such higher-level task switching designs in the narrow sense (i.e., switching between competing S-R mappings), it would be interesting to determine whether the engagement of prefrontal “cognitive control” areas decreases with increasing short-term task automatization, and how such patterns of task-automatization would compare to other types of paradigms investigating task automatization on different time scales (Cole, Bagic, Kass, & Schneider, 2010; Ruge & Wolfensteller, 2010; Schneider & Chein, 2003). For instance, Ruge & Wolfensteller (2010) found that large parts of prefrontal cortex disengaged after only four repetitions of the same arbitrary S-R link, suggesting that the recruitment of the lateral PFC is restricted to the initial practice of non-routine behaviour. Importantly though, stimuli in the Ruge & Wolfensteller study were not associated with multiple competing tasks as is the case in most task switching studies. Thus, it remains to be tested whether the observed rapid decline of PFC

recruitment also holds for longer sequences of task repetitions when stimuli are ambiguously linked to two competing tasks (e.g., the same digit stimulus is mapped onto a response in the magnitude task as well as in the parity task).

3. Key question 2: Is there evidence that some brain areas are relatively more activated proactively on switch trials than on repeat trials?

The relatively weak evidence for switch-*only* preparatory BOLD activation speaks against an all (switch) or none (repeat) implementation of proactive control processes. Rather, it supports a less radical view that proactive adjustments in switch trials may instead rely on the relatively greater recruitment of the same basic control processes that are also required for successful performance in repeat trials. Accordingly, the operation of proactive adjustment processes would be indicated by brain areas exhibiting *relatively* stronger preparation-related activation for switch as compared to repeat trials (but not necessarily in the absence of significant activation in repeat trials). The identification of such brain regions would explain the reduction of behavioural switch cost in prepared trials vs. unprepared trials in terms of increased employment of proactive control in switch relative to repeat trials. In fact, this view is common to many prominent theoretical accounts in the task switching literature. Specifically, accounts linked to the notion of "task set reconfiguration" (TSR) postulate a process of preparatory adjustment/reconfiguration of task representations (Meiran, 1996; Rogers & Monsell, 1995) whereas most accounts linked to the notion of "proactive task set interference" (PI) postulate the preparatory resolution of between-task competition (Gilbert & Shallice, 2002; Koch & Allport, 2006; Yeung & Monsell, 2003). Both views imply the need for increased control effort in switch trials as compared to repeat trials in order to establish the currently relevant task set, either in terms of re-configuring vs. configuring task sets (TSR) or in terms of resolving increased competition from the currently irrelevant task when it was the more recently performed one (PI)[9]. Accordingly, the greater recruitment of cognitive control processes in anticipation of a switch compared to a repeat should be indicated by switch-related activation in prepared trial conditions within a generic "cognitive control brain network" that would include prefrontal and parietal cortical regions (e.g., Cole & Schneider, 2007; Dosenbach, Fair, Cohen, Schlaggar, & Petersen, 2008). Moreover, the identification of switch-related activation in lower-level task-specific brain regions would reflect the outcome of these adjustment processes within the putative target areas of cognitive control.

There remains considerable discrepancy between fMRI studies as to whether there is any evidence in support of such proactive switch-related adjustment processes and, if so, which precise brain regions might be involved. In support of proactive switch-related adjustment processes, many studies have found evidence for switch-related activation in

[9] It is difficult to pinpoint the precise difference between "re-configuring task set" and "counteracting proactive task interference". One distinction that has often been made (not necessarily by those authors who introduced the term) is that TSR processes are engaged in switch trials only (Kiesel et al., 2010), yet this assumption is not always regarded mandatory (e.g., Koch & Allport, 2006). See also key question 1 in this review.

prefrontal and parietal brain regions for prepared trials with CTIs > 500 ms (Badre & Wagner, 2006; Barber & Carter, 2005; Braver et al., 2003; Chiu & Yantis, 2009; Crone et al., 2006; Forstmann, Brass, Koch, & von Cramon, 2005; Jamadar, Hughes, et al., 2010; Ruge et al., 2010; Rushworth, Hadland, Paus, & Sipila, 2002; Rushworth, Paus, & Sipila, 2001; Wylie, Javitt, & Foxe, 2006). The most consistently reported brain region exhibiting switch-related activation in these studies is the posterior parietal cortex (pSPL/pIPS), but most of the above studies also report switch-related activation in more anteriorly located parietal, premotor, and lateral and medial prefrontal regions. As discussed below (Section 3.1), the precise localization and strength of switch-related activation especially within the frontal cortex seems to depend strongly on the specific type of task switching required, whereas switch-related activation in the posterior parietal cortex occurs more broadly. Importantly though, many other studies have reported general trial-related activation for both switch and repetition trials in frontal and parietal areas, but *no* reliable activation differences between switch and repetition trials in any of these areas (Brass & von Cramon, 2002, 2004; Bunge et al., 2003; Cavina-Pratesi et al., 2006; Gruber, Karch, Schlueter, Falkai, & Goschke, 2006; Luks et al., 2002; Ruge et al., 2005; Ruge, Braver, & Meiran, 2009).

In part, this discrepancy might simply be due to a lack of statistical power in those studies that fail to detect significant switch-related BOLD activation (for further elaboration, see Section 3.1.1 and 3.1.2 below). Alternatively, it is noteworthy that a large proportion of studies that do report significant switch-related activation in prepared trial conditions have used designs and analysis procedures that do not allow for disentangling cue-related and target-related BOLD components (Badre & Wagner, 2006; Braver et al., 2003; Crone et al., 2006; Jamadar, Hughes, et al., 2010; Rushworth et al., 2002; Rushworth et al., 2001; Wylie et al., 2006). Consequently, as discussed Section 1.3 above, switch-related activation in such studies might possibly be attributable to reactive adjustment processes initiated after target onset rather than proactive adjustments completed during the CTI. Thus, the discrepancies might in part be due to uncontrolled study parameters that differentially affect the need for reactive control, that is, processes that are not primarily in the scope of the present review. However, such an explanation is unlikely to fully account for the variability of switch-related activation across studies, for two reasons. First, a subset of studies that attempted to explicitly disentangle cue-related and target-related BOLD response components (by use of partial trial designs, jittered CTI designs, or constant-long CTI designs; see Section 1.2) still show substantial inconsistencies, with some studies reporting reliable switch-related activation clearly linked to the preparation interval (Barber & Carter, 2005; Chiu & Yantis, 2009; Ruge et al., 2010) and others not (Bunge et al., 2003; Cavina-Pratesi et al., 2006; Ruge, Braver, et al., 2009). Second, another subset of studies that could not explicitly disentangle the compound cue-target BOLD response, but which examined RT-fMRI and ERP-fMRI relationships (see Section 1.3.1), suggest that the compound switch-related BOLD activation they observed does seem to be associated with *preparatory* switch-related processes. Specifically, a study by Braver et al. (2003) found that smaller residual behavioral switch cost was associated with greater switch-related activation in pSPL (for a similar finding, see Chiu & Yantis, 2009). This suggests that smaller residual switch cost in performance was caused

by stronger proactive adjustment processes as indicated by greater switch-related pSPL activation *during preparation*. Alternatively, if pSPL activation reflected reactive adjustments, it should have shown greater switch-related activation for *larger* residual switch cost, that is, when proactive adjustment processes had been relatively ineffective. Similarly, Jamadar, Hughes et al. (2010) reported that switch-related BOLD activation in a pSPL sub-region correlated positively with switch-repeat differences in a *cue*-locked but not *target*-locked ERP component, consistent with the interpretation that pSPL is involved in switch-related proactive preparatory processes.

3.1 Open questions and promising directions

The reasons why some studies do and some do not find reliable switch-related activation in prepared trial conditions still remains elusive. A few possible reasons are considered below.

3.1.1 Statistical uncertainty

Some of the inconsistencies in the above results could simply be related to statistical uncertainty. That is, some studies may report significant effects that have emerged by pure chance, whereas other studies may have failed to find significant effects because of insufficient statistical power, a problem prevalent in many domains of imaging research (Yarkoni, Poldrack, Van Essen, & Wager, 2010). This problem is often further complicated by the fact that studies apply different significance thresholds for dealing with multiple comparisons on the whole-brain level, thus differentially biasing the rejection of the null hypothesis[10]. Since the absence of a significant effect never justifies the acceptance of the null-hypothesis, studies that failed to find significant switch-related activation might be under-represented in published reports as such negative results can easily be refuted by postulating insufficient statistical power. The size of switch-related preparatory activation in previous studies, and hence its detectability, is likely to be affected by a host of study-specific procedural parameters. At present, however, the existing fMRI studies differ in too many features at once to be able to pin down which distinct procedural parameters might determine the presence or absence of significant switch-related preparatory activation.

This current state of affairs dramatically highlights the interpretative caveats of assessing main effects of trial type (i.e., switch>repeat). Clearer conclusions can be drawn by assessing interaction effects between trial type and conditions designed to differentially modulate the size of any basic trial type effect (i.e., differential size of switch>repeat effect in condition A vs. condition B). Accordingly, future fMRI studies should orthogonally vary the parameters that are likely to contribute to the discrepancy between existing studies. Importantly, rather than focussing on the absolute size of switch-related activation per se,

[10] The study by Bunge et al. (2003) is a good example for how the type of threshold can decisively influence the detection of preparatory switch-related activation. No significant results were obtained at a whole-brain threshold of $p<0.001$ (uncorrected) and at an ROI-based threshold of $p<.05$ (uncorrected) restricted to regions exhibiting preparatory activation for an independently defined contrast within the same study. When lowering the whole-brain threshold (uncorrected) down to $p<0.005$ or even down to $p<.05$ a number of significant voxels were found in various brain regions. Unfortunately, only few studies provide such transparent reports of stepwise thresholding procedures, which would enable the reader to pick the results that appear most appropriate for a particular purpose.

future studies should assess the *relative* size of switch-related preparatory activation under experimentally varied conditions. The relative size of switch-related preparatory activation might depend on parameters that generally affect the efficiency of proactive adjustment processes. Efficiency might be reduced by modifications to the task switching paradigm that are designed to make it more amenable to certain types of fMRI data analysis (see Sections 1.1 and 1.2.4 above), but there are certainly other parameters not specifically related to fMRI design considerations that might potentially affect preparatory efficiency, like, for example, the duration of cue presentation (Verbruggen, Liefooghe, Vandierendonck, & Demanet, 2007).

The relative size of switch-related preparatory activation can also be assessed by directly comparing prepared and unprepared conditions without necessarily being interested in the significance of switch-related activation in the prepared trial condition per se. Indeed, a fair number of studies have followed this approach as addressed extensively in Key Question 3 (Section 4 below).

3.1.2 Discrepancies between fMRI and ERP findings

In contrast to the rather heterogeneous results across different fMRI studies, virtually every ERP study reports switch-related modulations of cue-locked ERP components (Karayanidis et al., 2010). The highly consistent switch-related preparatory activation in ERP studies might indeed be due to the fact that ERP studies do not have to rely on design modifications (CTI and ITI lengths; target omission) to extract cue-related and target-related ERP components (see Sections 1.1 and 1.2.4 above). Yet, contrary to this speculation, a number of fMRI studies that relied most heavily on fMRI-specific design modifications *did* find switch-related preparatory BOLD activation in prefrontal and parietal brain regions (Barber & Carter, 2005; Chiu & Yantis, 2009; Ruge et al., 2010). Moreover, despite relatively modest modifications of the original behavioural task switching design, Ruge et al. (2005) did *not* find switch-related activation for prepared trials as compared to significant switch-related activation in unprepared trials.

Differences in statistical power between fMRI and ERP methodologies may also contribute to the discrepancy regarding switch-related preparatory activation. This is particularly likely as standard fMRI and ERP statistical analysis procedures apply different statistical thresholding and correction procedures. Typically, ERP studies apply local thresholds of $p<0.05$ and either do not correct for multiple comparisons across electrodes and/or timepoints or apply simple family-wise error rate correction. Therefore ERP studies are more likely to detect small effect sizes, and rely highly on replication to validate such small effects. Functional MRI studies involve an exponentially larger data set and typically control for the massive spatial multiple comparisons problem in imaging data sets, thus leading to higher *local* thresholds and increasing the likelihood of missing relatively weak true effects. Moreover, switch-related activation in circumscribed brain regions examined in fMRI studies could be expected to be weaker than suggested by switch-related activation in certain ERP components. The reason is that an ERP component is likely to results from the summation of switch-related signals elicited in spatially segregated, but functionally

associated brain regions, each of which exhibits only weak activation on its own. These relatively weak activation effects within each constituent brain region might be missed by the localized measure of brain activation obtained in fMRI. One way to reduce the difference in statistical power between ERP and fMRI studies would be to rely more heavily on fMRI region of interest (ROI) analyses which may detect smaller activation effects that would not survive more conservative whole-brain-corrected thresholds. Again, this discussion of power issues underlines the relative weakness of interpretations that are entirely based on assessing the presence of switch-related preparatory activation per se instead of identifying variables that modulate the relative size of switch-related activation (see Section 3.1.1 above).

3.1.3 Task switching without preceding task implementation

A distinctly different approach to identify switch-related preparatory activation was pursued by Brass & von Cramon (2004), using a "double-cue" paradigm and leading to some interesting conclusions beyond the typical task switching paradigm. In this novel paradigm, two task cues are presented consecutively during the preparation period and signal either the same task (cue meaning repeat) or different tasks (cue meaning switch). Contrasting these two cue conditions yielded significant switch-related activation in the posterior LPFC within the so-called "inferior frontal junction" area (IFJ, Derrfuss, Brass, Neumann, & von Cramon, 2005; Derrfuss, Brass, von Cramon, Lohmann, & Amunts, 2009) and within the parietal cortex[11]. This result may seem surprising in the light of behavioural findings (Schuch & Koch, 2003) which suggest that switch-related task adjustment processes depend on the actual implementation of the previously cued task, and therefore would not be expected to have been completed to the first cue in the Brass & von Cramon paradigm (for further elaboration on the distinction between task instruction and task implementation, see Brass, Wenke, Spengler, & Waszak, 2009). These contrasting outcomes suggest that switch-related adjustment processes as indicated by brain activation measures may not always be reflected in behavioural performance. If this conclusion is valid, an important caveat of the partial trial design appears less problematic. Specifically, the fact that trials after partial cue-only trials require a task switch without previous task implementation might not critically reduce the chance to detect switch-related preparatory BOLD activation when analysed together with trials following full cue-target trials. Indeed, the size of switch-related preparatory activation reported in Ruge et al. (2010) was not influenced by the presence or absence of previous task implementation as suggested by a separate analysis of switch-related preparatory activation following partial trials vs. full trials (Ruge & Braver, 2008). Similar results were obtained in a recent ERP study that implemented the Schuch & Koch (2003) paradigm and

[11] Interestingly, these activations were specific for switching the task indicated by the cues, as mere cue identity switches (i.e. the second cue was a different symbol as the first cue, but denoting the same task) did not activate these regions. Together with similar findings from other studies that disentangle cue switching and task switching (Jamadar, Hughes, et al., 2010; Wylie et al., 2006), this suggests that switch-related activations reported in fMRI studies are rather not reflecting mere cue switching effects (for a debate of this issue in the behavioral literature, see Logan & Bundesen, 2003; Mayr & Kliegl, 2003; Monsell & Mizon, 2006).

showed that switch-related preparatory brain activation was not influenced by completeness of task implementation in the preceding trial (Jamadar, Michie, et al., 2010b).

3.1.4 Does switch-related preparatory activation reflect stimulus-directed or response-directed adjustment processes?

Studies that have found significant switch-related preparatory BOLD activation typically report "some" lateral and medial frontal regions and "some" parietal regions within a generic "fronto-parietal cognitive control network". Yet, a closer look reveals a surprising heterogeneity concerning the precise localization of switch-related activation especially within the frontal cortex. In order to reconcile the discrepancies between the reported studies, it is essential to consider additional task parameters that may determine the nature of advance preparatory processes recruited in task switching.

One key task parameter that has been manipulated extensively in behavioural and ERP studies relates to whether the task requires switching between stimulus-directed (attentional) or response-directed (intentional) processes. Classical task switching paradigms involve switching between two different, but consistent, S-R mappings defined either on different stimulus dimensions of a single item (e.g. magnitude vs. parity of a single digit; Allport, Styles, & Hsieh, 1994) or on each dimension of a compound stimulus (e.g., vowel/consonant or odd/even for a letter/number combination; Rogers & Monsell, 1995). Thus, as suggested by Meiran (2000), preparation likely involves shifting attentional focus from one stimulus dimension to another (e.g. focus on magnitude but not parity or focus on letter not number). By contrast, other studies have used "rule switching", defined in terms of S-R reversal (circle=left, square=right vs. circle=right, square=left) or switching between abstract categorization rules (e.g. match vs. non-match) that cannot rely on attentional (i.e. stimulus-directed) preparatory mechanisms. Rather, these tasks rely on re-linking the same set of stimuli to different responses – processes that exclusively involve changes of "response set", or "response meaning" (i.e., R1 used to indicate presence of S1 vs. S2) rather than "stimulus set" (Brass et al., 2003; Meiran, 2000). Thus, one might expect partially different brain regions for switching paradigms that depend on attentional vs. intentional proactive adjustment processes. Indeed, using an S-R reversal task with constant CTI of 1.5 s, Crone et al. (2006) reported evidence for differential switch-related activation in mid-DLPFC/VLPFC (amongst other areas) when switching between bivalent targets (i.e., occurring under both S-R rules and thus likely involving intentional preparation) as compared to switching between univalent targets (i.e., that are linked to a constant S-R mapping and thus likely involved attentional preparation only). Similarly, using a partial trial design, Ruge et al. (2010) also found that the mid-DLPFC was associated specifically with intentional switch-related preparatory control. Specifically, there was additional switch-related preparatory activation in mid-DLPFC (amongst others) as compared to Pre-SMA only (amongst others) for an "intention-based" preparatory condition which differed from a purely "attention-based" preparatory condition with respect to the explicitness of task-specific response meanings. Rushworth et al. (2002; 2001) compared an S-R reversal condition with an attentional switching condition using a constant CTI of 1 s. They found different localisations for each

type of switching in the medial PFC and the PPC, but unfortunately did not examine whether there was differential involvement of mid-DLPFC in intentional task control.

The involvement of mid-DLPFC in response-related adjustment processes in task switching as suggested by the above studies is consistent with results from other research paradigms which suggest a general role of this region for action-direct control processes (e.g., Lau, Rogers, Ramnani, & Passingham, 2004; Pochon et al., 2001; Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000). Yet, despite this intriguing overlap of mid-DLPFC involvement across paradigms, the above task switching studies are not as consistent with regard to switch-related activations in other brain regions. On the one hand, this is not surprising as these studies employed quite different experimental manipulations to tease apart attentional and intentional processes and implemented rather different fMRI designs (constant CTI vs. partial trial). On the other hand, these different activation patterns across task switching procedures may suggest the existence of multiple action-related control processes. This is particularly likely with regard to fronto-medial regions that are implicated in models that postulate parallel and inter-related hierarchical organization of lateral PFC regions and medial PFC regions in cognitive control (Kouneiher, Charron, & Koechlin, 2009). Specifically, the rostral cingulate zone (RCZ) is implicated in intentional switch-related adjustment processes in both Rushworth et al. (2002) and Ruge et al. (2010). By contrast, these same studies implicated the Pre-SMA/SMA region in switch-related adjustment processes irrespective of specific intentional or attentional requirements. More importantly though, transcranial magnetic stimulation (TMS) application over that region disrupted only intention-related, but not attention-related adjustment processes (Rushworth et al., 2002), a finding that is consistent with Crone et al. (2006) who report an involvement of Pre-SMA/SMA in intention-related adjustment process. To further clarify this complex pattern of results, future research needs to tease apart different aspects of action-related preparatory adjustment processes, an endeavour that might also benefit from more precisely conceptualizing the notion of "response intention".

A related question is whether the same proactive adjustment processes are involved for task switching that involves a change in stimulus set (e.g., switching between letter and digit tasks without S-R reversals) and "lower-level" attribute switching tasks. Direct evidence in support of such a notion comes from Chiu & Yantis (2009), suggesting a common mechanism located in pSPL for both location-based attribute switching and classical task switching (digit categorisation). This result is in line with a common involvement of pSPL in lower-level attentional shifting situations irrespective of the target modality (Behrmann, Geng, & Shomstein, 2004). Interestingly, there is also evidence that the attentional switch-related preparatory processes interact with content-specific sensory areas for color vs. motion processing (Wylie et al., 2006; see also Yeung, Nystrom, Aronson, & Cohen, 2006 for similar material-specific effects in a blocked fMRI design).

3.1.5 Preparatory activation irrespective of switching or repeating

Many fMRI studies have focussed on preparatory BOLD activation in anticipation of the upcoming target irrespective of whether switching or repeating (Brass & von Cramon, 2002;

MacDonald, Cohen, Stenger, & Carter, 2000; Ruge, Braver, et al., 2009; Sakai & Passingham, 2003; Shi et al., 2010). Other studies included only switch trials making a comparison with repetition trials inherently impossible (Sakai & Passingham, 2006). Instead of examining possible differences in preparatory BOLD activation for switch and repeat trials, these studies examine differences in preparatory brain activation depending on different types of advance information (e.g., the specific task that is cued).

Generally, these studies can be grouped according to the specific type of preparatory activation they examine (see Figure 1 for different possible types of preparatory neural activation). Some studies focus on delay-related (i.e., working-memory-related) preparatory activation, and thus mostly use jittered CTI designs for explicitly extracting delay-related BOLD components. Other studies are interested in preparatory processes under minimized working memory load, and thus use partial trial designs with comparably short CTIs. Interestingly, preparatory activation within prefrontal cortex upon presentation of a typical task cue (e.g., a more or less abstract symbol denoting the currently relevant task) appears to systematically vary for partial trial designs and jittered CTI designs. In partial-trial studies there is a consistent overlap of preparatory activation related to task cue presentation in more posterior regions of PFC in the vicinity of the inferior frontal junction (IFJ) and the Pre-SMA (Brass & von Cramon, 2002; Ruge, Braver, et al., 2009; Shi et al., 2010). By contrast, studies based on wide CTI jittering report additional delay-related preparatory BOLD activation within more anterior ventro-lateral PFC regions extending into frontopolar cortex (Bengtsson, Haynes, Sakai, Buckley, & Passingham, 2009; Bunge et al., 2003; Chiu & Yantis, 2009; Sakai & Passingham, 2003, 2006). A plausible explanation for this striking difference is related to the fact that CTI jittering involves much longer CTIs (e.g., 4-12 seconds) than partial trial designs (e.g. 2 seconds) which have, in principle, no lower CTI limit. Additionally, these paradigms differ in that the cue remains on screen during the CTI in the partial trial studies but not in the jittered CTI studies, thus reducing the requirement for the active maintenance of cue identity. Thus, delay-related preparatory activation extending into more anteriorly located VLPFC regions likely reflects the need for active maintenance of task-related representations.

Beyond this general regional dissociation regarding the type of preparatory activation (i.e., cue-related vs. delay-related), the above studies yielded a number of interesting findings that could further constrain the role of prefrontal sub-regions for different aspects of task preparation. One such prefrontal sub-division in the context of high working memory demands was described by Sakai & Passingham (2003, 2006). Specifically, they showed that anterior LPFC activation (including BA10) was maintained during the delay irrespective of the currently cued task, but correlated in a task-*specific* manner with BOLD activation within more posteriorly located LPFC areas – both, during the delay and during subsequent task implementation (i.e., at the time of target presentation) as well as with behavioural task performance (for an extensive review of related research, see Sakai, 2008). Studies investigating task preparation under minimal WM demands and focusing on cue-related BOLD activation (instead of delay-related activation) did not typically examine the possible

task-specificity of preparation-related activation. In fact, these studies often seem to rather maximize task similarity (e.g., letter vs. digit categorization or horizontal vs. vertical placement) instead of maximizing task segregation in terms of processing modality (e.g., verbal vs. spatial tasks or color vs. motion tasks; but see previous section for Wylie et al., 2006, who compared color and motion tasks within a non-WM design). Thus, in these non-WM task preparation studies, the detection of task-specific preparatory activation might have been difficult in any case.

Another prefrontal sub-division was described in a partial-trials study by Ruge et al. (2009) which contrasted preparatory activation elicited by standard advance task cues (followed by target stimuli) with preparatory activation elicited by advance target stimuli (followed by task cues). On the one hand, the results suggested a strong functional-anatomical overlap between cue-related and target-related processes within posterior prefrontal (IFJ, Pre-SMA, dPMC) and posterior parietal areas (pIPS/pSPL). Specifically, these areas were engaged with advance task cues, re-engaged with the subsequent target, and also showed preparatory activation when the target stimulus appeared in advance of the cue. Moreover, there was no other brain region that was engaged exclusively for advance task cues. On the other hand, a number of more anterior brain regions within the PFC (DLPFC, RCZ) and parietal cortex (aIPS) were exclusively engaged with advance target stimuli. This pattern of results is consistent with a conceptual distinction between two "task set" components, that is, abstract task goals that specify "what to do next" and concrete task implementation rules that specify "how to do it" (cf., Rubinstein, Meyer, & Evans, 2001). While the advance activation of abstract task goals occurred for both cues first (single goal) and target first (two alternative goals) conditions, advance activation of implementation rules occurred exclusively for the target first condition, indicating stimulus-specific links to the respective task-appropriate response codes. The involvement of mid-DLPFC in preparatory activation of implementation rules is also directly supported by a recent study which found preparatory mid-DLPFC activation specifically for advance "rule cues" that explicitly denoted the currently relevant S-R rule as compared to standard advance task cues (Shi et al., 2010). Furthermore, it should be noted that particularly the mid-DLPFC and RCZ activations associated with the advance target condition in Ruge et al. (2009) overlap with areas of switch-related activation in prepared trial conditions reported in studies that more directly tap into the intentional aspect of response codes, that is "action sets" (Meiran, 2000; Meiran et al., 2008). Finally, as elaborated further below, the conceptual distinction between abstract task goals and implementation rules (i.e. action sets) might ultimately serve to explain why some studies did and some other studies did not observe switch-related preparatory activation indicative of proactive task adjustment processes.

4. Key question 3: Is there evidence for separable brain areas exhibiting switch-related activation in prepared vs. unprepared trial conditions?

Some studies directly compare proactive vs. reactive control adjustments by contrasting switch-related BOLD activation for prepared (i.e., trials with a long CTI>500ms where the cue

provides full information about the upcoming task) vs. unprepared task trials (i.e., trials with a short CTI<<500 ms or where the cue provides no information about the upcoming task). As discussed in detail in Section 1.3.2 above, a brain region primarily engaged in proactive control adjustments should exhibit stronger switch-related activation in prepared than in unprepared trials, whereas a brain region primarily engaged in reactive control adjustments should exhibit stronger switch-related activation in unprepared trials than in prepared trials. By extension, a region that exhibits similar switch-related activation for *both* prepared and unprepared trials is likely to be associated with control processes that are common to both proactive and reactive adjustment and are activated either before or after target onset depending on the time available for preparation. Interestingly, four studies that have directly compared prepared and unprepared trial conditions have found evidence for all three activation patterns partly even involving the same brain regions.

In support of *reactive* switch-related control adjustments Ruge et al. (2005) and Brass & von Cramon (2004) found widespread switch-related activation for unprepared trials (CTI = 100 ms) as compared to prepared trials (CTIs>800 ms) in multiple brain regions including parietal cortex (aIPS, pIPS/pSPL) and frontal cortex (mid-DLPFC, IFJ, Pre-SMA, dPMC). A similar, but regionally more confined reactive control pattern was found by Badre & Wagner (2006) specifically for the mid-VLPFC – a region not reported in the above two studies. The involvement of these brain regions in reactive adjustment processes is further supported by studies that included only unprepared trial conditions (i.e. no direct comparison with prepared trial conditions), most of which report switch-related activation in similar parietal and frontal regions (e.g., Brass et al., 2003; Dove, Pollmann, Schubert, Wiggins, & von Cramon, 2000; Hyafil, Summerfield, & Koechlin, 2009; Liston, Matalon, Hare, Davidson, & Casey, 2006; Smith, Taylor, Brammer, & Rubia, 2004). Importantly, a subset of these regions (IFJ, Pre-SMA, PMC, pIPS/pSPL) also showed *general* preparation-related BOLD activation in long CTI trials at similar levels for switch and repeat trials in some studies (e.g., Brass & von Cramon, 2002; Ruge et al., 2005; Ruge, Braver, et al., 2009). Thus, these areas do seem to play a role in proactive control – just not in terms of a substantially stronger recruitment in switch than repeat trials. However, to further complicate matters, some of the same regions (IFJ, Pre-SMA, mid-DLPFC, and pIPS/pSPL) that showed stronger switch-related activation for unprepared trials than for prepared trials in Ruge et al. (2005) and Brass & von Cramon (2004), exhibited similar switch-related activation levels in both prepared and unprepared trials in Badre & Wagner (2006). This latter result is consistent with a flexible engagement of these regions in both proactive and reactive switch-related adjustment processes depending on the time for advance preparation. As discussed in Section 3 above, the involvement in proactive switch-related adjustment processes is further supported by some studies that implemented prepared trial conditions only (e.g., Crone et al., 2006; Ruge et al., 2010; Rushworth et al., 2002). Finally, a recent study by Jamadar, Hughes et al. (2010) found a third pattern of switch-related activation comparing prepared and unprepared conditions. Specifically, there was switch-related activation in the pIPS/pSPL for prepared trials but not for unprepared trials (and no other areas showed switch-related activation for unprepared

trials), suggesting an exclusive role in proactive switch-related adjustments. This conclusion was also supported by analyses of fMRI-ERP correlations discussed in Section 3 above.

4.1 Open questions and promising directions

The complex pattern of the above results raises one particularly puzzling question: how can the same areas (IFJ, Pre-SMA, mid-DLPFC, pIPS/pSPL) appear to be involved in switch-related adjustment processes either only proactively (Jamadar, Hughes, et al., 2010, specifically the pSPL), only reactively (Ruge et al., 2005), or both proactively and reactively (Badre & Wagner, 2006). One immediately obvious implication is that none of these areas is likely to be specialized in either proactive or reactive switch-related adjustments. Instead, they seem to be able to play either role depending on the current experimental context.

An intriguingly simple explanation for the flexible recruitment of these brain areas in either proactive or reactive adjustment processes is that long CTI trials are not really "prepared trials" under all particular study conditions. Just as occasional failures to engage proactive adjustment processes on a few long CTI trials might explain residual behavioural switch cost despite sufficient preparation time (DeJong, 2000), a relatively high proportion of unprepared long CTI trials might explain the absence of significant switch-related preparatory BOLD activation in long CTI trials as observed in Ruge et al. (2005) or Brass & von Cramon (2004). In other words, switch-related preparatory neural activation associated with relatively few fully prepared long CTI trials might be too small to be detected when analysed together with the many unprepared long CTI trials. However, this explanation seems implausible for two reasons. First, studies that fail to identify *any* brain area associated with proactive adjustment processes (Brass & von Cramon, 2004; Ruge et al., 2005) still show a reduction in *behavioural* switch cost in long CTI trials as compared to short CTI trials suggesting that proactive adjustment is likely to have been undertaken on a considerable proportion of trials. Second, if subjects did not substantially adjust proactively during the long CTI in those studies, they must have adjusted reactively after the target arrived. This compensatory target-driven reactive adjustment in effectively unprepared long CTI trials should have been reflected by switch-related activation more or less equivalent to that observed for similarly unprepared short CTI trials. Yet, this was not the case in Ruge et al. (2005) and Brass & von Cramon (2004). Thus, paradoxically, although reduced behavioural switch cost and reduced switch-related activation in long as compared to short CTI trials suggests that subjects are prepared for the upcoming switch trial, long CTI trials show no sign of substantial switch-related enhancement of preparation-related BOLD activation. This suggests that under certain study conditions the need for switch-related reactive adjustments at the time of target presentation can be reduced via preparatory processes that are similarly engaged for both switch and repeat trials. Under other study conditions, however, the reduction of reactive adjustment demands in long CTI trials seems to rely on a type of preparation that does involve an increased recruitment of neural resources in switch relative to repeat trials as indicated by sizable switch-related BOLD activation in long CTI trials (Badre & Wagner, 2006; Jamadar, Hughes, et al., 2010). Below, we attempt to specify more clearly these different types of preparatory processes.

4.1.1 Multiple preparatory modes?

Many models of task-switching assume that preparation to repeat or switch tasks involves a number of different processes operating on different task set components. Rubinstein et al. (2001) distinguished between abstract task goals (i.e., a representation of "what to do next") and concrete task implementation rules (i.e., task-related action sets that determine "how to reach the activated task goal"). Similarly, Meiran et al. (2000; 2008) distinguished between abstract task goals, action sets and, as an additional third component, attentional sets that determine which stimulus dimension should be selectively processed. Rubinstein et al. and Meiran et al. agree that abstract goal representations can be activated in advance, but that action sets are not typically adjusted according to the active task goal in advance of target presentation. Additionally, Meiran et al. suggested that attentional sets are typically adjusted proactively in accordance with changed task goals. Notably, there are reasons to believe that the sequence of these processes can be flexibly aligned depending on the particular study conditions. Specifically, in Section 3.1.4 we reviewed evidence from fMRI studies suggesting that action sets can in fact be adjusted proactively under certain conditions – as evidenced by switch-related BOLD activation in long CTI conditions within a distinct set of brain regions (most reliably including mid-DLPFC and RCZ). By contrast, task preparation under other conditions rather seems to rely primarily on proactive adjustments of attentional sets as reflected by switch-related BOLD activation in long CTI conditions most reliably within pIPS/pSPL.

In addition to these two preparatory modes (i.e., proactive adjustments of attentional sets and proactive adjustments of action sets), we propose a third preparatory mode that relies on goal activation only (for conceptual considerations that might imply similar conclusions, see Gilbert & Shallice, 2002; Goschke, 2000; Rubinstein et al., 2001). This mode could explain the findings that suggest that the preparation-related reduction of residual reactive adjustment demands might be accomplished in the absence of substantial preparation-related enhancement of BOLD activation in switch relative to repeat trials. This explanation rests on the central assumption that the perseverative tendency to repeat the previous task is *not* related to lingering goal activation and a resulting difficulty in establishing a new task goal in switch trials. Instead, perseverative tendencies are assumed to be linked to lingering activation of "action set" and/or "attentional set" causing enhanced interference in switch trials which implies the need for switch-related adjustments either reactively during actual task implementation and/or proactively in case the respective preparation modes are engaged[12]. When subjects adopt the goal activation mode, the reduced interference during subsequent task implementation – as suggested by reduced

[12] Such a conceptualization is quite plausible in the light of Luria's classical characterization of prefrontal dysexecutive patients who often exhibit perseverative behaviour despite their preserved ability to verbally report the theoretically correct task goal (Luria, 1973). Accordingly, cognitive control is not so much required for establishing a new goal representation (patients' preserved ability to represent the task goal), but to effectively utilize an active goal representation for task implementation in the face of interference from the competing task in cases where the target stimulus is bivalent (problems in applying the respective task implementation rules in dysexecutive patients).

behavioural switch cost – can be explained by the interaction of different biases at the time of target presentation: Top-down bias from the proactively activated task goal and "bottom-up" (here: not proactively controlled) biases resulting from lingering activation of the previously active action set and attentional set. Importantly, due to the temporal priority of advance task goal activation in prepared trial conditions and due to the putative hierarchical dominance of this top-down bias, the target-evoked bottom-up biases may have no chance to develop a considerable impact. In prepared trials, this leads to a reduced need of counteracting target-induced interference in switch trials, and thus, entails reduced behavioural switch cost and reduced switch-related BOLD activation at the time of target presentation.

Importantly, the above considerations are not meant to imply mutually exclusive preparation modes. Rather, the relative preparatory involvement of each task set component (i.e., abstract goals, action set, attentional set) might vary as a function of task conditions. Even if the absence of *significant* switch-related BOLD activation in long CTI conditions implies a predominant engagement of the goal activation mode, this does not categorically exclude the additional, though comparably weak, involvement of proactive switch-related adjustment processes operating on attentional or action sets. These adjustment processes might however be too weak to be detected via measures of BOLD activation, whereas more sensitive ERP measures may reveal even small switch-related enhancement of neural activity (see Section 3.1.2 above).

For the notion of multiple preparatory modes to have strong explanatory power, two critical questions need to be addressed by future research. First, what are the critical variables that determine the relative preparatory involvement of each preparatory mode? Second, are these context variables indeed associated with different strengths of switch-related preparatory activation? Although there have been many variations of the task-switching paradigm, there has been little work trying to systematically identify the critical task variables that affect the type and strength of preparatory activation. For instance, one such variable might be the explicitness with which the task cue indicates the current implementation rule or action set (Meiran et al., 2008). In fact, a recent partial-trial fMRI study contrasted preparatory and target-related activation for standard advance task cues vs. "rule cues" that explicitly denoted the currently relevant implementation rule (Shi et al., 2010). Mid-DLPFC regions were sensitive to cue type in a way that suggested an involvement in preparatory rule activation rather than in preparatory task goal activation. However, as *switch-related* preparatory activation was not systematically analysed for each cue type (except for a Pre-SMA ROI yielding no significant differences in switch-related activation), this study does not really address the question whether advance rule cues might entail stronger switch-related proactive adjustment processes than advance task cues (see Section 5.1 in the General Conclusions for other important variables that may determine which preparatory mode(s) are adopted in a given study).

5. General conclusions

5.1 What kinds of processes are reflected by preparatory BOLD activation in task switching?

Much of the task switching literature for the last 15 years has been revolving around the notion of "task set reconfiguration" (TSR) – a concept encompassing executive control processes that serve to establish the currently relevant task set under task switching conditions. The reduction of behavioural switch cost with increasing *preparation time* can be interpreted as straight-forward evidence for the operation of such executive control processes. In functional-anatomical terms, executive control function in general is often ascribed to the prefrontal cortex (PFC) in concert with the posterior parietal cortex (PPC) (e.g., Cole & Schneider, 2007; Dosenbach et al., 2008).[13] However, the precise brain areas within this large generic control network specifically supporting preparatory control in task switching have not been clearly delineated. Moreover, it has been difficult to determine the degree of PFC involvement in preparing to switch tasks and possible sub-specializations within this or other brain structures. Beyond providing a comprehensive overview of the functional anatomical expressions of preparatory task control, the present review also aimed at evaluating how fMRI results might contribute to the clarification of conceptual issues concerning the specific properties of preparatory processes in task switching and whether the TSR metaphor might adequately capture the nature of these processes.

One conceptual issue concerns whether preparatory control (see Key Question 1; Section 2) is exclusively engaged in switch trials to establish the currently relevant task set – an implication that has often been derived from the "re-"configuration metaphor (cf., Kiesel et al., 2010). Accordingly, if a brain area existed (within PFC) for implementing such a switch-only preparatory mechanism, we should expect significant preparation-related BOLD activation in switch but in repeat trials. The available fMRI data are rather clear in refuting this strong prediction (at least with regard to preparation-related activation), both for PFC regions as well as other regions.

Alternatively, one might argue that a process that is defined as switch-only in procedural terms (indeed, nothing has to be *re*-configured in repetition trials), does not logically also imply the exclusive engagement of a particular (set of) brain region(s). In this sense, it is easily conceivable that an advance task cue triggers the engagement of certain higher-level brain regions that "guide the configuration" (i.e., "bias") processing pathways in accordance with the currently relevant task demands. There is no reason to assume that such a general "task set *con*figuration" process is exclusive to switch trials and cannot be activated on repeat trials as well. The only difference is that in switch trials it effectively results in a *re*-configured state of the brain, and that changing the brain state is likely to be associated with *relatively* stronger preparatory neural activity as compared to just "refreshing" the brain state as required in repetition trials. According to this more moderate

[13] In the behavioural task switching literature such a characterization of prepared task switching has not remained undisputed. There has been a longstanding dispute about whether executive control processes need to be invoked at all to explain performance on the task switching paradigm (Altmann, 2003; Logan & Bundesen, 2003; Monsell, 2003a). This issue seems to be mostly settled in the sense that it is commonly agreed that the reduction of behavioural switch cost likely reflects both automatic cue encoding processes and executive control processes (Kiesel et al., 2010).

view of the TSR metaphor, task preparation should be reflected by switch-related (i.e., *relatively* stronger for switch vs. repetition) preparatory BOLD activation within the fronto-parietal control network. Notably, as mention earlier, this interpretation of the TSR metaphor makes the same prediction of switch-related preparatory brain activation as proactive interference (PI) accounts of reduced behavioural switch cost (Gilbert & Shallice, 2002; Koch & Allport, 2006; Yeung & Monsell, 2003). This prediction, however, has not received ubiquitous support from the fMRI studies reviewed here, as only about half of the studies have reported significant switch-related BOLD activation in prepared trial conditions (see Key Question 2; Section 3). A similarly mixed (and even more complex) picture of results emerges when comparing the size of switch-related BOLD activation in prepared vs. unprepared trial conditions (see Key Question 3; Section 4). As discussed in detail earlier, the finding that the same brain regions (i.e., pIFS/IFJ, Pre-SMA, mid-DLPFC/mid-VLPFC, pIPS/pSPL) may be activated under conditions that promote proactive switch-related adjustments (i.e. reconfiguration), reactive adjustments, or a mixture of both, can be reconciled by invoking multiple preparatory modes leading to preparation-related reduction of behavioral switch cost. So, under some task conditions, behavioral switch cost may be reduced via a proactive goal activation process common to both switch and repeat that serves as an "advance bias in anticipation of subsequent competition". Such a mechanism may counteract or prevent the built-up of target-driven interference originating from lingering activation of previously active task set components (including action set and/or attentional set). By contrast, under other task conditions, the reduction of behavioral switch cost may be (additionally) mediated by advance adjustment (i.e. reconfiguration) of action sets and/or attentional sets according to the currently active task goal. These proactive adjustments would be associated with enhanced preparation-related BOLD activation in switch trials relative to repeat trials. At present it is unclear which particular task parameters might be responsible for a preference of one over the other preparation mode. Some likely variables may include (i) the explicitness of implementation rules cues, (ii) the duration of cue presentation in long CTI trials (iii) the amount of pre-scanning task practice, (iv) pre-experimental instructions (e.g., concerning speed/accuracy), and (v) overall biases towards more or less controlled information processing similar to that assumed in the conflict adaptation literature (Botvinick, Cohen, & Carter, 2004; Gratton, Coles, & Donchin, 1992). Research tools that are especially suited to tap possible preparatory strategy differences are discussed extensively in a previous paper focusing on multi-modal analysis approaches to examining preparatory processes in task switching (Karayanidis et al., 2010).

5.2. Which brain regions are involved in which preparatory sub-processes in task switching?

Despite a decade of research, it remains premature to make strong claims about one-to-one mapping between specific BOLD activation signatures and distinct components of preparatory task control. Nevertheless, we present a tentative summary of region-to-function assignments (from anterior to posterior) that might serve as working hypotheses for future studies:

- Anterior LPFC (BA10): Domain-independent maintenance of task goal information, especially when WM demands are high (as in widely jittered CTI designs); see especially Section 3.1.5.
- Mid-DLPFC: Preparatory activation of task-specific response intentions (i.e. action sets); implementation-directed preparation; an often observed parallel activation of the RCZ may reflect a mobilization of the motivational/energizing force behind mid-DLPFC engagement; see especially Section 3.1.4.
- Posterior LPFC/IFJ: Activation of abstract task goals; the often observed parallel activation of the Pre-SMA might possibly reflect a mobilization of the motivational/energizing force behind IFJ engagement; see especially Section 4.1.
- Posterior IPS/pSPL: Preparatory activation of attentional set; see especially Section 3.1.4.

Importantly, and consistent with the notion of multiple preparatory modes, the engagement of most of these regions in preparatory task switching is clearly not restricted to one distinct type of process. Instead, different regions might better be characterized in terms of the type of information or the type of task set component they are supposed to handle (except maybe anterior LPFC). Thus, the specific experimental context seems to determine (i) whether a specific brain region may be involved differentially with regard to switching/repeating (i.e., exhibit enhanced switch-related activation vs. similar activation levels for switch and repeat), (ii) the temporal locus of this engagement (i.e., exhibit preparatory and/or target-related activation), and (iii) its involvement in prepared and/or unprepared trial conditions. This diversity of processes within a certain region is illustrated here using the IFJ region as an example.

- General preparatory processes irrespective of switching or repeating; e.g., IFJ preparatory activation for advance task cues may reflect advance activation of abstract task goals in the context of a preparatory mode that does not involve the proactive adjustment of action sets or attentional sets.
- Proactive adjustment of task-related representations; e.g., switch-related preparatory activation in IFJ may reflect the imposition of goal-driven bias directing the proactive adjustment of action sets or attentional sets, which, in turn, are associated with concurrent switch-related preparatory activation in mid-DLPFC and pSPL, respectively.
- Non-preparatory processes during task implementation; e.g., target-related IFJ activation that may reflect reactivation of previously encoded goal information to ensure correct task implementation.
- The imposition of goal-driven bias directing the reactive adjustment of action sets or attentional sets; e.g., switch-related activation in IFJ for unprepared trial conditions.

5.3 Issues that need to be especially addressed by future research

Functional MRI design has come a long way since the first studies using the task-switching paradigm. Many clever design manipulations have been developed to overcome the tyranny of different timescales between fast, strategic and therefore variable cognitive processes and the relatively slow BOLD activation signal. However, a number of stubborn issues have remained resistant to these manipulations and future work is needed to systematically study the relationship between behavioural and BOLD activation phenomena.

A first issue is related to the fact that the consequences of certain fMRI design modifications necessary to isolate preparatory BOLD activation are not yet sufficiently understood (see Section 1). This issue requires further systematic examination (e.g., Goghari & MacDonald, 2008; Koch et al., 2003) – not least to better understand the apparent discrepancies between fMRI and EEG results. Currently emerging innovative fMRI analysis techniques might alleviate some of the limitations faced by more classical analyses. One such technique relies on multi-variate pattern classification procedures (Hanke, Halchenko, Haxby, & Pollmann, 2010) that has already yielded preliminary results in task switching studies (Bode & Haynes, 2009; Esterman, Chiu, Tamber-Rosenau, & Yantis, 2009). Another technique relies on independent component analysis (ICA), a multivariate approach that assumes that the fMRI data are a linear mixture of independent sources. ICA algorithms estimate an unmixing matrix to identify statistically independent components of the source signal. The strength of the approach lies in its potential to identify spatially or temporally coherent networks across the entire brain ('functional connectivity'). ICA may therefore be useful in the task-switching paradigm to extract networks related to temporally overlapping but apparently independent cognitive processes such as proactive and reactive control. This approach has been useful in extracting independent networks of activity in other cognitive paradigms, including working memory (Meda, Stevens, Folley, Calhoun, & Pearlson, 2009), auditory oddball (Meda et al., 2010), and semantic priming (Assaf et al., 2009). Recent advances in the development of algorithms for data fusion (e.g., joint ICA, Moosman et al. (2008); parallel ICA, Liu et al. (2009)) are also promising future directions that may build upon earlier attempts to multimodal imaging with this paradigm (Jamadar, Hughes, et al., 2010; Karayanidis et al., 2010).

A second issue involves the fact that due to the inherently multivariate nature of BOLD activation data, whole-brain analyses need to rely on statistical tools for handling the massive multiple-comparisons problem. As a consequence, statistical power is limited for detecting small activation effects in circumscribed brain regions. This might explain some inconsistencies across fMRI studies and across data modalities (especially comparing fMRI and EEG). Thus, future studies should rely more on ROI-based approaches to increase statistical power. Ideally, these ROIs should be informed by previous findings, which in turn highlights the need for better data-sharing solutions (e.g., Derrfuss & Mar, 2009; Yarkoni et al., 2010).

A third issue is related to the lack of comparability across fMRI task switching studies. While some inconsistencies across fMRI studies might be due to statistical uncertainty or fMRI-methodological limitations, many inconsistencies might simply be due to the fact that

any two existing fMRI task-switching studies differ in multiple procedural features. This makes it impossible to pinpoint the specific factors that might drive the observed differences in results. A systematic *within*-study examination of procedural differences that might impact the effectiveness of preparatory processes is strongly needed. Variables that need to be systematically investigated in fMRI studies include (cf., Vandierendonck et al., 2010): CTI length/distribution; ITI length/distribution; switch/repetition proportion; task practice; types of tasks (spatial, verbal, S-R reversal, etc.); similarity among involved tasks; duration of cue presentation (Verbruggen et al., 2007); types of cues (e.g., transition vs. task cues, Forstmann et al. (2005), informative vs. uninformative cues, Jamadar, Hughes et al. (2010), spatial vs. non-spatial cues, Arbuthnott & Woodward (2002)); nature of the cue-task association (i.e., 'arbitrary' vs. 'meaningful' cues Logan & Bundesen, 2004; Monsell & Mizon, 2006); ratio of cue-task mapping (Logan & Bundesen, 2004; Mayr & Kliegl, 2003; Nicholson et al., 2005); type of target (e.g., task dimensions within same item or segregated across different items); forced vs. voluntary task selection (Forstmann, Brass, Koch, & von Cramon, 2006); other modulatory variables on switch-related preparatory activation, like variable motivational states (Savine & Braver, 2010).

5.4 Final conclusions

Ten years of functional imaging research have made it clear that the functional neuroanatomy of preparatory task switching is multi-faceted. The available data suggest that different aspects of preparatory control are differentially localized within a generic fronto-parietal control network. However, it has also become clear that some brain regions can play different roles depending on the dominant preparatory mode engaged under particular study conditions. Moreover, different preparatory modes seem to imply different types of basic mechanisms of proactive interference control underlying the reduction of behavioural switch cost. One such mechanism may prevent task perseveration via an advance bias in anticipation of upcoming task competition, unfolding its impact *after target onset* during task implementation. This mechanism is supposed to be primarily engaged in a goal activation mode and relies on a similar recruitment of preparatory control for both switch and repeat trials. Another type of mechanism may prevent task perseveration by resolving task competition *during* preparation via directly adjusting the configuration of attentional set and/or action set, thus relying on stronger recruitment of preparatory control for switch than repeat trials.

It is important to acknowledge that these conclusions are largely based on comparisons across different studies that are plagued by a variety of confounding variables and involve a variety of fMRI-specific design modifications. Thus, as exemplified by the above admittedly incomplete list of still to-be-examined variables (Section 5.3, final paragraph), future research needs to systematically test these predictions using tightly controlled experiments that include suitable experimental manipulations of critical variables. In this way, it might be possible to overcome the often-criticised reality in fMRI research which typically yields conclusions by integrating findings across independent studies with highly dissimilar designs.

Acknowledgements:

Uta Zimmermann is supported by a Career ESF-fellowship (ESF 080938749) funded by the European Union and the Saxony State Ministry for Science and Art, Germany.

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-- Figure 1 --

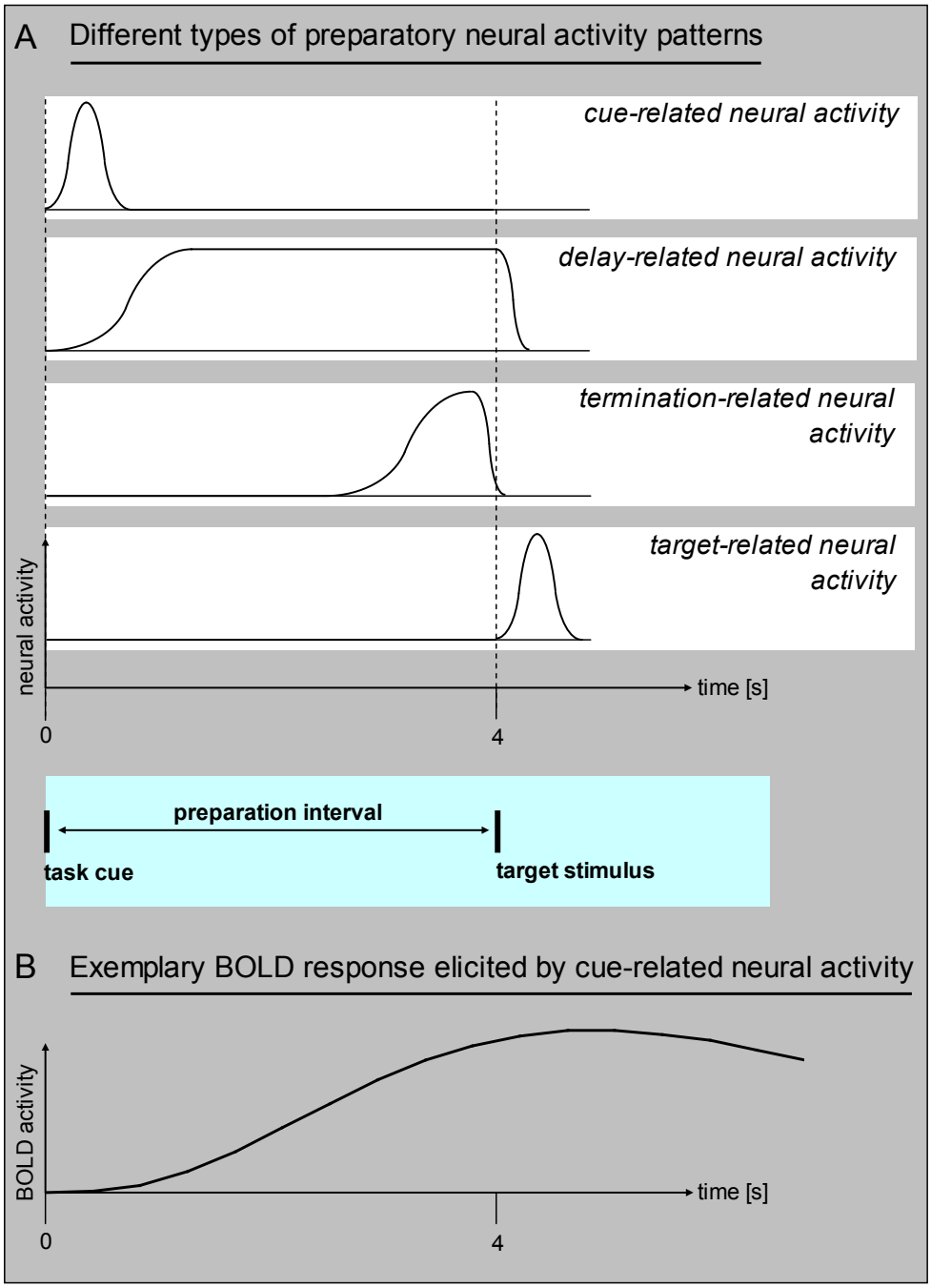

Figure 1. (A) Illustration of different types of neural activity that can occur during a cue-target trial in relation to (B) an exemplary BOLD response elicited by the cue. This schematic drawing highlights the analytical challenges of inferring the precise pattern of preparatory and target-related neural activity from the associated event-related BOLD response which evolves much slower than the underlying neural activity.