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Advance preparation and stimulus-induced interference in cued task switching: further insights from BOLD fMRI

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Abstract

To switch from one cognitive task to another is thought to rely on additional control effort being indicated by performance costs relative to repeating the same task. This switch cost can be reduced by advance task preparation. In the present experiment the nature of advance preparation was investigated by comparing a situation where an explicit task cue was presented 2000 ms in advance of the target stimulus (CTI-2000) with a situation where cue and target were presented in close succession (CTI-100). We mapped the blood-oxygenation-level-dependent (BOLD) activation correlates of switch-related control effort and advance task preparation to test alternative explanations why advance preparation is reducing switch costs. A previously reported control-related cortical network of frontal and parietal brain areas emerged that was more strongly activated for switching between tasks. However, this was true exclusively for CTI-100 where no advance task preparation was possible. At CTI-2000 these same brain areas were equally engaged in both switch and repeat trials. For some of these areas, this common activation was time-locked to the presentation of both the cue as well as the target. Other areas were exclusively associated with target processing. The overall pattern of results suggests that advance task preparation is a common process of pre-activating (cue-locked activation) the currently relevant task set which does not face interference from a persisting $N - 1$ task set. During target processing the same brain areas are re-engaged (subsequent target-locked activation) to apply the pre-activated task set. Though being common to repeat and switch trials, advance preparation has a differential benefit for switch trials. This is because the instructed task set has time to settle into a stable state, thus becoming resistant against disruption from the previous task set, which is retrieved by the current target stimulus.

Keywords: Executive control; Cognitive control; Reconfiguration; Task set; Action context; Set shifting; WCST; Prefrontal cortex; Parietal cortex

1. Introduction

Task switching is commonly held to be an appropriate paradigm for the exploration of executive control (e.g. Monsell, 2003a). Controlled information processing enables behavior that goes beyond inflexible stimulus-driven S–R association. Successful behavior in task switching would fail if subjects based their performance on fixed S–R mappings while ignoring task-specific contextual constraints on action. In compliance with 'contextual constraints', subjects are able to mentally structure the configuration of potentially available objects-for-action and potential response options (i.e. a task set is formed) in accordance with an internally represented goal.

Studies on brain-damaged patients (Milner, 1963; Stuss & Benson, 1986), non-human primates (Miller & Cohen, 2001; Stuss & Benson, 1986), and brain-imaging studies (Brass & von Cramon, 2002; Passingham, Toni, & Rushworth, 2000; Seitz & Binkofski, 2000; Toni, Rushworth, & Passingham, 2001) suggest an important role of the prefrontal cortex (PFC)

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subserving this kind of goal-directed behavior. Furthermore, studies that measure PFC and parietal cortex simultaneously usually show that the PFC acts in concert with the parietal cortex in order to implement control (Chafee & Goldman-Rakic, 1998; Dove, Pollmann, Schubert, Wiggins, & von Cramon, 2000; Sohn, Ursu, Anderson, Stenger, & Carter, 2000).

The task switching paradigm captures two core features of goal-directed behavior: flexibility and anticipatory control. Flexibility is realized by introducing frequent changes of the relevant goal (i.e. the task to be performed), which is operationalized by the independent variable task transition (task switch versus task repeat). Anticipatory control comes into play when the upcoming task can be prepared in advance, which is operationalized by the independent variable preparation interval with either a short interval (no advance preparation) or a long interval (advance preparation).

With this very basic design the present functional imaging study aimed at investigating the nature of advance task preparation and its relevance for flexibly switching between alternative tasks. This issue is central for understanding the basic cognitive mechanisms underlying task switching performance and has been causing severe controversy among theorists (Altmann, 2003; Monsell, 2003a, 2003b).

1.1. Two theoretical views of the relation between switch cost and task preparation

One basic empirical finding is that switching from one task to another task as compared to repeating the same task impairs behavioral performance. These 'switch costs' are supposed to reflect the need for a stronger engagement of control to enable a task switch. Or, in other words, switch costs reflect elevated control being necessary to counteract the tendency to repeat the previously performed task. The two scenarios outlined below make different assumptions about how this perseverative tendency is mediated.

Another important finding is that switch costs are often reduced with prolonged preparation intervals (e.g. Meiran, 1996; Rogers & Monsell, 1995). This observation suggests that a task switch can be prepared in advance. Two different explanations for this switch cost reduction are being contrasted in the present study.

According to the first scenario, the system tends to perseverate because the previously adopted task set is persisting over time into the next trial. Thus, establishing the competing task set in a current switch trial requires additional time-consuming control effort because proactive interference from the persistently activated, now misleading task set has to be overcome. With sufficient preparation time, this same process can be finished in advance of target presentation. As proactive interference has already been overcome during the preparation interval, it is no longer slowing down appropriate task implementation after the target has been presented. This notion to some degree resembles the concept of 'advance task set re-configuration' (Meiran, 1996; Rogers & Monsell, 1995).

According to the second scenario, a previously adopted task set is dissipating rapidly before the next trial is presented. Thus, it is not the persistently activated previous task set that causes interference in a current switch trial. Alternatively, as recent studies are suggesting, interference might be induced by the target stimulus itself which is retrieving the previous task set from memory (Allport & Wylie, 2000; Waszak, Hommel, & Allport, 2003, in press; Wylie & Allport, 2000). However, when every new trial starts with a neutral task set because interference is induced only after the target has been presented, there is nothing which can be done during preparation but biasing the initially neutral task set in the direction of the currently instructed task set—and this is equal for both switch and repeat trials. It is therefore not immediately clear why advance task preparation being equally engaged for both trial types should have a benefit that is differently stronger for switch trials compared to repeat trials as being indicted by reduced switch costs. A solution for this paradox is that a task switch can benefit differentially from advance preparation because the target-associated previous task set loses its potential to gain a misleading influence during task implementation. This is because the instructed task set has time to settle into a stable state, thus becoming resistant against later disruption (see also Koch & Allport, submitted for publication). A discussion of related notions can be found in other recent publications (Gilbert & Shallice, 2002; Goschke, 2000; Wylie, Javitt, & Foxe, 2003; Yeung & Monsell, 2003).

1.2. Brain activation correlates of task preparation

By measuring the subjects' behavioral performance, the involvement of a task preparation process can be inferred only indirectly from the beneficial impact it has during the subsequent task implementation. Functional MRI can be used to obtain a more direct record of the ongoing preparation process by measuring the correlated blood-oxygenation-level-dependent (BOLD) activation. In the present study we were measuring BOLD activation to distinguish between the two theoretical scenarios sketched above, which are both equally compatible with the reduction of behavioral switch costs.

We realized an explicitly cued task switching procedure (i.e. an unpredictable task cue indicated the current task) and introduced a long preparation interval of 2000 ms (CTI-2000) and a short preparation interval of 100 ms (CTI-100). An accumulating number of previous fMRI studies using cued task switching procedures did not find elevated BOLD activation for switch trials compared to repeat trials with long preparation intervals (Brass & von Cramon, 2002; Braver, Reynolds, & Donaldson, 2003; Dove, 2000; Luks, Simpson, Feiwell, & Miller, 2002).

This result intuitively appears to be incompatible with the notion that establishing the instructed task set in switch trials is facing interference from the persistently activated, now misleading previous task set. The advance resolution of this

interference should require more control effort during preparation than merely refreshing the task set in repeat trials. This should be paralleled by stronger BOLD activation for switch compared to repeat trials.

We suggest to explain this rather unexpected result in terms of the alternative scenario outlined above, which accounts for reduced behavioral switch costs without assuming that between-task interference is being resolved during preparation. This account predicts reduced or even absent additional switch-related control effort when advance preparation is possible, both during task preparation and during task implementation. Hence, being easily compatible with the absence of enhanced BOLD activation at long preparation intervals.

Furthermore, this account predicts that interference caused by the target-induced $N - 1$ task set impairs task implementation specifically when advance preparation is not possible. Thus, high switch-related control demands with a short preparation interval should be reflected by enhanced activation in switch trials compared to repeat trials. This is exactly the pattern Dove et al. (2000) observed for several frontal and parietal brain areas realizing a CTI of 0 s.

Different from previous fMRI studies we realized a short and a long CTI condition within the same subjects which allows to draw stronger conclusions regarding the comparison of switch-related BOLD effects for different CTIs. Moreover, as being delineated below, a fine-grained analysis of the temporal structure of the trial-related BOLD response was intended to bring about further theoretical constraints.

1.3. Determining the temporal structure of the trial-related BOLD response

As argued above, determining the pattern of switch-related BOLD activation for CTI-100 and CTI-2000 can reveal important information. However, it would be even more informative to know, whether brain areas that are engaged in the CTI-2000 condition are involved in cue-related and/or target-related processing. Unfortunately, the analysis of fMRI time courses notoriously faces problems of decomposing a trial-related BOLD response into sub-components associated with separate within-trial events (cue and target) when the events are not spaced generously or the event order is not counterbalanced. This problem also holds for the standard method based on multiple linear regression (Friston et al., 1998) which we applied for detecting relevant activations within the whole-brain volume. Any effect we observe for CTI-2000 thus always reflects the sum of effects caused by cue-related and target-related processing.

To gain at least partial information about the composition of the trial-related BOLD response at CTI-2000 we implemented a novel temporal analysis of trial-averaged time courses (Ruge, Brass, Lohmann, & von Cramon, 2003). This method allows to decide whether a brain area of interest is generally activated cue-related and/or target-related in terms of present–absent judgements.

However, if a brain area turns out to be engaged both in the cue phase as well as the target phase, even for this method, the 2000 ms CTI is too short to determine the relative quantitative contributions of the respective cue-related and target-related BOLD sub-components. In this case, the analysis can nevertheless tell that an activation of unspecified strength is associated with both the cue and additionally with the target.

Similarly, potential activation differences between switch and repeat trials at CTI-2000 can not differentially be assigned either to the cue period or to the target period. With regard to the hypothesis that the CTI-2000 condition would not differ between switch and repeat trials, this does not pose a major limitation. Furthermore, it should be noted that, though BOLD activation at CTI-2000 displays the sum of potential cue-related and target-related sub-components, activation effects that are associated with only one sub-component are still detected by both the standard regression-based whole-brain analysis as well as our additional temporal analysis.

2. Methods

2.1. Subjects

We measured 22 subjects who all gave written informed consent to participate in the present study. Four subjects were excluded due to movement artifacts, all during the second experimental block (see below). The mean age of the remaining 18 subjects was 25.5 (range 21–35), 10 were female. No subject had a history of neurological disorder, major medical disorder, or psychiatric disorder. All subjects were right-handed as assessed by the Edinburgh Inventory (Oldfield, 1971).

2.2. Experimental procedure

We adopted a spatial task-switching procedure, which has been introduced by Meiran (1996). The subjects had to obey one of two alternative rules: ‘judge if a filled white square appeared up or down’, or ‘judge if a filled white square appeared left or right’. Which task rule to apply next, was cued unpredictably from trial to trial with two different preparation intervals. Thus, in one half of the trials subjects had to change the rule from trial $N - 1$ to trial N in the switch condition. In the repeat condition the same rule was relevant in successive trials. The target stimulus could appear in one out of four positions of a two-by-two grid. Subjects had to press a button located down-left to indicate ‘down’ in one task and ‘left’ in the alternative task. By pressing the second button (located up-right) subjects had to indicate ‘up’ or ‘right’ corresponding to the target position (see Fig. 1). Which task rule to apply was indicated by arrow-cues directing left/right or up/down and being located at the edges of the grid. The task cue and the target were separated in time either by a cue-target interval (CTI) of 100 ms (condition CTI-100) or by a cue-target interval of 2000 ms (condition CTI-2000).

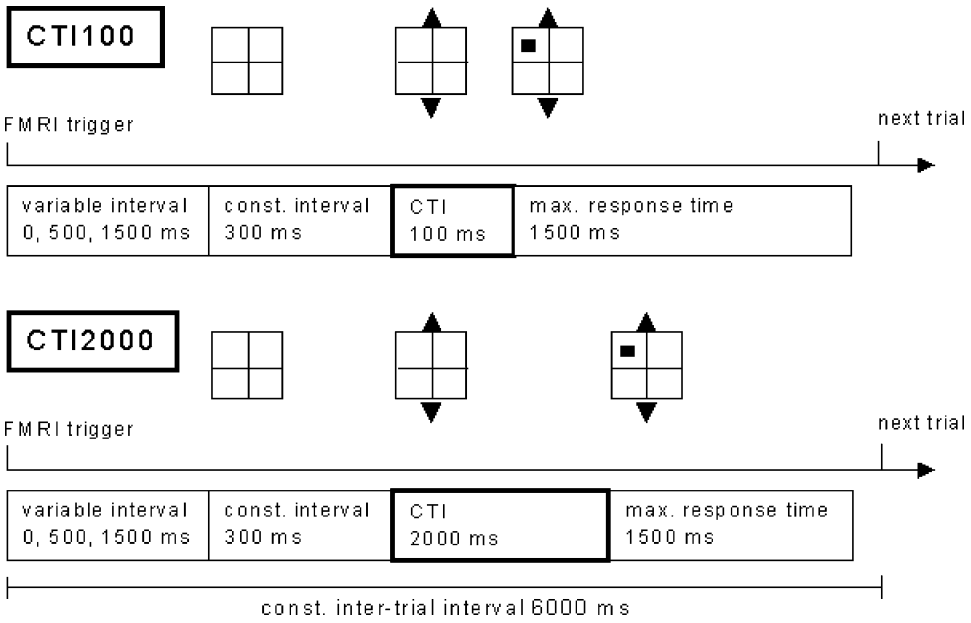

Fig. 1. Timing for the cue-target interval of 100 ms (CTI-100) and for the cue-target interval of 2000 ms (CTI-2000). In the left-right task subjects had to decide whether the small square appeared on the left or right side of the two-by-two grid. The up-down task required to indicate the position of the target on the vertical dimension. Which task to perform was indicated by arrow cues at the edge of the grid (the picture gives an example for the up-down task).

We did not vary the CTI independently from the response-target interval (RTI) as done in the original procedure (Meiran, 1996). Meiran, Chorev, and Sapir (2000) could show that the behavioral switch cost was only minimally affected by the inter-trial interval beyond an interval of 1 sec. However the benefit of a prolonged CTI was much more pronounced. In the present experiment the RTI varied within a relative large range (4–9 s), a period much longer than required for reaching asymptotic levels of behavioral switch cost. Moreover, this variation is considerably larger as compared to the CTI variation (100 or 2000 s). Thus, confounding CTI with RTI is supposed to be negligible.

At CTI-100, no or minimal advance task preparation should be possible before target presentation whereas at CTI-2000 subjects are supposed to have enough time to prepare for the next task in advance. In order to focus attention on the upcoming trial, the empty grid was displayed 300 ms before cue presentation. The final arrangement of grid, cue and target was maintained until response execution or timeout after 1500 ms. The timing of the sequence of trials was triggered from the MRI control every 6 s. The trials started with a variable over-sampling interval of 0, 500 or 1000 ms (time-to-repetition (TR) was 1.5 s) in order to obtain an interpolated temporal resolution of 500 ms (Josephs, Turner, & Friston, 1997). According to the TR of 1.5 s one data point is measured every 1.5 s and with 'jittering' the trial onset relative to the acquisition of the BOLD signal, the trial-related BOLD response is effectively measured at a greater number of different time points. Thus, a more accurate estimate of the time course can be achieved.

We implemented 128 experimental trials resulting in approximately (due to excluded error trials) 32 trials for each combination of the two independent variables preparation interval (CTI-100 versus CTI-2000) by task transition (switch versus repeat). The balanced number of 32 trials per condition (prior to the exclusion of error trials) was obtained by pseudo-randomization. We controlled for balanced absolute frequencies of the single tasks (approximately 64 trials each), the single target stimuli (approximately 32 trials each), the single responses (approximately 64 trials each). Furthermore, an equal number of the three over-sampling intervals (approximately 11 each) was pseudo-randomly assigned to the combinations of task transition and preparation interval. We created different trial sequences for each subject.

We also included 16 null-event trials pseudo-randomly interspersed (minimal distance of five trials between successive null-events). Pseudo-randomization guaranteed that the number of null-events following the four combinations of task transition and preparation interval was balanced. Following a null-event trial, we inserted a dummy trial which did not enter into the analysis. Depending on the temporal structure of the adjacent experimental trials, the duration of the no-stimulation period varied between 6.5 and 12 s. The null-events served as a baseline condition for comparison with the experimental conditions. Errors were followed by a feedback displayed for 700 ms. Error trials were not repeated and together with the following trial excluded from the analysis.

The conditions described above were realized as one block within a sequence of two different experimental blocks. The companion block is not analyzed or discussed in the present article. The results of a block comparison can be found elsewhere (Brass et al., 2003). The other block contained trials with 'univalent responses' (Meiran, 2000) as compared

to 'bivalent responses' used in the present block of interest. The order of blocks was balanced across subjects. In order to exclude transfer-effects, some analyses (specified below) were restricted to those 11 subjects (mean age 26.5, range 21–35, five female) who performed the relevant (i.e. bivalent response) block first. Both blocks were introduced to the subjects prior to the fMRI scanning procedure by presenting 20 practice trials each. Prior to the functional recording of each block, subjects performed another 60 practice trials with a short and constant response-cue interval of 800 ms.

2.3. FMRI procedure

The experiment was carried out on a 3T scanner (Medspec 30/100, Bruker, Ettlingen). Sixteen axial slices (19.2 cm FOV, 64 × 64 matrix, 5 mm thickness, 2 mm spacing) were acquired parallel to the AC–PC plane and covering the whole brain. We used a single shot, gradient recalled EPI sequence (TR 1500 ms, TE 30 ms, 90 flip angle). Prior to the functional runs, corresponding 16 anatomical MDEFT-slices and 16 EPI-T1 slices were acquired. Stimuli were displayed on a back-projection screen mounted in the bore of the magnet behind the participant's head by using an LCD projector. Participants viewed the screen by wearing mirror glasses.

2.4. Functional whole-brain-analysis

2.4.1. Pre-processing

The analysis of the fMRI data was performed using the LIPSIA software package (Lohmann et al., 2001). To align the functional dataslices with the Talairach 3D stereotactic coordinate reference system (Talairach & Tournoux, 1988), a rigid linear registration with six degrees of freedom (three rotational, three translational) was performed. The rotational and translational parameters were obtained on the basis of the MDEFT and EPI-T1 slices. The parameters were subsequently transformed to standard Talairach brain size by linear scaling. The resulting parameters were then used to transform the functional slices by using trilinear interpolation, so that the resulting functional slices were aligned with the stereotactic coordinate system. The functional data were first corrected for movement artifacts. Furthermore, the temporal offset between the slices acquired in one scan were corrected by using a sinc-interpolation algorithm. Data were smoothed using a spatial Gaussian filter with FWHM = 5.7 mm. A temporal highpass filter with a cutoff frequency ranging between 1/132 and 1/192 Hz was used for baseline correction. Considering the 'design frequency', the cutoff-frequency was determined for each subject individually, according to the maximal pairwise temporal distance of trials for the experimental condition with this distance being minimal. Both the analysis of whole-brain contrasts and the analysis of trial-averaged time courses were performed after these pre-processing steps had been finished.

2.4.2. Whole-brain contrasts

For the computation of whole-brain contrasts, we used the general-linear-model for serially auto-correlated observations (Friston et al., 1995). The design matrix for event-related analysis was based on a model of the hemodynamic response with a variable delay of the BOLD function (Friston et al., 1998).

The onsets of the single model BOLD responses for the construction of the model regressors were synchronized with the presentation of the task cue. We obtained highly similar results irrespective of either performing a target-locked or a cue-locked synchronization and also irrespective of the number of basis-functions included. This demonstrates the expected insensitivity of this method for differential contributions of within-trial events. Thus, any effect revealed in this analysis reflects the sum of effects caused by cue-related and target-related processing.

To meet a prerequisite of the multiple linear regression, the model equation including the observation data, the design matrix, and the error term, was convolved with a Gaussian kernel with a dispersion of 4 s FWHM. Contrast maps were generated for each subject. A one-sample *t*-test of contrast maps across subjects (random-effects-model considering subjects as a random variable) was computed to indicate whether observed differences between conditions were significantly different from zero. Subsequently, *t* values were transformed into *z* scores.

To obtain meaningful values of activation strength for significantly activated regions, we computed percent-signal-change values extracted from the peak amplitudes of trial-averaged time courses (see Section 2.5.2).

2.5. Post-hoc analysis of regions of interest (ROIs)

2.5.1. Temporal analysis of pre-processed trial-averaged time courses

We analyzed trial-averaged time courses in order to examine, whether those brain regions, that showed any switch-related activation difference were either engaged in cue processing, target processing, or both. The time courses were extracted from ROIs, which exhibited a stronger activation for switch than for repeat in the whole brain analysis. The detailed description and discussion of the procedure described below can be found in Ruge et al. (2003).

Below, we are sketching in three steps the basic reasoning behind the method. Firstly, model assumptions are formulated showing that a comparison of onset latencies and peak latencies between CTI-100 and CTI-2000 can provide useful (though not exhaustive) information about whether a brain area is activated by the cue, the target, or both. Secondly, we are describing how jackknife re-sampling can be used to determine and statistically assess onset latencies and peak latencies facing noisy single-subject data. Thirdly, we are describing how we dealt with the problem that BOLD onsets associated with the current trial are 'hidden' within the overlapping BOLD signal originating from the previous trial.

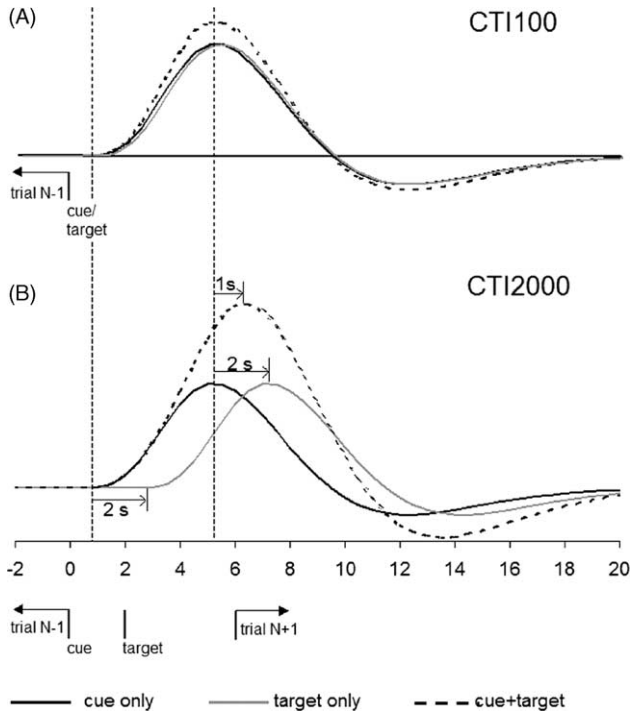

Fig. 2. Schematic model that illustrates how differences between the two cue-target-interval conditions (CTI-2000–CTI-100) of onset latencies on the one hand and peak latencies on the other hand, can be used to decide, whether a brain area is activated cue-locked and/or target-locked. For a full description of the decision scheme see main text. Both graphs (A and B) show three different curves (solid black, solid gray, dotted black) that depict different model time courses of trial-related BOLD activation depending on the differential contribution of one cue-related BOLD component and one target-related BOLD component. Three landmark patterns are illustrated: (i) Purely cue-locked activation (solid black), (ii) Purely target-locked activation (solid gray) and (iii) Combined cue-locked plus target-locked activation (dotted black). Time point zero refers to the onset of cue presentation. The *x*-axis is in units of seconds. Graph A depicts the situation for the cue-target interval of 100 ms (CTI-100). Graph B depicts the situation for the cue-target interval of 2000 ms (CTI-2000). The arrows illustrate the shift of both the onset latencies and the peak latencies at CTI-2000 referenced to the corresponding latencies at CTI-100.

2.5.1.1. Model assumptions. Fig. 2 depicts a schematic demonstration based on the assumption of two BOLD components associated with either the task cue or the target stimulus. Three different idealized landmark time courses of the trial-related BOLD response were constructed corresponding to a purely cue-locked activation (solid black), a purely target-locked activation (solid gray), and a combined cue-locked plus target-locked activation (dotted black).[1] These three patterns of trial-related BOLD activation are depicted for CTI-2000 (B) in relation to CTI-100 (A).

Fig. 2(A) shows that for CTI-100, each of the three landmark time courses has roughly comparable temporal characteristics as parameterized by onset latencies and peak latencies. Thus, onset latencies and peak latencies obtained for CTI-100 can be used as reference values which are not affected by the underlying event structure (i.e. despite of a purely cue-locked, a purely target-locked, or a combined activation). This is different for CTI-2000 (Fig. 2(B)) where onset latencies and peak latencies do depend on the underlying event structure. Thus, by comparing onset latencies and peak latencies at CTI-2000 to the reference values obtained for CTI-100, we are able to gain information about the underlying event structure.

Our schematic demonstration suggests an clear differentiation between the three landmark time courses that were considered. First, a purely cue-locked activation can be described by both equal onset latencies and equal peak latencies for both CTI conditions. Second, a purely target-locked activation is characterized by both a shift of onset latencies and a shift of peak latencies of about 2 s for CTI-2000 referenced to CTI-100. Third, a combined cue-locked plus target-locked activation is characterized by a relative shift of onset latencies of zero and a relative shift of peak latencies of about 1 s. In Ruge et al. (2003) we exemplified the validity of the general assumptions by demonstrating the expected temporal characteristics for visual cortex (cue-locked plus target-locked) and motor cortex (target-locked).

2.5.1.2. Limitations. First of all, the method relies on variable temporal offsets between two different event types (in the present experiment 100 ms versus 2000 ms offset between cue and target). Because the subjects' response is synchronized with the presentation of the target stimulus, these two events can in principle not be separated. Hence, referring to a 'target-locked' activation always means 'target/response-locked' activation.

Furthermore, in the case of a combined cue-locked and target-locked activation two questions can not be answered based on this decision scheme. First, it is not possible to quantify the relative contribution of each sub-component. Second, and related to the first limitation, it is also not possible to assign relative activation differences between switch and repeat to either of both sub-components.[2]

[1] When two events occur in close temporal succession, the BOLD activation induced by the second event is being increasingly suppressed the closer the events are spaced. At CTI-100, where cue and target are separated by only 100 ms, the target-induced BOLD activation can be assumed to be almost completely suppressed when the same brain area has been activated by the cue 100 ms before (Glover, 1999). See Fig. 2(A), where the combined cue/target activation (dotted black) is much smaller then would be expected for just adding up the two separate components. At CTI-2000 this suppression can be assumed to be much less pronounced (Dale & Buckner, 1997; Glover, 1999). See Fig. 2(B), where the combined cue/target activation (dotted black) approximately corresponds to the sum of the two separate components.

[2] These limitations could theoretically be overcome by counterbalancing the transitions between cue and target (Burock, Buckner, Woldorff, Rosen, & Dale, 1998). However, given the present experimental design, this is logically not possible for the cue always has to precede the target. Another option would be to vary the cue-target interval more widely, e.g. between 1 and 12 s (Toni et al., 2001). However, this (a) reduces the number of trials that can be presented given a limited amount of measurement time and (b) possibly introduces a strong working memory component and other uncontrolled intervening cognition.

In conclusion, given the experimental design we chose, the method we propose here, appears to be the only way to extract meaningful (though not complete) information about the underlying event structure from the observed BOLD response.

2.5.1.3. Jackknife resampling. In order to implement a quantitative analysis of onset latencies and peak latencies, we applied jackknife statistics, a procedure that has been successfully applied for similar problems arising in research based on event-related electrocortical potentials (Miller, Patterson, & Ulrich, 1998). The advantage of jack-knifing is that the parameters of interest are identified in time courses averaged across subjects (grand-averages). Thus, noise is reduced to an extent that allows to identify the relevant features reliably without any loss of data (e.g. as compared to smoothing single-subject data with broad filters). Estimation errors are obtained via the jackknife re-sampling procedure (Miller, 1974; Miller et al., 1998). Jackknife re-sampling provides an elegant tool to create a statistical distribution from grand-averaged values. Each of N subjects is excluded from grand-averaging once. The resulting distribution of N grand-averages (each omitting a different subject) can then be used to calculate estimates of standard-errors or other statistics. For our purposes we applied the appropriate algorithms for assessing means and mean-differences.

2.5.1.4. Considering inter-trial overlap of the BOLD signal. In Fig. 2 the trial-related BOLD activation is shown in isolation, not considering that this signal is embedded within activation that persists from trial $N - 1$ and activation that is associated with trial $N + 1$. As the inter-trial interval was only 6 s, a strong overlap of BOLD activation of successive trials has to be considered (Fig. 3).

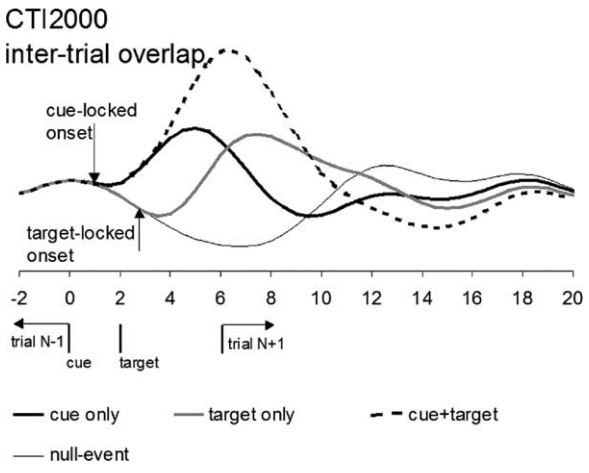

Fig. 3. Same as Fig. 2(B) but considering inter-trial overlap of the BOLD signal. The black dashed curve represents the null-event time course showing a passive decay of the activation associated with the previous trial. Onsets of the time courses associated with the experimental conditions CTI-100 and CTI-2000 are determined via the inflection point of the curves.

As being exemplified in Fig. 3, the onset of the trial-related BOLD response under investigation is hidden within the decreasing flank of the BOLD response associated with the previous trial. We considered the inflection point after the peak of the previous trial as being an appropriate measure of the onset of the BOLD response associated with the trial of interest. We did not use the time course of the null-event condition as a reference as it turned out that in particular this signal contained a high level of noise (only 16 trials per subject).

2.5.1.5. Concrete computations. To obtain the inflection point, we computed the interpolated accurate time-point when the second derivative crossed the x-axis within a time-window of 0–4000 ms. This was done separately for each jackknifed grand-average. The resulting values were then used to calculate standard errors via an appropriate jackknife algorithm.

Interpolation proceeded in two steps. First, we linearly interpolated the original individual time courses (Lohmann et al., 2001) resulting in one point every 125 ms (considering 500 ms oversampling due to variable jitter interval). The jackknifed grand-averages were smoothed (discrete gaussian approximation considering one adjacent time point) and derivatives were then obtained by discrete approximation. In a second step of interpolation, the accurate time point of zero-crossing was determined in the jackknifed grand-averaged second derivative. The zero-crossing was obtained by computing the crossing point of the time axis with the straight line which connected the values of two successive time-points. Peak latencies were determined correspondingly by estimating the interpolated zero-crossing of the 1st derivative within a time-window from 3 to 7 s.

2.6. Analysis of percent-signal-change amplitudes in trial-averaged time courses

In order to reveal the detailed structure of significant effects obtained in the whole-brain analysis, we extracted peak-values in units of percent-signal-change (PSC) from trial-averaged time courses. This was done for all those ROIs which showed a significant switch-related effect in the whole brain analysis. The PSC for single-subject trial-averages was referenced to the average signal in absolute units over the whole experimental block (Lohmann et al., 2001). Following this averaging process the signal level for each condition was normalized with reference to a baseline interval of [−0.5 to 0.5 s] to consider the relative deviation from cue onset at 0 s. To obtain discrete PSC-values representing the strength of activation for each single experimental conditions (‘baseline activation’) the difference between the condition-specific peak-value and the corresponding value for the null-event condition was computed. This was done to compensate distortions due to the inter-trial overlap of the BOLD signal. The peaks were identified in grand-average time courses and estimation errors were obtained by jack-knifing.

Table 1
Absolute values (RTs and errors) for the interaction task transition by preparation interval

	Switch (RT)	Repeat (RT)	Costs (RT)	Switch (errors)	Repeat (errors)	Costs (errors)
CTI-100	700.1	616.1	84.0	1.9	0.5	1.4
CTI-2000	572.7	553.8	18.9	1.0	0.2	0.8

3. Results

3.1. Behavioral data

As mentioned in the methods section the scanning session consisted of two different experimental blocks of which only the block with 'bivalent responses' is of interest in the present paper. The sequence of blocks was balanced across subjects implicating that the bivalent response block was either the first one or the second one to be performed by the subjects. In order to check for potential transfer effects we included the between-subjects variable block sequence into the analysis.

We computed an ANOVA including the factors task transition (switch vs. repeat), preparation interval (CTI-100 versus CTI-2000) and block sequence (first position versus second position).

3.1.1. Reaction times

Block sequence produced one marginally significant interaction, namely task transition by block sequence ($F(1, 16) = 3.4$ with $P(F) = .08$), indicating slightly longer RTs for switch compared to repeat if the relevant block was the second one. All three effects related to task transition and preparation interval were significant ($P(F) < 0.001$), including the main effect task transition ($F(1, 17) = 74.6$), the main effect preparation interval ($F(1, 17) = 61.1$), and the interaction task transition by preparation interval ($F(1, 17) = 17.0$). Switch costs were greater for CTI-100 than for CTI-2000 (see Table 1).

3.1.2. Proportion of errors

The interaction task transition by block sequence was significant ($F(1, 16) = 4.8$; $P(F) = 0.04$), indicating more errors for switch compared to repeat if the relevant block was the second one. All three effects related to task transition and preparation interval were significant ($P(F) < 0.05$), including the main effect task transition ($F(1, 17) = 32.3$), the main effect preparation interval ($F(1, 17) = 13.3$), and the interaction task transition by preparation interval ($F(1, 17) = 4.8$). Again, switch costs were greater for CTI-100 than for CTI-2000 (see Table 1).

The general pattern of behavioral results replicates previous observations (Meiran, 1996, 2000). The influence of block sequence on the effect of task transition indicates a transfer effect. To obtain more conclusive imaging results we restricted any analysis, which included the independent variable task transition to those 11 subjects who performed the block of interest first (i.e. both whole brain contrasts).

3.2. Whole-brain activation maps

We report two contrasts, which are relevant with respect to the hypotheses, namely the main effect of task transition and the interaction task transition by preparation interval. These contrasts are suited to reveal any significant switch-related activity present in both or in either of both CTI conditions.

A main effect of task transition was found in two regions (Table 2): the left IFJ ('inferior frontal junction', i.e. the junction of precentral sulcus and inferior frontal sulcus) and the left pSPL (posterior superior parietal lobule).

The interaction contrast of task transition by preparation interval revealed a widely distributed co-activation of parietal and frontal regions (Table 3 and Fig. 4). Importantly, this also included left IFJ and left pSPL, hence further qualifying the main effect of task transition observed for these two areas. The description of percent-signal change peak-values (Fig. 5 right panels) reveals the detailed structure of this interaction which is essentially the same for all brain areas. It appears that stronger activations for switch compared to repeat are evident for CTI-100 but no significant differences are present for CTI-2000.

Furthermore, the description of percent-signal change peak-values indicates baseline effects (compared against null-event activation) both for switch minus null-event and for repeat minus null-event in both CTI conditions (Fig. 5 middle panels). The only exception was the right mIFS (middle inferior frontal sulcus). However, visual inspection of the trial averaged time courses (Fig. 5, left panel, index #1) revealed that this was an artifact of the null event subtraction. In this region the null events were not an appropriate baseline.

3.3. Temporal analysis of pre-processed trial-averaged time courses

We furthermore aimed at assessing whether brain areas with significant stronger activation in switch compared to

Table 2
Brain areas significantly ($P(z) < 0.001$) activated in the main-effect contrast task transition

Index*	Brain region	Abbreviation	Talairach			z-value
3	Left inf. front. junction area	Left IFJ	−41	8	34	3.33
12	Left post. superior parietal lobe	Left pSPL	−16	−65	49	3.37

* Index numbers refer to Fig. 4.

Table 3
Brain areas significantly ($P(z) < 0.001$) activated in the interaction contrast task transition by preparation interval

Index	Brain region	Abbreviation	Talairach			z-value
1	Right middle inf. front. sulcus	Right mIFS	40	24	26	3.34
2	Left middle front. gyrus	Left MFG	−34	26	38	3.42
3	Left inf. front. junction area	Left IFJ	−41	6	29	3.59
4	Left ant. insula	Left aINS	−34	15	2	5.38
5	Right ant. insula	Right aINS	31	18	5	4.04
6	Ant. fronto-median cortex (BA32)	aFMC	4	18	41	4.38
7	Pre-supplementary motor area	Pre-SMA	1	12	50	3.57
8	Left ant. intraparietal sulcus	Left aIPS	−41	−39	38	3.61
9	Right ant. intraparietal sulcus	Right aIPS	49	−45	38	3.51
10	Left post. intraparietal sulcus	Left pIPS	−32	−51	44	3.95
11	Right post. intraparietal sulcus	Right pIPS	22	−57	47	3.60
12	Left post. superior parietal lobe	Left pSPL	−14	−63	50	3.25
13	Right post. superior parietal lobe	Right pSPL	16	−63	50	3.71

Index numbers refer to Fig. 4. See also Table 2.

repeat are generally involved in cue-related processing, target-related processing, or both.

For this purpose, we compared the temporal characteristics of pre-processed trial-averaged time courses for CTI-100 and CTI-2000 (see Section 2). Time courses were averaged across task switch trials and task repeat trials and all 18 subjects were included.

Fig. 5 (left panels) shows the grand-averaged time courses (i.e. trial-averages further averaged across subjects) of all relevant brain areas including the exact difference-

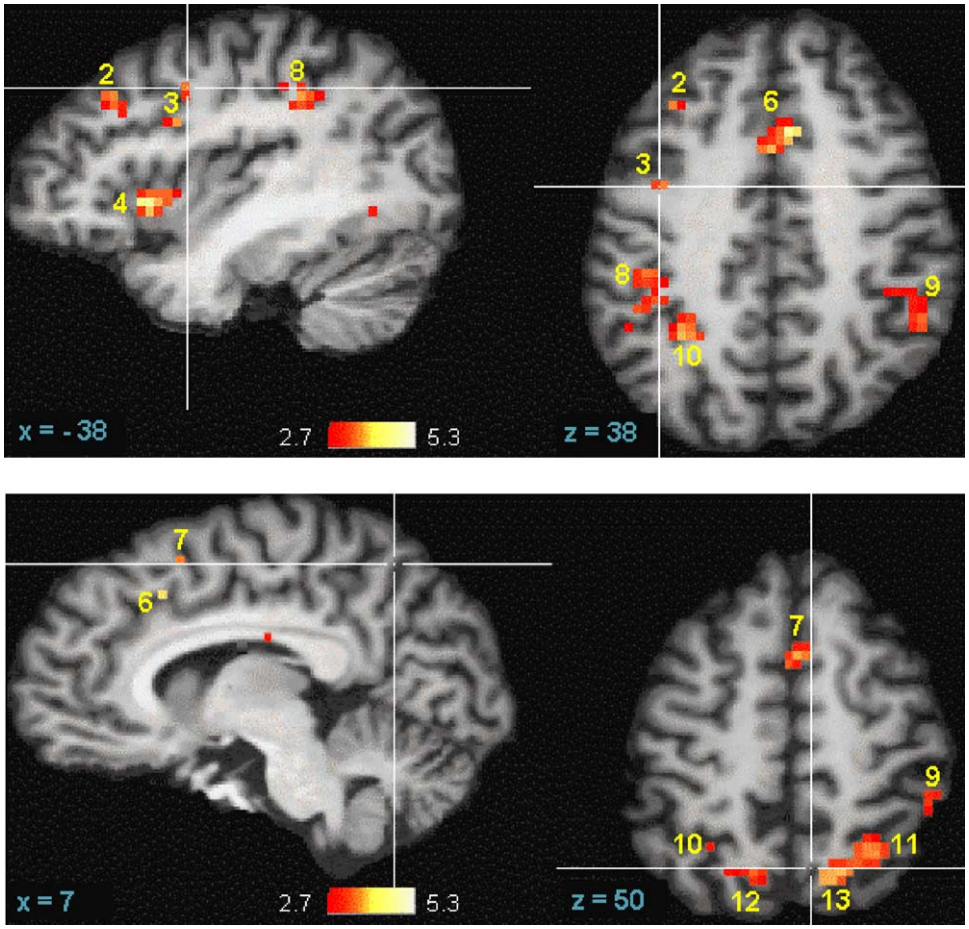

Fig. 4. Visualization of significant activations according to the interaction contrast task transition by preparation interval. The index numbers refer to the brain areas reported in Table 3. The cross-hairs indicate where the brain sections were cut in relation to each other (brain sections depicted on the right hand side compared to the left and vice versa).

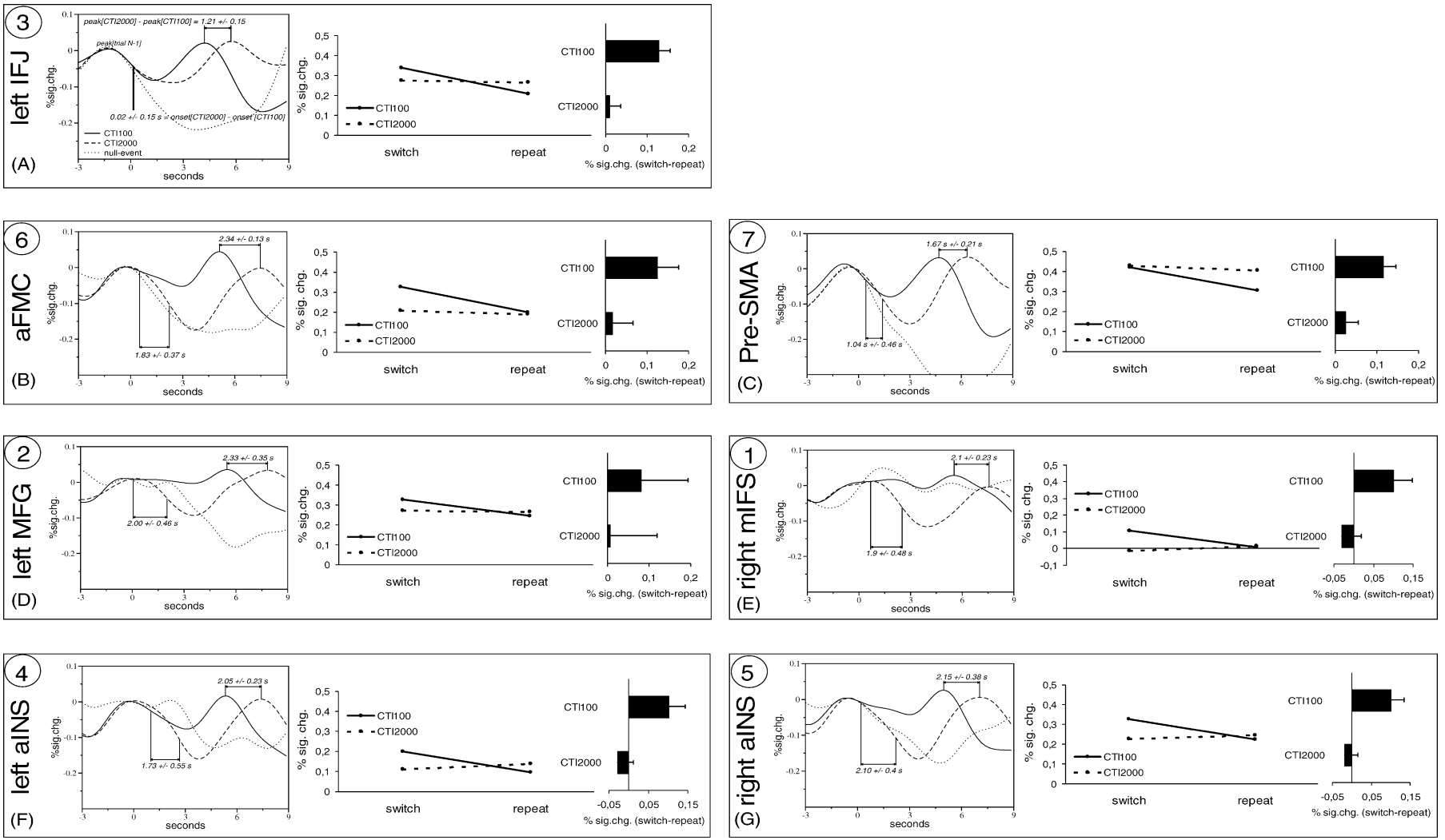

Fig. 5. Summary of the detailed analyses for all those brain areas that showed a significant effect of task transition by preparation interval in the whole-brain analysis. The encircled index numbers refer to the arrangement of brain areas in Table 3 and Fig. 4. Left panels: the depicted curves represent the grand-average time courses for CTI-100 (solid), CTI-2000 (dashed), and the null-event condition (dotted). The most upper-left panel (left IFJ, index number 3) highlights the relevant landmarks to be considered (onsets and peaks). Time point zero refers to the onset of cue presentation. Three different temporal activation patterns were observed: (i) cue-locked plus target-locked activation, i.e. same onset latencies for both CTI conditions paralleled by shifted peak latency at CTI-2000, observed for left IFJ, left/right pIPS, and left/right pSPL. (ii) purely target-locked activation, i.e. shifted onset latency (∼2 s) and shifted peak latency (∼2 s) at CTI-2000, observed for aFMC, left/right INS, left MFG, right mIFS, and left/right aIPS. (iii) An in-between pattern observed for pre-SMA. Middle panels: maximal percent-signal-change values extracted from trial-averaged time courses separately depicted for each single experimental condition relative to the null-event. Right panels: condensed version of the middle panel to highlight the relevant structure of the interaction contrast task transition by preparation interval. The error bars indicate the standard-error of the percent-signal-change difference-values for switch—repeat for each CTI condition.

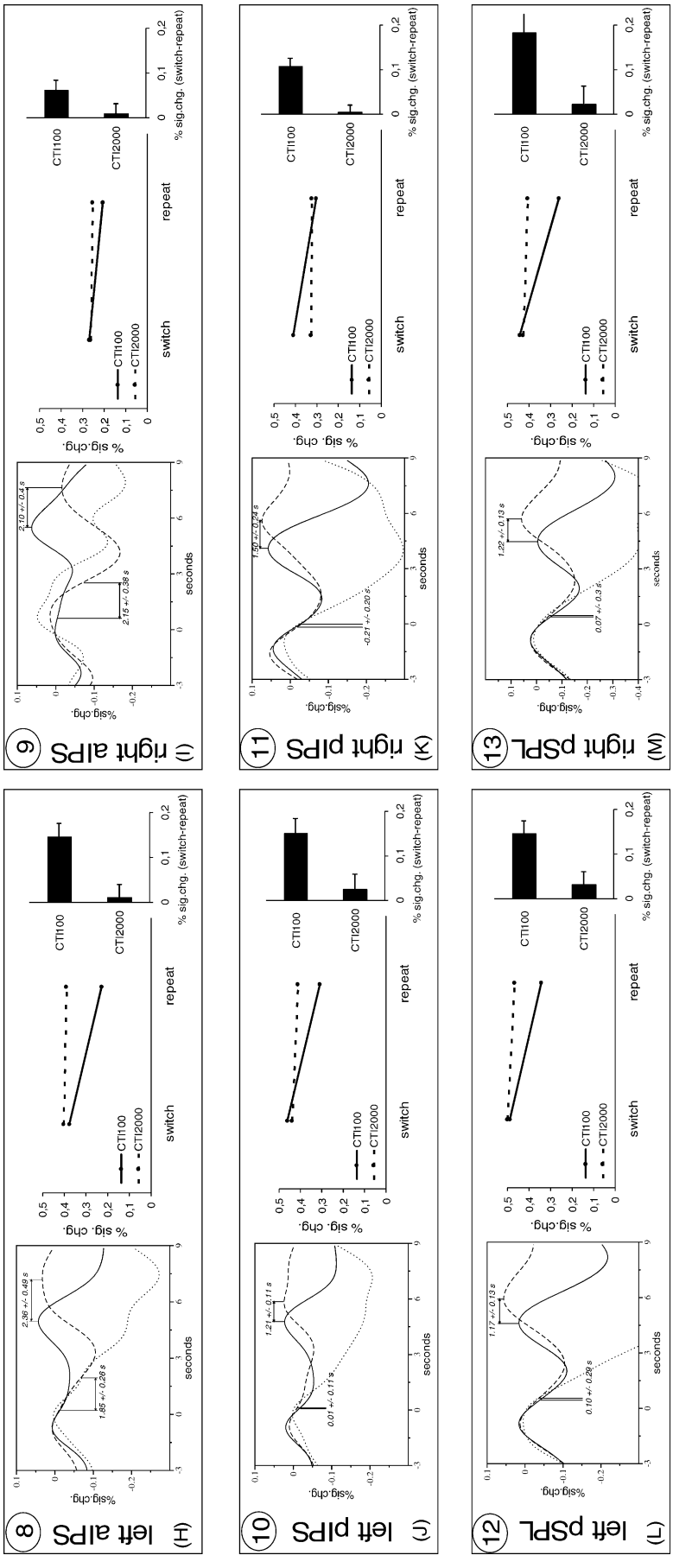

Fig. 5. (*Continued*).

values of onset latencies and peak latencies (±standard-error).

Brain areas that are activated time-locked to cue presentation are indicated by equal onset latencies for both CTI conditions (left IFJ, left/right pIPS, and left/right pSPL). Without exception each of these cue-locked areas is additionally activated target-locked, as being indicated by shifted peak latencies for CTI-2000 relative to CTI-100.

Brain areas that are activated purely target-locked are indicated by shifted onset latencies of about 2 s for CTI-2000 relative to CTI-100 (left MFG, right mIFS, aFMC, left/right INS, left/right aIPS).

The pre-SMA shows an in-between pattern with a difference of onset latencies of 1 s. This result is interpreted as BOLD activation that is elicited in anticipation of the upcoming target/response but triggered by predictive information delivered by the task cue.

Brain areas that showed a pattern of equal onset latencies and shifted peak latencies were classified as being activated cue-related and additionally target-related. However, there are two alternative interpretations that might potentially account for this pattern. While this pattern unequivocally indicates that neural activity at CTI-2000 does not cease after an initial cue-triggered BOLD response (otherwise peak latencies would be equal), it is ambiguous how exactly (neural) processing might have continued.

First, sustained neural activity during the 2 s preparation interval would also delay the peak latency at CTI-2000. However, we think this possibility is unlikely for the reason that the experiment was explicitly designed to avoid working memory to be necessary for maintaining the memory trace of the cue. On the one hand, the cue was displayed throughout the entire 2 s interval, and on the other hand, the CTI was comparably short. Thus, a transient cue encoding process should be sufficient to provide subsequent processing steps with the required cue-associated information.

Second, a preparation process with an onset that randomly varies between the time of cue presentation and the time of target presentation would also be reflected by equal onset latencies and a shifted peak latency at CTI-2000. Again, we think the present design is against this interpretation. One important argument for using cued task switching procedures (in particular compared to endogenous control procedures like the alternating runs paradigm) is that the preparation onset is thought to be well controlled by presenting the external task cue. Thus, task preparation in cued task switching is supposedly not subject to 'deliberate' decisions about when to start it. A possible scenario that to some degree assumes 'deliberate' temporal control, is that a preparation process is timed such that an optimal, internally determined preparation interval (e.g. 1 s instead of 2 s) is achieved. In this case, the CTI-2000 BOLD onset latency should be delayed as we observed for the pre-SMA. Moreover, the variability of this onset should be increased (due to the more variable internally driven time estimation) as is the case for the pre-SMA where the standard error for onset latencies is about twice as large as for the other cue-related brain areas.

In conclusion, we favor an interpretation that explains the temporal activation pattern for left IFJ, left/right pIPS, and left/right pSPL in terms of one initial, transient cue-locked BOLD response which merges with a subsequent transient target-locked BOLD response. In contrast, the pre-SMA might indeed be engaged in a more distributed kind of task preparation which depends on internally determined time estimation, thus being distributed over an interval ranging from 1 to 2 s after cue onset (peak latency is shifted by 1.67 s as compared to a shifted onset latency of 1.06 s).

4. Discussion

The aim of this study was to further elaborate how advance task preparation contributes to the flexibility of human behavior observed in task switching situations. Two different scenarios were sketched in the introduction which led to diverging predictions how advance task preparation should be reflected in BOLD activation. While both accounts agree that advance task preparation essentially means to establish the currently appropriate task set prior to the presentation of the target stimulus, the conditions under which this happens are fundamentally different implicating different control demands.

According to the first scenario, establishing a changed task set in switch trials faces proactive interference from the persistently activated misleading $N-1$ task set. Thus, additional control effort has to be applied to overcome this interference during the preparation interval (cf. 'advance task set re-configuration').

According to the second scenario, between-task interference is to be expected only after target presentation but not during the preparation interval because it is the current target stimulus that retrieves the previous and potentially conflicting task set. Thus, establishing a changed task set in advance does not require additional control effort. Virtually as a by-product, this also reduces the need for additional control during task implementation which would otherwise (at CTI-100) be required to overcome target-induced between-task conflict.

Our fMRI results confirm those obtained by other studies on explicitly cued task switching in showing enhanced activation for switch trials compared to repeat trials with short CTIs (Brass & von Cramon, 2004; Dove et al., 2000) but not with long CTIs (Brass & von Cramon, 2002, 2004; Braver et al., 2003; Dove, 2000; Luks et al., 2002).

We found several frontal (left IFJ) and parietal brain areas (bilateral pIPS, bilateral pSPL) that showed this CTI-100-specific switch-related activation while being engaged both cue-related and additionally target-related at CTI-2000.

We also found several frontal (left MFG, right mIFS, bilateral insula, aFMC) and parietal brain areas (bilateral aIPS) that showed the CTI-100-specific switch-related activation while being engaged purely target-related at CTI-2000.

We did not find any brain area that was engaged purely cue-related. No brain area was exclusively activated in switch trials (see also Dove et al., 2000; Dreher, Koechlin, Ali, & Grafman, 2002; Sohn et al., 2000).

The absence of enhanced activation in switch trials for the long CTI condition intuitively contradicts the notion that additional control effort is being raised during the preparation interval to overcome proactive interference from a persisting $N-1$ task set. This holds in particular for brain areas that are associated with cue processing, i.e. brain areas that are likely to be involved in advance task set re-configuration.

In contrast, our results confirm both the notion of task preparation being common to both switch and repeat trials (cf. Gilbert & Shallice, 2002; Goschke, 2000; Wylie et al., 2003) and the hypothesis that proactive interference is mediated by the target-induced re-activation of the competing task set (Allport & Wylie, 2000; Gilbert & Shallice, 2002; Wylie & Allport, 2000).

4.1. More detailed theoretical considerations

We are now describing in more detail a framework that tries to satisfy the observed pattern of BOLD activation suggesting a rather general role of those brain regions found to be involved in preparatory task control. This functional generality became evident in three brain areas (IFJ, pIPS, pSPL) that exhibited a clear directly cue-locked activation at CTI-2000 suggesting an involvement in advance task preparation. Moreover, these areas were not only engaged in preparatory cue-related processing but showed, (a) an additional target-related activation at CTI-2000 and (b) were also activated at CTI-100 where advance task preparation was not relevant. In addition, these areas exhibited at CTI-100 an enhanced activation in switch trials suggesting an involvement in the control of between-task interference. How does the scenario we sketched earlier relates to the general role these brain areas seem to play?

The basic aspect was the assumption that two interacting sources of information are involved in the specification of the current task set. On the one hand, there is the task cue that delivers definite information about the currently relevant task relying on unequivocal cue-task associations. On the other hand, there is the current target stimulus that retrieves the task set under which the stimulus itself, or any other stimulus sharing features of the previous task dimension[3] (cf. Waszak et al., in press) has been processed recently.

We suggest that the initial cue-locked activation reflects the encoding of the cue-associated task information by the posterior lateral prefrontal cortex (IFJ), which in turn is setting up parietal brain areas (pIPS, pSPL) being concerned with more basic task implementation issues. This fronto-parietal division of labor is based on the very general assumption of parietal cortices coding 'pragmatic stimulus properties' (i.e. how to utilize visual information for action) (Goodale & Milner, 1992) and fronto-lateral cortex coding the appropriate 'action context' (Miller & Cohen, 2001) or abstract 'conditional rules' (Monchi, Petrides, Petre, Worsley, & Dagher, 2001; Petrides, 1987). The flow of information is supposed to be directed from frontal cortex to parietal cortex (Miller, Erickson, & Desimone, 1996; Tomita, Ohabayashi, Nakahara, Hasegawa, & Miyashita, 1999).

In particular the concept of 'conditional rules' appears to be suited to specify what 'action context' means in the context of cued task switching where one out of two possible tasks has to be selected given one out of two different external cues. Interestingly, the specific prefrontal brain area we found to be engaged is consistently reported in other explicitly cued task-switching studies (Brass & von Cramon, 2002, 2004; Dove et al., 2000) and studies investigating more general aspects of implementing externally triggered abstract rules (Bunge, Kahn, Wallis, Miller, & Wagner, 2003; Koechlin, Ody, & Kouneiher, 2003)

The processes this fronto-parietal network is running through are supposed to be the same for repeat and switch trials: Activating the prefrontal context representation (cue-related activation) and utilizing this information for the control of basic task-related processes (additional target-related activation). When a strong influence of the target-associated competing task set at CTI-100 challenges appropriate task implementation, the same brain areas are in higher demand to enforce the cue-associated task set.

Why is it the cue-associated task set that is determined to win the competition against the inappropriate target-associated task set in switch trials? Regarding the rather unspecific processing architecture proposed above, this does not seem self-evident.

One reason is that the task set under which target(dimensions) are being processed changes during the sequence of trials. Thus, the association between target(dimensions) and task sets is supposed to be weaker than the unchanged cue-task associations. In fact, only a small bias in favor of either of both associations between target(dimensions) and task sets (the most recently reinforced) is to be expected. However, as the results for CTI-100 demonstrate, the misleading target-induced task set can still impair performance in switch trials resulting in prolonged response times and elevated BOLD activation for switch trials.

At this point, the role of advance preparation comes into play. Again, a special module or mode of advance preparation does not suit the proposed unspecific processing architecture. Therefore, just temporal priority is introduced as an

[3] The notion that target-task associations are generalizing to task-specific target-dimensions is important to explain trial-by-trial effects. Accordingly, any target stimulus (not only a repeating identical stimulus) in trial N is able to retrieve the $N-1$ task set. In the present experiment one target-dimension is the horizontal alignment of the target and the other dimension is the vertical alignment of the target. For instance, if the current target appears in left-upper position and the previous task was to make a 'left-right' judgment, the current target 'reminds' the subject of doing the left-right task again even if the previous target was presented in the right-lower position.

additional aspect (cf. Gilbert & Shallice, 2002). When the task cue is presented sufficiently early before the target stimulus, the cue-associated task set has time to settle into a stable state as specified by the task cue. Consequently, the target stimulus loses its potential to re-activate the previous task set although the strength of the target-task association has not been directly affected (e.g. in terms of re-configuring the target-task association). Thus, behavioral switch cost decreases and a change of the task does no longer pose an additional challenge for the fronto-parietal network indicating that the cue-associated task set does not need to be particularly enforced anymore (see also Koch & Allport, submitted for publication).

While this fronto-parietal preparation-related network is mediating the reduction of target-induced interference, interference-related processing demands posed on other purely target-locked task-implementation-related brain areas (MFG, mIFS, aFMC, and aIPS) are also relaxed as being reflected by the reduction of switch-related BOLD activation at CTI-2000 compared to CTI-100.

The involvement of the pre-SMA, however, is not fully clear. The temporal activation pattern of the pre-SMA is characterized by a one-second shift of the onset-latency at CTI-2000, indicating that activation starts in the middle of the preparation interval. This pattern suggests a temporal decoupling from external stimulation, but nevertheless this activation is supposed to be related to information carried by the cue, simply because no other information is available at this point in time. According to the literature, the pre-SMA might process cue information in anticipation of the upcoming target for the purpose of tuning the response-system in accordance with the currently relevant action context (Cunnington, Windischberger, Deecke, & Moser, 2002; Rushworth, Hadland, Paus, & Sipila, 2002). This is congruent with the view that the pre-SMA is engaged in order to cope with the anticipated competition between alternative response options (e.g. Ullsperger & von Cramon, 2001). Importantly, the temporal dissociation of pre-SMA and left IFJ further extents the finding of Brass and von Cramon (2002) who found both areas being undistinguishable (due to methodological constraints) involved in the same kind of cue-related task preparation.

The interpretation that advance preparation means to activate cue-task associations without directly affecting target-task associations suggests that these two types of associations are represented independently of each other. While cue-task associations might be encoded as abstract 'conditional rules', target-task associations might be more closely attached to concrete task representations or might be fixed in episodic memory traces (Waszak et al., 2003). This notion bears some relation to a proposal which distinguishes between a 'goal-activation' process (activating the cue-task association) and a 'rule-implementation' process (susceptible to target-induced re-activation of the $N-1$ task set) operating during task implementation (Rubinstein, Meyer, & Evans, 2001). However, this is an issue that should be addressed in more detail by future studies.

5. Conclusion

We presented an interpretation of the typical pattern of results obtained in fMRI studies of explicitly cued task switching which had been partly unexplained so far and which has often been thought to be incompatible with the typical pattern of behavioral results. The theoretical perspective we adopted is compatible with recent behavioral findings which (1) indicate that advance task preparation does not necessarily incorporate the re-configuration of a persistently activated previous task set and (2) indicate that control is needed to counteract target-induced between-task interference.

Our interpretation is applicable to one important aspect namely how control comes into play when the sequence of tasks is unpredictable and the task cue provides explicit task information. Under more 'endogenous' circumstances (i.e., the task sequence is memory-based) advance task preparation may encounter different demands. Furthermore, this interpretation makes the strong claim that a previously adopted task set decays rapidly implicating that there is no need for task set re-configuration in the current trial. It is likely that there are conditions with a different relationship between decay rate and control demands during the establishment of a changed task set.

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