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Attention, intention, and strategy in preparatory control

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ABSTRACT

The neural mechanisms underlying different forms of preparatory control were examined using event-related fMRI. Preparatory brain activation was monitored in relation to different types of advance information: (1) random task cues indicating which of two possible tasks to perform upon subsequent target presentation; (2) task-ambiguous target stimuli; or (3) targets for which the correct response could be pre-determined. Three types of activation pattern were observed in different brain regions. First, more posterior regions of lateral prefrontal cortex (LPFC) and parietal cortex were activated by both advance task cues and advance targets, but with increased and more sustained activation for the latter. Second, more anterior regions of LPFC and parietal cortex were selectively activated by advance targets. Importantly, in these regions preparatory activation was not further modulated by the availability of advance response information. In contrast, preparatory activation in a third set of brain regions, including medial frontal cortex, reflected the utilization of advance response information, but by only a subset of participants. These results suggest three types of preparatory control: attentional (stimulus-oriented), intentional (action-oriented), and a possibly strategic component that might determine inter-individual differences in response readiness. Notably, the absence of regions selectively or even preferentially activated during cue-based preparation argues against certain conceptualizations of task-selective attention under cued task-switching conditions.

1. Introduction

The ability to plan ahead in time, or prepare in advance, contributes importantly to the successful completion of many of our everyday activities. The ability to prepare prior to committing to the execution of a behavioral response depends on the consideration of (1) changing task priorities and (2) the affordances of potential target stimuli that become present in the environment (Fuster, 2000; Jennings & van der Molen, 2005; Norman & Shallice, 1986). The present study was designed to learn more about the neurocognitive implementation of these two generic aspects of preparatory control, and how such processes enable perception and action to be configured in advance of their actual demand. To this end, we employed the cued task-switching paradigm (Dove, Pollmann, Schubert, Wiggins, & von Cramon, 2000; Meiran, 1996; Monsell, 2003; Sudevan & Taylor, 1987).

In the cued task-switching paradigm, participants perform multiple (usually two) tasks in a randomly alternating manner. Task priority is determined by explicit cues that indicate which task to perform in a given trial. Target stimuli are typically task-ambiguous, suggesting actions according to multiple task rules which had been instructed prior to the start of the experiment. In the present study participants performed randomly intermixed letter and digit tasks (consonant/vowel or odd/even classification, with judgments indicated by a two-choice manual button press response). The target stimuli were always task-ambiguous, consisting of a letter-digit pair (e.g., A 2). Behavioral studies of cued task switching have investigated preparatory effects by presenting the task cue in advance of the target, at various intervals, in order to examine the impact of various experimental variables (Monsell, 2003). Likewise, cognitive neuroscience studies have investigated the neural mechanisms of preparation by isolating brain activity following advance task cues (Brass & von Cramon, 2002; Braver, Reynolds, & Donaldson, 2003; Bunge, Kahn, Wallis, Miller, & Wagner, 2003; MacDonald, Cohen, Stenger, & Carter, 2000; Nicholson, Karayanidis, Poboka, Heathcote, & Michie, 2005; Ruge et al., 2005; Rushworth, Passingham, & Nobre, 2002; Sakai & Passingham, 2003).

It is also possible to reverse the order of events such that task-ambiguous target stimuli are presented in advance of the task

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cue. Yet surprisingly, this preparatory paradigm has received little attention in the literature. To our knowledge, there is only a small number of behavioral studies examining the advance target condition during task switching (Gotler & Meiran, 2003, September; Shaffer, 1965, 1966), and no previous neuroimaging studies have been conducted. We believe that the direct comparison of cue-based and target-based preparation has the potential to provide novel insights on several levels. First and foremost it appears desirable to characterize a wider range of preparatory mechanisms that are relevant in multi-tasking situations. The investigation of cue-based preparation approximates one possible real-world scenario in which behavior is planned according to coarsely defined task goals (e.g., to prepare a cup of coffee) without knowing the specific stimulus conditions that might be present at the time of future task implementation (e.g., whether a clean cup will be available). Yet, an equally relevant scenario is captured by the advance target condition that approximates a situation in which new stimuli appear in the environment or enter the focus of attention (e.g., seeing an empty cup on the counter). These target stimuli may activate numerous potential action goals (e.g., a cup to be filled with fresh coffee, or a cup to be put away) even though it is oftentimes not instantly clear which particular action goal will become task-relevant at a later moment in time. Thus, a preparatory mechanism is needed that deals with stimulus-induced 'latent' action goals in a way that ensures optimal performance in case one of them will become relevant for accomplishing a future task.

Beyond the interesting, but purely descriptive characterization of the specific brain systems that implement each type of preparatory control, the comparison of preparatory neural activation in the standard advance cue condition and in the novel advance target condition allows us to tackle at least three conceptually important issues. The first two study aims concern clear-cut hypotheses about the functional significance of brain areas that have previously been shown to be involved in cognitive control processes in task switching. The third aim is more exploratory in nature and concerns a deeper analysis of target-based preparation by contrasting advance targets that do or do not allow for the possibility of unambiguous response preparation prior to the presentation of the task cue.

The first aim of the present study is to further clarify the functional role of certain frontal and parietal brain areas which have previously been shown to be engaged for *preparatory control in the standard advance cue condition*. One possible hypothesis is that such brain areas are *selectively* engaged for processes that are relevant for cue-based preparation, and thus are not engaged during target-based preparation. One such cue-specific process might be to establish attentional selectivity according to the task rule with currently higher priority (cf., Brass & von Cramon, 2004). This process may occur via top-down attentional control that serves to bias lower-level task-related processing pathways to operate preferentially on those target stimuli that match the currently task-relevant perceptual dimension (Meiran, 2000; Wylie, Javitt, & Foxe, 2006; Yeung, Nystrom, Aronson, & Cohen, 2006). In contrast, advance task-ambiguous target stimuli could not be used in this manner, since they lack any information that would allow for selecting one perceptual dimension over the other. Thus, brain areas that are supposed to be involved in the control of task-*selective* attention should remain silent during target-based preparation. Based on results from previous fMRI studies of cued task switching, there are several candidate brain regions that would be expected to show the predicted cue-specific pattern of preparatory activation, including a lateral PFC region located at the posterior end of the inferior frontal sulcus, sometimes referred to as 'inferior frontal junction' (IFJ), the pre-supplementary motor area (pre-SMA), and the posterior parietal cortex (PPC). These regions have shown most consistently preparatory activation following advance task cues (Brass & von Cramon, 2002, 2004; Bunge et al., 2003; Koechlin, Ody, & Kouneiher, 2003; Ruge et al., 2005; Yeung et al., 2006) and were more strongly activated under conditions requiring enhanced attentional control (Derrfuss, Brass, Neumann, & von Cramon, 2005; Ruge et al., 2005; Yeung et al., 2006).

Yet, despite this intuitively appealing hypothesis based on the notion of attentional selectivity, there are alternative views that imply rather different predictions for the same set of brain areas. In particular, the previously reported cue-related activation of IFJ and PPC may not reflect task-*selective* attention per se (i.e., selecting one task-related processing pathway over a competitor based on the priority cue). Instead, it may be that such brain activity more generally reflects the – not necessarily task-selective – top-down activation of task-related processing pathways in order to enable stimulus processing in accordance with the pre-experimentally instructed rules (Bunge, 2004; Bunge et al., 2003). That is, top-down attentional control serves to enable stimulus processing that goes beyond mere perceptual encoding (e.g., encoding the digit '2' as '2'), but proceeds to a stage at which task-related operations are being applied according to the instructed rules (e.g., classifying '2' as even and determining the appropriate response that maps to this stimulus category). Importantly, this theoretical stance implies a prediction that is critically different from accounts which assume a task-selective nature of attention. Specifically, attention-related brain areas, instead of being engaged exclusively for advance task cues, are predicted to be engaged equally or even stronger for advance targets than for advance cues. The reason is that in the advance target case two task-related pathways need to be activated in parallel, as opposed to only one in the cue-first condition (cf., Hübner, Kluwe, Luna-Rodriguez, & Peters, 2004).

So far, we have introduced two opposing predictions concerning the question whether or not *cue-based preparation* might involve distinct processes that are *not* engaged for target-based preparation. Analogously, one can ask whether *target-based preparation* might involve distinct processes that are *not* engaged during cue-based preparation. Answering this question constitutes the second aim of the present study. Indeed, there are reasons to hypothesize that advance target presentation might entail specialized preparatory processes that are distinctly *action*-oriented as opposed to the previously discussed *stimulus*-oriented top-down attentional activation of task-related processing pathways that are triggered by advance task cues and possibly also by advance targets. Such a hypothesis seems appealing under the assumption that advance target stimuli are actually processed according to the instructed task rules, whereas advance cues trigger processes that activate, but do not implement the currently relevant task rule (since there is no concrete stimulus the rule could be applied upon). Consequently, once rule application for the current target pair has led to the specification of response options for the digit and the letter, appropriate actions might be planned in anticipation of their potential implementation in case of future task-relevance.

In the previous task-switching literature such target-related action-planning processes (Brass et al., 2003; Meiran, 2000) have been linked to a conceptual framework in which action plans are conceptualized as representations of intended goals, or anticipated outcomes achieved by executing a particular action (Hoffmann, 1993; Hommel, Musseler, Aschersleben, & Prinz, 2001; James, 1890). Translated into a concrete example, this notion suggests that a target stimulus like '2 A' implies two alternative action plans, one to achieve the goal of 'even classification' (e.g., by pressing the right button) and another one to achieve the goal of 'vowel classification' (e.g., by pressing the left button). In the context of task switching, the relevance of such intentions has been demonstrated by contrasting conditions with univalent vs. bivalent responses. A bivalent response is one that can be used to achieve different goals depending on the currently performed task (e.g., a right button press is used to achieve both even classification and consonant classification).

In contrast, a univalent response only has meaning with respect to a single task. Results by Meiran (2000) suggest that cross-task interference associated with bivalent responses produces distinct behavioral performance costs during task switching. Analogously, an fMRI study by Brass et al. (2003), implementing the same manipulation of response valence, found specifically the mid-DLPFC to be engaged in bivalent conditions, suggesting a role in the 'intentional' control of cross-task interference on the level of action goal representations. Importantly, results from both, behavioral (Meiran, 2000) and imaging studies (Ruge et al., 2005) indicate that the activation of action goal representations (presumably in mid-DLPFC) is triggered by concrete target stimuli, but not by advance task cues.

Nevertheless, these prior results permitted only limited conclusions regarding the role of mid-DLPFC in task-related action planning, since targets occurred in the context of an advance cue condition—that is when action plans were being executed rather than prepared in advance. Yet, if the DLPFC was truly a neural substrate for the internal representation of action plans (i.e., intentions), then this region should show increased activation even when such plans are generated in a purely preparatory context (i.e., the advance target condition).

The third, more exploratory, aim of the present imaging study was to take advantage of a unique aspect of the advance target condition to examine the distinction between abstract action planning and a more concrete form of motor preparation. This is possible because advance target trials can be divided into those that are response congruent and those that are response incongruent. Response congruent letter-digit pairs are special in that they require the same response for both the letter and the digit task (e.g., 'A 3', when both vowels and odd digits require a left button response). In contrast, for incongruent letter-digit pairs different responses are required in the letter and digit tasks (e.g., 'A 2'). Thus, it is possible for congruent, but not for incongruent advance targets, to program a ready-to-execute motor response prior to cue presentation that can later be quickly released without considering which specific task the cue indicates. Indeed, in behavioral pilot studies we found that some participants showed extremely short response times, oftentimes <300 ms, for advance congruent targets suggesting that they had reached a high level of motor readiness prior to cue onset. Yet, surprisingly, in other participants there was almost no performance benefit of congruency, although post-hoc debriefing suggested that even these participants understood the distinction between congruent and incongruent targets.

One explanation for this behavioral pattern is that participants differed in the strategies they used to deal with advance targets. Specifically, those participants who were quick responders for congruent advance targets might rely on a preparatory strategy that attempts to maximize response readiness at the cost of accepting a higher risk of erroneous responding in case of incongruent targets. In contrast, participants who were slow responders for advance congruent targets might engage in only rather abstract action planning processes, and refrain from programming ready-to-execute motor programs. We examined the contrast between congruent and incongruent trials in the brain imaging data to provide more direct evidence for individual differences in task strategy regarding response preparation. Previous work has implicated the dorsal medial frontal cortex (MFC) as being involved in endogenous or volitional generation and/or selection of action plans (Barris & Schuman, 1953; Paus, 2001; Rushworth, Walton, Kennerley, & Bannerman, 2004). Thus, we predicted that this brain region might be importantly related to individual differences in task-related motor readiness in the advance target condition.

Besides the identification of brain areas related to preparatory motor readiness specifically in congruent trials (but not in incongruent trials), it appears similarly important to ensure that it is *not* this unique aspect of congruent advance targets that causes the predicted target-specific preparatory activation in areas like mid-DLPFC. Using a more sensitive regions-of-interest approach we therefore also evaluated whether such brain areas would be modulated by target congruency (possibly depending on group membership as defined above).

2. Methods

2.1. Participants

Twenty-two right-handed human participants with no evidence of neurological compromise took part in this study. All participants gave informed consent according to guidelines set by the Washington University Medical Center Human Studies Committee. The participants were paid US-$25 for each hour of participation. All reported analyses were based on 18 participants (age range 20–29, mean age 23, 7 male, 11 female) who survived the fMRI artifact rejection criteria (2 participants excluded) and who had overall error rates below 30% (2 participants excluded).

2.2. Procedure

The experiment consisted of two different blocked conditions, one involving advance cues and the other involving advance targets. The order of blocks was counterbalanced across participants. The two blocks were practiced (20 trials each) in the same order as the experimental blocks and practice was completed before participants entered the scanner. Each block included three types of trials (see Fig. 1).

In 50% of the trials the first stimulus (S1) preceded the second stimulus (S2) by a randomly chosen long preparation interval of either 1250 ms or 1875 ms (*long S1–S2 delay*). These two intervals were treated as one single condition for the purpose of data analysis. In another 25% of all trials S1 and S2 appeared simultaneously (*zero S1–S2 delay*). These zero delay trials were included in order to examine behavioral effects of preparation (i.e., as a function of preparatory interval duration), but were not a primary focus of the fMRI analyses. In the remaining 25% of trials the S2 was omitted, creating a partial trial condition (*S1-only*). Since responses were only to be made following S2 onset, the S1-only trials had no associated task response. Partial S1-only trials were included to be able to obtain independent estimates for S1-related activation and S2-related activation (see the following section on fMRI data analysis). The inclusion of a relatively high proportion of long S1–S2 delay trials was meant to encourage the use of advance S1 information to prepare for S2 despite the inclusion of zero S1–S2 delay and S1-only trials.

In all trials, the target stimulus consisted of a digit (ranging between 2 and 9) and a letter (vowels A, E, I, U and consonants H, K, N, S) presented left and right to each other (with the relative location of the digit and letter randomly alternating across trials). The task cue was placed centrally between the digit and the letter and consisted of either three vertically arranged copies of 'let' for the letter task cue or three vertically arranged copies of 'num' (for number) for the digit task cue. The particular cue that was presented varied pseudo-randomly from trial to trial so that an equal number of task repeat and task switch trials was obtained for each experimental block in each subject. In the letter task, the target letter had to be classified as vowel or consonant. In the digit task, the target digit had to be classified as odd or even. Digit and letter classification was achieved by manually pressing one of two response buttons on a hand-held response box. Thus, responses were bivalent, in that the same two responses were used in both tasks. One group of participants indicated vowel/odd with a left button press using the left index finger and consonant/even with a right button press using the right index finger. Another group of participants indicated vowel/odd with the right index finger and consonant/even with the left index finger.

Within each trial, the timing and sequence of events was constrained to achieve both, synchronization with fMRI data acquisition cycles (TR = 2500 ms) and increased temporal resolution. Each trial began with a blank interval that randomly varied between 0 and 1875 ms in steps of 625 ms to jitter the actual trial onset relative to the start of fMRI acquisition cycles. This jittering procedure enabled sampling of the trial-related BOLD response at a greater number of different time points relative to trial onset and can thus increase the effective temporal resolution of the BOLD signal (Josephs, Turner, & Friston, 1997; Miezin, Maccotta, Ollinger, Petersen, & Buckner, 2000). As discussed in Section 3, this increase in temporal resolution allowed for a more precise estimation of the duration of BOLD activation associated with S1 and S2 processing. Following the variable blank interval plus an additional constant 325 ms blank interval, a fixation cross ('+' sign) was presented in the center of the screen for 300 ms which alerted participants to the start of the trial. The fixation period was immediately followed by cue and target presentation as described above. Responses were only to be initiated following S2 onset. The cue and target stimulus remained on the screen until a response was executed or until timeout at 1875 ms after S2 onset. Manual responses executed in time were followed by a blank interval until the timeout point was reached. S1-only trials were matched in length to the long S1–S2 delay trials by having the S1 remain on screen until the S2 would normally occur, followed by a blank interval matched to the maximal response window of 1875 ms.

In addition to the 'real' experimental trials, 80 so-called 'null' trials per block were pseudo-randomly interspersed and matched in length to the different exper-

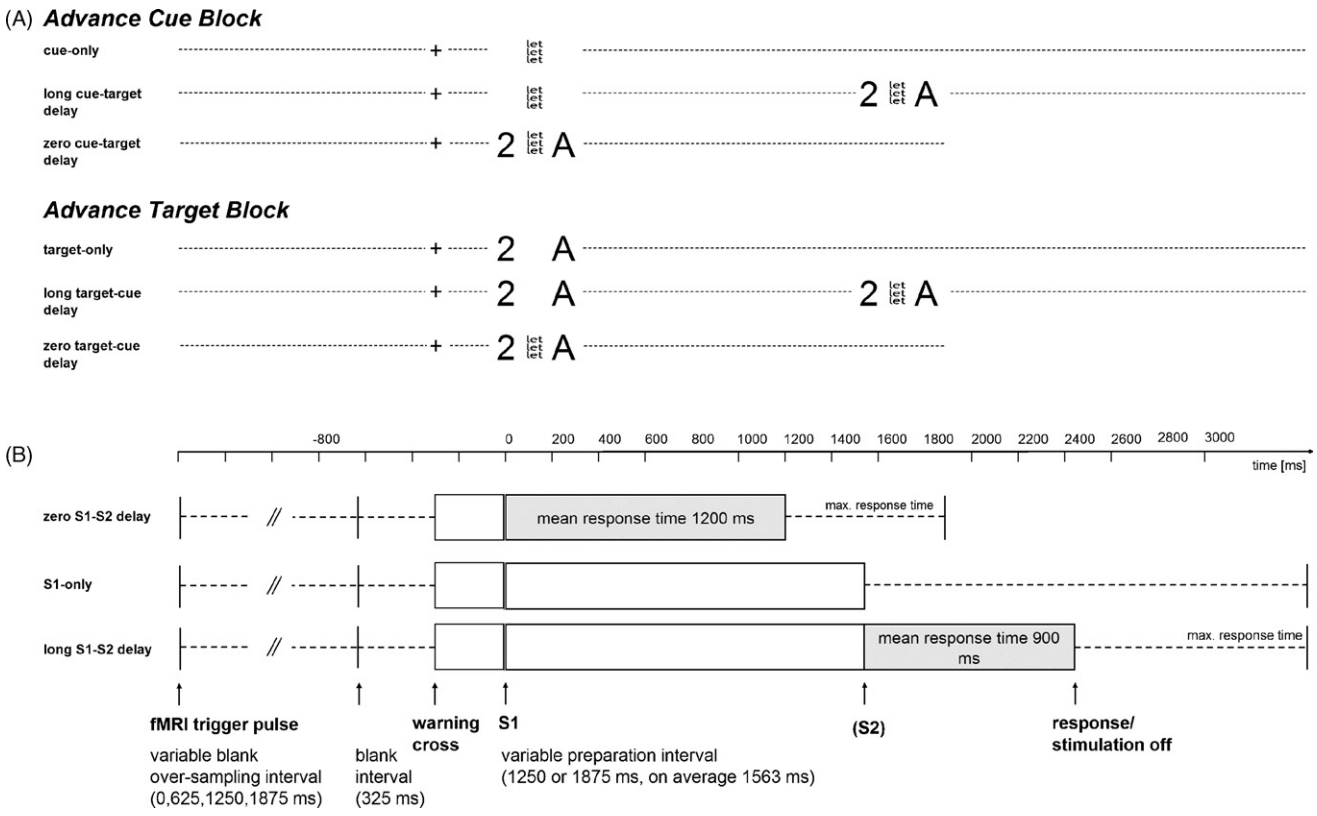

Fig. 1. Stimulation protocol for each of the three main trial types (zero S1–S2 delay, long S1–S2 delay, and S1-only) depicted for exemplary cases (A) and in detail (B).

imental trial types. During these no-event periods the screen remained black. The transitions between all trial types, including null trials, were counterbalanced. Therefore, the length of no-event periods could exceed the length of a single trial considering that a series of multiple null trials could occur in sequence. The use of no-event periods of variable length permitted the isolation of event-related BOLD responses for each of the experimental conditions (Miezin et al., 2000).

2.3. Functional imaging

Whole-brain images were acquired on a Siemens 3 Tesla head-only Allegra System (Erlangen, Germany) with a standard circularly polarized head coil. A pillow and tape were used to minimize head movement. Headphones and earplugs dampened scanner noise and enabled communication with participants. Both structural and functional images were acquired for each participant. High-resolution structural images (1.25 mm × 1 mm × 1 mm) were acquired using an MP-RAGE T1-weighted sequence (TR = 9.7 ms, TE = 4 ms, flip = 12°, TI = 300 ms) (Mugler & Brookeman, 1990). Functional images were acquired using an asymmetric spin-echo echo-planar sequence (TR = 2500 ms, TE = 25 ms, flip = 90°), sensitive to blood oxygen level-dependent (BOLD) magnetic susceptibility. Each volume contained 32, 3.75 mm thick slices (in-plane resolution 3.75 mm × 3.75 mm). Participants performed a total of eight functional scanning runs, which were separated into two blocks of four runs of each preparation condition (advance cue, advance target). The order of these condition blocks was counterbalanced across participants. Each scanning run consisted of 80 trials (320 total trials per blocked condition) and lasted approximately 6 min. The first four images in each run were used to allow for stabilization of magnetization, and hence were discarded. Additionally, the first five task trials of each scanning run were treated as a warm-up, and were excluded from analysis. An approximately 2 min delay occurred between scanning runs during which time participants rested.

Visual stimuli were presented using PsyScope software (Cohen et al., 1993) running on an Apple PowerMac G4. Stimuli were projected to participants with an AmPro LCD projector (model 150) onto a screen positioned at the head end of the bore. Participants viewed the screen through a mirror attached to the head coil. A fiber-optic, light-sensitive key press interfaced with the PsyScope Button Box was used to record participants' responses.

2.4. Data analysis

Behavioral performance data were analyzed for zero S1–S2 delay trials and long S1–S2 delay trials, excluding S1-only trials in which no response was emitted. Trials following errors were excluded. Average response times for each participant were based on arithmetic means computed for each condition of interest, excluding error trials. Error rates for each condition of interest were expressed as a percentage of all trials in that condition.

Functional imaging data were pre-processed prior to statistical analysis according to the following procedures using in-house software. All functional images were first corrected for movement using a rigid-body rotation and translation correction (Friston, Williams, Howard, Frackowiak, & Turner, 1996; Snyder, 1996), and then registered to the participant's anatomical images (in order to correct for movement between the anatomical and functional scans). The data were then temporally realigned using cubical spline interpolation, and temporally interpolated to a rate of one whole-brain image every 625 ms (i.e., TR/4), considering the variable jitter of trial onset time relative to fMRI acquisition onset time described earlier in Section 2.2. The data were then normalized, re-sampled into 3 mm isotropic voxels, and spatially smoothed with a 9 mm full-width half-maximum Gaussian kernel. Participants' structural images were transformed into standardized atlas space (Talairach & Tournoux, 1988), using a 12-dimensional affine transformation (Woods, Grafton, Holmes, Cherry, & Mazziotta, 1998). The functional images were then registered to the reference brain using the alignment parameters derived for the structural scans.

A general-linear model approach (Friston et al., 1995) was employed to determine event-related responses for each voxel by estimating values for consecutive data points within a 15 s hemodynamic response epoch using in-house software (Ollinger, Shulman, & Corbetta, 2001). Thus, given an interpolated temporal resolution of 625 ms, a total of 24 data points were estimated for each specified event type. A first GLM analysis was performed to isolate and compare preparatory BOLD activation elicited by advance cues and advance targets. To this end, three basic event types were defined separately for the advance cue block and for the advance target block, including (1) S1 events occurring in S1-only and long S1–S2 delay trials; (2) S2 events occurring in long S1–S2 delay trials; and (3) S1–S2 events occurring in zero S1–S2 delay trials. Because of our emphasis on neural activity related to preparation, zero delay trials were modeled but were not further analyzed, and will not be reported in the current results (except to serve as a common baseline for the two experimental blocks; see below). The GLM estimation procedure followed the de-convolution method described by Ollinger et al. (Ollinger, Corbetta, & Shulman, 2001; Ollinger, Shulman et al., 2001) and enabled the isolation of S1-related and S2-related activation despite the temporal dependency of both event types. A second GLM analysis was performed to investigate congruency effects specifically for the advance target block. Accordingly, the S1 (advance target) and S2 (cue-second) event types were further split into congruent and incongruent events.

After GLM estimation, the obtained time course estimates for the different event types were submitted to group analysis (in a condensed form, averaged across three consecutive time points) using voxel-wise repeated-measures random-effects ANOVAs. Event-related contrasts are determined in this approach by using time

Table 1
Classification system for five different patterns of preparatory activation.

	ANOVA 1 Main effect time point (S1 = advance cue)	ANOVA 2 Main effect time point (S1 = advance target)	ANOVA 3 Interaction time point X preparation type
(1) Selectively activated by advance cues	Sig. activation $p(z) < 0.001$	No activation $p(z) > 0.05$	Adv. Cue > Adv. Target $p(z) < 0.001$
(2) Preferentially activated by advance cues	Sig. activation $p(z) < 0.001$	Sig. activation $p(z) < 0.001$	Adv. Cue > Adv. Target $p(z) < 0.001$
(3) Selectively activated by advance targets	No activation $p(z) > 0.05$	Sig. activation $p(z) < 0.001$	Adv. Target > Adv. Cue $p(z) < 0.001$
(4) Preferentially activated by advance targets	Sig. activation $p(z) < 0.001$	Sig. activation $p(z) < 0.001$	Adv. Target > Adv. Cue $p(z) < 0.001$
(5) Equivalently activated by advance cues and targets	Sig. activation $p(z) < 0.001$	Sig. activation $p(z) < 0.001$	Adv. Cue <> Adv. Target $p(z) > 0.05$

point as a factor of interest and examining significant effects of this factor (both main effects and interactions with experimental factors). The primary advantage of this approach is that it makes no a priori assumptions about the particular shape of the hemodynamic response (Buckner & Braver, 1999).

To keep the results as concise as possible, we only report activation effects for those brain areas that are typically reported in studies of higher cognitive function, including the lateral prefrontal cortex, the pre-motor cortex, the medial frontal cortex, the pre-supplementary motor area, and the inferior and superior parietal lobules. The application of this criterion in the present study effectively excluded regions in the occipital lobe, the posterior temporal cortex, and sub-cortical structures in the thalamus, the basal ganglia and the brain stem. Furthermore, we only report activation effects for brain areas that exhibited *positive* BOLD amplitudes for the experimental conditions under consideration. Effectively, this criterion excluded areas located in the middle temporal lobe, the temporo-parietal junction area, the superior frontal gyrus, and the anterior fronto-median cortex. An exhaustive list of all identified regions in these analyses is available from the authors, upon request.

2.4.1. Contrasting advance cue vs. advance target activation

The primary aim of our analysis was to examine preparatory BOLD activation associated with advance cues vs. advance targets. To this end, three separate ANOVAs were conducted, including (1) a one-way (time point) ANOVA on the time course estimates for S1-related activation elicited by advance cues; (2) a one-way (time point) ANOVA on the time course estimates for S1-related activation elicited by advance targets; and (3) a two-factorial (time point X preparation type) ANOVA on the time course estimates for S1-related activation elicited by advance cues vs. advance targets. Based on the ANOVA results, we identified voxels belonging to one out of five different classes of activation patterns as depicted in Table 1. Significance tests were thresholded at $p(z) < 0.001$ on the whole-brain level. For example, to be classified as 'selectively activated by advance cues' a given voxel had to exhibit significant S1-related activation for advance cues with $p(z) < 0.001$ AND non-significant S1-related activation for advance targets with $p(z) > 0.05$ AND S1-related activation had to be significantly different for advance cues and advance targets with $p(z) < 0.001$. Image masks based on such logical conjunctions were then used to select relevant voxels from the *z*-maps reported in Table 2 and Fig. 3. For voxels falling into categories 1–4 (advance cue not equal to advance target) we report the masked *z*-map results for the interaction contrast time point X preparation type. For voxels falling into category 5 (advance cue equivalent to advance target) we report the masked *z*-map results for the main effect contrast time point (irrespective of preparation type). To insure that significant differences in preparatory activation for advance cues and advance targets were not due to global processing differences across experimental blocks (as advance cues and advance targets were presented in different blocks), we additionally assessed zero S1–S2 delay trials (cue and target simultaneously displayed) which were physically identical across both blocks. Using zero S1–S2 delay trials as a common baseline, we masked out all voxels from the advance cue vs. advance target contrast that exhibited a difference between zero S1–S2 delay trials across experimental blocks at a very liberal threshold of $p(z) < 0.05$. Effectively, no voxels were excluded due to this criterion.

Following the whole-brain level voxel classification, a second stage of analysis used a region-of-interest (ROI) approach for a more fine-grained characterization of activation profiles. This secondary data analysis was performed to clarify earlier interpretations of brain areas engaged in preparatory task control (Ruge et al., 2005). Specifically, due to a less powerful experimental design, the Ruge et al. study was somewhat inconclusive as to which of two possible models could best explain the temporal structure of neural events underlying the observed BOLD activation time courses of such brain areas. According to one model, the observed BOLD time courses resulted from two superimposed *transient* components, an initial component elicited by the task cue (S1) and a subsequent component elicited by the target stimulus (S2). An alternative model explained the same BOLD time course by a single component elicited by the task cue which was *sustained* throughout the preparation interval. As explained next, the current study design enabled us not only to determine independent activation components elicited by S1 and S2 (due to the partial trial logic) but also to infer from the temporal profile of S1-related BOLD time courses the relative duration of the underlying neural activation. Thus, we were able determine whether S1-related activation is transient or rather sustained throughout the preparation interval.

This analysis was based on ROI data sets that were created by first averaging time course estimates (including all 24 originally estimated time steps) across above-threshold voxels within an 8 mm sphere centered around the coordinates exhibiting the maximum *z*-value for selected brain regions from the whole-brain contrasts. For each ROI, time course estimates were first baseline-corrected relative to the average signal within the interval between time points 1–4 before being parameterized by peak amplitudes and peak latencies, using the R software package (R-Development-Core-Team, 2005). Although it is tempting to interpret amplitude and peak latency effects as being confounded, it has been well-established that a mere increase in activation strength does not imply a prolongation of the duration of BOLD activation (here, parameterized by peak latency). Thus, the duration of the underlying neural activity can be independently estimated (Miezin et al., 2000). Peak latencies were determined to estimate the duration of neural activation following event onset. Peak activation amplitudes were expressed in units of percent signal change relative to the signal average of the first three time points. Peak latencies were expressed relative to the onset time of S1 or S2, respectively. The statistical analysis of latency and amplitude estimates was based on jackknife re-samples of the original time course estimates extracted for each subject (Efron, 1981; Maertens & Pollmann, 2005; Ruge, Brass, Lohmann, & von Cramon, 2003). The jackknife procedure was useful for reliably identifying activation peaks, which are often difficult to determine within noisy single-subject time courses.

2.4.2. Contrasting congruent vs. incongruent advance target activation

A two-factorial (time point X congruency) ANOVA was conducted to isolate voxels that showed differential S1-related activation patterns for advance congruent targets as compared to advance incongruent targets. As we indeed found the expected group differences in congruency-related behavioral performance (see Section 3.1), we performed a three-factor ANOVA including group membership as an additional factor. The resulting contrast images were evaluated at two different significance levels. At a threshold of $p(z) < 0.001$ we identified significant voxels on the whole-brain level to reveal differential preparatory activation for congruent vs. incongruent advance targets. Additionally we applied a very liberal ROI-level threshold of $p(z) < 0.05$ selectively for those previously identified voxels that fell into any of the five classes of preparatory activation we had defined for the advance cue vs. advance target comparison. For voxels that missed this liberal ROI-level threshold, we felt relatively safe to conclude that differences in preparatory activation for advance cues vs. advance targets were not simply due to the special properties of congruent advance targets.

To answer important follow-up questions that arose from the observed S1-related activation effects, we performed an additional three-factor (time point X congruency X group) ANOVA on S2-related BOLD estimates.

Finally, we performed additional ROI-based analyses to determine the detailed structure of congruency X group interaction effects for brain areas that were identified in the whole-brain analyses for S1-related BOLD estimates (advance target) and/or S2-related BOLD estimates (cue-second). ROI data sets were created by first averaging time course estimates across above-threshold voxels within an 8 mm sphere centered around the coordinates exhibiting the maximum *z*-value for the selected brain areas. Such time courses were created for each subject separately for congruent and incongruent trials (S1-related and S2-related), were then baseline-corrected relative to the average signal within the interval between time points 1–4, and were finally parameterized by computing a single value representing the area under the curve (i.e., the sum of BOLD signal values across the time course). These summary values were then subjected to *t*-tests according to the four cells of the group X congruency interaction for both, S1-related and S2-related BOLD activation (depicted in form of bar graphs; see Fig. 4).

3. Results

3.1. Behavioral results

The behavioral signature of preparatory control was investigated by analyzing the effect of increased *preparation time* (long vs. zero S1–S2 delay) on response time (RT) and error rate, as a function of *preparation type* (advance cue vs. advance target). Additionally, we analyzed the modulatory effect of *response congruency* (congruent vs. incongruent) that we expected to be especially relevant in the advance target condition. Accordingly, two separate ANOVAs were conducted on mean RTs and error rates, including *preparation time, preparation type* and *response congruency* as experimental factors of interest.

3.1.1. Response times

The main effect of *preparation time* was significant ($F(1,17) = 131.83$; $p < 0.001$) reflecting that response times were almost 300 ms faster for long S1–S2 delay trials (877 ms) than for zero S1–S2 delay trials (1154 ms). This general preparation effect was not significantly modulated by *preparation type* (preparation type X preparation time interaction, $F(1,17) = 0.65$, n.s.). The main effect of preparation type was also not significant ($F(1,17) = 0.30$, n.s.).

There was also a significant triple interaction between *preparation time, preparation type, and congruency* ($F(1,17) = 16.63$; $p(F) < 0.001$). This interaction effect primarily reflected the fact that responses in congruent trials were almost 200 ms faster than in incongruent trials specifically in the advance target condition with a long preparation interval (782 ms vs. 964 ms). In all other conditions congruent and incongruent trials did not differ significantly (advance cue – long delay (881 ms vs. 882 ms; $F(1,17) = 0.01$, n.s.), advance cue – zero delay (1135 ms vs. 1154 ms; $F(1,17) = 0.8$, n.s.), and advance target – zero delay (1148 ms vs. 1177 ms; $F(1,17) = 2.5$, n.s.).

This result is relevant with regard to one of our original hypotheses stating that response time benefits for congruent relative to incongruent responses in long delay trials might be due to a voluntary strategy applied by some, but not all, participants to achieve a high degree of motor readiness. To further explore this notion, we additionally performed an RT distribution analysis to reveal the pattern of inter- and intra-subject variability that we considered to be indicative of strategy application. Specifically, we reasoned that a bi-modal distribution of RTs would reflect a mixture of two types of trials that are defined depending on whether or not the presumed motor preparation strategy was applied. In a first step, we computed the distribution of RTs across trials and participants (i.e., comprising each single RT of all the participants) for the critical advance target long delay condition separately for congruent and incongruent trials. Fig. 2 depicts these two distributions (thick solid curves) modeled according to Gaussian probability density functions (R-Development-Core-Team, 2005). Strikingly, we observed a bi-modal distribution across participants for congruent advance targets (thick solid curve, upper panel), but not for incongruent advance targets (thick solid curve, lower panel).

To answer the question whether the bi-modal distribution for congruent advance targets is due to variability *within* subjects or *between* subjects, Fig. 2 also depicts the RT distributions separately for each participant represented by the thin curves (i.e., each distribution contains all of the RTs for a single participant). The result of this analysis is clear-cut. The single-subject distributions for advance congruent targets are all approximately uni-modal, one set of distributions ($N = 8$) clustering around a median RT value of 435 ms and another set of distributions ($N = 10$) clustering around a median RT value of 1008 ms ($t(16) = 8.20$, $p(t) < 0.001$).

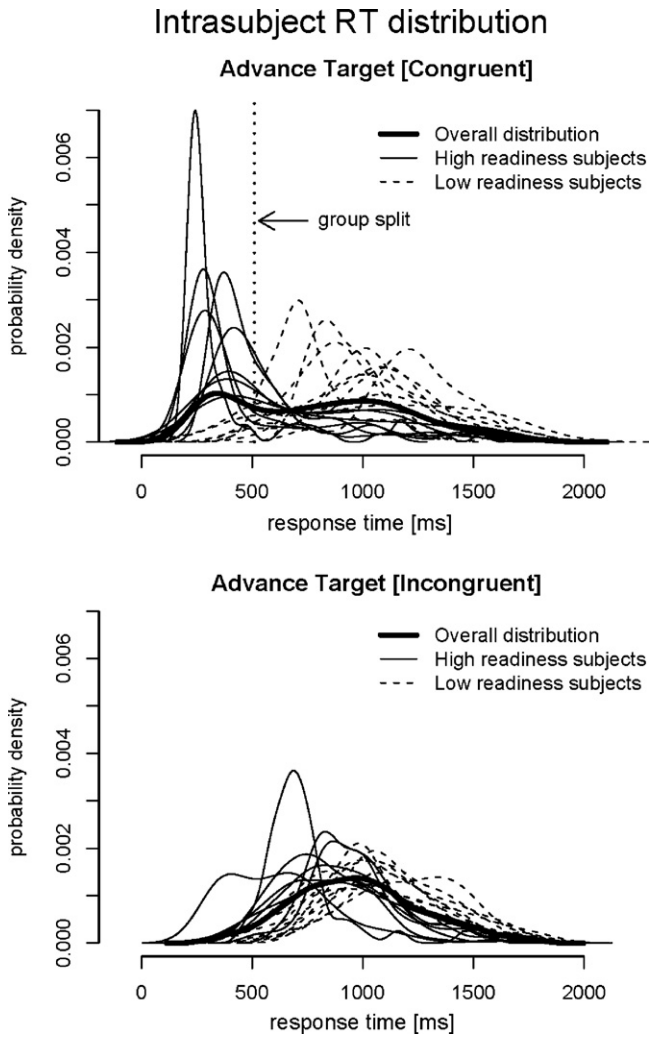

Fig. 2. Response time (RT) distributions modeled according to Gaussian probability density functions for congruent (upper panel) and incongruent (lower panel) advance targets in the long S1–S2 delay condition. The two thick curves depict the overall RT distributions comprising each single trial from each subject. The thin curves represent the RT distributions separately for each subject. According to the bi-modal RT distribution for congruent targets, subjects fall into one out of two categories. 'high-readiness' (i.e., well prepared) subjects are characterized by excessively short RTs whereas 'low-readiness' (i.e., less well prepared) subjects consistently exhibit much longer RTs.

This pattern suggests that some subjects ($N = 8$) are responding consistently fast in every congruent trial ('high-readiness' group), whereas some other subjects ($N = 10$) are responding consistently slow in every congruent trial ('low-readiness' group). There is, in contrast, no indication of the opposite possibility, that at least some subjects would exhibit very fast RTs in some trials and very slow RTs in other trials. In that case, the bi-modality of the overall distribution should have been replicated in the single-subject distributions. Notably, although there was no clear bi-modal distribution pattern for incongruent advance targets (Fig. 2, lower panel), 'high-readiness' participants as compared to 'low-readiness' participants (defined according to their performance in congruent trials) were also significantly faster on incongruent trials (876 ms vs. 1026 ms; $t(16) = 2.20$, $p(t) < 0.05$). Finally, the interaction of group X congruency (based on long delay trials only) was significant ($F(1,16) = 110.22$, $p(F) < 0.001$) reflecting that 'high-readiness' participants responded much faster for advance congruent than for advance incongruent targets (435 ms vs. 876 ms; $t(7) = 10.23$, $p(t) < 0.001$), whereas RTs of 'low-readiness' participants did not

differ between advance congruent and advance incongruent targets (1008 ms vs. 1026 ms; $t(9) = 1.66$, n.s.).

In summary, the results of the distribution analysis are consistent with the hypothesis that some participants (8 out of 18) engaged in a voluntary strategy to achieve a high degree of response readiness, which allowed them produce exceedingly fast RTs for advance congruent targets and (albeit to a much smaller extent) also for advance incongruent targets.

3.1.2. Error rates

Overall error rates reached 9.9% in the advance cue condition and 10.8% in the advance target condition, which was not a significant difference ($F(1,17) = 0.48$; n.s.). There were significant and expected main effects of *preparation time* (less errors with longer preparation time: 13.0% vs. 7.4%, $F(1,17) = 12.60$; $p(F) < 0.002$) and *response congruency* (more errors on incongruent trials: 11.6% vs. 8.8%, $F(1,17) = 7.55$; $p(F) < 0.01$). None of the interaction effects reached significance. Thus, the error rate data indicate that the more specific interaction effects observed for the response time data were not due to speed-accuracy tradeoffs. Finally, a comparison of high-readiness and low-readiness groups for the advance target condition (group X congruency ANOVA for long preparation interval only) revealed that the high-readiness group was not only faster than the low-readiness group but also committed fewer errors (4.5% vs. 9.4%, $F(1,16) = 5.4$; $p(F) < 0.05$). This suggests that the RT group difference was not due to a speed-accuracy tradeoff. Interestingly, the factor group did not interact significantly with congruency ($F(1,16) = 0.3$; $p(F) = 0.59$). Thus, the high-readiness group was able to reduce the error rate to a similar extent for both congruent and incongruent trials.

3.2. Imaging results

The primary analyses for this study focused on the neural correlates of preparatory control, contrasting S1-related activation for advance target and advance cue events. Secondary ROI-based analyses examined (i) the temporal activation profile for S1-related activation and (ii) S2-related activation for cue-second and target-second events. A further set of analyses was performed to determine the influence of response congruency

Table 2
Activation foci from whole-brain contrast of advance target vs. advance cue events.

Brain region	Brodmann area	*x*	*y*	*z*	*z*-max (advance target vs. advance cue)
Selectively target-related					
Dorso-lateral prefrontal cortex					
Left aIFS	BA46/BA10	−45	42	12	5
Right aIFS	BA46/BA10	30	45	9	3.8
Left mIFS	BA46	−42	30	18	5.7
Right mIFS	BA46	42	36	24	4.9
Left mMFG	BA46/BA9	−42	27	39	5.4
Right mMFG	BA46/BA9	36	24	39	3.6
Left pIFG	BA44	−51	6	15	4.7
Left dPMC-d	BA6	−30	6	57	4.7
Right dPMC-d	BA6	21	6	48	4.2
Left MFC	BA32/BA8	−6	24	44	4.2
Left aInsula		−30	18	9	4.6
Right aInsula		33	18	9	3.9
Left aIPS-d	BA40	−51	−39	51	6.4
Right aIPS-d	BA40	42	−39	45	5.5
Preferentially target-related					
Left IFJ	BA9/BA6	−42	6	30	5.6
Right IFJ	BA9/BA6	42	3	36	4.3
Left MFC	BA32/BA8	−6	15	45	3.6
Left aInsula		−36	15	0	3.5
Intra-parietal sulcus					
Left mIPS	BA7	−30	−48	48	5.5
Right mIPS	BA7	30	−48	48	6.6
Left pIPS	BA7/BA19	−27	−69	42	5.5
Right pIPS	BA7/BA19	24	−66	42	6.5
Left pSPL	BA7	−27	−60	54	5.2
Right pSPL	BA7	24	−63	57	5.5
Left pre-Cuneus	BA7	−12	−69	51	5.8
Right pre-Cuneus	BA7	6	−69	51	4.9
Selectively cue-related					
None					
Preferentially cue-related					
None					
					Mean *z*-max (advance cue, advance target)
Equally cue-related and target-related					
Left dPMC-v	BA6	−52	−3	48	8.6
Right dPMC-v	BA6	45	−3	54	9
Pre-SMA	BA6	−3	3	54	10.8

Abbreviations: a, anterior; p, posterior; r, rostral; c, caudal; m, mid; l, lateral; d, dorsal; v, ventral; IFS, inferior frontal sulcus; IFG, inferior frontal gyrus; IFJ, inferior frontal junction; MFG, middle frontal gyrus; PMC, pre-motor cortex; MFC, medial frontal cortex; Pre-SMA, pre-supplementary motor area. IPS, intra-parietal sulcus; SPL, superior parietal lobule.

on BOLD activation specifically in the advance target condition.

3.2.1. Cue-based vs. target-based preparation

The first step of the analysis classified the pattern of S1-related activation into one of five different categories (see Table 1). The first two categories were included to identify brain areas more strongly associated with cue-based preparation, including (1) selective activation for advance cues and (2) preferential activation for advance cues (i.e., activation for advance cues *and* advance targets, but increased for the former). Categories 3 and 4 were included to identify brain areas more strongly associated with target-based preparation, including (3) selective activation for advance targets and (4) preferential activation for advance targets (i.e., activation for advance targets *and* advance cues, but increased for the former). Finally, we included a fifth category to identify brain regions that exhibited equivalent preparatory activation for advance cues and advance targets. A summary of all identified regions in each of the five categories is provided in Table 2 and shown localized on the brain surface in Fig. 3.

The key finding of this analysis was the identification of a number of brain regions that exhibited selective activation for advance targets (category 3), including bilateral regions within the DLPFC along the inferior frontal sulcus, extending posteriorly into BA44 and further into ventral pre-motor cortex (vPMC). Selective target activation was also observed in the medial frontal cortex, the dorsal portion of the dorsal pre-motor cortex (dPMC-d), and anterior regions of parietal cortex in the vicinity of the intra-parietal sulcus (aIPS). In stark contrast, no brain regions were found to be selectively or even preferentially activated for advance cues (categories

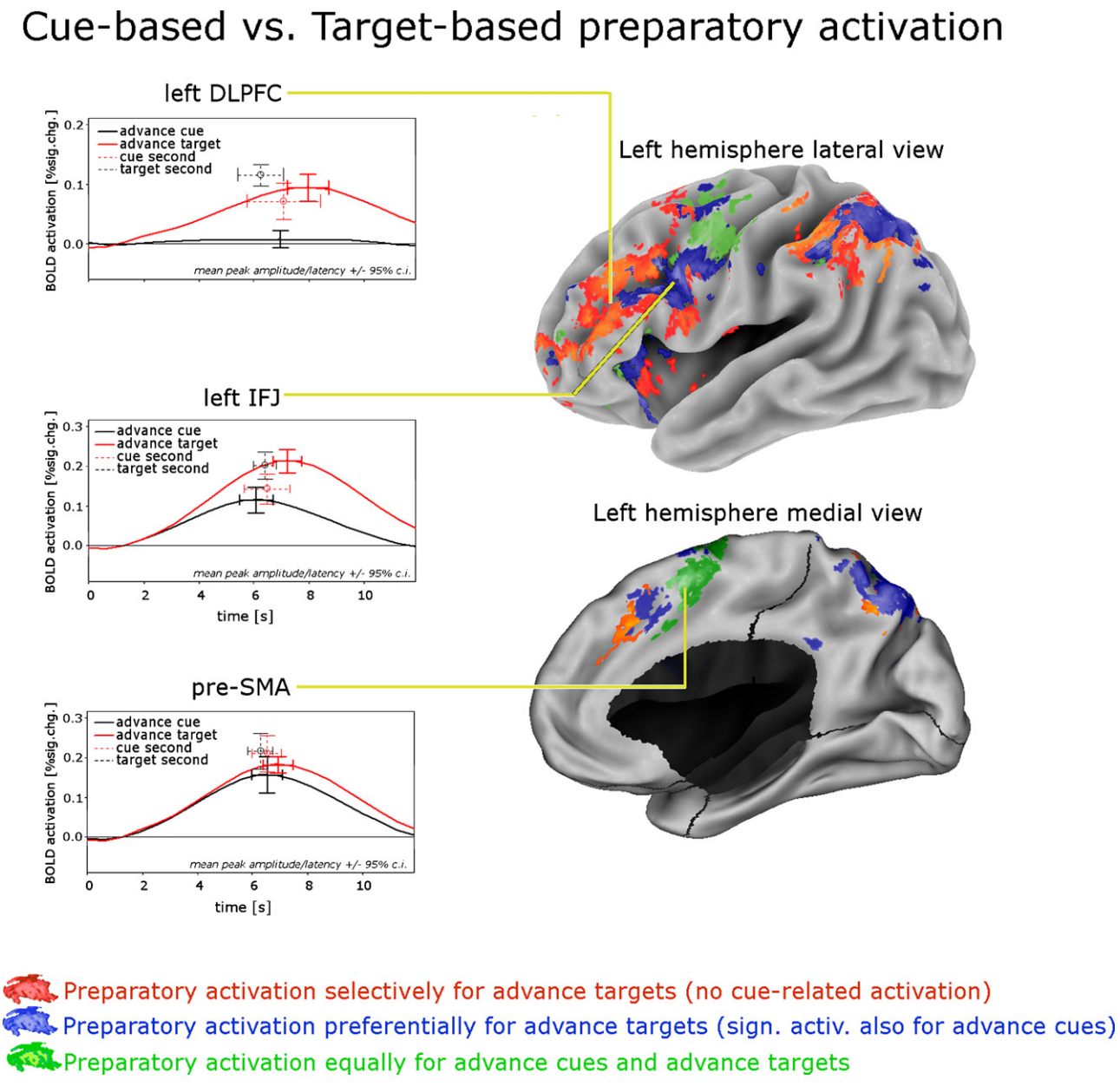

Fig. 3. Whole-brain map of preparatory activation for the comparison of advance target vs. advance cue events in two brain renderings using the Caret Software (Van Essen et al., 2001). Three cases are distinguished, as indicated by separate color codes: selectively target-related activation (red), preferentially target-related activation (blue), and equal activation for both advance cues and advance targets (green). Selectively or preferentially cue-related activation was not observed. Additionally, time course estimates are shown for representative brain areas, including the full activation profiles for the advance target and the advance cue events, plus the peak amplitude/latency estimates for the target-second and cue-second events. The parameterized time course data (peak amplitude/latency) for all identified regions is reported in Tables 3 and 4. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Table 3
Peak latencies associated with S1 and S2 events for previously identified brain areas.

Brain region	Advance target	Advance cue	Advance target–advance cue	Advance target – target 2nd	Advance cue – cue 2nd
Selectively target-related					
Dorso-lateral prefrontal					
Left aIFS	8.8 ± 1.6	\	\	1.7 ± 1.9	\
Right aIFS	8.5 ± 0.8	\	\	**1.8 ± 1.6**	\
Left mIFS	8.0 ± 0.7	\	\	**1.7 ± 0.9**	\
Right mIFS	6.6 ± 1.1	\	\	**1.5 ± 1.3**	\
Left mMFG	9.1 ± 1.1	\	\	**2.1 ± 2.0**	\
Right mMFG	9.1 ± 0.7	\	\	**3.1 ± 1.2**	\
Left pIFG	8.3 ± 1.1	\	\	**1.9 ± 1.1**	\
Left dPMC-d	9.5 ± 1.8	\	\	**3.4 ± 1.7**	\
Right dPMC-d	8.1 ± 1.1	\	\	**1.8 ± 1.2**	\
Left MFC	8.3 ± 0.7	\	\	**1.8 ± 1.0**	\
Left aIPS-d	8.5 ± 0.7	\	\	**1.6 ± 0.8**	\
Right aIPS-d	7.3 ± 0.6	\	\	**0.9 ± 0.6**	\
Preferentially target-related					
Left IFJ	7.2 ± 0.5	6.1 ± 0.6	**1.1 ± 0.7**	**0.8 ± 0.4**	−0.4 ± 0.8
Right IFJ	6.8 ± 0.6	6.3 ± 0.5	**0.5 ± 0.5**	0.6 ± 0.8	−0.8 ± 1.2
Intra-parietal sulcus					
Left mIPS	6.9 ± 0.5	6.4 ± 0.7	**0.5 ± 0.4**	**0.6 ± 0.4**	−0.2 ± 0.6
Right mIPS	7.0 ± 0.4	6.2 ± 0.6	**0.9 ± 0.5**	**0.7 ± 0.5**	**−0.6 ± 0.6**
Left pIPS	7.4 ± 0.5	6.5 ± 0.8	**1.0 ± 0.4**	**0.8 ± 0.4**	−0.5 ± 0.7
Right pIPS	6.9 ± 0.3	6.0 ± 0.6	**0.9 ± 0.5**	**0.6 ± 0.4**	**−0.8 ± 0.6**
Left pSPL	7.1 ± 0.5	6.5 ± 1.0	**0.7 ± 0.6**	**0.7 ± 0.5**	−0.4 ± 0.9
Right pSPL	7.4 ± 0.6	6.3 ± 0.7	**1.1 ± 0.6**	**0.8 ± 0.7**	**−0.7 ± 0.5**
Left pre-Cuneus	8.0 ± 0.6	5.9 ± 0.7	**2.1 ± 0.9**	**1.1 ± 0.7**	**−1.2 ± 0.8**
Right pre-Cuneus	8.5 ± 0.6	7.2 ± 1.2	**1.3 ± 0.9**	0.7 ± 0.9	−0.8 ± 1.1

Mean peak latency (difference) [s] ± 95% C.I. (significant differences are in bold font). *Abbreviations*: a, anterior; p, posterior; r, rostral; c, caudal; m, mid; l, lateral; d, dorsal; v, ventral; IFS, inferior frontal sulcus; IFG, inferior frontal gyrus; IFJ, inferior frontal junction; MFG, middle frontal gyrus; PMC, pre-motor cortex; MFC, medial frontal cortex; Pre-SMA, pre-supplementary motor area. IPS, intra-parietal sulcus; SPL, superior parietal lobule.

1 and 2). The only exception was a small region within the posterior calcarine sulcus, that most likely reflected the more foveal location occupied by visual presentation of the cue.

The lack of selective or preferential cue-related activation does not reflect the absence of cue-related preparatory activation at all. Indeed, a number of regions exhibited substantial activation for advance cues. Yet in many of these regions there was more pronounced activation for advance targets (category 4). These preferentially target-related regions included the inferior frontal junction area (IFJ) located at the posterior end of the inferior frontal sulcus and several foci along the intra-parietal sulcus (IPS) extending into the pre-cuneus. Finally, there were a few brain regions that showed equal activation for advance cues and advance targets (category 5), including the pre-supplementary motor area (pre-SMA) and the ventral portion of the dorsal pre-motor cortex (dPMC-v).

For each of these identified brain regions we performed secondary, ROI-based analyses to determine (i) whether S1-related BOLD activation reflects sustained or rather transient neural activation and (ii) whether brain areas exhibiting S1-related activation would be re-activated following the S2.

3.2.2. Is preparatory activation sustained?

To determine the extent to which preparatory activation in the identified brain regions was sustained throughout the preparation interval, we quantified peak latencies of the S1-related activation time courses. Given a maximal preparation interval of 1875 ms, neural activity underlying the observable S1-related BOLD time courses can be maximally sustained for that time period. The comparison of peak latencies associated with the advance cue vs. advance target conditions provided a way of estimating the relative difference in duration of preparatory activation for these two conditions. As an additional independent reference, we used the peak latencies of S2-related BOLD time courses (i.e., cue-second and target-second) which should be maximally sustained only for the duration between S2 presentation and average response times (i.e., ∼900 ms). Fig. 3 shows a graphical depiction of these activation dynamics for representative regions, namely left-hemisphere IFJ and DLPFC. Table 3 summarizes the results of the peak latency analysis for all identified brain regions.

For those brain areas that were *selectively* activated for advance targets (category 3), we found a general trend of sustained activation (i.e., longer duration for advance target stimuli than target-second stimuli) that was statistically significant for most of the regions. For those brain areas that were *preferentially* activated for advance targets (category 4), we directly compared peak latencies for advance targets vs. advance cues, in a first analysis step. All identified brain areas exhibited a more sustained activation pattern for advance targets as compared to advance cues. In a second analysis step, we separately compared target-related and cue-related preparatory activation to the respective reference time courses (i.e., target-second and cue-second, respectively). This analysis revealed a general trend for advance target-related activation to be significantly *more* sustained than the reference and advance cue-related activation to be *less* sustained than the reference. Given that average response time latencies were ∼900 ms following S2 onset, it can be concluded that advance target activation was sustained longer than maximally ∼900 ms whereas advance cue activation was sustained for less than maximally ∼900 ms.

3.2.3. Are preparation-related brain areas re-activated at S2?

A further question of interest concerns the relationship of S1 to S2 activation strength. In particular, it is of interest to know whether brain areas showing S1-related preparatory activation would be re-activated by the subsequent S2 stimulus. In the current study, estimates of peak amplitudes for S2-related activation indicated the presence of substantial S2 re-activation following both advance

Table 4
Peak amplitudes associated with S1 and S2 events for previously identified brain areas.

Brain region	Advance target	Cue-second	Advance cue	Target second
Selectively target-related				
Dorso-lateral prefrontal cortex				
Left aIFS	**0.12 ± 0.03**	**0.07 ± 0.03**	\	**0.13 ± 0.03**
Right aIFS	**0.08 ± 0.02**	0.01 ± 0.02	\	**0.02 ± 0.02**
Left mIFS	**0.09 ± 0.02**	**0.07 ± 0.03**	\	**0.12 ± 0.02**
Right mIFS	**0.12 ± 0.05**	**0.06 ± 0.03**	\	**0.09 ± 0.02**
Left mMFG	**0.12 ± 0.02**	**0.04 ± 0.02**	\	**0.08 ± 0.03**
Right mMFG	**0.09 ± 0.02**	0.01 ± 0.01	\	**0.03 ± 0.02**
Left pIFG	**0.07 ± 0.02**	**0.08 ± 0.03**	\	**0.1 ± 0.04**
Left dPMC-d	**0.08 ± 0.02**	**0.04 ± 0.02**	\	**0.09 ± 0.03**
Right dPMC-d	**0.06 ± 0.01**	**0.03 ± 0.01**	\	**0.05 ± 0.02**
Left MFC	**0.1 ± 0.06**	**0.07 ± 0.04**	\	**0.12 ± 0.05**
Left aIPS-d	**0.16 ± 0.04**	**0.17 ± 0.03**	\	**0.2 ± 0.03**
Right aIPS-d	**0.09 ± 0.02**	**0.07 ± 0.02**	\	**0.09 ± 0.03**
Preferentially target-related				
Left IFJ	**0.21 ± 0.03**	**0.14 ± 0.04**	**0.11 ± 0.03**	**0.2 ± 0.03**
Right IFJ	**0.15 ± 0.03**	**0.05 ± 0.01**	**0.09 ± 0.04**	**0.07 ± 0.03**
Intra-parietal sulcus				
Left mIPS	**0.2 ± 0.03**	**0.14 ± 0.02**	**0.1 ± 0.03**	**0.18 ± 0.04**
Right mIPS	**0.19 ± 0.03**	**0.08 ± 0.02**	**0.09 ± 0.03**	**0.12 ± 0.02**
Left pIPS	**0.22 ± 0.02**	**0.17 ± 0.04**	**0.13 ± 0.04**	**0.23 ± 0.03**
Right pIPS	**0.2 ± 0.03**	**0.09 ± 0.03**	**0.1 ± 0.03**	**0.15 ± 0.03**
Left pSPL	**0.26 ± 0.03**	**0.17 ± 0.03**	**0.13 ± 0.04**	**0.23 ± 0.04**
Right pSPL	**0.28 ± 0.06**	**0.15 ± 0.05**	**0.14 ± 0.05**	**0.23 ± 0.06**
Left pre-Cuneus	**0.18 ± 0.03**	**0.15 ± 0.04**	**0.09 ± 0.03**	**0.21 ± 0.05**
Right pre-Cuneus	**0.26 ± 0.06**	**0.15 ± 0.04**	**0.15 ± 0.06**	**0.22 ± 0.07**

Mean peak amplitude [%sig. chg.] ± 95% C.I. (significant activations are in bold font). *Abbreviations*: a, anterior; p, posterior; r, rostral; c, caudal; m, mid; l, lateral; d, dorsal; v, ventral; IFS, inferior frontal sulcus; IFG, inferior frontal gyrus; IFJ, inferior frontal junction; MFG, middle frontal gyrus; PMC, pre-motor cortex; MFC, medial frontal cortex; Pre-SMA, pre-supplementary motor area; IPS, intra-parietal sulcus; SPL, superior parietal lobule.

cues and advance targets in all regions that showed S1-related preparatory activation (see Table 4 and Fig. 3 for an illustration of this effect in left IFJ and mid-DLPFC). This pattern of activation dynamics rules out an exclusive role in preparatory control for the set of regions engaged by advance information, and instead suggests that these regions are re-engaged during processes that occur following S2 onset.

3.2.4. Congruency-related effects in the advance target condition

The behavioral performance data indicated that participants could be subdivided into two discrete groups according to whether they were sensitive to congruency information in the advance target condition. This finding seems to suggest that the two groups of participants may have differed in the extent to which they strategically engaged voluntary response preparation processes. To add further detail to this interpretation we examined how this behavioral group difference was reflected in differential patterns of preparatory BOLD activation. A whole-brain ANOVA was conducted for S1-related activation specifically in the advance target condition using both group (high-readiness vs. low-readiness) and response congruency (congruent vs. incongruent) as factors.[1] Surprisingly, neither the group X congruency interaction, nor the main effect of congruency identified any significant activation at the whole-brain significance threshold. Even at a very liberal ROI-level threshold of $p(z) < 0.05$, selectively including the subset of voxels that were identified in the advance cue vs. advance target contrast, only the pSPL showed significant S1-related activation for the group X congruency interaction with $p(z) < 0.01$. As the respective bar graph in Fig. 4 shows, this effect was mainly due to a relative signal increase for incongruent trials in the high-readiness group. This striking absence of significant effects at a very low threshold of $p(z) < 0.05$ (except for the pSPL) suggests that preparatory activation in none of the preferentially or selectively target-related brain areas differed between congruent and incongruent advance targets. Thus, it seems relatively safe to conclude that the widespread increase of preparatory activation for advance target as compared to advance cues is not due to the special properties of advance *congruent* targets.

Yet, despite the almost complete absence of differential preparatory activation for congruent vs. incongruent advance targets, there were many brain areas that showed a significant ($p(z) < 0.001$) main effect of group, with stronger activation in the 'high-readiness' group for both congruent and incongruent trials (Table 5, Fig. 4). Brain areas exhibiting this activation pattern included two foci within the right ACC, plus regions in the left IFJ, the left anterior IFS, the right dPMC, the ventral aIPS bilaterally, and two foci within the right inferior parietal lobule (IPL). Notably, some of these areas (rostral ACC and aIFS) showed no significant activation at all in the 'low-readiness' group at a threshold of $p(z) < 0.05$.

This finding of stronger target-related preparatory activation for high-readiness participants begs the question whether target-related preparatory activation for the *low*-readiness group would still be more pronounced in contrast to the advance *cue* condition (as was true for all group-sensitive regions except ACC-r in the original analysis including all 18 subjects). The overall finding of stronger preparatory activation for advance targets as compared to advance cues was replicated for the low-readiness group, except for

[1] It turned out that many brain areas exhibited differential congruency-related activation effects that continued to evolve later than approximately 9 s after advance target presentation and well beyond the activation peak of the target-related BOLD response. This indicates that these effects were most likely to be associated with the subsequent trial. While such effects are certainly interesting, and in fact not entirely unexpected (e. g., Kerns et al., 2004), we nevertheless decided to ignore them for the purpose of the present paper. Therefore, we restricted the ANOVA model to the first 9 s after S1 presentation to obtain a more pure estimate of effects associated with the current trial.

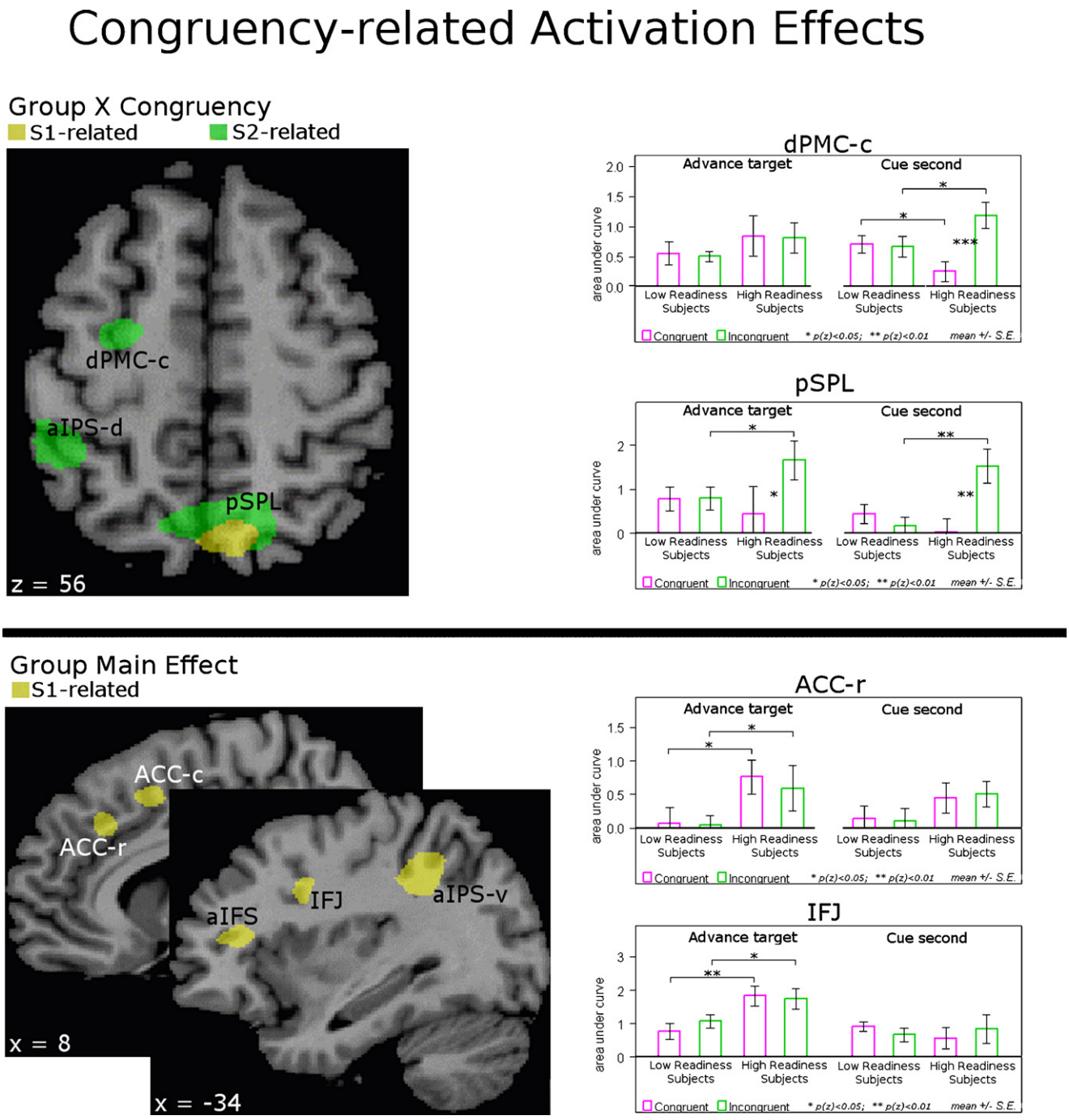

Fig. 4. Whole-brain activation maps for congruency-related activation effects as a function of group membership (defined according to behavioral performance of individual participants). The two groups of subjects were defined according to the presence or absence of a behavioral congruency effect at the long preparation interval (see Fig. 2). The upper panel depicts results from the group X congruency interaction contrast for both, S1-related BOLD estimates (yellow; ROI-level threshold at $p < 0.01$) and S2-related BOLD estimates (green; whole-brain threshold at $p < 0.001$). The lower panel depicts results from the group main effect contrast for S1-related BOLD estimates only. Bar graphs for representative brain areas depict the detailed pattern of BOLD activation for the relevant conditions, parameterized by the area under the curve. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

the anterior IFS which did not even exhibit significant activation at $p(z) < 0.05$ for advance targets. This conclusion holds for both, overall activation strength parameterized by the area under the curve (all $p(z) < 0.024$) as well as duration parameterized by peak latency (all $p(z) < 0.022$).

The presence of a group main effect in preparatory activity but no interaction with congruency might seem somewhat surprising, given the strong interaction effect in behavioral performance. A possible interpretation is that the 'high-readiness' group engaged the same extra preparatory process on both congruent and incongruent advance targets (as suggested by the common group-specific BOLD increase in a number of brain areas). Yet, this common preparatory process might differentially impact subsequent processes initiated after S2 (cue) onset depending on whether the trial was congruent or incongruent, thereby producing the behavioral congruency effect. To test this hypothesis, we again examined the group X congruency interaction, but this time for S2-related rather than S1-related activation. As hypothesized, several brain areas were identified in this analysis that exhibited a significant group X congruency effect, including the posterior superior parietal lob-

Table 5
Activation foci from whole-brain contrasts for congruency-dependent target-based preparation (considering group-differences according to behavioral performance).

Brain region	Brodmann area	*x*	*y*	*z*	*z*-max
Main effect Group at S1 (advance target)					
Right ACC-r	BA32	6	30	33	3.9
Right ACC-c	BA32	3	12	45	3.6
Right dPMC	BA6	30	6	54	3.7
Left IFJ	BA9/BA6	−48	9	33	3.7
Left aIFS	BA10/BA46	−36	36	12	3.7
Left_aIPS-v	BA40	−36	−42	36	5.5
Right_aIPS-v	BA40	42	−33	42	4.5
Right mIPL	BA7	30	−51	39	4.8
Right pIPL	BA7/BA39	30	−66	33	5.7
Group × Congruency at S2 (cue-second)					
Left dPMC-c	BA6	−27	−6	54	3.1
Right dPMC-c	BA6	18	−6	69	3.9
Left aIPS-d		−48	−39	54	4.3
Left pSPL	BA7	−9	−60	63	3.7
Right pSPL	BA7	9	−63	63	3.8
Group × Congruency at S1 (advance target)					
Left pSPL	BA7	−3	−69	−57	2.6
Right pSPL	BA7	9	−66	60	3.0

Abbreviations: a, anterior; p, posterior; r, rostral; c, caudal; m, mid; d, dorsal; v, ventral; IFJ, inferior frontal junction; PMC, pre-motor cortex; ACC, anterior cingulate cortex; IPS, intra-parietal sulcus; SPL, superior parietal lobule; IPL, inferior parietal lobule.

ule (pSPL) bilaterally, the caudal portion of the dPMC bilaterally, and the left dorsal aIPS.

A ROI-based examination of the detailed activation pattern in these identified regions confirmed without exception that the group X congruency interaction was due to the presence of a congruency effect selectively in the 'high-readiness' group (Fig. 4; bar graphs for representative brain regions). However, there was a further distinction in the interaction pattern exhibited by different regions. Specifically, in pSPL the congruency effect was primarily due to increased activity for incongruent trials in the 'high-readiness' group relative to the 'low-readiness' group (with activity only slightly, and non-significantly, reduced in congruent trials). In contrast, for dPMC-c and aIPS-d the interaction effect was due to both, significantly reduced S2 activation on congruent trials as well as significantly increased activation on incongruent trials for the 'high-readiness' group relative to the 'low-readiness' group.

4. Discussion

In this study we contrasted the neural correlates of two preparatory conditions within the cued task-switching paradigm: (1) preparation based on advance task cues and (2) preparation based on advance task-ambiguous target stimuli. The central hypothesis was that cue-based preparation would mainly rely on attentional, stimulus-oriented mechanisms whereas target-based preparation would rely more on intentional, action-oriented mechanisms. Furthermore, we wanted to clarify whether cue-related attentional processes are specialized for the selection of one task-processing pathway over another, a hypothetical mechanism unlikely to be involved in case of advance targets (since such stimuli were task-ambiguous). Finally, action-oriented preparation was hypothesized to comprise an additional process component engaged for achieving a high level of response readiness and that might be sensitive to individual differences in cognitive strategy.

The results revealed clear distinctions in preparatory brain activation, both in terms of anatomical localization and in terms of the temporal dynamics of activation. Strikingly, no brain area was selectively or even preferentially activated by advance task cues. Instead, it was the advance target condition that we found to be associated with a more extended activation pattern that included both the recruitment of additional brain areas not activated in the advance cue condition, as well as more sustained activation in brain areas that were only transiently activated by advance cues. Importantly, we could exclude that this enhanced target-related preparatory activation was due to the unique properties of congruent advance targets in terms of complete response foreknowledge. This was true even when inter-individual differences in response readiness were considered (defined via qualitative differences in the effect of response congruency on task performance). At the same time, we also found that some brain areas involved in target-based preparation were in fact modulated by such inter-individual differences in response readiness—in terms of generally increased preparatory activation in high-readiness participants for *both*, congruent and incongruent advance targets. Yet, even low-readiness participants, like high-readiness participants, still exhibited significantly stronger preparatory activation for advance targets as compared to advance cues in these brain areas.

These findings have a number of conceptually relevant implications that we will discuss next. First, we consider the possible functional role of brain areas that had previously been observed during cue-based preparation, but which were found to be equally or even more strongly activated during target-based preparation in the current study. Second, we discuss the functional role of brain areas that were selectively activated by advance targets. Finally, we address the complex pattern of activation observed in the advance target condition after taking into account the inter-subject variability in congruency-related behavioral performance.

4.1. Preparatory brain activation for advance cues: attentional, stimulus-oriented control

Previous cued task-switching studies have consistently demonstrated that certain prefrontal and parietal brain areas exhibit preparatory activation following advance task cues. Not surprisingly, we found a similar set of regions showing cue-based activation, including the IFJ, the pre-SMA, and a more posterior section of the IPS extending into the posterior superior parietal lobule (pSPL). The role of these regions in attentional control seems to be well-established by the prior literature (Derrfuss et al., 2005; Wager, Jonides, & Reading, 2004; Yantis & Serences, 2003). Yet, as we have argued in the introduction, such results are equally consistent with at least two opposing interpretations regarding the exact functional role this 'dorsal fronto-parietal network' might play during attentional task control. One conceptualization holds that the control processes implemented by these brain areas are specific for situations in which unambiguous priority information is available (e.g., via an explicit task cue) that allows for selective attention to one task-related stimulus dimension over another (cf., Brass & von Cramon, 2004). In other words, such brain areas might be defined by their role in establishing attentional selectivity according to the task rule that has higher priority in a given trial. If this functional–anatomical characterization were true, then no preparatory activation should be observed for advance targets, since such stimuli are, by definition, task-ambiguous and do not convey information about the current task priority.

This hypothesis of selective cue-related preparatory activation was definitively not borne out by the present results. None of the candidate frontal or parietal areas (nor any other brain region, for that matter) showed selective or even preferential activation for advance cues as compared to advance targets. Instead, the dominant pattern we observed was that the brain areas showing cue-related preparatory activation were equally or even more strongly activated by advance targets. This finding is more consistent with the alternative possible view: that the dorsal fronto-parietal attentional network might serve more generally to configure task-related processing pathways so that stimulus input can be processed according

to the pre-experimentally instructed task rules (Bunge, 2004). In this sense, task-selectivity resulting from cue-based preparation is just a special case of the more general process of re-activating representations of task rules, be it a single rule (advance cues) or multiple rules (advance targets). Thus, it should be expected that the strength of preparatory activation depends on the number of rules to re-activate. Consistent with this prediction we found significantly stronger preparatory activation for advance targets (two task rules) than for advance cues (single task rule) in the IFJ and the posterior SPL.

Interestingly, a more fine-grained temporal analysis of the activation time courses revealed that preparatory activation persisted throughout the preparation interval in the advance target condition, but not in the advance cue condition. This finding, although not part of our initial hypothesizing, is consistent with the general interpretation proposed above. Specifically, the assumed concurrent activation of multiple task rules in case of advance targets is likely to place a greater on-going demand on active maintenance and control processes to manage potential interference between the two tasks.

Lastly, a more detailed examination of the pattern of the temporal dynamics in regions showing cue-related preparatory activation revealed that in these regions cue-related activity was transient (short activation duration), and then followed by significant re-activation following the S2 (i.e., target-second presentation). Thus, we could clarify previous results (Ruge et al., 2005) that were somewhat inconclusive in this respect.

4.2. Selective preparatory activation for advance targets: intentional, action-oriented control

A second hypothesis that we examined in this study was that the advance target condition would engage a unique set of preparatory processes not engaged during the advance cue condition. Specifically, we reasoned that target presentation would entail specific action-oriented processes based on actual 'rule implementation' (as compared to mere 'rule activation' in case of advance cues). In particular, rule implementation following target presentation would result in the generation of concrete action plans (or intentions) associated with each dimension of the target (e.g., the goal to achieve either 'even classification' by pressing the right button or 'vowel classification' by pressing the left button). Based on previous imaging results manipulating action-related variables during task switching (Brass et al., 2003; Ruge et al., 2005), we predicted preparatory activation in mid-DLPFC for advance targets, but not for advance cues, reflecting the involvement of action-oriented preparation. This is exactly what we found, thus supporting the original hypothesis.

The interpretation that the DLPFC and other areas might be involved with action planning or intentional control processes is consistent with findings from a variety of paradigms, in addition to the previous task-switching results already mentioned. One class of relevant studies are those employing free selection tasks (Frith, Friston, Liddle, & Frackowiak, 1991; Jahanshahi & Dirnberger, 1999; Lau, Rogers, Ramnani, & Passingham, 2004). Such studies, which have reliably observed DLPFC activation, are of particular theoretical interest, as they seem well suited to isolate a central aspect of intentional control, namely that an action is specified by anticipating its future effects, or goals that are expected to be achieved (Hommel et al., 2001; James, 1890). This is because informative stimulus input is lacking and thus, free action selection needs to rely on the choice among anticipated future action effects.

Another source of support for our interpretation comes from consideration of the full network of regions exhibiting the target-selective activation pattern, which includes, in addition to mid-DLPFC, including ventral pre-motor cortex (extending into Broca's area, BA 44) and anterior IPS. Interestingly, this network closely overlaps the network that is thought to comprise the 'mirror neuron' system (Arbib, 2005; Rizzolatti & Craighero, 2004). Studies of the 'mirror neuron' system have suggested that both the anterior parietal and ventral pre-motor cortex (extending in humans into Broca's area, BA 44) as critical regions for coding the relationship between actions (either one's own or others') and their effects (Arbib, 2005; Buccino et al., 2001; Hamilton & Grafton, 2006; Jeannerod, Arbib, Rizzolatti, & Sakata, 1995; Manthey, Schubotz, & von Cramon, 2003; Rizzolatti & Luppino, 2001). While the DLPFC does not seem to be as consistently implicated in human activation studies of the mirror system, this discrepancy could reflect that 'mirror-neuron' studies typically use rather passive action observation tasks which might not require a great deal of prefrontal top-down guidance. However, cortical connectivity studies in monkeys suggest that the mid-DLPFC has strong projections to the aIPS, and also, to a lesser degree, to ventral pre-motor area F5 (Rizzolatti & Luppino, 2001), thus suggesting a common functional basis.

The current results also contribute to an ongoing theoretical debate in the cognitive neuroscience literature. One popular view appears to be a monolithic account of lateral PFC (including mid-DLPFC and IFJ) as being primarily concerned with attentional control and active maintenance in working memory without making the attention/intention distinction. One of the most typical examples is the interpretation of DLPFC activation in the Stroop task as being critical for active maintenance of task information used for attentional biasing (e.g., Banich et al., 2000; MacDonald et al., 2000). Yet, another line of research has been emphasizing the specific role of DLPFC in action-planning processes (e.g., Genovesio, Brasted, Mitz, & Wise, 2005; Lau et al., 2004; e. g., Pochon et al., 2001; Rowe, Toni, Josephs, Frackowiak, & Passingham, 2000), rather than attention or working memory per se (Postle, 2006). The present findings seem to add further support for the latter theoretical position.

Another recent theoretical account of lateral PFC cognitive architecture suggests a functional differentiation along the anterior–posterior axis (Koechlin et al., 2003; Koechlin & Summerfield, 2007). Specifically, more anterior regions (mid-DLPFC) are supposed to establish a form of episodic context, whereas more posterior LPFC regions establish the immediate task context. Both contextual control mechanisms serve to select the currently appropriate action facing ambiguous stimulus situations. As far as the posterior section of LPFC (i.e., IFJ) is concerned, our interpretation of the present results seems to accord well with the notion of immediate task context which ensures that action selection is guided by the currently appropriate stimulus properties. In contrast, with respect to mid-DLFPC function, future research needs to clarify whether the concepts of episodic control and intentional control (i.e., future-directed action control via goal/effect anticipation) might be reconciled by identifying a common functional basis.

4.3. Individual differences in response readiness: voluntary strategy at work?

A final aim of our study was to analyze the relevance of response congruency for preparatory activation in the advance target condition, considering inter-individual differences in response readiness. Specifically, we found that some participants showed a strong facilitation in response times on response congruent trials—indicating that they had achieved a high degree of response readiness during the preparatory interval—whereas other participants showed almost no facilitation in such conditions. The underlying bi-modal distribution of performance across participants allowed us to divide the sample into two subgroups according to the presence or absence of congruency effects ("high-readiness" vs. "low-readiness" groups). As predicted, the high-readiness group

showed increased preparatory brain activation in a number of regions, including the medial frontal cortex. Yet, most interestingly, this group effect occurred not only in congruent trials, but also to a similar extent in incongruent trials. This finding of equivalent preparatory activation increase for both congruent and incongruent advance targets in the 'high-readiness' group argues against the possibility that complete foreknowledge of the correct upcoming motor response in congruent trials might involve a distinct preparatory process. Instead, it suggests the presence of a more global strategy undertaken by some participants in both, congruent *and* incongruent trials. This interpretation was also supported by the observation that high-readiness participants also showed significantly faster response times and reduced error rates on incongruent advance target trials.

The MFC, including two separate foci in the 'dorsal ACC' (BA32), was one of the most prominent regions showing increased preparatory activity in the high-readiness group. The MFC has long been thought to be essential for the initiation of action (Barris & Schuman, 1953). This view is supported by recent brain imaging studies that emphasize the role of MFC in volitional and motivational processes (Forstmann, Brass, Koch, & von Cramon, 2005; Nachev, Rees, Parton, Kennard, & Husain, 2005; Paus, 2001; Winterer, Adams, Jones, & Knutson, 2002). More specifically, the MFC has been hypothesized to implement cost–benefit computations which determine whether or not to commit to a certain behavior, based on the evaluation of expected outcome (Brown & Braver, 2005; Paus, 2001; Rushworth et al., 2004). Applied to the present context, such an interpretation of MFC functionality suggests that some participants might have spent additional effort to achieve a high degree of response readiness because the relevant MFC sub-regions indicated that this additional processing is advantageous. Specifically, we hypothesize that the MFC may have computed a cost–benefit tradeoff weighing increased preparatory effort following S1 (especially on incongruent trials) against reduced response selection demands following S2 (especially on congruent trials).

Another set of brain regions (pSPL, aIPS-d, and dPMC-c) did show differential effects of congruency across the two groups, most of them exclusively during the S2 period (i.e., with cue presentation) when actual motor implementation processes were initiated. This effect was due to stronger activation for incongruent relative to congruent targets exclusively in the high-readiness group. All three regions exhibiting S2-related congruency effects in the high-readiness group showed increased activation on incongruent trials relative to the activation level in the low-readiness group. A similar pattern was observed for *S1-related* preparatory activation specifically in the pSPL. In addition, left aIPS-d and bilateral dPMC-c exhibited reduced S2-related activity in congruent trials for the high-readiness group as compared to the low-readiness group. This pattern of findings appears to be consistent with a cost–benefit tradeoff at work. In particular, the increased activity for incongruent advance targets may reflect the cost of an explicit motor preparation strategy that results in increased competition on incongruent trials (due to the concurrent activation of competing motor programs). Conversely, the reduced S2-related activation of dPMC-c and aIPS-d for congruent advance target trials may indicate the benefits that accrue from such strategy—presumably in terms of a reduced demand on motor generation and initiation processes in congruent trials (since in these trials the S2 task cue only needs to serve as a trigger for activation of the relevant motor program, rather than providing information about which motor program is relevant). The finding that activation differences between congruent and incongruent trials mainly played out after S2 presentation but not during the preparation interval suggests that activation in areas like dPMC is not primarily sensitive to the number of potential responses prepared in advance but rather to the number of prepared responses to select among at the time of actual motor generation. The involvement of dPMC, especially its more caudal part (Picard & Strick, 2001), in both initial action preparation and final action selection is consistent with the previous literature (Cisek & Kalaska, 2005; Toni, Thoenissen, & Zilles, 2001). Moreover, the dPMC, as compared to the more ventral PMC, seems to support conditional motor behavior controlled by arbitrary stimulus–response associations like those used in present study (Hoshi & Tanji, 2004). Our observation that *preparatory* dPMC activation was not sensitive to target congruency and the resulting competition among alternative responses during a preparatory period seems to be consistent with some recent fMRI results (Mars, Piekema, Coles, Hulstijn, & Toni, 2007), but not others (Cavina-Pratesi et al., 2006).

Finally, it should be noted that our interpretation of inter-individual differences in congruency-related behavior and brain activation builds partly on exploratory analyses and recourse to the existing literature on MFC functionality. Thus, future work based on explicit manipulations of cost–benefit tradeoffs needs to be done to confirm the present interpretation in terms of voluntary strategy at work.

5. Conclusions

The present study results demonstrate that differential patterns of preparatory activation can occur during task switching, depending on the type of advance information available. Thus, preparatory task control seems to be multi-faceted rather than monolithic. We propose that the identified distinct neural pathways may correspond to a distinction between attentional, intentional, and strategic control mechanisms. Attentional control mechanisms, supported by areas such as IFJ and pIPS/pSPL, are stimulus-oriented and serve to configure task-related neural pathways so that present (advance target condition) or future (advance cue condition) stimulus input can be processed according to the instructed task rules. Importantly, by demonstrating the absence of selectively cue-related preparatory activation, the current results argue against the notion that such regions might have an exclusive role in task-*selective* attention engaged only when unambiguous priority information is available. Intentional control mechanisms, supported by areas such as DLPFC and aIPS, are output-oriented and serve to generate plans for future action as is the case for advance target stimuli but not for advance task cues. Finally, strategic control mechanisms, related to areas such as MFC, can provide a means of passing from abstract action planning to concrete response preparation, and might be triggered by cost–benefit computations specifying the value of pursuing a high level of response readiness.

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