

Attentional control of task and response in lateral and medial frontal cortex: Brain activity and reaction time distributions

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ABSTRACT

It is unclear whether task conflict is reflected in the anterior cingulate cortex (ACC) or in more dorsal regions of the medial frontal cortex (MFC). When participants switch between tasks involving incongruent, congruent, and neutral stimuli, it is possible to examine both response conflict (incongruent vs. congruent) and task conflict (congruent vs. neutral). Here, we report an event-related functional magnetic resonance imaging (fMRI) study that examined which areas in frontal cortex, including MFC, are implicated in response conflict, task conflict, or both. Stimuli were incongruent and congruent arrow-word combinations, or arrows and words only in a neutral condition. Participants responded manually to the arrow or word. The task varied every second trial. The behavioral data revealed response conflict (incongruent > congruent) and task conflict (congruent > neutral) in mean reaction times and ex-Gaussian latency distribution components. The imaging data revealed activity in both the ACC and a more dorsal region in the MFC (the medial superior frontal gyrus) related to response conflict as well as task conflict. These conflict effects were observed independent of the task performed (arrow or word) or the trial type (repeat or switch). In lateral prefrontal cortex (LPFC), response conflict was associated with activity in ventral LPFC, whereas task conflict activated both ventral and dorsal regions. Thus, whereas the type of conflict (response vs. task) was differentiated in LPFC, no such differentiation was found in MFC, including the ACC. Models of ACC functioning may require modification to take account of these findings.

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1. Introduction

Attentional control refers to the regulatory processes that ensure that our actions are in accordance with our goals. Attentional control implies flexibility to switch rapidly between tasks and the ability to resolve conflict when stimulus dimensions are competing for control of the output. Previous research has implicated regions in the dorsal medial frontal cortex (MFC) and the anterior cingulate cortex (ACC, Brodmann areas [BA] 24 and 32) in attentional control (for reviews, see Bush, Luu, & Posner, 2000; Mansouri, Tanaka, & Buckley, 2009; Miller & Cohen, 2001; Paus, 2001; Posner & Raichle, 1994; Ridderinkhof, Ullsperger, Crone, & Nieuwenhuis, 2004). The exact role of these areas has remained unclear, however.

A task often used in studying attentional control is the Stroop task (Stroop, 1935). In the original color-word version of this task, participants name the ink color of written color words or read the words aloud (MacLeod, 1991). Stimuli can be congruent (e.g., the

word 'red' in red ink), incongruent (e.g., the word 'blue' in red ink), or neutral (e.g., a row of Xs in red ink for color naming or the word 'red' in black ink for word reading). In a blocked-task design, only the color-naming task elicits interference effects, that is, participants are slower when naming the color of incongruent Stroop stimuli compared with neutral or congruent stimuli, whereas there are no effects in word reading. Throughout neuroimaging history, the ACC is typically found to be more active for the incongruent than the congruent or neutral conditions in Stroop color naming, implying a role of the area in dealing with response conflict (Bench et al., 1993; Carter, Mintun, & Cohen, 1995; Kerns et al., 2004; MacDonald, Cohen, Stenger, & Carter, 2000; Pardo, Pardo, Janer, & Raichle, 1990).

Regions in MFC have also been implicated in conflict at the level of tasks. In Stroop paradigms, the difference between word reading and color naming is less when the tasks are mixed than when they are blocked. In particular, when tasks are blocked, Stroop interference is absent in word reading, but when word reading and color naming are mixed, or participants switch between tasks, Stroop interference occurs in word reading (Allport & Wylie, 2000; Gilbert & Shallice, 2002; Yeung & Monsell, 2003): the so-called reverse Stroop effect. Woodward and colleagues have conducted several experiments to elucidate the role of the ACC in Stroop task-switching (Ruff, Woodward, Laurens, & Liddle, 2001;

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Woodward, Metzack, Meier, & Holroyd, 2008; Woodward, Ruff, & Ngan, 2006). In particular, they have demonstrated that the ACC/pre-supplementary motor area (pre-SMA) not only reflects Stroop conflict in color naming, but also the reverse Stroop conflict in word reading when participants switch between the tasks (Ruff et al., 2001). Furthermore, they have shown that the ACC/pre-SMA activation for the reverse Stroop effect decreased as a function of the number of trials since a task switch, suggesting a role for this MFC region in resolving competition between tasks (Woodward et al., 2006). However, in these studies, the authors contrasted incongruent with neutral stimuli, that is, a bivalent stimulus containing conflicting response and task dimensions (i.e., a color word in a conflicting ink color) with a univalent stimulus containing no conflicting response and task dimensions (i.e., a color word in black ink). This contrast not only involves task conflict but also response conflict in the word reading task. Thus, it is unclear whether brain activity related to task or response conflict was measured in these studies.

In a more recent study, Woodward et al. (2008) contrasted neutral trials in a univalent block context with neutral trials in a bivalent block context. This contrast revealed dorsal ACC (dACC, which was actually medial BA 9) activity, interpreted as a role for dACC in signaling a break in task inertia. Although this is convincing evidence for a role of the MFC in task conflict, the exact locus of the effect is still unclear because the activation in the dACC included the ACC (BA 32) and the medial superior frontal gyrus (BA 8). In the previously mentioned studies, Woodward and colleagues (Ruff et al., 2001; Woodward et al., 2006) also found activity for the reverse Stroop effect in ACC/pre-SMA voxels that were located more in the pre-SMA than in the ACC. Thus, the question arises whether the task-conflict effect is actually located in the ACC, in more dorsal regions of the MFC, or both. This question is especially important in light of the results of Milham and Banich (2005). They used congruent, incongruent, and neutral (color-unrelated) color-word Stroop stimuli, which made it possible to contrast bivalent (incongruent and congruent) with univalent (neutral) stimuli and to contrast stimuli involving conflict (incongruent) with stimuli not involving conflict (congruent and neutral). The authors found that for the valency contrast (i.e., congruent > neutral and incongruent > neutral) a region nearby the pre-SMA was activated, while for the conflict contrast (i.e., incongruent > congruent = neutral) a more anterior and ventral region in the ACC was active (Milham & Banich, 2005). Hence, the activity in the ACC was suggested to be conflict specific, while the activity nearby the pre-SMA was suggested to be more generally related to valency (i.e., task conflict). However, although this latter dorsal (and caudal) region in MFC was more active for congruent than for neutral stimuli, participants still responded faster to congruent than neutral stimuli (i.e., an RT facilitation effect was found). Thus, it is not clear whether the manipulation really induced reliable task conflict, which may explain the absence of an effect in the ACC. To conclude, from the studies of Woodward et al. (2008, 2006) and Milham and Banich (2005) it is unclear whether task conflict is reflected in the ACC or in more dorsal regions of the MFC. In several studies, Banich and colleagues (Liu, Banich, Jacobson, & Tanabe, 2006; Milham, Banich, & Barad, 2003; Milham et al., 2001) compared performance on incongruent and neutral Stroop trials. However, the neutral stimuli used were colored non-color words (e.g., the word 'lot' in green ink), affording both color naming and word reading. Thus, it remains unclear to what extent the neutral stimuli evoked response conflict, task conflict, or both in these studies.

To resolve these issues, we used a design with incongruent, congruent, and neutral Stroop-like stimuli, in which participants switched between responding to the two dimensions of the stimuli (Fig. 1) (see also, Aron, Monsell, Sahakian, & Robbins, 2004). Switching between tasks creates conflict at the level of the whole

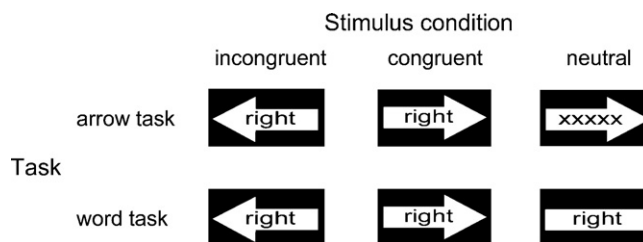


Fig. 1. Examples of incongruent, congruent, and neutral stimuli in the arrow and the word tasks. Incongruent and congruent stimuli are both bivalent, whereas neutral stimuli are univalent. In the study, the words were given in the participants' native language, i.e., Dutch.

task set and at the level of individual responses (e.g., Allport & Wylie, 2000; Monsell, 2003; Rogers & Monsell, 1995). Our incongruent and congruent stimuli afforded both tasks in the experiment (i.e., they were bivalent), whereas our neutral stimuli afforded only one task (i.e., they were univalent) (Allport & Wylie, 2000; Pashler, 2000). When people switch between tasks involving incongruent, congruent, and neutral stimuli, it is possible to examine both response- and task-related activity evoked by the stimuli (Aron et al., 2004). Because bivalent incongruent and congruent stimuli are equally associated with the two tasks, slower responding to incongruent than to congruent stimuli must reflect response conflict. Bivalent congruent stimuli create no conflict at the response level but are associated with both tasks, whereas univalent neutral stimuli are associated with only one task. Therefore, slower responding to bivalent congruent than to univalent neutral stimuli can only reflect conflict at the task level (Aron et al., 2004; Monsell, 2005; Rogers & Monsell, 1995): "In task-switching experiments, competition from stimulus→task associations is revealed by a pattern Rogers and Monsell (1995) observed: RTs substantially shorter for neutral (N) than for congruent (C) stimuli... Hence we argued that observing a positive C–N contrast (i.e., C slower than N) is a marker for competition at the task-set level" (Monsell, 2005, p. 184).

Our use of the term 'response conflict' refers to conflict at the level of individual response tendencies as opposed to conflict at the level of task set ('task conflict'), which by definition involves multiple stimulus-response mappings. Conflict at the individual response level may occur at one or more processing stages, including conceptual processing, response selection, and motor programming of the manual response (see Roelofs, 2003; Roelofs & Hagoort, 2002; Roelofs, van Turennout, & Coles, 2006, for a computational model of performance on Stroop-like tasks). Milham et al. (2001) provided evidence that the ACC and right dorsal lateral prefrontal cortex (LPFC) are specifically involved in conflict during response selection, whereas left dorsal LPFC is implicated in conflict at other processing levels. Our design (i.e., the contrast between incongruent and congruent trials) does not allow a distinction between response selection and other processing stages, although the findings of Milham et al. (2001) make it likely that conflict relates to response selection in our experiment as well.

We employed an arrow-word Stroop task, allowing for manual responding in the scanner with non-arbitrary mapping of responses onto buttons (see also, Aarts, Roelofs, & van Turennout, 2008; Baldo, Shimamura, & Prinzmetal, 1998; Roelofs et al., 2006; Turken & Swick, 1999). Participants were presented with bivalent incongruent or congruent combinations of left- or right-pointing arrows and the words 'left' or 'right' (e.g., a right-pointing arrow combined with the word 'left') or univalent arrows and words only in a neutral condition (e.g., a right-pointing arrow combined with a row of Xs). A task cue presented on each trial reminded the subjects whether they had to respond to the direction denoted by the arrow or by the word. Although the tasks switched predictably every two trials, we used external cues to not make the task too difficult to perform

with long inter-trial intervals. We were, however, only interested in the stimulus-related activity.

We hypothesized that response conflict is indexed by the difference in performance between incongruent and congruent conditions, while task conflict is indexed by the difference between the congruent and neutral conditions. To obtain converging evidence for this assumption in our experiment, we performed ex-Gaussian distribution analyses on the response times (Ratcliff, 1979). The ex-Gaussian is a mathematical model used to describe response time distributions. Ex-Gaussian functions provide good fits of empirical response time distributions and have been widely adopted (e.g., Heathcote, Popiel, & Mewhort, 1991; Hohle, 1965; Luce, 1986; Spieler, Balota, & Faust, 1996; Yap & Balota, 2007). The ex-Gaussian distribution is a convolution of a Gaussian and an exponential distribution, and it has three parameters: μ , σ , and τ . The μ and σ parameters reflect, respectively, the mean and standard deviation of the Gaussian portion, and τ reflects both the mean and standard deviation of the exponential portion. Theoretically, the sum of μ and τ is equal to the mean of the overall distribution (Hohle, 1965; Luce, 1986). Ex-Gaussian analyses allow differences between conditions to be separated into distributional shifting, reflected in μ , and distributional skewing, reflected in τ . Whereas μ has been associated with the process of resolving response competition in Stroop-like tasks (e.g., Kane & Engle, 2003; Roelofs, 2008b), τ has been associated with processes at the level of task set, such as goal maintenance (Duncan, Emslie, Williams, Johnson, & Freer, 1996; Kane & Engle, 2002, 2003; Schmiedek, Oberauer, Wilhelm, Suss, & Wittmann, 2007). Thus, according to our assumptions, response conflict (i.e., incongruent > congruent) should be reflected in μ , and task conflict (congruent > neutral) should be apparent in τ in our experiment.

The present design allowed us to directly test whether the ACC region typically involved in response conflict (incongruent > congruent) is also involved in task conflict (congruent > neutral) or whether task conflict is associated with a more dorsal region in MFC. We also assessed these effects in LPFC, where processes at the level of response selection are often associated with ventral regions and processes at the level of task set with dorsal regions, although the distinction need not be absolute (for reviews, see Kane & Engle, 2002; Roelofs, 2008a; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997).

2. Methods

2.1. Participants

Twelve neurologically healthy Dutch subjects (10 female, mean age 21.2 years, range 19–25) participated in the experiment. All participants were right-handed and native speakers of Dutch. They were compensated for participation and gave written informed consent in a manner approved by the Dutch Central Committee on Research Involving Human Subjects (CCMO).

2.2. Design and procedure

The participants were scanned while performing a manual arrow-word version of the Stroop task. The stimuli consisted of written words superimposed onto arrows, or arrows and words only (Fig. 1). The lines and letters of the stimuli were white on a blue background. The arrows pointed to the left or to the right. The words were the Dutch words for right ('rechts') and for left ('links'). Participants responded manually to the Stroop-like stimuli by pressing a left or a right button on a scanner-compatible button box. Participants responded either to the direction of the arrow (arrow task) or to the direction indicated by the word (word task). Participants were told to respond as quickly and accurately as possible with the left middle finger (for left response) and the left index finger (for right response). This button-box response was executed with the left hand (right motor cortex) because the stimuli themselves were language-related (left hemisphere). In the congruent Stroop condition, the arrow and the word denoted the same direction (e.g., the word 'right' in an arrow pointing to the right). In the incongruent Stroop condition, the arrow and the word denoted a different direction (e.g., the word 'left' in an arrow pointing to the right). In the neutral Stroop condition, the stimuli consisted of words ('left' or 'right') in rectangles without arrow heads or rows of five or six Xs in arrows. In both tasks,

each of the three conditions included 40 stimuli (240 trials in total). Congruent, incongruent, and neutral stimuli were presented randomly intermixed.

The task switched predictably every two trials (order: arrow arrow word word arrow arrow, etc.), following the alternate runs paradigm (Rogers & Monsell, 1995). Half of the participants started the experiment with the arrow task, the other half with the word task. Although the task switched predictably, a cue at the beginning of each trial indicated what task to perform next. The cue was the Dutch word for word ('woord'), which instructed the subjects to respond to the word, or the Dutch word for arrow ('pijl'), instructing them to respond to the arrow. The Stroop stimulus followed the cue after a variable delay of minimally 2 and maximally 7 s long. Similarly, a variable delay of 2–7 s was used between a Stroop stimulus and the next task cue, in which participants made their response. Participants were not limited in their response times. The jitter between cue and stimulus and the inter-trial interval was calculated with a simulation of the blood oxygenation level-dependent (BOLD) response in SPM99 (Wellcome Dept. of Cognitive Neurology, London). The variable delays enabled us to characterize the hemodynamic responses at a fine temporal resolution (Josephs, Turner, & Friston, 1997) and thus allowed us to reliably distinguish the BOLD response to the cue from the BOLD response to the Stroop stimulus (see for a similar procedure: Mars et al., 2005; Toni, Schluter, Josephs, Friston, & Passingham, 1999). This calculation was repeated several times, generating a random sequence with appropriate delays for every participant separately. Because the delay between cue and Stroop stimulus could not be predicted, the participant needed to be ready to respond at any time. Stimuli remained on the screen for 600 ms.

Conflict processes were indexed by differences in activity among incongruent, congruent, and neutral Stroop stimuli. As indicated, bivalent incongruent and bivalent congruent stimuli afford and activate both tasks in an experiment, whereas univalent neutral stimuli afford and activate only one of the tasks. Thus, more activity for incongruent than congruent stimuli indexes response conflict, whereas more activity for congruent than neutral stimuli indexes conflict between task sets. These contrasts are closely related to, respectively, the conflict contrast and the valency (or 'competition') contrast of Milham and Banich (2005).

2.3. fMRI data acquisition

Whole-brain imaging was performed on a 3T Siemens Trio MRI system. Functional data were acquired using a gradient-echo echo-planar scanning sequence (30 axial slices, 3.5 mm thick, interslice gap = 0.35 mm, repetition time = 2210 ms, echo time = 40 ms, voxel size = 3.5 mm × 3.5 mm × 3.5 mm, field of view = 224 mm, flip angle = 70°). All functional images were acquired in a single run with a duration of 40 min. Visual stimuli were projected on a screen and were viewed through a mirror attached to the head coil. After the acquisition of functional images, high-resolution anatomical images were acquired using an MP-RAGE sequence (192 sagittal slices, repetition time = 2300 ms, echo time = 3.03 ms, voxel size = 1.0 mm × 1.0 mm × 1.0 mm, field of view = 256 mm).

2.4. Behavioral data analysis

2.4.1. Mean response times and error rates

The mean latencies of the correct manual responses to the arrows and words in the two tasks (arrow task, word task) and error rates were analyzed using repeated-measures analyses of variance (ANOVA) with the factors STROOP CONDITION (congruent, incongruent, neutral), TASK (word, arrow), and TRIAL TYPE (switch, repeat). All variables were tested within participants. *T*-Tests were performed one-tailed unless mentioned otherwise.

2.4.2. Ex-Gaussian parameters

In addition, the data were examined at the level of distributional characteristics using ex-Gaussian analyses. These analyses characterize a response time distribution by assuming an explicit function for the shape of the distribution. The ex-Gaussian function consists of a convolution of a Gaussian and an exponential distribution and it has three parameters, μ and σ (characterizing the Gaussian distribution) and τ (characterizing the exponential distribution). Previous research has associated μ with the process of resolving response competition in Stroop-like tasks and τ has been associated with processes at the level of task set. The distributional parameters of the present data were estimated using the quantile maximum likelihood estimation method proposed by Brown and Heathcote (2003). The ex-Gaussian parameters (μ , σ , and τ) were obtained per condition for each participant individually using the program of Brown and Heathcote. All estimations converged within 31 iterations. Condition differences in the parameters were then examined by conducting analyses of variance.

2.5. fMRI data analysis

2.5.1. Image processing

Data were analyzed using SPM2 (Wellcome Dept. of Cognitive Neurology, London). The first five volumes of each participant's data set were discarded to allow for T1 equilibrium. Functional images were corrected for differences in slice acquisition timing, followed by motion correction. Structural and functional data were co-registered and spatially normalized to a standard stereotaxic space (Montreal Neurological Institute (MNI) template), using a 12-parameters affine transformation.

Table 1
Regions showing an effect of both task conflict and response conflict determined by the contrast congruent > neutral stimuli inclusively masked (at $p = .01$) by the contrast incongruent > congruent stimuli, and regions activated for either task conflict or response conflict.

Region	BA	Task + response conflict					Task conflict (con > neu)					Response conflict (inc > con)				
		Cluster size	Voxel <i>T</i> -value	MNI coordinates			Cluster size	Voxel <i>T</i> -value	MNI coordinates			Cluster size	Voxel <i>T</i> -value	MNI coordinates		
				x	y	z			x	y	z			x	y	z
ACC	32/24	13	3.84*	-6	38	28	10	3.67*	-6	34	10	91	4.41	-10	42	26
meSFG	8	460	5.80*	-2	26	44	1295	5.80*	-2	26	44	116	3.87	2	30	46
IFG - L	47	161	4.23*	-32	26	-14						150	4.14	-40	22	-14
IFG - R	47	56	4.41*	36	24	-18						308	5.13	34	24	-14
IFG - L	45	72	4.49*	-44	22	24						31	3.67	-42	28	6
												10	3.62	-42	20	14
IFG - R	45						271	4.65*	36	24	8					
IFG - L	44	149	5.21*	-36	10	28	1591	5.32*	-34	8	30					
IFG - R	44						25	3.50*	58	16	28					
MFG - L	10						10	3.67*	-40	60	2					
MFG - R	10						574	4.40*	32	58	4					
MFG - R	8	22	4.28*	44	6	44	26	3.43*	26	16	42					
MFG - R	6						1287	5.26*	38	2	48					
preCG - L	6											19	3.86	-54	4	38
												22	3.45	-46	4	30
STG - L	22						15	3.45*	-60	-50	8					
Ang G - L	39											44	4.26	-28	-60	36
IPL - L	40	426	4.91*	-32	-54	44	857	4.91*	-32	-54	44	118	4.25	-36	-38	40
												176	4.12	-48	-52	30
IPL - R	40						450	4.55*	36	-48	44					
SPL - L	7											20	3.66	-32	-64	54
												16	3.53	-26	-66	46
SPL - R	7						10	3.50*	32	-68	52					
preCun - R	7						454	4.88*	12	-64	58					
Caud - L							63	4.15*	-8	0	4	18	3.74	-8	10	-2
Caud - R							53	3.68*	14	2	6	42	3.73	10	12	6
Thal - L							27	3.47*	-8	-14	10					
Cerebel - R							15	3.46*	34	-64	-36					

Note: This table presents the results of the 2nd level random effects group analysis. The *T* values represent the value for local maxima at $p < .001$ (only one peak per activated cluster is shown here). The cluster size refers to the total number of (2 mm × 2 mm × 2 mm) voxels included in the cluster (minimum of 10 voxels). The MNI coordinates are measured in mm. BA = Brodmann areas, con = congruent stimuli; neu = neutral stimuli; inc = incongruent stimuli; ACC = anterior cingulate cortex; meSFG = medial superior frontal gyrus; IFG = inferior frontal gyrus; MFG = middle frontal gyrus; preCG = precentral gyrus; STG = superior temporal gyrus; Ang G = angular gyrus; IPL = inferior parietal lobule; SPL = superior parietal lobule; preCun = precuneus; Caud = caudate nucleus; Thal = thalamus; Cerebel = cerebellum; L = left; R = right.

* Voxel *p*-value is <.05 (false discovery rate corrected).

After normalization, voxels were resampled with a 2 mm × 2 mm × 2 mm voxel size. Images were spatially smoothed with a 6 mm full-width at half-maximum (FWHM) isotropic Gaussian kernel. High-pass filtering (128 s) was applied to the time series of the functional images to remove low-frequency drifts.

2.5.2. Statistical model

Statistical analyses were performed in the context of the general linear model in SPM2. On the first level, all event-types were modeled. Stimulus-related predictors included word congruent, neutral, and incongruent, and arrow congruent, neutral, and incongruent stimuli for each trial type (switch and repeat). Trials on which participants had made an error were put together as a separate regressor of non-interest. All predictors of interest were modeled as a stick function (duration=0) convolved with a canonical HRF (Friston et al., 1998) and its temporal derivative to account for variance due to different slice timings as well as to different HRF delays/shapes for different regions. The first derivatives of the six motion parameters were included as covariates. Effects were estimated using a subject-specific fixed-effects model.

Consistent effects across subjects were tested using a random effects analysis. A within-subject ANOVA was performed on the second level with first-level contrast images for every subject, corresponding to the 12 cells of the 3 × 2 × 2 design [STROOP CONDITION (congruent, incongruent, neutral) × TASK (word, arrow) × TRIAL TYPE (switch, repeat)]. We report the results of this random effects analysis with the statistical threshold set at $p < .001$ at the voxel level and a minimum cluster size of 10 voxels (Forman et al., 1995). We also mention the false discovery rate (FDR) corrected p -value at the voxel level in the text for the ROIs in MFC and in Table 1.

2.5.3. Contrasts

First, we looked at the contrasts for task conflict (congruent > neutral stimuli) and response conflict (incongruent > congruent stimuli) separately. However, we specifically wanted to test whether a region in the ACC typically involved in response conflict is also involved in task conflict. To that end, we specified the contrast congruent > neutral (i.e., task conflict) inclusively masked (at $p = .01$) by the contrast incongruent > congruent (i.e., response conflict). This way, we could identify regions that were responsive to both types of conflict.

2.5.4. Region-of-interest analysis

To test whether the effects of response and task conflict in the MFC regions were influenced by task or trial type, we performed a ROI analysis using MarsBaR (Brett, Anton, Valabregue, & Poline, 2002). From the 2nd level group analysis ($P_{FDR} < .05$), we chose the regions within the MFC and LPFC (with a minimum cluster size of 10 voxels) that responded to both response and task conflict, determined with the contrast specified above (congruent > neutral, masked inclusively by incongruent > congruent [at $p = .01$]). Mean beta weights from all voxels in these regions were extracted for all event types and all subjects. These regionally averaged beta-weights were analyzed in repeated-measurement ANOVAs.

To ascertain whether or not task conflict would activate more dorsal levels of the MFC and response conflict more ventral levels, we also used anatomically defined AAL ROIs (Tzourio-Mazoyer et al., 2002). To investigate conflict effects in MFC, we performed analyses on the left and right anterior cingulum ROIs and left and right medial superior frontal ROIs. With a repeated-measurement ANOVA on the regionally averaged beta-weights, we investigated region by conflict effects. To establish a possible dissociation between task conflict and response conflict in lateral prefrontal cortex (LPFC), a similar analysis was done with LPFC ROIs. We used the left and right middle frontal ROIs (dorsal LPFC), and left and right inferior frontal pars triangularis and inferior frontal pars orbitalis ROIs (ventral LPFC). The dorsal LPFC is often associated with processes at the level of task set, and the ventral LPFC with processes at the level of response selection.

3. Results

3.1. Behavioral data

Fig. 2 shows the mean response latencies and error rates for each Stroop condition on switch and repeat trials, separately for each task.

3.1.1. Mean response times

Response times were longer on switch than on repeat trials and longer in the incongruent condition than in the other conditions (Fig. 2). There were main effects of TRIAL TYPE [$F(1,11) = 70.45$, $p < .001$] and STROOP CONDITION [$F(2,22) = 38.92$, $p < .001$]. There was, however, no main effect of TASK [$F(1,11) = 2.95$, $p > .1$]. There was no TRIAL TYPE × TASK interaction [$F(1,11) = 1.86$, $p > .1$], but there was a TRIAL TYPE × STROOP CONDITION interaction [$F(2,22) = 3.98$, $p = .03$] and a TASK × STROOP CON-

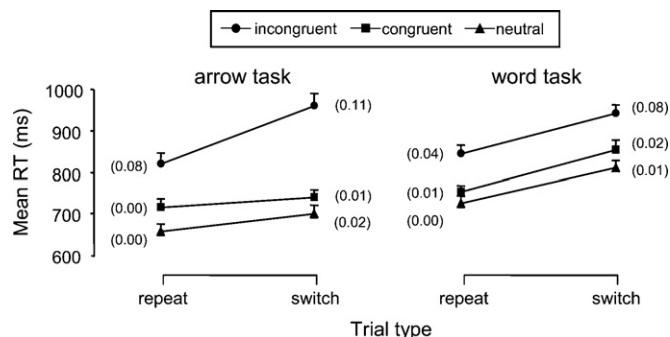


Fig. 2. Mean reaction times (RT) for the three Stroop conditions on repeat and switch trials in the arrow and word tasks. Error rates are given between parentheses. Error bars represent the standard error of the mean.

DITION interaction [$F(2,22) = 4.91$, $p = .02$]. There was no TRIAL TYPE × TASK × STROOP CONDITION interaction [$F(2,22) = 2.38$, $p > .1$].

In the arrow task, responses were slower for incongruent than for congruent stimuli on both repeat [$t(11) = 3.9$, $p < .001$] and switch trials [$t(11) = 5.09$, $p < .001$], and slower for congruent than for neutral stimuli on repeat trials [$t(11) = 3.3$, $p = .004$], and there was a trend towards this effect on switch trials [$t(11) = 1.66$, $p = .06$]. The difference between incongruent and congruent trials was greater on switch than on repeat trials [$t(11) = 3.3$, $p = .007$]. The congruent and neutral conditions did not differ between switch and repeat trials [$t(11) < 1$]. In the word task, responses were slower for incongruent than for congruent stimuli on both repeat [$t(11) = 2.96$, $p = .007$] and switch trials [$t(11) = 2.51$, $p = .01$]. Response times did not differ between congruent and neutral stimuli on repeat trials [$t(11) = 1.03$, $p > .1$], but they were slower for congruent than for neutral stimuli on switch trials [$t(11) = 1.82$, $p = .05$]. The difference between the incongruent and congruent conditions, and between the congruent and neutral conditions, did not differ between switch and repeat trials [both $t(11) < 1$].

To summarize, responding was slower on switch than repeat trials for both tasks, replicating the standard switch cost in the literature. Moreover, response times differed among the Stroop conditions in both tasks, indicating effects of both response conflict and task conflict.

3.1.2. Error rates

Fig. 2 (error rates between parentheses) shows that more errors were made on switch than on repeat trials. Also, more errors were made in the incongruent condition than in the other conditions. The error rates exhibited main effects of TRIAL TYPE [$F(1,11) = 7.65$, $p < .018$] and STROOP CONDITION [$F(2,22) = 18.78$, $p < .001$], but there was no TRIAL TYPE × STROOP CONDITION interaction [$F(2,22) = 1.42$, $p = .26$]. For the error rates, there was no main effect of TASK [$F(1,11) = 1.61$, $p = .23$], and there was no TASK × STROOP CONDITION interaction [$F(2,22) = 1.70$, $p = .21$]. Also, the TRIAL TYPE × TASK × STROOP CONDITION interaction was not significant [$F(2,22) < 1$].

Overall, participants made more errors when there was response conflict, i.e., incongruent vs. congruent Stroop stimuli [$t(11) = 4.33$, $p = .001$]. However, there was no difference between the congruent and neutral condition [$t < 0$], so no effect of task conflict in the error rates.

3.1.3. Ex-Gaussian parameters

We also investigated the conflict effects on the three ex-Gaussian parameters, μ , σ , and τ . The values of these parameters for the incongruent, congruent, and neutral conditions are shown in Fig. 3. Note that the congruent condition was slower than the neutral

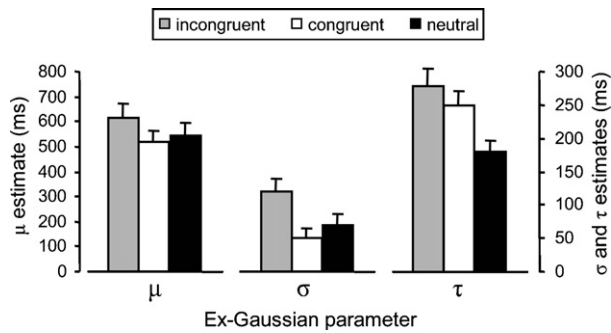


Fig. 3. Mean ex-Gaussian parameter estimates as a function of Stroop condition. Error bars represent the standard error of the mean.

condition in the mean RTs (765 ms vs. 723 ms, respectively), but the congruent condition was numerically faster than the neutral condition in μ . For μ , there was a main effect of STROOP CONDITION [$F(2,22)=7.96, p=.003$]. This effect on μ was caused by a difference between the incongruent and congruent conditions [$F(1,11)=8.13, p=.016$] and not by the congruent and neutral conditions [$F(1,11)=2.25, p=.162$]. There was an interaction of STROOP CONDITION and TRIAL TYPE in μ [$F(2,22)=5.12, p=.015$], revealing that the difference between incongruent and congruent trials in μ was greater on switch trials (160 ms) than repeat trials (67 ms), like in the mean RTs (see Fig. 2). There was no interaction of STROOP CONDITION and TASK in μ [$F(2,22)=1.70, p=.21$]. For σ , there was also a main effect of STROOP CONDITION [$F(2,22)=4.32, p=.026$], which was also caused by a difference between incongruent and congruent trials [$F(1,11)=5.9, p=.033$] and not by congruent

and neutral trials [$F(1,11)<1$]. There was no interaction of STROOP CONDITION and TRIAL TYPE in σ [$F(2,22)=1.63, p=.28$]. STROOP CONDITION interacted with TASK in σ [$F(2,22)=5.55, p=.011$], which occurred because σ was larger for the incongruent condition in the arrow task than in all other conditions of both tasks. For τ , there was again a main effect of STROOP CONDITION [$F(2,22)=13.4, p<.001$]. However, in contrast to the effects on μ and σ , the effect on τ was caused by a difference between congruent and neutral trials [$F(1,11)=20.1, p=.001$] and not by incongruent and congruent trials [$F(1,11)=1.53, p=.242$]. There was no interaction of STROOP CONDITION and TRIAL TYPE in τ [$F(2,22)=1.30, p=.29$] and also not of STROOP CONDITION and TASK [$F(2,22)<1, p=.66$].

To summarize, the difference in performance between the incongruent and congruent conditions in the experiment was uniquely associated with the μ and σ parameters of the ex-Gaussian distribution. In contrast, the difference in performance between the congruent and neutral conditions was uniquely associated with the τ parameter. Given that earlier research has associated μ with the process of resolving response competition, and τ with processes at the level of task set (such as goal maintenance), the results of the ex-Gaussian analyses provide converging evidence for our hypothesis that response conflict is indexed by the difference in performance between the incongruent and congruent conditions, and that task conflict is indexed by the difference between the congruent and neutral conditions.

3.2. Imaging data

Areas activated by response conflict, task conflict, or both are shown in Table 1 and Fig. 4. Response conflict and task conflict

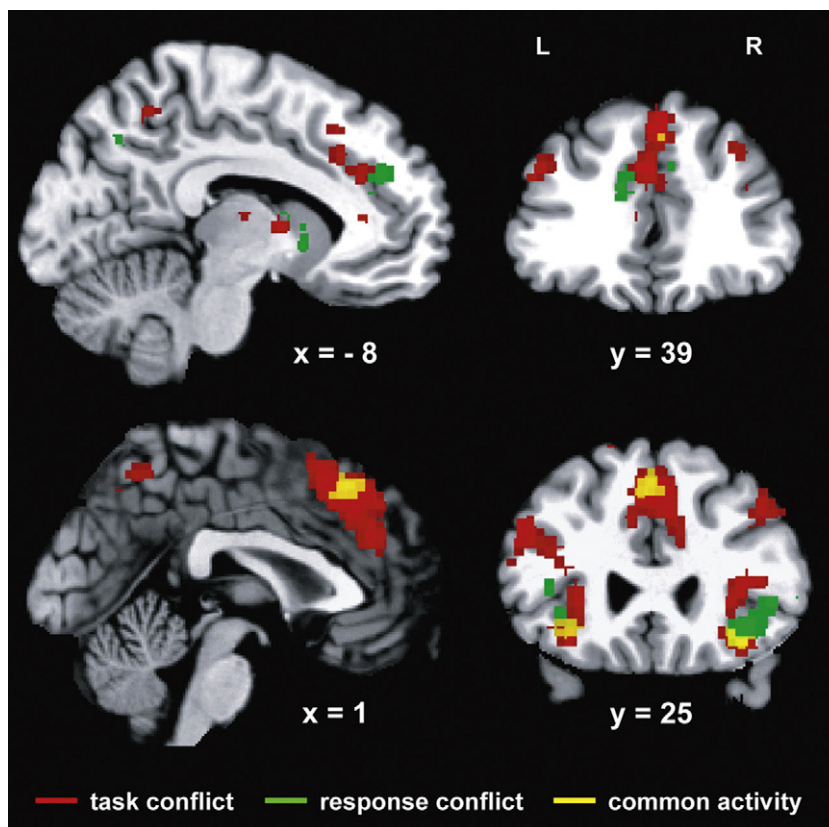


Fig. 4. Contrasts of response and task conflict overlaid on two sagittal (left) and two coronal sections (right), thresholded at $t=3.16$ at the voxel level. Red denotes activity for the task conflict contrast (congruent > neutral stimuli). Green denotes activity for the response conflict contrast (incongruent > congruent stimuli). Yellow denotes common activity for task and response conflict. The sagittal sections show adjacent and overlapping activity for task and response conflict in the anterior cingulate cortex (ACC; top) and in the medial superior frontal gyrus (meSFG; bottom). The coronal sections show effects of task conflict in dorsal parts of the lateral prefrontal cortex (LPFC), and common activity for task and response conflict in ventral parts of LPFC (bottom).

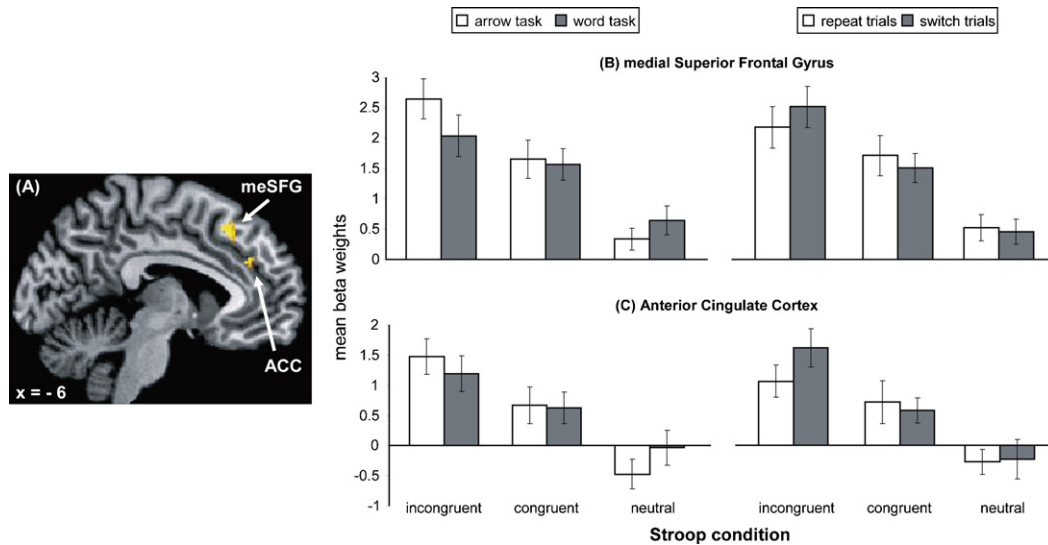


Fig. 5. Response and task conflicts in medial frontal cortex. (A) Sagittal section showing increased medial Superior Frontal Gyrus activity (meSFG/BA 8; MNI: $x = -2, y = 26, z = 44$) and increased anterior cingulate activity (ACC/BA 32; MNI: $x = -6, y = 38, z = 28$) for the contrast congruent vs. neutral stimuli (thresholded at $p < .001$ and 10 contiguous voxels), inclusively masked by the contrast incongruent vs. congruent stimuli (at $p < .01$) in the random effects group analysis. (B) Mean beta weights of all active voxels in meSFG and (C) ACC are plotted separately for the three Stroop conditions in the arrow and word task (left) and in repeat and switch trials (right). There were no interactions of task or trial type with Stroop condition. BA = Brodmann area. MNI = coordinates of the peak voxel in the random effects group average. Error bar represents the standard error of the mean.

both activated areas in dorsal and ventral MFC and in ventral LPFC (inferior frontal gyrus), while areas in dorsal LPFC (middle frontal gyrus) seemed to be primarily activated by task conflict. In the MFC, two regions showed an effect for response conflict and were also activated for conflict at the task level, as revealed by the masking contrast used (Fig. 5). This was the ACC (BA 32; MNI: $-6, 38, 28$; $p(\text{FDR corrected}) = .009$) and a more dorsal and caudal region in the medial superior frontal gyrus (meSFG, BA 8; MNI: $-2, 26, 44$; $p(\text{FDR corrected}) = .002$). To examine whether these conflict effects were influenced by the task that had to be performed (arrow or word) or by the trial type (repeat or switch), we performed an ANOVA on the regionally averaged beta weights of these two MFC regions (see Fig. 5). As can be seen in Table 2, the effects of response and task conflict were independent of task or trial type in both regions of the MFC (ACC and meSFG). We performed a similar functional

ROI analysis with regions in LPFC (BA 44–47) activated by both response conflict and task conflict (see Table 1). Table 2 shows that in these LPFC regions, conflict effects were also not considerably influenced by the task that had to be performed (arrow, word). In the inferior frontal gyrus (IFG) pars triangularis (BA 45), there were only trends towards interaction effects of task by response conflict [$F(1,11) = 3.43, p = .091$] and task by task conflict [$F(1,11) = 3.7, p = .081$]. In the IFG pars orbitalis (BA 47), there was no interaction of task by task conflict [$F(1,11) < 1$], but only an interaction of task by response conflict [left: $F(1,11) = 7.94, p = .017$; right: $F(1,11) = 3.36, p = .094$]. This occurred because these regions in ventral LPFC were more activated for the incongruent condition in the arrow task than in the word task. Similar to the regions in MFC, trial type (switch or repeat) did not interact with Stroop condition in the functionally defined regions in LPFC.

Table 2

Main effects, interaction effects and effects of task conflict and response conflict in functionally and anatomically defined regions in medial and lateral frontal cortex.

Region	Stroop condition $F(2,22)$	Task $F(1,11)$	Trial type $F(1,11)$	Task \times Stroop condition $F(2,22)$	Trial type \times Stroop condition $F(2,22)$	Task-set conflict $t(11)$	Response conflict $t(11)$
ACC ($-6, 38, 28$)	25.37***	<1	1.03	1.33	<1	4.17**	3.68**
A: Cing Ant L	9.40**	<1	<1	1.49	1.29	2.67*	2.33*
A: Cing Ant R	8.93**	<1	<1	1.33	1.07	2.83*	1.86
meSFG ($-2, 26, 44$)	38.98***	<1	<1	2.76	<1	5.19***	4.22**
A: Front Sup Med L	14.32***	<1	<1	1.21	<1	4.25**	2.17
A: Front Sup Med R	8.23**	1	<1	1.74	1.31	3.11*	1.43
IFG-L ($-32, 26, -14$)	25.18***	<1	2.60	6.80**	1.51	14.45**	33.27***
A: Front Inf Orb L	20.26***	<1	<1	5.02*	1.33	4.00**	3.55**
IFG-R ($36, 24, -18$)	24.90***	<1	3.27	3.60*	1.69	14.04**	25.92***
A: Front Inf Orb R	14.98***	<1	<1	2.47	<1	3.66**	2.69*
IFG-L ($-44, 22, 24$)	22.79***	3.63	<1	6.40**	<1	13.99**	11.96**
A: Front Inf Tri L	20.69***	1.13	<1	7.32**	<1	3.75**	3.69**
A: Front Inf Tri R	12.37***	<1	1.14	2.67	<1	3.06*	2.29*
A: Front Mid L	9.21**	1.71	2.6	2.25	<1	3.64**	<1
A: Front Mid R	9.65**	1.12	2.58	1.17	<1	3.64**	<1

ACC = anterior cingulate cortex (MNI coordinates x, y, z); meSFG = medial superior frontal gyrus (MNI coordinates x, y, z); A = "AAL" ROI (Tzourio-Mazoyer et al., 2002); Cing Ant = anterior cingulum; Front Sup Med = medial superior frontal; Front Mid = middle frontal; Front Inf Tri = inferior frontal (pars triangularis); Front Inf Orb = inferior frontal (pars orbitalis); L = left; R = right.

* $p < .05$
 ** $p < .01$
 *** $p < .001$

To investigate conflict effects with functionally unbiased ROIs, we performed similar analyses on anatomical (AAL) ROIs in dorsal and ventral MFC and LPFC (see Table 2). In MFC, especially the left anterior cingulum ROI showed effects of both response and task conflict. On a more dorsal level in MFC, the medial superior frontal ROI showed effects of task conflict and a trend towards a response conflict effect on the left ($p = .053$, 2-tailed). Both dorsal and ventral ROIs in LPFC showed effects of task conflict, while response conflict was clearly associated with ventral instead of dorsal LPFC (Table 2). Again, whether participants had to perform the arrow or word task only interacted with the Stroop condition in left ventral LPFC regions (inferior frontal pars triangularis and pars orbitalis), but task and trial type (switch or repeat) did not interact with Stroop condition in the MFC regions.

To investigate whether task conflict and response conflict could be dissociated in dorsal and ventral MFC and LPFC, we directly compared these conflict effects between the left-lateralized (most activated) anatomically defined ventral and dorsal regions. Although more dorsal levels of the MFC (medial superior frontal ROIs) showed only a marginally significant response conflict effect, there was no region by response conflict effect when comparing the left medial superior frontal ROI with the left anterior cingulum ROI [$F(1,11) < 1$], and no region by task conflict effect either [$F(1,11) < 1$]. Similarly, between the functionally defined regions in ACC and meSFG, there was no difference in response conflict [$F(1,11) < 1$] or task conflict effect [$F(1,11) = 2.32$, $p = .156$]. Thus, although it seems apparent from Fig. 4 and Table 1 that task conflict more extensively activates dorsal regions in MFC than the ACC, we do not find any differences for either measure of conflict between anatomically and functionally defined ROIs in MFC. The anatomically defined LPFC regions, on the other hand, demonstrated a clear dissociation in conflict effects. The dorsal LPFC regions showed less response conflict than the ventral regions in LPFC [left middle frontal vs. left inferior frontal pars triangularis: $F(1,11) = 18.47$, $p = .001$; left middle frontal vs. left inferior frontal pars orbitalis: $F(1,11) = 41.01$, $p < .001$], while there was no difference between regions within ventral LPFC [left inferior frontal pars triangularis vs. left inferior frontal pars orbitalis: $F(1,11) < 1$]. In contrast, task conflict was equally associated with dorsal and ventral regions in LPFC [left middle frontal vs. left inferior frontal pars triangularis: $F(1,11) = 1.39$, $p = .263$; left middle frontal vs. left inferior frontal pars orbitalis: $F(1,11) < 1$].

4. Discussion

The present fMRI study examined the role of the ACC in attentional control during response conflict and conflict at the level of task sets. We mixed arrow and word Stroop tasks with bivalent incongruent, bivalent congruent, and univalent neutral stimuli. Our behavioral data yielded the expected patterns of switch costs and measures of both response conflict and task conflict in the mean RTs. Furthermore, the ex-Gaussian analyses of the response times demonstrated that our measure of response conflict (incongruent > congruent) was uniquely associated with the μ and σ parameters, which have previously been linked to the resolution of response competition. Moreover, our measure of task conflict (congruent > neutral) was uniquely associated with the τ parameter, which has previously been linked to processes at the level of task set. The fMRI findings indicate that the ACC is activated by both response conflict and task conflict, independent of the particular task (word or arrow task) and trial type (repeat or switch). Using anatomical ROIs, there was no difference in conflict effects between ventral and dorsal MFC regions. In contrast, there was a difference between ventral and dorsal LPFC regions: response conflict was associated with ventral rather than dorsal LPFC, whereas there was no such regional dissociation for task conflict.

4.1. Behavioral data

We found reliable effects of response and task conflict in the mean RTs. Converging evidence that we correctly measured response conflict and task conflict came from the ex-Gaussian analyses that we performed. In these analyses, response conflict was reflected in the Gaussian parameters of the distribution (μ and σ), while task conflict was reflected in the exponential parameter τ , which has previously been associated with processes at the level of task set (e.g., Kane & Engle, 2003; Schmiedek et al., 2007).

This conclusion was further corroborated by comparing the direction of the difference between the congruent and neutral conditions in μ and τ . Numerically, the congruent condition was faster than neutral in μ , but the congruent condition was slower than neutral in τ . Thus, the slower responding on congruent than neutral trials in the mean RTs was driven by the slower responding on congruent than neutral trials in τ . For μ , there was Stroop facilitation. The pattern of numerical facilitation in μ and interference in τ replicates previous results obtained with standard Stroop color naming (Heathcote et al., 1991; Spieler et al., 1996). When participants only perform the Stroop color naming task, the magnitude of the facilitation in μ tends to equal the interference in τ , which leads to a null effect in the mean RTs. In the current task switching experiment, where there was presumably much more competition between tasks, the interference in τ was much larger than the facilitation in μ , yielding a net interference effect in the mean RTs. Relative to neutral trials in a task switching situation, congruent trials yield both task competition (because they activate the competing task) and response facilitation (because they activate the appropriate response). In the mean RTs, we found faster responses on neutral trials than on congruent trials, indicating that a lack of task conflict on neutral trials outweighed the response facilitation on congruent trials.

To conclude, the results of the ex-Gaussian analyses provide converging evidence for our hypothesis that response conflict is indexed by the difference in performance between the incongruent and congruent conditions, and that task conflict is indexed by the difference between the congruent and neutral conditions. Moreover, a tradeoff between task competition and response facilitation on congruent trials was observed in the ex-Gaussian parameters: the congruent condition was faster than neutral in μ (reflecting response facilitation), but slower than neutral in τ (reflecting task competition).

Task conflict (congruent > neutral) in RTs did not differ between switch and repeat trials in either task. This may come as a surprise given the presence of an RT switch cost, which seems to suggest greater competition at switch than repeat trials. However, Monsell (2005) argued that the task conflict caused by stimulus-task associations cannot account for the type of residual switch cost that we observed. When a small number of bivalent stimuli occur in both task contexts (in our experiment, there were only two stimuli per task), they soon become asymptotically associated with both task sets. Consequently, the task conflict caused by stimulus-task associations will not differ between repeat and switch trials, exactly as we (and Aron et al., 2004) observed.

To conclude, our behavioral data yielded the expected patterns of switch costs and Stroop-like effects. The difference in response time among all three Stroop conditions and the additional ex-Gaussian analyses suggest that the stimuli evoked response conflict as well as conflict at the level of task sets.

4.2. Task conflict in the MFC

We found effects of both response and task conflict in the ACC and in the meSFG. An anatomical ROI analysis confirmed that response and task conflict were equally associated with more ven-

tral regions of the MFC (ACC) and more dorsal regions of the MFC (meSFG). Our finding of task conflict in the meSFG replicates previous studies (Milham & Banich, 2005; Woodward et al., 2008). Woodward and colleagues found a region in meSFG when they contrasted neutral trials in a univalent context with neutral trials in a bivalent context. Milham and Banich found a region close to the pre-SMA when contrasting bivalent vs. univalent Stroop stimuli (congruent > neutral and incongruent > neutral). However, in both studies no effects of task conflict were found in the ACC, whereas we did find such an effect in the present study.

The differences between these previous studies and ours might be related to differences in experimental design. Woodward et al. (2008) did not compare bivalent and univalent trials directly, but looked at block-context effects, which may have been weaker than the effects from our direct comparisons. Thus, we may have observed differential ACC activity because of greater experimental power. The discrepancy with the results of Milham and Banich (2005) might be due to the fact that these authors used unrelated words as neutral stimuli instead of the row of Xs that were used in the present experiment. In contrast to a row of Xs, an unrelated word still evokes the word reading task (Monsell, Taylor, & Murphy, 2001). This diminishes or removes the task conflict difference between neutral and congruent stimuli. Furthermore, the experiment of Milham and Banich did not use task switching, i.e., the only task was to name the color of the word. Hence, they observed a behavioral facilitation effect (i.e., faster responding to congruent than to neutral stimuli). In the present task-switching design, both tasks were active, resulting in a behavioral task conflict effect (i.e., faster responding to neutral than to congruent stimuli). Thus, we found faster responses and less ACC activity on neutral trials than on congruent trials, indicating that a lack of task conflict on neutral trials outweighed the response facilitation on congruent trials. The fact that we did find a behavioral index for task conflict might be related to our observation of task conflict activity in the ACC.

4.3. The role of the ACC in attentional control

It is often claimed that the ACC is a response conflict monitor, signaling other brain regions – like the lateral prefrontal cortex – to execute control when conflict is detected (Botvinick, Braver, Barch, Carter, & Cohen, 2001; Carter, Botvinick, & Cohen, 1999; MacDonald et al., 2000; Miller & Cohen, 2001). The present findings show that ACC activity was not only greater for incongruent than for congruent stimuli (i.e., response conflict), but also greater for congruent than for neutral stimuli (i.e., task conflict), in the absence of response conflict. That ACC activity can be independent of response conflict was also observed by Roelofs et al. (2006) using a version of the arrow-word Stroop paradigm in which the trials were blocked by task. Others have also observed increased ACC activity in contexts requiring increased attentional control, where the level of response conflict was kept the same (Badre & Wagner, 2004).

Recent evidence indicates that the ACC is differentially active for decision conflict even before a response is made (Pochon, Riis, Sanfey, Nystrom, & Cohen, 2008). Similarly, the ACC was demonstrated to be differentially active in anticipation of Stroop stimuli, again when no response had to be given yet (Aarts et al., 2008). Importantly, this anticipatory ACC activity was independent of upcoming response conflict. In contrast to a conflict monitoring role, effective connectivity studies provided evidence for a function of the ACC in regulating or top-down modulation of activity in modality-specific sensory areas (Crottaz-Herbette & Menon, 2006), the amygdala (Etkin, Egner, Peraza, Kandel, & Hirsch, 2006), and the caudal cingulate (motor) zone (Fan, Hof, Guise, Fossella, & Posner, 2008). These findings are in agreement with monkey electrophysiology studies. While two studies have failed to identify populations

of neurons in the ACC specialized for monitoring response conflict (Ito, Stuphorn, Brown, & Schall, 2003; Nakamura, Roesch, & Olson, 2005), a recent study found differential preparatory activity in ACC neurons in a task-switching task (Johnston, Levin, Koval, & Everling, 2007). The authors argued for a role of the ACC in the implementation of top-down control. In line with above mentioned evidence, it is plausible to assume that our results of response and task conflict in the ACC reflect regulatory processes that resolve conflict rather than merely detect conflict. Our results then suggest that the ACC is implicated in the resolution of conflict evoked both by stimulus-response associations (i.e., response conflict, indexed by the positive incongruent-congruent contrast) and stimulus-task associations (i.e., task conflict, indexed by the positive congruent-neutral contrast), following the reasoning of Monsell and colleagues (Aron et al., 2004; Monsell, 2005; Rogers & Monsell, 1995).

Although task and response conflict both engaged the ACC, it is not clear from the present study whether these types of conflict are associated with different sub-regions in the ACC. Fig. 4 (at $x = -8$) shows that the clusters for response conflict and task conflict within the ACC are non-overlapping, with response conflict activating a more anterior region of the ACC and task conflict activating a bordering posterior region. However, when comparing response conflict activity from numerous other studies, clusters are found throughout the whole ACC region (Ridderinkhof et al., 2004). Future studies may further test whether functional heterogeneity exists within the ACC. Important for now is that both task and response conflict activate the ACC.

4.4. ACC vs. meSFG

The present results indicate a role for both the ACC and a more dorsal (and caudal) region in the MFC, the meSFG ($z = 46$), in conflict tasks. Others have suggested that conflict is better associated with activations at a more dorsal level ($z > 45$) in the SFG than activations in the ACC (Rushworth, Walton, Kennerley, & Bannerman, 2004; Ullsperger & von Cramon, 2001). Indeed, several studies found regions rostral to the pre-SMA in meSFG for conflict processing (Nachev, Rees, Parton, Kennard, & Husain, 2005; Ullsperger & von Cramon, 2001). This is in line with our findings of meSFG activity for response and task conflict. Yet, our present experiment and previous studies have consistently found the ACC to be differentially active in conflict tasks (Aarts et al., 2008; Roelofs et al., 2006).

Rushworth et al. (2004) proposed that the meSFG is involved in task control and selection of action sets, whereas the ACC guides decisions while taking the reward history into account (see also Rushworth & Behrens, 2008). During response or task conflict both types of processes could actually play a role, which would explain the present finding of the involvement of both MFC regions in conflict.

4.5. Conflict-related processes in the LPFC

In contrast to the MFC, we did find a dissociation regarding conflict-related processes in LPFC. While task conflict was observed in both ventral and dorsal LPFC, response conflict was only observed in ventral LPFC. The inferior frontal gyrus (ventral LPFC) has been shown to be involved in Go/NoGo tasks (Konishi, Nakajima, Uchida, Sekihara, & Miyashita, 1998; Menon, Adelman, White, Glover, & Reiss, 2001; Rubia et al., 2001) and lesions in the inferior part of the frontal cortex cause utilization behavior. This impulse-control disorder is characterized by a lack of goal-directed behavior (Lhermitte, 1983; Shallice, Burgess, Schon, & Baxter, 1989). Therefore, it seems that ventral LPFC regions have a role in the suppression of inappropriate responses in case of response conflict and in the suppression of inappropriate task sets in case of task conflict. Furthermore, some findings suggest that the (left) ventral

LPFC plays an important role in controlled retrieval and selection processes (Badre, Poldrack, Pare-Blagoev, Inslar, & Wagner, 2005; Crone, Wendelken, Donohue, & Bunge, 2006; Thompson-Schill et al., 1997). It is no surprise that task conflict was also associated with dorsal regions of the LPFC in our study. Dorsal LPFC has typically been associated with goal maintenance and working memory (e.g., D'Esposito, Postle, & Rypma, 2000), see Kane and Engle (2002) for a review. Banich et al. (2000a, 2000b) have argued that dorsal LPFC regions are involved in imposing an attentional set (i.e., task set). The association in our study of the dorsal LPFC with task conflict, but not with response conflict, provides further converging evidence that the congruent > neutral contrast indexes task conflict.

5. Conclusion

Our behavioral data showed that we were successful in manipulating response and task conflict within one paradigm. The imaging data revealed that the ACC is not only activated by response conflict but also by conflict at the level of task sets. Whereas the LPFC showed a functional dissociation in conflict effects when comparing ventral and dorsal regions, such dissociation between ventral and dorsal regions could not be observed in the MFC. That is, like in the ACC, a more dorsal region in the MFC, the meSFG, was activated by both response and task conflict. Models of attentional control should take account of these key properties of the ACC and meSFG.

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