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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.

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, Metzak, 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

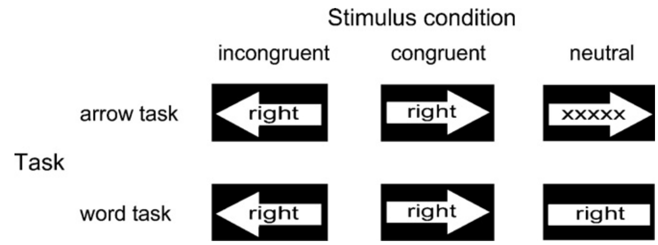

Fig. 1. Examples of incongruent, congruent, and neutral stimuli in the arrow and the word tasks. Incongruent and congruent stimuli are both bivalent, whereas neutral stimuli are univalent. In the study, the words were given in the participants' native language, i.e., Dutch.

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