THE NE AL C ELATE F E CE T AL L AD IND CED ATTENTI NAL ELECTI N: AN FM I T D

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Rees et al., 1997; Chen, 2003; Schwartz et al., 2005). The software (http://nbs.neuro-bs.com/). Each trial lasted for 2500 ms. At the start of a search trial, a white fixation dot, 0.05° in visual angle, appeared at the center of the black screen for 500 ms. Six dots around the central fixation then appeared for 200 ms, indicating the six locations of the central display at which the target and the five distractor items were presented. After another 100 ms in which only the fixation dot was shown, the search display was presented for 500 ms. The search display consisted of a central fixation dot surrounded by the search array, that is, 6 bar stimuli (at an eccentricity of 1.2° from central fixation, see Fig. 1). A flanker was presented to the left or the right side of the search array (at an eccentricity of 3.2°). Each bar of the search array, as well as the flanker bar in the periphery, subtended 0.8 × 0.2° of visual angle. The search array always contained a target stimulus which was randomly either a horizontal or vertical bar. At the same time, five distractor bars were presented. In the low load condition, all distractors had the same orientation so that the task was basically a 'pop-out' search (Treisman, 1988 randomized and divided up between two fMRI runs, with each run acquiring 525 volumes. An anatomical scan was obtained between the two sessions. Only the made more errors in the high- than in the low-load condition (9.8% vs. 4.5%), and more in the incongruent than in the congruent condition (8.2% vs. 6.1%). The interaction was not significant.

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In accordance with the analyses of the behavioral data, the main effects of perceptual load [(High_con + High_incon) vs. (Low_con + Low_incon)] and of flanker congruency [(High_incon + Low_incon) vs. (High_con + Low_con)], and the interaction between them [(Low_incon – Low_con) vs. (High_incon – High_con)] were computed in the whole-brain analysis (see Table 2 and Fig. 2). Compared with the low-load condition, bilateral inferior frontal junction (IFJ), bilateral anterior insula, bilateral PPC, ACC, and right frontal eye field (FEF) were activated in the high-load condition, indicating these areas to be involved in visual search for a predefined target (or one of two predefined alternatives) among heterogeneous distractors. The ACC was more activated in the incongruent compared to the congruent condition, which is consistent with the idea that this area is involved in the processing of conflicting information. Importantly, the interaction between perceptual load and flanker congruency was significant for the ACC, and the bilateral anterior insula. Follow-up analyses for these areas showed that the difference between the activation values in the incongruent compared to the congruent conditions was higher for the low-load condition compared to the high load condition. Parameter estimations from the activated clusters in these regions are illustrated in Fig. 2 for the four experimental conditions.

DISCUSSION

2001). In this adjustment process, ACC is responsible for detecting response conflict and signal this to brain areas subserving conflict resolution, such as the dorsolateral prefrontal cortex (DLPFC).

et al., 1998), a target-like distractor has a greater chance of falsely activating the target template, which may then lead to inappropriate response tendencies (e.g., false alarms in a target present/absent task). In the current experiment (with the two alternative targets, only one of which was presented), the chance of false responses was increased in the high-load (heterogeneous-distractor) condition, where a distractor similar in orientation to the alternative, but not presented target might induce a tendency toward an incorrect response, causing ‘response’ conflict within the central (search) task. ACC might also be responsible for detecting such conflicting response tendencies (only one of which can be correct). Consistent with this, as mentioned in the Introduction, heightened ACC activation has also been observed in a pure visual-search task (without any flankers) under conditions of heterogeneous, as compared to homogeneous, distractors (Wei et al., 2009).

It should be noted, though, that even with the extensions sketched above, the role of ACC is restricted to ‘detecting’ conflict according to the conflict monitoring theory. However, recent evidence and models suggest that ACC may not be exclusively involved in conflict detection, but also in the focusing attention on the task-relevant information (Paus et al., 1998; Posner and DiGirolamo, 1998), or in the implementation and maintenance of task goals (Weissman et al., 2003; Dosenbach et al., 2006, 2007, 2008). For example, a study examining the time course of activity in ACC and right anterior insula/frontal operculum demonstrated that these regions are engaged throughout the performance of a task, from stimulus perception to response planning and execution and to evaluation of feedback and post-task adjustments (Dosenbach et al., 2007). Additionally, ACC and anterior insula have been found to modulate the activity of other brain areas during challenging tasks (Dosenbach et al., 2007; Sridharan et al., 2008; Eckert et al., 2009). Thus, ACC and anterior insula have been suggested to form a putative task-control network (Dosenbach et al., 2006), and to play a causal role in the initiation of cognitive control, in particular for task-set implementation in coordinating goal-directed performance (Corbetta et al., 2008; Sridharan et al., 2008). Consistent with this proposal, our results also showed concurrent activations of ACC, anterior insula, and fronto-parietal regions such as FEF and PPC in the contrast between the high-load and low-load conditions, indicative of these areas’ involvement in attentional control.

Moreover, ACC, or at least part of ACC, was not only activated in the main effects of perceptual load and flanker congruency, but also sensitive to the interaction between these factors. In fact, activations in ACC and bilateral anterior insula mirrored the interaction pattern in the behavioral data. While activations were generally stronger for the high load than for the low load condition, the level of activation was higher for incongruent relative to congruent stimuli only in the low load condition, not in the high load condition. Previous neuroimaging studies on the role of perceptual load in bottom-up salience value of the peripheral flanker, the flanker could be more likely to win competition within its vicinity and the response conflict induced by the flanker might be readily registered in ACC, yielding differential activations in this area for incongruent as compared to congruent trials.

On the other hand, according to models that assume ACC and anterior insula are involved in the actual implementation of task goals (Dosenbach et al., 2006, 2007, 2008), activations in these areas might be taken to represent the mental effort in different task conditions. Indeed, a recent model of hierarchical reinforcement learning (Holroyd and Yeung, 2012) proposes that ACC not only chooses between possible options in attentional selection or cognitive control, but also motivates and energizes behavior by determining the level of effort to be applied toward executing the policy, and maintaining this signal until the chosen option has been carried through. The similar interaction patterns in the behavioral data and the activations in ACC and anterior insula are consistent with this proposal.

The present study does not allow us to choose between the (amended) conflict monitoring theory and the other accounts discussed above, which might in any case not be mutually exclusive in understanding the role of ACC and related brain areas in attentional selection (Botvinick, 2007). The pattern of results that we report here may be simulated or validated in future, computational-modeling studies on the role of ACC.

To conclude, by asking participants to search for a vertically or horizontally oriented bar in the central display and by presenting a congruent or incongruent flanker in the periphery, we demonstrated an interaction between the load of attentional selection and the effect of conflict control not only at the behavioral level, but also at the neural level. The anterior cingulate cortex (ACC) and bilateral anterior insula were found to be sensitive to the interaction between perceptual load and flanker congruency. The activations were larger for the incongruent stimuli, relative to the congruent stimuli, but only when the perceptual load in searching for the central target was low. These results suggest that ACC and bilateral anterior insula may exert executive control by selectively biasing processing in favor of task-relevant information, and this biasing depends on the resources currently available to the control system.

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