

THE NEURAL CORRELATES OF PERCEPTUAL LOAD INDUCED ATTENTIONAL SELECTION: AN FMRI STUDY

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Abstract—The neural correlates of perceptual load induced attentional selection were investigated in an functional magnetic resonance imaging (fMRI) experiment in which attentional selection was manipulated through the variation of perceptual load in target search. Participants searched for a vertically or horizontally oriented bar among heterogeneously (the high load condition) or homogeneously (the low load condition) oriented distractor bars in the central display, which was flanked by a vertical or horizontal bar presented at the left or the right periphery. The search reaction times were longer when the central display was of high load than of low load, and were longer when the flanker was incongruent than congruent with the target. Importantly, the flanker congruency effect was manifested only in the low load condition, not in the high load condition, indicating that the perceptual load in target search determined whether the task-irrelevant flanker was processed. Imaging analyses revealed a set of fronto-parietal regions having higher activations in the high than in the low load condition. Anterior cingulate cortex (ACC) was more activated for the incongruent than for the congruent trials. Moreover, ACC and bilateral anterior insula were sensitive to the interaction between perceptual load and flanker congruency such that the activation differences between the incongruent and congruent conditions were significant in the low, but not in the high load condition. These results are consistent with the claim 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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Key words: visual search, perceptual load, flanker effect, ACC, anterior insula.

INTRODUCTION

The extent to which individuals can focus attention in face of distracting information depends on the information load imposed by the current task. The ‘perceptual load theory of attention’ (Lavie and Tsai, 1994; Lavie, 1995, 2005, 2010) provides a framework which combines the early-selection assumption (e.g., Broadbent, 1958) that perception is a limited-capacity process with the late-selection assumption (e.g., Deutsch and Deutsch, 1963) that perception is an automatic process, attempting to resolve the longstanding antagonism between early- and late-selection theories of attention. According to perceptual load theory, a task with high perceptual load that engages all available processing resources would leave effectively no spare capacity for the perception of task-irrelevant information, giving rise to a pattern of performance indicative of early attentional selection. In contrast, a task with low perceptual load would leave spare capacity that (unintentionally) spills over to irrelevant information; processing of this information could interfere with the processing of the target, yielding a pattern of performance indicative of late attentional selection.

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Abbreviations: ACC, anterior cingulate cortex; ANOVA, analysis of variance; DLPFC, dorsolateral prefrontal cortex; FEF, right frontal eye field; FWE, family-wise error; GLM, general linear model; IFJ, inferior frontal junction; PPC, posterior parietal cortex; SPM, Statistical Parametric Mapping.

Rees et al., 1997; Chen, 2003; Schwartz et al., 2005). The absence or presence of a congruency effect (i.e., a reaction time (RT) difference between incongruent and congruent conditions) has been taken as an indicator of whether the peripheral flanker is processed up to the response level. The flanker congruency effect has been found to be larger when processing of the central display and identifying the target are of low perceptual load, and smaller or entirely absent when the current task is of high perceptual load (Lavie, 2005; Wei and Zhou, 2006).

At the neural level, neuroimaging studies on the role of perceptual load in attentional selection have mainly shown activation in stimulus processing areas for task-irrelevant stimuli to be reduced with high, relative to low, perceptual load (Rees et al., 1997; Schwartz et al., 2005; Bahrami et al., 2007). For example, Rees et al. (1997) asked participants to perform a linguistic task of either low or high load in processing a word presented in the center of the screen, while ignoring irrelevant visual motion in the periphery. Although the linguistic task and distractor processing were unrelated, functional imaging of activity in cortical area V5 revealed reduced motion processing during the high load task. Schwartz et al. (2005) varied the attentional load in a visual monitoring task performed on a rapid serial visual presentation (RSVP) stream at central fixation and measured brain responses to task-irrelevant checkerboards in the periphery. They found that activation in the visual cortex for the irrelevant peripheral stimuli decreased when the attentional load at fixation increased. Taken together, these studies validated the load theory (Lavie and Tsal, 1994; Lavie, 2005) by showing reduced perceptual processing of the irrelevant information when the central task load was high. However, to the best of our knowledge, none of the previous neuroimaging studies did examine whether and, if so, how the neural activation related to response congruency between the target and the task-irrelevant stimuli is modulated by the perceptual load.

The need to resolve behavioral conflict arises in many everyday circumstances. A large body of neuroimaging studies has reported activations of the medial prefrontal cortex (mPFC) and especially the anterior cingulate cortex (ACC), dorsolateral prefrontal cortex (DLPFC), and posterior parietal cortex (PPC) in incongruent (or conflict) conditions as compared to congruent conditions (see Nee et al., 2007, for a meta-analysis). ACC activation is widely observed in tasks requiring participants to resolve response conflict (e.g., in Flanker or Stroop tasks) elicited by automatic processing of the task-irrelevant objects/dimensions, which is consistent with the conflict monitoring theory (Botvinick et al., 1999, 2001, 2004; van Veen et al., 2001; Ridderinkhof et al., 2004; Chen et al., 2006; Botvinick, 2007; Carter and van Veen, 2007). Furthermore, ACC activation is also associated with other cognitive functions, such as detecting discrepancies between actual and intended responses (Scheffers and Coles, 2000), predicting error likelihood (Brown and Braver, 2005, 2007), biasing attentional selection toward task-relevant information

(Frith et al., 1991; Paus et al., 1998; Posner and DiGirolamo, 1998; Roelofs et al., 2006; Wei et al., 2009), and implementing and maintaining task-goals (Weissman et al., 2003; Dosenbach et al., 2006, 2007; Dosenbach et al., 2008). For example, a recent fMRI study found that ACC was more activated when participants searched for a target among heterogeneous, rather than homogeneous, distractors in visual search (Wei et al., 2009). This suggests that this area may play a general role in biasing target template matching in conditions with heterogeneous distractors, as false activation of the target template by a distractor is more likely when the distractors are heterogeneous. Given this, it is of theoretical interest to examine how activation of the ACC, and related brain areas, would be modulated by the current demands of searching for a task-relevant target under different perceptual load conditions and by possible conflict elicited by the processing of the task-irrelevant flankers.

In the present fMRI experiment, we asked participants to search for a vertically or horizontally oriented bar in the central search display consisting the target and distractors, while a task-irrelevant flanker (a vertical or horizontal bar) was presented to the left or the right of the central display, creating congruent and incongruent conditions (Fig. 1). Crucially, we manipulated the perceptual load of target search by embedding the target among distractors of either the homogeneous orientation (the low load condition) or heterogeneous orientations (the high load condition) in the central display. For the main effect of perceptual load, we expected to observe higher activations in brain regions involved in attentional selection in the high load, relative to the low-load, condition. For the main effect of target-distractor congruency, we expected higher ACC activation on incongruent, compared to congruent, trials. In addition, we expected an interaction between load and congruency, characterized by a robust congruency effect in the ACC in the low-load condition, but no (or a reduced) effect in the high load condition because in that condition there should be no conflict arising from the target flanker.

EXPERIMENTAL PROCEDURES

Participants

Sixteen undergraduate and graduate students (11 female; aged between 22 and 31 years) participated in the experiment. All of them were right-handed, had normal or corrected-to-normal vision, and had no known neurological or psychiatric disorders. All participants gave written informed consent before the scanning.

Design and procedures

Fig. 1 depicts the trial sequence and sample display. Visual stimuli were presented through an liquid-crystal display (LCD) projector onto a rear projection screen located behind the participant's head. Participants viewed the screen through an angled mirror on the head-coil. Presentation of the stimuli and recording of the responses were controlled by the Presentation

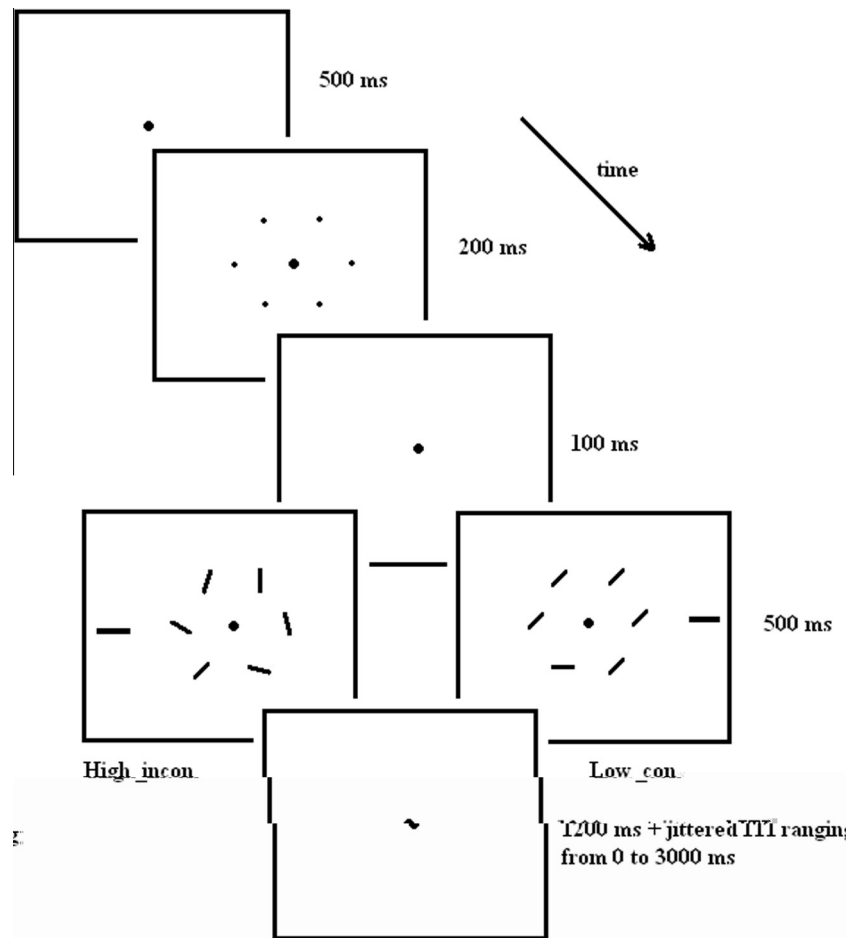


Fig. 1. Example of trial sequence and example display with high load incongruent and low load congruent conditions.

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 $0.8 \times 0.2^\circ$ 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). In the high load condition, all distractor bars had randomly heterogeneous orientations, requiring a rather serial search for the target (Duncan and Humphreys, 1989; Wolfe, 1994). After the search display, a 1200-ms blank display with the fixation dot was presented.

Participants were instructed to respond as quickly and as accurately as possible upon the presentation of the search display, by pressing the left button of the computer mouse for horizontal (target) bar and the right button for vertical (target) bar. In a null trial, only the fixation dot was presented for 2500 ms. For the purpose of jittering in fMRI design, additional blank displays lasting between 0 ms and 3000 ms were added randomly to the end of each trial, yielding a mean inter-trial-interval of 1500 ms.

A 2×2 fast event-related design was used. The first factor was the perceptual load of the search display (high vs. low). For the high load conditions, the five distractor bars always had different orientations. For the low load conditions, although the distractor bars in each trial had the same orientation, bars with different orientations were equally likely used over different trials. The second factor was the congruency between the target and the flanker, which could be the same (congruent) or different (incongruent) in orientation. The location of the target in the central search display was randomly selected, and the flanker was presented randomly on the left or the right side of the central display.

The total 432 experimental trials (108 trials for each perceptual load \times congruency condition) were intermixed with 48 null trials. All these trials were

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 fixation point was displayed during the first 10 s of each session for participants to become accustomed to the scanning noise and for the MR signal to reach a steady state. During each scan, participants had two breaks lasting 40 s each without the scanner stopping. All participants completed a training session of 10 min before the scanning.

Data acquisition

A 3T Siemens Allegra system with a standard head coil at the MRI Center of Regensburg University, Germany, was used to obtain T2*-weighted echo-planar images (EPI) with blood oxygenation level-dependent (BOLD) contrast (matrix size: 64×64 , pixel size: 3×3 mm). Thirty-four transversal slices of 4-mm thickness, oriented parallel to the anterior and posterior commissures, were acquired interleaved with a 1-mm gap (repetition time (TR) = 2 s, echo time (TE) = 30 ms, field of view (FOV) = 256 mm, flip angle = 90°), enabling whole-brain coverage. High-resolution anatomic images were obtained using a 3D T1-weighted MPRage sequence (FOV = 256 mm, 160 slices, TR = 2250 ms, TE = 2.6 ms, flip angle = 90° , 256×256 matrix, 1 mm^3 voxel size). The first five functional volumes were discarded to allow for T1 equilibration effects. Images were spatially realigned to the sixth volume for head movement correction, and co-registered with the anatomical 3D image. The functional images were then normalized, by applying the transforming matrix obtained through normalizing anatomical scans to a standard T1 template (Montreal Neurological Institute template provided by Statistical Parametric Mapping [SPM], see below) using the “unified-segmentation” function of SPM5 (see below) with resampling of $2 \times 2 \times 2 \text{ mm}^3$ voxels. The data were then smoothed with a Gaussian kernel of 8-mm full-width half-maximum to accommodate inter-subject anatomical variability.

fMRI data analysis

Data were analyzed by using the Statistical Parametric Mapping software SPM5, Wellcome Department of Imaging Neuroscience, London (Friston et al., 1995), employing a general linear model (GLM). At the first level, the GLM was used to construct a multiple regression design matrix that included the four experimental conditions: high-load condition, congruent trials (High_con); high-load condition, incongruent trials (High_incon); low-load condition, congruent trials (Low_con); and low-load condition, incongruent trials (Low_incon). All events were time-locked to the onset of the search display by a canonical synthetic hemodynamic response function (HRF) and its first-order temporal derivative, with event duration of 0 s. All error trials and instructions for the starting of scanning and were included as extra regressors of no interest in the design matrix. The six movement parameters of the realignment (rigid body translation in the x-, y-, and z-planes as well as rotation around the x-, y-, and z-axes) were also included

in the design matrix as additional regressors. Data were high-pass filtered at 1/128 Hz. Temporal autocorrelation was modeled using an autoregressive model of order 1 (AR(1)) process. Parameter estimates were calculated for each voxel using weighted least squares to provide maximum likelihood estimators based on the temporal autocorrelation of the data. No global scaling was applied. For each participant, simple main effects for each of the four experimental conditions were computed by applying the “experimental condition vs. implicit baseline (null trials)” contrasts. The four first-level individual contrast images were then submitted to the 2×2 within-participants analysis of variance (ANOVA) at the second group level, employing a random-effects model (flexible factorial design in SPM5, including an additional factor modeling the participant means of activation). In modeling variance components, we allowed for violations of sphericity by modeling nonindependence across parameter estimates from the same participant, and allowed unequal variances between conditions and participants using the standard implementation in SPM5. The activations are reported below with voxel-wise FWE (family-wise error) corrected threshold of $p < .05$, with a minimum cluster size of 15 voxels.

RESULTS

Behavioral

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.

Imaging

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

By asking participants to search for a vertically or a horizontally oriented bar in the central display while

ignoring a response-congruent or -incongruent flanker in the periphery, we found that RTs were affected by both the perceptual load of the central search task and the flanker congruency, replicating previous behavioral studies (e.g., Lavie, 2005; Wei and Zhou, 2006). RTs were longer when the central display induced a high load rather than a low load, and longer when the target and the flanker were incongruent than when they were congruent. Moreover, the flanker congruency effect on RTs was manifested in the low load condition, but not in the high load condition. As hypothesized, imaging results revealed a set of fronto-parietal regions, including right FEF, bilateral IFJ, bilateral PPC, bilateral anterior insula, and ACC, to be more activated in the high load, compared to the low load, condition. Furthermore, ACC was more strongly activated on incongruent trials than on congruent trials. Importantly, activity in ACC and bilateral anterior insula also exhibited an interaction between perceptual load and flanker congruency, with greater activation on incongruent than on congruent trials only in the low load, but not in the high load, condition.

The ACC activation seen in the main contrast between incongruent and congruent conditions is consistent with previous studies. Greater ACC activation on incongruent than on congruent trials has been observed repeatedly in Stroop tasks (Barch et al., 2001), flanker tasks (Botvinick et al., 1999, 2001; van Veen et al., 2001), and Simon tasks (Kerns, 2006), as well as in other tasks in which an inappropriate response tendency elicited by the processing of task-irrelevant information must be overridden. According to the conflict monitoring theory (Botvinick et al., 1999, 2001, 2004; Botvinick, 2007), conflicts arising from processing the task-irrelevant as well as the relevant information, and mapping of the respective processing outcomes onto conflicting responses, would trigger adjustments in the activation of strategic, task-regulating representations, which in turn would bias processing toward the task-relevant stimulus-response pathways (Botvinick et al.,

Table 2. Brain areas activated in the main effect of perceptual load, the flanker effect, and the interaction between perceptual load and flanker effect. Activations were reported with FWE correction of $p < .05$, and extent threshold of 20 voxels. Peak coordinates (x, y, z) correspond to the MNI (Montreal Neurological Institute) space

Contrast/anatomical regions	L/R	BA	x	y	z	Z-value	Voxel No.
<i>High load vs. low load</i>							
Inferior frontal junction	L	48/44	-35	11	29	5.69	56
	R	44	40	11	30	6.71	633
Frontal eye field	R	6	24	2	47	6.59	184
Anterior insula	L	47	-29	25	-5	6.06	105
	R	47	31	27	-2	5.48	511
Anterior cingulate cortex	L/R	32	1	27	44	6.95	576
Posterior parietal cortex	L	7	-23	-64	47	6.86	176
	R	7	26	-61	47	5.92	733
<i>Incongruent vs. congruent</i>							
Anterior cingulate cortex	L/R	32/8	6	25	45	5.18	74
<i>Low load (incon-con) vs. high load (incon-con)</i>							
Anterior cingulate cortex	L/R	8/32	4	24	44	6.31	460
Left anterior insula	L	48	-34	16	4	5.57	22
Right anterior insula	R	47/45	36	28	0	5.82	201

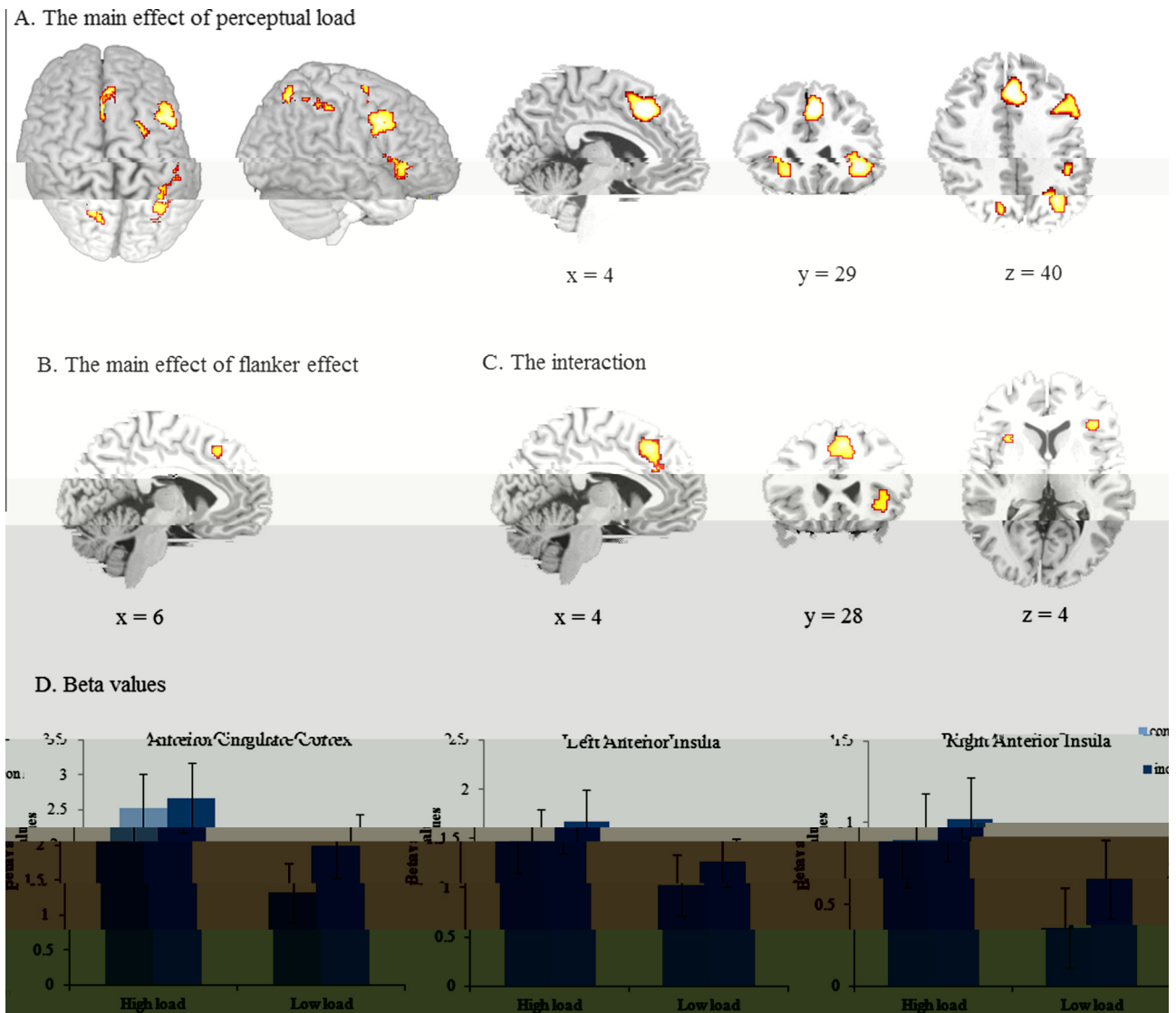


Fig. 2. The activated regions in (A) the main effect of perceptual load, (B) the main effect of flanker congruency, and (C) the interaction. (D) Parameter estimations extracted from the activated areas are shown as a function of the experimental conditions.

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).

In the current experiment, the main contrasts between the high-load and low-load conditions revealed a pattern of activations in ACC and other fronto-parietal regions, e.g., the right FEF, bilateral IFJ, bilateral PPC, and bilateral anterior insula. The observation of the latter is consistent with previous studies that examined the neural correlates of perceptual load (Schwartz et al., 2005), attentional selection (e.g., Corbetta and Shulman, 2002), and visual search (Wojciulik and Kanwisher, 1999; Donner et al., 2000, 2002; Leonards et al., 2000; Nobre et al., 2003; Müller-Plath, 2008; Wei et al., 2009). In fact, the greater ACC activation in the high-load compared to the low-load condition is not readily consistent with the conflict monitoring theory in its original form (Botvinick et al., 2001), in which the role

attributed to ACC was to detect 'response' conflict. However, the conflict monitoring theory might be extended in two ways to accommodate the current findings. First, conflicts in information processing may arise at various stages, or levels, of processing, from stimulus encoding, through target detection and response selection to response execution (Eriksen and Schultz, 1979; Milham et al., 2001; van Veen et al., 2001; Chen et al., 2006). Thus, in the current high load condition, heterogeneous distractors in the central display may cause difficulty in stimulus encoding at the perceptual level. ACC might also detect this 'perceptual' conflict and signal this to fronto-parietal regions for exerting more attentional control, in order to focus processing on the search display and select and identify the search target. Second, according to the SERR (SEArch via Recursive Rejection) model of visual search (Humphreys and Müller, 1993; Müller et al., 1994; for overviews, see Müller and Humphreys, 1993, and Müller

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 attentional selection have mainly shown activations in

stimulus processing areas for task-irrelevant stimuli to be reduced with high, relative to low, perceptual load (Rees et al., 1997; Schwartz et al., 2005; Bahrami et al., 2007). The relevant studies used peripheral dot motion (Rees et al., 1997) or peripheral checkerboards (Schwartz et al., 2005) as task-irrelevant stimuli, that is, there was no manipulation of the response congruency between the target and the irrelevant stimuli. Although ACC was found to be activated in the main contrast of high vs. low load conditions, these studies did not demonstrate an 'interaction between central load and peripheral stimulation' (Schwartz et al., 2005, p. 774). By contrast, the present results show, for the first time, that the neural activation related to response congruency between the target and the task-irrelevant stimuli is modulated by perceptual load.

How can this pattern of interaction in ACC and anterior insula be explained by the theoretical approaches outlined above? On the one hand, according to extended versions of the conflict monitoring theory and the perceptual load theory, this interaction might suggest that the ability to detect conflict is subject to resource limitation. In the high load condition, searching for the target among heterogeneous distractors engages all available processing resources and leaves effectively no spare capacity for the perception of task-irrelevant flanker, resulting in the null effect in the activation of ACC and anterior insula. In contrast, in the low load condition, searching for the target among homogeneous distractors would leave spare capacity that (unintentionally) spills over to irrelevant flanker, which in turn causes conflict that is readily detected by ACC. Although one may argue that the definition of perceptual load and the consumption of attentional resources are rather descriptive and "unfalsifiable" (Tsal and Benoni, 2010), this deficiency might be compensated for by analyzing the cognitive processes and mechanisms underlying the consumption of resources. The salience-based model of attention, the Guided Search model (Wolfe, 1994), assumes that feature contrast values, signaling the extent to which an item differs from other items in its vicinity, are computed not only for the target, but also in parallel for the other presented items, i.e., the distractors and the flanker. In the high load condition, each item in the central display, the target, and the flanker were different from each other, yielding comparable bottom-up salience values for these items. However, in the low load condition, only the target in the central display and the flanker in the periphery were different from other items in the vicinity, yielding higher bottom-up salience values for these two items. Accordingly, in the high load condition, the relatively higher bottom-up salience of heterogeneous distractors results in the occurrence of strong perceptual conflicts in finding and discriminating the target and the high level of ACC activity signaling the general level of conflicts (Fig. 2D); this in turn may cause the potentially conflicting flanker, which is presented in the display periphery, to be excluded from further processing. By contrast, in the low load condition, with little or no conflict in the central display and with the higher

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.

Acknowledgements—This study was supported by grants from the DFG (Research Group FOR480 and Excellence Cluster 142) and by grants from Natural Science Foundation of China (31000502, 30110972, 91232708) and the Ministry of Science and Technology of China (2010CB833904).

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