Differentiating allocation of resources and conflict detection within attentional control processing

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Abstract

Increasing demands for conflict detection and for allocation of attentional resources increase the need for attentional control. While prior evidence suggests that different cortical regions are preferentially engaged by these two attentional processes, the effect of increasing demand for conflict detection and/or allocation of attentional resources has been relatively unexplored. We designed a novel task (the 'variable attentional control' – VAC – task) that varies the demand for attentional control by increasing conflict detection and allocation of attentional resources within the same stimuli. We studied 34 subjects who underwent event-related functional magnetic resonance imaging while performing the VAC task. Increasing demand for attentional control, as reflected by longer reaction time and reduced accuracy, was associated with greater activation in the dorsolateral prefrontal cortex, parietal cortex and dorsal cingulate. Furthermore, an increase in conflict detection was associated with greater dorsal cingulate activity, whereas an increase in demand for allocation of attentional resources implied greater activation in the dorsolateral prefrontal and parietal cortices. In essence, in addition to allowing the exploration of the overall effects of increasing demand for attentional control, our novel task also allowed parsing of the neural components of attentional control into those related to allocation of attentional resources and those related to conflict detection.

Introduction

Attentional control is the capacity to flexibly orientate thoughts and behaviors towards a goal by selecting and integrating relevant contextual information. This cognitive process provides a top-down bias for analysis and representation of relevant information in the face of concurrent and non-relevant information (Desimone & Duncan, 1995). Two complementary subprocesses are involved in attentional control: (1) allocation of attentional resources, i.e. a representation of the attentional demands of a task that can be used to bias processing in favor of task-relevant stimuli; and (2) conflict detection, i.e. the ability to detect conflicting information within the task (MacDonald *et al.*, 2000). Earlier studies on attentional control with electrophysiology in non-human primates (for review, see Desimone & Duncan, 1995; Corbetta & Shulman, 2002) and with functional neuroimaging in humans implicate a network of brain regions, including the dorsolateral prefrontal cortex (DLPFC), parietal and cingulate cortices (Carter *et al.*, 1998; 2000; Botvinick *et al.*, 1999; Casey *et al.*, 2000; MacDonald *et al.*, 2000; Ullsperger & von Cramon, 2001; Bunge *et al.*, 2002; Milham *et al.*, 2002; Peterson *et al.*, 2002; Durston *et al.*, 2003; Fan *et al.*, 2003; Hazeltine *et al.*, 2003; Weiss *et al.*, 2003; Weissman *et al.*, 2003; Kerns *et al.*, 2004; Langenecker *et al.*, 2004). These studies also suggest that each of these regions play a relatively specific role. The DLPFC, in concert with the parietal cortex (Corbetta & Shulman, 2002), is thought to be important for top-down modulation of stimulus processing (Miller & Cohen, 2001; Corbetta & Shulman, 2002; Kerns *et al.*, 2004). The

dorsal cingulate, on the other hand, has been implicated in conflict monitoring (Carter *et al.*, 1998; 2000; Botvinick *et al.*, 1999; MacDonald *et al.*, 2000; Durston *et al.*, 2003; Kerns *et al.*, 2004), and in error processing (Carter *et al.*, 1998; Kiehl *et al.*, 2000; Braver *et al.*, 2001; Ullsperger & von Cramon, 2001; Garavan *et al.*, 2003; Mathalon *et al.*, 2003; Holroyd *et al.*, 2004).

Relatively few studies have been performed to explore the neurophysiological correlates of increasing demands for attentional control. For example, Durston *et al.* (2003) increased the demand for attentional control by parametrically increasing the level of perceived conflict using a version of the flanker task. Based on the interference effect demonstrated by Gratton *et al.* (1992), the authors found a monotonic increase in activation of the DLPFC, parietal cortex and dorsal cingulate by increasing the number of congruent stimuli prior to an incongruent stimulus. However, their task did not vary the demand for attentional control within the target stimulus and did not allow to fully differentiate the contribution of an increase in demands for different cognitive subprocesses within the attentional control domain.

In the present study, we further explored the functional magnetic resonance imaging (fMRI) BOLD response to increasing demands for attentional control. We used a novel task that allows varying the degree of conflict detection and allocation of attentional resources required for each stimulus. More specifically, we varied conflict detection by increasing the level of perceptual conflict within the stimulus. With this aim, we based task manipulation on the so-called flanker effect (Eriksen, 1974). A number of behavioral and imaging studies have shown that surrounding flankers are involuntarily processed even if they are irrelevant to the task at hand (Eriksen, 1974). In particular, it has been found that reaction time increases

when flankers are incongruent with the central target. Therefore, we hypothesized that stimuli that are incongruent in direction to the target stimulus might generate cognitive conflict during stimulus processing. Furthermore, we also hypothesized that incongruent stimuli closer in the visual field might generate more cognitive conflict relative to those more distant.

We also varied allocation of attentional resources in our task taking advantage of the global precedence effect (Navon, 1977). According to Desimone & Duncan (1995), objects in the visual field compete for limited processing capacity and control of behavior. This competition is biased by both bottom-up and top-down mechanisms. Bottom-up information processing tends to separate figures from their background, while top-down neuronal mechanisms select objects of relevance to current behavior. Brain networks associated to executive function, possibly located in the prefrontal cortex, probably concur in building top-down selection templates (Desimone & Duncan, 1995). The global-precedence effect is related to the development of the percept claiming that global properties have temporal precedence during the microgenesis of percept (Navon, 1977). For example, Navon (1977) used an interference task showing that conflicting information between global and local levels slows the identification of local but not of global characteristics of the stimulus. Thus, the global precedence is relative to bottom-up aspects of attentional processing, suggesting that attention may be first captured by global aspects of stimuli. Therefore, forcing attention via top-down representations may affect global–local processing. Several experiments have indicated that attentional manipulations affect global–local processing. For example, dividing attention on both global and local levels implicates no advantage for global processing, while allocating attention to a single level equally facilitates performance for global and local targets (Hoffman, 1980; Kimchi, 1993). Ward (1982) identified a level-readiness effect, i.e. performance for both global and local levels improves if the previous stimulus had just been processed at the same level. Kinchla (1983) showed that the use of information to process one level is slowed by directing attention to the other level, while information to process the latter is used more rapidly. Furthermore, other results (Paquet, 1988) show that attentional allocation to either local or global levels of attended stimuli determines which level of unattended stimuli between the local and the global ones is harder to ignore. Han (2003) showed that top-down attention on pop-out local items weakens the global reaction time advantage. In summary, all these findings suggest that attentional allocation affects global–local processing, and that differential demand for top-down allocation of attentional resources may be present if top-down attentional bias on either local or global aspects of the stimulus is requested. Our aim was to study such differential top-down modulation of attentional resources. Therefore, to specifically investigate the contribution of allocation of attentional resources, we required resources allocation on either global or local features within the stimuli.

Based on previous studies, we hypothesized that activity in the DLPFC, parietal cortex and dorsal cingulate would vary according to demands for attentional control. We also hypothesized that activity in the dorsal cingulate would be preferentially sensitive to increasing conflict detection, while the DLPFC and parietal cortex would be more engaged by varying attentional allocation.

Materials and methods

Subjects

Forty healthy control subjects (23 males, age ± SEM 27.9 ± 0.9 years, IQ 105.1 ± 1.5, handedness 0.93 ± 0.01) who had undergone extensive clinical evaluation were recruited. Inclusion criteria were the absence of any neurological and psychiatric disorder and any other medical condition, absence of any pharmacological treatment that could influence cerebral metabolism or blood flow, and history of drug abuse, age < 45 years and handedness > 0.8 as measured with the Edinburgh Handedness Inventory (Oldfield, 1971).

All subjects gave written informed consent to the study after the procedure had been fully explained. The protocol was approved by the National Institute of Mental Health Institutional Review Board. Data from 23 of these subjects were included in an earlier report on the effects of catechol-O-methyltransferase val[158]met genotype on cortical processing during this task (Blasi et al., 2005).

Variable attentional control (VAC) task

Subjects performed the VAC task depicted in Fig. 1. Briefly, each stimulus was composed of arrows of three different sizes (one large, six medium, 42 small-sized arrows) pointing either to the right or to the left; seven small arrows were embedded in each medium-sized arrow; and six medium-sized arrows were embedded in each large arrow. The direction of the arrows of each particular size (i.e. small or medium) was always the same. Subjects were instructed by a cue word (either big or medium or small) displayed above each stimulus to press a button corresponding to the direction of the large, medium or small arrows, respectively.

Stimuli were manipulated to obtain increasing demands for attentional control. With this aim, both allocation of attentional resources and conflict detection demands were varied: (i) to elicit differential allocation of attentional resources, the subjects were instructed to focus on either more local (stimulus 2, 4 and 5 in Fig. 1) or more global (stimulus 1 and 3 in Fig. 1) characteristics of stimuli and (ii) to obtain differential conflict detection, the congruency⁄incongruency of hierarchical stimuli was manipulated. We hypothesized a lower demand for conflict detection if arrows at the target level were congruent with those at the next hierarchical level (stimulus 1 and 2 in Fig. 1, e.g. if the target level small arrows are congruent in direction with the medium arrows, etc.); on the other hand, a higher demand for conflict detection was hypothesized if arrows at the target level were incongruent with those at the next hierarchical level (stimulus 3, 4 and 5 in Fig. 1, e.g. if the target level small arrows are incongruent in direction with the medium arrows, etc.). Further, we hypothesized a relatively less effect on conflict detection at the more distant hierarchical level. Therefore, a lower level of conflict was obtained with the congruency between arrows at the target level and those at the closest hierarchical level, while those at the more distant hierarchical level could be congruent or incongruent with arrows at the target level. On the contrary, a higher level of conflict was obtained with the incongruency between arrows at the target level and those at the closest hierarchical level, while those at the more distant hierarchical level could be congruent with arrows at the target level.

These stimulus manipulations were aimed to obtain varying levels of allocation of attentional resources and conflict detection. The increase in demand for both these cognitive processes implies an increase in demand for attentional control. Therefore, five stimulus types, in which allocation of attentional resources and conflict detection were manipulated, were chosen to study the neurophysiological correlates underlying an increase in demand for attentional control with fMRI (Blasi et al., 2005) (Fig. 1).

Low level of attentional control (LOW): all three sizes of arrows were congruent in direction with each other and the stimuli were cued with the word BIG (Fig. 1, stimulus 1).
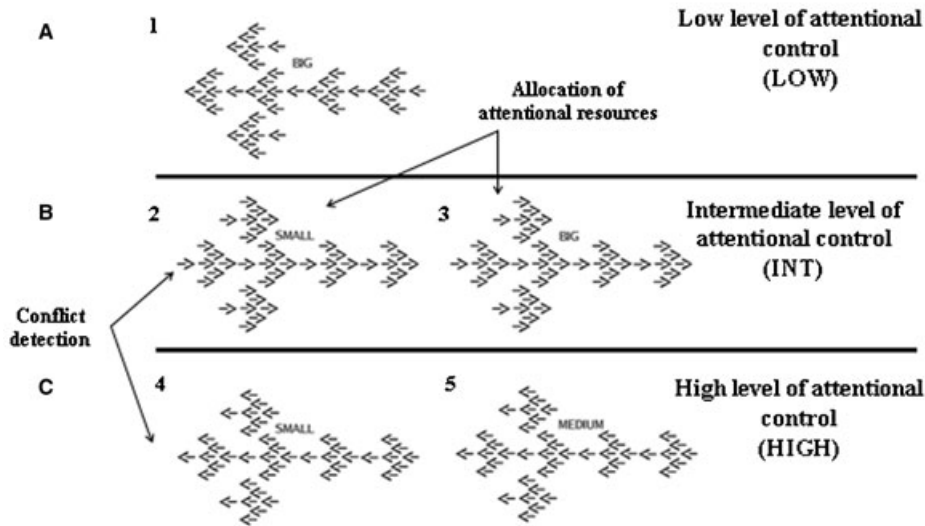
FIG. 1. VAC task. This task is aimed to measure the following. (A) increasing demands for attentional control. With this purpose, stimulus 1 was designed to obtain a low level of attentional control (LOW), stimuli 2 and 3 an intermediate level of attentional control (INT), stimuli 4 and 5 a high level of attentional control (HIGH). (B) increasing demands for conflict detection. With this aim, stimulus 2 was designed to obtain a lower level of conflict detection (CON-L), stimulus 4 a higher level of conflict detection (CON-H). (C) varying demands of allocation of attentional resources. Stimulus 2 was designed to obtain allocation of attentional resources on local characteristics (LOC), stimulus 3 to measure allocation of attentional resources on global features (GLO). See text for details.

Intermediate level of attentional control (INT): two stimuli were used: the big arrow was incongruent in direction to the small and the medium arrows in both; the cue was BIG in one of them, SMALL in the other one (Fig. 1, stimulus 2 and 3).

High level of attentional control (HIGH): two stimuli were used: the medium-size arrows were incongruent in direction to the big and the small arrows in both; the cue was SMALL in one of them, MEDIUM in the other one (Fig. 1, stimulus 4 and 5).

A behavioral pilot study confirmed that the stimuli enumerated above were associated with increasing reaction time (RT) with the increase in demand for attentional control. Furthermore, among all the possible stimuli, RT relative to the stimulus used for LOW was the fastest, to the stimuli used for HIGH the slowest, and to the stimuli used for INT in the middle-range.

Some of the enumerated stimuli were also parsed to disambiguate the role of varying demand for allocation of attentional resources and conflict detection within increasing demand for attentional control. The choice of these stimuli was made according to their characteristics allowing to control for allocation of attentional resources while evaluating increasing demand for conflict detection, and to control for the general characteristics of the stimulus while evaluating varying allocation of attentional resources.

Increasing conflict detection was evaluated comparing two of the stimuli used in this task in which the target stimuli were at the same hierarchical level, allowing to control for allocation of attentional resources (the instruction was 'SMALL' for both). In particular, in the low degree of conflict detection (CON-L), the big arrow was incongruent in direction to the small and the medium arrows and the cue was SMALL (Fig. 1, stimulus 2). In the high degree of conflict detection (CON-H), the medium-size arrows were incongruent in direction to the big and the small arrows and the cue was again SMALL (Fig. 1, stimulus 4).

The physiological response related to varying allocation of attentional resources was measured controlling for the perceptual characteristics of the stimulus. With this aim, allocation of attentional resources on global characteristics of the stimulus (GLO) was

evaluated using the stimulus in which the big arrow was incongruent in direction with the small and the medium arrows and the cue was BIG (Fig. 1, stimulus 3). Allocation of attentional resources on local characteristics of the stimulus (LOC) was instead evaluated using the stimulus in which, as for GLO, the big arrow was incongruent in direction to the small and the medium arrows, but the cue was SMALL (Fig. 1, stimulus 2).

In summary, this task was aimed to measure the physiological response related to three levels of attentional control, two levels of allocation of attentional resources and two levels of conflict detection (Fig. 1).

Subjects were instructed to respond as quickly and as accurately to the stimuli as possible by pressing either the left or right button on a response pad using their right thumb. They were also instructed to move their thumb to a small plastic knob placed in the center of the response pad between responses. All subjects were trained on the rules of the task prior to the fMRI session.

Each stimulus was presented for 800 ms, with the interstimulus interval (ISI) randomly jittered between 1.2 and 7.1 s (mean ISI: 1.7 s), and the order of the stimuli was randomly distributed across the session (Friston *et al.*, 1999). The visual angle of stimuli was 10 °. The randomization of this sequence was specified according to the stochastic design option in SPM99. The total number of stimuli was 241: 50 HIGH (25 each of the two stimuli that required a HIGH degree of attentional control), 68 for INT [34 each of the two stimuli that required an intermediate degree (based on RT from the pilot study – vide supra) of attentional control], 57 for LOW, 66 for the control condition. The total duration of the task was 10 min 8 s. A fixation cross-hair was presented during the ISI.

BOLD fMRI

BOLD fMRI was performed on a GE Signa 3T scanner (gradient echo-planar imaging sequence, TR/TE = 2000/28; 26 interleaved slices, thickness = 4 mm, gap = 1 mm; voxel size $3.75 \times 3.75 \times 5$; scan repetitions = 300; flip angle = 90°; field of view = 24 cm;

matrix = 64×64), while subjects performed the VAC task. The first four scans were discarded to allow for signal saturation. Stimuli were presented via a back-projection system, and the responses were recorded through a fiber optic response box that allowed the measurement of the accuracy and reaction time for each trial.

Data analysis

Behavioral data

Effect of increasing demand for attentional control A repeated-measures ANOVA with the three conditions (LOW, INT and HIGH) of the task as the within-effect factor was performed on both accuracy and reaction time measures. Only correct responses were used in the reaction time analysis. *Post hoc* analyses were performed using Tukey Honest Significance Difference (HSD). Accuracy was measured as the percentage of correct responses relative to the total number of stimuli for each demand of general attentional control.

Effect of increasing demand for conflict detection A repeated-measures ANOVA with the two degrees of perceived conflict (CON-L vs. CON-H) as within-effect factors was performed on both accuracy and reaction time (for correct responses) measures.

Effect of varying allocation of attentional resources A repeated-measures ANOVA with LOC and GLO was performed on both accuracy and reaction time for correct responses only.

fMRI analysis

Whole-brain image analysis was completed using SPM99 (http://www.fil.ion.ucl.ac.uk/spm). Images for each subject were slice time corrected, realigned to the first volume in the time series to correct for head motion, and spatially normalized into a standard stereotactic space using a 12-parameter affine model. Spatial smoothing was also applied with a Gaussian filter set at 12 mm full width at half maximum to minimize noise and residual differences in gyral anatomy. After realignment, data sets were also screened for high quality (scan stability) as demonstrated by small motion correction (< 2 mm translation, < 1.5° rotation).

fMRI responses were modeled using a canonical hemodynamic response function, and temporally filtered using a SPM default high-pass filter based on the frequency of the events and a hrf-shape low-pass filter. Vectors were created for each condition using the timing of the correct responses for each stimulus type. The timing of the incorrect responses and the residual movement were also modeled as regressors of no interest. Predetermined condition effects at each voxel were created using a *t*-statistic, producing a statistical image for the following contrasts for each subject: HIGH > baseline (cross-hairs), INT > baseline, LOW > baseline, CON-L > CON-H, GLO > LOC, LOC > GLO. A second-level random effects model that accounts for both scan-to-scan and subject-to-subject variability was then used for group analyses. The contrast HIGH > baseline, INT > baseline and LOW > baseline for each individual was entered in an ANOVA (HIGH > INT > LOW) to evaluate the effect of increasing level of attentional control. The resulting activation map was then used to constrain the subsequent analyses exploring the effect of increasing conflict detection, varying allocation of attentional resources and their relative comparison. To evaluate the effects of increasing conflict detection, the contrasts CON-H > CON-L and CON-L > CON-H for each individual were entered in one-sample *t*-tests. To evaluate the effect of varying allocation of attentional resources, the contrast LOC > GLO and GLO > LOC were also entered in one-sample *t*-tests.

Finally, ANOVAs between increasing conflict detection and varying allocation of attentional resources [(CON-H > CON-L) > (LOC > GLO) and the inverse contrast] were performed to compare the activity of brain regions preferentially involved in either subprocess.

Because of our strong *a priori* hypothesis regarding the differential response of the DLPFC, parietal and cingulate cortices during attentional control and our use of a rigorous random effects statistical model, a statistical threshold of $P < 0.005$, $k = 6$, with a further Family Wise Error (FWE) small volume correction for multiple comparisons using a 10 mm radius sphere centered around the coordinates found by MacDonald *et al.* (2005) in the dorsal cingulate and the DLPFC, and by Durston *et al.* (2003) in the parietal cortex, $P = 0.05$ was used to identify significant responses for all comparisons in these anatomical regions.

Spearman's correlation analysis was then performed between the signal change extracted using MarsBar (http://marsbar.sourceforge. net/) from the brain regions showing differential activity within the DLPFC, the cingulate as well as the parietal cortices, and behavioral data in performing the VAC task.

Results

All the subjects underwent fMRI while performing the VAC task. Six subjects did not demonstrate the expected behavioral responses across the various levels of demand for attentional control. In particular, the RT from one of the two stimuli in the INT attentional control category showed longer RT than one of the two stimuli in the HIGH attentional control category. It is not clear to us why these six subjects had a different response relative to the rest of the group (34 subjects). Because the main aim of this paper was to explore neurophysiological correlates associated with an increase in attentional control demand and responses from these six subjects were clearly different from the rest of the group, we chose not to include the imaging data from these six subjects at this time.

Thus, 34 subjects (20 males, age ± SEM 26.0 ± 0.8 years, IQ 105.4 ± 1.5, handedness 0.93 ± 0.01) were utilized in the final analyses.

Behavioral data

Effect of increasing demand for attentional control

Accuracy. There was a main effect of an increase in demand for attentional control ($F_{2,66} = 57.918$; $P < 0.0001$). As predicted, subjects performed worse on the HIGH condition relative to the INT and LOW conditions (% correct responses ± SEM: HIGH 86.76 ± 1.42; INT 94.46 ± 0.76; LOW 99.79 ± 0.10). *Post hoc* analysis revealed a statistically significant difference across all three levels of demand for attentional control (HIGH > INT: $P < 0.0002$; HIGH > LOW: $P < 0.0002$; INT > LOW: $P < 0.0003$).

Reaction time. There was also a main effect of increasing demand for attentional control on RT ($F_{2,66} = 146.60$; $P < 0.0001$). RT was significantly longer for the HIGH condition relative to the INT and LOW conditions (reaction time ± SEM: HIGH 1033.14 ± 22.71 ms; INT 853.73 ± 18.90 ms; LOW 703.26 ± 19.14 ms). *Post hoc* analysis revealed a statistically significant difference across all three levels of demand for attentional control (all $P < 0.0002$).

Effect of level of conflict detection (CON-L vs. CON-H)

While there was no significant difference in accuracy between the CON-L vs. CON-H conditions ($F_{1,33} = 2.66$; $P = 0.11$) (CON-H

95.29 ± 1.11; CON-L 97.06 ± 0.55), there was a significant difference in RT between the two conditions, with greater RT during the CON-H condition relative to the CON-L condition (CON-H 951.20 ± 21.69 ms; CON-L 864.76 ± 18.25 ms; $F_{1,33} = 104.81$, $P < 0.0001$).

Effect of varying allocation of attentional resources

There was a significant main effect of accuracy ($F_{1,33} = 17.99$; $P < 0.0002$), with better performance at LOC vs. GLO (GLO 91.87 ± 1.27; LOC 97.06 ± 0.55). There was also a significant main effect of RT ($F_{1,33} = 8.21$; $P < 0.008$), with faster responses at GLO vs. LOC (GLO 842.70 ± 20.28 ms; LOC 864.76 ± 18.25 ms).

Imaging data

Main effect of increasing demand for attentional control (HIGH > INT > LOW)

A main effect of increase in demand for attentional control was found in several regions, including the DLPFC, the dorsal cingulate, the parietal cortex, the supplementary motor area and the ventrolateral prefrontal cortex bilaterally (Table 1, Figs 2A and 3A).

Main effect of increasing conflict detection (CON-H vs. CON-L)

CON-H showed relatively higher activation only in the dorsal cingulate (BA32) (Table 1, Figs 2B and 3B). No local maxima were found in the opposite comparison (CON-L > CON-H).

Main effect of varying allocation of attentional resources (LOC vs. GLO)

LOC showed relatively higher activation in the left dorsolateral prefrontal, parietal and premotor cortices (Table 1, Figs 2B and 3B). No local maxima were found in the opposite comparison (GLO > LOC).

Comparison between increasing conflict detection and varying allocation of attentional resources

Direct comparisons further confirmed greater activity in the dorsal cingulate during conflict detection, and greater activity in the dorsolateral prefrontal and parietal cortices during allocation of attentional resources (Table 1, Figs 2C and 3B). In these two comparisons, there was no significant difference in activation of the supplementary motor area or ventrolateral prefrontal cortex, the other two regions that showed a main effect of attentional load.

Correlation analysis

There was a trend for a significant positive correlation between signal change in the cingulate cortex and RT costs (RT for HIGH minus RT for LOW conflict trials; $r = 0.31$, $P = 0.068$) (Fig. 4). No correlation was found between conflict-related RT costs and DLPFC activity, or between allocation of attentional resources, RT costs and cingulate activity.

Discussion

Consistent with prior evidence (Carter *et al.*, 1998, 2000; Botvinick *et al.*, 1999; Casey *et al.*, 2000; MacDonald *et al.*, 2000; Ullsperger & von Cramon, 2001; Bunge *et al.*, 2002; Milham *et al.*, 2002; Durston *et al.*, 2003; Fan *et al.*, 2003; Hazeltine *et al.*, 2003; Weissman *et al.*, 2003; Kerns *et al.*, 2004), our results show that a circumscribed network of brain regions is involved in attentional control as assayed with our task. These brain regions include the DLPFC, the parietal cortex and the dorsal cingulate. Importantly, we observed that these regions show an increase in activity with increasing demand for attentional control. Our novel task also allowed parsing of the neural components of attentional control into those related to allocation of attentional resources and those related to conflict detection. Thus, we observed that the dorsal cingulate showed a preferential increase in

TABLE 1. Local maxima of activated areas related to increasing demand of attentional control (HIGH > INT > LOW), to conflict detection (CON-H > CON-L) and to allocation of attentional resources (LOC > GLO)

Brain area	BA	Talairach coordinates			Z-value
		x	y	z	
Increasing attentional control demand (HIGH > INT > LOW)					
R medial frontal/cingulate gyrus	6/32	8	13	45	5.70
R inferior/medial frontal gyrus	9/46	49	12	27	5.46
R superior parietal lobule	7	30	−52	53	5.43
R middle frontal gyrus	6	38	−1	51	5.33
L middle frontal gyrus	6/9	−34	3	51	4.94
L inferior frontal gyrus	44/9	−49	12	22	4.72
L inferior parietal lobule	40	−38	−51	58	4.69
Conflict detection (CON-H > CON-L)					
R cingulate gyrus	32	4	10	41	2.90
Allocation of attentional resources (LOC > GLO)					
L inferior parietal lobule	40	−45	−46	39	4.42
L middle frontal gyrus	6	−30	6	50	4.14
L middle frontal gyrus	46	−45	30	17	3.36
Conflict detection > allocation of attentional resources					
R cingulate gyrus	32	4	6	41	3.46
Allocation of attentional resources > conflict detection					
L inferior parietal lobule	40	−45	−46	39	4.74
L middle frontal gyrus	46	−41	19	18	3.48

There were no significant areas of activation on the inverse contrasts. Furthermore, local maxima associated to the comparison between allocation of attentional resources and conflict detection [(LOC > GLO) > (CON-H > CON-L)] are presented. L, left; R, right.

activity during conflict detection, and the DLPFC and the parietal cortex during allocation of attentional resources. In our study, the physiological response related to allocation of attentional resources is obtained by top-down attentional bias on either local or global aspects
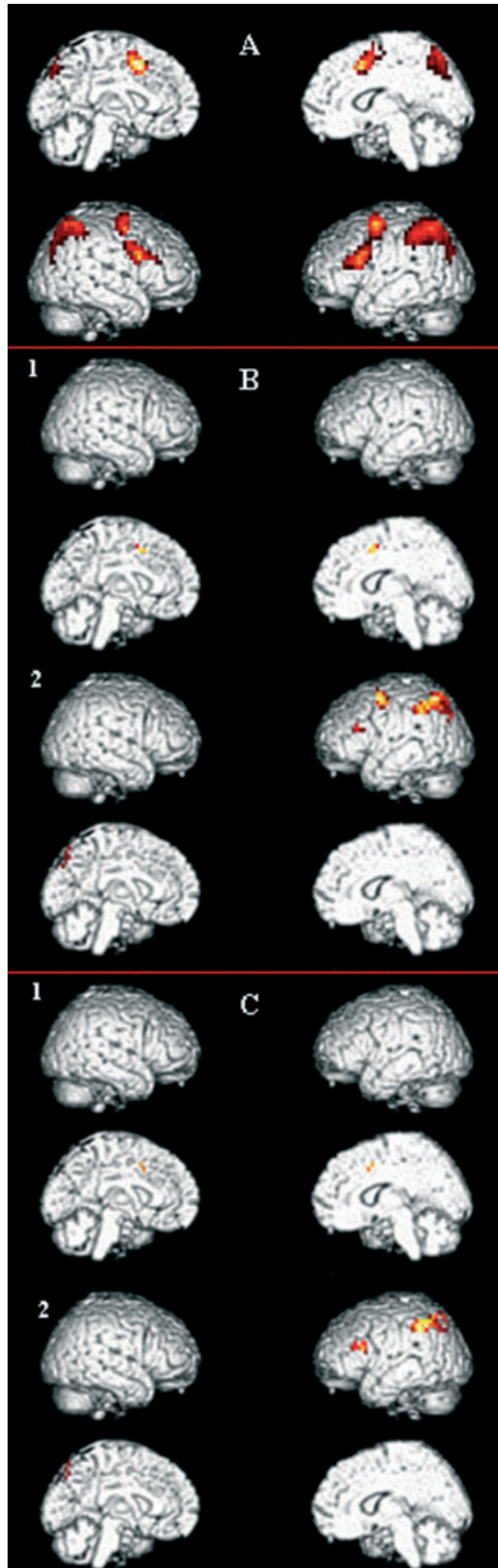
of the stimulus. According to the global precedence effect (Navon, 1977), global characteristics of stimuli are more readily processed relative to local ones. Therefore, higher cognitive effort in allocating attentional resources on local characteristics might be required. Our data seem to be in line with this contention. In fact, allocating attentional resources on local characteristics of the stimuli in our paradigm is associated with increasing activity in the DLPFC and parietal cortices relative to resources allocation related to global features.

These results are unique for several reasons. First, few studies have parametrically manipulated the demand for attentional control. Parametric designs allow the study of capacity limitation in cognitive processing. Furthermore, they permit to analyse the physiological response related to multiple levels of cognitive load, allowing in turn to compare neural responses related to different levels of behavioral performance. Furthermore, designs with these characteristics make it possible to compare the effect of increasing demands of cognitive load between groups, exploring differential physiological correlates of capacity limitation (Manoach, 2003). In our task, parametric manipulations were also performed to create conditions that differentially challenged the subprocesses underlying attentional control. Prior studies that explored the neurophysiological correlates of increasing task demands in other cognitive domains have shown either a linearly increasing or an 'inverted-U'-shaped response in the activity of brain regions canonical for a particular cognitive process. For example, Callicott et al. (1999), using a version of the 'n-back' task providing parametric increases of working memory load, showed that increasing the load elicited an apparent 'inverted-U'-shaped response in DLPFC. However, activity in the pericingulate cortex increased linearly with increasing working memory load. Culham et al. (2001) demonstrated that increasing attentional demands in a visual tracking task is associated with a linear increase in activation in frontal and parietal areas. Similarly, Durston et al. (2002) used a parametric manipulation of the go-no go paradigm to examine the effect of preceding context on inhibitory processes; they demonstrated increasing activation in the ventral prefrontal cortex, parietal cortex and dorsal cingulate. More specific to attentional control, Durston et al. (2003) showed increasing activation in the DLPFC, parietal cortex and dorsal cingulate with increasing level of conflict. This study used a version of the flanker task that allowed modulation of the level of conflict by increasing the number of congruent stimuli before the actual incongruent stimulus. In contrast, we manipulated each stimulus to modulate the level of attentional control independent from the previous context, reducing confounds related to priming effects (Mayr et al., 2003). Our results show increasing activity in the DLPFC, dorsal cingulate and parietal cortex associated with increasing demands for attentional control. Therefore, these findings are consistent with those indicating that

FIG. 2. (A) Rendered images of group maps showing significant areas of activation primarily in the DLPFC, parietal cortex and dorsal cingulate with increasing demand for attentional control (HIGH > INT > LOW). (B) Rendered images of group maps showing: (1) areas of significantly greater activation during increasing conflict detection (CON-H > CON-L), i.e. dorsal cingulate; and (2) areas of significantly greater activation during differential allocation of attentional resources (LOC > GLO), i.e. DLPFC, parietal and premotor cortex. The inverse contrasts did not show any significant differences. (C) Rendered images of group maps showing areas of significantly greater activation during: (1) conflict detection relative to allocation of attentional resources; and (2) the inverse contrast. Activation maps show relative higher activity in the dorsal cingulate during conflict detection, and relative higher activity in the DLPFC and parietal cortex during allocation of attentional resources. A statistical threshold of $P < 0.005$, $k = 6$ was used for these rendered images. Significant clusters of activity survived after a small volume correction at $P = 0.05$.
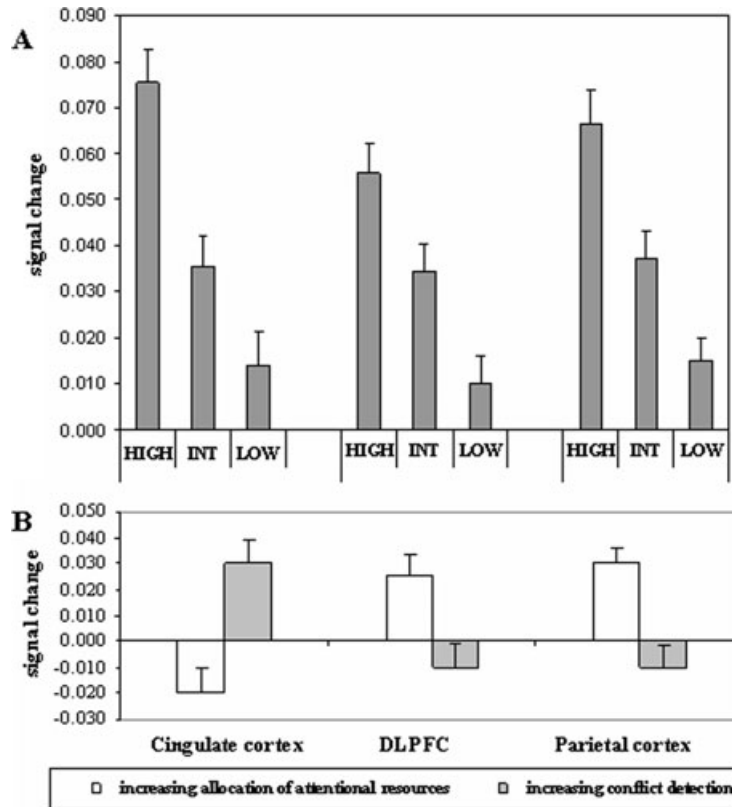
FIG. 3. For representative purposes, bar graphs showing signal changes with SEM extracted using MarsBar (http://marsbar.sourceforge.net/) during performance of the VAC task plotted from the dorsolateral prefrontal (DLPFC), cingulate and parietal cortices. (A) In the DLPFC (x, 49; y, 12; z, 27), cingulate (x, 8; y, 13; z, 45) and parietal cortices (x, 30; y, −52; z, 53) signal change increases with the increase in demand for attentional control. (B) During varying allocation of attentional resources, activity increases only in the DLPFC (x, −41; y, 19; z, 18) and in the parietal cortex (x, −45; y, −46; z, 39). On the other hand, during increasing conflict detection, activity increases only in the cingulate cortex (x, 40; y, 6; z, 41).
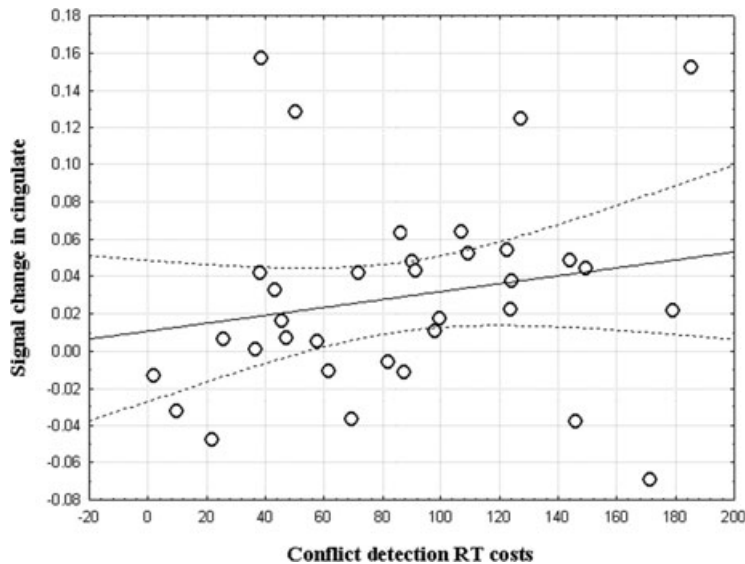

FIG. 4. Scatterplot showing positive correlation approaching significance between signal change in the cingulate cortex during performance of the VAC task and reaction time (RT) costs for conflict detection (RT for CON- H minus RT for CON-L). See text for r and P-values.

greater neuronal activity with increasing task demands is observed across a variety of cognitive functions and during increasing demands for attentional control in specific brain regions.

The second reason for which our results may be of relevance is that previous studies trying to disambiguate the relative contribution of

different brain regions to attentional control processing have produced results with some inconsistencies. For example, while some findings do not suggest differential engagement of distinct regions of the prefrontal cortex by processing of conflictual information and top-down attentional biasing processes (Weissman *et al.*, 2002), other

results are more consistent with this view (MacDonald *et al.*, 2000; Durston *et al.*, 2003). In particular, activation in the dorsal cingulate has been associated with interference monitoring and suppression (Blasi *et al.*, 2006), with the presence of conflict and with conflict detection and monitoring (Carter *et al.*, 1998, 2000; Botvinick *et al.*, 1999; Casey *et al.*, 2000; MacDonald *et al.*, 2000; Milham *et al.*, 2002; Durston *et al.*, 2003; Fan *et al.*, 2003; Weissman *et al.*, 2003; Kerns *et al.*, 2004), with error processing (Carter *et al.*, 1998), but also with decision making (Walton *et al.*, 2004). The DLPFC, on the other hand, has been specifically implicated in implementing control (MacDonald *et al.*, 2000; Durston *et al.*, 2003; Kerns *et al.*, 2004) and in top-down modulation of attention (Desimone & Duncan, 1995; Miller & Cohen, 2001; Corbetta & Shulman, 2002). In particular, the prefrontal cortex has been involved in sending excitatory bias signals to other brain regions to resolve competition between cognitive and visual stimuli (Miller, 1999; Miller & Cohen, 2001). Together with the prefrontal cortex, the superior parietal region also has been implicated in the top-down modulation of attentional control (Desimone & Duncan, 1995; Corbetta & Shulman, 2002). In support of this hypothesis, using the classic flanker task with fMRI, Casey *et al.* (2000) demonstrated that the superior parietal lobe is important for orienting attention to critical areas of the visual field. Additionally, in a study specifically addressing neural responses to an increase in perceived conflict, Durston *et al.* (2003) showed that activity in this region increases linearly with an increase in the degree of conflict.

In summary, the above studies suggest specific roles for the cingulate cortex, the DLPFC and the parietal cortex for specific subprocesses within attentional control. In particular, the superior parietal cortex, thought to be responsible for orientation and top-down modulation of attention (Desimone & Duncan, 1995; Corbetta & Shulman, 2002), might act in concert with the DLPFC in allocating attentional resources (Botvinick *et al.*, 1999; Carter *et al.*, 2000; MacDonald *et al.*, 2000; Durston *et al.*, 2003; Kerns *et al.*, 2004). On the other hand, the cingulate cortex may be involved in detecting or resolving conflict generated by the presence of incongruent information within the stimulus. Consistent with this theory, MacDonald *et al.* (2000) performed an event-related fMRI study with the Stroop task to evaluate the differential roles played by the DLPFC and the cingulate cortex during conflict and instruction processing. Using specific manipulations of task instructions and manipulation of the stimuli, they demonstrated greater engagement of the DLPFC during instruction processing and greater engagement of dorsal cingulate during conflict processing. Based on these results, the authors proposed that the cingulate cortex may be responsible for conflict monitoring/detection, and the DLPFC for processes representing and maintaining the attentional demands of the task. Our findings are consistent with this study. LOC vs. GLO comparison in the task used here permits evaluation of the physiological response during allocation of attentional resources. This analysis revealed greater activation in the DLPFC and parietal cortex during LOC relative to GLO. These results support the notion that these regions play a more significant role in allocation of attentional resources. On the other hand, analysis of conflict detection (CON-H > CON-L) showed a differential activation in the dorsal cingulate, but not in the DLPFC and parietal cortices. These results support the contention that activity in this brain region may be related to conflict detection. The results obtained by correlation analysis may be consistent with this interpretation. In fact, the positive relationship between signal change in the cingulate cortex and RT costs related to conflict detection further suggests association between increasing effort in performing conflict-related cognitive processing and cingulate activity. On the other hand, no correlation was found between conflict-related RT costs and DLPFC activity.

In sum, our results seem consistent with those showing functional dissociation between distinct regions within the attentional control brain network. Furthermore, they suggest a specific link between conflict processing and the cingulate cortex. In particular, the fact that we find an increase in activity only in the cingulate cortex with an increase in perceived conflict may suggest that this region is involved not only in conflict detection, as suggested by previous studies (Botvinick *et al.*, 1999; Carter *et al.*, 2000; MacDonald *et al.*, 2000; Durston *et al.*, 2003; Kerns *et al.*, 2004), but also in conflict resolution. This interpretation, that is consistent with results from other studies (e.g. Walton *et al.*, 2004), is also supported by correlation analysis between behavioral and physiological data, showing that only cingulate cortex activity is linked to conflict-related behavior in our study. However, a possible role of the DLPFC in resolving conflict cannot be ruled out based solely on these data.

Third, our design is different from those previously used in that the differential demand for attentional control is obtained by varying demands for two specific components of attentional control (i.e. attentional allocation and conflict detection) within the same stimuli. On the other hand, previous studies on the subject have used designs in which brain activity related to different cognitive subprocesses was investigated manipulating different components of the task. For example, MacDonald *et al.* (2000) manipulated a Stroop-like task to temporally separate instruction-related strategic processes, including those responsible for representing and maintaining the attentional demands of the task from response-related, including evaluative, processes However, in their design there was no behavioral performance during instruction-related processes, raising the question if other ongoing cognitive processes were present during this component of the task. In contrast, our design allowed us to explore attentional allocation as well as conflict detection within each stimulus, isolating the physiological response related to each of these processes from one another. All these characteristics may further help to associate specific brain regions to differential demand for specific cognitive processes.

A limitation of the LOC vs. GLO contrast to evaluate behavior and physiology during attentional allocation is that behavioral data in these two conditions demonstrate better accuracy but longer RT for LOC compared with GLO. These results are suggestive of a speed–accuracy trade off, i.e. increasing effort in allocating attentional resources (as reflected by prolonged RT) may lead to better accuracy to LOC relative to GLO. In essence, the speed–accuracy trade off may be resulting in a more efficient and productive allocation of attentional resources.

Earlier studies have demonstrated that activity in the dorsal cingulate may vary during error detection (Carter *et al.*, 1998) Therefore, a limitation of this study may be that it is also possible that our findings may be related to error processing during the task. However, we limited our analyses only to the BOLD response during correct responses, making it less likely that our results are affected by error processing. Another limitation may be that the role of two different cognitive processes is parsed by studying the effects of one factor while keeping the level of the second factor constant. However, previous studies document that in order to examine factor independence a full factorial design is required. Only if two factors produce additive effects can one conclude that the factors have different and independent effects. However, this study was not powered to perform this analysis as we were interested in specific aspects of attentional control processing.

In conclusion, this study shows that increases in demand for attentional control are associated with increases in activity of a network of brain regions including the DLPFC, the cingulate cortex and the parietal cortex. Our data also support the notion that, among these cortical areas, specific brain regions increase their activity with

the increase in demands for specific cognitive processes within attentional control.

Abbreviations

DLPFC, dorsolateral prefrontal cortex; fMRI, functional magnetic resonance imaging; ISI, interstimulus interval; RT, reaction time; VAC, variable attentional control.

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