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Common regions of dorsal anterior cingulate and prefrontalparietal cortices provide attentional control of distracters varying in emotionality and visibility

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Abstract

Top-down attentional control is necessary to ensure successful task performance in the presence of distracters. Lateral prefrontal cortex, parietal cortex and anterior cingulate cortex have been previously implicated in top-down attentional control. However, it is unclear whether these regions are engaged independent of distracter type or whether, as has been suggested for anterior cingulate cortex, different regions provide attentional control over emotional versus other forms of salient distracter. In the current task, subjects viewed targets that were preceded by distracters that varied in both emotionality and visibility. We found that behaviorally, the presence of preceding distracters significantly interfered with target judgment. At the neural level, increases in the emotional and visual saliency of distracters were both associated with increased activity in proximal regions of prefrontal, parietal cortex and anterior cingulate cortex responding to distracters of increased emotionality and visibility.

Keywords

attention; emotion; visibility; top-down attentional control; fMRI

INTRODUCTION

Top-down attentional control is needed to suppress the influence of distracters to ensure successful task performance. It has been suggested that such top-down control is mediated by prefrontal-parietal attention network (Hopfinger et al., 2000;Kastner & Ungerleider, 2000;Luck et al., 1997;Marois et al., 2000,2004; Moran & Desimone, 1985; Reynolds et al., 1999) as well as the anterior cingulate cortex (ACC) (Gitelman et al., 1999;Kastner & Ungerleider, 2000;Marois et al., 2000;2004;Posner & Petersen, 1990). But are these attentional areas engaged independent of distracter type? For example, are prefrontal, parietal cortex and ACC engaged by both increasingly emotional and increasingly visible distracters? This issue has direct implications for the understanding of a variety of psychiatric disorders including anxiety disorders and posttraumatic stress disorder. Individuals with these disorders are characterized by increased susceptibility to emotional interference relative to healthy

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individuals (Armony et al., 2005;Phan et al., 2006;Williams et al., 2006) even when the emotional stimuli are subliminal (Armony et al., 2005;Bradley et al., 1995;Mineka & Ohman, 2002;Mogg et al., 1993). It is important to determine whether there are systems which specifically respond to emotional distracters (and which, when dysfunctional, might lead to this increased susceptibility in anxiety disorders) or whether responding to emotional distracters recruits general attentional systems (indicating more general attentional difficulties in anxiety disorders or that the increased susceptibility reflects increased emotional responding). This issue also has implications for understanding emotional regulation, which stresses a role for attentional control over the emotional stimulus (Ochsner et al 2002;Ochsner & Gross, 2005).

Previous work has shown that emotional stimuli cause greater interference than neutral stimuli (Blair et al., 2007;Erthal et al., 2005;Harris & Pashler, 2004;Mitchell et al 2006,2007;Pessoa et al., 2003;Vuilleumier et al., 2001). This is thought to reflect reciprocal connections between the amygdala and temporal and occipital cortex; the amygdala augments the activation of sensory representations of emotional distracters within occipital and temporal cortex (Blair et al., 2007;LeDoux, 1996;Mitchell et al., 2007;Pessoa et al., 2002;Vuilleumier et al., 2004). Indeed, this augmentation of the sensory representations of emotional stimuli by the amygdala appears to allow the enhanced perception of emotional, relative to neutral, stimuli following target stimuli in attentional blink paradigms (Anderson & Phelps, 2001).

But what are the systems involved in the top-down attentional control of emotional distracters? This issue has been investigated through Stroop-type (Blair et al., 2007;Bremner et al., 2004;Etkin et al., 2006;Shin et al., 2001;Whalen et al., 1998) and other attentional paradigms (Bishop et al., 2004;Mitchell et al 2007;Simpson et al., 2000;Vuilleumier, et al., 2001). These studies suggest that systems involved in the top-down attentional control of emotional distracters include ACC (Blair et al., 2007;Bremner et al., 2004;Etkin et al., 2006;Shin et al., 2007;Bremner et al., 2004;Etkin et al., 2006;Shin et al., 2007;Bremner et al., 2004;Etkin et al., 2006;Shin et al., 2001;Whalen et al., 1998), PFC (Bishop et al., 2004;Blair et al., 2007;Shin et al., 2001;Simpson et al., 2000;Vuilleumier, et al., 2001;Whalen et al., 1998) and parietal cortex (Blair et al., 2007;Bremner et al., 2001;Whalen et al., 1998) and parietal cortex (Blair et al., 2007;Bremner et al., 2007;Bremner et al., 2004). However, very little work has addressed if regions providing attentional control of emotional distracters are similar to those responding to other features that increase the salience of the distracter, for example visibility level.

A distinction has been drawn between rostral and dorsal regions of cingulate cortex (rACC and dACC); it has been argued that they subserve distinct affective and cognitive processes (Bush et al. 2000;Whalen et al. 1998). In particular, it has been argued that attentional control of emotional distracters recruits rACC (Bishop et al., 2004;Etkin et al., 2006;Shin et al., 2001;Vuilleumier et al., 2001;Whalen et al., 1998). In contrast, attentional control of non-emotional distracters is thought to implicate dACC (Bush et al. 1998;Carter et al. 1995, 2000;Durston et al., 2002;MacDonald et al. 2000;Menon et al., 2001). However, some studies report dACC rather than rACC activity in response to emotional distracters (Blair et al., 2007;Davis et al., 2005;Haas et al., 2006;Mitchell et al., 2007). Moreover, work has shown that rACC shows increased responding to emotional stimuli even in contexts where attentional control is not required (Nakic et al., 2006;Kosson et al., 2006;Pissiota et al., 2003). Importantly, very few studies have manipulated distracter salience through emotional and non-emotional manipulation in the same study (Compton et al., 2003).

Previous investigations examining the response to emotional distracters have involved stimuli at the supraliminal level. However, neuroimaging data suggest that subliminally presented stimuli are cortically represented (e.g. Dehaene et al., 2001;Luo et al., 2004) and that emotional stimuli at the subliminal level also activate the amygdala (Liddell et al., 2005;Morris et al., 1999;Whalen et al., 2004;Williams et al., 2005). If the prefronto-parietal network is recruited whenever top-down control is necessary to "attend" to the target stimulus in the face of

competing cortical representations, then if subliminal distracters are cortically represented, they too may demand prefronto-parietal top down control, particularly if they are emotional. Moreover, increasing the visibility of distracters provides an interesting comparison condition to increasing the emotionality of distracters. It is suggested that emotional distracters cause more representational interference than neutral distracters because the activity of the neurons within visual and temporal cortex representing them receives additional input from the amygdala (Mitchell et al., 2006;Pessoa et al., 2003). Surpraliminal distracters should cause more representational interference than subliminal distracters because the supraliminal stimuli themselves should more strongly activate the neurons within visual and temporal cortex representing them (cf. Dehaene et al., 2001).

In the present study, an event-related fMRI study was conducted to investigate the effect of distracters with different emotionality (emotional vs. neutral) and visibility level (supraliminal vs. subliminal) on target processing. A temporal distraction paradigm was employed, i.e., the target was preceded by a distracter. Distracters immediately preceding target stimuli detrimentally impact the processing of the target stimuli (Broadbent & Broadbent, 1987). Indeed, while emotional distracters presented simultaneously with task relevant stimuli cause interference infrequently (Bar-Haim et al., 2007; Williams et al., 1996; though see, Erthal et al., 2005;Harris & Pashler, 2004;Okon-Singer et al., 2007). However, when emotional distracters and the target stimuli are presently serially in a rapid visual stream, interference is frequently reported (Blair et al 2007, Mitchell et al., 2006, 2007; Strange et al., 2003). Two contrasting sets of predictions were made. On the basis of the emotional Stroop literature, we predicted that attentional control of emotional relative to neutral distracters would be associated with increased rACC activity while attentional control of supraliminal relative to subliminal distracters would be associated with increased dACC activity. Alternatively, if attentional control of emotional distracters is mediated by similar regions to attentional control of increasingly visible distracters, we predicted interference by both types of distracters would be associated with increased activation of dACC as well as regions of lateral PFC and parietal cortex. Moreover, if this second hypothesis is correct, a conjunction analysis examining all four distracter conditions vs. a non distracter control condition should identify regions commonly activated to control all distracter types.

Materials and Methods

Subjects

Fourteen volunteers, 7 males and 7 females, between the ages of 20 to 36 participated in this study. All gave written informed consent to participate in the study, which was approved by the National Institute of Mental Health Institutional Review Board.

Design and procedures

The study involved an event-related fMRI design. The subject was presented with a target (letter strings in upper case) that was either preceded by distracters (words in lower case) or without any distracters. See Fig. 1 for a description of stimulus sequence. We adopted a 2 (emotion/neutral) \times 2 (supraliminal/subliminal) design (in the four conditions, a target was preceded by distracters varying in valence and visibility) plus a control condition (only a target was shown, without preceding distracters). Therefore, there were five conditions: supraliminal emotional distracter condition (SUPEM), supraliminal neutral distracter condition (SUPNE), subliminal emotional distracter condition without distracters (CONTROL).

Supraliminal and subliminal distracters were distinguished by presentation duration: 200 ms or 30 ms respectively. Target stimuli were present for 120 ms. There were 60 trials in each of

the five conditions. Each trial in total corresponded to 1 TR (2000 ms; see Figure 1). The baseline was 200 fixation point trials, each also lasting 2000 ms. There were two runs. Each involved 150 trials and 100 fixations. Stimuli presentation was randomized across subjects.

The subjects were told to make lexical decisions with respect to the upper case letter strings. They were to ignore the lower-case letter strings. They made one response for a word, a second for a non word.

The word stimuli were chosen from the ANEW (Affective Norms for English words) (Bradley & Lang, 1999). The valence, arousal level, concreteness, length and frequency were shown in Table 1. The 60 emotional (negative) and 60 neutral distracter words were matched for concreteness, length and frequency using the MRC Psycholinguistic Database (http:// www.psy.uwa.edu.au/mrcdatabase/uwa_mrc.htm). The 60 emotional (negative) and 60 neutral distracter words were matched for concreteness, length and frequency. See Table 1. The same emotional/neutral words were used in both the supraliminal and subliminal conditions (i.e., the distracter words were presented twice). Targets consisted of a different set of 30 neutral words and 30 non-words. Non-words were created from the word targets used in the experiment by swapping the position of any of the two letters in the word). The same targets (30 words and 30 nonwords) were used for each of the five conditions (i.e., the target words were repeated five times). The subjects were familiarized with the testing procedure through a short training session before entry into the scanner.

After the fMRI study, while still lying in the scanner, the subject was required to perform a post-test designed to test whether they could report the subliminal/supraliminal distracters, unknown to them before. This involved 40 distracter trials (10 trials from each of the 4 distracter conditions) taken from the previous fMRI experiment. In the post-test, subjects were asked to ignore upper-case targets, but to focus on lower-case words (distracters in the fMRI experiment). Their task was to report, if they saw a lower-case word, what the word was.

FMRI data acquisition

The study was performed on a 3 Tesla GE scanner. Functional scans were obtained by using a single-shot T2* weighted gradient-echo planar imaging (EPI) sequence (29 contiguous axial slices, slice thickness = 4 mm, in plane resolution = 3.75×3.75 , TR/TE/theta = 2000 ms/30 ms/90, FOV = 240×240 mm², Matrix = 64×64). A series of 250 volumes were acquired during each of the 2 functional runs. The high-resolution anatomical images were acquired using a T1-weighted, three-dimensional, Spoiled GRASS imaging (spgr) sequence ($1 \times 1 \times 1.5$ mm³). The stimuli (font size = 36 mm), in black, were shown centrally on the screen against a white background using a laptop computer connected to a LCD projector. Stimuli were projected through a collimating lens (Buhl Optical) onto a screen attached to the head coil during data acquisition.

Data Processing

The AFNI software package (http://afni.nimh.nih.gov/afni) was used for image data processing. The 2 times series were motion corrected and reregistered and spatially smoothed with Isotropic Gaussian blur with FWHM = 6 mm. They were then normalized to signal percent change (this was done by dividing the signal intensity of a voxel at each time point by the mean signal intensity of that voxel for each run and multiplying the result by 100). The two runs were then concatenated. The haemodynamic response function and multivariate statistics corresponding to each condition were obtained by deconvolving the input for each from the concatenated time series using a least squares procedure within a General Linear Model.

Individual images were spatially normalized to the standard coordinate space of Talairach and Tournoux (Talairach and Tournoux, 1988) before group analysis. A 2 (emotional, neutral) \times 2 (supraliminal, subliminal) random-effects ANOVA was performed. The threshold was set at p < .005 (corrected for multiple comparisons at p < .05). Because of our a priori hypotheses regarding ACC and our interest in the amygdala given the emotional nature of the task, more lenient thresholds were adopted for these structures (p < 0.005 and p < 0.01 uncorrected respectively). A subset of clusters showing significant differential activation were selected according to a priori hypotheses about the regions involved in effects of attentional control, emotionality and visibility. These clusters were used to define functional regions of interest (ROIs). Average activation levels for individual subjects within these ROIs were calculated for each condition.

To see if there was overlap in the distraction effect of each of the four distracter conditions versus the non-distracter condition, a conjunction analysis was also performed. The contrasts between each of the four distraction condition versus the non-distracter condition were obtained first. Computations were then performed to obtain overlapping activations.

Results

Behavioral

A one way ANOVA conducted on the RT (response time) data across the 5 conditions revealed no significant difference (F (4, 52) = .902, p = .47). A 2 (Valence: emotional vs. neutral) \times 2 (Visibility: supraliminal, subliminal) ANOVA was also performed on the RT data. This revealed no significant main effects for emotional valence (F (1, 13) = .367, p = .555) or visibility (F (1, 13) = .419, p = .529) or significant interaction (F (1, 13) = 3.055, p = .104).

A one way ANOVA conducted on the error rate data across the 5 conditions did reveal significant differences (F (4, 52 = 4.415, p < .005). Follow-up t-tests revealed significant differences between the SUPEM and CONTROL (p < .001), SUPNE and Control (p < .025) and SUBEM and CONTROL (p < .034) condition. However, there was no significant difference between the SUBNE and CONTROL condition (p = .208). A 2 (Valence: emotional vs. neutral) \times 2 (Visibility: supraliminal, subliminal) ANOVA was also performed. A marginally significant main effect was found for visibility, F (1, 13) = 4.320, p = .058) but not for emotional valence, F (1, 13) = 1.163, p = .300) or their interaction (F (1, 13) = .160, p = .696). See Table 2 for behavioral results.

Visibility test results

A 2 (Valence: emotional vs. neutral) \times 2 (Visibility: supraliminal, subliminal) ANOVA revealed a significant main effect for visibility (F (1, 13) = 439.45, p < .0001): the report rate for supraliminal distracters (93%±10%; most of the trials were reported) was significantly higher than that for subliminal distracters (15%±15%). However, there was no main effect of valence (F (1, 13) = 1.28, p = .278; reportable trials were incidental) or significant interaction.

FMRI results

A 2 (Valence: emotional, neutral) \times 2 (Visibility: supraliminal, subliminal) ANOVA conducted on the BOLD response revealed significant main effects for both valence and visibility. Areas showing the main effects were shown in Table 3. However, there were no regions which showed significant valence by visibility interaction. The threshold was set at p < .005 (corrected for multiple comparison at p < .05).

Areas showing a main effect of valence (emotional > neutral) included left prefrontal cortex (BA 8, 9), right prefrontal cortex (BA 8, 9, 10, 44), right posterior parietal cortex (the inferior

parietal lobule, BA 40) and left posterior parietal cortex including inferior parietal lobule (BA 40) and precunues (BA7), right dACC (BA 24), fusiform gyrus (BA 37) and the left amygdala (showing activation at a p < .01). Areas activated also included the pre- and post- and paracentral gyrus (bilateral BA 3, right BA 5 and left BA6), medial frontal gyrus (right BA 6), left thalamus, left lentiform nucleus and left insular cortex.

In regard to the left amygdala, interestingly, the between-condition contrasts within ANOVA in the voxel-wise analysis revealed that it was significantly active not only in response to supraliminal emotional (p < .05, in the contrast of SUPEM vs. SUPNEU) but also to subliminal emotional trials (p < .05, in the contrast of SUBEM vs. SUBNEU).

Areas showing a main effect of visibility (supraliminal > subliminal) included left prefrontal cortex (BA9, 46), right posterior parietal cortex (superior parietal lobule, BA 7), right lingual gyrus (BA 18), right dACC, (BA 32, significant at p < .005 uncorrected). Areas activated also included right medial frontal gyrus (BA6), right insular cortex and the left cerebellum-declive region.

To better illustrate the results, signal intensity of interested areas is shown in Fig. 2. The signal intensity of the areas was obtained from the clusters showing the main effect of valence and visibility respectively identified in the fMRI ANOVA analysis.

To explore whether there was overlap in the regions responding to the different types of distraction, a conjunction analysis was conducted examining each of the four distraction conditions versus the control condition. This revealed significant conjunction (p < .005) in the right posterior parietal cortex (BA 7) and the left lingual gyrus (BA 19) (See Fig 3 c and d). The SUPEM, SUPNE and SUBEM versus the CONTROL also shared significant conjunction (p < .005; uncorrected) within middle frontal cortex (BA 10). Dorsal ACC (BA 32/24) was significant at p < .01 (uncorrected). (See Fig 3 a and b)

DISCUSSION

The present study investigated the effect of a distracter's emotionality and visibility on topdown attentional control. We found that increasing both the emotional and visual saliency of distracters was associated with increased activity in regions of occipital and temporal cortex. In line with predictions generated from the hypothesis that attentional control of emotional distracters is mediated by similar regions to attentional control of increasingly visible distracters, increases in the emotional and visual saliency of distracters (with target type held constant) were also both associated with increased activity in proximal regions of prefrontal, parietal and cingulate cortex, regions typically associated with attentional control. Increased activity within the amygdala was only seen to emotional distracters. The conjunction analyses also indicated considerable overlap in regions of parietal and frontal cortex responding to distracters of increased emotionality and visibility. The results of this conjunction analysis were thus also consistent with predictions generated from the hypothesis that attentional control of emotional distracters is mediated by similar regions to attentional control of increasingly visible distracters.

Previous work has found that when emotional distracters and the target stimuli are presently serially in a rapid visual stream, emotional distracters will cause significant behavioral interference (Blair et al 2007,Mitchell et al., 2006,Strange et al., 2003). However, this was not found in the current study. Of course, many emotional interference paradigms have not reported significant behavioral interference by emotional distracters. Thus, two reviews of the emotional Stroop literature report that significant emotional interference is only shown by clinical populations, not by healthy comparison individuals (Bar-Haim et al., 2007;Williams et al, 1996). Indeed, there have been suggestions that distracters will only cause interference in

emotional Stroop paradigms if they are response competitors for the target words (Algom et al., 2004; cf. Etkin et al., 2006;Haas et al., 2006). However, this was not an emotional Stroop paradigm and previous work has demonstrated that emotional distracters can cause representational interference (Blair et al 2007,Erthal et al., 2005;Harris & Pashler, 2004;Mitchell et al., 2006,Okon-Singer et al., 2007,Strange et al., 2003). Of course, in many of these studies the emotional distracters have been visual images (Blair et al 2007,Erthal et al., 2005;Mitchell et al., 2006; though see Harris & Pashler, 2004;Strange et al., 2003). It is possible that while the distracters were sufficiently salient to require additional attentional control, they were not sufficiently salient to actually interfere with behavioral performance.

Previous work has reported that emotional relative to neutral distraction is associated with activity in amygdala and occipital and temporal cortex (Blair et al., 2007;Pessoa et al., 2003;Vuilleumier et al., 2001). This is thought to reflect reciprocal connections between the amygdala and temporal and occipital cortex (Blair et al., 2007;Mitchell et al 2007;LeDoux, 1996;Pessoa et al., 2002;Vuilleumier et al., 2004). In the current study, we found that trials with emotional relative to neutral distracters were associated with significantly greater activation in the amygdala as well as fusiform cortex. Interestingly, and in line with some previous work (Naccache et al., 2005), the amygdala activation was observed independent of the impact of increased visibility; i.e., the amygdala showed a response to subliminal emotional distracters.

Increasing the visibility of distracters was associated with increased activity in visual cortex (lingual gyrus). This is consistent with previous work showing increased visual cortex activation to stimuli whose visual salience has been increased; e.g., through changes in luminance contrast (Marios et al., 2004), relative contrast (Reynolds & Desimone, 2003), contour saliency (Li et al., 2006) or shape saliency (Altmann et al., 2004). Interestingly, the conjunction analysis revealed that all distracter conditions were associated with significantly greater activity in the lingual gyrus of occipital cortex than control trials (where no distracters were presented). This suggests that even the subliminal distracter trials evoked increased activation in visual cortex. This supports previous suggestions that non-conscious events are not filtered out of cortex but rather represented weakly in visual areas (Dehaene et al., 2001;Luo et al., 2004).

The control of task-irrelevant distracters on target processing has been consistently associated with the fronto-parietal network (Kastner & Ungerleider, 2000; Marois et al., 2004; Moran & Desimone, 1985) as well as the ACC (Botvinick et al., 2004;Cohen et al., 2000;Kastner & Ungerleider, 2000; Marois et al., 2000; 2004;). Previous studies investigating the response to emotional distraction have also identified the recruitment of frontal, parietal and cingulate cortex (Bishop et al., 2004;Blair et al., 2007;Etkin et al., 2006;Mitchell et al 2007;Whalen et al., 1998; Vuilleumier, et al., 2001). However, to our knowledge, no previous work has investigated the effect of distracter visibility on target processing; though related work has shown the increased recruitment of frontal and parietal areas in response to stimuli of increased visual salience (Constantinidis, 2006;Gottlieb et al., 1998;Indovina & Macaluso, 2006). Also, very little work has directly compared the impact of increasing distracter salience nonemotionally and emotionally within the same study (Compton et al 2003). We found, in this study, that proximal regions of frontal, parietal and cingulate cortex were identified by the main effects of both emotionality and visibility. Moreover, the conjunction analyses indicated considerable overlap in regions of parietal and frontal cortex responding to trials with distracters of increased emotionality and visibility. These data suggest that comparable regions of the fronto-parietal network exert top-down control over increasing emotional and increasingly visible distracters. As such, these data are consistent with those of Compton et al (2003) who observed increased recruitment of dorsolateral prefrontal cortex in response to both emotional and color incongruent in a Stroop paradigm.

It has been suggested that rostral and dorsal cingulate cortex subserve distinct processes: 'affective' and 'cognitive' respectively (Bush et al. 2000; Whalen et al. 1998). According to one view, while dACC is involved in dealing with non-emotional distraction (as considerable data suggests; e.g., Bush et al. 1998;Carter et al. 2000), rACC is involved in dealing with emotional distracters (cf. Bishop et al., 2004;Etkin et al., 2006;Whalen et al., 1998). In contrast to this view, in the current study regions of dorsal ACC were identified by the main effects of both visibility and emotionality, though the dACC region identified by the emotional main effect was slightly more posterior than to that identified by the visibility main effect. In addition, our conjunction analyses identified a region of dACC that showed significantly greater activation to the three distracter conditions that led to significant behavioral interference as indexed by error rate (supraliminal emotional/neutral and subliminal emotional) relative to the trials where no distracters were presented. Taken together, our results do not support the suggested dichotomy within ACC for the attentional control of emotional relative to neutral interference. As such they are in line with some other recent reports indicating dACC rather than rACC activity in response to emotional distracters (Blair et al., 2007;Davis et al., 2005; Haas et al., 2006; Mitchell et al., 2007). The study by Davis et al (2005) is particularly noteworthy as it involved single cell recording in humans in a region of ACC proximal to that implicated in the current study. Neurons within this region were responsive to both emotional and numerical distracters in an emotional Number Stroop paradigm. Moreover, it is interesting that emotional regulation has stressed attentional control as a mechanism by which this might be achieved (Ochsner et al., 2002). Studies of emotional reappraisal frequently implicate dACC (Phan et al., 2005; Ochsner et al., 2002; 2004).

It is worth briefly considering potential functions of dACC. Considerable stress has been placed on a role for dACC in the mediation of response conflict, especially when activity in this region is seen in the context of Stroop tasks (e.g., Botvinick et al., 2004; Cohen et al., 2000). Indeed, it could be argued that the failure to see dACC activity in emotional Stroop paradigms (e.g., Whalen et al., 1998) reflects the absence of response conflict between the emotional distracters and the target stimuli (cf. Algom et al., 2004). When the emotional distracters are response competitors with the target stimuli, dACC activity can be seen (Etkin et al., 2006;Haas et al., 2006). However, dACC appears to be involved in attentional control more generally (Kastner & Ungerleider, 2000; Marois et al., 2000; Posner and DiGirolamo, 1998; Weissman et al., 2005), perhaps responding to representational conflict (cf. Desimone & Duncan, 1995). We assume that it was this latter function of dACC that is being recruited in the current task by both increasingly visible and increasingly emotional distracters. It is worth noting however that the conditions showing an overlap of activity within dACC in the conjunction analysis were all those where error rates were significantly elevated relative to the control condition. Dorsal ACC has also been implicated in error detection (Brown and Braver, 2005 Holroyd et al., 2004). As such the increased dACC activation in these conditions might reflect an increased risk for error.

The inconsistency within the literature with respect to the role of rACC in attentional control of emotional distracters could reflect methodological issues. In many of the previous studies reporting rACC activation as a response to emotional distraction, the distracters were presented simultaneously with the target stimuli (e.g., Bishop et al., 2004;Etkin et al., 2006;Whalen et al., 1998). In addition, several studies indicating a role for rACC adopted a blocked design (Bishop et al., 2004;Whalen et al., 1998) rather than the event related design adopted here (though this is not the case for all studies indicating a role for rACC - Etkin et al., 2006;Vuilleumier et al., 2001). Some studies used ROIs that included only part of dACC (Bishop et al., 2004). Moreover, it does not appear that the amygdala and rACC are exclusively mutually inhibitory. There are also data suggesting that they may also be mutually excitatory, or at least that the amygdala may excite rACC (Budhani et al, 2007;Nakic et al, 2006;Pezawas et al, 2005). Specifically, rACC is found active in affective stimuli processing (Breiter et al.

1996;Dolan et al. 1996;Elliott et al. 2000;George et al. 1993). It is therefore possible that some of the results that were suggested to indicate control over the amygdala's response actually represented excitatory activation from the amygdala. In short, the issue of the rACC/dACC divide for emotional and cognitive interference requires additional attention in the future.

Finally, it is worth noting that while the current data support the suggestion of a similar frontoparietal network involved in the attentional control of both emotional and non-emotional distracters, this does not imply that there are not also additional systems involved in top-down modulation of emotional responding (cf. Blair et al., 2006; Pessoa et al., 2005). Indeed, in the current study, several regions of middle frontal cortex showed a response for increasingly emotional but not increasingly visible distracters (see Table 2).

Conclusion

In this study, we observed the recruitment of similar regions of lateral frontal cortex, anterior cingulate cortex and parietal cortex to trials with distracters of both increasing emotion and visibility. Our results did not suggest that differential regions of ACC (rACC vs. dACC) respond to emotional and non-emotional distracter trials. We found that both distracter emotionality and visibility were associated with increased activity in dorsal anterior cingulate, lateral prefrontal and parietal cortices.

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References

- Algom D, Chajut E, Lev S. A rational look at the emotional stroop phenomenon: a generic slowdown, not a stroop effect. J Exp Psychol Gen 2004;133:323–338. [PubMed: 15355142]
- Anderson AK, Phelps EA. Lesions of the amygdala impair enhanced perception of emotionally salient events. Nature 2001;411:305–309. [PubMed: 11357132]
- Altmann CF, Deubelius A, Kourtzi Z. Shape saliency modulates contextual processing in the human lateral occipital complex. J Cogn Neurosci 2004;16:794–804. [PubMed: 15200707]
- Armony JL, Corbo V, Clement MH, Brunet A. Amygdala response in patients with acute PTSD to masked and unmasked emotional facial expressions. Am J Psychiatry 2005;162:1961–3. [PubMed: 16199845]
- Bar-Haim Y, Lamy D, Pergamin L, Bakermans-Kranenburg MJ, van I, Jzendoorn MH. Threat-related attentional bias in anxious and non-anxious individuals: A meta-analytic study. Psychological Bulletin 2007;133:1–24. [PubMed: 17201568]
- Bishop S, Duncan J, Brett M, Lawrence AD. Prefrontal cortical function and anxiety: controlling attention to threat-related stimuli. Nat Neurosci 2004;7:184–188. [PubMed: 14703573]
- Blair KS, Smith BW, Mitchell DGV, Morton J, Vythilingam M, Pessoa L, Fridberg D, Zametkin A, Sturman D, Nelson EE, Drevets WC, Pine DS, Martin A, Blair RJR. Modulation of Emotion by Cognition and Cognition by Emotion: An MRI investigation. Neuroimage 2007;35:430–40. [PubMed: 17239620]
- Botvinick M, Cohen J, Carter C. Conflict monitoring and anterior cingulate cortex: an update. Trends Cogn Sci 2004;12:539–546. [PubMed: 15556023]
- Bradley, MM.; Lang, PJ. Affective norms for English words (ANEW): Stimuli, instruction manual and affective ratings. Technical report C-1. Gainesville, FL: The Center for Research in Psychophysiology, University of Florida; 1999.
- Bradley BP, Mogg K. Mood and personality in recall of positive and negative information. Behav Res Ther 1994;32:137–141. [PubMed: 8135712]
- Bradley BP, Mogg K, Millar N, White J. Selective processing of negative information: effects of clinical anxiety, concurrent depression, and awareness. J Abnorm Psychol 1995;104:532–6. [PubMed: 7673577]

- Breiter HC, Etcoff NL, Whalen PJ, Kennedy WA, Rauch SL, Buckner R, Strauss MM, Hyman SE, Rosen BR. Response and habituation of the human amygdala during visual processing of facial expression. Neuron 1996;17:875–887. [PubMed: 8938120]
- Bremner JD, Vermetten E, Vythilingam M, Afzal N, Schmahl C, Elzinga B, Charney DS. Neural correlates of the classic color and emotional stroop in women with abuse-related posttraumatic stress disorder. Biol Psychiatry 2004;55:612–20. [PubMed: 15013830]
- Broadbent DE, Broadbent MH. From detection to identification: Response to multiple targets in rapid serial visual presentation. Perception & Psychophysics 1987;42:105–113. [PubMed: 3627930]
- Brown JW, Braver TS. Learned predictions of error likelihood in the anterior cingulate cortex. Science 2005;307:1118–1121. [PubMed: 15718473]
- Budhani S, Marsh AA, Pine DS, Blair RJ. Neural correlates of response reversal: Considering acquisition. Neuroimage 2007;34:1754–65. [PubMed: 17188518]
- Bush G, Luu P, Posner MI. Cognitive and emotional influences in anterior cingulate cortex. Trends Cogn Sci 2000;4:215–222. [PubMed: 10827444]
- Bush G, Whalen PJ, Rosen BR, Jenike MA, McInerney SC, Rauch SL. The counting Stroop: an interference task specialized for functional neuroimaging-validation study with functional MRI. Hum Brain Mapp 1998;6:270–282. [PubMed: 9704265]
- Carter CS, Macdonald AM, Botvinick M, Ross LL, Stenger VA, Noll D, Cohen JD. Parsing executive processes: strategic vs. evaluative functions of the anterior cingulate cortex. Proc Natl Acad Sci U S A 2000;97:1944–8. [PubMed: 10677559]
- Carter CS, Mintun M, Cohen JD. Interference and facilitation effects during selective attention: an H2150 PET study of Stroop task performance. Neuroimage 1995;2:264–272. [PubMed: 9343611]
- Cohen JD, Botvinick M, Carter CS. Anterior cingulate and prefrontal cortex: who's in control? Nat Neurosci 2000;3:421–423. [PubMed: 10769376]
- Constantinidis C. Posterior parietal mechanisms of visual attention. Rev Neurosci 2006;17:415–27. [PubMed: 17139842]
- Compton RJ, Banich MT, Mohanty A, Milham MP, Herrington J, Miller GA, Scalf PE, Webb A, Heller W. Paying attention to emotion: an fMRI investigation of cognitive and emotional stroop tasks. Cognitive, Affective, & Behavioral Neuroscience 2003;3:81–96.
- Davis KD, Taylor KS, Hutchison WD, Dostrovsky JO, McAndrews MP, Richter EO, et al. Human anterior cingulate cortex neurons encode cognitive and emotional demands. Journal of Neuroscience 2005;25:8402–8406. [PubMed: 16162922]
- Dehaene S, Naccache L, Cohen L, Bihan DL, Mangin JF, Poline JB, Riviere D. Cerebral mechanisms of word masking and unconscious repetition priming. Nat Neurosci 2001;4:752–8. [PubMed: 11426233]
- Desimone R, Duncan J. Neural mechanisms of selective visual attention. Annual Review of Neuroscience 1995;18:193–222.
- Dolan RJ, Fletcher P, Morris J, Kapur N, Deakin JF, Frith CD. Neural activation during covert processing of positive emotional facial expressions. Neuroimage 1996;4:194–200. [PubMed: 9345509]
- Durston S, Thomas KM, Worden MS, Yang Y, Casey BJ. The effect of preceding context on inhibition: an event-related fMRI study. NeuroImage 2002;16:449–453. [PubMed: 12030830]
- Eisenberger NI, Lieberman MD. Why rejection hurts: A common neural alarm system for physical and social pain. Trends in Cognitive Sciences 2004;8:294–300. [PubMed: 15242688]
- Elliott R, Rubinsztein JS, Sahakian BJ, Dolan RJ. Selective attention to emotional stimuli in a verbal go/ no-go task: an fMRI study. Neuroreport 2000;11:1739–1744. [PubMed: 10852235]
- Erthal FS, de Oliveira L, Mocaiber I, Pereira MG, Machado-Pinheiro W, Volchan E, Pessoa L. Loaddependent modulation of affective picture processing. Cognitive Affective & Behavioral Neuroscience 2005;5:388–395.
- Etkin A, Egner T, Peraza DM, Kandel ER, Hirsch J. Resolving emotional conflict: a role for the rostral anterior cingulate cortex in modulating activity in the amygdala. Neuron 2006;51:871–82. [PubMed: 16982430]
- George MS, Ketter EA, Gill DS, Haxby JV, Ungerleider LG, Herscovitch P, Post RM. Brain regions involved in recognizing facial emotion or identity: An oxygen-15 PET study. J Neuropsychiatry Clin Neurosci 1993;5:384–394. [PubMed: 8286936]

- Gitelman DR, Nobre AC, Parrish TB, LaBar KS, Kim YH, Meyer JR, Mesulam M. A large-scale distributed network for covert spatial attention. Brain 1999;122:1093–1106. [PubMed: 10356062]
- Gottlieb JP, Kusunoki M, Goldberg ME. The representation of visual salience in monkey parietal cortex. Nature 1998;39:481–4. [PubMed: 9461214]
- Haas BW, Omura K, Constable RT, Canli T. Interference produced by emotional conflict associated with anterior cingulate activation. Cogn Affect Behav Neurosci 2006;6:152–6. [PubMed: 17007235]
- Harris CR, Pashler HE. Attention and the processing of emotional words and names: Not so special after all. Psychological Science 2004;15:171–178. [PubMed: 15016288]
- Holroyd CB, Nieuwenhuis S, Yeung N, Nystrom L, Mars R, Coles MGH, Cohen JD. Dorsal anterior cingulate cortex shows fMRI response to internal and external error signals. Nat Neurosci 2004;7:497–498. [PubMed: 15097995]
- Hopfinger JB, Buonocore MH, Mangun GR. The neural mechanisms of top-down attentional control. Nat Neurosci 2000;3:284–291. [PubMed: 10700262]
- Indovina I, Macaluso E. Dissociation of Stimulus Relevance and Saliency Factors during Shifts of Visuospatial Attention. Cereb Cortex. in press
- Kastner S, Ungerleider L. Mechanisms of visual attention in the human cortex. Annu Rev Neurosci 2000;23:315–341. [PubMed: 10845067]
- Kosson DS, Budhani S, Nakic M, Chen G, Saad ZS, Vythilingam M, Pine DS, Blair RJL. The role of the amygdala and rostral anterior cingulate in encoding expected outcomes during learning. Neuroimage 2006;29:1161–72. [PubMed: 16387514]
- Itti L, Koch C. Computational modelling of visual attention. Nat Rev Neurosci 2001;2:194–203. [PubMed: 11256080]
- LeDoux, JE. The Emotional Brain. New York: Simon and Schuster; 1996.
- Li WV, Piech. Contour saliency in primary visual cortex. Neuron 2006;50:951-62. [PubMed: 16772175]
- Liddell BJ, Brown KJ, Kemp AH, Barton MJ, Das P, Peduto A, Gordon E, Williams LM. A direct brainstem-amygdala-cortical 'alarm' system for subliminal signals of fear. Neuroimage 2005;24:235–43. [PubMed: 15588615]
- Luck SJ, Chelazzi L, Hillyard SA, Desimone R. Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. J Neurophysiol 1997;77:24–42. [PubMed: 9120566]
- Luo Q, Peng D, Jin Z, Xu D, Xiao L, Ding G. Emotional valence of words modulates the subliminal repetition priming effect in the left fusiform gyrus: an event-related fMRI study. Neuroimage 2004;21:414–21. [PubMed: 14741678]
- MacDonald AW, Cohen JD, Stenger VA, Carter CS. Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. Science 2000;288:1835–1838. [PubMed: 10846167]
- Marois R, Chun MM, Gore JC. A common parieto-frontal network is recruited under both low visibility and high perceptual interference conditions. J Neurophysiol 2004;92:2985–92. [PubMed: 15486425]
- Marois R, Chun MM, Gore JC. Neural correlates of the attentional blink. Neuron 2000;28:299–308. [PubMed: 11087002]
- Menon V, Adleman N, White CD, Glover GH, Reiss AL. Error-related brain activation during a Go/ NoGo response inhibition task. Hum Brain Mapp 2001;123:131–143. [PubMed: 11170305]
- Mineka S, Ohman A. Phobias and preparedness: the selective, automatic, and encapsulated nature of fear. Biol Psychiatry 2002;52:927–37. [PubMed: 12437934]
- Mitchell DG, Richell RA, Leonard A, Blair RJ. Emotion at the expense of cognition: psychopathic individuals outperform controls on an operant response task. J Abnorm Psychol 2006;115:559–66. [PubMed: 16866596]
- Mitchell DGV, Nakic M, Fridberg D, Pine DS, Blair RJR. The impact of processing load on emotion. Neuroimage 2007;34:1299–309. [PubMed: 17161627]
- Mogg K, Bradley BP, Williams R, Mathews A. Subliminal processing of emotional information in anxiety and depression. J Abnorm Psychol 1993;102:304–311. [PubMed: 8315143]
- Moran J, Desimone R. Selective attentiongates visual processing in the extrastriate cortex. Science 1985;229:782–784. [PubMed: 4023713]1985

- Morris JS, Ohman A, Dolan R. A subcortical pathway to the right amygdala mediating "unseen" fear. Proceedings of the National Academy of Science USA 1999;96:1680–1685.
- Naccache L, Gaillard R, Adam C, Hasboun D, Clemenceau S, Baulac M, Dehaene S, Cohen L. A direct intracranial record of emotions evoked by subliminal words. Proc Natl Acad Sci U S A 2005;102:7713–7. [PubMed: 15897465]
- Nakic M, Smith BW, Busis S, Vythilingam M, Blair RJ. The impact of affect and frequency on lexical decision: The role of the amygdala and inferior frontal cortex. Neuroimage 2006;31:1752–61. [PubMed: 16647271]
- Ochsner KN, Bunge SA, Gross JJ, Gabrieli JDE. Rethinking feelings: An fMRI study of the cognitive regulation of emotion. Journal of Cognitive Neuroscience 2002;14:1215–1299. [PubMed: 12495527]
- Ochsner KN, Ray RD, Robertson ER, Cooper JC, Chopra S, Gabrieli JDE, Gross JJ. For better or for worse: Neural Systems Supporting the Cognitive Down- and Up-regulation of Negative Emotion. Neuroimage 2004;23(2):483–499. [PubMed: 15488398]
- Ochsner KN, Gross JJ. The cognitive control of emotion. Trends Cogn Sci 2005;9:242–249. [PubMed: 15866151]
- Okon-Singer H, Tzelgov J, Henik A. Distinguishing between automaticity and attention in the processing of emotionally-significant stimuli. Emotion 2007;7:147–157. [PubMed: 17352570]
- Pessoa L, Kastner S, Ungerleider LG. Neuroimaging studies of attention: from modulation of sensory processing to top-down control. J Neurosci 2003;23:3990–3998. [PubMed: 12764083]
- Pessoa L, McKenna M, Gutierrez E, Ungerleider LG. Neural processing of emotional faces requires attention. Proc Natl Acad Sci U S A 2002;99:11458–11463. [PubMed: 12177449]
- Pezawas L*, Meyer-Lindenberg A*, Drabant EM, Verchinski B, Mattay VS, Hariri AR, Kolachana B, Egan MF, Weinberger DR. 5-HTTLPR polymorphism impacts human cingulate-amygdala interactions: a genetic susceptibility mechanism for depression. Nat Neurosci 2005;8:828–834. [PubMed: 15880108]
- Phan KL, Fitzgerald DA, Nathan PJ, Moore GJ, Uhde TW, Tancer ME. Neural substrates for voluntary suppression of negative affect: a functional magnetic resonance study. Biological Psychiatry 2005;57:210–219. [PubMed: 15691521]
- Phan KL, Fitzgerald DA, Nathan PJ, Tancer ME. Association between amygdala hyperactivity to harsh faces and severity of social anxiety in generalized social phobia. Biol Psychiatry 2006;59:424–9. [PubMed: 16256956]
- Posner, MI.; DiGirolamo, GJ. Executive attention: Conflict, target detection, and cognitive control. In: Parasuraman, R., editor. The Attentive Brain. MIT Press; 1998.
- Posner MI, Petersen SE. The attention system of the human brain. Annu Rev Neurosci 1990;13:25–42. [PubMed: 2183676]
- Reynolds JH, Chelazzi L, Desimone R. Competitive mechanisms subserve attention in macaque areas V2 and V4. J Neurosci 1999;19:1736–1753. [PubMed: 10024360]
- Reynolds JH, Desimone R. Interacting Roles of Attention and Visual Salience in V4. Neuron 2003;37:853–63. [PubMed: 12628175]
- Shin LM, Whalen PJ, Pitman RK, Bush G, Macklin ML, Lasko NB, et al. An fMRI study of anterior cingulate function in posttraumatic stress disorder. Biol Psychiatry 2001;50:932–942. [PubMed: 11750889]
- Simpson JR, Ongur D, Akbudak E, Conturo TE, Ollinger JM, Snyder AZ, Gusnard DA, Raichle M. The emotional modulation of cognitive processing: An fMRI study. Journal of Cognitive Neuroscience 2000;12:157–170. [PubMed: 11506655]
- Strange BA, Hurlemann R, Dolan RJ. An emotion-induced retrograde amnesia in humans is amygdalaand beta-adrenergic-dependent. Proceedings of the National Academy of Sciences of the United States of America 2003;100:13626–13631. [PubMed: 14595032]
- Talairach, J.; Tournoux, P. A co-planar sterotactic atlas of the human brain. Stuttgart, Germany: Thieme; 1988.
- Vuilleumier P, Richardson MP, Armony JL, Driver J, Dolan RJ. Distant influences of amygdala lesion on visual cortical activation during emotional face processing. Nat Neurosci 2004;7:1271–8. [PubMed: 15494727]

- Vuilleumier P, Armony JL, Driver J, Dolan RJ. Effects of attention and emotion on face processing in the human brain: an event-related fMRI study. Neuron 2001;30:829–41. [PubMed: 11430815]
- Weissman DH, Gopalakrishnan A, Hazlett CJ, Woldorff MG. Dorsal anterior cingulate cortex resolves conflict from distracting stimuli by boosting attention toward relevant events. Cereb Cortex 2005;15:229–237. [PubMed: 15238434]
- Whalen PJ, Kagan J, Cook RG, Davis FC, Kim H, Polis S, McLaren DG, Somerville LH, McLean AA, Maxwell JS, Johnstone T. Human amygdala responsivity to masked fearful eye whites. Science 2004;306:2061. [PubMed: 15604401]
- Whalen PJ, Bush G, McNally RJ, Wilhelm S, McInerney S, Rauch SL. The emotional counting Stroop paradigm: An fMRI probe of the anterior cingulate affective division. Biological Psychiatry 1998;44:1219–1228. [PubMed: 9861465]
- Williams LM, Das P, Liddell BJ, Kemp AH, Rennie CJ, Gordon E. Mode of functional connectivity in amygdala pathways dissociates level of awareness for signals of fear. J Neurosci 2006;26:9264–71. [PubMed: 16957082]
- Williams MA, McGlone F, Abbott DF, Mattingley JB. Differential amygdala responses to happy and fearful facial expressions depend on selective attention. NeuroImage 2005;242:417–425. [PubMed: 15627583]
- Williams JM, Mathews A, MacLeod C. The emotional Stroop task and psychopathology. Psychological Bulletin 1996;120(1):3–24. [PubMed: 8711015]



Fig 1. Stimuli presentation Sequence

SUPEM-supraliminal emotional; SUPNE-supraliminal neutral; SUBEM-subliminal emotional; SUBNE- subliminal neutral.



Fig 2. Brain areas showing the valence and visibility effect

a) Regions showing the emotion effect. b) Signal percent change in regions shown in a. The signal intensity of the areas was obtained from the clusters showing the main effect of emotion. c) Regions showing the visibility effect. d) Signal percent change shown in regions in c. The signal intensity of the areas was obtained from the clusters showing the main effect of visibility. Abbreviations: PFC- prefrontal cortex; PPC-posterior parietal cortex; ACC-anterior cingulate cortex; AMY-amygdala. R refers to the left hemisphere and L to the right.



Fig 3. Brain areas showing overlapping distraction effect

Map a and b showed overlapping distraction effect of SUPEM, SUPNE, SUBEM. Map c and d showed overlapping distraction effect of all the four conditions. a) Right ACC (BA32/24); x, y, z = 10, -1, 37; p < .01. b) Middle frontal gyrus (BA 10); x, y, z =38, 52, 11. p < .005. c) Precuneus (BA 7); x, y, z = 24, -69, 32; p < .005. d) Lingual gyrus (BA 19), x, y, z = -28, 64, 0; p < .005. R refers to the left hemisphere and L to the right hemisphere.

controlled aspects of stimuli

	Emotional distracters	Neutral distracters		
	Mean	Mean	F	р
Valence	2.31	4.12	636.75	.0001
Arousal	5.24	4.02	31.36	0001
Concreteness	405.48	418.47	.818	.368
Length	5.17	5.28	.184	.668
Frequency	214.88	221.15	.009	.927

Behavioral results

	RT		ER	
	Mean	Std.	Mean	Std.
SUPEM	604.00	131.98	9.88%	4.78%
SUPNE	580.94	146.28	9.41%	4.83%
SUBEM	575.20	80.83	8.69%	5.36%
SUBNE	585.03	86.32	7.62%	4.97%
CONTROL	572.13	86.21	5.83%	4.37%

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Regions that showed a significant main effect in voxel-wise analysis

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Structure	L/R	BA	v alence effect, p < .005 x	у	Z	F
Middle/Superior frontal Gyrus	Г	8/6	-39	41	29	36.60
Middle Frontal	Я	9/8/44	49	12	36	40.83
Superior Frontal Gyrus	Я	10	37	52	14	31.42
Inferior Parietal Lobule	R	40	39	-51	36	112.68
Precuneus	Г	7	-4	-58	64	33.24
Inferior Parietal Lobule	Г	40	-53	-45	28	35.86
Cingulate Gyrus	R	24	4	10	35	23.23
Fusiform Gyrus	R	37	49	-40	-12	31.95
Precentral Gyrus	L	ю	-31	9–	36	42.02
Postcentral Gyrus	R	σ	19	-25	47	48.61
Paracentral Lobule	R	5	6	-37	51	27.65
Precentral Gyrus	L	9	-32	-13	62	30.86
Medial Frontal Gyrus	R	9	4	-4	60	41.27
Thalamus	L		8-	-16	17	21.86
Thalamus/Pulvinar	Γ		L	-29	-2	25.54
Lentiform Nucleus	L		-27	1	13	25.10
Insula	L	13	-42	8	18	56.46
amygdala	Γ		-29	-8-	-19	10.49, p < .01
			Visibility effect, $p < .005$			
Middle Frontal Gyrus	Г	46	-45	18	25	27.74
Middle Frontal Gyrus	L	6	-42	9	31	31.65
Superior Parietal Lobule	R	7	22	-66	52	25.34
Medial Frontal Gyrus	R	9	15	ر ا د	52	24.77
Anterior Cingulate Gyrus	Я	32	18	33	17	22.87, p < .005 uncorrected
Lingual Gyrus	R	18	20	-72	-12	35.06
Caudate Body	R		1	L	16	-46.46
Insula	R	13	42	-21		31.98
Declive	L		-28	-66	-18	45.16
Declive	Г		-2	-59	-11	25.23

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