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A Common Parieto-Frontal Network Is Recruited Under Both Low Visibility and High Perceptual Interference Conditions

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Marois, René, Marvin M. Chun, and John C. Gore. A common parieto-frontal network is recruited under both low visibility and high perceptual interference conditions. *J Neurophysiol* 92: 2985–2992, 2004; 10.1152/jn.01061.2003. A fundamental property of visual attention is to select targets from interfering distractors. However, attention can also facilitate the detectability of near-threshold items presented in isolation. The extent to which these two perceptually challenging conditions are resolved by the same neural mechanisms is not well known. In the present event-related fMRI experiment, subjects performed a letter identification task under two perceptually challenging conditions; when the luminance contrast of a target letter was reduced (perceptual visibility manipulation) and when the target letter was flanked by distractors (perceptual interference manipulation). Perceptual interference recruited the right parietal and mid-lateral frontal cortex, while perceptual visibility activated these regions bilaterally. The overlap of activated areas between the two perceptual manipulations suggests that a single parieto-frontal network is summoned under both perceptual visibility and interference conditions.

INTRODUCTION

The goal of this study is to determine how the brain can successfully detect a target under two types of perceptually challenging conditions: the first, *perceptual interference*, occurs when the target to be detected is presented among competing distractors, whereas the second, *perceptual visibility*, arises when the target is barely visible. Target detection, whether it occurs under perceptual interference or low visibility conditions, can be dramatically enhanced by attention (Duncan 1980; Hawkins et al. 1990; Lu and Dosher 1998; Posner et al. 1980). Attentional enhancements under perceptual interference and low visibility conditions have been characterized as attentional selection and attentional facilitation, respectively (Reynolds et al. 2000). However, despite that fact that these two roles of attention have long been characterized behaviorally, it is not well understood whether resolutions of perceptual interference and low visibility arise from mechanistically distinct attentional mechanisms or whether they are mediated by the same fundamental process (Reynolds et al. 1999, 2000).

Single-cell studies in monkeys indicate that the effect of attention is to suppress the activity associated with distractors presented along with the target in the cell's receptive field (Luck et al. 1997; Moran and Desimone 1985; Reynolds et al. 1999), as if the cell's receptive field shrunk around the attended stimulus. These and other results have led to a biased competition model of attention (Desimone and Duncan 1995), according to which *1*) objects in the visual field compete for representation in the cortex, and *2*) this competition is biased in favor of the behaviorally relevant object by top-down attentional mechanisms, effectively leading to the selective processing of the target and filtering out of irrelevant stimuli. However, in addition to suppressing distractor activity, attention can also enhance the response of visual cells to targets under perceptually difficult conditions in the absence of distractors (Martinez-Trujillo and Treue 2002; Reynolds et al. 2000; Spitzer et al. 1988). Indeed, it has been suggested that the role of attention is essentially one of enhancing the effective contrast of a stimulus (Martinez-Trujillo and Treue 2002; Reynolds and Desimone 2003; Reynolds et al. 2000).

In summary, the single-cell studies raise the possibility that the effects of attention onto visual neurons could be at least partly distinct under perceptual interference and low visibility conditions, with the former associated primarily with filtering out of distractor activity and the latter with target signal enhancement.

The source of the biasing signals to the visual cortex in attentional selection is thought to arise from the frontal cortex and perhaps from the parietal cortex as well (Kastner and Ungerleider 2000; Kastner et al. 1999; Miller and Cohen 2001). Although some regions of the parietal cortex exhibit similar characteristics to the visual cortex (Kastner et al. 1999), the dorsal parietal cortex in particular seems associated with the control of attentional selection: it is activated in tasks requiring subjects to select a target among distractors (Corbetta et al. 1993, 2000; Hopfinger et al. 2000; Kastner and Ungerleider 2000; Kastner et al. 1999; Marois et al. 2000; Nobre et al. 1997), regardless of whether the stimuli are presented or not (Kastner et al. 1999). Consistent with these results, it has been proposed that a fundamental role (Friedman-Hill et al. 2003; see also Marois et al. 2000), if not the fundamental role (Wojciulik and Kanwisher 1999), of the intra-parietal cortex in visual attention is to suppress task-irrelevant distractors. However, it is currently unknown whether the same parietal (and frontal) cortical regions are also recruited under perceptually challenging conditions in the absence of distractors.

In a previous study, we identified a parieto-frontal network that was activated under two types of distractor interference (Marois et al. 2000); temporal interference, in which distractors temporally interfere with target identification during a rapid

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serial visual presentation (RSVP), and spatial interference, in which distractors interfere with target identification by lateral masking. The same parieto-frontal network was activated under both interference types, although spatial interference effects were more robustly observed in the parietal than in the frontal cortex (Marois et al. 2000). In the present study, we determined whether this parieto-frontal network is specifically recruited under perceptual (spatial) interference conditions or whether it is activated with perceptual visibility manipulations as well. The perceptual interference condition consisted in a lateral masking manipulation, in which the distance between the target and distractors was varied, while the perceptual visibility manipulation varied the luminance contrast and/or size of the target.

METHODS

Behavioral experiment

All subjects provided informed consent in accordance with procedures and protocols approved by the Yale University School of Medicine Human Investigation Committee and Vanderbilt University Institutional Review Board.

An initial behavioral task measured the attentional effects of our distractor interference and perceptual visibility manipulations (Fig. 1). When subjects are required to identify two targets presented in rapid succession, attentional processing of the first target (T1) often triggers a transient impairment for reporting the second target (T2), a dual-task deficit known as the attentional blink (AB) (Chun and Potter 1995; Raymond et al. 1992). T2 performance therefore provides a measure of the attentional demands of the first task. Eleven subjects searched for both T1 (letters B, C, or D) and T2 (letter Y present or absent) presented in a short RSVP of distractor items. A trial consisted of fixation for 1,000 ms, blank screen for 200 ms, T1 presentation for 100 ms to preclude eye movements, blank screen for 300 ms, followed by successive presentation of three letters for 100 ms each, with all stimuli shown at fixation. When present, T2 was the first of the three letters. The response panels for T1 (B__C__D) and T2 (YES__NO) were subsequently shown for 1,300 and 1,080 ms, respectively. The T1 panel consisted of a horizontal string of 17 white consonants (0.5° high, 0.3° wide; letter center-to-letter center distance, 0.375°; visual angle of entire letter string, 7.5°) on a black background, with the target letter always appearing in the center at fixation. As shown in Fig. 1*A*, there were three T1 displays: *baseline display*, with the target letter separated from the distractor letters by a 1.1° gap (letter center-to-letter center); *low-visibility display*, with a T1 panel identical to the baseline condition except that the contrast of the central target letter was reduced from 100 to 25% and its size to 35%; and *high-interference display*, with a T1 panel identical to the baseline display except that two of the eight distractors on either side were positioned between the 100% contrast target letter and the 1° gap. The three self-paced trial types were randomly intermixed, and subjects performed 70 trials per condition. On 20% of the trials, T2 was replaced by another letter to calculate T2 false alarm rate. The comparison between the visibility and baseline trial performance corresponds to the perceptual visibility manipulation, whereas the comparison between the interference and baseline trial performance corresponds to the perceptual interference manipulation.

To insure that deficits in T2 detection in the dual-task experiment were caused by the attentional demands of T1 instead of forward masking of T2 by T1 displays, nine additional subjects performed the same experiment except that they were told to detect the presence of T2 only, ignoring the T1 display.

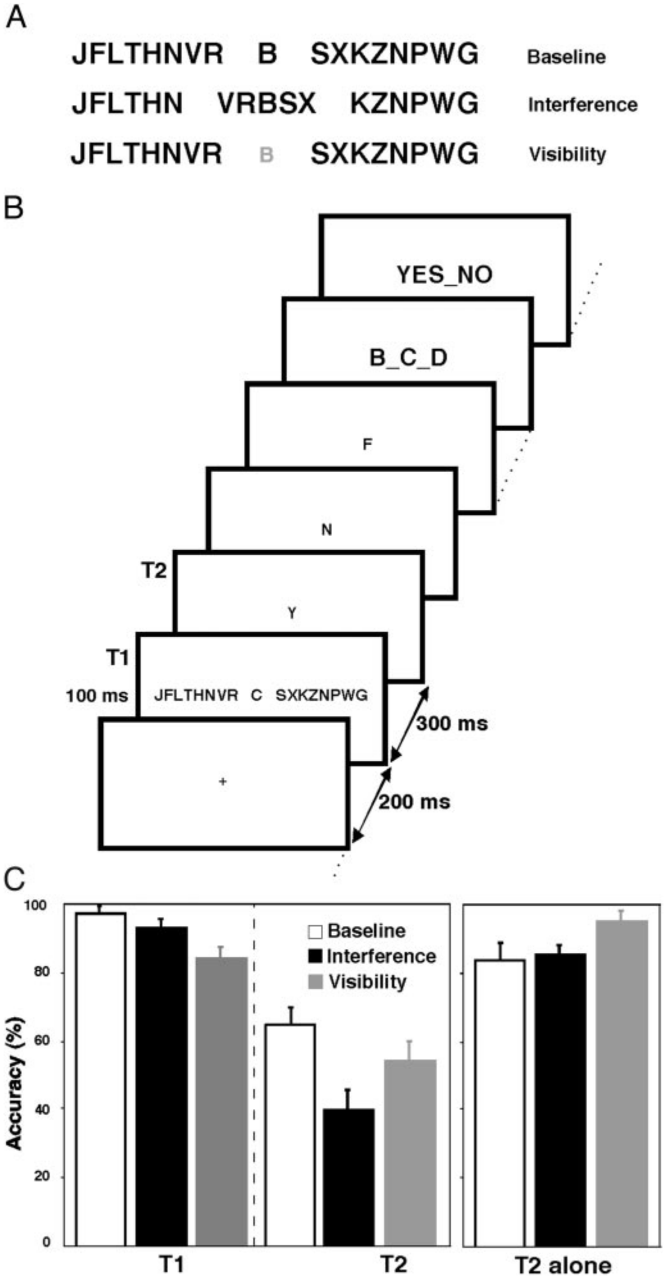

FIG. 1. Attentional effects of perceptual interference and visibility. *A*: Target 1 (T1) displays for the baseline, interference, and visibility conditions. In the experiment, the letters were bright and the background was dark, but for illustration purposes, the brightness levels have been reversed in this figure. *B*: trial design. Subjects identified T1, searched for the presence of target 2 (T2; letter Y), and responded at the end of each trial. *C*: behavioral performance. *Left*: T1 performance was better in the baseline condition than in both interference and visibility conditions. T2 performance was also better in the baseline condition than in both interference and visibility conditions. All T2 performances were above their respective false alarm rates (8, 8, and 11%, $P < 0.0001$). *Right*: when subjects performed the T2 task alone, the interference and visibility conditions no longer led to poorer performance compared with the baseline condition.

Functional MRI experiments

EXPERIMENT 1: VISIBILITY MANIPULATION. This experiment had two purposes. First, using a region of interest (ROI) analysis, it aimed at determining whether the perceptual visibility manipulation activated the same brain regions previously implicated in perceptual interference (Marois et al. 2000). Second, by using a voxel-based exploratory analysis, it also aimed at determining whether other brain regions than the parieto-frontal ROIs would be activated by a perceptual visibility manipulation.

The functional MRI (fMRI) parameters are described in detail elsewhere (Marois et al. 2000). Briefly, subjects ($n = 10$) were scanned with a 1.5-T GE MRI system (Advanced NMR, Wilmington, MA) equipped with EPI. T1-weighted images were first acquired using conventional parameters. Eight axial slices (9 mm thick, 0.5 mm skip) encompassed the dorsal apex of cortex to the middle/inferior temporal cortex. Image acquisition consisted of a gradient echo single-shot sequence [echo time, 60 ms; flip angle, 60°; repetition time (TR), 1,750 ms; and 102 images/slice]. Each image was 128×64 pixels over a field of view of 40×20 cm (in-plane resolution: 3.12 mm^2).

Each trial consisted of 3 s of small fixation cross, blank for 150 ms, target for 100 ms, blank for 200 ms, and large fixation cross for 8.8 s, during which subjects made a nonspeeded button press response (total of 12.25 s per trial). The two T1 trial types, high visibility (baseline) and low visibility, were randomly intermixed. There were seven trials per condition per fMRI run, with six to eight runs per subject. Image acquisition was synchronized to stimulus presentation, and error trials were discarded from further analysis.

Images acquired from 2 to 9 s after T1 presentation were used for voxel-based statistical parametric mapping (SPM). The voxel-based SPMs of blood oxygenation level-dependent (BOLD) activation were created for each subject using a skew-corrected percentage signal difference. The anatomical and Gaussian-filtered (full width at half-maximum = 4.0 mm) BOLD images were transformed into standardized Talairach space. The resulting maps from all subjects were superimposed to create cluster-filtered (6 contiguous pixels) composite maps. The probability that the mean percentage signal change of activation across subjects was significantly different from zero was calculated using a t-test for each composite pixel. The parieto-frontal ROIs previously shown to be involved in perceptual interference (Marois et al. 2000) were overlaid on the composite maps. To determine how well the voxel-based activations were confined to the ROIs, the voxel-based analysis was thresholded at the same level as the ROI analysis ($P < 0.05$, corrected for the number of ROI comparisons). However, activations that fell outside of the ROIs were only considered to be significant if they survived a $P < 0.001$ threshold. No significant activations outside the ROIs were observed at that threshold (for either high minus low visibility or low minus high).

To provide a more comprehensive account of the ROI activations with the perceptual visibility manipulation, the activation time courses were extracted for each subject in each ROI and normalized to the image acquired 250 ms following stimulus onset. Each signal was time-smoothed with a Gaussian filter half width half maximum [(HWHM) = 0.2s] prior to slice interpolation. The time intervals corresponding to the signal peaks (images acquired within the central 4 s of the peak) across conditions for each ROI were first isolated, and t-tests between the signal peaks of the two perceptual visibility conditions (low vs. high) were performed with significance level set at $P < 0.05$.

EXPERIMENT 2: VISIBILITY VERSUS INTERFERENCE MANIPULATIONS. Thirteen participants volunteered for this event-related fMRI experiment, which consisted in the presentation of two pairs of trial types, one each for the perceptual interference and visibility manipulations. Specifically, the perceptual visibility manipulation consisted of the low and high contrast T1 targets presented alone without any distractors, while the perceptual interference manipulation included the high and low T1 interference displays used in the behavioral experiment. The presentations of the four T1 trial types were randomly intermixed.

The experimental protocol was as described in the previous fMRI experiment, except for the following modifications: TR = 2,000ms, 120 images/slice, the large fixation period was 9,500 ms, and small fixation period was 4 s (for total trial duration of 14 s), permitting the second TR of each trial to coincide with stimulus presentation. There were four repetitions of each of the four trial types per fMRI run, with six to eight runs per subject.

Activation time courses were extracted for each subject in each parieto-frontal ROI, normalized to each trial onset, and analyzed as described in the previous fMRI experiment. t-test between the signal peaks of the two interference conditions (high vs. low interference) and perceptual conditions (low vs. high visibility) were performed separately. Since we were interested not only in testing the separate effects of the perceptual visibility and interference manipulations, but also whether the effect of the interference was significantly larger than that of perceptual visibility, t-test were selected instead of ANOVAs. However, ANOVAs yielded qualitatively similar results.

Since this second fMRI experiment used perceptual visibility displays that were different from those used in the previous behavioral and fMRI experiments, we ascertained in a separate behavioral dual-task experiment that the specific perceptual manipulations employed in this new fMRI experiment were also attention demanding. Twelve subjects performed both T1 and T2 (letter Y) detection tasks as described in the initial behavioral experiment (Fig. 1), except that there were four randomly intermixed T1 display conditions (high/low contrast, high/low interference), with 50 trials per T1 condition.

EXPERIMENT 3: CONTROL STUDY. A control experiment was conducted on six subjects to rule out the possibility that low-level physical differences between the high and low interference displays could account for the activations observed in *experiment 2*. This experiment aimed at measuring the level of activation associated with the two interference displays under conditions where attention was diverted away from the interference manipulation. The experimental design and data analysis was as described in *experiment 2*, except that only the interference displays were presented, and for each of the high and low interference displays, one-half of the stimulus set was colored light red and the other one-half was colored light green, with this color stimulus pairing counterbalanced between subjects. As a result, the correlation between stimulus color (red/green) and interference level (high/low) was zero. Subjects' task consisted simply in identifying the color of the stimulus display by pressing one of two buttons. Accuracy was ~98% for each of the two types of color trials.

RESULTS

Behavioral studies

To measure the attentional costs of the distractor interference and perceptual visibility manipulations, we used a dual-task attentional blink paradigm (Fig. 1), in which the costs of attending to the first of two targets in an RSVP stream is indexed by the detection performance with the second target (Chun and Potter 1995; Raymond et al. 1992). Specifically, we determined how perceptual interference and perceptual difficulty manipulations of Task1 affected T2 detection performance. In this behavioral experiment, subjects performed target letter identification for Task1 in three different conditions: In the baseline condition, a high-contrast target letter was flanked distally by distractor letters (Fig. 1); in the interference condition, the target was flanked proximally by distractor letters (Marois et al. 2000); and in the visibility condition, the display was identical to the baseline condition except for the use of a low-contrast and small-size target. Task2, identical for all conditions, consisted of detecting the presence of the letter Y shown 300 ms after T1. Interference effects were revealed by lower T1 and T2 performance in the interference condition compared with the baseline condition (T1: $t = 3.5$, $P = 0.005$; T2: $t = 8.0$, $P < 0.0001$; Fig. 1*C*). The visibility manipulation (visibility vs. baseline conditions) also led to poorer T1 and T2 detection, confirming the increased attentional demands for identifying a low-contrast letter (T1: $t = 3.1$, $P = 0.01$; T2: $t = 3.0$, $P = 0.01$). These deficits resulted from the attentional demands of Task1 rather than sensory masking effects of Task 1 on Task 2 since T2 detection dramatically improved for all three conditions when subjects performed Task2 alone compared to when Task2 was performed together with Task1 (pooled *t*-test, baseline: $t = 2.3$, $P = 0.03$; visibility: $t = 6.3$, $P < 0.0001$; interference: $t = 6.4$, $P < 0.0001$). Most importantly, the interference ($t = 0.7$, $P = 0.49$) and visibility ($t = -2.8$, $P = 0.99$) condition performances were no longer worse than baseline performance when Task2 was performed alone (Fig. 1*C*). These results indicate that increasing attentional demands for T1 identification, either via distractor interference or by degrading target visibility, leads to deficits in perceiving subsequently presented items (an attentional blink).

Imaging studies

EXPERIMENT 1. Given that both the perceptual visibility and interference conditions require attention, do they recruit the same neural substrates? A previous study indicated that perceptual interference recruits a parieto-frontal network consisting of the intra-parietal/intra-occipital cortex (predominantly in the right hemisphere), the mid-lateral frontal cortex, and anterior cingulate cortex (AC) (Marois et al. 2000). In the present experiment, we investigated whether these parieto-frontal ROIs would also be recruited under perceptual visibility manipulations. Subjects ($n = 10$) were scanned while identifying a high-visibility (high-contrast, large-size) or low-visibility (low-contrast, small-size) target letter flanked by distal distractors (Fig. 2, *A* and *B*). Comparison of the low versus high perceptual visibility conditions revealed activations overlapping with the parieto-frontal ROIs (Fig. 2*C*). Peak time course analysis confirmed the SPM results, showing greater response under low visibility condition in several of the parieto-frontal ROIs (left parietal: $t = 3.5$, $P < 0.01$; right lateral frontal: $t = 2.9$, $P < 0.05$; right AC: $t = 4.7$, $P = 0.001$; left AC: $t = 3.1$, $P < 0.05$), except for the left lateral frontal ($t = 1.6$, not significant) and right parietal cortex ($t = 1.7$, not significant) ROI (Fig. 2*C*). Importantly, no brain regions outside of these ROIs were activated by the perceptual visibility manipulation when using a voxel-wise analysis thresholded at $P < 0.001$. These results indicate that low perceptual visibility seems to recruit a very similar neural network to that observed during perceptual interference (Marois et al. 2000) and that the visibility manipulation did not recruit brain regions other than those activated under perceptual interference conditions. Finally, the absence of significant right parietal activation with the visibility manipulation is noteworthy given that this area was consistently observed in several perceptual interference manipulations (Marois et al. 2000).

EXPERIMENT 2. While the above findings point to potential similarities and differences in the neural network engaged by low visibility and high interference, they are nevertheless limited in their interpretability given that the results from the two types of manipulation originated from separate experiments. To provide a more direct test of the functional relationship between perceptual interference and visibility, we carried out a second event-related fMRI experiment during which subjects were exposed to both manipulations in a mixed-trial design. Unlike in the previous experiment, the visibility manipulation consisted of a pure contrast manipulation (high: 100% vs. low: 20% contrast) without letter size differences and in the complete absence of lateral flankers to eliminate any possibility of distractor interference. The perceptual interference manipulation consisted of a central high contrast target letter flanked either distally (low interference) or proximally

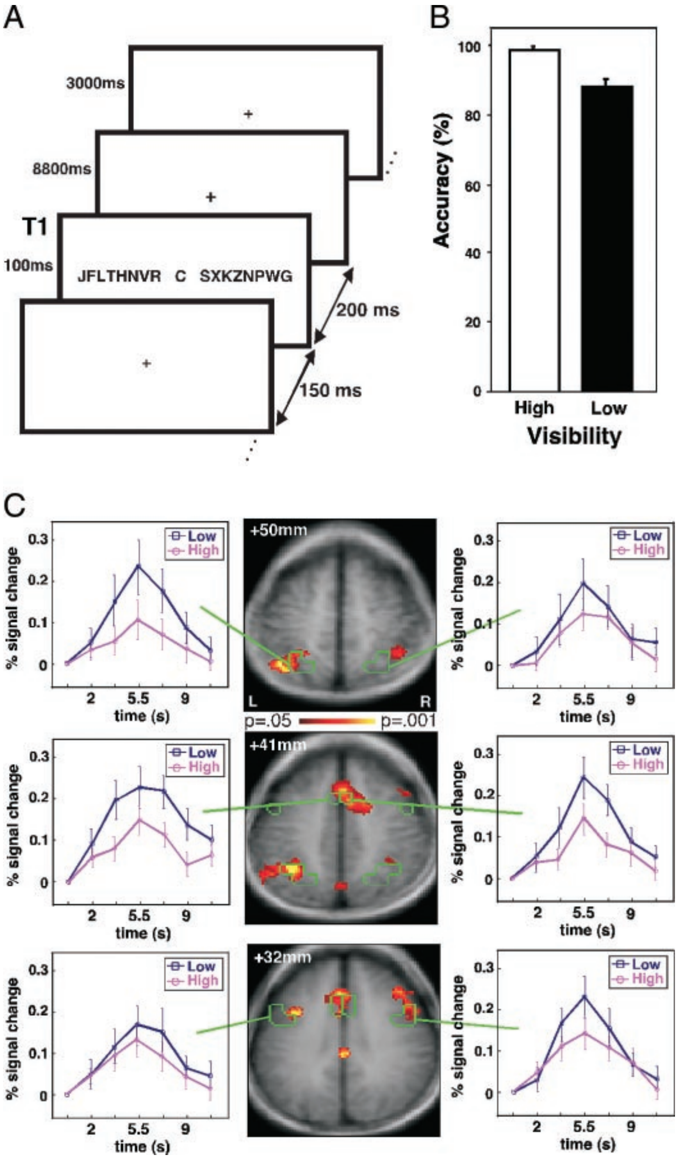

FIG. 2. Perceptual visibility activations. *A*: trial design. Subjects responded to T1 identity (letter B, C, or D) after the display presentation. *B*: behavioral performance during the functional MRI (fMRI) session. Subjects' accuracy was poorer in the low visibility condition than in the high visibility condition ($t = 4.8$, $P < 0.001$). *C*: brain activation group composites for low minus high visibility [$n = 10$; $P < 0.05$, corrected for the number of region of interest (ROI) comparisons], and activation time courses in the parieto-frontal ROIs (Marois et al. 2000), identified by green outlines. *Top*: intra-parietal ROI. *Middle*: anterior cingulate ROI. *Bottom*: lateral frontal ROI. Approximate Talairach coordinates (x,y,z) of the ROI centroids: IPS: ±30, −58, +45; lateral frontal: ±48, +8, +35; anterior cingulate cortex (AC): ±3, +20, +36.

(high interference) by distractor letters (see Fig. 1; Marois et al. 2000). Given that the present visibility manipulation was different from those used in the previous behavioral and fMRI experiments, we ascertained in a separate behavioral experiment that it was still attention-demanding since it generated substantial dual-task costs (Fig. 3*A*). Specifically, both the visibility (low vs. high) and interference (high vs. low) manipulations led to poorer T1 and T2 performances (visibility manipulation T1: $t = 4.6$, $P < 0.001$; T2; $t = 3.3$, $P < 0.01$; interference manipulation T1: $t = 2.3$, $P < 0.05$; T2: $t = 5.1$, $P < 0.001$). Similarly, T1 performance suffered under both perceptual manipulations during the fMRI experiment (Fig. 3*B*), although target accuracy was worse for the perceptual visibility manipulation than the perceptual interference manipulation ($t = 5.0$, $P < 0.001$).

The activation time courses for the interference and visibility manipulations in the parietal and frontal ROIs are shown in Fig. 4. Perceptual interference (high vs. low) engaged the right intra-parietal sulcus (IPS) ($t = 2.4$; $P = 0.03$) and showed a similar trend in the right lateral frontal ROI ($t = 1.85$; $P = 0.08$). These results replicate previous findings of robust right parietal activation but weaker frontal activation with spatial interference (Marois et al. 2000). The perceptual visibility manipulation (low vs. high) engaged both the left ($t = 2.2$, $P < 0.05$) and marginally the right IPS ($t = 2.14$, $P = 0.05$), as well as the anterior cingulate cortex bilaterally (left: $t = 2.28$, $P < 0.05$, right: $t = 2.2$, $P < 0.05$). There was also a trend for increased right lateral frontal activation with decreased visibility ($t = 1.88$, $P = 0.08$). Direct comparison between the interference and visibility manipulations averaged across difficulty levels revealed no significant differences in any of the ROIs ($P > 0.1$). Finally, no brain regions outside the ROIs were activated with either manipulation when using a voxel-based analysis thresholded at $P < 0.001$. Taken together, these results provide further evidence that a single parieto-frontal cortical network is recruited under both interference and visibility manipulations.

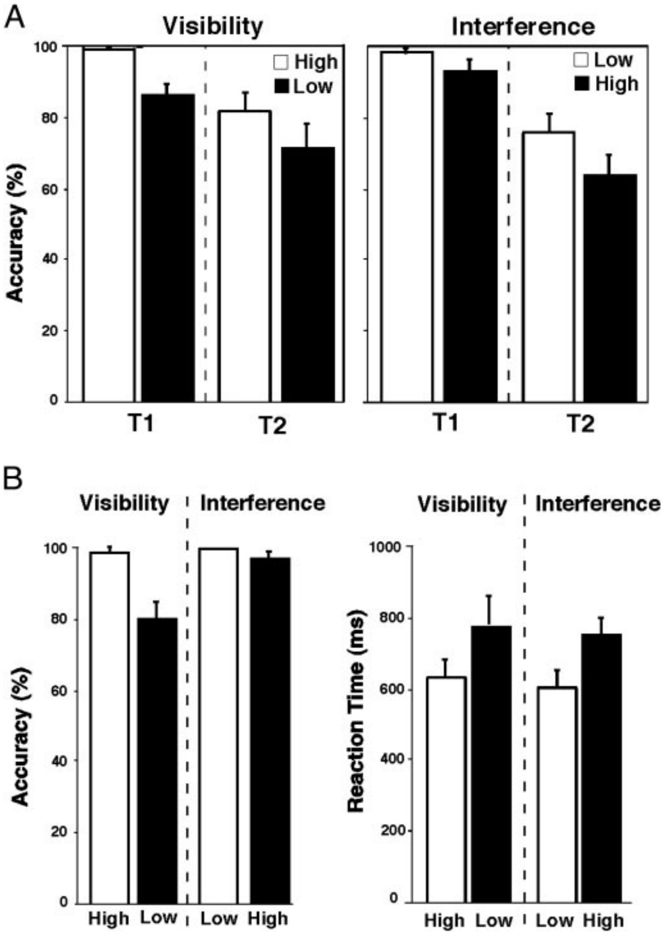

FIG. 3. Perceptual visibility and interference manipulations: behavioral results. *A*: performance with visibility and interference manipulations under dual-task conditions. Both T1 and T2 accuracy were worse in the more difficult visibility (low contrast) and interference (high interference) conditions. *B*: behavioral performance in fMRI session. *Left*: accuracy was worse in the low than in the high visibility condition ($P < 0.05$), and in the high than in the low interference condition ($P < 0.05$). *Right*: reaction time (RT) for correct trials only. Subjects' RTs were longer in the low than in the high visibility condition ($t = 6.9$, $P < 0.001$), and in the high than in the low interference condition ($t = 2.7$, $P = 0.02$).

EXPERIMENT 3. The parieto-frontal cortex activations observed in *experiments 1* and *2* are consistent with the view that this neural network is involved in target identification under attention-demanding conditions. However, since the stimulus displays physically differed across manipulation levels (high vs. low contrast; proximal vs. distal lateral masking), it is conceivable that differences in physical energy of the stimuli may also have contributed to the brain activations. While this reasoning is unlikely to apply to the visibility manipulation given that the firing rate of visually responsive neurons diminishes with decreased stimulus contrast (Albrecht and Hamilton 1982; Sclar et al. 1990), it is more difficult to rule out this possibility for the interference manipulation: a lateral shift in the center of mass of the letter string between the high and low interference displays could in principle differentially activate the parieto-frontal cortex. To examine this possibility, we carried out a control fMRI experiment in which six naive subjects were exposed to the same low and high interference stimuli as before but performed an attention-demanding task that was irrelevant to the interference manipulation. Specifically, subjects performed a color identification task (green vs. red) instead of a letter identification task on the letter string stimuli. Importantly, the color assignments of the stimuli were uncorrelated to their interference levels. It was therefore possible to assess the hemodynamic consequences of the interference manipulation under conditions where the displays were attended, but the interference levels (high vs. low) were task irrelevant. When comparing the activations associated with the high and low interference stimuli under such conditions (Fig. 4), no significant differences in activation were found in any of the ROIs ($P > 0.1$). In fact, any activation trends were opposite those of the target letter identification task, with increased activation for the low interference condition (Fig. 4). Thus stimulus differences in physical energy cannot, per se, account for the parieto-frontal activations observed with the perceptual visibility and interference manipulations.

DISCUSSION

This study investigated how the brain responds to two very distinct perceptual challenges: when a target is presented among distractors and when the target is of low visibility. The principal finding is that both attention-demanding conditions

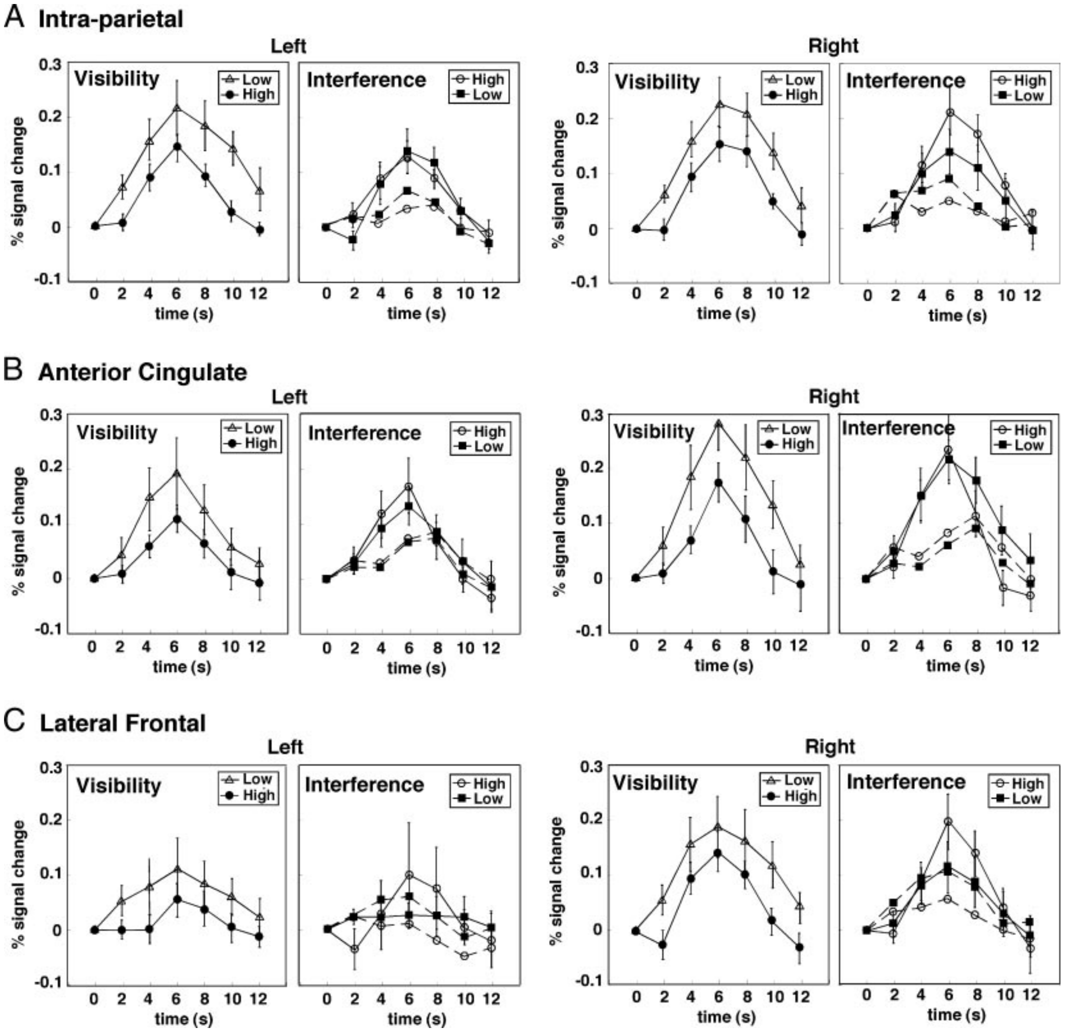

FIG. 4. Activation time courses for the perceptual visibility and interference manipulations in left and right (*A*) intra-parietal, (*B*) anterior cingulate, and (*C*) lateral frontal cortex ROIs. Stippled lines represent activation time courses for interference stimuli when subjects are attending to the color of the letters instead of the central target letter in a control experiment (see METHODS).

recruit the same parieto-frontal network. As such, our results have important implications about the neural basis of perceptual interference and perceptual visibility resolution and about the role of the parieto-frontal cortex in selective attention.

Perceptual interference

The activation of a parieto-frontal network under spatial interference conditions, with activation most robustly observed in parietal cortex of the right hemisphere, replicates previous interference manipulation studies (Marois et al. 2000). Since the targets were briefly presented at fixation, the parietal activation is unlikely to be due to spatial shifts of attention, and since the high and low interference stimulus presentations were randomly intermixed, the activation observed is associated with the brain's response to a perceptually challenging condition. These results therefore suggest that the right parietal cortex is an important locus for resolving perceptual-spatial interference between target and distractors. While the effects of distractor interference have been well characterized in the inferior and middle temporal cortex (Luck et al. 1997; Maunsell 1995; McAdams and Maunsell 1999a; Moran and Desimone 1985; Reynolds et al. 1999; Treue and Maunsell 1996) as well as in the frontal cortex (Schall et al. 1995), modulation of target-related neuronal activity in parietal cortex by distractors has not been so evident (Constantinidis and Steinmetz 2001a,b; Gottlieb et al. 1998; Kastner et al. 1999). Although few imaging studies specifically investigated the effects of distractor interference in the parietal cortex (Kastner et al. 1999), several others have shown a right hemisphere activation bias in parietal cortex with spatial attention tasks (Corbetta et al. 1993; Coull et al. 1996; Nobre et al. 1997). In addition, lesions of the parietal cortex frequently lead to perceptual deficits when there are multiple visual items that compete for attention (Kinsbourne 1987; but see Duncan et al. 1997) and to deficits in distractor filtering (Friedman-Hill et al. 2003). Taken together, these findings suggest that the right parietal cortex plays an important role in selecting a target among interfering distractors, perhaps by filtering out irrelevant visual information (Friedman-Hill et al. 2003) or by disambiguating neural signals associated with each object when multiple items (e.g., target and distractors) are present in the display (Luck and Ford 1998). In support of this possibility, a recent study showed that a feature conjunction task that required disambiguating the shape and color features of each object presented in a visual scene recruited the right parietal cortex (Shafritz et al. 2002).

Perceptual visibility

The perceptual visibility manipulation recruited the entire parieto-frontal network, with the exception of the left lateral frontal ROI. The extensive activation of the parieto-frontal network with the contrast manipulation could be related to the higher difficulty of this task, especially relative to the interference condition. Indeed, although the interference and visibility manipulations were equated in reaction time, accuracy was lower in the perceptual visibility than in the interference manipulation. The recruitment of the anterior cingulate with the visibility manipulation but not with the easier interference manipulation is consistent with these behavioral results: the AC has been associated with monitoring conflict and/or error detection (Botvinick et al. 1999; Carter et al. 1998; Ghering et al. 1993), both of which would be expected to increase with task difficulty. It is more tenuous at this stage to ascribe specific functions to the other ROIs activated by the visibility manipulation. For instance, the left parietal cortex has not only been associated with linguistic processing (Binder et al. 1997), but with nonspatial (object-based) forms of attention as well (Humphreys et al. 1994). Further experiments involving objects with little or no verbal codes will be required to discern more accurately the role of the left parietal cortex in the current visibility manipulation. In any events, in keeping with the single-cell work in the visual cortex (Martinez-Trujillo and Treue 2002; Reynolds et al. 2000; Spitzer et al. 1988), it is conceivable that the primary function of the parieto-frontal cortex during low visibility is to enhance the neural response to the visually impoverished target (see *Role of the parieto-frontal cortex in visual attention*).

Role of the parieto-frontal cortex in visual attention

Although the right parietal cortex was the region most robustly activated by the perceptual interference task, it was also recruited by a perceptually challenging condition in the absence of distractors (visibility manipulation). Thus there is no evidence that the parietal cortex, or any of the frontal cortex regions examined here, is *specifically* involved in resolving interference or competition between objects in the visual scene.

The selection of a visual target presented among distractors items is a fundamental role of attention (Friedman-Hill et al. 2003). Indeed, attention is regarded as the mechanism that biases the neural competition between objects for limited processing resources (Desimone and Duncan 1995; Reynolds et al. 1999), and that serves to resolve ambiguities in neural coding when multiple objects are processed simultaneously (Luck and Ford 1998). In accordance with these views, several neuroimaging studies have shown a parieto-frontal network of areas activated in selective attention tasks (Corbetta et al. 1993, 2000; Hopfinger et al. 2000; Kastner and Ungerleider 2000; Kastner et al. 1999; Marois et al. 2000; Nobre et al. 1997). Findings such as these have led to the hypothesis that the basic function of this parieto-frontal network is to resolve perceptual interference among objects (Wojciulik and Kanwisher 1999). Our results lead us to propose instead that the activity of this parieto-frontal network is modulated by perceptually demanding attentional tasks, regardless of the nature of the perceptual challenge, perhaps in an analogous way to the one proposed for the visual cortex (McAdams and Maunsell 1999a,b). This notion is more consistent with findings that dorsal parietal cortex is activated in a wide range of perceptual and cognitive tasks (LaBar et al. 1999; Simon et al. 2002; Wojciulik and Kanwisher 1999).

Our results do not rule out the possibility that perceptual interference and visibility may be separately resolved at early stages of visual cortical processing or even encoded differentially at the cellular level within the same regions of the parietal and frontal cortex. They do rule out, however, the prospect that distinct parieto-frontal networks are recruited to select a target under low visibility conditions or high interference conditions. Our results are therefore consistent with the contention that the intra-parietal cortex exerts a general role in visual attention (Wojciulik and Kanwisher 1999). However, this role does not boil down to attentional selection of targets among distractors. Instead, we propose that this function should be more generally cast as enhancing the processing of behaviorally relevant visual signals (targets), whether these correspond to visually impoverished stimuli (i.e., that must be distinguished from internal processing noise) or whether they are concealed among distractor items (i.e., that must be distinguished from external noise).

Interestingly, it has recently been suggested that the effect of attention during object competition in the visual cortex may be akin to a gain in the contrast of the attended stimulus (Reynolds and Desimone 2003). If so, this mechanism would provide a potential cellular link between attentional selection and facilitation, in that both forms of attention would trigger a contrast gain of the target. This gain would in turn favor cortical processing of the target, which, under interference conditions, would lead to suppression and filtering out of distractor items. Thus the biased competition model, derived from single-cell data, could accommodate both forms of attention if one holds that attention's primary role in perceptually challenging conditions is akin to a stimulus contrast gain. Here, we show a corresponding mechanistic convergence of attentional selection and facilitation at the neural network level; the same regions of parietal and frontal cortex respond to challenges in target identification under distractor interference and low visibility. Taken together, both the cellular and imaging work suggests that attentional selection and attentional facilitation may very well be, mechanistically speaking, one and the same.

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