

# Neural Correlates of the Attentional Blink

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## Summary

Attending to a visual event can lead to functional blindness for other events in the visual field. This limit in our attentional capacities is exemplified by the attentional blink (AB), which refers to the transient but severe impairment in perceiving the second of two temporally neighboring targets. Using functional magnetic resonance imaging (fMRI), we observed predominantly right intraparietal and frontal cortex activations associated with the AB. We further demonstrate that an AB can be elicited by both temporal and spatial distractor interference on an attended target and that both of these interference mechanisms activate the same neural circuit. These results suggest that a (right) parietofrontal network previously implicated in attentional control and enhancement is also a locus of capacity-limited processing of visual information.

## Introduction

Visual scenes contain far more information than we can consciously perceive at any given instant. The information that does reach visual awareness is selected by our attentional systems (Driver and Mattingley, 1998; Treisman and Kanwisher, 1998). However, our attentional capacities are limited (Broadbent, 1958; Kahneman, 1973; Duncan, 1980). As a result, the cost of attentional selection to a visual stimulus can be functional blindness to other unattended stimuli (Kanwisher, 1987; Joseph et al., 1997; Rensink et al., 1997; Simons and Levin, 1997; Mack and Rock, 1998). Such costs are especially acute in the attentional blink paradigm, which reveals a severe but transient impairment in detecting the second of two targets presented among a rapid sequence of distractor items (Broadbent and Broadbent, 1987; Weichselgartner and Sperling, 1987; Raymond et al., 1992). The blink occurs when attentional mechanisms are consumed by the processing of the first target (T1), leaving little attention available for the next 500 ms or so to process the second target (T2) (Raymond et al., 1992; Duncan et al., 1994; Chun and Potter, 1995; Shapiro et al., 1997; Jolicoeur, 1998). Detection performance for the second target is poorest at short temporal lags of 200–300 ms between T1 and T2,

and it improves monotonically with increasing lags of up to about 600–700 ms. The transient graded impairment in perceiving the second target demonstrates that attentional processing of the first target is a capacity-limited operation.

While much imaging work has been devoted to understanding attentional mechanisms of orienting and enhancement (Corbetta et al., 1993, 1995, 1998; Coull et al., 1996; Nobre et al., 1997; Coull and Nobre, 1998; Kastner et al., 1998, 1999; Kim et al., 1999; Wojciliuk and Kanwisher, 1999), no previous study has investigated the AB, which emphasizes the capacity-limited nature of attentional processing. In five experiments, we use fMRI to identify the neural activity associated with the processing limitations that produce the AB deficit. Past psychophysical work has revealed two conditions necessary for the attentional blink. First, T1 must be attended (Raymond et al., 1992; Duncan et al., 1994; Luck et al., 1996; Joseph et al., 1997). Second, distractor items, particularly ones that appear immediately after T1, must be present to interfere with the identification of this target. Distractor interference increases the duration of attentional processing of T1, thereby amplifying the processing bottleneck that prevents T2 from entering awareness (Raymond et al., 1992; Chun and Potter, 1995; Moore et al., 1996; Grandison et al., 1997; Seiffert and Di Lollo, 1997; Jolicoeur, 1998; Breitmeyer et al., 1999). Our experiments will make use of this temporal distractor interference effect to determine the neural correlates of the capacity-limited process underlying the AB.

In addition, we will also determine whether spatial interference can induce an attentional blink. Although past work on the AB has focused on the role of temporal interference, evidence from other paradigms suggests that target identification is also severely affected by *spatial* interference from simultaneous, neighboring distractors (Eriksen and Hoffman, 1972; Eriksen and Eriksen, 1974; Miller, 1991). Thus, the presence of distractors can interfere with, and in extreme cases may even prevent, target awareness, a phenomenon known as attentional crowding (Bouma, 1970; He et al., 1996). We will test whether spatial interference produces an AB and, if so, whether it utilizes the same neural substrates engaged by the capacity-limited mechanisms associated with temporal interference.

## Results

The attentional blink is caused by the processing demands of T1 (Raymond et al., 1992; Duncan et al., 1994; Chun and Potter, 1995; Ward et al., 1996; Jolicoeur, 1998, 1999). T2 and the masking of T2 serve to probe the attentional limitations arising from the processing of T1 (Chun and Potter, 1995; Giesbrecht and Di Lollo, 1998). Therefore, the identification of the associated neural correlates requires the isolation of T1, not T2, processing. Moreover, given the poor temporal resolution of fMRI, the variable hemodynamic response to T2

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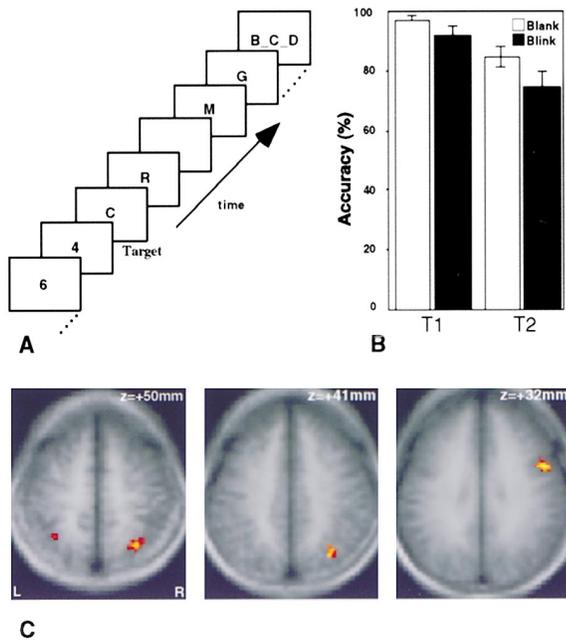


Figure 1. Distractor Interference Manipulation

(A) Trial design. For HIGH interference trials (depicted), a letter distractor was presented between the target (letter B, C, or D) and the blank. In LOW interference trials, the positions of this distractor and the blank were switched. Subjects responded during the B-C-D panel presentation at the end of each trial.

(B) Behavioral performance outside the scanner. T2 accuracy was significantly lower in the HIGH interference than in the LOW interference conditions ( $p < 0.05$ ).

(C) Group composites of brain activation. The HIGH interference condition posteriorly engaged the intraparietal sulcus and anteriorly engaged the lateral frontal cortex.

processing would contaminate the T1-related activations. For both of these critical reasons, subjects performed only T1 processing during the fMRI experiment. We demonstrate for each of our experiments that the same manipulation used during the fMRI experiment led to the expected behavioral deficit when a second target was added in a psychophysical experiment held inside or outside the magnet. We also confirmed that subjects' T1 performance during the psychophysical testing and the fMRI experiment was comparable.

To isolate the neural substrates that form the attentional limitations revealed by the AB, we compared brain activation in two conditions that were as identical as possible but differed in the severity of the AB they produced. In experiment 1, we took advantage of the fact that the attentional blink critically depends on the perceptual interference generated by the presence of a distractor item immediately following T1 (Raymond et al., 1992; Chun and Potter, 1995; Moore et al., 1996; Breitmeyer et al., 1999). Performance in identifying T2 is substantially improved if a blank interval is inserted at the place of a distractor item immediately following T1. Thus, manipulations of perceptual interference on T1 can reveal the neural substrates of the attentional processes that modulate the blink. Ten subjects were scanned while identifying a single target (letter B, C, or D) appearing within a rapid serial visual presentation sequence of digits and letters (Figure 1A). In half of the

trials, the target letter (T1) was immediately followed by a blank (LOW interference), while in the other half, a distractor letter was inserted between the target letter and the blank (HIGH interference). Thus, the two trial types differed only by the relative position of the blank in the visual stream. Due to the low temporal resolution of the BOLD signal, this subtle manipulation predicts no detectable difference in activation based on low-level physical differences in the displays. However, the interference manipulation has a sizeable impact on the attentional demands of processing T1, and this would be revealed by comparing neural activation between HIGH and LOW interference conditions. While subjects performed only T1 detection in the fMRI experiment, we confirmed that, when subjects searched also for a second target, T2 detection accuracy was significantly lower in the HIGH than in the LOW interference condition (Figure 1B), replicating prior psychophysical studies (Raymond et al., 1992; Chun and Potter, 1995; Moore et al., 1996; Breitmeyer et al., 1999).

Two areas were more activated in the HIGH than in the LOW interference condition: the intraparietal sulcus (IPS) and a lateral frontal area, with the center of mass at the intersection between the middle, inferior frontal, and precentral gyri (Figure 1C; Table1). At lower thresholds ( $p < 0.005$ ), the anterior cingulate (AC) demonstrated activation (Table1). The activations for these areas were stronger in the right hemisphere, although these hemispheric differences were not statistically significant ( $p = 0.3$  and  $p = 0.8$  for the IPS and frontal activations, respectively). The mean percent signal difference between the HIGH and LOW interference conditions was 0.16%, 0.19%, and 0.09% for the spatially filtered bilateral IPS, lateral frontal, and AC ROIs, respectively.

To further confirm and generalize these findings, we replicated these results using a different manipulation. The magnitude of the blink is also highly dependent on the global (overall) discriminability between the targets and distractors (Chun and Potter, 1995). In a second experiment, eight subjects were scanned while identifying a target letter (B, C, or D) embedded in a stream of digits (which leads to HIGH target-distractor interference and hence, substantial AB) or of keyboard symbols (which leads to LOW interference and significantly diminished AB) (Figure 2A). Behavioral data collected outside the scanner confirmed a significant difference in T2 detection (Figure 2B). During the fMRI experiment, subjects performed similarly with target accuracy (98.7% versus 97.8% for the symbol and digit distractors, respectively). A region of interest analysis (based on the first experiment) demonstrated that the right intraparietal sulcus ( $t = 5.0$ ,  $p = 0.0016$ ), the anterior cingulate ( $t = 3.8$ ,  $p = 0.0067$ ), and the left middle frontal region ( $t = 5.8$ ,  $p = 0.001$ ) were significantly more activated in the HIGH interference condition than in the LOW interference condition (Figure 2C). Although the ROI analysis did not demonstrate significant activation in the right middle frontal gyrus, examination of the group composites at  $p < 0.001$  revealed a single activation site in the right middle frontal gyrus ( $x = 38$ ,  $y = 34$ ,  $z = 32$ ) that was anterior to the ROI-defined site (Figure 2C).

The first two experiments revealed the brain regions recruited by distractors' temporal interference with the target in a classical AB paradigm. We next determined

Table 1. Regions of Activation in Experiment 1: HIGH Interference to LOW Interference

ROI Name	Mean t Value	Talairach Coordinates		
		x	y	z
Right intraparietal sulcus	5.7	29	-59	50
Right intraparietal sulcus	5.0	31	-65	41
Left intraparietal sulcus	5.1	-34	-51	50
Right lateral frontal area	5.3	47	9	32
Right lateral frontal area*	3.7	51	7	41
Anterior cingulate*	3.9	2	21	41
Anterior cingulate*	3.8	4	19	32
Middle temporal gyrus	-4.0	-56	-52	23

The Talairach coordinates of the center of mass of significantly activated ( $p < 0.001$ ) ROIs. Marginally significant ROIs ( $*p < 0.005$ ) are also listed. Negative t values refer to ROIs activated by the reversed condition.

whether spatial interference with the target would also generate an attentional blink. In this behavioral experiment, we designed the spatial equivalent of an AB paradigm (Figure 3). Instead of inducing interference with distractors that temporally preceded or followed the first target, the letter distractors were presented simultaneously with T1. Since interference with target processing increases as the distance between target and distractors decrease (Eriksen and Hoffman, 1972; Eriksen and Eriksen, 1974; Miller, 1991), we compared T2 identification accuracy in two conditions in which we manipu-

lated the target-distractor distance. In the LOW interference condition, the central target letter was separated from the distractors on either side by a  $1^\circ$  gap, while in the HIGH interference condition, two distractor letters immediately flanked the target on either side, followed by the  $1^\circ$  gap and the rest of the string of distractors (Figure 3A). Thus, the two conditions are identical except for the relative position of the gap on either side of the target. The subjects' task consisted of identifying the first target (either the letter B, C, or D) and then determining whether the letter X (T2) was present after the first target (Figure 3B). The results of this spatial interference task mirror those obtained in the traditional temporal interference task. Although subjects performed extremely well at identifying the first target in both conditions, they were significantly more impaired at detecting T2 in the HIGH interference than in the LOW interference condition (Figure 3C).

We first determined the brain regions that were more activated in the HIGH than in the LOW interference con-

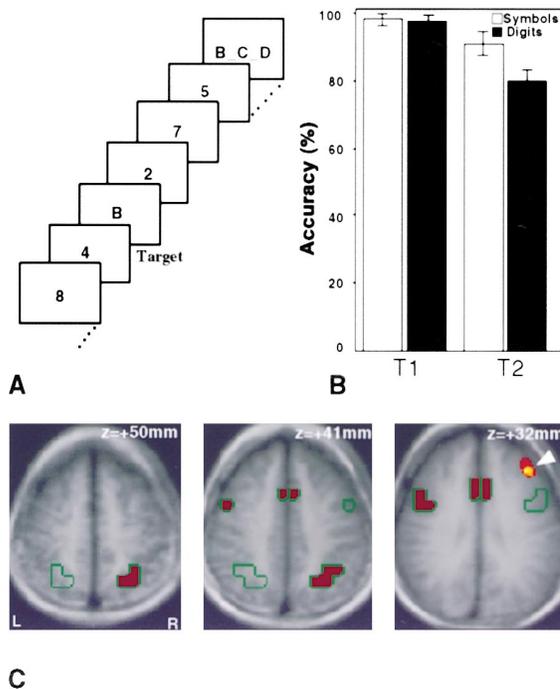


Figure 2. Global Distractor Interference Manipulation (A) Trial design. The target (B, C, or D) was embedded in a stream of digits (depicted) for the HIGH interference trials and in a stream of keyboard symbols for the LOW interference trials. (B) Behavioral performance outside the scanner. T2 accuracy was significantly lower in the HIGH interference condition ( $p < 0.05$ ). (C) Group composites of brain activation. Filled ROIs (dark red in green outlines) were significantly more activated in the HIGH than in the LOW interference condition ( $p < 0.05$ ). Arrowhead shows right middle frontal gyrus activation at  $p < 0.001$ .

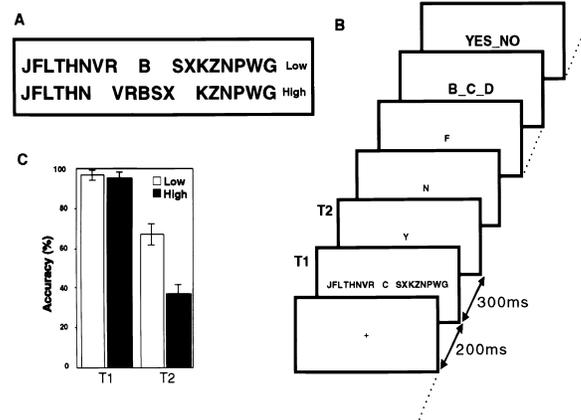


Figure 3. Experimental Design for Spatial Interference Manipulation (A) Stimuli. A  $1^\circ$  gap separated the central target (letter B, C, or D) from the flanking distractors in the LOW interference condition. Two of the distractor letters immediately flanked the central target on either side in the HIGH interference condition. (B) Trial design. In the behavioral experiment, subjects monitored for both T1 and T2 (letter Y). Subjects responded by button press during the response panel presentations. (C) Behavioral performance outside the scanner. T2 accuracy was significantly lower in the HIGH interference condition ( $t = 8.01, p < 0.0001$ ).

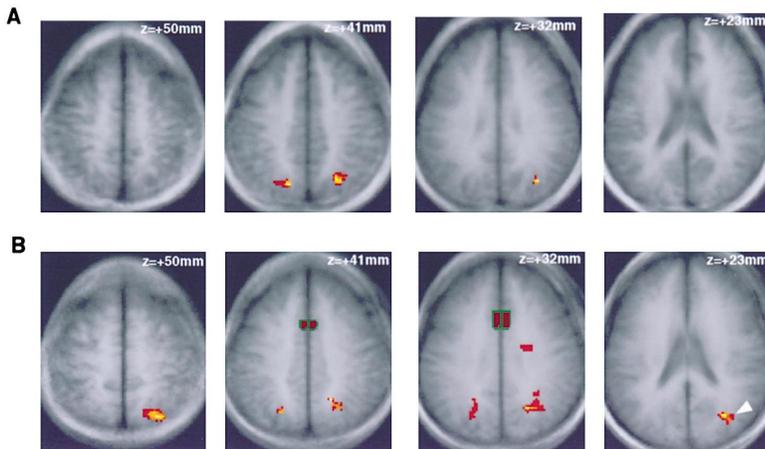


Figure 4. Group Composites of Brain Activation for Spatial Interference Manipulation

(A) Block design. The HIGH interference condition engaged the intraparietal sulcus.  
(B) Event-related design. The intraparietal sulcus activation extends ventrally in the intraoccipital sulcus (arrowhead). The ROI analysis also showed significant activation in the anterior cingulate (dark red fill in green outlines).

dition, using an ABAB block design (ten 1.5 s long trials per block). As in the previous experiments, subjects ( $n = 7$ , two females) performed only T1 identification in the scanner. T1 accuracy was very high in both conditions (HIGH = 96.4%, LOW = 98.0%, NS,  $p = 0.14$ ). Nevertheless, comparisons of HIGH versus LOW interference showed activation in the intraparietal sulcus (Figure 4A). The spatial overlap of this activation with the parietal region activated in the first two experiments was confirmed with the ROI analysis ( $t = 2.5$ ,  $p < 0.05$ ). There was also significantly more activation in the right parietal than in the left parietal ROI ( $t = 3.1$ ,  $p < 0.05$ ). The frontal ROIs were not significantly activated. To determine whether this activation pattern is specific to the blocked design (e.g., differences in attentional set or oculomotor control between blocked conditions), we performed the same experiment in an event-related mixed-trial design in a separate group of subjects ( $n = 10$ , five females). As in the blocked-design experiment, the intraparietal sulcus was more activated in the HIGH than in the LOW interference condition (Figure 4B). Furthermore, the ROI analysis shows that this activation significantly overlaps with the parietal ROI drawn from the first experiment ( $t = 2.0$ ,  $p < 0.05$ ). The anterior cingulate ROI was also significantly activated ( $t = 2.6$ ,  $p < 0.05$ ), while the lateral frontal ROI was marginally activated ( $t = 1.4$ ,  $p = 0.09$ ).

Taken together, the first two experiments demonstrated activation of the intraparietal sulcus, lateral frontal cortex, and anterior cingulate in two different temporal interference manipulations of the attentional blink. The last two experiments confirmed that an AB can also be obtained with a homologous spatial interference paradigm. Moreover, the new spatial interference manipulation recruited the same intraparietal area activated by the traditional temporal interference paradigm.

Although the present interference manipulations play a causal role in modulating the magnitude of the AB (Raymond et al., 1992; Chun and Potter, 1995; Moore et al., 1996; Grandison et al., 1997; Seiffert and Di Lollo, 1997; Breitmeyer et al., 1999), it is conceivable that the neural activations associated with these interference manipulations may not solely reflect attentional limitations but, also, general effort or task difficulty that is not directly associated or causally linked with the AB. To examine this possibility, we conducted an additional

experiment that varied the difficulty of the T1 task but did not influence the visual AB for T2. Subjects performed a lexical decision task on a word presented as T1 (Figure 5A) (Wojciulik and Kanwisher, 1999). In the HIGH difficulty condition, the subjects determined whether the T1 word could be both a noun and a verb (e.g., “search”). In

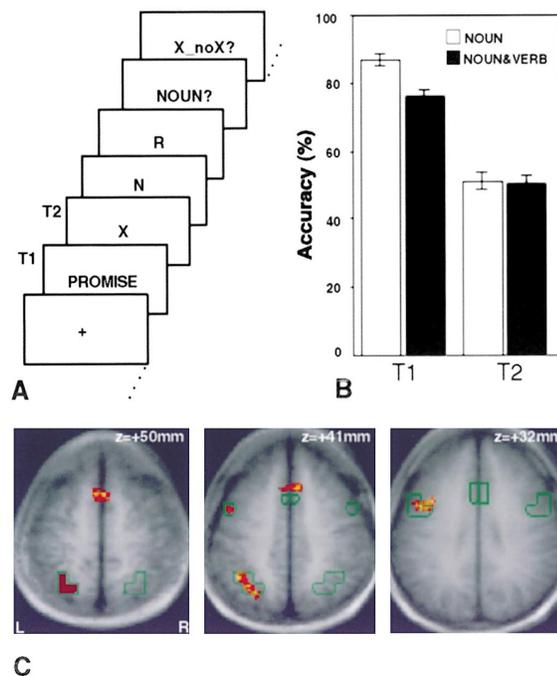


Figure 5. Task Difficulty Control

(A) Trial design for the behavioral task. The word (T1) was presented at the beginning of each trial for 100 ms, followed 300 ms later by T2 (letter X) and by two other letter distractors. The trial ended with the response panel presentations.

(B) Behavioral performance outside the scanner. T1 accuracy was significantly lower in the HIGH than in the LOW difficulty condition ( $t = 7.81$ ,  $p < 0.0001$ ), yet T2 performance was equivalent in both tasks ( $t = 0.71$ ,  $p = 0.50$ ).

(C) Group composites of brain activation. The left but, importantly, not the right parietal and frontal ROIs were significantly more activated in the HIGH than in the LOW difficulty conditions. The HIGH difficulty condition also activated an anterior cingulate area dorsal and anterior to the AC ROI.

the LOW difficulty condition, the subjects simply judged whether T1 was a noun or not. As in the spatial interference experiments, T1 was followed 300 ms later by the rapid successive presentation of three letters, with the first of the three occupied by T2 (letter X) on 80% of the trials. Although the HIGH and LOW difficulty conditions should lead to different T1 performances, the magnitude of the attentional blink should not differ between these two conditions, since they both contain the same perceptual processing demands. Despite significant differences in T1 performance, behavioral data collected outside the scanner confirmed that the difficulty manipulation did not differentially affect T2 performance (Figure 5B). The false alarm rates for the HIGH and LOW conditions (0.12 and 0.14) were significantly lower ( $p < 0.001$ ) than their respective T2 accuracy (0.52 and 0.53), confirming that subjects were not simply guessing the T2 identity. In the scanner, comparison of HIGH versus LOW difficulty conditions demonstrated significant activation in the left intraparietal sulcus (ROI analysis:  $t = 5.67$ ,  $p < 0.001$ ) and left middle frontal gyrus ( $t = 5.12$ ,  $p < 0.001$ ) (Figure 5C). The left hemisphere lateralization of the activation is not surprising, given the linguistic nature of the task (e.g., Binder et al., 1997). In sharp contrast to earlier experiments, however, no significant activity was observed in the right parietal or frontal cortex, and the difference between right and left hemispheres was significant ( $t = 2.4$ ,  $p < 0.05$ ). The anterior cingulate activation observed with the lexical decision task did not significantly overlap with the AC ROI that was engaged in the temporal interference tasks. Thus, task difficulty per se can only account for the left parietal and frontal activations. The right intraparietal sulcus (and, to a less consistent extent, the anterior cingulate and right lateral frontal gyrus) is specifically associated with manipulations of perceptual interference that modulate the AB.

## Discussion

Although attentional selection can occur at several stages of visual information processing (Pashler, 1998; Luck and Hillyard, 2000), the attentional blink is widely acknowledged to occur at a capacity-limited stage (or bottleneck of attention) that constrains the ability to explicitly perceive multiple visual targets (Duncan, 1980; Broadbent and Broadbent, 1987; Duncan et al., 1994; Shapiro et al., 1994; Chun and Potter, 1995; Jolicoeur, 1998). The present fMRI data suggest that the right intraparietal sulcus and, to a less consistent extent, the frontal areas represent the neural correlates of the capacity-limited process that underlies the AB deficit. This activation pattern was observed in several manipulations of the attentional blink, attesting to its generality, but not in an experiment that controlled for task difficulty or arousal effects, demonstrating specificity for the attentional processes summoned by the AB task.

While the neural basis of the attentional blink is just beginning to be unraveled, other attentional paradigms have long been the focus of functional imaging studies. Several of these have investigated the neural correlates of orienting attention to targets either in space or time (Corbetta et al., 1993, 1995; Coull et al., 1996; Pugh et

al., 1996; Nobre et al., 1997; Corbetta, 1998; Coull and Nobre, 1998; Kastner et al., 1999; Kim et al., 1999; Wojciulik and Kanwisher, 1999), and yet others have examined the effects of dividing attention across multiple features or objects (Corbetta et al., 1991; Vandenberghe et al., 1997). Interestingly, the right parietal and frontal cortical areas activated in the present AB study are very similar to the brain regions recruited by attentional orienting. This convergence of findings leads us to hypothesize that the neural network involved in the control of visuospatial attention may also form a capacity-limited bottleneck of visual information processing that is revealed by the AB. However, it is important to emphasize that the present study does not directly query the neural correlates of explicit visual perception. In addition, we do not suggest that the parietofrontal circuit revealed here serves as an omnibus capacity-limited stage for all information processing. Given that there are multiple attentional systems in the human brain (Posner, 1980; Posner and Dehaene, 1994; Luck and Hillyard, 2000), it is likely that other types of processing limitations are mediated by brain regions distinct from those isolated by the present psychophysical manipulations. It is also unknown whether the present brain areas may represent a bottleneck specific to visual processing or whether they might also mediate capacity-limited processing observed in other modalities as well (e.g., Duncan et al., 1997; Arnell and Jolicoeur, 1999; but see Potter et al., 1998). Finally, while different forms of capacity-limited processes such as graded sharing and bottleneck models have been proposed (e.g., Pashler, 1998), it is not clear which type of capacity-limited process best characterizes the AB (Raymond et al., 1992; Chun and Potter, 1995; Ward et al. 1996; Jolicoeur, 1998; Vogel et al., 1998). Our study is agnostic to this debate, and, hence, here we interchangeably use the terms “bottleneck” and “capacity-limited process” to simply refer to the processing limitations causing the AB.

## The Nature of Limited Capacity Processing: Spatial and Temporal Interference

There is broad consensus that the attentional blink is triggered by perceptual interference (Raymond et al., 1992; Chun and Potter, 1995; Moore et al., 1996; Grandison et al., 1997; Seiffert and Di Lollo, 1997; Breitmeyer et al., 1999) as well as by global target-distractor discriminability (Chun and Potter, 1995). This interference arises from the backward masking of T1 by an ensuing distractor. The role of masking is to increase the attentional demands of target processing, leaving little attention available for subsequent targets (Raymond et al., 1992; Chun and Potter, 1995). The first experiment examined the effects of such masking-induced temporal interference. We emphasize, however, that it is unlikely that the resulting parietofrontal activations could be due to sensory masking per se. If subjects were not specifically attending to a target, the sole difference in physical presentation between the HIGH and LOW interference conditions would be far too subtle (100 ms shift in the relative position of a blank interval) to differentially affect their hemodynamic response, especially given the low temporal resolution of fMRI. We therefore conclude that the resulting activations directly reflect attentional pro-

cessing of the temporally masked target. This point is further reinforced by the finding that the activations in *both* our temporal and spatial interference manipulations were localized to areas previously implicated in a wide variety of attentional tasks (see above).

Relative to temporal interference, the role of spatial interference in the AB is poorly understood, as previous studies were restricted to interference manipulations by simultaneous, spatially overlapping distractors (Seiffert and Di Lollo, 1997) or nonsimultaneous, nonoverlapping distractors (Raymond et al., 1995). However, experiments 3 and 4 clearly demonstrate that an attentional blink can be triggered by simultaneous presentation of nonoverlapping flankers. Although flanker tasks are commonly used to study interference for response selection (Eriksen and Eriksen, 1974; Eriksen et al., 1982; Miller, 1991), our study used a variant of this task to focus on the perceptual interference component inherent to the flanker paradigm (Eriksen and Hoffman, 1972; Eriksen and Eriksen, 1974). Our behavioral results demonstrate that this perceptual interference component can generate an attentional blink to the perception of subsequent targets and, moreover, that spatial interference activates the same neural circuits recruited by the temporal interference of the classical AB paradigm. These findings strongly suggest that our different temporal and spatial attentional blink manipulations are tapping into the same mechanisms used to resolve distractor interference. The present spatial interference manipulation is also important for linking our results to the attentional crowding phenomenon. The intraparietal (and intraoccipital) sulcus activation observed in the spatial interference task supports recent suggestions that the dorsal visual system may be involved in attentional resolution of crowding effects or distractor interference (He et al., 1996; Wojciulik and Kanwisher, 1999).

Our results do not allow us to determine whether the intraparietal area actually processes target identity (Maunsell, 1995) or whether it controls and modulates the processing of target representations in downstream visual cortical areas (Corbetta, 1998). Current evidence points in both directions: the intraparietal cortex responds to target presentation (e.g., Corbetta et al., 2000) and, at least in monkey, encodes stimulus saliency (e.g., Gottlieb et al., 1998) and even shape selectivity (Serenio and Maunsell, 1998). On the other hand, the role of the inferior temporal and lateral occipital cortex in visual stimulus identification is very well established (e.g., Ungerleider and Mishkin, 1982; Treisman and Kanwisher, 1998), and it has been suggested that the parietal cortex may be modulating the processing of information in the inferior temporal cortex (e.g., Hopfinger et al., 2000). However, in contrast to the consistent activation of parietal cortex by our interference manipulations, corresponding activations were not reliably observed in the inferior temporal cortex. This might seem surprising, given that activity associated with stimulus presentation in the temporal cortex is well known to be suppressed by the presence of distractors (Miller et al., 1993; Reynolds et al., 1999). However, this suppressive effect is eliminated by attending to the stimulus (Moran and Desimone, 1985; Kastner et al., 1998; Reynolds et al., 1999). Thus, the inferior temporal cortex may not have been (de-)activated in the present experiments because the

suppressive effects were counteracted by the attentional effects (Kastner et al., 1998). In parietal cortex, recent neuroimaging evidence suggests that the IPS may not show suppressive effects (Kastner et al., 1999). As a result, the IPS may have been activated in our manipulation because the attentional effects were not opposed by suppressive effects.

The effects of spatial distractor interference in nonhuman primates have not only been studied in the inferior temporal cortex (e.g., Moran and Desimone, 1985; Miller et al., 1993; Reynolds et al., 1999), but also in frontal eye field (Schall et al., 1995) and MT (Treue and Maunsell, 1996). However, to our knowledge, spatial interference effects have not been studied in the (intra-)parietal cortex. Temporal interference (backward masking) has also been studied neurophysiologically in several brain areas (Schiller, 1968; Rolls and Tovee, 1994; Kovacs et al., 1995; Macknik and Livingstone, 1998; Rolls et al., 1999; Thompson and Schall, 1999) but, again, not in parietal cortex. Although the above studies have not directly compared temporal and spatial interference, they generally demonstrate that both types of interference lead to suppressive activity. In light of our present results indicating that distractor interference produces a consistent increase in activation in the (right) parietal cortex, single-cell recordings of target-distractor interference in this brain region should prove very fruitful.

It is important to distinguish the effects of general task difficulty and effort from the specific effects of perceptual interference on attentional processing (Wojciulik and Kanwisher, 1999). Increasing perceptual interference across the first four experiments served to increase the difficulty in resolving T1. Several studies have demonstrated a positive correlation between task difficulty and the magnitude of the attentional blink (Chun and Potter, 1995; Moore et al., 1996; Grandison et al., 1997; Seiffert and Di Lollo, 1997; Jolicoeur, 1998, 1999). Since perceptual interference covaried with perceptual difficulty in experiments 1–4, the relative contribution of these two factors remains to be established. The potential importance of perceptual difficulty is illustrated by a neurophysiological study demonstrating that increased perceptual difficulty is met with enhanced neuronal response to stimulus presentations (Spitzer et al., 1988). Nevertheless, the results of the lexical decision control task (experiment 5) demonstrate that the attentional blink is not modulated by general effort or arousal effects (Shapiro et al., 1994). Correspondingly, the right parieto-frontal cortex activation cannot be interpreted as a non-specific response to general effort, since it was only associated with those difficulty manipulations that modulate the AB.

#### **Parietal versus Frontal Activations**

While the IPS was activated in all of our four experiments, activations of the lateral frontal and cingulate areas were less consistent. For instance, the lateral prefrontal cortex was activated in both of the temporal interference experiments but not by the spatial interference tasks. The anterior cingulate was activated in all but one (the blocked spatial-interference task) of our experiments. The anterior cingulate has generally been considered as the central executive and evaluative com-

ponent of the attentional system (Posner, 1994) and may perform specific functions such as error detection (Gehring et al., 1993) and conflict monitoring (Carter et al., 1998; Botvinick et al., 1999), while the lateral frontal areas have been associated with a motor/intentional and/or working memory component of the attentional network (Mesulam, 1981; Posner and Dehaene, 1994; Rafal, 1996). Our experiments were not designed to dissociate the relative contributions of the parietal and frontal areas to the formation of an AB, and future work should further elucidate this. Given that these frontal regions are highly interconnected with the parietal cortex (Pandya and Yeterian, 1985) and are also limited in capacity (Rainer et al., 1998), it may not be surprising that they were coactivated in the present studies. However, since the right IPS was significantly activated in all of our perceptual interference manipulations but not in the difficulty control task, it is likely to be a key neural component of the capacity-limited process revealed by the attentional blink.

### Implications for Visual Awareness

The importance of distractor interference in generating the AB, as well as the location of the activation in the parietal lobe and its right-hemisphere bias, suggests strong parallels with the neural substrates affected in hemispatial neglect (Robertson and Marshall, 1993). One hallmark of neglect is extinction: the loss of visual awareness for a stimulus presented in the neglected visual hemifield when a competing stimulus is presented simultaneously in the intact hemifield. In the attentional blink, T2 is essentially extinguished from visual awareness by the competition for attention between T1 and its neighboring distractors. In support of this proposal, neglect patients show abnormally long attentional blinks (Husain et al., 1997). The similarities between the attentional blink and neglect further underscore the role of attention in visual awareness (Posner, 1994; Rafal, 1996; Driver and Mattingley, 1998). Conditions that tax limited temporospatial processing capacity to select targets among distractors, as in the attentional blink and attentional crowding paradigms, conspire to limit our awareness of visual stimuli. Our findings with the AB paradigm suggest that the intraparietal sulcus, a key region of the cortical network for the control of attentional deployment and selection (Corbetta et al., 1993, 1998; Coull et al., 1996; Pugh et al., 1996; Courtney et al., 1997; Nobre et al., 1997; Coull and Nobre, 1998; Kastner et al., 1999; Kim et al., 1999; Wojciulik and Kanwisher, 1999), may also be characterized as a limited-capacity channel for visual information processing under conditions of perceptual interference, producing a cost that prevents conscious perception of other stimuli.

### Experimental Procedures

Prior to their participation in this study, all subjects provided informed consent in accordance with procedures and protocols approved by the Yale University School of Medicine Human Investigation Committee.

#### Trial Design

##### Experiment 1

The rapid serial visual presentation (RSVP) sequence consisted of black digits and capitalized letters (0.6° high and 0.4° wide) shown

at fixation on a white background with no interstimulus interval. Stimulus duration was fixed at 100 or 120 ms for each subject, depending on their performance in pilot testing. The visual stream began with digits and then switched to letters, with the first letter presented always being the target (B, C, or D). This design made the first target slightly more discriminable from the distractors and was used to alleviate fatigue incurred from the high attentional demands required throughout the fMRI sessions. Subjects detected a single target presented between 5.0 and 5.5 s into a 10.5 s long RSVP trial. A response panel, presented for 1500 ms at the end of the RSVP stream, prompted subjects to enter their response by button press. In the LOW interference trials, the target was followed by the blank(s) instead of distractor letters (Figure 1A). In the HIGH interference trials, the target was followed by a distractor letter and then by the blank(s). Four subjects were exposed to single blanks, while six other subjects were exposed to two consecutive blanks. The double-blank condition only accentuated the interference manipulation (Raymond et al., 1992) and fMRI signal differences (data not shown). The results are presented for the combined ten subjects (three women, ages 20–42). There were 15 trials per fMRI run (trial duration: 12 s) and ten runs per subject, with the number of HIGH and LOW interference trials counterbalanced between runs and their order of presentation randomized within runs.

##### Experiment 2

The target (letter B, C, or D) appeared anywhere between serial position 4 and 9 of a 1200 ms long stream of either digits (HIGH interference condition) or symbols (LOW interference condition: #, %, &, \*, /, =, +, >, <), followed by the response panel for 1800 ms (Figure 2A). A fixation cross was presented for 9 s between trials. Eight subjects (three women) were cued for the next trial by enlargement of the cross 3 s prior to the onset of a new trial. There were 16 trials per run (trial duration: 12 s) and ten runs per subject.

For the psychophysical experiments performed outside the scanner, a separate group of subjects ( $n = 7$ ) also searched for the presence of a second target (the letter X), which was shown at lag 4 and at lags 2–3 after T1 for experiments 1 and 2, respectively.

##### Experiment 3

A run consisted of alternating blocks of LOW and HIGH interference trials (ten trials per 15 s block), with a 3 s rest period (fixation) between blocks. A trial consisted, in order, of a 150 ms blank screen, 100 ms stimulus presentation, 200 ms blank screen, and a fixation cross for 1150 ms (total trial duration: 1500 ms), during which the subjects ( $n = 7$ , two women) responded to the target identity in a nonspeeded fashion. The trial panel consisted of a string of 17 nonrepeated consonants (total visual angle: 7.5°), with the target letter (either letter B, C, or D) appearing in the center of the screen at the previous location of the fixation cross (Figure 3A). The target letters never appeared among the flanking letters. The white letters (0.5° high and 0.3° wide) and fixation cross (0.25° visual angle) were presented on a black background. Letter-to-letter distance: 0.085° edge-to-edge, and 0.375° center-to-center. In the LOW interference condition, a gap (0.815° edge-to-edge, and 1.105° center-to-center) occurred between the central target and the eight distractors on either side. In the HIGH interference condition, two of the eight distractor letters were positioned between the target letter and the gap on either side. Thus, the panels in the two conditions were identical, except for the relative spatial position of the 1° gap.

##### Experiment 4

Experiment 4 was very similar to experiment 3, except that trials were presented in an event-related design instead of a block design. A trial consisted of a 200 ms blank, 100 ms stimulus presentation, 200 ms blank, 8750 ms large fixation cross (0.5°), and by a 3000 ms small fixation cross (total trial duration: 12.25 s). The size decrease in the fixation cross was used to signal the imminent presentation of a new stimulus. The task of the subjects ( $n = 10$ , five women) consisted of identifying which of the letters (X, Y, or Z) was presented at the center and to respond by a button press in a nonspeeded fashion. The order of trial presentation (nine trials of each condition per run, with nine runs per subject) was randomized.

For the psychophysical experiment performed outside the scanner, a separate group of subjects ( $n = 8$ ) searched for both a first (letter B, C, or D) and a second target (letter Y). A trial consisted of fixation for 1000 ms, blank screen for 200 ms, T1 presentation for 100 ms, and blank screen for 300 ms, followed by successive pre-

sentation of three letters for 100 ms each. When present, T2 was always the first of the three letters shown. Following these letters, the response panels for T1 ("B-C-D") and T2 ("YES-NO") were subsequently shown for 1300 ms and 1080 ms, respectively. The order of trial presentations for each condition was randomized.

#### Experiment 5

Sixteen subjects participated in the behavioral experiment. Trials began with fixation cross for 1 s then word presentation for 100 ms, interstimulus interval for 300 ms, T2 (letter X) for 100 ms, and by two distractor letters for 100 ms each. Response panels for T1 and T2 were presented for 4 s each. Ten trials were presented per block, and blocks of HIGH ("Is word both a noun and verb?") and LOW difficulty ("Is it a noun?") conditions were alternated. For each of the two conditions, 50% of the trials were "yes" trials for T1, and 20% of the trials had no T2 for determining the rate of false alarms (FA).

Nine subjects (four females) participated in the blocked-design fMRI experiment. There were 12 blocks (six blocks  $\times$  two conditions) per run, with six trials per block. A panel presented for 3 s at the beginning of each block instructed the subject about the task identity. A trial consisted of word presentation for 100 ms, followed by an ISI of 300 ms and a 3 s long fixation period for response generation. Subjects' T1 accuracy in the fMRI experiment was 89.5% and 82.7% for HIGH and LOW difficulty conditions,  $t = 3.71$ ,  $p < 0.01$ .

#### fMRI Design

Subjects were scanned with a 1.5T GE MRI system with resonant gradients for echoplanar imaging (Advanced NMR, Wilmington, MA). T1-weighted structural images were first acquired using conventional parameters. Imaging parameters for experiment 1: eleven 9 mm thick axial slices (0.5 mm skip) encompassing all of the cerebral cortex but the ventral part of the temporal poles. Image acquisition consisted of a gradient echo single-shot sequence (echo time, 60 ms; flip angle, 60°; repetition time (TR), 2000 ms; and 90 images/slice). Each image was 128  $\times$  64 pixels over a field of view of 40  $\times$  20 cm (in-plane resolution: 3.12 mm<sup>2</sup>). Experiment 2 had identical parameters as experiment 1, except for TR, 1500 ms; slice number, eight most dorsal; and number of images per slice, 128. Experiment 3: TR, 1500 ms; slice number, ten most dorsal; and number of images per slice, 102. Experiment 4: TR, 1750 ms; slice number, eight most dorsal; and number of images per slice, 126. Experiment 5: TR, 1750 ms; slice number, eight most dorsal; and number of images per slice, 158.

To ensure time locking of image acquisition to trial presentation, trial onsets were triggered by the MR scanner pulses. Stimuli were presented using RSVP software (P. Williams and M.J. Tarr, RSVP: Experimental Control Software for MacOS [<http://psych.umb.edu/rsvp/>]) with a MacIntosh PowerPC 7100 and back-projected from an LCD panel onto a screen that was viewed by the supine subject in the MR scanner through a prism mirror.

#### Data Analysis

For event-related experiments (experiments 1, 2, and 4), images taken at ~4–8 s after T1 presentation (experiment 1), 3–9 s (experiment 2), and 3.5–8.75 s after T2 presentation (experiment 4) were selected for fMRI data analysis. The image selection was determined a priori, to account for the delay of the hemodynamic response and to minimize cross-contamination between neighboring trials. Trials in which the target was incorrectly identified were discarded (less than 5% of all trials). For the blocked-design experiments (experiments 3 and 5), images taken from 3 s after the start of the first trial to 1.5 s after the end of the last trial of each block were selected.

Statistical parametric maps of BOLD activation for each subject were created using a skew-corrected percent signal difference. The anatomical and Gaussian-filtered (full-width at half-maximum = 4.0 mm) BOLD images for each subject were transformed into standardized Talairach space. The resulting maps from all subjects were superimposed to create cluster-filtered (six contiguous pixels) composite maps.

For all experiments, the probability that the mean percent signal change of activation across subjects was significantly different from zero was calculated using a  $t$  test for each composite pixel. The composite maps shown in all figures reveal pixels with  $p$  values  $< 0.001$  (uncorrected for the number of comparisons). For experiments

2–5, a region of interest (ROI) analysis was also performed, based on the brain regions activated below  $p < 0.005$  in experiment 1 (Table 1). The mean percent signal change for each ROI of each subject was first computed, and statistical differences in the group mean percent change between the two interference conditions were calculated with  $t$  tests (with significance level set at  $p < 0.05$ ). ROIs that were significantly activated based on this analysis are illustrated in the figures by a dark red fill of the green outlines.

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