The Neural Fate of Consciously Perceived and Missed Events in the Attentional Blink

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Summary

Cognitive models of attention propose that visual perception is a product of two stages of visual processing: early operations permit rapid initial categorization of the visual world, while later attention-demanding capacity-limited stages are necessary for the conscious report of the stimuli. Here we used the attentional blink paradigm and fMRI to neurally distinguish these two stages of vision. Subjects detected a face target and a scene target presented rapidly among distractors at fixation. Although the second, scene target frequently went undetected by the subjects, it nonetheless activated regions of the medial temporal cortex involved in high-level scene representations, the parahippocampal place area (PPA). This PPA activation was amplified when the stimulus was consciously perceived. By contrast, the frontal cortex was activated only when scenes were successfully reported. These results suggest that medial temporal cortex permits rapid categorization of the visual input, while the frontal cortex is part of a capacity-limited attentional bottleneck to conscious report.

Introduction

Virtually all cognitive models of attention posit that human perception proceeds along at least two stages (Broadbent and Broadbent, 1987; Chun and Potter, 1995; Duncan, 1980; Neisser, 1967; Rensink, 2002; Shiffrin and Gardner, 1972; Treisman and Gelade, 1980; Wolfe et al., 1989). The first stage of perceptual analysis is considered to be largely unconscious and allows for the rapid, global, and highly efficient categorization of items and events in a visual scene. The second "attentional" stage is necessary for the thorough identification, consolidation, and conscious report of visual events.

The dual nature of perception is clearly illustrated by the attentional blink (AB) paradigm: when subjects search for two targets presented in a rapid serial visual display of distractor items, they are severely impaired at detecting the second of the two targets when it is presented within 500 ms of the first target (Chun and Potter, 1995; Raymond et al., 1992). The deficit with the

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second target (T2) is a result of attending to the first target (T1): subjects have no difficulties in reporting T2 when it is the only target to be detected (Joseph et al., 1997; Raymond et al., 1992). Thus, T2 can easily be singled out of an RSVP of distractor items, unless attention is engaged in processing a previously presented target (T1). These results support a two-stage model of the AB, consisting of the rapid and initial representation of visual items followed by the slow, capacity-limited and attention-demanding consolidation of these items for conscious report (Chun and Potter, 1995; Jolicoeur et al., 2001; Shapiro et al., 1997b).

Although such a dual mode of visual information processing figures prominently in cognitive models of the AB and of attention in general, it is not yet clear whether it also characterizes the underlying functional neuroarchitecture. In support of a first stage of information processing, there is both electrophysiological (Luck et al., 1996) and behavioral (Shapiro et al., 1997a) evidence that visually presented words which are not explicitly perceived in the attentional blink are nonetheless processed up to their semantic identity. However, these studies could not determine the functional neuroanatomy of unconsciously processed events under conditions of inattention nor could they reveal how it differs from that of consciously perceived events. In support of a second, attention-demanding stage, manipulations that affect the magnitude of the AB recruit a parietofrontal cortical network (Marois et al., 2000a) previously implicated in the control of visuospatial attention (Corbetta et al., 1993, 1998; Kastner et al., 1999; Nobre et al., 1997). However, the Marois et al. (2000a) study focused on neural processing of T1, namely, the attentional limitations that cause the AB. The present study now examines the effects of divided attention on T2, both when it is consciously perceived and when it is missed.

Few imaging studies have investigated the neural fate of consciously perceived and missed visual events under conditions of divided attention, and they have yielded inconsistent results. One study reported no evidence that foveally presented words are semantically processed by the brain in the absence of attention (Rees et al., 1999). Although another observed distinct inferior temporal and parietofrontal activation patterns for consciously and unconsciously perceived face changes (Beck et al., 2001), that study could not distinguish between neural activity associated with awareness of the change versus activity associated with spatial shifts of attention toward the change since the objects were not presented at the focus of attention.

Thus, the goal of the present study is to determine whether the two stages of visual information processing predicted by cognitive models of attention are implemented by different neural substrates under experimental conditions that eliminate contributions of spatial shifts of attention. Specifically, we used an AB paradigm to test whether the neural activation associated with consciously reported and unreported targets presented at fixation is different in regions of the inferior temporal cortex involved in visual categorization and representa-
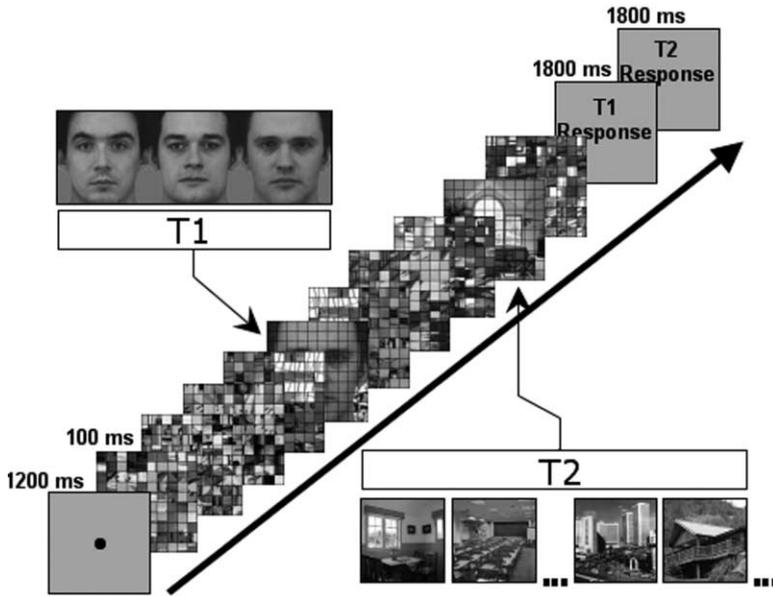
Figure 1. Experimental Design

In the dual-task experiment, subjects searched for a face target (T1) and a scene target (T2) presented in an RSVP of scrambled distractor scenes. The SOA between T1 and T2 was varied. The single-task experiment was identical except that subjects searched only for the target scene. Insets show the three face targets and examples of both indoor and outdoor scene targets.

tion, than in the parietofrontal cortical network previously hypothesized to represent a capacity-limited attention-demanding stage (Marois et al., 2000a). The hypothesis that the AB bottleneck occurs at a late locus of processing predicts that (1) both reported and unreported visual items should engage even high-level stages of visual event representation in ventral regions of the occipitotemporal cortex (Treisman and Kanwisher, 1998; Malach et al., 2002) and that (2) the neural distinction between reportable and unreportable items should occur later along the information processing pathway, specifically in the parietofrontal network of visuospatial attention (Beck et al., 2001; Marois et al., 2000a).

Results

The task consisted of searching for two targets presented among a 1 s long rapid serial display of scrambled scenes (Figure 1). The first target (T1) was a face, the second (T2) a scene, and distractors consisted of scrambled versions of scenes. This design bestowed several crucial experimental advantages for this study. First, since the scenes activate a canonical region of the visual cortex, namely the parahippocampal place area (PPA) (Epstein and Kanwisher, 1998), the brain response to T2 stimulus presentations can be easily localized. Second, the use of scenes as T2 and faces as T1 permits the assessment of the brain response to scenes uncontaminated by the processing of T1, since faces produce negligible activation of the PPA (Epstein et al., 1999; Epstein and Kanwisher, 1998), a finding we confirmed in pilot scanning sessions (data not shown). Third, since the PPA is involved in high-level perception, namely in the perceptual encoding (Epstein et al., 1999) and representation (Epstein et al., 2003) of visual scenes, it is ideally suited to test whether high-level visual representation can occur even in the absence of conscious report. Finally, scrambled scenes conceal intact scenes sufficiently to render detection of the latter difficult (see

below) but not enough to obscure intact scene-related activity, as the PPA activates significantly more to intact than scrambled scenes (Epstein and Kanwisher, 1998).

Although in principle T1-related activity could also be examined, since face stimuli activate a well-defined region of the fusiform gyrus (Kanwisher et al., 1997; Sergent et al., 1992), this is not feasible in the present experiment since the face-sensitive area also responds to buildings/scenes (Ishai et al., 2000; Kanwisher et al., 1997), thereby preventing the independent assessment of T1-related brain activity from T2 performance and activity. Instead, the design of the experiment and the results described below focus on isolating the neural response to T2 processing.

Behavioral Experiment

A behavioral experiment performed outside the scanner room established that an attentional blink can be obtained with this experimental paradigm (Figure 2). Scene detection performance was substantially lower when subjects were required to detect both T1 and T2 than
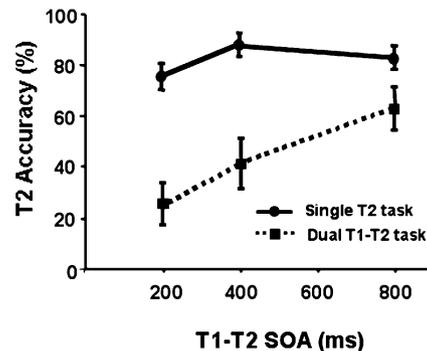
Figure 2. Behavioral T2 Performance under Single- and Dual-Task Conditions

T2 performance was worse in the dual-task than in the single-task condition, especially at small SOAs. Error bars: ± SEM.

when they were required to detect only T2 [F(1,16) = 22.7, p < 0.001, ANOVA with condition (single/dual task) as between-subject and SOA as within-subject factors]. Furthermore, in the dual-task condition, performance increased with greater SOA between T1 and T2 [F(2,32) = 15.4, p < 0.001]. These two results are trademark features of the AB (Chun and Potter, 1995; Raymond et al., 1992).

fMRI Experiment: Behavioral Performance

A similar dual-task experiment was carried out in the scanner. Mean T1 accuracy was 86%, with a 2% false alarm rate. T2 accuracy was experimentally held around 50% detection to yield similar number of trials in T2-detected and T2-undetected conditions by adjusting the T1-T2 SOA between fMRI runs (mean T1-T2 SOA: 450 ms). Presumably, for any set SOA, whether T2 is detected or missed on any given trial is governed by stochastic variations in the activity levels of the neural substrates involved in T1 and T2 identifications (Dehaene et al., 2003). With this SOA manipulation, T2 was detected on 52% (27% correctly and 25% incorrectly identified scenes) of the trials and was missed on 48%. The mean T2 false alarm rate was 24%, which was significantly below the T2 detection rate [F(1,18) = 8.920, p < 001]. Finally, as expected, subjects performed very well with T2 (82% accuracy) in trials where T1 was absent, demonstrating again that T2 performance is impaired by attention to T1.

fMRI Experiment: T2-Related Brain Activations

Medial Temporal Cortex. The PPA region of each subject was first isolated in a localizer task by contrasting the brain activity in blocked presentations of faces and scenes. The mean Talairach coordinates of the isolated region (right PPA: x = 21.4 mm, y = −53.1 mm, z = −5.38 mm; left PPA: x = −22.8 mm, y = −56.6 mm, z = −5.38 mm) is consistent with the known location of the PPA (Epstein et al., 2003; Epstein and Kanwisher, 1998).

The isolated PPAs from both left and right hemispheres were collapsed and probed in the dual-task experiment for scene-related activity under three different T2 performance conditions: (1) subjects successfully detected the presentation of a scene (Hit), regardless of whether the scene was correctly identified as indoor or outdoor (see Experimental Procedures); (2) subjects failed to detect the scene (Miss), and (3) subjects correctly reported the absence of a scene (CR). Too few false alarm trials (scene was reported when none was shown) were obtained per subject (mean = 7.4) to yield a stable response for this condition. The PPA was activated even when no scenes were presented and detected (CR, Figure 3). This activation likely resulted from the entire sequence of scrambled scenes since we observed in preliminary scanning sessions similar responses even when neither any scenes nor faces were presented (data not shown), confirming that scrambled scenes activate the PPA (Epstein and Kanwisher, 1998). The CR condition provides the baseline on which the other two conditions can be compared. As expected, the PPA was more activated when subjects detected the presence of a scene [Hit > CR, t(18) = 4.38, p < .001]. Most importantly, scenes that were not detected
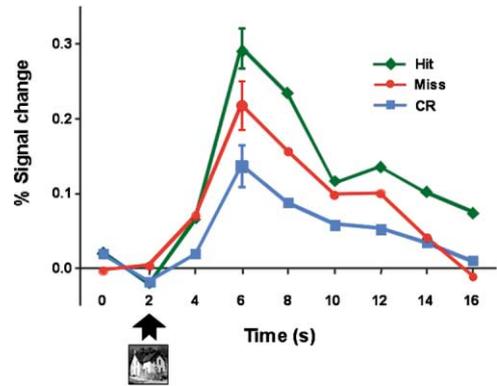
Figure 3. Timecourse of the Hemodynamic Response in the Parahippocampal Place Area under Hit, Miss, and CR T2 Conditions
Error bars: ± SEM.

by the subjects (Miss) still activated the PPA more than when no scenes were presented (CR) [Miss > CR, t(18) = 2.19, p < 0.05], suggesting that the PPA responds to scenes even when they are not consciously perceived. Moreover, this subliminal PPA activation was enhanced when subjects consciously perceived the scenes [Figure 3; Hit > Miss, t(18) = 2.31, p < 0.05], suggesting that conscious scene perception amplified the PPA response elicited by subliminal scene perception.

Parietofrontal Cortex. The results in the PPA suggest that the medial temporal cortex discriminates between scenes and nonscenes even when these are not consciously perceived by the subjects under conditions of divided attention. Based on previous findings (Marois et al., 2000a), we postulated that a network of lateral frontal, anterior cingulate (AC), and intraparietal areas may represent the attentional bottleneck to perceptual awareness. This hypothesis predicts that the parietofrontal network should respond differently than the medial temporal cortex under the three T2 conditions. Specifically, activity in this network should be the comparable in Miss and CR trials, whereas conscious scene detection (Hit) should recruit these brain regions more than either of the two other conditions. A voxel-based approach did not reveal any parietofrontal regions that were significantly more activated in the Hit than in the Miss and CR conditions (p < 0.05, corrected). However, a more sensitive ROI approach, using regions of interest defined in a previous AB study (Marois et al., 2000a), revealed activation in part of this parietofrontal network with T2 response (Figures 4A and 4B). Specifically, the bilateral frontal cortex activation conformed [F(1,18) = 5.12, p < 0.05] to the predicted response function (ANOVA with 2Hit, -1Miss, -1CR contrast weights), and the anterior cingulate (AC) showed a similar though marginal effect [F(1,18) = 4.39, p = 0.051]. These results were also generally supported by paired t tests analysis for both the lateral frontal (Miss-CR p = 0.339, Hit-CR p < 0.05, Hit-Miss p = 0.054) and AC (Miss-CR p = 0.068, Hit-CR p < 0.05, Hit-Miss p = 0.221). The greater response in the frontal cortex with Hits than with Misses and CRs is evidenced not only by higher peak amplitude but also by a prolonged response (Figure 4A).

In contrast to the frontal areas, the parietal ROI did
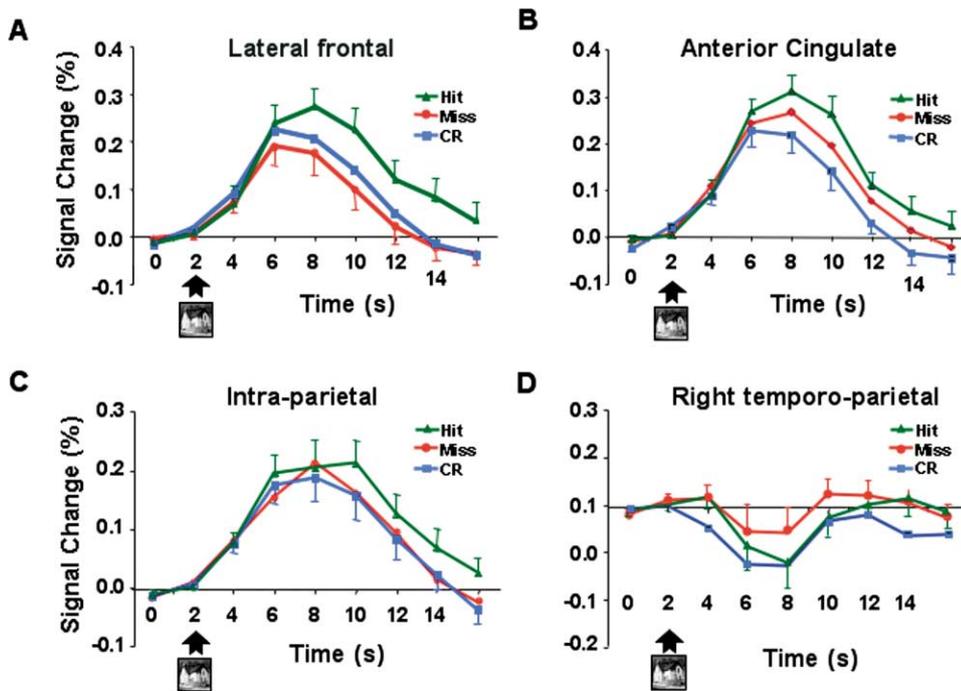
Figure 4. Timecourse of the Hemodynamic Response in the Parietal and Frontal Cortex under Hit, Miss, and CR T2 Conditions

(A) Intraparietal cortex, Talairach coordinates (x, y, z) of the ROI centroid (Marois et al., 2000a): ±30, −58, +45; (B) lateral frontal cortex, ±48, +8, +35; (C) anterior cingulate, ±3, +20, +36; (D) right temporoparietal junction, +53, −34, +21. Error bars: ± SEM.

not show significant activation differences between any of the three conditions [$F_{(1,18)} = 0.12$, $p = 0.913$ for the linear contrast analysis, $ps > 0.25$ for pair-wise t tests], although it did show a prolonged response as well (Figure 4C). Finally, given recent reports that patients with lesions in the temporoparietal cortex may exhibit abnormally long ABs (Husain et al., 1997; Shapiro et al., 2002), we also examined this region (Marois et al., 2000b) and found no systematic differences between the three conditions (Figure 4D), either with the contrast analysis [right TPJ, $F_{(1,18)} = 0.407$, $p = 0.53$; left TPJ, $F_{(1,18)} = 0.456$, $p = 0.508$] or pair-wise t tests (all $ps > 0.05$).

Overall, these results indicate that, unlike the medial temporal cortex, the frontal cortex activation is mainly dictated by the subjects' explicit perception of the stimulus rather than by its physical presentation. Importantly, the distinct activation pattern in the frontal and medial temporal cortex argues against a simple account of detection bias for the results in the PPA, i.e., that activation in Miss trials might not be due to processing of unattended scenes but instead to subjects adopting a conservative criterion for the report of the target scene, leading them to classify trials for which they were uncertain about the presence of a scene as Miss. Since this bias is not reflected in the activity of the frontal cortex, where decision making is thought to be more prevalent than in visual cortex (Gold and Shadlen, 2001; Schall, 2001), it is unlikely to account for the PPA activity.

Discussion

The findings of this study clearly establish that the medial temporal cortex can be activated even when sub-jects fail to consciously perceive foveated stimuli under divided attention. By contrast, the frontal cortex's response to the stimulus is primarily contingent on whether that stimulus is consciously reported by the subject. Thus, activity in the inferior/medial temporal cortex primarily reflects the physical visual world, while the frontal cortex predominantly represents the consciously reported world.

Parahippocampal Cortex

The greater activation of the PPA in Miss than in CR trials suggests that the visual cortex can categorize visual input under conditions of high attentional load that prevents awareness and report. These results are consistent with behavioral and electrophysiological work suggesting that stimuli that fail to be explicitly reported during the AB are nevertheless registered by the brain (Luck et al., 1996; Shapiro et al., 1997a) but inconsistent with the idea that the brain is unresponsive to stimuli that the mind is inattentive to (Rees et al., 1999). This finding supports the view that visual cortex activation is not sufficient for visual awareness (Beck et al., 2001; Dehaene et al., 2001) even when the stimuli are foveated. They also demonstrate that, unlike previous reports (Beck et al., 2001), scenes can activate the medial temporal cortex during inattention, raising the possibility that scenes are automatically categorized by the PPA.

Importantly, these results do not imply that the medial temporal cortex is not critical for conscious, attentive perception of the visual world, as has been evidenced with brain lesion (Farah and Feinberg, 1997) and physiological studies (Bar et al., 2001; Kleinschmidt et al., 2002; Logothetis, 1998; Lumer et al., 1998; Moutoussis and

Zeki, 2002; Pins and Ffytche, 2003; Tong et al., 1998). Furthermore, the visual cortex in general (Chawla et al., 1999; Kastner et al., 1998; Luck et al., 1997; Spitzer et al., 1988), and the PPA in particular (O'Craven and Kanwisher, 2000; see also Figure 3), is strongly modulated by attention and imagery. Correspondingly, PPA activity was enhanced above and beyond the activation levels of the Miss condition when subjects consciously perceived the scenes (Figure 3), perhaps as a result of attentional top-down modulation of the PPA with scene detection. Taken together, these results clearly indicate that PPA activity represents a conflation of automatic/bottom-up and conscious/top-down sources of activation.

Parietofrontal Cortex

In contrast to the medial temporal cortex, the lateral frontal cortex activation was strongly dependent on whether the target scenes were explicitly reported. These results are consistent with the involvement of this brain region in the control of visuospatial attention (Corbetta et al., 1993; Kastner et al., 1999; Nobre et al., 1997) and suggest that the frontal cortex is particularly important for conscious target report (Beck et al., 2001; Dehaene et al., 2001; Weiskrantz et al., 2003). The precise function played by the lateral frontal cortex in the present task remains to be determined, although it is likely to be associated with some aspects of reporting the conscious perception of the target, such as the consolidation and maintenance of the target in working memory for subsequent report (Courtney et al., 1998). Consistent with an involvement in working memory, the frontal cortex showed a prolonged hemodynamic response with hits relative to misses or correct rejections (Figure 4), which may reflect further decision making about scene category (indoor/outdoor) following an initial judgment about the presence or absence of a scene. This is a testable hypothesis, since one would predict that larger but not prolonged responses should be observed when subjects are only asked to perform a judgment about the presence or absence of a scene. The anterior cingulate cortex showed a similar response trend to the lateral frontal cortex. Viewed in the light of the involvement of the AC in response conflict and/or performance/error monitoring (Carter et al., 1998; Gehring et al., 1993; Paus, 2001), it is possible that the AC activation in this study may be response related, perhaps reflecting indecision or monitoring processes.

The response of the intraparietal cortex did not distinguish between the different T2 conditions, although it showed the same trend of prolonged Hit activation observed in the frontal cortex. This suggests that the IPS may not be as involved in conscious target report as the lateral frontal cortex. On the other hand, T1 manipulations of perceptual interference that affect the magnitude of the AB modulate IPS activation (Marois et al., 2000a). It is therefore conceivable that the parietal cortex is important for resolving perceptual interference (Friedman-Hill et al., 2003; Marois et al., 2000a; Shafritz et al., 2002; Wojciulik and Kanwisher, 1999) or, more broadly speaking, in controlling the distribution of attentional resources among visual events, rather than in explicit target perception per se. In support of this hypothesis,

the intraparietal cortex appears to be primarily engaged by temporal and spatial changes of attentional demands (Corbetta et al., 1993; Coull and Nobre, 1998; Yantis et al., 2002). Since the attentional demands were constant across all T2 conditions in the current experiment, this hypothesis would predict little activation difference among these conditions. The attentional demand hypothesis is also consistent with the observation of IPS activation with detection of scene changes (Beck et al., 2001), since the detection of a change may lead to a shift of visuospatial attention to the location of the change.

Neural Substrates of the Attentional Blink

The attentional blink reveals a central processing limitation in attending to two targets presented in an RSVP of distractor items. Consistent with a central limitation, the AB is a robust phenomenon that has been observed with a wide variety of target objects and events (Joseph et al., 1997; Ross and Jolicoeur, 1999; Shapiro et al., 1997b; Sheppard et al., 2002). Our behavioral results extend the generality of the attentional blink in demonstrating that it not only applies to the perception of objects but to the perception of complex scenes as well. As such, these results challenge a recent finding that scenes can be overtly categorized in the absence of attention (Li et al., 2002). In contrast to their null finding, we observed pronounced scene detection deficits, probably because our procedures—namely, the sustained RSVP task and robust masking of the target scenes by scrambled scene distractors—were more effective at taxing attention.

The results also provide neural support for two-stage models of visual attention. More specifically, the two-stage model of the attentional blink proposed that stimuli are initially characterized and registered at an early stage of visual information processing, but explicit report of the stimuli requires attentional consolidation of the stimuli into a durable form (working memory) (Chun and Potter, 1995; Jolicoeur and Dell'Acqua, 1998, Vogel et al., 1998). This model echoes other attention models that distinguish between efficient, preconscious and more capacity-limited, attention-demanding stages of vision (Broadbent and Broadbent, 1987; Duncan, 1980; Neisser, 1967; Rensink, 2002; Shiffrin and Gardner, 1972; Treisman and Gelade, 1980; Wolfe et al., 1989). Consistent with this two-stage progression of attentional processing, the present results demonstrate different response patterns in visual and frontal cortex: the lateral frontal cortex is activated when subjects can successfully report the target, while high-level visual cortex still registers the visual stimuli even when they are not reportable. It should be noted that these findings do not imply that the two stages of information processing with the attentional blink are necessarily discrete, as the results are not inconsistent with graded models of activation to awareness. Our experimental design and analysis may simply reveal extremes of a continuum, although recent modeling and behavioral evidence suggests that the attentional blink may result from a nonlinear transition from nonconscious processing to explicit perception (Dehaene et al., 2003).

More broadly speaking, the frontal cortex may be associated with capacity-limited attentive vision, while the

visual cortex registers the input in an efficient, precon-
scious manner that guides selection for report (Chun
and Marois, 2002; Marois et al., 2000a). Accordingly,
activation of the visual cortex is not sufficient for con-
scious vision, which would necessitate the recruitment
of the frontal cortex (Beck et al., 2001; Dehaene et al.,
2001, 2003; Lumer et al., 1998; Rees et al., 2002). Clearly,
the explicit perception of a visual stimulus is likely to
result from the interaction between a sensory represen-
tation of the visual stimulus in visual cortex and the
attentional network necessary to consolidate that stimu-
lus for full report in the frontal cortex.

Experimental Procedures

Behavioral Experiments
Nine paid subjects from the Vanderbilt University commu-
nity volunteered for each of the single- and dual-task experiments. In the
dual-task experiment, subjects searched for two targets presented
among an RSVP of eight distractor items at fixation for 100 ms each
with no interstimulus interval. The first target (T1) was a face, the
second (T2) a scene, and the distractors were scrambled versions
of scenes, with each grayscale stimulus subtending 12.8° × 12.8°.
The scrambled scenes originated from a pool of 120 scenes and
were created by dividing each quadrant of the image into 25 squares,
inverting these squares, and randomly scrambling their positions.
Thin black grids were drawn over the scrambled (and intact) images
to occlude the boundaries of blocks. When present, the scene target
was shown at the second-to-last position in the RSVP, while the
face target was presented 200, 400, or 800 ms before the scene
target. A trial began with presentation of a fixation point for 1200
ms before the onset of the RSVP and ended with the presentation
of both T1 response and T2 response displays, each for 1800 ms.
During the T1 displays (labeled "Face1_Face2_Face3"), subjects
decided by keypress which of the three faces was presented, while
during the T2 response displays ("NoScene_Indoor_Outdoor") they
selected whether no scene, an outdoor scene, or an indoor scene
was presented. A face target was present on every trial and a scene
target on 67% of the trials, with equal probability of indoor and
outdoor scene presentation. When absent, T2 targets were replaced
by a scrambled scene. Subjects were instructed to emphasize task
1 over task 2. For T2 performance, only T1-correct trials were ana-
lyzed. The single-task experiment was identical to the dual-task
experiment except that subjects were instructed to search for the
scene target only. A total of 180 trials were presented in each exper-
iment.

fMRI Experiment
Twenty paid subjects (9 females) from the Vanderbilt University
community performed a similar dual-task in an fMRI experiment.
The 12.8° × 12.8° stimuli were viewed by the subjects on a projection
screen through a mirror mounted on top of the RF coil above their
head. Stimuli were projected onto the screen by means of an LCD
projector located outside the scanner room.
fMRI Parameters
Subjects were scanned on a 3T whole-body GE/Magnex (Milwau-
kee, WI). Anatomical images were acquired using conventional pa-
rameters. T2* scan parameters: TR 2 s, TE 25 ms, FA 70°, 197
images/slice, with 19 axial slices (7 mm thick, 0 mm skip) acquired
parallel to the AC-PC line.
Localizer Task
Subjects were first presented with two runs of a one-back repetition
detection task in order to localize the PPA (Epstein et al., 1999,
2003; Levy et al., 2001). The design consisted of alternating blocked
presentation of faces and scenes, with each block containing 18
scenes or faces presented at fixation for 800 ms followed by a blank
of 200 ms. Subjects searched for consecutive repetitions of stimuli,
with two such repetitions occurring in each block. There were nine
blocks each of faces and scenes in one fMRI run. The PPA was
localized in each individual by contrasting the averaged brain activity
in scene blocks with face blocks. Statistical parametric maps of

BOLD activation for each subject were created using a skew-cor-
rected percent signal difference. The PPA ROI was defined as the
voxel with the peak activation and its eight surrounding voxels, such
that each subject provided a 3 × 3 voxel grid from each hemisphere.
For all subjects, the activated region was found in the parahippo-
campal gyrus/collateral sulcus region.
Dual Task
Subjects subsequently performed four to eight runs of an event-
related dual-task experiment similar to the behavioral experiment
except for the following modifications. The response panels were
followed by a 12.7 s fixation period and by a 1000 ms blank period,
which signaled the beginning of the next trial (total trial duration =
18 s). Nineteen trials were presented in each fMRI run, including
five T1-only trials and four T2-only trials. After each run, the temporal
lag between the T1 face target and the T2 scene target was adjusted
by the experimenter in order to yield a scene detection performance
around 50%, and the hit and false alarm rates for the face task were
given to subjects as feedback. Unlike for the behavioral experiment,
"no_face" and "unknown_scene" response options were added for
the T1 and the T2 task, respectively. The "unknown_scene" re-
sponse was included in case subjects perceived the layout of a
scene but were not certain whether it was indoor or outdoor. For
data analysis, selection of this response option was classified as
an incorrect scene identification, where it accounted for 64% of this
category's trials. However, since all ROIs showed indistinguishable
responses to correctly identified and incorrectly identified scenes
(data not shown), these two responses were combined into the
category of correct scene detection.
Data Analysis
One predictable consequence of the lag manipulation for keeping
subjects' T2 performance around 50% is that it led to a difference
(t test, p < 0.05) in T1-T2 SOA between the Hit (mean SOA: 452 ms)
and Miss (mean SOA: 435 ms) conditions. Even though this differ-
ence in mean stimulus onset asynchronies is small, to prevent such
differences in stimulus presentations from influencing the activation
differences between Hits and Misses, we equated the Hits and
Misses SOAs by extracting fMRI runs which showed the longest lag
as well as the greatest hit rate, or the shortest lag as well as the
greatest miss rate. Nine runs from eight subjects were thereby elimi-
nated from further analysis. One subject was removed from further
analysis, as the resulting number of CR trials was excessively low (a
priori criterion that subjects with fewer than eight trials per condition
would be discarded). The group average SOA for Hits and Misses
were no longer significantly different from each other (SOA differ-
ence: 9 ms, p = 0.155). The SOA difference between Correct Rejec-
tion and Miss trials was also not significant (SOA difference: 4 ms,
p = 0.220).
   For each ROI of each subject, the BOLD percent change was
calculated by averaging the time courses of each T2 condition (Hit,
Miss, CR) and normalizing them to the averaged value of the first
two TRs after trial onset (Figure 3). ROI time courses were then
averaged across all subjects. Statistical analysis (paired t tests and
contrast analysis) between conditions was performed on the peak
amplitude response (Epstein et al., 2003), the time point of which
was first determined by collapsing all T2 conditions together. An
area under the curve (AUC) analysis yielded qualitatively similar
results to the peak analysis. Only T1-correct trials were examined
for T2-related brain activity.

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