Regional Brain Activity Associated with Visual Backward Masking

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Abstract

In visual backward masking, the visibility of a briefly presented visual target is disrupted by a mask that is presented shortly thereafter. The goal of the current study was to identify regions in the human cortex that may provide the neural basis of visual masking. We searched for areas whose activity correlated with perception as we systematically varied the strength of masking. A total of 13 subjects performed a backward masking task during functional magnetic resonance imaging. Target and mask were presented at three delay intervals (34, 68, and 102 msec) and behavioral measures confirmed that the targets were more visible at longer masking intervals. Two sets of regions of interest were identified: Distinct regions in the visual cortex (V1/V2, LO, hMT+) were segregated using scans to localize visual processing drawn from the existing literature. Additional cortical regions were selected in a data-driven approach based on their activity during the backward masking task. For each set, we determined the regions whose magnitude of activation increased at longer masking intervals. Nine of the subjects provided valid behavioral performance data on the visual masking task and imaging data from these subjects were used for subsequent analysis. The scans of visual processing areas identified four regions, including: early visual areas (V1 and V2), the motion-sensitive regions in the lateral occipital (LO) lobe (hMT+), and two components (dorsal and ventral) of the object-sensitive region, LO. Of these, the ventral and dorsal LO regions were sensitive to the strength of the mask. For the data-driven approach, six regions were identified on the basis of a difference map in which all masking intervals were contrasted with rest. These included the inferior parietal, anterior cingulate, precentral, insula, thalamic, and occipital areas. The predicted effects of more activity with weaker masking were seen in the thalamus, inferior parietal, and anterior cingulate. This study isolated three types of visual processing areas. The first included regions that subserve key stages of vision (including object and motion processing). The second type responded to the presentation of briefly presented visual stimuli, regardless of masking interval. The third type (selected from the first two) included regions sensitive to the interval between the target and mask. These latter regions (including ventral LO, inferior parietal, anterior cingulate, and thalamus) may form the neural substrate of backward masking.

INTRODUCTION

In visual masking, the salience of a briefly presented visual “target” is reduced by a visual “mask” presented very shortly before or after the target (Breitmeyer & Ogmen, 2000; Purushothaman, Ogmen, & Bedell, 1997; Breitmeyer, 1984). The effect is called “backward” masking when the mask follows the target, and “forward” masking when the mask precedes the target. Visual masking is of theoretical interest for several reasons. It occurs over time intervals less than 100 msec, but can extend longer depending on the complexity of the stimuli. With strong masking effects, subjects are unaware of the target, or experience an ambiguous sense of stimulus simultaneity. Visual masking is a very sensitive indicator or abnormalities in early visual processing and has been used to document deficits in clinical populations, including schizophrenia and bipolar disorder (Green, Nuechterlein, & Mintz, 1994; Braff, Saccuzzo, & Geyer, 1991). Although backward masking is a highly robust behavioral phenomenon, little is known about the nature of the central brain mechanisms that subserve it.

Visual masking likely results from a disruption of the neural pathways responsible for object recognition; the so-called “what” or ventral stream in the cortex (Ungerleider & Mishkin, 1982). This consists of a series of densely interconnected cortical regions that can be organized into a roughly hierarchical arrangement from early (e.g., cortical areas V1 and V2), to late (e.g., IT) visual processing (Felleman & Van Essen, 1991). In humans, the areas comprising some of the later stages of the “what” stream have been divided into two separate anatomical regions: the LO
cortex, and regions in the lingual and fusiform gyri on the ventral surface of the posterior temporal lobe (for a recent survey, see Hasson, Levy, Behrmann, Hendler, & Malach, 2002). Aberrant processing at any point along this stream could explain the masking phenomenon. Although theories about the mechanisms of visual masking have typically emphasized disruption in early stages of feed-forward processing, more recent formulations have also suggested the importance of feedback, or reentrant, processing as a source for the masking effect (e.g., Di Lollo, Enns, & Rensink, 2000; Enns & Di Lollo, 2000).

Prior neurophysiological studies have found effects of visual masking at different stages in the visual pathways. Recordings from single units in macaque VI revealed that backward masking reduced the transient response associated with the removal of a stimulus (the “off-response”), but did not greatly affect responses to the onset or sustained portion of the stimulus (Macknik & Haglund, 1999). At later stages of visual processing, in the inferotemporal cortex, masking has a larger effect upon single-unit responses: It reduces their duration, peak firing rate, and stimulus selectivity (Rolls, Tovee, & Panzeri, 1999; Kovacs, Vogels, & Orban, 1995).

Recent neuroimaging studies of visual masking have mainly focused on the activation of stimuli that do not reach conscious awareness. For example, Whalen et al. (1998) used functional magnetic resonance imaging (fMRI) to demonstrate that the amygdala, a region that is activated by a range of emotional stimuli, was activated by emotional stimuli (faces) even when they were masked and unconscious. Sheline et al. (2001) used a similar procedure to demonstrate that depressed patients had increased activation in the left amygdala in response to masked emotional faces. Recent studies have also indicated that masked stimuli can still have priming effects on a simple motor response decision task, and that these effects can be measured with fMRI (Dehaene, Ward, Owen, & Rafal, 2001; Dehaene, Naccache, Le Clec’h, et al., 1998).

Two prior studies have attempted to identify brain regions whose activity correlates with recognition of masked stimuli. One study (Grill-Spector, Kushnir, Hendler, & Malach, 2000) manipulated the duration of the target (a photo of an object) from 20 to 500 msec, and found that activity in the LO cortex was greater at longer durations when stimuli could be recognized. Activity in the LO cortex was also greater for stimuli that subjects had practiced recognizing than for novel stimuli. The second study (Bar et al., 2001) kept the duration of masked stimuli constant, but manipulated recognition by presenting stimuli repeatedly. Activity both in the LO cortex and in more anterior regions of the fusiform gyrus was higher when subjects recognized stimuli than when they did not.

Although these studies provide evidence that the LO cortex is important for object recognition, they do not identify it as a neural basis of masking itself. This is because they did not explicitly manipulate the effectiveness of the masks; but instead manipulated the effectiveness of the targets by lengthening presentation time, by having subjects train on some of the stimuli, or by repeating presentation of some of the stimuli. To see this more clearly, let us define a neural masking effect as a reduction in response to a target produced by the subsequent presentation of a mask. In the previous imaging studies mentioned above, it is entirely possible that neural masking was equivalent in all conditions, but that neurons in the LO cortex nevertheless responded more strongly when stimulus duration, learning, or priming were increased. The locus of neural masking in humans, therefore, remains unknown.

The goal of the current study was to identify regions in the human cortex where a mask reduces neural response to a target. To this end, we kept the duration and intensity of both target and mask constant, but manipulated the “effectiveness” of the mask by delaying its onset (i.e., increasing the stimulus onset asynchrony [SOA]). We expected that signal in brain regions affected by masking would increase with SOA, as the masking became weaker.

We examined the effects of SOA in masking within several regions of interest in the cortex. We used two approaches to identify the regions. In one approach, we selected regions a priori on the basis of reference scans that used previously validated stimuli designed to activate specific visual areas. By focusing on a small number of areas associated with visual processing, this a priori method provided enhanced power to examine the effects of masking. However, it is entirely possible that regions outside classical visual processing areas may be involved with processing a masked target (e.g., areas involved with reentrant processing). For this reason, we also used a data-driven approach in which we selected regions that were generally active during the backward masking task (all intervals of masking minus rest) and then determined which areas showed the predicted pattern of greater activation with longer SOA.

RESULTS

Behavioral Performance in the Scanner

The subjects showed a consistent SOA-dependent masking effect. Mean performance for the group was 43.5%, 64.5%, and 75.9% for the 34, 68, and 102 msec SOAs, respectively, compared to 25% chance accuracy. These differences across conditions were significant with repeated-measures analysis of variance ($F = 26.2, df = 2, 16, p < .001$). Follow-up contrasts revealed that performance at each condition was significantly different from each other (all $p$ values < .05).
The A Priori Approach to Defining Regions

The scans that were designed to localize visual processing identified four interpretable regions known to be associated with visual processing (shown in Figure 1 and Table 1). The scan of retinotopic areas identified a region associated with early visual processing (V1 and V2) along the calcarine fissure. The “motion” procedure identified bilateral regions in the LO lobe consistent with previous reports of the location of hMT+ (e.g., Tootell et al., 1995). The “LO” scan identified two separate areas, both also in the LO region. These locations are comparable to results in previous reports of dorsal and ventral components of the LO lobe (e.g., Hasson et al., 2002).

After these four regions were localized, the time series of activation in each region was examined to determine whether any had the predicted response to the three SOAs. Specifically, we examined whether these areas showed increased response with longer (weaker) masking intervals. All four regions showed a clear hemodynamic time course with curves that peaked 4.5 to 7.5 sec after presentation of stimuli (Figure 2). Of these, the ventral LO region ($t = 2.40; \text{df} = 1,8; p < .04$) and, to a lesser extent, the dorsal LO cortex ($t = 1.92; \text{df} = 1,8; p < .09$), showed the largest response with the longest SOA and the smallest response with the shortest SOA.

Data-driven Approach

In a separate analysis, we identified regions on the basis of a difference map in which all SOAs were contrasted with rest. In this way, six regions were identified that were activated by the masking stimuli regardless of their sensitivity to SOAs (see Table 2). These are shown in Figure 3 and included the inferior parietal, anterior cingulate, precentral, insula, thalamic, and occipital regions. Some of these areas of activations were expected on the basis of the visual nature of the task (inferior parietal, thalamus, and occipital regions) or the manual response (precentral).

Time-course analyses were conducted with each of these areas and shown in Figure 4. The predicted effects of increased activity with weaker masking were seen with the thalamus (SOA 3 – SOA 1, $t = 1.96; \text{df} = 1,8; p < .09$), inferior parietal ($t = 2.90; \text{df} = 1,8; p < .022$), and anterior cingulate ($t = 2.52; \text{df} = 1,8; p < .04$). Based on its anatomy (Figure 3), it appears that the activation in the thalamus was primarily localized to the pulvinar.

DISCUSSION

This study investigated the neural bases of backward masking. We used simple stimuli, and importantly, kept the duration of the target and mask constant (34 and 68 msec, respectively) to generate a masking effect that varied predictably with SOA. The goal of this study was to systematically manipulate the effectiveness of the

Table 1. Coordinates for A Priori Regions of Interest

<table>
<thead>
<tr>
<th>Region of Interest</th>
<th>Hemisphere</th>
<th>Volume (mm$^3$)</th>
<th>x, y, z</th>
<th>BA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Retinotopic areas</td>
<td>Bilateral</td>
<td>22,013</td>
<td>−4, 89, 2</td>
<td>17 and 18</td>
</tr>
<tr>
<td>MT+</td>
<td>Right</td>
<td>1450</td>
<td>−43, 68, 0</td>
<td>19</td>
</tr>
<tr>
<td>MT+</td>
<td>Left</td>
<td>1156</td>
<td>39, 74, 0</td>
<td>19</td>
</tr>
<tr>
<td>Dorsal LO</td>
<td>Right</td>
<td>2584</td>
<td>−41, 80, 5</td>
<td>18</td>
</tr>
<tr>
<td>Dorsal LO</td>
<td>Left</td>
<td>1123</td>
<td>40, 79, 4</td>
<td>18</td>
</tr>
<tr>
<td>Ventral LO</td>
<td>Right</td>
<td>2888</td>
<td>−40, 64, −9</td>
<td>37 and 19</td>
</tr>
<tr>
<td>Ventral LO</td>
<td>Left</td>
<td>1397</td>
<td>31, 72, −6</td>
<td>19</td>
</tr>
</tbody>
</table>

x, y, z = Talairach coordinates: x (right–left), Y (anterior–posterior), z (inferior–superior); BA = Brodmann’s areas.

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Figure 1. Regions defined by the a priori method using three types of scans to localize visual processing. The scan for retinotopic areas identified a region along the calcarine fissure, the hMT+ procedure identified bilateral regions in the LO lobe, and the LO scan identified two separate areas consistent with previous reports of dorsal and ventral components of the LO.
mask. It would have been possible to influence the degree of masking through other methods such as altering the type or contrast of the mask, but our intention was to keep the stimuli constant and to manipulate only SOA. Regions were identified through two different approaches: (1) an a priori approach using reference scans designed to activate known visual processing areas, and (2) a data-driven approach that identified regions activated during presentation of target and mask.

The procedures in this project isolated three types of visual processing areas. The first, identified with the a priori approach, were regions that subserve key stages of visual processing (including object and movement recognition). The second type responded to the presentation of briefly presented visual stimuli, regardless of the SOA. The third type was a subset of the first two and represented areas that were sensitive to the interval between the target and the mask. Hence, these are the areas that respond to parametric changes in the visibility of the target on the basis of SOA. It is this third type of region that the current study sought to identify because these regions appear to reflect the substrates of the backward masking effect.

Among the regions identified with the a priori approach, the ventral LO region showed a consistent relationship to the strength of the masking effects. That is, the LO cortex was less active when stimuli were less visible. We did not observe such a pattern in the earlier visual cortex, making the LO cortex the likely source of the neural masking effect. A simple model can explain why masking effects arose in the LO cortex but not in the earlier visual cortex. Many neurons in the visual cortex respond less to a preferred stimulus when a nonpreferred and a preferred stimulus are presented simultaneously within their receptive fields (e.g., Moran & Desimone, 1985). This phenomenon can account for our results in regions where: (1) neurons exist that prefer the target over the mask and (2) neurons integrate information over an extended temporal window leading our short SOAs to reduce neural response in a similar way to simultaneous presentation or preferred and nonpreferred stimuli. Our results suggest that the LO cortex is the first location in the cortex where both
these assumptions hold. That is, it contains large numbers of neurons that are sufficiently specialized to respond differentially to our (very similar) target versus mask and that integrate information over at least the 30–60 msec of our shorter delays.

Our results allow us to localize the neural correlates of interactions between stimulus and mask. Prior work (Bar et al., 2001; Grill-Spector et al., 2000) varied the strength of the stimulus while keeping the mask and SOA constant. Stronger stimuli produced greater activity in the LO cortex and better recognition performance, suggesting that the LO cortex plays an important role in object recognition. However, because the mask parameters (and possibly the strength of masking itself) were held con-

<table>
<thead>
<tr>
<th>Region of Interest</th>
<th>Hemisphere</th>
<th>Volume (mm$^3$)</th>
<th>$x$, $y$, $z$</th>
<th>BA</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inferior parietal</td>
<td>Left</td>
<td>13,074</td>
<td>43, 30, 37</td>
<td>40</td>
</tr>
<tr>
<td>Inferior parietal</td>
<td>Right</td>
<td>6741</td>
<td>−47, 30, 32</td>
<td>40 (2)</td>
</tr>
<tr>
<td>Anterior cingulate</td>
<td>Bilateral</td>
<td>3140</td>
<td>1, −3, 35</td>
<td>32 and 24</td>
</tr>
<tr>
<td>Insular cortex</td>
<td>Left</td>
<td>7002</td>
<td>38, −4, −2</td>
<td>13</td>
</tr>
<tr>
<td>Insular cortex</td>
<td>Right</td>
<td>3850</td>
<td>−37, −11, −3</td>
<td>13 (22)</td>
</tr>
<tr>
<td>Precentral gyrus</td>
<td>Right</td>
<td>1208</td>
<td>−53, −4, 12</td>
<td>6</td>
</tr>
<tr>
<td>Thalamus (subcortical)</td>
<td>Bilateral</td>
<td>5090</td>
<td>4, 25, −1</td>
<td>NA</td>
</tr>
</tbody>
</table>

$x$, $y$, $z = $ Talairach coordinates: $x$ (right–left), $y$ (anterior–posterior), $z$ (inferior–superior); BA = Brodmann’s areas.

Figure 3. Regions identified based on a difference map in which all SOAs were contrasted with rest, including the inferior parietal, anterior cingulate, precentral, insula, thalamic, and occipital regions.
stant, changes in activity could not be attributed to changes in masking effects, and the studies could not reach conclusions about the basis of masking. Because only SOA was varied in our study, we can attribute observed changes in activity to interactions between stimulus and mask. Our data show that this interaction occurs in area LO.

Several regions identified with the data-driven approach also showed a predicted relationship to SOA, including the inferior parietal, thalamus (particularly the pulvinar), and anterior cingulate. These regions may be more closely associated with reentrant processing that provides informational feedback to early visual processing areas and allows stimulus recognition (Di Lollo et al., 2000; Enns & Di Lollo, 2000). Along these lines, it can be argued that some of these regions identified with the data-driven approach may be involved with differences in the allocation of attention between conditions. It is possible that as stimuli became more recognizable, they drew more attention, and this would naturally occur more often in the long SOA conditions. Among the active regions we observed that may play a role in attentional allocation, the inferior parietal cortex is one of the classical areas in the attention shifting network that has been identified through lesion, single-unit, and imaging studies (Yantis et al., 2002; Corbetta, Miezin, Shulman, & Petersen, 1993). The anterior cingulate has also been implicated in allocation of attention through modulatory effects on the effective connectivity among brain regions (Peterson et al., 1999), and also as a source for error detection or in resolution of conflict in task performance (Carter et al., 1998). The pulvinar is viewed as a component of the ascending visual stream, receiving afferent input from the lateral and medial geniculate nuclei, and projecting to the striate cortex, temporal lobe, and posterior parietal cortex. There also exists a tectothalamic pathway which appears to transmit visual information from the superior colliculi to the extrastriate visual cortex (Harting, Diamond, & Hall, 1973). Lesions to the pulvinar have been observed to result in impaired redirection of attention to visual stimuli (Danziger, Ward, Owen, & Rafal, 2001; Michael, Boucart, Degrefe, & Godefroy, 2001), a finding supported by electrophysiological studies that suggest that pulvinar neurons show attentional modulations in firing rate (Bender & Youakim, 2001).

In general, the a priori approach may implicate regions of early and middle stages of visual processing involved

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**Figure 4.** Time-series plots for activation in each region identified by the data-driven method. The last point is the first scan of the following trial. The time courses were examined separately for each SOA to determine which areas showed increased response to the longer (weaker) masking intervals. The longest SOA (102 msec) is indicated by the dotted line, and the shortest SOA (34 msec) is indicated by the solid line.
with masking, in particular, the LO region. In contrast, the regions defined by the data-driven approach may result from higher-level attentional processes linked to a degree of stimulus ambiguity. This study, like many others, cannot determine whether the pattern of activation in the LO region across SOAs is the result of feedback from higher-level attentional centers. Electrophysiological procedures that have much greater temporal resolution than fMRI would be needed to distinguish the timing of activation patterns across regions.

Although the current study sheds light on the neural substrates of visual masking, future studies would benefit from increased sample size and an increased range in performance with increasing SOA; ideally, performance would range from chance (25%) to near 100% accuracy. In addition, subsequent studies may wish to equate subjects on unmasked performance. In studies of visual masking, especially those that use clinical samples, it is helpful to control for variance across subjects in basic input of stimuli by using psychophysical procedures to equate subjects on initial (unmasked) performance (Green, Nuechterlein, & Breitmeyer, 2002). This study intentionally selected very simple stimuli, so it is not known if the same brain regions would be activated with more complex targets.

This study is part of a larger program of research that is dedicated to understanding early visual processing deficits in schizophrenia (Keri, Kelemen, Benedek, & Janka, 2001; Green, Nuechterlein, Breitmeyer, & Mintz, 1999; Green, Nuechterlein, Breitmeyer, et al., 1997; Miller, Saccuzzo, & Braff, 1979). A first step towards understanding the physiological basis of masking deficits in schizophrenic patients is to identify the areas in the brain that show regional activation that correlates with the strength of the mask. This initial study used two separate methods to identify several areas that show such a pattern. Specifically, the LO, inferior parietal, pulvinar, and anterior cingulate appear to be linked to the perceptibility of the target. We speculate that LO activity reflects basic visual analysis of the target, whereas the other regions reflect allocation of attention. This distinction between visual processing areas and areas that are involved with attentional (or reentrant) processes may be helpful in identifying the nature of visual processing abnormalities in clinical conditions that have abnormalities in visual processing, such as schizophrenia.

**METHODS**

**Subjects**

A total of 13 subjects were recruited from approved flyers placed around the UCLA Medical Center and the Veterans Administration Greater Los Angeles Healthcare System. All of the subjects read and signed informed consent documents that were approved by the Institutional Review Boards of both institutions. Some subjects reported difficulty seeing the stimuli through the goggles in the scanner. Following scanning, the performance data from all subjects were reviewed for validity. Four subjects were dropped from further analysis due to invalid behavioral data (i.e., performance that was close to chance and did not improve with increasing intervals between target and mask). The remaining 9 subjects included 4 men and 5 women, 8 were right handed, their mean age was 31.0 (range = 25–41) years and their mean educational level was 14.0 (range = 12–16) years.

**Stimuli for Masking Procedure**

The target was a circle with a gap in one of four locations (top, bottom, left, and right) and the mask consisted of 12 overlapping circles that covered the area of the target (see Figure 5). Each trial lasted 15 sec. First, a blinking fixation point was presented for 4.5 sec. The target was presented for 34 msec and the mask was presented for 68 msec at one of three possible SOAs: 34, 68, or 102 msec.

Stimuli were presented with an LCD-based video system (Resonance Technology, Northridge, CA). The images ultimately were composited as interlaced NTSC.

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**Figure 5.** Stimuli and timing for the masking task. The target was a circle with a gap in one of four locations (top, bottom, left, and right) and the mask consisted of overlapping circles that covered the area of the target. Each trial lasted 15 sec (5 scans). A blinking fixation point was presented for 4.5 sec before each target. The target was presented for 34 msec and the mask was presented for 68 msec at one of three possible SOAs: 34, 68, or 102 msec.
video, which limited the minimum display time and update to 34 msec (two screen sweeps). The optics of this device produce a screen image approximately 25° across. The displays were controlled using MacStim (White Ant Software).

**Stimuli for the Scans to Localize Visual Processing**

To identify regions of interest according to the a priori approach, three procedures were used to generate activity in regions involved in distinct aspects of visual processing.

**Retinotopic Areas**

Early and middle visual areas were identified using a rotating wedge of contrast reversing checkerboard; this stimulus has been used previously to identify retinotopically organized brain regions (Engel, Glover, & Wandell, 1997; DeYoe et al., 1996; Sereno et al., 1995; Engel, Rumelhart, et al., 1994). Subjects fixated at the center of the display as the wedge completed 4 revolutions at a rate of one every 48 sec.

**Object Processing**

Late visual areas involved in object processing (referred to in the text as “LO”) were identified by contrasting the cortical responses to images of three-dimensional objects to those elicited by images containing texture patterns. This is now a standard method of measuring object areas in the LO cortex (Malach et al., 1995). Comparing the responses to these conditions at high threshold can also reveal object-related areas in the lingual/fusiform region (Martin, Wiggs, Ungerleider, & Haxby, 1996). Subjects viewed 36-sec blocks of images in alternation with 36-sec blocks of viewing a uniform gray field. Alternate image blocks contained either gray-scale objects or texture patterns.

**Human Area MT**

The human area MT region (referred to in the text as “hMT+”) is highly sensitive to visual motion and can be identified by comparing activity when subjects view moving rings to activity when subjects view stationary rings (Tootell et al., 1995). Because hMT+ has high motion sensitivity, but low contrast and luminance sensitivity, these maps were improved by displaying the rings at relatively low contrast and brightness levels. Subjects viewed 36-sec blocks of moving rings in alternation with 36-sec blocks of stationary rings.

**Functional MRI Procedures**

All scanning was carried out on a 3 Tesla General Electric (Waukesha, WI) scanner modified for echo-planar imaging (EPI) by Advanced NMR Systems, and located in the UCLA Ahmanson Lovelace Brain Mapping Center. Prior to each functional study, a high-resolution EPI axial T2-weighted series was obtained for each subject and used for anatomical reference (TR = 6000 msec, TE = 54 msec, flip angle 90°, 30 axial slices, FOV 20 cm). Functional imaging utilized a gradient-echo, EPI sequence sensitive to the BOLD signal (Kwong et al., 1992) acquiring 16 slices parallel to the AC–PC plane (TR = 3000 msec, TE = 42 msec, flip angle 80°, voxel size of 3.125 × 3.125 × 4.00 mm with a 1-mm gap). Backward masking data were collected in three separate 6-min scans, resulting in 360 images per subjects. The identical EPI sequence was used to acquire each of the three scans used to identify visual processing.

**Functional Image Analysis**

For each subject, 6 series of functional images were collected: 3 runs of backward masking and 3 scans for visual processing references (retinotopic areas, LO and hMT+). Each of these time series was processed with the same basic procedures. To combat potential motion artifacts, each BOLD image in a time series underwent a 3-D spatial registration (6-parameter rigid-body) to the middle data point in the time series (Jenkinson, Bannister, Brady, & Smith, 2002). Data were smoothed with a nonlinear algorithm designed to preserve image structure by only smoothing over voxels thought to be of the same tissue type (5 mm kernel) (Smith & Brady, 1997). Each dataset was subjected to a multiple regression analysis, using a prewhitening technique (Bullmore et al., 1996) to account for the intrinsic temporal autocorrelation of BOLD imaging (Zarahn, Aguirre, & D’Esposito, 1997). For each intracranial voxel, least-squares coefficients were generated independently reflecting each task condition (Woolrich, Ripley, Brady, & Smith, 2001). Statistical images, including percent signal change and Student’s t-statistic images, were created for all trials and each of the three SOAs contrasted with an implied baseline for each run of the backward masking task and for the LO and hMT+ reference scans. The scan of retinotopic areas used a somewhat different analysis procedure described elsewhere (Engel, Glover, et al., 1997).

To facilitate multisubject analysis, a common space brain was defined which approximated the average size, shape, and orientation of each subject’s higher-resolution T2-weighted image (Woods, Dapretto, Sicotte, Toga, & Mazziotta, 1999). Based on the parameters created from the higher-resolution image, statistical images created for each subject were normalized into this common space (12-parameter model). Higher-level multisubject analysis utilized a mixed-effects model (Behrens, Woolrich, & Smith, 2003) and provided t-images reflecting group activation patterns for each SOA of the backward masking task and for each of the scans used to localize visual processing.
processing. To make the results from this study comparable with others in the literature, the common space brain was normalized into a standard stereotactic space (Talairach & Tournoux, 1988) to report locations of active regions.

For the a priori analyses, the group activation maps for each of the scans to localize visual processing areas were thresholded on the basis of the magnitude (t = 3.0) and extent (cluster significance p < .05) of activation (Poline, Worsley, Evans, & Friston, 1997; Forman et al., 1995). The remaining activation clusters were constrained to anatomical regions associated with the primary or secondary cortex and orthogonal to one another. These analyses produced four anatomically and functionally distinct regions of interest (see Figure 1).

The search space for the data-driven analyses was reduced by masking the group statistical image for each SOA with an image reflecting activation on all trials versus rest. Statistic images were subsequently thresholded on the basis of the magnitude (t = 3.0) and extent (cluster significance p < .05) of activation (Poline et al., 1997; Forman et al., 1995). The spatially distinct clusters generated through this procedure were treated as functionally defined regions of interest.

The motion-corrected and smoothed time-series echo-planar data collected while subjects performed the backward masking paradigm were divided into 18-sec blocks corresponding to each trial (i.e., 15 sec for each trials plus the first 3-sec scan of the subsequent trial). Data from similar SOA trials were averaged together and normalized (at the voxel level) to express the percentage deviation from the mean time-series signal intensity. Regions of interest generated from the a priori and data-driven approaches were used to interrogate these average SOA time-course data. Within each region, voxels associated with the masking task were identified (showing a t > 2.0 on the all trials vs. rest contrast) and average time courses were constructed. For each subject, a subtraction score (SOA 1 – SOA 3) was created at the point of maximum deviation from the time-series mean. A t test was performed to determine whether that subtraction score was different from 0.

Behavioral Methods

Subjects viewed the stimuli in the scanner through goggles and responded with a four-way response pad held in their dominant hand. The buttons were arranged in a diamond shape so that each button corresponded to the gap in each possible target (e.g., a gap at the top indicated to press the top button). Eight trials were administered at each SOA in a randomized sequence in a run of 24 trials (6 min of scanning). Three different runs, each with a separate randomized sequence, were administered during a session. Hence, across the runs, each subject saw a total of 24 trials at each of the three SOAs. Accuracy of response was the dependent measure.

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The data reported in this experiment have been deposited in the FMRI Data Center (http://www.fmridc.org). The accession number is 2-2004-117BB.

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