Research Report

No Representation Without Awareness in the Lateral Occipital Cortex

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ABSTRACT—*Recent research has shown that four small dots presented in the vicinity of, but not adjacent to, a target stimulus can banish that stimulus from conscious awareness. It is thought that the mental representation of the masked stimulus is "erased" by the trailing quartet of dots. Using functional magnetic resonance adaptation, we show that there is no persisting neural representation of the successfully masked stimulus in lateral occipital cortex, a region that has been implicated in the processing of object structure. This finding rules out the alternative interpretation that a lingering neural representation is merely rendered inaccessible to consciousness, as is the fate, for example, of monocular information under conditions of binocular rivalry.*

When a visual stimulus interferes with the apprehension of a prior visual stimulus, the earlier stimulus is rendered consciously unavailable through a process termed visual masking (Breitmeyer, 1984). Visual masking is a popular tool in the study of visual perception because it allows the experimenter to limit the amount of visual information available to observers or to manipulate observers' awareness of a stimulus. Increasingly, however, masking has become an object of investigation in its own right, precisely for the same reasons. Masking appears to tap into aspects of the mental architecture that are closely tied to conscious awareness (Di Lollo, Enns, & Rensink, 2000), and it is capable of curtailing observers' awareness of a stimulus that was presumably processed at least to some extent (Dehaene et al., 1998). Earlier attempts to investigate masking at a neural level

produced some interesting results that revealed potential mechanisms by which a mask might obliterate a neural response to a masked stimulus via interruption (Kovacs, Vogels, & Orban, 1995) or competition (Keysers & Perrett, 2002). With the advent of neuroimaging techniques, the study of the neurophysiology of masking has been expanded to include investigations of masking phenomena in the human cortex (Bar et al., 2001; Dehaene et al., 1998; Green et al., 2005; Grill-Spector, Kushnir, Hendler, & Malach, 2000).

What is common to both studies of monkey physiology and neuroimaging approaches is that, typically, a pattern mask is used to limit visibility of the masked stimulus. In pattern masking, the mask is presented in the same spatial location as the to-be-masked stimulus. Given the retinotopic organization of early visual cortex (DeYoe et al., 1996), the neuronal response to the masking stimulus presumably occurs in largely the same population of neurons as the response to the masked stimulus, potentially leading to "retinotopic overwriting" (Breitmeyer, Ro, & Ogmen, 2004). In strong contrast to pattern masking stands the recently discovered object-substitution masking (OSM), in which four small dots, presented spatially surrounding, but not abutting, a to-be-identified stimulus, manage to mask that stimulus even though they are neither sufficiently close nor sufficiently large to overwrite it retinotopically. Di Lollo, Enns, and their colleagues have proposed that the masking dots and the masked target are in "competition for consciousness" under conditions of distributed attention (Di Lollo et al., 2000; Enns & Di Lollo, 1997), and that the mask "wins" if it trails the display by a sufficient duration, making it the only item in the observer's consciousness. They have furthermore suggested that the underlying (neural) representation of the masked item is erased as the now-dominating mask stimulus is substituted for it. Di Lollo, Enns, and their colleagues argue that although retinotopic overwriting is ruled out in this form of masking, the overwriting

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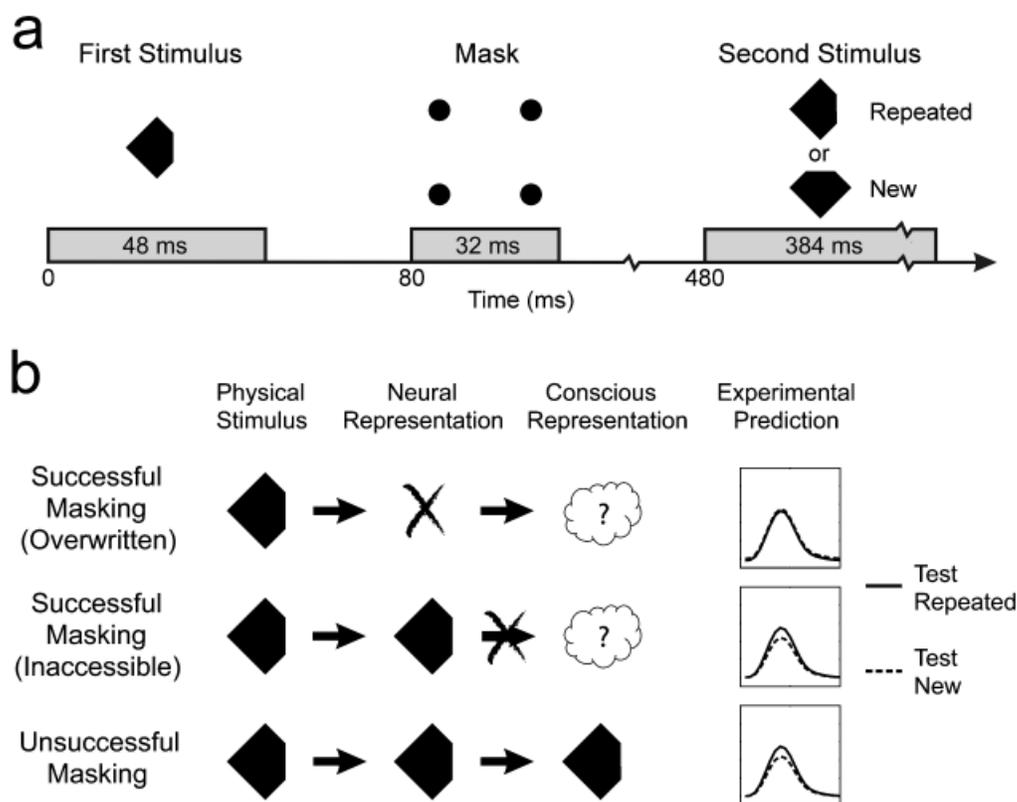
Fig. 1. Experimental design (a) and predictions (b). Each trial began with presentation of a notched diamond, which was followed by a four-dot mask and then a second notched diamond that either did or did not have the same orientation as the first. If masking was successful and the representation of the first stimulus was overwritten by the trailing mask, a repeated stimulus would not be expected to result in an attenuated hemodynamic response (relative to the response to a new stimulus). In contrast, if masking was successful and the mask rendered the neural representation of the first stimulus inaccessible to conscious inspection but otherwise intact, the response for repeated representations would be expected to be attenuated, as it would be on trials on which masking was unsuccessful.

occurs at the (high) level of object representations—a claim for which there is increasing evidence (e.g., Lleras & Moore, 2003).

Although the phenomenon of OSM now has ample support from behavioral studies, the conjecture that the neural representation of the masked target is erased by substitution lacks empirical support. Indeed, an alternative account is that OSM simply bars the masked target from conscious awareness and the underlying neural representation remains intact at some level of the visual system. It is known, for example, that information at a very high spatial frequency is represented in early visual cortex yet lacks access to conscious awareness (He & MacLeod, 2001), as does monocular information in binocular rivalry (Blake, 1997). OSM might constitute another example of such a dissociation between neural representation and awareness.

To test between these alternatives, we employed functional magnetic resonance adaptation (fMR-A), which permits inferences about the nature of the underlying neural representation of a given stimulus. The logic of fMR-A is based on the observation that the sequential presentation of two stimuli that are functionally equivalent along some critical dimension evokes a hemodynamic response (HDR) that is attenuated compared with

that evoked by two stimuli that are not functionally equivalent along that dimension (Grill-Spector & Malach, 2001). Figure 1a shows a schematic illustration of a single trial in the experiment. If the first presentation of a stimulus is successfully masked and its neural representation is overwritten, that stimulus should no longer function as equivalent to a physically identical second stimulus, so this second stimulus should produce no evidence of HDR attenuation. In other words, it should not matter whether the physical stimulus presented after the mask is repeated or new, because this distinction is rendered moot by successful masking. The distinction should be relevant only for trials on which masking fails (and therefore no overwriting occurs).

Alternatively, if the first stimulus is successfully masked (perceptually) but its neural representation is not overwritten (i.e., the neural representation remains intact but is barred from consciousness), the HDR should be attenuated when the two stimuli are identical, compared with when they are different. In this case, the distinction between a repeated versus new second stimulus remains relevant even when masking is successful. What determines the presence or absence of attenuation is the underlying neural representation, which is dissociable from

conscious awareness of the stimulus in this alternative scenario. These competing scenarios are summarized in Figure 1b. As illustrated in the figure, two different variables were crossed in the experiment: the success of OSM and the relation between the first and second stimuli (repeated vs. new second stimulus). The former variable was created by sorting trials post hoc into error trials (on which masking presumably succeeded) and correct trials (on which OSM failed). A study by Grill-Spector et al. (2000) suggests that it may not be appropriate to compare HDRs directly across successful- and unsuccessful-masking conditions, because responses may be lower overall in the former condition. However, this concern does not apply if one compares responses to repeated versus new stimuli within each of the two masking conditions separately.

In our study, we concentrated on lateral occipital cortex (LO) as our region of interest (ROI). This focus was motivated in part by claims that OSM is a high-level phenomenon that occurs at the level of object description (Enns & Di Lollo, 1997; Lleras & Moore, 2003) and by evidence that clearly implicates LO in object processing (Grill-Spector, 2003; Kourtzi & Kanwisher, 2001; Rauschenberger, Liu, Slotnick, & Yantis, 2006). In addition, we selected LO because of reports that early visual areas (V1, V2) appear to be insensitive to masking manipulations (Grill-Spector et al., 2000).

METHOD

Seven volunteers (5 male, 2 female), each of whom gave written consent, participated in the experiment. The study was approved by the Institutional Review Board of the Boston University Medical Campus. Each subject participated in three functional imaging runs of the OSM task, as well as two localizer scans to identify LO and the regions stimulated in V1. Subjects were scanned on a 3-T magnetic resonance imaging (MRI) scanner at the Boston University Center for Biomedical Imaging. Functional imaging was conducted using an echo-planar imaging sequence (repetition time = 2,500 ms, echo time = 30 ms, flip angle = 90°, field of view = 192 mm, matrix size = 64 × 64). Scanned volumes were 30 axial slices (in-plane resolution of 1.8 × 1.8 mm, 2.5 mm thick; interslice gap of 1 mm). Functional runs in the main experiment comprised 264 functional acquisitions (660 s). Localizer scans had shorter scan durations (200 and 132 acquisitions, respectively) and a shorter repetition time (2 s). The first four images of each functional run were discarded to allow for T1 equalization. High-resolution T1-weighted structural scans (1 × 1 × 1 mm) were also acquired for each subject to verify the anatomical locations of selected ROIs.

Stimuli were generated on a computer and presented via MATLAB (The MathWorks, Natick, MA) utilizing functions provided in the Psychophysics Toolbox (Brainard, 1997). Stimuli were displayed on a translucent screen by means of an LCD projector. Subjects viewed the screen through a mirror mounted onto the head coil, with a field of view of 20° of visual angle.

LO was localized using a block design. Subjects passively viewed images of faces, natural scenes, common objects, and scrambled images. Images were presented at a rate of 2 Hz in 24-s blocks. Blocks of images were shown consecutively and repeated four times during the functional imaging run. To identify LO, we generated a model of the expected response of LO using previously reported properties of LO responses to the four classes of stimuli (Grill-Spector, 2003). LO was defined by voxels activated at a p-value threshold of less than 10^{-4} (uncorrected).

Regions in V1 corresponding to the four spatial locations stimulated in the main experiment (upper left, upper right, lower left, and lower right) were localized using a block design. The eccentricity of the four spatial locations was determined individually for each subject on the basis of the subject's performance in the OSM task (described next). Checkerboard patterns flickering at a rate of 4 Hz were shown at each of the spatial locations for 4 s, and each of these locations was stimulated 16 times during the localizer scan. Voxels activated at a significance level of $p < 10^{-4}$ (uncorrected) were selected.

In the OSM task, subjects viewed a rapid succession of pairs of notched diamond stimuli, a new trial occurring every 2,500 ms. On each trial, the first notched diamond in the pair was presented for 48 ms and followed, 32 ms later, by the mask (four dots surrounding the stimulus), which was presented for 32 ms. In turn, the mask was followed, 368 ms later, by a second notched diamond, which was presented for 384 ms (see Fig. 1a). On each trial, the orientation of the second stimulus was randomly determined to be either identical to or different from the orientation of the first stimulus. After viewing the second stimulus, subjects were instructed to make a key-press response indicating the orientation of the first stimulus.

Stimuli were presented in one of four randomly selected spatial locations on each trial, in order to introduce the spatial ambiguity considered necessary for OSM (Enns & Di Lollo, 1997). The spatial uncertainty also ensured that subjects' attention was evenly distributed across the display, ruling out any attentional confounds. The four target positions were located in the four corners of the screen and were offset from a central fixation point by a fixed distance. The eccentricity of the four spatial positions was adjusted individually for each subject so as to achieve a level of performance of approximately 65% correct. In the actual experiment, subjects' performance ranged from 51% to 80% correct, with a group mean of 70% correct (chance = 25%). Each subject performed 771 trials (3 imaging runs × 257 trials per run). Subjects trained on the task for roughly 30 min on a desktop computer prior to the functional imaging experiment. Subjects received additional training in the scanner during the anatomical scan (approximately 8 min).

Data analysis was performed using Brainvoyager QX (Brain Innovation, Maastricht, The Netherlands). Data preprocessing consisted of motion correction and linear trend removal. For the
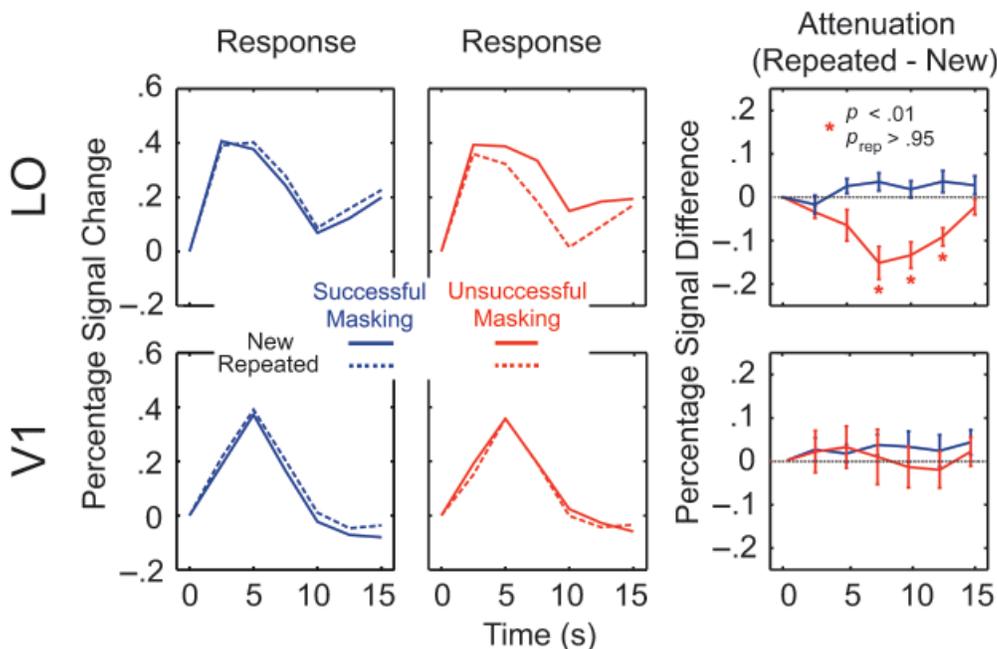
Fig. 2. Functional magnetic resonance imaging results for lateral occipital cortex (LO; top) and V1 (bottom). The graphs on the left show the time course of response to repeated and new presentations, respectively, for trials on which masking was successful. The middle graphs show the corresponding results for unsuccessful-masking trials. The graphs on the right present the magnitude of response attenuation for repeated presentations (response for repeated presentations minus response for new presentations) on successful- and unsuccessful-masking trials, respectively. Error bars denote ± 1 *SEM*. For inferential statistics, see Table 1.

rapid-event-related runs, the data were deconvolved to extract the HDR for each of the ROIs (left hemifield LO, right hemifield LO, and the regions stimulated in the upper right, upper left, lower right, and lower left visual fields of V1).

RESULTS

The results for LO are shown in the top row of Figure 2 (see also Table 1). In the successful-masking condition, the important thing to note is the absence of HDR attenuation for the repeated condition relative to the new condition. This outcome strongly suggests that the neural representation of the first stimulus was either erased or significantly altered by the mask—so that it was no longer functionally equivalent to the representation of the

physically identical second stimulus—rather than merely barred from awareness. By comparison, we did observe the typical attenuation on repeated trials, relative to new trials, in the unsuccessful-masking condition; thus, the two successive stimuli were treated as functionally equivalent on trials on which masking did not occur and therefore did not affect the representation of the first (i.e., potentially masked) stimulus. To isolate this effect, we plotted the magnitude of attenuation (i.e., the response on repeated trials minus the response on new trials) for successful and unsuccessful masking, respectively (Fig. 2, right). As the plot shows, no significant attenuation was present when masking was successful. In contrast, significant attenuation was observed for trials on which masking was unsuccessful, and this attenuation occurred during the period

TABLE 1

Inferential Statistics for the Attenuation Results Shown in Figure 2

	Time point (seconds)					
Region	2.5	5.0	7.5	10.0	12.5	15.0
Lateral occipital cortex: successful masking	0.82	−1.57	−1.80	−0.98	−1.51	−1.36
Lateral occipital cortex: unsuccessful masking	2.57	1.86	4.16*	4.59**	4.59**	1.29
V1: successful masking	−1.12	−0.92	−1.75	−1.03	−0.72	−1.66
V1: unsuccessful masking	0.90	−0.02	0.03	0.58	0.41	−0.82

Note. All t tests are one-tailed; $df = 13$ for lateral occipital cortex and 6 for V1. The p_{rep} statistic is the probability of obtaining a result of the same sign (see Killeen, 2005).
*$p = .001$, $p_{rep} = .99$. **$p = .0003$, $p_{rep} = .99$.

of time when other fMR-A studies have found that the HDR normally peaks and recovers (Kourtzi & Kanwisher, 2001; Rauschenberger et al., 2006). No corresponding effects were observed in V1 (Fig. 2, bottom row; Table 1).

DISCUSSION

These results are striking because, contrary to the pattern masks typically employed in neurophysiological studies of masking, the four-dot mask used in the present experiment is spatially separated from the masked stimulus, and the two are represented in retinotopically distinct loci. Retinotopic overwriting or interference is therefore unlikely. Yet the four-dot mask is still effective in significantly altering the neural representation of the masked stimulus, which does indeed appear to be overwritten, as proposed by accounts of OSM. The most explicit of these accounts suggests that OSM is instantiated through feedback projections to V1 (Di Lollo et al., 2000). However, we found no evidence of any effect of the mask in early visual areas (Fig. 2, bottom row), whereas we observed masking effects as "late" as LO. Although our null results in early visual areas do not allow us to generate strong recommendations for theories of OSM, it is possible that the locus of object substitution in the cortex needs to be adjusted slightly upward along the pathway of visual information processing. Such a readjustment would make sense in any case because the phenomenon is considered to be fairly high level and is frequently situated at the level of object descriptions.

Our results do not rule out the possibility that neuronal activation precipitated by the eventually masked stimulus lingers elsewhere in the brain, despite successful masking and successful substitution of the new neural representation in LO. For example, priming effects at a postperceptual level of processing may be observed in the face of a loss of the neural representations at a perceptual level of processing. Using pattern masks, Dehaene et al. (1998), for instance, found neurophysiological evidence of priming in human subjects who lacked conscious access to the prime. This finding does not contradict our results, if one assumes that awareness is supported by perceptual representations and that whatever representations drive priming are dissociable from these perceptual representations and do not contribute to awareness.

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