

Unconscious Processing of Unattended Features in Human Visual Cortex

Tatiana Aloï Emmanouil¹, Philip Burton², and Tony Ro¹

Abstract

■ Unconscious processing has been convincingly demonstrated for task-relevant feature dimensions. However, it is possible that the visual system is capable of more complex unconscious operations, extracting visual features even when they are unattended and task irrelevant. In the current study, we addressed this question by measuring unconscious priming using a task in which human participants attended to a target object's shape while ignoring its color. We measured both behavioral priming effects and priming-related fMRI activations from primes that were unconsciously pre-

sented using metacontrast masking. The results showed faster RTs and decreases in fMRI activation only when the primes were identical to the targets, indicating that primes were processed both in the attended shape and the unattended color dimensions. Reductions in activation were observed in early visual areas, including primary visual cortex, as well as in feature-responsive areas for shape and color. These results indicate that multiple features can be unconsciously encoded and possibly bound using the same visual networks activated by consciously perceived images. ■

INTRODUCTION

In most circumstances, we are exposed to large amounts of visual information, only a small fraction of which reaches our consciousness. However, several studies have shown that much of the information that does not reach consciousness can nevertheless be processed unconsciously, including basic visual properties, such as brightness, color, and shape (Persuh & Ro, 2012; Ro, Singhal, Breitmeyer, & Garcia, 2009; Breitmeyer, Ro, & Singhal, 2004; Klotz & Wolff, 1995), as well as semantic information (Abrams, Klinger, & Greenwald, 2002; Dehaene et al., 1998; Luck, Vogel, & Shapiro, 1996). Although it is now widely accepted that the visual system can process some information unconsciously, it remains unclear whether entire objects are unconsciously processed, including the unattended dimensions. We therefore investigated whether unconscious processing occurs not only for features that are relevant but also for those that are irrelevant for behavior.

Unconscious processing of individual features is often shown using an unconscious priming paradigm in which masked primes are followed by visible targets. In this design, primes that are associated with the same response as the target (congruent primes) produce faster RTs than primes of the opposite response (incongruent primes). For example, Klotz and Wolff (1995) demonstrated unconscious processing of shape by showing faster RTs for square and diamond targets preceded by unconscious same-shape primes. Additionally, Schmidt (2002) found faster pointing movements to a color target when it fol-

lowed the presentation of congruent color primes. In our experiment, we used an unconscious priming design in which primes and masks varied in both shape and color. Importantly, participants were asked to respond only to the shape of the target and to ignore the color. On the basis of several studies that have shown extensive unconscious processing of complex information (Dijksterhuis & Nordgren, 2006), we hypothesized that priming would occur not only for the task-relevant shape but also for the task-irrelevant color dimension.

In addition, we investigated unconscious shape and color priming at the neural level using fMRI. Previous fMRI studies have shown reduced neural activations associated with behavioral priming (Buckner et al., 1998). This “repetition suppression” is related to a general property of neurons to adapt to objects repeated over time (Grill-Spector et al., 1999; Miller & Desimone, 1994) and occurs for both consciously and unconsciously presented stimuli (Henson, 2003). Several fMRI studies have investigated unconscious priming of words (Dehaene et al., 2001), numbers (Naccache & Dehaene, 2001), and common objects (Eddy, Schnyer, Schmid, & Holcomb, 2007). However, no studies have examined unconscious priming of simple visual features, such as shape and color, in specific brain areas that process these features, such as the shape-selective lateral occipital complex (LOC) and the color-selective fusiform gyrus (FG).

In the current study, we investigated unconscious priming for shape and color within areas that selectively respond to these features, as well as within retinotopically defined areas of the visual cortex. We predicted that repetition suppression would be measured for both the

¹The City University of New York, ²University of Minnesota

task-relevant shape and task-irrelevant color in the LOC and FG regions of visual cortex, respectively. Using a whole-brain analysis, we also evaluated the effects of repetition priming in areas beyond the visual cortex.

Previous studies have shown that the behavioral and neural effects of priming are modulated by attention and appear absent or reduced for unattended stimuli, whether consciously or unconsciously presented (Henson & Mouchlianitis, 2007; Lachter, Forster, & Ruthruff, 2004; Murray & Wojciulik, 2004; Naccache, Blandin, & Dehaene, 2002). In our study, because the primes were always presented at fixation and thus always appeared at an attended location, the amount of spatial attention to the stimuli remained constant. However, we manipulated attention to features by asking participants to respond to shape but not color. According to evidence that unconscious processing is influenced by task and attention, we might expect little or no priming for the unattended color feature (Kiefer, Adams, & Zovko, 2012; Tapia, Breitmeyer, & Shooner, 2010).

However, a large literature on consciously perceived objects shows that, given sufficient attentional resources, features of an object are selected together, regardless of attention (O’Craven, Downing, & Kanwisher, 1999). Furthermore, integrated features form “object” or “event” files, which result in expedited processing when presentations of the same object are repeated, as well as RT costs for partially or entirely different objects (Hommel, 2004; Kahneman, Treisman, & Gibbs, 1992). We therefore reasoned that if unconscious processing is similar to conscious perception, the color of attended shapes would be automatically processed regardless of attention, especially because both the attended and the unattended features belong to the same object (Egly, Driver, & Rafal, 1994; Duncan, 1984). Thus, we should find that responses to targets that share both the attended and unattended features produce more priming and repetition suppression than targets that have one or both incongruent features.

To test for unconscious processing of attended and unattended features, we orthogonally manipulated the shapes and colors of primes and masks/targets such that the primes could be identical in shape and color to the masks/targets or one or both features could differ. We therefore assessed whether priming occurs only for identical primes and costs incur for partially or entirely different primes, which would suggest that both the shape and color were selected together and possibly bound in the absence of awareness.

METHODS

Participants

Eight participants (24–29 years, 4 men) gave informed consent and participated in the experiment for monetary compensation. All had normal or corrected-to-normal vision. The data from one male participant were excluded

from the analysis because of large amounts of head motion. Also, the fMRI data from the second run of another participant was excluded because of signal artifacts.¹

Stimuli and Design

The experiment was run using E-Prime software (Psychology Tools, Inc., Pittsburgh, PA), and stimuli were rear-projected onto a screen that was centered behind the MRI scanner. The stimuli were primes and masks subtending 0.7° and 1.5° of visual angle from edge to edge, respectively. The primes and targets, which also served as the masks, were blue or green squares or diamonds (Figure 1) presented on a black background. A cross subtending 0.6° of visual angle served as the fixation point and was always visible except when the primes and masks were presented. We used a metacontrast masking paradigm in which the mask overlaps only with the contours of the prime and also serves as the target (Ro et al., 2009; Breitmeyer et al., 2004; Schmidt, 2002; Klotz & Wolff, 1995). This method reduces interference from an irrelevant mask and is known to produce strong masking effects while also leaving a large degree of prime processing intact (Fehrer & Raab, 1962).

The prime stimulus was presented for 16.7 msec and was immediately followed by a mask that was presented for 50 msec. The trial ended 2 sec from the onset of the prime. To measure the hemodynamic response in a fast event-related design, the interval between trials was jittered between 2, 4, 6, and 8 sec, with each interval used an equal number of times. Shape and color congruency were varied orthogonally resulting in four conditions: (1) shape

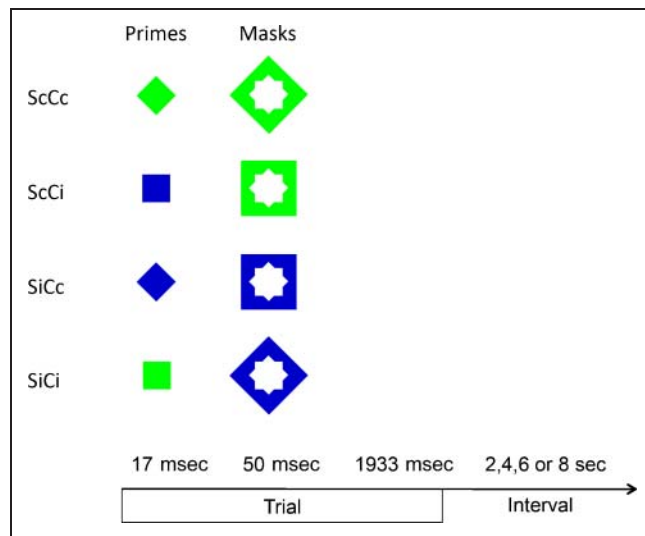


Figure 1. Stimuli and design. The primes and masks varied orthogonally along two features: shape (square or diamond) and color (blue or green). There were thus four conditions in which primes and masks were (1) congruent in both shape and color (ScCc), (2) congruent in shape but incongruent in color (ScCi), (3) incongruent in shape but congruent in color (SiCc), and (4) incongruent in both shape and color (SiCi). The timeline for a trial is shown at the bottom of the figure.

congruent/color congruent (ScCc), (2) shape congruent/color incongruent (ScCi), (3) shape incongruent/color congruent (SiCc), and (4) shape incongruent/color incongruent (SiCi).

In the main part of the experiment, participants were asked to identify only the shape of the mask by pressing keys on an MRI-compatible button box using their right hand. Note that the color of the mask was unattended insofar as it was task irrelevant and that participants were never instructed to attend or process it. In the prime identification task, which was always conducted after the mask shape identification task, visual awareness of the primes was objectively measured by having participants report the shape of the prime in a two-alternative forced-choice (2AFC) task.

fMRI Procedures

Participants took part in a scanning session that lasted approximately 2 hr. For each participant, we obtained a structural scan, three localizer scans, and two experimental scans. After these six scans, participants performed the two-alternative forced-choice prime identification task while remaining in the scanner. For four of the participants, two additional structural scans were acquired while the prime identification task was being performed.

The three localizer scans, each lasting 492 sec, were acquired to delineate the borders of early visual cortex and color- and shape-sensitive regions. The localizers were always acquired in a fixed order. First, a retinotopic scan was acquired during which participants viewed alternating blocks of horizontally and vertically oriented flickering checkerboard wedges (10 Hz). Next, we localized color-sensitive regions in each participant by having them view alternating blocks of colored and achromatic flickering checkerboards (20 Hz). Following the retinotopy and color localizer scans, participants viewed blocks of object drawings and scrambled images to localize shape-sensitive regions of the brain. All three localizers consisted of 10 blocks of 12 sec, each preceded by a 12-sec fixation period. The blocks in the retinotopic scan alternated between horizontally and vertically oriented checkerboards and the blocks in the color localizer alternated between colored and achromatic full-field checkerboards, whereas the object and scrambled image blocks in the LOC localizer were shown in random order. The scans ended with a 12-sec fixation period to allow the hemodynamic response to return to baseline.

Following the localizers, participants completed two main experimental scans lasting 560 sec. The participants completed 40 trials for each condition (ScCc, ScCi, SiCc, and SiCi) in random order, for a total of 160 trials across the two scans. The prime identification task was performed in the scanner immediately after the experimental scans. The stimuli in the prime identification task were identical to those in the experimental scans, but the participants were instructed to identify the shape of

the prime instead of the mask. As in the main experimental scans, 160 trials were shown (40 trials of each condition) in random order. No fMRI data were collected during the prime identification task.

The fMRI data were collected at the Baylor College of Medicine's Human Neuroimaging Laboratory. Each participant was scanned in one of two identical 3-T Siemens Allegra (Munich, Germany) head-only scanners. The structural images were acquired using a magnetization-prepared 180° radio frequency pulses and rapid gradient-echo (MPRAGE) sequence with 1-mm-thick axial slices and an in-plane resolution of 0.5 × 0.5 mm (field of view = 240 mm, repetition time = 1200 msec, echo time = 2.93 msec). Functional images were acquired using an EPI sequence (echo time = 40 msec, flip angle = 90°) sensitive to the BOLD signal. Twenty-six contiguous whole-brain axial slices, with a slice thickness of 4 mm, were collected in each 2-sec repetition time. These parameters yielded an in-plane resolution of 3.4 mm × 3.4 mm.

fMRI Data Analysis

All fMRI data were analyzed using AFNI (Cox, 1996) (afni.nimh.nih.gov/afni). The 3-D cortical surface models were created with FreeSurfer and visualized in SUMA (Saad, Reynolds, Argall, Japee, & Cox, 2004; afni.nimh.nih.gov/afni/suma). We performed both an ROI and a whole-brain analysis.

For the ROI analysis, the data were analyzed in native participant space without any spatial normalization. The functional data were motion corrected, smoothed (4 mm FWHM), and scaled to the average of each functional run before they were submitted to a multiple regression analysis. For the main experimental runs, we included regressors for each condition of interest (ScCc, ScCi, SiCc, SiCi). For the localizer scans, we submitted regressors for the horizontal and vertical checkerboard blocks, the colored and achromatic checkerboard blocks, and the object and scrambled image blocks.

The ROIs were areas V1, V2, V3, defined by retinotopy, the color-responsive FG, defined by the color localizer, and the shape-responsive LOC, defined by the shape localizer. The use of separate and independent localizers from our main task allowed us to better isolate our ROIs and to avoid the bias that is inherent in selecting voxels based on experimental conditions (Kriegeskorte, Simmons, Bellgowan, & Baker, 2009; Vul, Harris, Winkielman, & Pashler, 2009). The ROIs were drawn on individual cortical reconstructions based on significant activations ($p < .01$). In addition, because our stimuli covered only part of the visual field, we selected only those voxels in each area (V1–V3, FG, and LOC) that showed activation to our stimuli collapsed across all conditions (ScCc, ScCi, SiCc, SiCi), using a lenient threshold ($p < .2$). This lenient threshold was chosen to ensure that we were not overly biasing our voxel selection to only a few highly responsive voxels. Using these conservatively defined voxels in each ROI, we estimated a hemodynamic response function (HRF) for

each condition by fitting a finite impulse response model to the motion corrected, unsmoothed, and detrended data averaged across all voxels and scaled to the mean of each run. The fit was computed using ordinary least squares. Statistical analyses were then performed on the activation for each condition within each ROI averaged across three points in the HRF beginning at 2 sec after trial onset, which yielded similar but more reliable results as compared with analyses using individual beta weights. Activation differences between conditions were evaluated using two-way ANOVAs with shape and color congruency as the within-subject factors. We also evaluated our a priori hypothesis, which was based on pilot experiments showing an identical object advantage. This hypothesis was tested by using complex contrasts ($\alpha = .05$) to examine whether the shape-congruent/color-congruent (ScCc) condition would show decreased activation compared with any of the other conditions with at least one incongruent feature.

For the group analysis, the functional data in original subject space were motion corrected, smoothed by 6 mm, scaled to the mean of the functional run, and submitted to a regression analysis. The resulting statistical maps were spatially normalized to Talairach coordinates (Talairach & Tournoux, 1988) and submitted to an ANOVA ($\alpha = .05$). Significant cluster sizes ($\alpha = .01$) were determined using a Monte Carlo simulation (Alphasim) of 1000 iterations.

RESULTS

Behavioral Data

As predicted, faster RTs (i.e., priming) were measured only when the primes were identical in both shape and color to the target mask (Figure 2). A 2×2 ANOVA with Shape and Color Congruency as factors did not show main effects of Shape, $F(1, 6) = 2.59, p = .16$, or Color, $F(1, 6) = 1.5, p = .27$, and no significant interaction, $F(1, 6) = 2.17, p = .19$. However, a planned contrast based on our a priori hypothesis that only entirely congruent

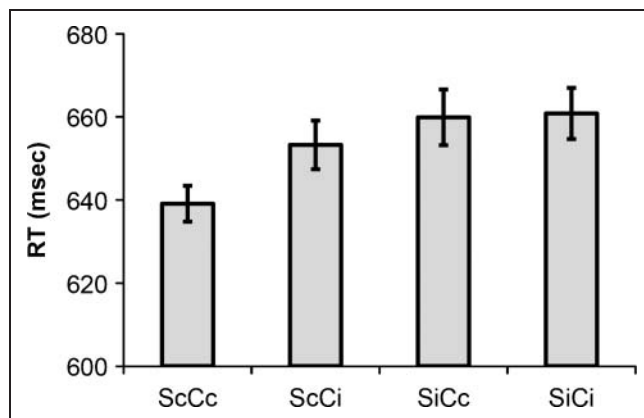


Figure 2. RT data for the four conditions (ScCc, ScCi, SiCc, SiCi). Error bars indicate the within-subject SEM (Loftus & Masson, 1994).

Table 1. Mean Accuracy for Shape Judgments in Each of the Conditions

	Mean	SE
ScCc	0.96	0.02
ScCi	0.97	0.01
SiCc	0.97	0.01
SiCi	0.97	0.01

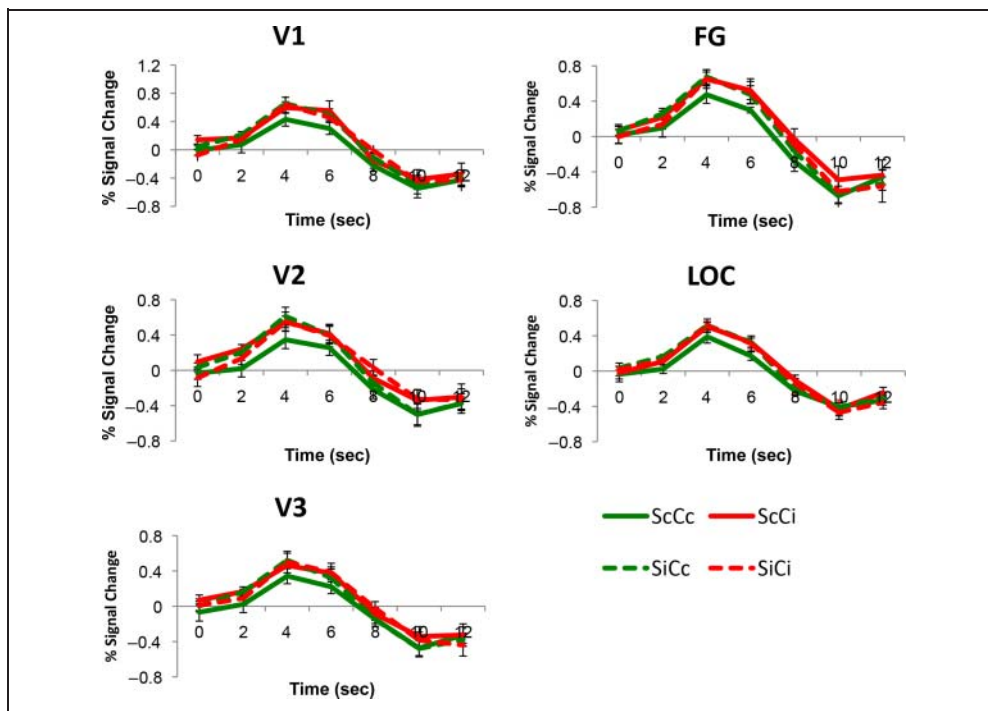
objects would result in priming showed a significant difference between the ScCc and the other three conditions (ScCi, SiCc, and SiCi; $F(1, 6) = 10.76, p = .017$). This behavioral result suggests that unconscious priming occurs for visually identical objects. Accuracy remained at ceiling for all conditions (Table 1); thus, there were no effects on accuracy for either Shape, $F(1, 6) = 0.21, p = .67$, or Color Congruency, $F(1, 6) = 0.2, p = .9$, and no interaction, $F(1, 6) = 0.15, p = .71$. Performance in the two-alternative forced-choice prime identification task was at chance (49%), confirming that the primes were unconsciously processed.

fMRI Data

The activation pattern in visual cortex (Figure 3) closely reflects the behavioral RT pattern. Across all areas, even as early as primary visual cortex (V1), the ScCc condition showed decreased activation compared with the other three conditions. We conducted 2×2 ANOVAs with Shape and Color Congruency as the two within-subject factors in each of the five predefined visual areas (V1, V2, V3, FG, LOC). The main effect of Shape reached significance in V1, $F(1, 6) = 6.18, p < .05$, and V2, $F(1, 6) = 7.38, p < .05$, and was marginally significant in the LOC, $F(1, 5) = 5.64, p = .06$. The main effect of Color was significant in V1, $F(1, 6) = 8.85, p < .05$, and marginally significant in V2, $F(1, 6) = 5.81, p = .053$, and in the LOC, $F(1, 5) = 4.67, p = .08$. The Shape \times Color interaction did not reach significance in any of the areas. Neither the main effects nor the two-way interaction was significant in FG. On the basis of our hypothesis that only objects that are congruent in both shape and color would show unconscious priming, we performed contrasts in each area comparing the ScCc condition with the other three conditions in which one or both features were incongruent. The contrasts, corrected for multiple comparisons using a reversed sequential Bonferroni procedure (Hochberg, 1988), showed a significant difference in all areas, in V1, $F(1, 6) = 22.50, p = .003$; V2, $F(1, 6) = 17.95, p = .005$; and V3, $F(1, 5) = 7.34, p = .042$ in FG, $F(1, 5) = 7.67, p = .039$, and in LOC, $F(1, 5) = 51.62, p = .001$.

To explore other brain areas that would show identity effects, we also conducted a group analysis on the fMRI data comparing the ScCc with the other three conditions. The results (Figure 4) showed a cluster of significantly

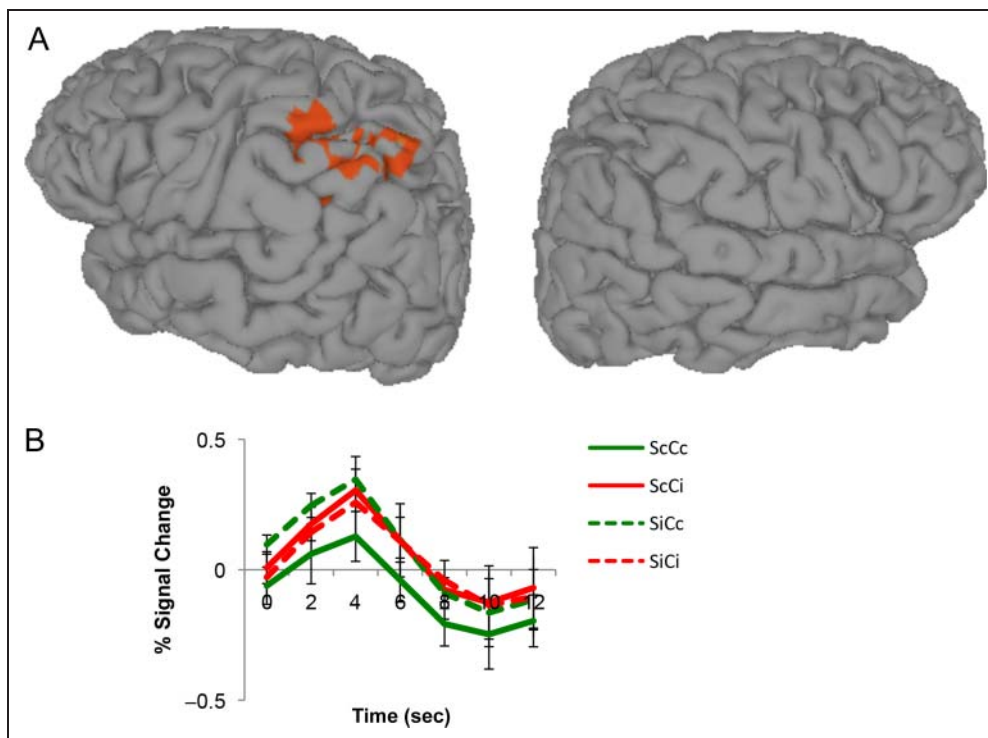
Figure 3. Time series data (estimated HRFs) in each of the visual areas V1, V2, V3, FG, and LOC. Solid lines denote shape congruent conditions, whereas dashed lines show shape-incongruent conditions. Green lines represent color-congruent conditions, and red lines represent color-incongruent conditions (ScCc, solid green; ScCi, solid red; SiCc, dashed green; SiCi, dashed red). Error bars indicate *SEM*.



activated voxels ($p < .05$), with a center of mass in the left inferior parietal lobule ($x = -37, y = -51, z = 44$). As for the visual ROIs, we analyzed the peak activity within this parietal area using a 2×2 ANOVA with Shape and Color Congruency as the within-subject factors. The ANOVA showed a main effect of Shape, $F(1, 6) = 22.50, p = .003$, but not of Color, $F(1, 6) = 1.72, p = .24$. Inter-

estingly, there was also a significant interaction between Shape and Color, $F(1, 6) = 15.54, p = .008$. The interaction was due to a significant difference in shape congruency when color was congruent, $F(1, 6) = 75.27, p < .001$, as opposed to when it was incongruent, $F(1, 6) = .47, p = .52$. Although in this whole-brain analysis some activation was observed in the visual cortex, consistent with

Figure 4. (A) The results of a whole-brain analysis overlaid on a spatially normalized cortical surface. The analysis compared the condition in which primes and targets were identical in shape and color (ScCc) to the other three conditions in which one or both features differed (ScCi, SiCc and SiCi). A significant cluster of activated voxels ($p < .05$) was observed with a center of mass in the left inferior parietal cortex ($x = -37, y = -51, z = 44$); significant cluster size at $p < .01$. (B) The activity within this inferior parietal area showed a similar pattern as the visual ROIs (same conventions as in Figure 3). Error bars indicate *SEM*.



the results of the ROI analysis, it remained below the threshold for significance, which was expected given the corrections for cluster size.

DISCUSSION

In the current study, we investigated the unconscious processing of objects that varied along multiple feature dimensions. Participants performed shape judgments on larger colored shapes that were preceded by smaller colored shape primes. We measured faster RTs when primes were congruent in the attended shape dimension, but only when the unattended color dimension was also congruent. When the shape was congruent, but the color was incongruent, there were no priming effects. These results extend previous findings (Tapia et al., 2010; Ro et al., 2009; Breitmeyer et al., 2004; Klotz & Wolff, 1995) by demonstrating unconscious priming from primes that are identical to targets not only in task relevant but also in task-irrelevant features.

Similar to the behavioral results, the fMRI data showed reductions in activation, likely related to repetition suppression, when the primes were identical to the masks. We observed effects in several visual areas, including primary visual cortex, consistent with previous fMRI studies showing V1 activity for unconscious visual stimuli (Watanabe et al., 2011; Tse, Martinez-Conde, Schlegel, & Macknik, 2005). Given the known orientation and color selectivity of neurons in V1 (Livingstone & Hubel, 1984), adaptation in primary visual cortex may have been partly driven by bottom-up stimulus factors. However, because the primes did not spatially overlap with the masks in our experiment, they would not have been within the same receptive fields of the majority of neurons in V1. Therefore, activation differences in V1 may have also been partly modulated by top-down processes.

We also measured adaptation in feature-responsive areas. fMRI activity was lower in the LOC (Grill-Spector et al., 1999; Malach et al., 1995) and the FG (Hadjikhani, Liu, Dale, Cavanagh, & Tootell, 1998; Zeki et al., 1991) for targets that followed shape- and color-congruent primes. Note that, although the LOC and FG are considered to be responsive for shape and color, respectively, both areas showed repetition suppression to both features. This result is consistent with fMRI and neurophysiology studies that suggest some overlap in shape and color selectivity in the FG and inferior temporal cortex (Cavina-Pratesi, Kentridge, Heywood, & Milner, 2010; Edwards, Xiao, Keyser, Foldiak, & Perrett, 2003; Pasupathy & Connor, 1999; Komatsu & Ideura, 1993). One possibility may be that different neurons or voxels within LOC and FG show varying levels of selectivity to different types of features. To better separate color- and shape-related activations, future studies will require color and shape localizers with comparable stimuli (Cavina-Pratesi et al., 2010) and higher-resolution fMRI.

Unexpectedly and interestingly, the whole-brain analysis showed a significant cluster of activation in the left parietal cortex for the three incongruent conditions compared with the identical prime condition. The posterior parietal cortex has been previously shown to be involved with adaptation to repeated presentations of the same object, regardless of size and viewpoint (Konen & Kastner, 2008). Our study is the first to show adaptation for unconsciously presented objects in this inferior region of the parietal cortex. Furthermore, the analysis of activity within this area showed an interaction between shape and color congruency, suggesting that this area may encode feature combinations. Future studies are necessary to more precisely determine how and why this particular region of the brain is particularly sensitive to unconsciously presented objects.

Our results provide an important link between findings of unconscious object encoding and unattended visual feature processing. Marois, Yi, and Chun (2004) showed that objects rendered unconscious through the attentional blink still activate feature-responsive areas of the visual cortex. On the other hand, O'Craven et al. (1999) found that feature-selective areas respond to unattended properties of conscious objects, especially when these objects are selected for an attended property. Our study complements and extends these findings by demonstrating that task-irrelevant features of objects can be processed even when the objects are unconscious.

The chance performance obtained in the prime identification task performed at the end of our experiment constitutes evidence that participants had no conscious perception of prime shape. Although we did not conduct a similar prime identification task for the color, we believe that participants were unlikely to have conscious color experiences for several reasons. First, color information was task-irrelevant and thus remained unattended throughout the experiment. Second, the SOA used was in the range known to maximally suppress consciousness of color (Ro et al., 2009; Breitmeyer et al., 2004; Schmidt, 2002). Finally and most importantly, participants did not report any awareness of the primes, which suggests that both color and shape remained below the threshold of awareness.

Although our results convincingly show unconscious processing of the task-irrelevant unattended color dimension, we cannot conclude that all unattended features would be equally analyzed at the unconscious level. First, it is likely that the difficulty and encoding speed of the attended relative to the unattended feature would play a role in unconscious processing. For example, if shape information is processed slower than color information, we should expect irrelevant color information to be processed when performing a shape task, but not an irrelevant shape to be processed when performing a color task. In fact, some pilot behavioral results using stimuli similar to the ones in the current experiment suggest that when color is attended and shape is unattended, shape

does not influence RTs in a color discrimination task, possibly because shape is processed slower or is less salient than the surface property of color. Second, the perceptual load when discriminating the attended feature may determine whether the unattended feature is processed (Lavie, 1995). The fact the perceptual load in our experiment was low and that color influenced priming suggests that it may have been automatically selected and thus possibly attended to unconsciously. Consistent with this possibility, a recent study has shown that unattended feature processing decreases with increasing perceptual load for consciously presented objects (Xu, 2010). We believe that similar attentional load effects may hold for unconscious stimuli and that attention and consciousness may be dissociable, as previous studies have suggested (Koch & Tsuchiya, 2007; Lamme, 2003; Kentridge, Heywood, & Weiskrantz, 1999). Finally, as in most previous priming studies, there was a limited set of stimuli, and the shapes and colors of the primes were identical to the targets apart from their size and their centers. With this limited number of stimuli, it is possible that the processing of the primes was influenced by the amount of practice with the same stimuli as targets (Damian, 2001), and that feature binding for both the primes and the masks only occurred in our experiment when the targets were presented. It will be important for future studies to investigate whether unattended features would be unconsciously processed even when they have never been perceived consciously as targets.

Note that our behavioral results are different from those reported using a very similar design in a recent psychophysical study (Tapia et al., 2010), which found no evidence of unconscious priming from either unattended shape or color. These contrasting results are likely because of differences in SOAs between the two studies (53 msec in Tapia et al., as compared with 17 msec in our study); the longer SOA in their study may have allowed for sufficient time for subjects to filter out task-irrelevant information. Additionally, their participants judged both the shape and color of the masks, albeit in different blocks, which may have resulted in more response interference (i.e., carryover effects) when these features were supposed to be irrelevant.

One intriguing question is whether multiple features are unconsciously integrated into object representations (Treisman & Gelade, 1980). To our knowledge, feature binding has never been shown for unconsciously presented stimuli. Our results are consistent with the possibility that priming occurred at the level of bound objects because we did not find intermediate priming effects when only one of the features was congruent. Thus, priming was not linearly additive but rather “all-or-none,” occurring only when primes and targets were identical objects. If, indeed, the visual system has the capability of resolving not just features but integrated objects at an unconscious level, it would suggest that sophisticated processing and complex scene analysis can occur in the absence of awareness.

It is also possible that, in our experiment, features were independently encoded and produced separate priming effects. One reason that priming may not have been additive is that priming may reach a critical threshold only when both features were identical. Alternatively, it might be that incongruity in one feature dimension overrides the effects of congruency in the other. To clarify whether features were independently represented or unconsciously bound, experiments that present displays of multiple unconscious objects, in which several combinations of the same features can be compared, are necessary. Nonetheless, our results tentatively and most parsimoniously suggest that the visual system encodes integrated objects.

In conclusion, the psychophysical and neuroimaging evidence presented here demonstrate that the visual system has the ability to unconsciously process objects across multiple task relevant and irrelevant properties. The current results provide evidence that the visual system can unconsciously encode entire objects, abstracting from their overall size and using the same feature responsive network that has been shown to respond to supraliminal, consciously perceived images.

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Reprint requests should be sent to Tony Ro, Department of Psychology, NAC 7/120, 160 Convent Ave., New York, NY 10031, or via e-mail: tro@ccny.cuny.edu.

Note

1. Data from the LOC and FG were also excluded in one participant because of insufficient slice acquisition in the inferior occipital cortex and from V3 in a second participant because of insufficient activation.

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