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Visual Feature Binding Requires Reentry

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Abstract

Reentrant processing has been proposed as a critical mechanism in feature binding. To test this claim, participants were shown arrays of six pairs of crossed vertical and horizontal bars. In each pair, one bar was white; one was red, green, or blue. Identifying the orientation, but not the color, of the nonwhite bar in the target item required correct binding. Four dots appeared around one of the items (the target) and either disappeared with it or persisted for 300 ms after the array disappeared. This type of trailing mask is thought to interfere with target processing by disrupting reentry. Consistent with the hypothesis that binding requires reentrant processing, the trailing mask significantly reduced the accuracy of orientation but not color judgments. In a control condition, when the white bar was omitted, binding was no longer required, and both color and orientation were accurately reported.

Keywords

feature binding; feature integration; reentry; attention; object substitution masking

As a critical early step in object perception, separate visual features must be properly integrated. There is considerable evidence that the correct binding together of features into objects is a challenging task for the visual system (Wolfe & Cave, 1999). However, the neural mechanisms that underlie visual feature binding are not known. One possible mechanism of feature binding, according to feature integration theory, is reentrant processing (Treisman, 1996). According to this hypothesis, the first response to visual stimulation activates feature detectors in early striate and extrastriate areas that connect automatically to the temporal lobe object nodes with which they are compatible and perhaps inhibit those with which they conflict. To check whether the conjunctions are real, the features must be retraced to the early visual areas where localization is more precise. So far, however, there has been no behavioral demonstration that reentry is required for feature binding.

Until recently, showing that a process depended on reentry was difficult. Di Lollo, Enns, and Rensink (2000) presented the results from a series of experiments using a new form of masking, which they called object substitution masking (OSM). In a typical example, an item in a display was surrounded by four small dots. If the dots disappeared at the same time as the item, the item was easily seen. However, if the dots persisted after the array disappeared, they made the target much more difficult to see. The authors concluded that

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their data were better explained as a disruption of feedback, rather than feed-forward, processing. Their suggestion was that the first pass through the visual system generates a hypothesis about what was presented and that this hypothesis is then verified by sending a prediction back to early visual areas (reentry) to be compared with the stimulus effects that are still present. If the top-down hypothesis is consistent with the evidence from the currently selected location, it is confirmed and can be consciously experienced. The trailing mask disrupts these stimulus effects, and the mask itself is substituted for the stimulus in the conscious percept. The hypothesis we tested is that this reentry check is particularly necessary for feature binding and may not be required for simple feature detection, which can often be achieved on the first feed-forward pass.

In the present experiment, participants performed a behavioral task that required feature detection and on some trials feature binding. We tested whether a trailing mask selectively disrupted feature binding relative to feature detection. If binding depends on reentry, it should be particularly vulnerable to object substitution, whereas the stimulus features might be registered on the first pass through the visual system and thus remain available even in the presence of a trailing mask.

Method

Participants

Ten individuals with normal or corrected-to-normal vision (including Seth Bouvier) participated in Experiment 1. All but Seth Bouvier were naive to the purpose of the experiment. A new group of 15 individuals participated in Experiment 2.

Stimuli and procedure

Stimuli were presented on an 18-in. CRT monitor (Samsung) using MATLAB (Version 2007b; The MathWorks, <http://www.mathworks.com/>) and the Psychophysics Toolbox extensions (Brainard, 1997). Observers' heads were positioned 56 cm from the screen.

The stimuli consisted of an array of six elements, equidistant from the center of the screen (see Fig. 1). Each element was composed of a cross with vertical and horizontal bars. One of the bars was white, and the other was randomly selected from the set (red, green, or blue). The orientations of the white and colored bars were randomly determined for each element. Each bar subtended 1.4° of visual angle in length and 0.3° in width. The center of each item (where the two bars crossed) was located 2.3° from the center of the screen.

One of the six items was designated as a target by the location of four white dots. Each dot had a diameter of 0.28° . The dots were present at the corners of the imaginary square defined by the extent of the target item and thus never occluded the item. Although the positions of the six items did not vary from trial to trial, the location of the target item varied randomly. The task was to identify the color and orientation of the colored bar in the target item.

In Experiment 1, the target was followed by either no mask or a trailing mask. For each mask type, there were two types of trials (for a total of four conditions). In two-bar trials, the target item included a white distractor bar. In one-bar trials, the target item did not include a white bar. In all conditions, the five nontarget items always contained the white distractor bar, and the color and orientation of the nonwhite bar were randomly chosen on each trial and at each location.

At the start of each trial, a small circle appeared at the center of the screen. Participants were instructed to fixate the circle. After 750 ms, the circle disappeared, and the stimulus array

appeared. The array was on the screen for 75 ms. During the no-mask trials, the four small dots disappeared at the same time as the stimulus array. During trailing-mask trials, the dots persisted for an additional 300 ms. Participants were asked to report, with separate keypresses, the color and orientation of the nonwhite bar in the target item. Participants performed 150 trials of no-mask and trailing-mask conditions.

In Experiment 2, the procedure was the same, but a second type of mask was also tested, in addition to the trailing-dot mask (for a total of six conditions). In this noise-mask condition, the dots and the target item appeared for 75 ms, then were immediately replaced with a noise mask composed of a 5×5 grid of square elements; the color of each square was randomly drawn from the set (red, green, blue, or white). The noise mask remained on the screen for 300 ms. Participants performed 500 trials of each of the three masking types. Conditions were presented in random order.

Performance was computed separately for each response type (color and orientation) in each condition. In our analyses, we did not include the first 10 trials from Experiment 1 or the first 20 trials from Experiment 2. Statistical comparisons between conditions were made using paired *t* tests; replicability statistics were also calculated (Killeen, 2005).

Results and Discussion

Participants were asked to report the color and orientation of the target item. When the target contained a single bar, the task was straightforward: Only a single color and orientation were present, so any errors were due to a failure to identify these features. However, when the target item also contained a white distractor bar, two colors and two orientations were present at the same location. Preattentively, this type of stimulus is represented as a loose collection of its component features (Wolfe & Bennett, 1997). The correct combinations of color and orientation must then be bound to properly perceive the item. In our task, identifying the color of the target bar did not require binding, because knowing which of the two bars was colored was not task relevant; white was not a possible response. But in the two-bar condition, identifying the orientation of the target bar did require binding, because the relevant bar was defined as the target only by its color. Thus, some binding errors were expected with no mask because of the brief exposure, but if reentry is critical for binding, we predicted a much more severe impairment with the trailing mask.

We look first at no-mask trials in which reentry is assumed to proceed normally. On one-bar no-mask trials, performance on both the color and the orientation tasks was at ceiling (see Fig. 2a). Likewise, in two-bar no-mask trials, color judgments were at ceiling. However, in two-bar no-mask trials, the presence of the white bar did slightly reduce participants' ability to judge the orientation of the nonwhite bar ($p < .05$, $p_{\text{rep}} = .915$). To identify the relevant orientation, participants had to bind the color to the colored bar. The error rate (7%) is consistent with illusory conjunction rates previously reported with brief presentations and no trailing dots (Treisman & Schmidt, 1982).

The addition of the trailing mask had no effect in one-bar trials. We conclude that reentry is not critical for the acquisition of either color or orientation features in this task. In two-bar trials, however, the trailing mask dramatically impaired the orientation judgments ($p < .001$, $p_{\text{rep}} = .995$), which were dependent on feature binding, but not the color judgments for which binding was not required. Thus, reentry is critical specifically for feature binding.

Could this performance difference be due to greater vulnerability to masking for orientation than for color judgments, regardless of the need to bind the features? There is some evidence that OSM may function somewhat independently for color and orientation (Gellatly, Pilling, Cole, & Skarratt, 2006), and here, we found that OSM affected orientation but not color

judgments. However, we found no masking of orientation in one-bar trials, which makes the account in terms of special vulnerability of orientation unlikely. In these trials, binding errors are not possible because only a single color and a single orientation are present in the target item.

In Experiment 2, we replicated the results of Experiment 1 (see Fig. 2b). In addition, we compared the effect of a more traditional backward mask, which occupied the same location as the target (unlike the trailing mask, which did not overlap with the target). For this reason, we predicted that the noise mask might disrupt feed-forward processing, making it difficult for participants to report the features as well as their binding. As predicted, the presence of the noise mask seriously impaired both color and orientation judgments in both one-bar and two-bar trials (all comparisons: $p < .001$, $p_{\text{rep}} = .999$). These data were consistent with the view that backward pattern masking disrupts feed-forward processes, but OSM leaves them relatively intact (Enns, 2004). They also showed that both color and orientation features are highly maskable by conventional overlapping masks.

We have suggested that feature detection is relatively immune to OSM. Is this consistent with previous research? In previous OSM studies, the trailing mask was said to disrupt the perception of stimulus features (Di Lollo et al., 2000). One possible explanation of the discrepancy is that their tasks also involved binding to some degree, as they asked participants to locate a feature (gap or line) relative to a target circle rather than to detect the presence of a feature. Another possibility is that the difference reflects the longer time that our participants were given before the OSM mask (75 ms compared with the 10–45 ms used by Di Lollo et al., 2000). The increased exposure may have allowed sufficient time for feature identification, explaining the relative resistance of features to substitution masking in our experiment. At the least, our results show that binding is substantially more vulnerable to interference with reentry than are features.

At what level of processing would we expect to find OSM effects if our account is correct? There should be an initial unimpaired response to the features in the feed-forward sweep in whatever areas register the features. OSM should affect area V1, not immediately but a brief interval after the target onset when the reentry pathway is activated. It could also affect any later stages after reentry if the relevant information was destroyed by the object substitution mask at the time of the reentry check. The neural data are consistent with these predictions. A recent article reports that a trailing mask disrupted activity in V1 occurring after the initial feed-forward activity (Boehler, Schoenfeld, Heinze, & Hopf, 2008). Other studies found effects of OSM outside primary visual cortex. Woodman and Luck (2003) showed that scalp-recorded N2pc potentials were not eliminated in response to stimuli followed by a trailing mask, suggesting that the feed-forward representation was disrupted only after participants had directed attention, perhaps to control the choice of locations for the reentry check. Another study found reduced N170 potentials (thought to localize to lateral occipital cortex) to masked items (Reiss & Hoffman, 2007), probably reflecting the loss of identifiable information due to failures of reentry. A functional neuroimaging study found that the representation of masked and unmasked stimuli did not differ in V1 but did differ in portions of the lateral occipital complex (Carlson, Rauschenberger, & Verstraten, 2007).

The reentrant process disrupted during OSM experiments depends on attention, because the effect is reduced or eliminated when the target location is known in advance (Di Lollo et al., 2000). The fact that attention is important for feature binding (Corbetta, Shulman, Miezin, & Petersen, 1995; Treisman & Gelade, 1980) is consistent with the idea that the trailing mask disrupted attention-related processing in our experiments and also with many feedback models of visual attention (Hamker, 2005; Sprattling & Johnson, 2004). Many studies have shown that regions in parietal and frontal cortex modulate visual cortex activity during

spatial attention; these regions may be the source of reentry during binding. Neuropsychological studies suggesting that the parietal lobes are important for feature binding are also consistent with our account. A patient with bilateral parietal lesions resulting in Balint's syndrome exhibited the typical simultanagnosia and inability to localize visual objects spatially, but in addition he had great difficulty in correctly binding features. He saw a large number of illusory conjunctions, even when the stimuli were presented for as long as 10 s (Friedman-Hill, Robertson, & Treisman, 1995). Ashbridge, Walsh, and Cowey (1997) induced selective disruption of search for conjunction targets (requiring feature binding) by transcranial magnetic stimulation (TMS) to the parietal cortex of normal participants 100 or 160 ms after the presentation of the display. Similarly, Braet and Humphreys (2009) showed increased illusory conjunctions when they applied TMS to the right parietal lobe 150 to 200 ms poststimulus. Thus, neurons in parietal cortex are necessary for feature binding, especially during a critical 100- to 200-ms poststimulus time window. In our task, signals sent from parietal to visual cortex during this 100- to 200-ms poststimulus time window would arrive while only the trailing mask persisted.

These findings underscore what may be a limitation of purely feed-forward models of object recognition. In hierarchical models of object perception, neurons may become tuned to conjunctions of features by combining afferents from lower level neurons with different selectivities. For example, Serre, Oliva, and Poggio (2007) built a feed-forward model of visual processing that closely matched human performance on a rapid object categorization task. However, there is evidence that the type of task used by Serre et al. may be based primarily on the early detection of characteristic features (Evans & Treisman, 2005). Our data indicate that when binding is an essential element of the task, reentrant processing is needed to confirm the correct binding of features.

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Fig. 1.

Illustration of the stimuli in Experiments 1 and 2. During each trial, an array of six items appeared for 75 ms on a computer screen. One of the items was cued by four small dots. Participants' task was to report the color and orientation of the nonwhite bar at the cued location. In no-mask trials (a and b), the four dots disappeared with the stimulus array. In trailing-mask trials (c and d), the four dots persisted for 300 ms after the offset of the array. In noise-mask trials (e and f; Experiment 2 only), the dots and target item were replaced by a 5×5 grid for 300 ms. On half the trials, the cued item had a single bar only (b, d, and f).

Fig. 2. Percentage of correct responses in (a) Experiment 1 and (b) Experiment 2 as a function of the type of task (one bar or two bars), the type of judgment (color or orientation), and the type of mask (no mask, trailing mask, or noise mask). Error bars represent $\pm 1 SE$.