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Brief communication

Subthreshold features of visual objects: Unseen but not unbound

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Abstract

The object is a basic unit that is thought to organize the way in which we perceive and think about the world. According to theories of object-based attention, perception of unified objects depends on the binding together of the disparate features of each object via attention. Here we show that a visual feature that is not consciously perceived is nonetheless modulated by object-based attention: the influence of a subthreshold motion signal (prime) on subsequent motion perception depended critically on whether it was associated with the attended object or another, spatially overlapping object. These results show that invisibly weak features of attended objects are not lost, but are organized by and selected together with the object by attention.

Keywords: Attention; Visual features; Object perception; Motion

1. Introduction

While our perceptual experience is of a world constituted of coherent objects and surfaces, independent visual attributes such as color, motion or surface texture are processed in parallel, specialized neural subsystems (Felleman & Van Essen, 1991; Livingstone & Hubel, 1988). According to the theories of object perception, visual objects are perceived as coherent entities because all the features that belong to the same objects are bound and selected simultaneously by visual attention (Desimone & Duncan, 1995; Duncan, 1996). Both behavioral and physiological evidence provide strong support for the existence of feature binding and object-based attentional selection. For example, it is well documented that we are more efficient in making simultaneous judgments about two features when they belong to the same compared to when they belong to different objects (Blaser, Pylyshyn, & Holcombe, 2000; Duncan, 1984, 1996; Reynolds, Alborzian, & Stoner, 2003). Likewise, attentional selection of a specific feature of an object also affects the processing of other, task-irrelevant features of this object (O'Craven, Downing, & Kanwisher, 1999; Sohn, Papathomas, Blaser, & Vidnyánszky, 2004; Valdés-Sosa, Bobes, Rodriguez, & Pinilla, 1998), suggesting that features that belong to the same object are bound and selected together by attention.

A crucial question that remains to be answered, however, is whether those features of an object that are subthreshold, i.e., too weak to be consciously perceived, are also bound together with the other visible features of the object and selected by object-based attention. It is not clear, based on previous studies, whether object-based effects result because it is easier to simultaneously select features of the same object, or, instead, that paying attention to an object automatically results in a spreading of these attentional effects to all the features of that object. In the first case, top-down attention is more efficient when two separate features happen to belong to the same object, perhaps because of a shared representation or binding of those features in higher areas of visual cortex.

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An altogether different possibility is that directing attention to one feature automatically results in a spreading of attentional modulation across different features of the selected object. This would involve an active mechanism of spreading attention across features processed in specialized visual areas, as it was suggested in the case of global implicit selection (Melcher, Papathomas, & Vidnyánszky, 2005).

To address the question of how object-based attention selects for features, we took advantage of the fact that a subthreshold motion prime can influence subsequent motion perception (Melcher & Morrone, 2003). According to the first model of object-based attention, in which top-down selection is easier for two features of the same object, one would predict that only superthreshold stimuli could be actively selected by attention (Alais & Blake, 1999). If object-based effects involve automatic spreading of features of the same object, then even a subthreshold signal might be influenced by whether or not it belongs to the attended object. In the present study, the prime could be associated, i.e., can share the color, with one of two differently colored surfaces of dots. Perceptually, the two surfaces were transparent, making it possible to select one or the other of the surfaces despite the fact that they were spatially superimposed. Similar displays have been used to isolate object-based mechanisms of visual attention, since spatial-based selection of one or the other surfaces of such transparent stimuli can be excluded (Reynolds et al., 2003; Sohn et al., 2004; Valdés-Sosa et al., 1998). To maintain perceptual segmentation, one set of dots was in random motion while the other surface of dots was either moving coherently or was completely stationary. Thus, on a given trial, the observer was able to pay attention to only one of the two dot surfaces to detect a contrast increment or decrement that occurred during the first part of the trial.

In the second phase of the trial—which was signalled with a short beep—each dot moved randomly and the observer's task was to discriminate the direction of a brief motion probe (direction discrimination task). To measure the influence of object-based attention, motion coherence thresholds were measured with and without the brief subthreshold motion prime presented during the first phase of the trials (Melcher & Morrone, 2003). In the prime present trials, a small group of flickering dots moved coherently for a brief period (150 ms). In the first experiment, these prime dots moved orthogonally to the large group of dots that were moving coherently throughout the trial. It has been shown that in the case when the motion of both dot populations of a bivectorial transparent display is suprathreshold, directing attention to the color of one of the dot fields results in automatic selection of the motion signal that was associated with the attended color, providing support for object-based selection with this type of stimulus (Sohn et al., 2004). Thus, if one could show that the processing of the subthreshold motion prime is modulated depending on whether the attended color matches the color of the prime dots or not, it would provide evidence that even invisible features of the same surface/object are bound and selected by attention together with the whole object.

2. Methods

2.1. Participants

One author (DM) and three naïve observers participated in the experiment. All had normal or corrected to normal vision. Informed consent was obtained for all participants, in accordance with institutional ethics guidelines. Three observers participated in the first experiment and two in the second. The second experiment was run with a new naïve observer (AB), since the two naïve observers from the previous experiment were no longer available.

2.2. Stimuli

Images were displayed on a BARCO calibration monitor using VSG framestore (Cambridge Research Graphics), with the timing and order of events controlled by a PC running MATLAB software. The stimulus was presented at the center of fixation and contained 50 dark and 50 white dots displayed within a 10×10 cm aperture against a background of mean gray (28 cd/m^2). In the case of random noise dots, the location of each dot was re-plotted randomly on each frame at 63 Hz. The vertically drifting dots were randomly plotted on the first frame and then displaced vertically (deg/s or pixels) until they reached the bottom of the aperture, at which point they were once again re-plotted at a random location to continue drifting. This gave the impression of a single drifting surface moving upwards or downwards (direction was randomized across trials). During the motion prime or test, a subset of the randomly moving points were displaced horizontally (left or right), creating motion at 10deg/s. This limited lifetime motion involved a single dot being displaced on a second frame but then randomly plotted on the third frame.

2.3. Procedure

Each trial contained two sequential tasks: contrast change discrimination and motion direction discrimination (Fig. 1A). During the first part (contrast task), the display contained two differently colored (black and white) dot fields that were perceptually segmented. In the first experiment, one dot field consisted of dots moving incoherently and the other dot population was moving coherently, while in the second experiment the incoherent noise population was paired with a set of stationary dots. In the second half of the trial (motion task) both colors of dots moved incoherently as a single undifferentiated surface. In the initial contrast discrimination task, observers paid attention to either the black or white dots in order to detect a brief (150 ms) increment or decrement in contrast. The white dots, for example, turned either whiter or more similar to the background grey. During the contrast task one set of dots (white or black) was slowly drifting up or down (5deg/s) while the other dots were randomly re-plotted every two frames to give the appearance of random noise. The instruction to pay attention to either the dark or white dots was given before each block of 40 trials.

The second task was motion direction discrimination, in which the black and white dots returned to incoherent noise for 950 ms. A single motion probe was presented for 150 ms in the middle of that time period after either 300 or 400 ms. This motion test consisted of a subset of the dots that briefly translated to the right or to the left.

Unknown to the observer, a subthreshold motion prime was presented in the random dot population on some trials during the contrast test in the first part of the trial. The strength of the prime was chosen after determining threshold detection for each observer during pilot trials and then choosing the highest motion strength that yielded chance performance (Fig. 1B). Critically, the prime was presented in either the white or the black dots, but not both. Thus it was possible to measure the role of attention, which was given preferentially to either the black or white dots, on the effect of the motion prime on the later motion task. When attended, the

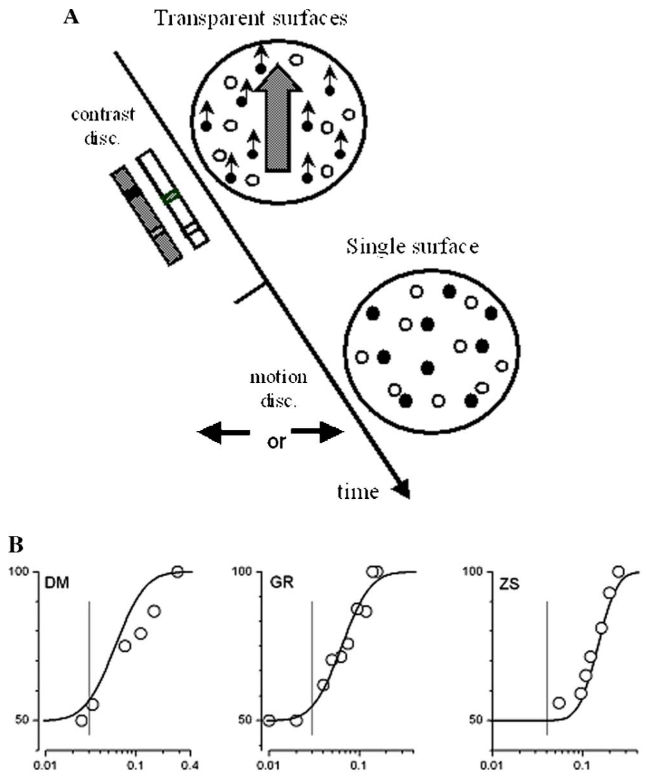

Fig. 1. (A) Schematic representation of experimental events. In the first part of each trial, two perceptually transparent surfaces were visible and observers were instructed to attend to one of these surfaces to judge whether a change in color was an increment or decrement. Then the dots all began to move incoherently in the second half of the trial, to give the impression of random noise. Near the end of this period, a brief (150 ms) motion stimulus was presented for a direction discrimination test. (B) Calculation of the strength of the subthreshold prime. Motion coherence sensitivity was measured initially in a set of two sessions, with the motion signal presented either near the end of the trial or during the contrast test (40 trials each). The curve shows the final measure of motion sensitivity for trials with no prime across the entire experiment for three observers, along with the prime strength (vertical line) calculated after the first set of trials. Any change in overall motion sensitivity was monitored throughout the experiment to ensure that the prime remained subthreshold.

prime was expected to be integrated with the subsequently presented probe and to lead to decreased thresholds in the motion discrimination task (Melcher & Morrone, 2003; Melcher, Crespi, Bruno, & Morrone, 2004; Melcher et al., 2005), while it was hypothesized that the unattended prime would fail to influence motion thresholds. The prime was presented in one of four different time periods (randomized across trials): 300 ms before the contrast test, during the contrast test or 150 or 300 ms after the contrast change.

In the second experiment, during the first part of the trials the non-prime color dots were stationary, rather than drifting up or down. This was to ensure that any lack of prime effect when attending to the non-prime dots was due to object-based attentional selection, rather than masking of the prime motion by the orthogonal drifting motion.

3. Results

When the color of the dots that formed the subthreshold motion prime matched the attended color, motion direction discrimination thresholds were lower compared to trials with no prime (Fig. 2A). There was a significant effect of the matching prime (DM: $p < 0.005$; GR: $p < 0.001$; ZS: $p < 0.001$). On average, thresholds were about half of those found without the motion test, showing that the prime and the test signals were temporally integrated (Burr & Santoro, 2001; Melcher & Morrone, 2003). As shown in Fig. 2B, there was no influence of the prime when observers were paying attention to the other color (DM: $p = 0.427$; GR: $p = 0.360$; ZS: $p = 0.227$). Thus, the influence of the subthreshold prime depended critically on whether or not it occurred in the attended surface of dots. Importantly, the observers' performance in the contrast discrimination task was similar when they attended to the black dots to that when white dots were attended, excluding the possibility that the observed attentional effects are due to different attentional loads in the two conditions.

To ensure that the attentional effects were not due to the modulation of the strength of the motion signal associated with the coherently moving dot field by attentional selection, we ran an additional condition in which the display contained a stationary—replacing the coherently moving—and a flickering dot field. Importantly, in this case stationary and flickering dots were again segmented and perceived as two transparent surfaces, similarly to the display with coherently moving and flickering dots used in the first experiment. We found the same pattern of results (Fig. 3). The prime in the attended color improved subsequent motion discrimination (AB: $p < 0.005$; DM: $p < 0.005$), while a prime presented in the unattended color had no effect on thresholds (AB: $p = 0.104$; DM: $p = 0.184$). Again, this showed that visual processing of a subthreshold motion signal was influenced by whether or not it matched the attended color. Similarly to the first experiment, the observers' performance in the contrast discrimination task was not different depending on whether they were attending to the black or white dots.

4. Discussion

The results show that when attention is directed to specific features (color) of one of the surfaces of a transparent random dot display, the attentional modulation is not restricted to this feature but spreads automatically to another subthreshold feature (motion) that is associated with this surface. Importantly, attentional selection of the motion prime cannot be explained based on spatial attention. The transparent random dot displays used in the present study exclude the possibility that selection of one of the transparent surfaces could be spatial based, since the two dot populations forming the two surfaces spatially overlapped and the short lifetime dots were placed in random position within the display aperture (Reynolds et al., 2003; Sohn et al., 2004; Valdés-Sosa et al., 1998). Thus any spatial-selection mechanisms would result in similar attentional modulation of the motion prime independently of which dot population is actually attended.

The current results are compatible with the theory that visual feature binding consists of two different stages (Wolfe & Cave, 1999). Recent evidence for this idea comes

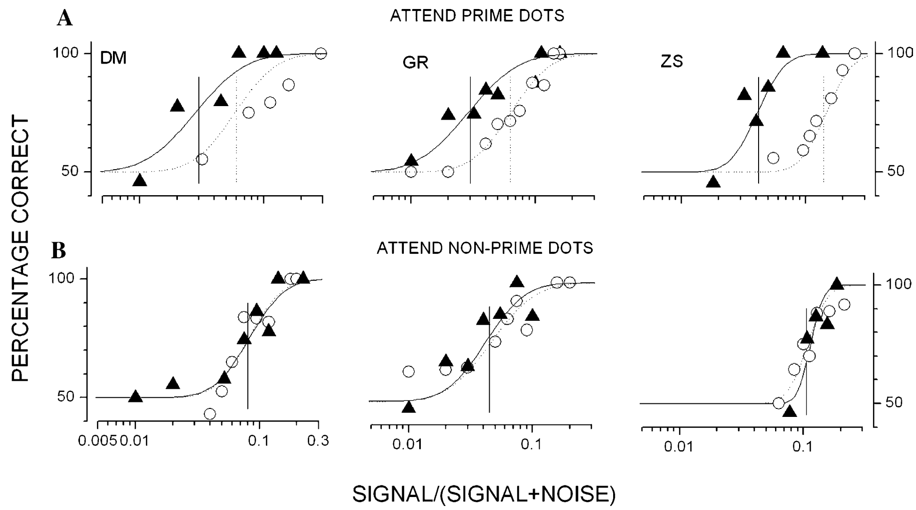

Fig. 2. Motion direction discrimination performance as a function of motion signal strength for experiment 1. (A) Performance when the color of the dots forming the subthreshold motion prime matched the color of the attended dot surface (triangles) compared to trials in which no prime was presented (circles). (B) Direction discrimination when the color of the prime matched the color of the non-attended dot surface (triangles) compared to trials with no prime.

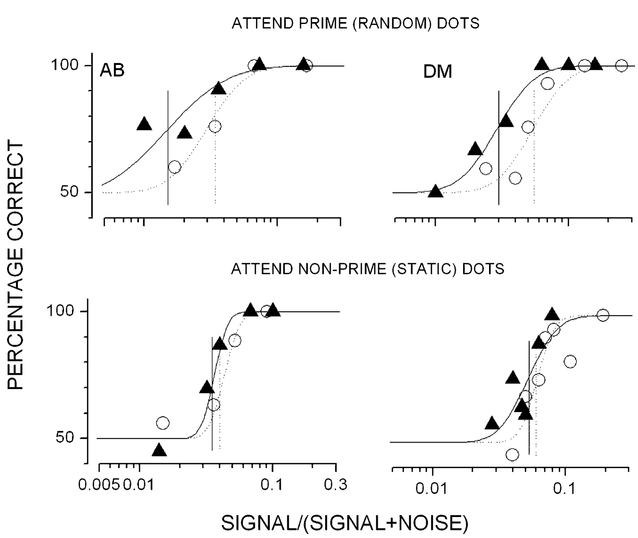

Fig. 3. Motion direction discrimination performance as a function of motion signal strength for experiment 2, in which one surface moved randomly and the other remained fixed and static. Notation is the same as in Fig. 2.

a study of color-motion binding inside and outside the focus of attention (Melcher et al., 2005). In the case of transparent random dot displays used here, the first stage of feature binding would be between the different local feature information associated with a single dot, based on the spatiotemporal co-occurrence of these features. The second stage would involve binding of all the feature information associated with one or the other dot populations based on object-based grouping. Based on the evidence for attentional modulation of subthreshold features, it appears that paying attention to an object automatically results in a spreading of these attentional effects to all the features of that object, even though they are processed in separate cortical areas. The finding that even weak visual signals are bound to specific objects is in agreement with the theory that objects serve as an a priori, organizing principle of human perception (Kant, 1781, 1789).

Our findings have important implications regarding the potential mechanisms that lead to simultaneous attentional selection of all the visual features of the attended object. There are at least two possible mechanisms that could account for object-based attentional selection. On the one side, object-based attention might be thought of as operating “vertically” within the visual processing hierarchy. One can suppose that due to object-based organization of the representations in fronto-parietal cortical network—responsible for the guidance of attention (Corbetta & Shulman, 2002; Pessoa, Kastner, & Ungerleider, 2003; Yantis & Serences, 2003)—directing attention to a specific feature of the object may result in automatic and simultaneous direct attentional modulation of all the features that belong to this object. On the other side, it is possible that only the processing of the task-relevant feature of the object may be modulated by attention directly but, due to the fact that different features of the same object are bound at the stage of sensory processing, this attentional modulation automatically spreads to other task-irrelevant features of the attended object (Duncan, 1996; Schoenfeld et al., 2003; Sohn et al., 2004). This would imply that object-based attention involves selection mechanisms operating “horizontally,” within the network of visual cortical areas specialized for processing of different visual features. The results of the present study show that even subthreshold features that could not be attended directly are selected together with the associated object. This provides novel evidence that object-based attentional selection involves the horizontal mechanism of automatic spreading of attentional modulation from the attended feature of an object to its other, task irrelevant features.

To conclude, our results provide evidence that even subthreshold features of the objects are part of the bound object representations and are selected by attention whenever the object, or any of its features is in the focus of attention. Although at first glance it might appear redundant, the processing and selection of invisibly weak features together with the objects they belong to might play important role in detecting important information about an object by integrating it over time. Temporal integration that is tied to a specific object could be useful in maintaining its identity and in detecting and predicting possible changes in location, velocity, and viewpoint of that object. Since observers and objects in the world are frequently in motion, object representations must be equally dynamic, allowing specific features that were not previously perceived or diagnostic to become visible and heuristic markers of the same object in another instant of time.

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