

Implicit Attentional Selection of Bound Visual Features

Report

David Melcher,^{1,2,*} Thomas V. Papathomas,³
and Zoltán Vidnyánszky^{4,5,*}

¹Department of Psychology
Oxford Brookes University
Gipsy Lane
Oxford OX3 0BP
United Kingdom

²Faculty of Psychology
San Raffaele University
Milan
Italy

³Laboratory of Vision Research and
Department of Biomedical Engineering
Rutgers University
Piscataway, New Jersey 08854

⁴Neurobiology Research Group
Hungarian Academy of Sciences -
Semmelweis University
1094 Budapest
Hungary

⁵Faculty of Information Technology
Peter Pazmany Catholic University
1083 Budapest
Hungary

Summary

Traditionally, research on visual attention has been focused on the processes involved in conscious, explicit selection of task-relevant sensory input. Recently, however, it has been shown that attending to a specific feature of an object automatically increases neural sensitivity to this feature throughout the visual field. Here we show that directing attention to a specific color of an object results in attentional modulation of the processing of task-irrelevant and not consciously perceived motion signals that are spatiotemporally associated with this color throughout the visual field. Such implicit cross-feature spreading of attention takes place according to the veridical physical associations between the color and motion signals, even under special circumstances when they are perceptually misbound. These results imply that the units of implicit attentional selection are spatiotemporally colocalized feature clusters that are automatically bound throughout the visual field.

Introduction

James (1890) has argued that “Everyone knows what attention is; it is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought.” Indeed, we all have an experience of “explicit” attentional selection: focusing attention on a specific object,

location, or feature of the environment or disengaging and shifting it to another target. However, there is a line of experimental results on “feature-based” attentional selection (Corbetta et al., 1991; Motter, 1994; Treue and Martinez-Trujillo, 1999; McAdams and Maunsell, 2000; Saenz et al., 2002) that can hardly be accommodated in this framework of explicit selection. It has been shown that attending to a specific feature of an object modulates neural sensitivity for this feature globally, throughout the visual field, even if the objects that are associated with it are outside the focus of attention and are believed to be ignored.

This implies that attentional selection is not restricted to the objects that we believe we attend explicitly. In parallel with the explicit selection, there is always an implicit attentional selection (IAS)—of which we are not aware and have no volitional control—affecting the processing of visual information outside the attentional focus. Importantly, studying the effects of IAS requires a different approach from that used to investigate explicit selection. Instead of comparing the perceptual and neural processes inside the focus of attention to those found outside of it, studying IAS involves measuring the processing of the visual input outside the focus of attention as a function of what is attended inside the attentional focus. In this study, we adopted this strategy to determine the units of implicit attentional selection.

Since attentional effects outside the focus of attention have previously been studied under the framework of feature-based attention, it is widely believed—although not directly tested—that the units of selection are isolated features identical to those that are explicitly, focally attended (Treue and Martinez-Trujillo, 1999; McAdams and Maunsell, 2000; Saenz et al., 2002). However, there are several lines of research suggesting that the processing of different visual feature information does not occur independently and that, even in the absence of attention, visual features might be bound and processed jointly (Humphrey and Goodale, 1998; Wolfe and Cave, 1999; Holcombe and Cavanagh, 2001). Here we directly tested whether global attentional modulation is indeed restricted to the specific feature that is attended inside the focus or, instead, spreads to other task-irrelevant features that are associated with the attended one. If the latter turns out to be the case, it would provide evidence that the units of implicit attentional selection are not isolated features but are bound clusters of spatiotemporally colocalized features.

Another crucial question that our study aimed to elucidate is whether IAS is determined by early feature binding that is based on the physical, spatiotemporal correlation between the different features or by higher-level binding mechanisms that link features that belong to the same unified perceptual object. Both possibilities appear plausible, since electrophysiological studies in macaques have found strong global feature-based attentional modulation at different stages of the visual cortical hierarchy, including the intermediate stage of visual processing (areas V4 and MT) as well as in the

*Correspondence: dmelcher@brookes.ac.uk (D.M.); vidnyanszky@ana.sote.hu (Z.V.)

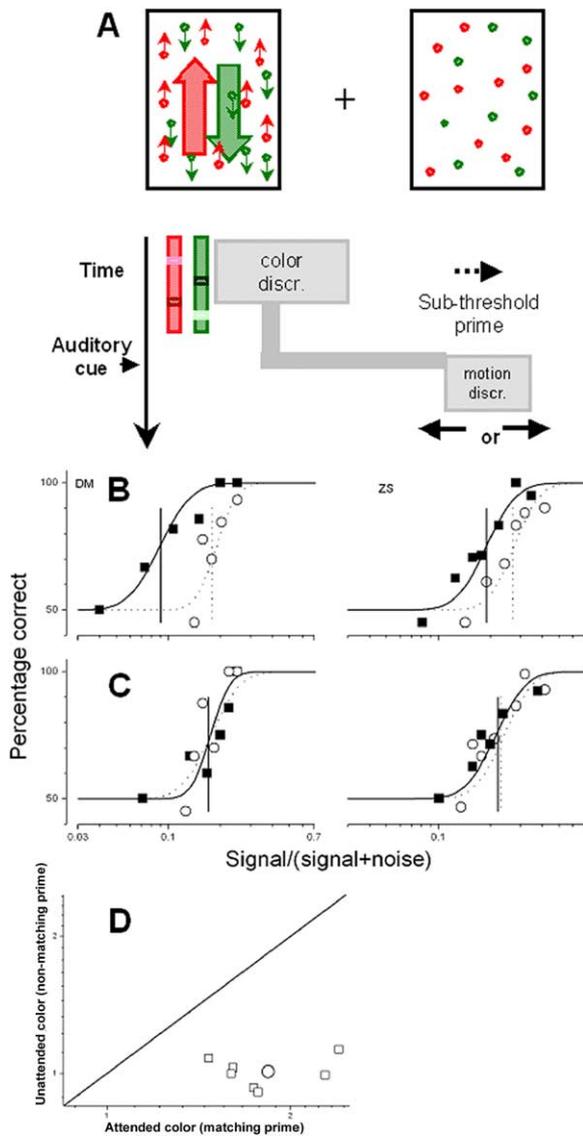


Figure 1. Cross-Feature Attentional Effects on Motion Priming Outside the Focus of Attention

(A) Schematic representation of stimuli.

(B) Motion discrimination performance versus motion strength when the attended color matched the color of the motion prime dots (data are shown for two typical observers). Open circles and dotted lines show performance without prime; filled squares and solid lines show performance with prime. Fitted curves are integrals of Gaussian functions; vertical lines show 75% correct threshold values, with standard error in threshold estimate ranging from 0.0015 to 0.0037. Thresholds were significantly lower for trials containing a matching prime compared to trials with no prime (DM: $p < 0.001$; ZS: $p < 0.01$).

(C) Results when the attended dots did not match the color of the prime dots. The unmatched prime had an insignificant effect on thresholds compared to trials with no prime ($p > 0.05$). The subthreshold prime values both in (B) and (C) were 0.10 for DM and 0.13 for ZS.

(D) Scatterplot of the normalized effect of the prime on motion sensitivity for trials with a prime matching the attended color or the other color. Here, 1.0 signifies no effect of the prime (sensitivity was equivalent to trials with no prime), while 2.0 indicates a doubling of sensitivity (complete temporal integration of prime and probe).

primary visual cortex (Motter, 1994; Treue and Martinez-Trujillo, 1999; McAdams and Maunsell, 2000).

The basic stimulus design in our psychophysical studies was similar to that used in previous neurophysiological (Treue and Martinez-Trujillo, 1999) and fMRI (Saenz et al., 2002) experiments, which provided evidence that directing attention to a visual feature of an object results in a global modulation of the neural responses to this feature across the entire visual field. However, while previous studies investigated global attentional effects outside the focus of attention on the processing of the same visual feature (intra-feature attentional effects), we tested whether global attentional selection affects other, task-irrelevant features of unattended objects that share the attended feature (cross-feature attentional effects).

Results

Cross-Feature Effects of Implicit Attentional Selection

The stimulus in our first experiment consisted of two populations of differently colored dynamic dots displayed on each side of the fixation point (Figure 1A). One aperture contained flickering dots with one or two brief (150 ms) bursts of coherent horizontal motion. The aperture on the other side contained transparently moving red and green dots (upward and downward). Each trial lasted for 3 s. Observers first attended selectively to one of the dot populations of the opposite-motion display in order to detect a brief color contrast increment or decrement that occurred after a variable delay (attention task). Then, observers were cued by a beep to switch attention to the stimulus on the other side of the fixation point to discriminate the direction of a brief motion probe, containing equal numbers of red and green dots (direction discrimination task). Motion coherence thresholds in the direction discrimination task were measured with and without a brief subthreshold motion prime containing dots of one color (Melcher and Morrone, 2003). The subthreshold prime on the unattended side was presented at exactly the same time as the color change on the attended side, and its strength was determined for each subject in pilot studies (see the Supplemental Data available with this article online) to ensure that it was below detection threshold.

It was found that the addition of the prime boosted performance significantly in the motion discrimination task, but only when the prime dots' color matched the color of the attended dot field in the attention task (Figure 1B, squares), and not when it did not (Figure 1C, squares). It is known that two sequentially presented weak motion signals can be temporally integrated, doubling motion coherence sensitivity for a given signal strength (Burr and Santoro, 2001; Melcher and Morrone, 2003). The results of our first experiment show that only when the color of the prime dots matched

Squares show data for seven subjects, and the circle shows the average value, which was significantly higher for the matching prime than for the unmatched prime ($t = 6.356$, $p < 0.001$).

the attended color—and not when they were different—was the subthreshold prime temporally integrated with the subsequent motion probe, resulting in a nearly 2-fold increase in motion coherence sensitivity (Figure 1D), as predicted from linear integration of motion (Burr and Santoro, 2001; Melcher and Morrone, 2003). These results show that implicit attentional selection can affect the processing of task-irrelevant subthreshold motion prime outside the focus of attention and that this depends on whether the prime motion was associated with a color that is attended or neglected inside the focus of attention.

An important question is whether the cross-feature attentional effects outside the focus of attention of our first experiment could be due to spared attentional resources allocated to the aperture containing the prime while observers were performing the color contrast detection task in the other hemifield. In light of previous research showing that selection inside the focus of attention is object based (Duncan, 1984; Valdés-Sosa et al., 1998; O’Craven et al., 1999; Blaser et al., 2000; Schoenfeld et al., 2003), this possibility appears unlikely. On the side where the coherent motion prime occurred, the superimposed red and green dots were both flickering and thus were not perceptually segmented into two different surfaces. Therefore, object-based selection would predict that if attention was directed to the flickering dot field when the motion prime occurs, then the red and green dots would be integrated into a single surface, so attention to either of the colors would result in an equal attentional modulation. To test this prediction, in the second experiment we changed the display so that the color changes and coherent motion prime occurred on the same side that contained flickering dots, with attention always directed only to this aperture (Figure 2A). Under these conditions, the prime increased the performance in the motion discrimination task independently of whether the color of the prime dots and the attended color were the same or different (Figures 2B–2D). These results exclude the possibility that the cross-feature attentional effects found in our first experiment were due to spared attentional resources directed to the aperture with the motion prime. This is because such spared attention would tend to induce a priming effect irrespective of attended color, masking any color-specific global attention modulation.

Feature Binding that Mediates Implicit Attentional Selection

The results of our first and second experiment suggest that the spreading of implicit attentional modulation might be determined by the physical spatiotemporal association between the different features. Our third experiment was aimed at directly testing this possibility. For this, we adopted the stimulus that was shown to induce steady-state perceptual misbinding of color and motion features (Wu et al., 2004). This stimulus contains two differently colored random dot populations that are moving in different directions and are displayed in a large aperture. What is special about this stimulus is that the colors of the two moving dot populations in the periphery are interchanged with respect

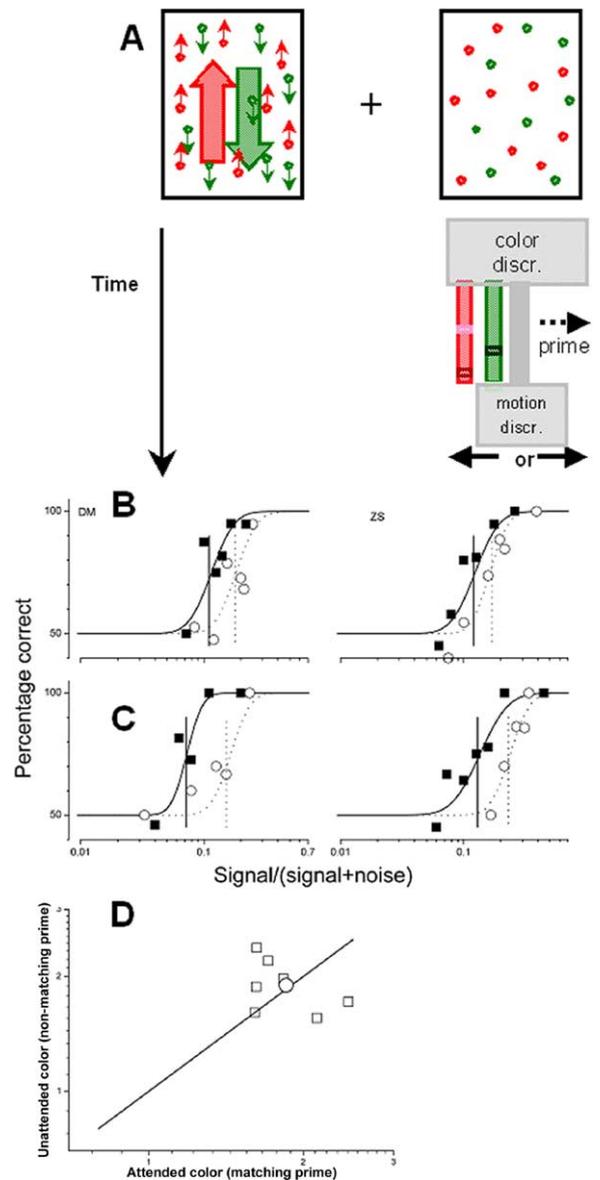


Figure 2. Cross-Feature Attentional Effects on Motion Priming Inside the Focus of Attention

- (A) Schematic representation of stimuli.
- (B) Results when attended dots matched the color of prime dots (data are shown for two typical observers).
- (C) Results when attended dots did not match the color of prime dots. Notation is the same as in Figure 1. The subthreshold prime values both in (B) and (C) were 0.06 for DM and 0.13 for ZS. Thresholds were significantly lower for trials containing both the matching and unmatching prime, compared to trials with no prime (DM: $p < 0.005$; ZS: $p < 0.05$).
- (D) Scatterplot of normalized effect of the prime on motion sensitivity for trials with a prime matching the attended color or the other color. Squares show data for seven subjects, and the circle shows the average, which was not significantly different for trials with matched and unmatched primes ($t = 0.251$, $p = 0.810$). Notation is the same as Figure 1.

to the color of the dots in the central region; i.e., if red dots move upward and green dots move downward in the central region, the periphery contains red dots mov-

ing down and green dots moving up. Strikingly, however, when one looks at this stimulus, there is a misbinding of the color and motion signals in the periphery: all dots moving in one direction are perceived to have the same color, consistent with the color-motion pairing in the central region. Thus, in this display the actual spatiotemporal association between the color and motion signals in the periphery is different from the perceived association. This stimulus provides a unique opportunity to test whether spreading of implicit attentional modulation occurs according to the *physical* associations between the different features—as is suggested by the results of our first two experiments—or according to the *perceived* feature binding.

The stimulus in our third experiment was a slightly modified version of that used by Wu et al. (2004). Instead of having oppositely moving dot populations, in our stimulus one dot field moved coherently and the other population flickered randomly. In a pilot experiment we verified that for all participants this modified stimulus evoked misbinding of color and motion in the periphery. During the main experiment, observers attended to the color of the coherently moving dots in the central region and performed the color contrast detection task as in the first two experiments, as shown in Figure 3A. A percentage of the randomly moving dots in the rightmost peripheral region formed the motion prime, and it was presented simultaneously with the color transient in the central region. Following the color task, observers were cued to attend to the rightmost peripheral region that had contained the prime and performed a motion direction discrimination task for the probe, which contained equal numbers of red and green dots. There were two different stimulus conditions: in one case the attended color in the central aperture matched the color of the randomly moving dots in the rightmost peripheral region (illustrated in Figure 3A), while in the other case it matched the color of the coherently moving dots.

It was found that the addition of the prime affected performance significantly in the later motion discrimination task, but only when the attended color in the central region matched the color that was physically associated with the moving prime dots (Figure 3B, squares), and not when it matched the color that was spatiotemporally linked to the unattended dots (Figure 3C, squares). As shown in Figure 3D, the mean effect of the color-matched prime in the third experiment (a 44% increase in sensitivity to the probe) was only about half of that in the first two experiments. The effective strength of the prime in this experiment may have been weakened because the total number of dots at the time of the prime more than doubled compared to the earlier experiments (see Experimental Procedures), and added noise reduces motion coherence sensitivity (Burr and Santoro, 2001). However, with respect to the question we addressed in our third experiment, the relevant finding is that the subthreshold prime motion signal was modulated by implicit attention according to its veridical spatiotemporal association with the color signal, not its perceptual association.

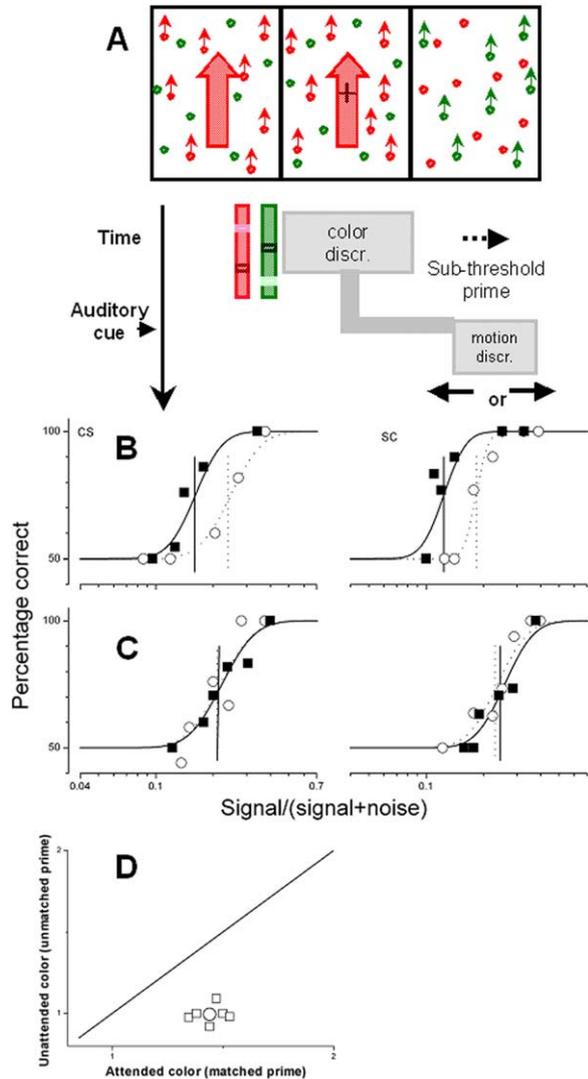


Figure 3. Cross-Feature Attentional Effects during Perceptual Misbinding

(A) Schematic representation of stimuli. (B) Motion discrimination performance versus signal strength (data are shown for two typical observers). Circles show performance (percent correct direction discrimination) with no added motion prime; squares show performance when the prime was in the attended color. Motion thresholds were significantly lower for trials containing a matching prime compared to trials with no prime (CS: $p < 0.05$; SC, $p < .005$). (C) Same as in (B), but squares show results for trials containing a prime in the nonattended color. The unmatched prime had an insignificant effect on thresholds compared to trials with no prime ($p > 0.05$). The subthreshold prime value was 0.13 for CS and 0.15 for SC. (D) Scatterplot of normalized effect of the prime on motion sensitivity for trials with a prime matching the attended color or the other color. Sensitivity was on average much higher for matched primes than for unmatched primes ($t = 13.344$, $p < 0.001$). Notation is the same as Figure 1.

Discussion

Our results show that implicit attentional modulation spreads to task-irrelevant visual features that are spa-

tiotemporally linked with the attended features throughout the visual field. Our findings have important implications regarding the potential mechanisms that lead to cross-feature attentional selection of task-irrelevant visual features that are associated with the attended one. In previous studies showing cross-feature attentional effects inside the focus of attention (O'Craven et al., 1999; Schoenfeld et al., 2003; Sohn et al., 2004), although the affected features were task irrelevant, they were still clearly visible and were associated with the attended object. Therefore, there are at least two possible mechanisms that could account for the cross-feature attentional selection found in these studies: (1) object-based selection mechanisms originating from the frontoparietal cortical network, responsible for the guidance of attention (Corbetta and Shulman, 2002; Pessoa et al., 2003; Yantis and Serences, 2003), may result in simultaneous direct attentional modulation of all the features that belong to the selected object; or (2) 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). In our experiments, cross-feature attention effects were found outside the focus of attention even for subthreshold motion signals that could not be attended directly as a feature. This provides evidence that one of the mechanisms behind selection of task-irrelevant features is an automatic spreading of attentional modulation at the level of visual processing from the attended feature to other features that are bound with it.

This study used temporal summation of two motion signals as a measure of visual processing outside the focus of attention. Previous studies have shown that a weak motion prime increases coherence sensitivity and reduces discrimination thresholds, as shown here (Melcher and Morrone, 2003), while a strong prime motion signal leads to reduced sensitivity to the prime motion direction (Raymond et al., 1998). Interestingly, the effect of both types of motion primes can be modulated by explicit attentional selection (Melcher et al., 2004; Raymond et al., 1998). Here we have shown that IAS also modulates motion priming. These results suggest that IAS can facilitate the processing of the unattended motion prime and its integration with the subsequently presented probe, which in turn would lead to an interesting prediction: namely, that in the case of a stronger motion prime, IAS would lead to *decreased* sensitivity to the subsequently presented motion probe, because further increasing the strength of the motion prime would result in motion contrast. In fact, this is exactly what we found in an experiment similar to experiment 3, with a stronger, although still not consciously detected, motion prime (see [Supplemental Data](#)).

Our findings also imply that feature binding *inside* the focus of attention is object based and links all features belonging to the same surface or object, whereas binding *outside* the attentional focus is based on the physical spatiotemporal relationship between the features. While there are several lines of evidence suggesting

that visual features are bound automatically at the early stages of visual processing in the fovea (Humphrey and Goodale, 1998; Wolfe and Cave, 1999; Holcombe and Cavanagh, 2001), our study provides evidence that color and motion are bound in the periphery even when they are outside the focus of attention. The importance of these findings is evident in light of the fact that most of the examples of feature misbinding found in the literature originate from studies that tested peripheral visual perception under limited or disturbed explicit attention (Treisman, 1999; Wolfe and Cave, 1999; Robertson, 2003). Our results are in agreement with the suggestion that visual feature binding, as measured by performance in a visual search task, consists of two different components: one occurring “preattentively” (i.e., automatically throughout the visual field) and another mechanism that is under attentional control (Wolfe and Cave, 1999).

Based on the available data, one can think of two plausible explanations that could account for the early and automatic linkage between the processing of color and motion found in the present study. The first is based on the existence of double-duty neurons that are selective simultaneously both for color and direction of motion, which have been found to exist in different visual cortical areas (Desimone and Schein, 1987; Cheng et al., 1994; Dobkins and Albright, 1994; Ferrera et al., 1994; Gegenfurtner and Kiper 2003). Another possible explanation is that active binding mechanisms exist to link the processing of neurons that are tuned to a single feature dimension, such as color or motion direction. Our new approach for examining cross-feature attentional effects may provide an effective tool in further studies to characterize the different stages and mechanisms of feature binding both inside and outside the locus of attention.

Finally, our results also clearly show that cross-feature spreading of the implicit attentional modulation is determined by the physical, spatiotemporal association between the different features, rather than by object-level feature binding, which determines consciously perceived feature associations. This property of IAS makes it different from the explicit attentional selection inside the focus of attention (Sohn et al., 2004). We believe that there is a good reason for why implicit attentional selection is based on the veridical physical associations between the visual features. Due to the attentional capacity limitations, binding at the higher stages of visual processing outside the focus of attention can be erroneous or overwhelmed by object-grouping principles—as is vividly demonstrated by the Wu et al. (2004) display—and can lead to false feature associations. Thus, implicit selection based on the physical relationship between the different features appears as a heuristic strategy that avoids potentially erroneous cross-feature attentional selection of visual features at the higher stages of visual processing and may also help to explain the phenomenological absence of a “binding problem” in everyday visual perception.

Experimental Procedures

Experiments 1 and 2

Cross-feature attentional effects on motion priming. One author (D.M.) and six naive observers participated in the first two experi-

ments. The experiments were approved by the ethics boards at San Raffaele University (Milan, Italy) and Oxford Brookes University (Oxford, UK). All participants signed an informed consent form.

Stimuli

Stimuli were generated using VSG Framestore (Cambridge Research Graphics) and displayed on a Barco Calibrator monitor subtending $38^\circ \times 28.5^\circ$, viewed from 60 cm (mean luminance of 28 cd/m²). Dots were presented in two $6^\circ \times 6^\circ$ apertures, 12° apart center-to-center (see Figure 1A). Each region contained 100 dots, half red and half equiluminant green. One region contained dots of one color moving upward and dots of the other color moving downward at 3° /s. Dots in the other region were replotted at 63 Hz, creating the impression of incoherent flickering noise. The motion prime and probe each contained a subset of dots moving coherently either to the right or left at 10° /s for 150 ms before returning to incoherent noise (for details, see Melcher and Morrone, 2003). The motion strength of the prime was determined independently for each observer to get the maximum value that would lead to chance performance (see Supplemental Data). The prime and probe were separated by 500–700 ms (exact timing of probe was chosen randomly on each trial). The attended region of dots contained a brief (150 ms) color change, which was either an increment (i.e., the dot color became more saturated) or decrement (less saturated). The prime and the color contrast discrimination task occurred simultaneously to ensure that attention was focused on the color-change task during the prime. The magnitude of color change was determined during pilot trials independently for each subject to maintain performance at 75%–85% correct. There was no significant difference in performance in the attention task across conditions.

Procedure

Each trial contained a color contrast discrimination task followed by a motion direction discrimination task. The color increment or decrement (150 ms) occurred after 900–1100 ms. In the first experiment, where the motion prime was presented outside of the locus of attention, the color change always occurred in the aperture containing red and green dots drifting in opposite directions. A beep cued the participant to switch attention from the drifting-dot aperture to the incoherently moving dot aperture for the motion test. In the second experiment, the change in color occurred in the incoherently moving dot aperture.

Simultaneous with the color change, the 150 ms subthreshold motion prime was presented in only one color of dots in the incoherently moving dot aperture, followed by a 500–700 ms delay. Then the 150 ms motion probe, containing equal numbers of red and green dots, was displayed in the same aperture as the prime. The strength of the motion probe (percentage of coherently moving dots) varied across trials using the QUEST adaptive staircase method (Watson and Pelli, 1983). A minimum of three QUEST sessions of 41 trials each was run for each condition. Data were fitted with a cumulative Gaussian function weighted by the number of trials for each $S/(S + N)$ value using a simplex algorithm; threshold values were obtained at the 75% correct performance. In separate interleaved blocks of trials (50% of total trials), the motion prime was absent. Naive observers were unaware that a motion prime would be presented in any of the trials. Eye movements were recorded with three observers to ensure steady fixation (ViewPoint video-based eye tracker). Observers successfully maintained stable fixation at the central point (average variability in fixation position within a trial was less than 10 min of arc), and there was no difference in the variability in fixation position in trials with and without the subthreshold prime ($F_{(1,2)} = 0.45$, $p = 0.85$).

Experiment 3

Cross-feature attentional effects during perceptual misbinding. One author (D.M.) and five naive observers participated in this experiment.

Stimuli

In this experiment, there were three regions of dots (left, center, right). The three $6^\circ \times 6^\circ$ apertures were displayed spatially contiguous along the horizontal meridian. Each of the three apertures contained a population of vertically drifting dots of one color and a population of flickering dots of the other color. The number of dots was increased in each aperture from 100 to 150 dots, and the back-

ground was changed from mean gray to black to better replicate the conditions for perceptual misbinding in the periphery (Wu et al., 2004). To maintain similar motion coherence thresholds as in the first two experiments, the test period involved only the rightmost peripheral region of dots. While the estimated prime strength for each observer was calculated as in the first two experiments (see Supplemental Data) to facilitate comparison, the effective signal-to-noise strength of the prime was weakened because there were 450 total dots rather than 200.

Procedure

The tasks and timing were identical to the first experiment. First, there was a color contrast task (center), followed by a beep that cued the observer to shift attention to the rightmost region for a motion test. On each trial, the color of the moving and nonmoving dots was switched in either the left- or rightmost region of dots (i.e., the drifting dots were made red instead of green, while the random noise dots were made green instead of red). Perceptually, this change had no noticeable effect, with all of the vertically translating dots appearing to be of the same color. Subjects were tested on the ability to judge which region was “odd” in separate blocks of trials and performed at chance (average for six observers was 51% correct). On trials containing a motion prime, the prime was presented in the noise dots in the rightmost region of dots.

Supplemental Data

The Supplemental Data for this article can be found online at <http://www.neuron.org/cgi/content/full/46/5/723/DC1>.

Acknowledgments

We thank D. Burr, C. Morrone, and E. Kowler for comments and assistance in the statistical analyses. This work supported by MUIR (project PRIN) and by grants from the Royal Society and British Academy to D.M.; U.S. NEI/NIH (EY 013758-01) to T.V.P.; and Hungarian National Research and Development Program (2/046) to Z.V. The authors declare that they have no competing financial interests.

Received: November 11, 2004

Revised: March 9, 2005

Accepted: April 20, 2005

Published: June 1, 2005

References

- Blaser, E., Pylshyn, Z.W., and Holcombe, A.O. (2000). Tracking an object through feature space. *Nature* **408**, 196–199.
- Burr, D.C., and Santoro, L. (2001). Temporal integration of optic flow, measured by contrast and coherence thresholds. *Vision Res.* **41**, 1891–1899.
- Cheng, K., Hasegawa, T., Saleem, K.S., and Tanaka, K. (1994). Comparison of neuronal selectivity for stimulus speed, length, and contrast in the prestriate visual cortical areas V4 and MT of the macaque monkey. *J. Neurophysiol.* **71**, 2269–2280.
- Corbetta, M., and Shulman, G.L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nat. Rev. Neurosci.* **3**, 201–215.
- Corbetta, M., Miezin, F.M., Dobmeyer, S., Shulman, G.L., and Petersen, S.E. (1991). Selective and divided attention during visual discriminations of shape, color, and speed: functional anatomy by positron emission tomography. *J. Neurosci.* **11**, 2383–2402.
- Desimone, R., and Schein, S.J. (1987). Visual properties of neurons in area V4 of the macaque: sensitivity to stimulus form. *J. Neurophysiol.* **57**, 835–868.
- Dobkins, K.R., and Albright, T.D. (1994). What happens if it changes color when it moves? The nature of chromatic input to macaque visual area MT. *J. Neurosci.* **14**, 4854–4870.
- Duncan, J. (1984). Selective attention and the organization of visual information. *J. Exp. Psychol. Gen.* **113**, 501–517.

- Duncan, J. (1996). Cooperating brain systems in selective perception and action. In *Attention and Performance YVI*, T. Inui and J.L. McClelland, eds. (Cambridge, MA: MIT Press), pp. 549–578.
- Ferrera, V.P., Rudolph, K.K., and Maunsell, J.H. (1994). Responses of neurons in the parietal and temporal visual pathways during a motion task. *J. Neurosci.* *14*, 6171–6186.
- Gegenfurtner, K.R., and Kiper, D.C. (2003). Color vision. *Annu. Rev. Neurosci.* *26*, 181–206.
- Holcombe, A.O., and Cavanagh, P. (2001). Early binding of feature pairs for visual perception. *Nat. Neurosci.* *4*, 127–128.
- Humphrey, G.K., and Goodale, M.A. (1998). Probing unconscious visual processing with the McCollough effect. *Conscious. Cogn.* *7*, 494–519.
- James, W. (1890). *The Principles of Psychology* (New York: Dover Publications).
- McAdams, C.J., and Maunsell, J.H. (2000). Attention to both space and feature modulates neuronal responses in macaque area V4. *J. Neurophysiol.* *83*, 1751–1755.
- Melcher, D., and Morrone, M.C. (2003). Spatiotopic temporal integration of visual motion across saccadic eye movements. *Nat. Neurosci.* *6*, 877–881.
- Melcher, D., Crespi, S., Bruno, A., and Morrone, M.C. (2004). The role of attention in central and peripheral motion integration. *Vision Res.* *44*, 1367–1374.
- Motter, B.C. (1994). Neural correlates of attentive selection for color or luminance in extrastriate area V4. *J. Neurosci.* *14*, 2178–2189.
- O'Craven, K., Downing, P., and Kanwisher, N. (1999). fMRI evidence for objects as the units of attentional selection. *Nature* *401*, 584–587.
- Pessoa, L., Kastner, S., and Ungerleider, L.G. (2003). Neuroimaging studies of attention: from modulation of sensory processing to top-down control. *J. Neurosci.* *23*, 3990–3998.
- Raymond, J.E., O'Donnell, H.L., and Tipper, S.P. (1998). Priming reveals attentional modulation of human motion sensitivity. *Vision Res.* *38*, 2863–2867.
- Robertson, L.C. (2003). Binding, spatial attention and perceptual awareness. *Nat. Rev. Neurosci.* *4*, 93–102.
- Saenz, M., Buracas, G.T., and Boynton, G.M. (2002). Global effects of feature-based attention in human visual cortex. *Nat. Neurosci.* *5*, 631–632.
- Schoenfeld, M.A., Tempelmann, C., Martinez, A., Hopf, J.M., Sattler, C., Heinze, H.J., and Hillyard, S.A. (2003). Dynamics of feature binding during object-selective attention. *Proc. Natl. Acad. Sci. USA* *100*, 11806–11811.
- Sohn, W., Papathomas, T.V., Blaser, E., and Vidnyánszky, Z. (2004). Object-based cross-feature attentional modulation from color to motion. *Vision Res.* *44*, 1437–1443.
- Treisman, A. (1999). Solutions to the binding problem: progress through controversy and convergence. *Neuron* *24*, 105–110.
- Treue, S., and Martinez-Trujillo, J.C. (1999). Feature-based attention influences motion processing gain in macaque visual cortex. *Nature* *399*, 575–579.
- Valdés-Sosa, M., Bobes, M.A., Rodriguez, V., and Pinilla, T. (1998). Switching attention without shifting the spotlights object-based attentional modulation of brain potentials. *J. Cogn. Neurosci.* *10*, 137–151.
- Watson, A.B., and Pelli, D.G. (1983). QUEST: a Bayesian adaptive psychometric method. *Percept. Psychophys.* *33*, 113–120.
- Wolfe, J.M., and Cave, K.R. (1999). The psychophysical evidence for a binding problem in human vision. *Neuron* *24*, 11–17.
- Wu, D.A., Kanai, R., and Shimojo, S. (2004). Vision: steady-state misbinding of colour and motion. *Nature* *429*, 262.
- Yantis, S., and Serences, J.T. (2003). Cortical mechanisms of space-based and object-based attentional control. *Curr. Opin. Neurobiol.* *13*, 187–193.