Cross-feature spread of global attentional modulation in human area MT+

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Feature-based attention affects the processing of the selected feature throughout the visual field. Here, we show that such global attentional modulation is not restricted to the attended feature but spreads to task-irrelevant features that are bound to the attended one. Attention to a color in one of the visual hemifields affected the processing of task-irrelevant motion in the other hemifield when it was associated with a stimulus that shared the attended color. This cross-feature global attentional selection increased the duration of the motion aftereffect and the strength of functional magnetic resonance imaging responses in the motion-sensitive area MT+, evoked by the task-irrelevant motion. These findings imply that features belonging to the same object are bound and selected jointly even outside the focus of attention. *NeuroReport* 16:1389–1393 © 2005 Lippincott Williams & Wilkins.

Key words: Feature-based attention; Functional magnetic resonance imaging; Motion aftereffect; MT+

INTRODUCTION

Attending to a feature in one location increases neural sensitivity to this feature throughout the visual field [1–4]. Such global attentional modulation was believed to be restricted to the feature selected inside the focus of attention [1,3,5]. However, a recent study [6] reported that global attentional modulation automatically spreads to task-irrelevant features that are spatiotemporally associated with the attended feature. Attending to a color in one location increased the sensitivity in motion discrimination at another location, only when the subthreshold motion prime was of the attended color. The goal of the present study was to test the behavioral and neural effects of cross-feature (color-to-motion) spreading of attentional modulation for suprathreshold motion stimuli.

We modified the paradigm of previous studies on global feature-based attention [1,3,7], in which attentional modulation outside the focus of attention was measured for the feature attended inside the focus of attention. To study attentional modulation across different features, we measured the processing of task-irrelevant motion signals that are spatiotemporally associated with the globally selected color. Observers attended to one of two colors, red or green, in a random-dot field placed in an aperture on one side of a central fixation mark. They were asked to ignore the stimulus presented simultaneously in an aperture on the other side of fixation, containing two transparent red and green dot fields. We compared the motion signal strength evoked by one of the motion components in the ignored area, using motion aftereffect (MAE) and functional magnetic resonance imaging (fMRI) responses, when its color matched the attended color, to that when it did not. If attention spreads to task-irrelevant features that are associated with the attended feature, the task-irrelevant moving dot field would evoke a stronger MAE, and larger fMRI responses in the motion-sensitive area MT+, when the color of the dots matches the globally selected color.

METHODS

Experiment 1: psychophysics

Observers Two authors (W.S., Z.V.) and two naïve observers participated in the experiment. All had normal or corrected-to-normal visual acuity and gave written consent, approved by the Rutgers University Ethics Committee.

Stimuli During motion adaptation, random dots (3.6 arcmin) with limited lifetime (200 ms) drifted at 0.8°/s against a black background in two rectangular apertures (6° × 8°), one on each side of fixation (Fig. 1a). In the attended field, colored dots (80 red, 80 green) moved randomly. Occasionally, 70% of dots within each colored field increased their luminance for 200 ms. In the unattended field, one colored group of dots (n=100), say red, moved upward, and the other (n=60), say green, moved horizontally, alternating direction (left, right) every 4 s. Because the horizontal motion was balanced over time, any directional MAE was due to the upward motion. The MAE test consisted of a static field of 100 random dots only in the unattended aperture, identically colored to the dots moving upward.

Procedure The green dots' luminance was adjusted to have the same perceptual luminance as red (fixed at 5.52 cd/m^2)

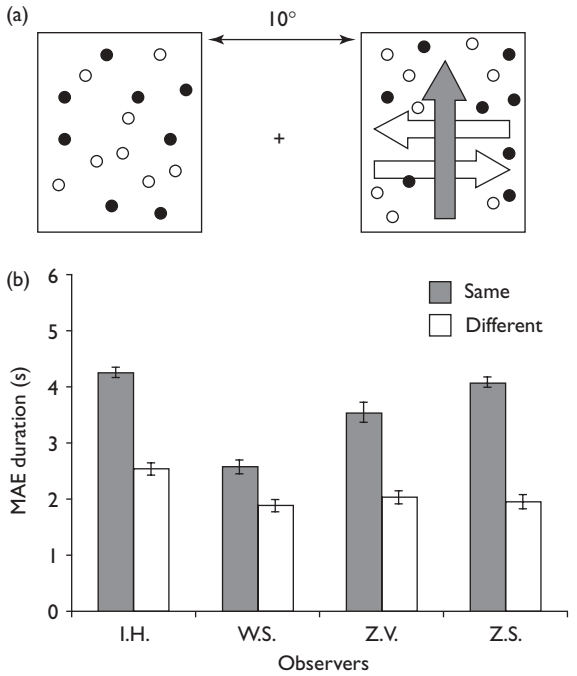

Fig. 1. Experiment 1: psychophysics. (**a**) Adaptation stimuli. Red/green dots are shown as black/white, respectively. Left aperture is attended area, where luminance increment events occurred in randomly moving dots. Right aperture is unattended. Gray and white arrows indicate motion directions of colored dot populations. After adaptation, the test stimulus was presented only in the unattended area. (**b**) MAE durations for four observers in the unattended area are shown for 'same' (gray bars) and 'different' (white bars) conditions. Error bars show standard error of the mean.

for each observer, using a locally paired dot display [8]. During 40 s of adaptation, observers fixated a central point and performed the luminance-increment detection task in red or green dots in the attended aperture. Luminance increments producing 75%–85% correct performance were determined for each observer. Observers pressed a key as soon as they detected a luminance-increase event in the attended color. Responses within 1 s from event onset were scored as hits [9]. We used the terms 'same' and 'different' for conditions in which the color of the upward motion in the ignored area matched and did not match the attended color, respectively. A 600-ms blank screen preceded the MAE test, where observers reported the MAE duration by pressing a key to indicate MAE cessation. The next trial began 1 s after the observer's response. The location of the attended visual field (left or right of fixation), the attended dots' color (red or green), and the color of the upward moving dots were counterbalanced across blocks. Observers performed 16 six-trial blocks, yielding 48 MAE duration measurements per condition.

Experiment 2: functional magnetic resonance imaging

Observers One author (S.C.) and five naïve observers participated in the experiment. All had normal or corrected-to-normal visual acuity, and were in good health, with no past history of psychiatric or neurological diseases. They gave informed written consent, approved by the Princeton University Ethics Committee.

Stimulus During the stimulus presentation period, there were two rectangular apertures (6.2×9.7), each containing 160 random dots (5.8 arcmin, 80 red, 80 green) with limited lifetime (200 ms) (Fig. 2a). In the attended field, all dots were flickering asynchronously, with the same luminance-increase events as in Experiment 1. In the ignored aperture, 80 dots of one color were flickering. The other 80 moved coherently (0.9°/s), changing their direction every 4 s by 30° (CW or CCW) to avoid motion adaptation. The initial direction was randomly determined in each trial.

Procedure Each observer had at least a two-hour practice session outside the scanner. Equiluminance and task-difficulty were adjusted inside the scanner (see Experiment 1 for details). In the main experiment, an 8-s resting period preceded each stimulus presentation. During the resting period, only a white fixation point was present. At the end of the resting period, the fixation point changed to red or green for 2 s, indicating the to-be-attended color in the trial. During the 24 s of stimulus presentation, observers fixated the central point while detecting luminance increases in the attended color. Stimulus configuration was the same throughout a scan; only the attentional target alternated between red and green. Thus, the condition in which the attended color matched the color of the coherently moving dots in the ignored field ('same') and in which it did not ('different') alternated. The location of the attended visual field (left, right), the color of the attended dots (red, green) and the color of the moving dots were counterbalanced across scans.

Image acquisition: The 3.0 T head-dedicated Siemens MAGNETOM Allegra scanner was used at Princeton University. A Macintosh G4, synchronized with the scanner, drove an LCD projector to present the visual stimuli on a translucent screen located at the back of the scanner. Stimuli were viewed from inside the magnet bore by a mirror system attached to the head coil. We collected functional images using 25 coronal slices (slice thickness 3 mm, inter-slice distance 1 mm and in-plane resolution 3×3 mm). We used standard T2-weighted echoplanar imaging to acquire all functional scans (TR=2000 ms, TE=30 ms, flip=90). Participants completed at least nine 228-s scans [4 s of initial resting period + (24 s of stimulus presentation + 8 s of resting period) $\times$ 7], each acquiring 114 volumes for the functional scans of the main experiment, and two additional 268-s scans [12 s of initial resting period + (16 s of moving/static dots + 16 s of resting period) $\times$ 8], each acquiring 134 volumes for the functional scans of the MT+ localizer. The first resting and experimental blocks were discarded in the analysis to exclude the task-irrelevant, initial attentional effects [10]. A T1 magnetization-prepared gradient echo scan was acquired for more accurate localization of brain structures.

Localizing retinotopic areas Flattened retinotopy maps were obtained for three of six observers from separate scan sessions, following well established methods [11,12]. To visualize retinotopy measurements, a high-resolution magnetic resonance imaging of each observer's brain was computationally flattened [11].

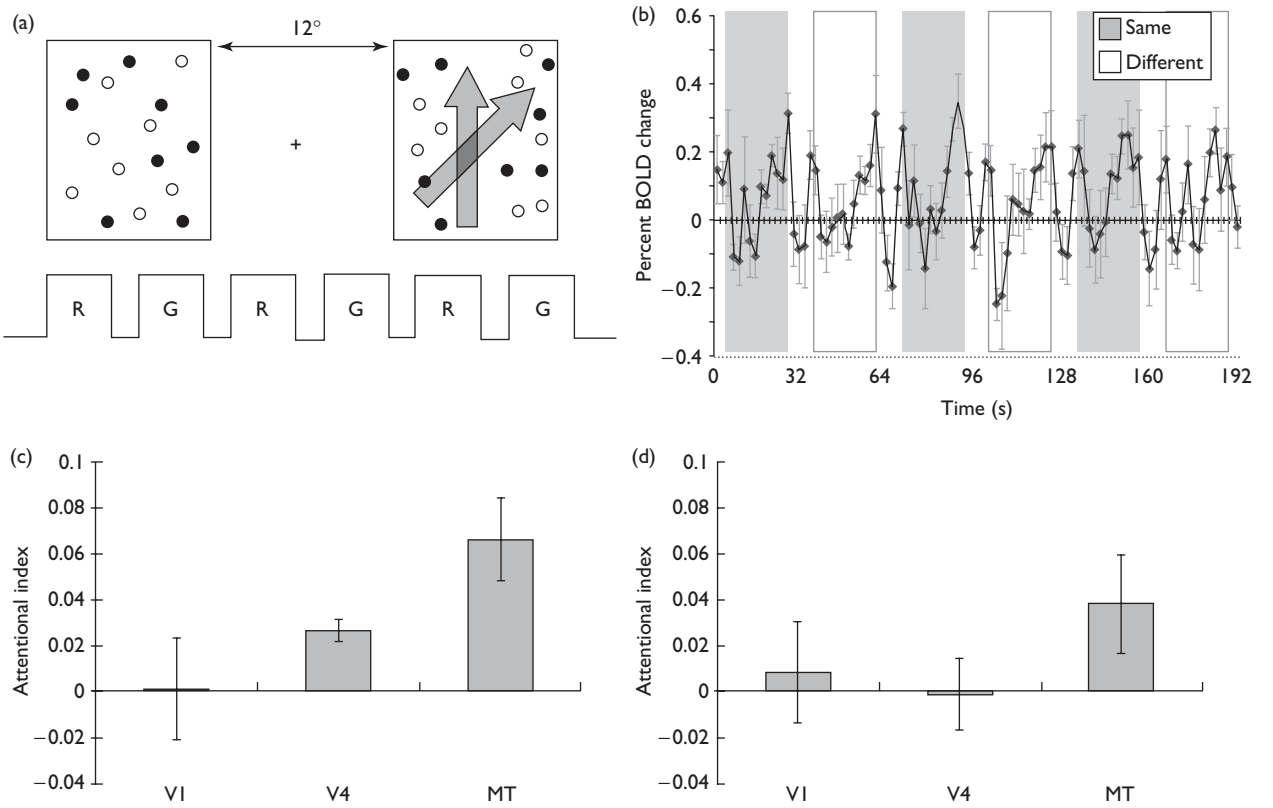

Fig. 2. Experiment 2: functional magnetic resonance imaging (fMRI). (**a**) Stimuli for 'stimulus presentation' interval. Red/green dots are shown as black/white, respectively. Left aperture is attended area. Observers detected luminance increment events in flickering dots of one color. Right aperture is unattended. Gray arrows indicate two consecutive directions of the coherently moving dots of one color, say red; the other dots (green) were flickering. Scan profile is shown in the lower panel. 'Attend-to-red' and 'attend-to-green' conditions alternated; thereby 'same' (coherently moving dots matched attended color) and 'different' conditions (did not match) alternated. (**b**) fMRI time series of %blood oxygen-level-dependent (BOLD) change to the unattended area is shown for MT+, averaged across five observers' mean values. Shaded area indicates 'same', and boxed area 'different' conditions. Attentional modulation in the tested visual areas for the unattended (**c**) and for the attended stimulus aperture (**d**). Error bars show standard error of the mean.

Localizing MT+ The human homolog of the MT/MST complex (MT+) was defined on the basis of fMRI response to stimuli that alternated in time between moving and stationary dot patterns. Three intervals, motion, static, and the resting period, existed, each lasting 16 s. In the motion sequence, white dots moved coherently (0.9°/s) against a black background, changing direction randomly every 4 s. In the static sequence, static dots regenerated their positions every 4 s. In the resting period only the fixation point was present. Motion and static intervals alternated with a resting period in-between. A single scan consisted of four motion and static intervals and nine resting intervals (initial and eight in-between). We selected the voxels beyond the retinotopically organized visual areas that produced significantly larger percent blood oxygen-level-dependent (BOLD) change to the motion than the static stimulus ($p<0.000083$). Average Talairach coordinates of six participants' MT+ were 46 ± 4 (X), -63 ± 5 (Y), and -1 ± 3 (Z), which were consistent with findings from previous studies [13,14].

Data analysis: We discarded data from scans in which observers' behavioral performance fell below 60% correct. After screening such scans, we excluded an observer from analysis because only two scans were left for this observer. The number of scans considered in the data analysis was 5–12 per observer. All analyses were conducted using Brain Voyager (Brain Innovation, Maastricht, Netherlands). Functional data were motion-corrected and linear trends were removed. Temporal smoothing with a high-frequency pass filter (3 Hz) and spatial smoothing with a 4 mm Gaussian filter were applied. Functional data were aligned to the structural three-dimensional image and transformed into Talairach coordinates. The data were analyzed using the general linear model and specified contrasts for ;each condition. We analyzed the BOLD response to the attended and unattended stimulus separately in each of three visual areas, V1, V4, and MT+. For the retinotopic areas V1 and V4, we restricted the analysis to the voxels within each visual area that showed significantly larger responses to the visual stimuli than to the blank screen, regardless of the two different experimental conditions ($p<0.016$).

Attentional index To quantify attentional effects, an attentional index (AI) was calculated as follows:

$$AI = (\%BOLD_{same} - \%BOLD_{diff})/[abs(\%BOLD_{same}) + abs(\%BOLD_{diff})],$$

where $\%BOLD_{same}$ and $\%BOLD_{diff}$ are the signals in the 'same' and 'different' conditions, respectively. Positive AI

indicates higher fMRI responses during the 'same' than during the 'different' condition.

RESULTS

The results of Experiment 1 (Fig. 1b) show strong color-to-motion cross-feature attentional effects on the unattended hemifield. The MAE in the 'same' condition was on average about 70% longer than the 'different' condition. The results suggest that the global color-specific attentional modulation outside the locus of attention spreads to the motion signal of the dots whose color matches the attended one. Importantly, observers' performance in the attentional task was not significantly different in the two conditions [$t(3)=2.324$, $p=0.103$], excluding the possibility that the observed attentional effects are due to different attentional loads in the two conditions.

Analogous findings were observed in the fMRI experiment (Fig. 2b–d). The time series of fMRI responses in contralateral MT+ to the ignored stimulus is shown in Fig. 2b. Because MT+ is more responsive to coherent motion than flickering patterns [15], larger MT+ responses to this stimulus are expected when the coherent motion, rather than the flickering dots, is selected by global attention. fMRI responses to the ignored visual display were larger in the 'same' than in the 'different' condition; significantly higher than zero AI was observed in the motion-sensitive area MT+ ($p=0.032$) and area V4 ($p=0.043$), but not in V1 ($p=0.90$) (Fig. 2c). In all tested visual areas that are contralateral to the attended display, on the other hand, the average AI for the attended stimulus was not significantly different from zero ($p=0.74$, 0.95, and 0.18, for V1, V4, and MT+, respectively) (Fig. 2d). Behavioral performances for the luminance-increment detection indicated no difference in the attentional load between the two conditions (same: 72.4% correct, different: 71.9%, $p=0.88$).

DISCUSSION

Attention to a specific feature of a stimulus triggers global attentional modulation leading to increased neural responses to the same feature throughout the visual field, in early visual areas V1, V2, V3, V4 and MT [1,4,16–18]. The present study supports a recent finding [6] that such attentional modulation outside the focus of attention is not restricted to the selected feature, but also affects the processing of task-irrelevant features that are associated with the attended one. We observed that attentional spread from color to motion affects the strength of the MAE and the magnitude of the fMRI responses in human area MT+. The results of our study extend our knowledge on global cross-feature attention by showing that it affects the processing of suprathreshold motion stimuli, analogously to the case of subthreshold motion signals [6]. Moreover, we provide the first fMRI evidence for cross-feature spreading of attention outside the attentional focus.

Attentional effects in task-irrelevant motion processing observed in the fMRI experiment cannot be explained solely on the basis of the global selection of color, without invoking cross-feature mechanisms. Because the ignored stimulus contained the same number of red and green dots, even when direct effects of color-based global selection are observed in the motion-sensitive area MT+ [3], such attentional effects would be balanced for 'same' and 'different' conditions. In addition, the observed attentional effects cannot be due to larger MT+ responses to one color versus the other, because we alternated the colors that were associated with coherent moving and flickering dots across scans. Therefore, we conclude that the attentional effects found in MT+ should be mediated by color-to-motion cross-feature spreading of global attentional modulation.

Interestingly, the 'same' condition evoked significantly stronger fMRI responses than the 'different' condition in area V4 as well, which is known to be involved in color processing. Because the stimuli in these two conditions differed only along the motion but not the color dimension, the attentional effects in V4 cannot be explained on the basis of global color-specific selection mechanisms. A previous study [3] also reported that global color-specific attention resulted in increased fMRI responses not only in color-sensitive area V4 but also in motion-sensitive area MT+. A possible explanation for these results might be based on binding mechanisms that link all the visual features that belong to the same visual object/surface [19–21]. If the neural responses in a visual area that is selective to a particular feature of a stimulus are increased by attention, this increase may be transmitted – by reciprocal connections – to other feature-specific areas that are activated by the same stimulus. In our experiment, increased responses in MT+ due to cross-feature spreading of global attention (larger responses in 'same' than in 'different' conditions) may have in turn generated increased responses in the subset of V4 neurons that are responsive to the same dot field.

In conclusion, our results provide both behavioral and fMRI evidence for color-to-motion cross-feature spread of global attentional modulation. Our findings imply that visual features that belong to the same object are bound together and modulated jointly by global attentional mechanisms, even when they are outside the focus of attention.

REFERENCES

1. Treue S, Martinez-Trujillo JC. Feature-based attention influences motion processing gain in macaque visual cortex. *Nature* 1999; **399**:575–579.
2. McAdams CJ, Maunsell JH. Attention to both space and feature modulates neuronal responses in macaque area V4. *J Neurophysiol* 2000; **83**:1751–1755.
3. Sáenz M, Buracas GT, Boynton GM. Global effects of feature-based attention in human visual cortex. *Nat Neurosci* 2002; **5**:631–632.
4. Liu T, Slotnick SD, Serences JT, Yantis S. Cortical mechanisms of feature-based attentional control. *Cereb Cortex* 2003; **13**:1334–1343.
5. Reynolds JH, Chelazzi L. Attentional modulation of visual processing. *Annu Rev Neurosci* 2004; **27**:611–647.
6. Melcher D, Papathomas TV, Vidnyánszky Z. Implicit attentional selection of bound visual features. *Neuron* 2005; **46**:723–729.
7. Sáenz M, Buracas GT, Boynton GM. Global effects of feature-based attention for motion and color. *Vision Res* 2003; **43**:629–637.
8. Sohn W, Papathomas TV, Blaser E, Vidnyánszky Z. Object-based cross-feature attentional modulation from color to motion. *Vision Res* 2004; **44**:1437–1443.
9. Neisser U, Becklen R. Selective looking: attending to visually specified events. *Cogn Psychol* 1975; **7**:480–494.
10. Kastner S, DeWeerd P, Desimone R, Ungerleider LG. Mechanisms of directed attention in the human extrastriate cortex as revealed by functional MRI. *Science* 1999; **282**:108–111.

11. Engel SA, Glover GH, Wandell BA. Retinotopic organization in human visual cortex and the spatial precision of functional MRI. *Cereb Cortex* 1997; **7**:181–192.
12. Sereno MI, Dale AM, Reppas JB, Kwong KK, Belliveau JW, Brady TJ *et al*. Borders of multiple visual areas in humans revealed by functional MRI. *Science* 1995; **268**:889–893.
13. Tootell RB, Reppas JB, Kwong KK, Malach R, Born RT, Brady TJ *et al*. Functional analysis of human MT and related visual cortical areas using magnetic resonance imaging. *J Neurosci* 1995; **15**: 3215–3230.
14. Kourtzi Z, Bulthoff HH, Grodd W. Object-selective responses in the human motion area MT/MST. *Nat Neurosci* 2001; **5**:17–18.
15. Muckli L, Singer W, Zanella F, Goebel R. Integration of multiple motion vectors over space: an fMRI study of transparent motion perception. *Neuroimage* 2002; **16**:843–856.
16. Beauchamp MS, Cox RW, DeYoe EA. Graded effects of spatial and featural attention on human area MT and associated motion processing areas. *J Neurophysiol* 1997; **78**:516–520.
17. Motter BC. Neural correlates of attentive selection for color or luminance in extrastriate area V4. *J Neurosci* 1994; **14**:2178–2189.
18. Martinez-Trujillo JC, Treue S. Feature-based attention increases the selectivity of population responses in primate visual cortex. *Curr Biol* 2004; **14**:744–751.
19. Duncan J. Cooperating brain systems in selective perception and action. In: Inui T, McClelland JL (eds). *Attention and Performance XVI*. Cambridge: MIT Press; 1996, pp. 549–578.
20. Wolfe JM, Cave KR. The psychophysical evidence for a binding problem in human vision. *Neuron* 1999; **24**:11–17.
21. Robertson LC. Binding, spatial attention and perceptual awareness. *Nat Rev Neurosci* 2003; **4**:93–102.

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