Feature-based attention involuntarily and simultaneously improves visual performance across locations

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Selective attention can selectively increase sensitivity to particular visual features in order to prioritize behaviorally relevant stimuli. Moreover, neural responses to attended feature values are boosted even at ignored locations. We provide behavioral evidence for involuntary and simultaneous effects of this "global" feature-based attention on visual performance. Observers were cued to attend to dots moving in a particular direction at one location (the primary task), while discriminating which of two groups of moving dots on the other side of the screen contained coherent motion (the secondary task). An analogous experiment tested selective attention to orientation. The secondary tasks did not require observers to discriminate or selectively attend to the particular feature values present. Nonetheless, sensitivity was highest when the direction or orientation happened to match the one cued in the primary task. By comparing performance to a neutral condition, we revealed more enhancement of attended feature values than suppression of others.

Introduction

An ideal visual system would not waste metabolic resources on analyzing the images of objects that have no bearing on current or future decision-making. The ideal level of efficiency is out of reach because it is difficult to predict which objects will become relevant and where they will be. Nonetheless, several visual functions help prioritize behaviorally relevant stimuli. First, eye movements center the high-resolution fovea on important locations. Second, without eye movements, covert spatial attention facilitates processing at some locations at the expense of others (e.g., Pestilli & Carrasco, 2005; Posner, 1980). Third, feature-based attention selectively increases sensitivity to the features of relevant objects, such as their orientations, motion directions, and colors (e.g., Maunsell & Treue, 2006). Note that the term feature-based attention sometimes is used to describe attention to one feature dimension or another (e.g., motion vs. color; Serences, Liu, & Yantis, 2005), whereas in this paper, like those reviewed below, we are concerned with attention to particular feature *values* within a dimension (e.g., upward vs. downward motion).

Advance knowledge of an upcoming object's features boosts sensitivity in the sensory channels best tuned for those features relevant to the task at hand (Baldassi & Verghese, 2005; Ling, Liu, & Carrasco, 2008; Scolari & Serences, 2009; Shulman & Wilson, 1987). Feature-based selection is especially useful in visual search, when an object's features are known but its location is not (Bichot, Rossi, & Desimone, 2005; Buracas & Albright, 2009; Wolfe & Horowitz, 2004). Furthermore, observers can selectively process targets that are spatially coextensive with distractors of different feature values. Such selection modulates adaptation (Alais & Blake, 1999; Lankheet & Verstraten, 1995), neural responses (David, Hayden, Mazer, & Gallant, 2008; Fallah, Stoner, & Reynolds, 2007; Haenny & Schiller, 1988; Hayden & Gallant, 2005; Kamitani & Tong, 2006; Liu, Larsson, & Carrasco, 2007; Müller et al., 2006; Patzwahl & Treue, 2009; Serences, Saproo, Scolari, Ho, & Muftuler, 2008), and perceptual performance (Felisberti & Zanker, 2005; Ling et al., 2008; Liu, Stevens, & Carrasco, 2007). Feature-based attention is, therefore, distinct from spatial selection, in that it operates even when the location of the target is unknown or competing features are superimposed. Does this imply that it is completely unconstrained in spatial extent, such that it modulates perception beyond the location where selective feature-based attention is willfully deployed?

The properties of visual cortex seem to allow for such a possibility. Middle temporal (MT) neurons in macaque monkeys respond more strongly to an ignored moving stimulus if they prefer directions similar to that of an attended stimulus in the opposite hemifield, and they are suppressed if they prefer very different directions, relative

to when the monkeys attended only to a fixation mark (Martinez-Trujillo & Treue, 2004; Treue & Martinez-Trujillo, 1999). These effects formed the basis of Treue and Martinez-Trujillo's "feature-similarity gain model" of attention: The responses of visual neurons are modulated by the similarity between the attended feature values and the values they prefer, independently of the stimulus present in the receptive field and its location.

Human neuroimaging experiments have also demonstrated this "global spread" of feature-based attention. When observers selectively attend to one of two superimposed dot fields, the BOLD response to an ignored stimulus in the other hemifield is strongest if it has the same direction or color (Saenz, Buracas, & Boynton, 2002; for similar EEG findings, see Zhang & Luck, 2008). In a similar paradigm, the attended direction has been classified from cortical regions that received no sensory stimulation at all, suggesting that direction-specific attentional signals bias baseline activity levels across the visual field (Serences & Boynton, 2007).

These neurophysiological studies imply that entire retinotopic areas become more responsive to the feature values of an attended object. What are the perceptual consequences of these neural activity patterns? Behavioral studies on the phenomenon have mostly used two indirect strategies: measuring perceptual aftereffects and measuring performance in simultaneous discriminations of spatially separated stimuli.

Adaptation aftereffects have demonstrated that feature-based attention applied at one location modulates processing of an ignored adaptor in the other hemifield (Boynton, Ciaramitaro, & Arman, 2006; Kanai, Tsuchiya, & Verstraten, 2006; Liu & Mance, 2011; Zirnsak & Hamker, 2010). In addition, subthreshold moving dots at an ignored location have a greater priming effect on subsequent test stimuli if they move in the same direction as another attended stimulus (Melcher, Papathomas, & Vidnyanszky, 2005). These aftereffect experiments are consistent with the neurophysiological studies, but as they measure perception of other stimuli after the deployment of feature-based attention, they do not address how the involuntary spatial spread simultaneously affects visual performance.

Another line of research has sought to demonstrate effects of global feature-based attention on visual performance with dual discrimination tasks. In these studies, two stimuli are displayed simultaneously and observers are better able to discriminate a feature of both of them if they are similar rather than different (Lu & Itti, 2005; Saenz, Buracas, & Boynton, 2003; Sally, Vidnyanszky, & Papathomas, 2009). Performance benefits for similar stimuli are consistent with the global nature of feature-based attention: for example, a relative increase in sensitivity to the orientation of stimulus A at the location of stimulus B will help performance if B's orientation is similar to A's and hinder performance otherwise.

These dual-task experiments are interesting in their own right, but they differ in important ways from the neurophysiological experiments reviewed above: (1) The neurophysiology shows *involuntary* spreading of gain changes, whereas in these performance studies observers willfully attended to the same features of both stimuli. Therefore, these results are also consistent with the theoretically distinct hypothesis that attempting to divide attention within feature space is more difficult than attending to only one feature value. (2) In some studies (Lu & Itti, 2005; Sally et al., 2009), the pairs of stimuli may perceptually group and, thus, be easier to process when they share features than when they do not (e.g., Ben-Av & Sagi, 1995; Carrasco & Chang, 1995). Such a stimulus-based effect could contribute to the effects on performance, as the physical display and the attended features covaried. Furthermore, no study with human observers (behavioral or neuroimaging) has tested whether the relative benefit for attended or matching feature values is due in part to a suppression of others, relative to a neutral condition.

The goal of the current study was to investigate how global feature-based attention concurrently affects visual performance with a design that allows for a closer link with the neurophysiological data. In two dual-task experiments, we studied attentional selection by motion direction and orientation. In the primary tasks, observers were cued to monitor stimuli with one feature value (direction or orientation) at a location that was also occupied by distractors. To measure the effect of feature-based cues at that location, we compared performance to a neutral condition in which observers attended equally to both directions or both orientations. For the secondary tasks, two noisy stimulus arrays appeared in the other hemifield during the presentation of the primary stimuli and observers reported which contained coherent motion or orientation. We evaluated how sensitivity to each direction/orientation in the secondary stimuli was increased by switching attention in the primary task from the opposite to the same direction/orientation, while keeping the display constant. Differences between the secondary and primary stimuli prevented grouping. Furthermore, the particular feature values of the secondary stimuli were task-irrelevant, so observers had no reason whatsoever to willfully attend to them in a selective manner. Comparison with the neutral condition allowed us to determine whether the effects were caused more by enhancement of similar features or suppression of dissimilar features.

Experiment 1—Motion direction

Methods

Observers

Thirteen observers (five females) with normal or corrected-to-normal vision participated. Nine were graduate students or postdoctoral fellows in the NYU Psychology Department (including one author), and eight were

experienced in psychophysical tasks. All observers (but one author) were naive to the purposes of the study.

Apparatus

Stimuli were presented in a darkened room with an Apple Macintosh iMac on a calibrated and linearized CRT monitor (ViewSonic P810) with a refresh rate of 75 Hz and mean luminance of 47 cd/m^2, viewed at a distance of 57 cm with a chin rest. Stimuli were programmed in MATLAB (The MathWorks, Natick, MA) using the MGL toolbox (http://gru.brain.riken.jp/mgl).

Stimuli and trial sequence

Figure 1 shows a sample trial sequence. Observers fixated the central cross (0.3°), while the primary stimuli appeared for a random duration between 800 and 1290 ms. These were composed of random dots (0.09° × 0.09°; 12 dots/deg^2) confined within a circular aperture 8.3° in diameter centered at 7° eccentricity on the horizontal midline. Half of the dots moved upward and half downward, with unlimited lifetimes. Dots that reached the edge of the aperture were moved to the opposite side and redrawn. Their luminance (14 or 80 cd/m^2) and starting speed (3.75, 4, or 4.25 deg/s) varied randomly in each trial (but were the same for all dots). On a random half of trials, the speed of one of the two groups of dots increased 293 ms before stimulus offset.

The secondary stimuli were moving dots (9 dots/deg^2) of the same size presented within two circular apertures 8.3° in diameter, positioned 7° in eccentricity at a 45° angle from the horizontal midline, one above and one below. To reduce grouping by similarity, the dots' contrast polarity was always the opposite of the primary dots on that trial (luminance = 14 or 80 cd/m^2), but their speed was always equal to the primary dots' starting speed.

In one of the secondary apertures, the direction of each dot was selected independently from a uniform distribution (0–360°). In the other, a fraction of the dots moved coherently either upward or downward. This coherence level varied randomly by trial among a set of 7–9 equally spaced values between 5% and 100% chosen to span the dynamic range of each observer's psychometric function. The secondary stimuli appeared for 293 ms at a pseudorandom time between 200 ms after the onset and 293 ms before the offset of the primary stimuli. Their onset occurred before the speed change in the primary stimuli 60% of the
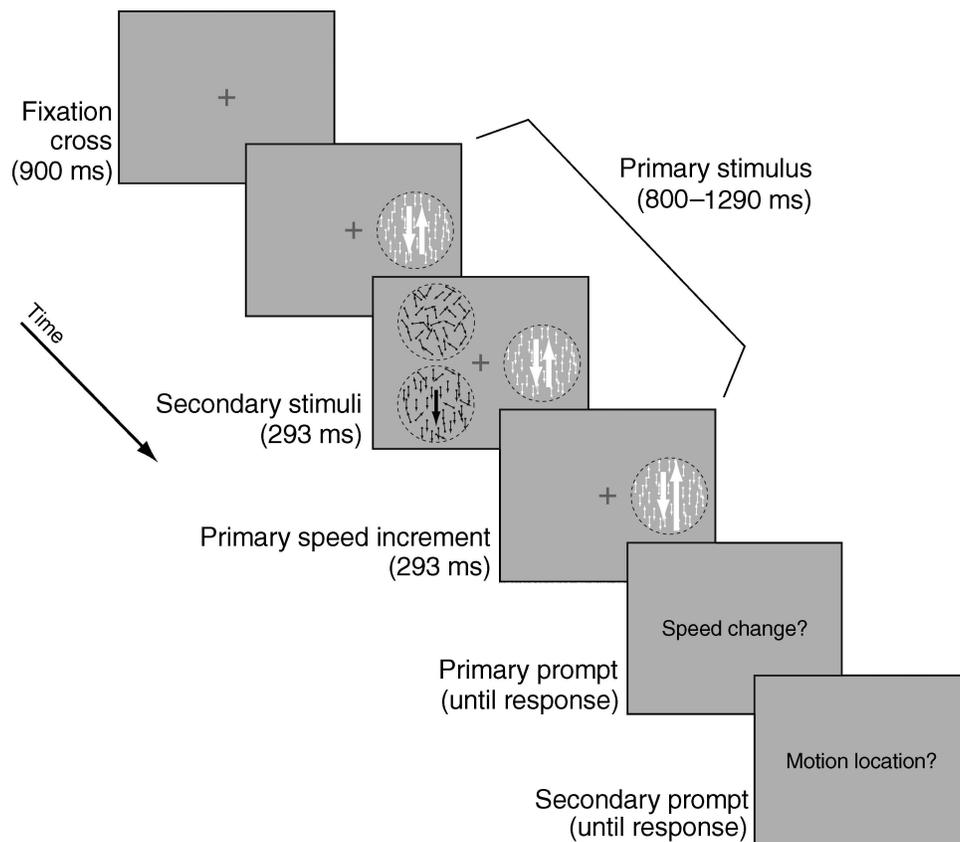

Figure 1. Sample trial sequence for Experiment 1. The length of arrows (not present in the actual experiment) indicates relative speed; their thickness indicates relative proportions of dots. Dashed outlines were not present in actual experiment. This is a mismatch trial because the primary target dots move upward and the secondary coherent dots move downward.

time. In addition, on 60% of trials, they were still visible on at least 1 display frame after the speed change.

Tasks

The *primary* task was to report whether or not there was a speed increment in one of the primary groups of dots. QUEST staircases (Watson & Pelli, 1983) brought the ratios of incremented speed to starting speed to an estimate of the 85% correct threshold, separately for the downward- and upward-moving dots. The *secondary* task was to report which aperture (top or bottom) contained coherent motion. Observers were informed that the particular direction of the coherent motion was equally likely to be up or down, was task-irrelevant, and had no relation to the direction of the target dots in the primary stimuli. After each trial, observers responded first to the primary task and then to the secondary task with two key presses. Response time was unlimited, and auditory feedback was provided for the primary task only.

Procedure and attention conditions

Blocks of 105 trials were sequenced in groups of 3, one of each attention condition: neutral, cued up, and cued down, in pseudorandomized order without sequential repeats. In neutral blocks, the primary dots that increased speed were moving upward in a random half of trials and downward in the rest, and observers were instructed to attend equally to both at the block's start. In cued blocks, the speed change was always in dots of one direction, which observers were instructed to attend to. The color of the fixation mark indicated the potential speed change direction: white for either (in neutral blocks), red for downward, and green for upward. The primary stimulus alternated between the left and right sides of the screen every 3 blocks (the secondary stimuli were always on the opposite side).

At the start of each session, observers were given 90–200 practice trials (with auditory feedback on both tasks) until performance stabilized. At the end of each block, the screen displayed the overall percent correct in the primary task and in the secondary task for the highest coherence level. If the latter fell below 90%, observers were asked to try to increase secondary task performance. Each observer completed 2 to 3 1-h-long sessions of 6 blocks each.

Data analysis

Thresholds (85% correct) in the primary task were established via QUEST. For the secondary task, we obtained 75% correct thresholds by fitting Weibull curves to the patterns of performance as a function of motion coherence, using Psignifit version 2.5.6 (http://bootstrap-software.org/psignifit/; see Wichmann & Hill, 2001).

To test whether sensitivity in the secondary task was higher for coherent motion in the direction attended in the primary task, we separately analyzed trials in which the directions of the primary and secondary targets were the same ("match") or opposite ("mismatch"). Because similar effects occurred for each secondary stimulus direction, we report thresholds computed from data collapsed across both. Given the substantial theoretical work and empirical evidence regarding feature-based attention reviewed in the Introduction section, there is reason to predict that the feature cue enhances the attended features but no reason to expect that it suppresses them. Hence, we tested unidirectional hypotheses (*p*-values are one-tailed).

As a complementary, non-parametric analysis of the secondary task data, we computed bootstrapped confidence intervals of the mean difference in thresholds between each pair of conditions. To do this, we sampled with replacement from the set of threshold differences (one value per observer) 10,000 times, and on each repetition, we computed the mean of resampled differences. We then computed the 95% confidence interval (CI) of this distribution of mean differences and determined that a difference in threshold was significant if its CI did not include zero.

Results and discussion

Primary task

Figure 2A displays the speed-change detection thresholds averaged across directions and observers. Thresholds were significantly lower in the cued condition than in the neutral condition ($t(12) = 2.45$, $p = 0.015$, one-tailed). Thus, observers were better able to detect the speed change when they knew its direction in advance.

Secondary task

Figure 2B plots the average coherence thresholds for discriminating which aperture contained a coherent motion signal (average Weibull fit $R^2 = 0.91$). Thresholds were significantly lower in the cued match condition than in the cued mismatch condition ($t(12) = 2.32$, $p = 0.019$), which indicates that sensitivity was higher for motion in the direction that was attended on the other side of the display. Thresholds were lower in the cued match condition than in the neutral condition ($t(12) = 2.09$, $p = 0.029$), but there was no difference between cued mismatch and neutral thresholds ($t(12) < 1$). This suggests that attention enhanced sensitivity to the cued direction but hardly suppressed the opposite direction.

To confirm that the difference between cued match and mismatch thresholds depended on attentional selection of primary stimuli, we separately analyzed the 50% of trials in which no speed change was present, and thus, stimuli were identical between conditions (average $R^2 = 0.84$). The difference was still robust (match = 47.7%,
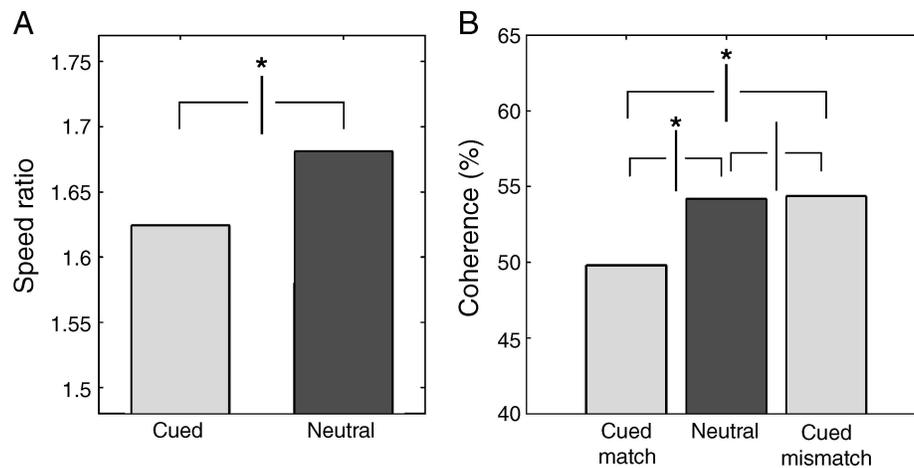
Figure 2. Results of Experiment 1. (A) Primary task. Speed ratio thresholds for the speed-change detection task for the average of the two directions. (B) Secondary task. Coherence thresholds were computed from both directions pooled. Error bars are ±1 standard deviation of the within-subject differences of the indicated conditions, and asterisks indicate $p < 0.05$.

mismatch = 53.8%; $t(12) = 2.16$, $p = 0.026$). To determine whether the effect remains with the same stimuli but without direction cues, we also analyzed trials from the neutral condition separately by whether primary and secondary target directions matched (average $R^2 = 0.81$). The difference in thresholds was slightly inverted and not significant (match = 55.2%, mismatch = 53.3%; $t(12) < 1$).

The bootstrapping analysis confirmed the results of these t-tests: whenever p was < 0.05, the 95% bootstrapped CI on threshold differences did not include zero and vice versa.

Experiment 2—Orientation

Methods

Experiment 2 tested attention to orientation rather than direction. Procedures were identical to Experiment 1 except as noted here.

Observers

Thirteen observers (four females) participated; five also participated in Experiment 1 (including one author). Seven were graduate students or postdoctoral fellows. All observers (but one author) were naive to the purposes of the study.

Stimuli and trial sequence

Figure 3 displays a sample trial sequence. Observers fixated the central cross (0.4°) during the appearance of the primary stimuli, which were rapid sequences of 4 circular sinusoidal gratings presented at 7° eccentricity on the horizontal midline. These were 6° in diameter, 1.9 cycles/

degree in spatial frequency, and 60% contrast; at their edges, contrast was ramped down linearly to zero over a 0.6° strip. Two gratings in the sequence were oriented (near) horizontally and two (near) vertically, in random order with blank frames in between. Three were exactly horizontal or vertical, but one (the target) was slightly tilted away from its cardinal axis.

The secondary stimuli were two 8×10 grids or "textures" of Gabor patches (sinusoidal gratings in Gaussian windows; $SD = 0.24°$; spatial frequency = 1.9 cycles/deg, cosine phase; contrast = 60%). The Gabors' center-to-center distance was 1.26°. Each texture subtended 10.02° × 12.54°. Their inner vertical and horizontal edges were 0.75° from the display's vertical and horizontal midlines, respectively. In one of the textures, the orientation of each Gabor was chosen independently from a uniform distribution (0–180°), with the constraint that at least one was exactly horizontal or vertical. In the other, a fraction of the Gabors (at randomly chosen positions) were all either horizontal or vertical. This coherence level was selected randomly on each trial from 6 to 9 values (5%–100%). The secondary textures appeared for 200 ms simultaneous with a random primary grating.

Tasks

The *primary* task was to report whether the target grating was tilted clockwise or counterclockwise relative to its closest cardinal axis. QUEST staircases brought the tilt magnitude to an estimate of the 85% correct threshold, separately for horizontal and vertical axes. The *secondary* task was to report which texture (top or bottom) contained coherent orientation. Observers were informed that the particular coherent orientation present in the texture was equally likely to be horizontal or vertical, was task-irrelevant, and had no relation to the orientation of the primary target.
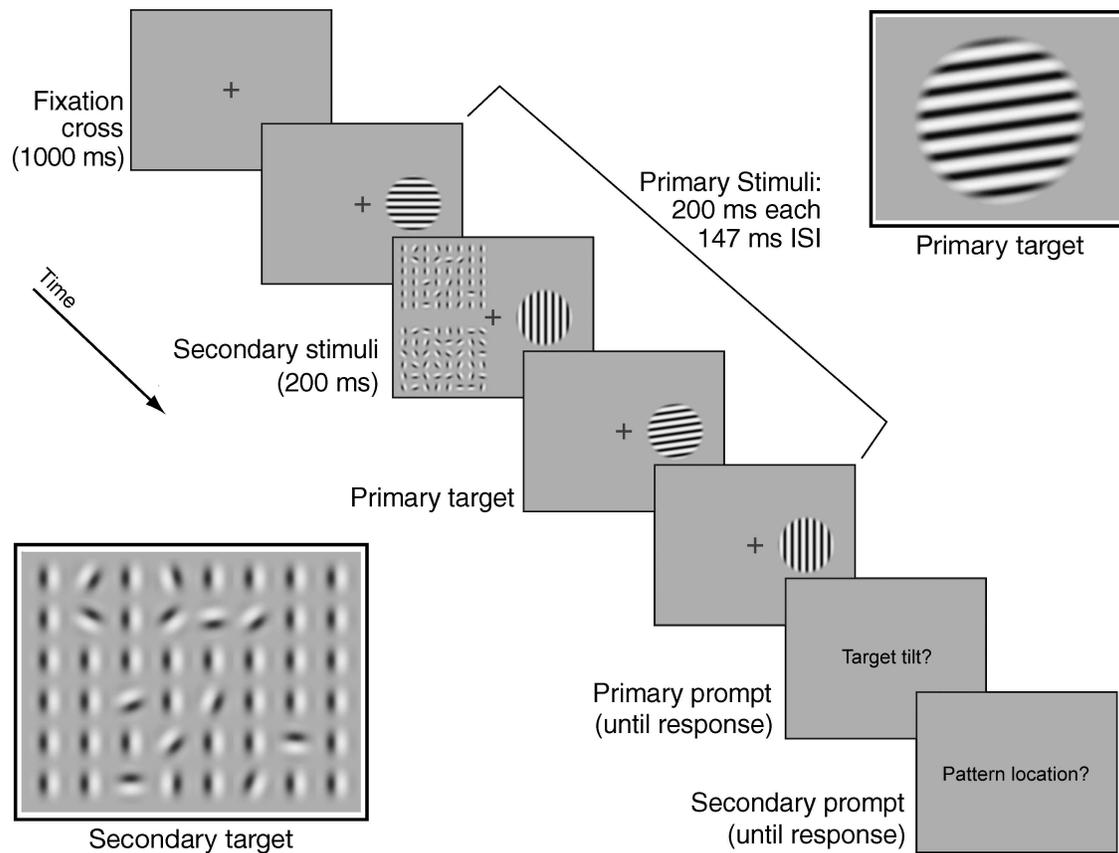
Figure 3. Sample trial sequence for Experiment 2 (not to scale). The top right inset shows the primary tilted target. The bottom left inset shows the secondary target texture (the uppermost of the two in the 3rd frame). This is a "mismatch" trial because the primary target is near horizontal and coherence in secondary target is vertical.

Procedure and attention conditions

In neutral blocks, the primary tilted target was near horizontal on a random half of the trials and near vertical on the rest. Within each cued block, the target's orientation was always near the same axis and observers were instructed to attend to gratings with orientations near that axis. The fixation mark's color indicated which axis the target could be near: white for either (neutral blocks), red for horizontal, and green for vertical.

Results and discussion

Primary task

Figure 4A displays tilt discrimination thresholds averaged across axes and observers. Thresholds were significantly lower in the cued condition than in the neutral condition ($t(12) = 4.59$, $p = 0.0003$). Therefore, attending selectively to stimuli near a cued axis improved orientation discrimination.

Secondary task

Figure 4B plots the average coherence thresholds for determining which of two textures had coherent orientation (similar results were found for each orientation so we report collapsed data; average $R^2 = 0.95$). Thresholds were significantly lower in the cued match condition than in the cued mismatch condition ($t(12) = 1.82$, $p = 0.047$), demonstrating that sensitivity was higher for the orientation attended in the primary task. Thresholds were lower in the cued match condition than in the neutral condition ($t(12) = 1.90$, $p = 0.041$), but there was no difference between cued mismatch and neutral thresholds ($t(12) < 1$), again demonstrating more enhancement than suppression.

To confirm that the difference between cued match and mismatch thresholds reflects feature-based attention rather than the presence of the primary targets, we separately analyzed the trials in which the secondary stimuli did not appear simultaneously with the primary target (average $R^2 = 0.93$). In these trials, the stimuli were identical between conditions, but the difference is robust (match = 26.3%, mismatch = 30.5%; $t(12) = 2.06$, $p = 0.031$). The critical role of attention is also supported by the fact that match and mismatch thresholds were nearly identical within the neutral condition (30.3% vs. 29.5%; $t(12) < 1$; average $R^2 = 0.88$).

The bootstrapping analyses confirmed these t-tests: whenever p was < 0.05, the 95% bootstrapped CI on threshold differences did not include zero and vice versa
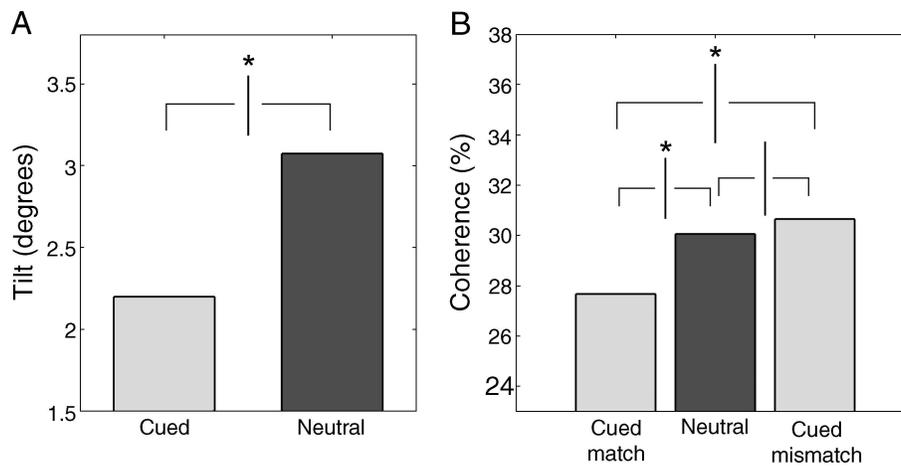
Figure 4. Results of Experiment 2. (A) Primary task. Tilt thresholds for the orientation discrimination task (average of the two axes). (B) Secondary task. Coherence thresholds were computed from both orientations pooled. Error bars are ±1 standard deviation of the within-subject differences of the indicated conditions, and asterisks indicate $p < 0.05$.

(except in the comparison of thresholds in the cued match and neutral conditions, in which the CI barely included zero [−0.0005 to 0.0459]).

Finally, there was a correlation between the individual observers' effects of attention in the primary task (ratio of neutral to cued thresholds) and in the secondary task (ratio of cued mismatch to cued match thresholds; Spearman's $\rho = 0.70$, $p < 0.01$). This suggests a common underlying mechanism.

General discussion

Summary

These experiments show how feature-based attention affects visual performance voluntarily at the location where targets are selected from distractors and, at the same time, involuntarily in the other hemifield where there were no task demands for selection. The "local" effect of feature-based attention was manifest in the primary tasks by lower thresholds for detecting a speed change when its direction was cued (Experiment 1) and by lower tilt discrimination thresholds when the nearest cardinal axis was cued (Experiment 2).

The global spread of feature-based attention was demonstrated with the secondary tasks, which required observers to determine which of two noisy stimulus arrays contained a coherent signal within the relevant feature dimension. In the cued condition, but not in the neutral condition, we found that coherence thresholds were lower when the particular direction or orientation of that signal matched that of the primary target than when it was the opposite. Thus, feature-based attention deployed to the primary stimuli also selectively increased sensitivity for particular feature values of the secondary stimuli.

Could uncertainty reduction explain the observed effects of feature cues? In the primary task, the cues allowed observers to discount half of the primary stimuli when making decisions about the speed and orientation changes, and this reduction in uncertainty could have improved performance. However, the underlying cause of the effects on primary task performance is not central to the goal of this paper. The primary tasks were designed only to manipulate feature-based attention so that its effects could be measured in secondary task performance. Crucially, the secondary task effects cannot be explained by reductions in stimulus uncertainty at the decision-making stage. Both directions (Experiment 1) and both orientations (Experiment 2) provided the same information. Thus, it would not have been useful for even an ideal observer to allocate more weight to one or the other. Moreover, the attentional modulations of sensitivity in the secondary tasks suggest that at least part of the primary task effects was due to changes in sensitivity as well. It is hard to imagine that feature-based attention would not affect sensitivity (but only reduce decision uncertainty) at the location where that feature is relevant but, nonetheless, selectively increase sensitivity in the opposite hemifield.

The feature-similarity gain model

We propose that the performance benefits for matching features reflect the global nature of the "feature-similarity gain model" of attention (Treue & Martinez-Trujillo, 1999), which has been supported with fMRI (Saenz et al., 2002; Serences & Boynton, 2007), EEG (Zhang & Luck, 2008), and perceptual aftereffects (e.g., Boynton et al., 2006; Melcher et al., 2005). Our experiments are the first to demonstrate with a comparable paradigm that human abilities to perceive distant stimuli are affected by the simultaneous deployment of feature-based attention elsewhere.

Experiment 2 is consistent with the previous finding that when observers discriminate the orientation of a central Gabor patch, they have highest hit rates for detecting subsequently flashed peripheral gratings that have similar orientations (Rossi & Paradiso, 1995). However, given the impossibility to measure false alarm rates for each orientation, those results could have reflected changes in decisional criteria rather than sensitivity. We circumvented this methodological limitation by using a two-alternative forced-choice discrimination task.

Our performance effects are more closely related to the neurophysiology than previous studies using dual discrimination tasks, which found that observers are better able to simultaneously judge the feature values of two stimuli that are similar rather than different (Lu & Itti, 2005; Saenz et al., 2003; Sally et al., 2009). Their findings could be explained, at least partially, by voluntary feature-based attention to both stimuli, the relative difficulty of dividing attention within a feature dimension, and/or perceptual grouping between similar stimuli. We eliminated these factors by making the feature values of the secondary stimuli task-irrelevant, by manipulating attention without changing the physical display, and by rendering the primary and secondary stimuli very different from each other (see Figures 1 and 3).

It is important to note that observers must have been voluntarily distributing some *spatial* attention to the location of the secondary stimuli, knowing as they did that stimuli relevant to their secondary task would appear there at some point in time. Our design was, therefore, different from those of neurophysiological studies that measured responses to ignored stimuli. This difference was necessary because our goal was to measure visual performance. However, for the following three reasons, we conclude that the effect of feature-based cues on secondary task performance was involuntary—i.e., that it did not depend on a conscious decision to attend selectively to a particular feature value in the hemifield opposite to the primary stimuli: First, observers knew that the primary target features could not predict which of the two coherent directions or orientations would be in the secondary stimulus. Both possible feature values were equally likely to occur and, in any case, did not have to be distinguished from one another. Second, the secondary stimulus locations were blank for the majority of each trial and the stimuli appeared there at an unpredictable time. This further reduced the motivation to attend selectively at their location while focusing on the continuously present primary stimuli. Third, the duration of the secondary stimuli was too brief to allow for a voluntary deployment of feature-based attention after their onset (Liu, Stevens et al., 2007).

There are several viable models of the underlying mechanisms causing the global spread of feature-based attention. One is that attention to an object engages long-distance lateral connections that activate similarly tuned detectors across retinotopic cortex and perhaps suppress others (suggested by Serences & Boynton, 2007). Under

this hypothesis, the global spread of feature-based attention is truly "automatic" and indirectly caused by the voluntary deployment of attention to the primary stimulus. Some recent evidence indirectly supports this theory, in particular the findings that values of task-irrelevant (and presumably ignored) features of an attended object are also boosted across the visual field (Katzner, Busse, & Treue, 2009; Melcher et al., 2005; Sohn, Chong, Papathomas, & Vidyansky, 2005). Another possibility consistent with the present results is that the same attentional signals that select the important features of the target object (as in Liu, Hospadaruk, Zhu, & Gardner, 2011) are applied to the whole visual field. In this case, the attentional effects we observed in secondary as well as primary task performance would have been caused by top-down feature-specific signals applied within one wide spatial "window" that covered the entire display. According to this model, our behavioral results would demonstrate that this window is diffuse even when there is no task-related reason to deploy it beyond one location.

It would be parsimonious to assume that all reports of global enhancements of the features of attended objects are related to the same underlying mechanisms. However, these models have not been directly tested, and studies with different dependent variables and task designs could be tapping into different attentional phenomena. For instance, we manipulated *selective* attention in the presence of distractors with the opposite feature value, whereas other studies measured the global effects caused by attention to a single object (e.g., Treue & Martinez-Trujillo, 1999). There is currently some discrepancy in the literature as to whether competing distractors strengthen the global spread (Saenz et al., 2003; Zhang & Luck, 2008) or whether attention to any feature of a single object is sufficient to increase sensitivity to any similar stimuli across the visual field (e.g., Katzner et al., 2009; Melcher et al., 2005). Further research will be necessary to elucidate the relation between these manifestations of feature-based attention.

Benefits versus costs

Martinez-Trujillo and Treue (2004) reported enhanced responses in MT neurons that prefer the attended feature value as well as suppression in neurons that prefer very different values, relative to "sensory" responses in which only the fixation mark was attended. This pattern predicts a performance benefit for attended feature values and a cost for others, relative to a neutral condition. Ours is the first behavioral study to test that prediction, but we found only a performance benefit for attended orientations and directions. Note that in our neutral conditions the distribution of spatial attention was the same as in the cued conditions, and QUEST staircases always maintained primary task difficulty at 85% correct. In contrast, Martinez-Trujillo and Treue (2004) measured firing rates in response to an ignored stimulus while the monkeys attended to another stimulus

on the other side of fixation. They compared those firing rates to a condition in which the monkeys ignored both stimuli and attended to the central fixation mark, which was closer to the stimulus in the receptive field than the dots that were attended in the first condition. This difference in the distribution of spatial attention could have elevated sensory responses overall in the attend-fixation condition and, thus, exaggerated the degree of relative suppression when the more distant target was attended and moving in the anti-preferred direction.

Conclusion

Our findings provide a novel behavioral demonstration of how feature-based attentional selection at one location simultaneously alters perception of the rest of the scene. At locations distant from the stimuli that are selectively attended, the presence of the attended feature value is more easily detected than the presence of the opposite feature value. A comparable neutral condition revealed that the effect is due more to enhancement of the attended feature value than suppression of others. These are the first effects of global feature-based attention on visual performance that cannot be explained by criterion shifts, differences in the display, voluntary attention to particular feature values at the secondary locations, or task difficulty levels. This study helps narrow the gap between perception and known neurophysiological phenomena and further establishes how basic visual mechanisms automatically adapt to the observer's goals.

Acknowledgments

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