

Global feature-based attention to orientation

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Selective attention to motion direction can modulate the strength of direction-selective sensory responses regardless of their spatial locations. Although such spatially global modulation is thought to be a general property of feature-based attention, few studies have examined visual features other than motion. Here, we used an adaptation protocol combined with attentional instructions to assess whether attention to orientation, a prominent feature in early visual processing, also exhibit such spatially global modulation. We adapted observers to an orientation by cuing them to attend to the orientation in a compound grating that was presented at a peripheral location. We then assessed the size of the tilt aftereffect at three locations that were never stimulated by the adapter. Attending to orientation produced a tilt aftereffect in these locations, indicating that attention modulated orientation-selective mechanisms in remote locations from the adapter. Furthermore, there was no difference in the magnitude of the tilt aftereffect for test stimuli that were located at different distances and hemifields to the adapter. These results suggest that attention to orientation spreads uniformly across the visual field. Thus, spatially global modulation seems to be a general property of feature-based attention, and it provides a flexible mechanism to modulate feature salience across the visual field.

Keywords: attention, spatial vision, visual cortex

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Introduction

Visual scenes generally contain much more information than we can process at once. Attention allows us to select certain aspects of the visual scene for prioritized processing. Both psychophysical and neurophysiological studies have shown that attention can affect early visual processing (Carrasco, 2006; Reynolds & Chelazzi, 2004). Although the majority of studies typically manipulate covert spatial attention, i.e., selecting a location in space without overt eye movement, recent work has also examined attention to visual features (Maunsell & Treue, 2006).

An interesting property of such feature-based attention is that it exhibits spatially global modulation of visual processing. This has been demonstrated in neurophysiological and imaging studies. For example, attending to a direction of motion in one hemifield modulates neuronal and fMRI response to a motion stimulus in the opposite hemifield (Saenz, Buracas, & Boynton, 2002; Treue & Martinez-Trujillo, 1999). Such modulations are captured by the feature-similarity gain model (Martinez-Trujillo & Treue, 2004; Treue & Martinez-Trujillo, 1999), which proposes that attending to a feature enhances firing in neurons preferring that feature and suppresses firing in

neurons preferring very different features. Psychophysical studies have also provided behavioral correlates for spatially global modulation due to feature-based attention (Arman, Ciaramitaro, & Boynton, 2006; Liu & Mance, 2011; Saenz, Buracas, & Boynton, 2003; Zirnsak & Hamker, 2010).

To date, most studies on feature-based attention have focused on attention to direction of motion. It can be argued that motion is an inherently global feature as veridical motion perception requires integrating local motion signals over space (Movshon, Adelson, Gizzi, & Newsome, 1986). Psychophysical studies have shown that adapting to motion in one location can induce motion aftereffect (MAE) in a separate, non-stimulated, location (Bex, Metha, & Makous, 1999; Snowden & Milne, 1997; Weisstein, Maguire, & Berbaum, 1977). The existence of such “phantom MAE” suggests that motion processing involves spatially global mechanisms. Physiologically, motion processing has been linked to MT/MST areas in the primate brain, and mapping studies show that neurons in these areas have large receptive fields that sometimes cross over to ipsilateral hemifield (Albright & Desimone, 1987; Komatsu & Wurtz, 1988; Tanaka & Saito, 1989). These observations suggest that the global nature of motion processing could facilitate spatially global attentional modulations to motion.

Thus, a question remains whether spatially global modulation is a general property of feature-based attention, or it only holds for features like motion that tend to be processed on a global scale. To test these alternatives, in the current study, we examined whether attention can globally modulate features that are processed on a more local scale. Orientation is a fundamental feature in vision, and it is prominently represented at the earliest stage of cortical visual processing—the primary visual cortex. The majority of V1 neurons have strong orientation tuning and have much smaller receptive fields than those of MT/MST (Hubel & Wiesel, 1968). Thus, orientation can be considered a feature that entails more local processing than motion. Given these considerations, it would be useful to know whether attention to orientation modulates visual processing in a spatially global fashion.¹

Our first goal is to examine whether feature-based attention to orientation spreads to distant locations. In addition, we seek to further characterize such spread by systematically testing multiple locations. Previous studies on global feature-based attention have generally tested one location, usually in the opposite hemifield of the attended stimulus (Arman et al., 2006; Saenz et al., 2002, 2003; Treue & Martinez-Trujillo, 1999). Thus, although they demonstrated a spatial spread of attentional modulation, it is not clear whether such spread is uniform or exhibits certain spatial gradient across the visual field.

Here, we employed an adaptation protocol to examine the spread of attentional modulation. The basic logic is the following: if attending to a specific feature selectively increases the activity of neurons preferring that feature, those neurons will become more adapted, as neural adaptation tends to increase with stronger neuronal response (e.g., Gardner et al., 2005; Sclar, Lennie, & DePriest, 1989). Behaviorally, such selective adaptation should lead to perceptual aftereffects due to unbalanced activity from neuronal subpopulations (Clifford, 2002). Thus, it has been shown that attending to one direction in a compound motion stimulus produces a motion aftereffect (Lankheet & Verstraten, 1995), and attending to an orientation in a compound grating stimulus produces a tilt aftereffect (Liu, Larsson, & Carrasco, 2007; Spivey & Spirn, 2000). These previous studies only tested the aftereffect at the adapter location; here, we used attention-induced tilt aftereffect to measure the spread of orientation-based attention across the visual field. Furthermore, we tested tilt aftereffect in remote locations that were never stimulated, which allowed us to obtain a pure measure of the spread of feature-based attention without local sensory adaptation. This technique has been demonstrated in previous studies on attention to motion (Arman et al., 2006; Liu & Mance, 2011). Finally, because the tilt aftereffect has been linked to neuronal population responses in V1 (e.g., Dragoi, Sharma, & Sur, 2000; Jin,

Dragoi, Sur, & Seung, 2005), our psychophysical measurement can be considered to index attentional modulation in V1.

Methods

Participants

Five observers participated in the experiment, including one author (YH). All participants had normal or corrected-to-normal vision and had extensive experience in psychophysical experiments. They gave informed consent according to the study protocol that was approved by the Institutional Review Board at Michigan State University. Observers were compensated at \$10/hr for their participation.

Stimulus and display

Visual stimuli were generated using MGL (<http://gru.brain.riken.jp/doku.php?id=mgl:overview>), a set of custom OpenGL libraries running in Matlab (Mathworks, Natick, MA), and were presented on a 21" CRT monitor (resolution: 1024 × 768, 60-Hz refresh rate). Participants viewed the screen at a distance of 57 cm with their heads stabilized by a chin rest. The screen was covered with a circular aperture to eliminate cues provided by the edges of the monitor.

Stimuli were square-wave gratings (duty cycle: 40%, luminance: 22.7 cd/m²) in a circular aperture (5° diameter), presented on a gray background (45.4 cd/m²). The adapting stimulus (adapter) consisted of two gratings, tilted 15° clockwise (CW) and counterclockwise (CCW) off the vertical orientation (0°), here labeled −15° and +15° (Figure 1A). The luminance of the intersection of the two component gratings was set to mimic surface transparency. The spatial frequency of each component grating was continuously modulated over time, in a sinusoidal profile with opposite phases. The duration of each cycle was 4 s, during which time the spatial frequencies of the two component gratings were smoothly modulated between 0.5 and 2.5 cycles/degree. The spatial phase (the relative location of light/dark bars in a grating) of the component gratings was randomized on each trial to ensure no systematic luminance difference in retinal stimulation. The test stimulus was a single, static, square-wave grating (1.5 cycles/degree) in the same annulus, whose spatial phase was also randomized on each trial. The square-wave gratings were rendered with anti-aliased polygons such that the edges appeared smooth.

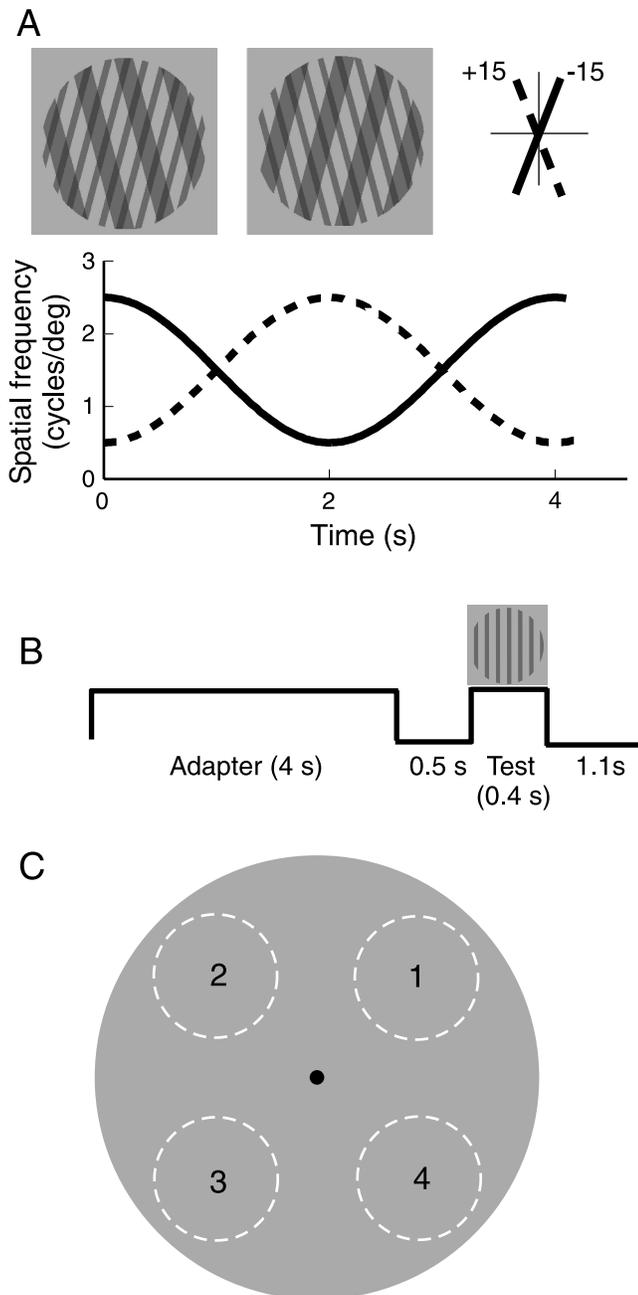


Figure 1. Experimental setup. (A) The adapter stimulus was a compound grating containing two orientations whose spatial frequencies were modulated smoothly over time. (B) Timing diagram on each trial of the experiment. Note that the test stimulus was a single orientation grating. (C) The four possible stimulus locations on the screen (covered with a circular cutout to remove edges of the screen).

Procedure and task

Attention experiment

We measured attention-induced tilt aftereffect (TAE) in blocks of trials. At the beginning of each block, a prompt

indicated to participants which orientation in the adapter (either clockwise or counterclockwise) to attend throughout the block. A 20-s pre-adaptation period then followed in which the spatial frequency of the two component gratings continuously changed. This was followed by 32 experimental trials, each consisting of a 4-s display of the adapter stimulus (“top-up”), a 0.5-s fixation period, a 0.4-s test stimulus, and a 1.1-s intertrial interval (Figure 1B). Participants were instructed to selectively attend to the prompted orientation whenever they viewed the adapter stimulus (i.e., during pre-adaptation and top-up). They were also instructed to report the perceived orientation of the test stimulus (relative to vertical), by pressing the left and right arrow keys on a computer keyboard to indicate “counterclockwise” and “clockwise,” respectively. The orientation of the test stimulus was controlled by a 1-up 1-down adaptive staircase, which approaches the 50% threshold (i.e., point of subjective vertical). The starting orientation of the test stimulus was 0° (physical vertical). Participants responded during the 1.1-s intertrial interval. In each session, participants attended to one orientation for two blocks of trials, followed by attending to the other orientation for two more blocks of trials. They took a 2-min break between orientations for the adaptation effect to dissipate. The order of attended orientations was randomized for each session. Participants performed 128 trials in each session, 64 trials per orientation.

The adapter and test locations were fixed within a session but were varied across sessions in order to examine the spatial spread of attentional modulation. There were four possible stimulus locations in the experiment, located at 7° eccentricity on the intercardinal axes (Figure 1C). The adapter was presented in either location 1 or 3, while the test stimulus was presented in one of the three remaining locations. This created six possible adapter–test location pairs (2 adapter locations \times 3 test locations), which were run in separate sessions in a random order for each participant.

Baseline adaptation

We also ran a baseline condition to assess possible differences in adaptability in the four stimulus locations. The baseline trials were identical to the attention trials, with two exceptions: (1) there was only one grating in the adapter (undergoing the same modulation in spatial frequency); (2) the adapter was presented in the same location as the test stimulus. Participants were instructed to attend to the fixation point during the adapter presentation and perform the same orientation discrimination task on the test stimulus as in the attention trials. There were four adapter–test location pairs (with both stimuli residing in the same location), which were run in separate sessions in a random order for each participant. Participants ran the baseline condition first before running the attention experiment.

Eye tracking

Participants were instructed to maintain central fixation throughout the experiment. All participants have extensive experience in psychophysical experiments, and we were confident that they followed the instruction. We verified their fixation pattern in a subset of attention blocks, by monitoring their eye position with a video-based eye tracker (Eyelink II, SR Research, Ontario, Canada). Eye position data were analyzed offline using custom Matlab code. All participants were able to maintain stable fixation throughout a trial, with the mean eye position less than 0.5° from fixation.

Results

For each individual condition (participant, location pair, attention vs. baseline), we first calculated the proportion of observers' "counterclockwise" response as a function of the orientation of the test stimulus. We then fitted a cumulative Gaussian function to these data with a maximum likelihood method as implemented in `psignifit` (Wichmann & Hill, 2001).

Sample data from a single observer (one location pair) are presented in Figure 2. In the baseline condition (Figure 2A), adapting to the $+15^\circ$ grating shifted the psychometric function rightward, meaning observers were less likely to report "counterclockwise" (note CCW was labeled as positive). The reverse was found when observers adapted to -15° grating. This is the standard TAE, where adaptation causes a "repulsion" effect in the apparent

orientation of a test stimulus. Interestingly, when observers attended to one of the orientations in the compound adapter stimulus, a shift in psychometric function was also found (Figure 2B). This shift was in the same direction as the basic adaptation effect, except that the magnitude was smaller. The shift in perceived vertical in Figure 2B can be attributed purely to an attentional modulation as the physical stimulus was identical across the two attention conditions. Importantly, the adapter and test stimuli were presented in different locations, thus demonstrating that the attention-induced TAE can spread to remote locations.

We quantified the strength of adaptation as the change in the point of perceived vertical (50% threshold) between adapting to the two orientations (TAE). Figure 3 displays individual data from the five observers who participated in the experiment. In the baseline condition, where the adapter and test were in the same location, adaptation produced a robust TAE (Figure 3, right column). In the attention experiment, where the adapter and test were in different locations, attention also produced a TAE in the same direction as the baseline but with a smaller magnitude (Figure 3, left column). The baseline TAE did not show much variation across different locations, as would be expected for these isoecentric locations. The attention-induced TAE also did not show systematic variation across adapter–test location pairs. In particular, there was no obvious pattern in TAE as a function of adapter–test distance or hemifield. The largest variation among conditions was found in observer JK's data; however, it was mainly due to a large TAE in the upper left quadrant rather than a systematic pattern of variation.

To evaluate the reliability of these effects, we averaged the TAE across observers and performed statistical analysis. The averaged attention-induced TAE was around

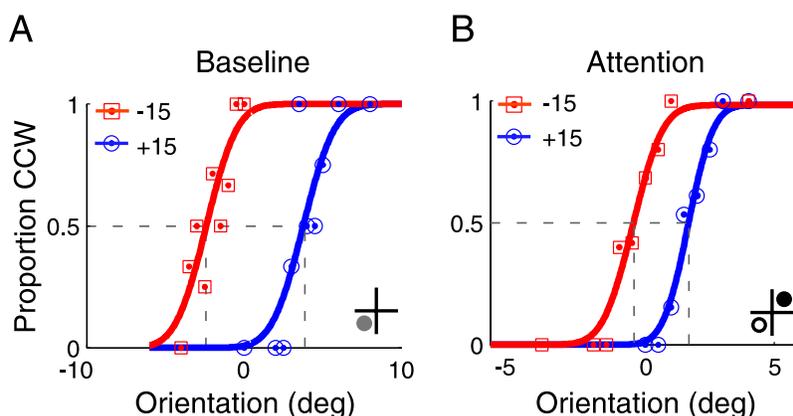


Figure 2. Sample data from a single observer. (A) Data in the baseline condition, when the adapter and test stimuli were presented in the lower left location (indicated by the gray circle in the inset). Data points represent proportion of "counterclockwise" responses as a function of the orientation of the test stimulus (note that positive numbers denote counterclockwise orientation). (B) Data in the attention condition, when the adapter stimulus was presented in the upper right location and the test stimulus was presented in the lower left location (locations indicated by the black and empty circles in the inset). Location circles correspond to four stimulus locations (see Figure 1C). Smooth curves are maximum likelihood fits of cumulative Gaussian functions. Note that the range of the x-axis is different in (A) and (B); this reflects the different magnitude of the adaptation effect (smaller effect in the attention than the baseline condition).

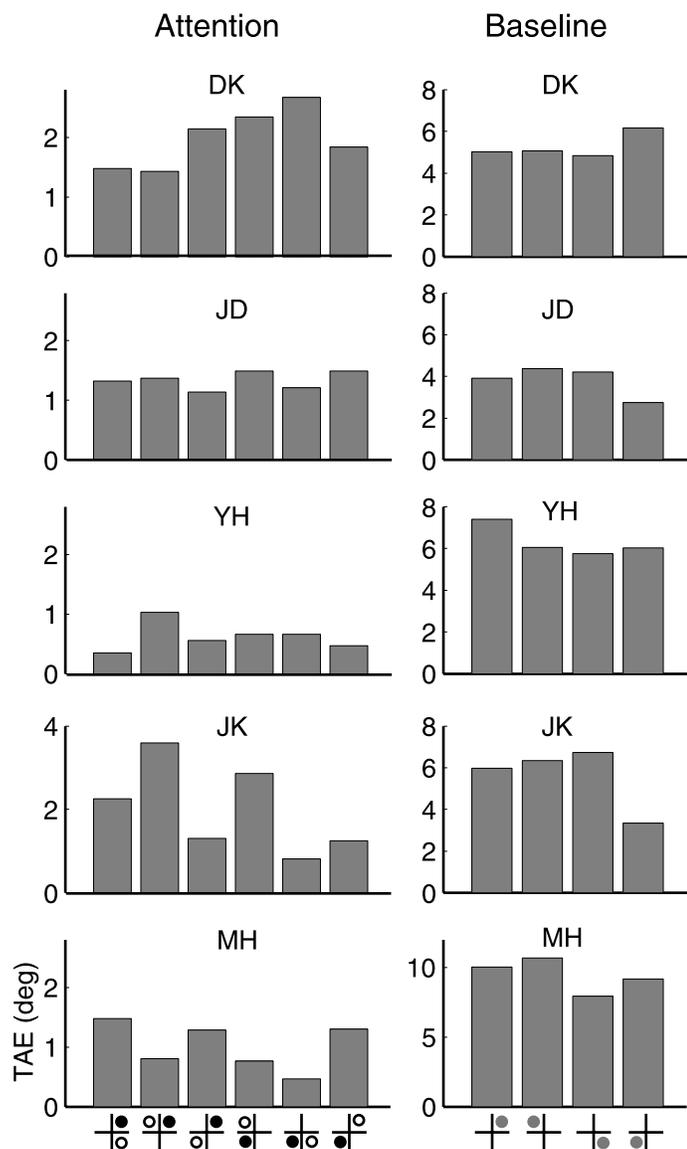


Figure 3. Individual observer data. Each row shows data from an observer. Each bar shows the change in perceived vertical (TAE) between adapting or attending to two orientations. The location information is shown by the diagrams below the horizontal axis. In the attention experiment (left column), black circle indicates adapter location and empty circle indicates test location. In the baseline experiment (right column), gray circle indicates the location of both the adapter and test. Note that the scale is larger for the baseline experiment than the attention experiment, indicating a larger effect. The scales for JK’s attention data and MH’s baseline data are also larger than other observers to accommodate their larger individual effects in those conditions.

1–1.5° (Figure 4A) and was significantly different from 0 for all location pairs (*t*-test, all *p* < 0.05). This shows that attention to orientation induced a reliable TAE at remote locations. Furthermore, there was no significant difference between the TAE among location pairs (one-way repeated-measures ANOVA, *F*(5,20) < 1). Baseline TAE

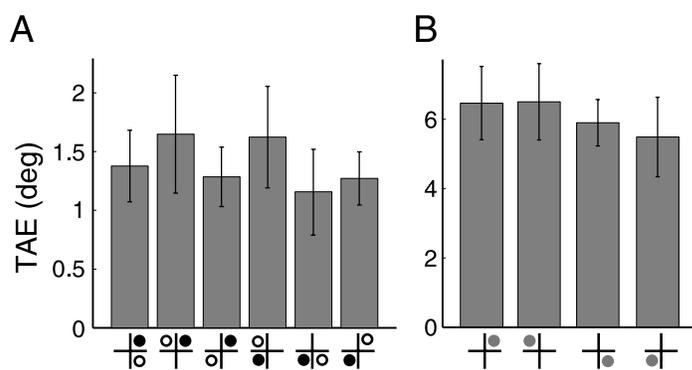


Figure 4. Averaged data for each location pair across observers. (A) Average TAE in the attention experiment. (B) Average TAE in the baseline experiment. Location information is in the same format as Figure 3. Error bars are standard error of the mean across observers.

showed a larger overall effect around 6° (Figure 4B), which was significantly different from 0 for all locations (*t*-test, all *p* < 0.01) but not different from each other (one-way repeated-measures ANOVA, *F*(3, 12) = 1.18, *p* = 0.36). The baseline result showed that the stimulus locations were equally adaptable, hence making it possible to directly compare the magnitude of attention-induced TAE across locations.

We further averaged the attention data across the two adapter locations, thus yielding three conditions according to adapter–test location pairing: same hemifield, near location (nearSH), different hemifield, near location (nearDH), and different hemifield, far location (farDH). All conditions exhibited a robust TAE that was signifi-

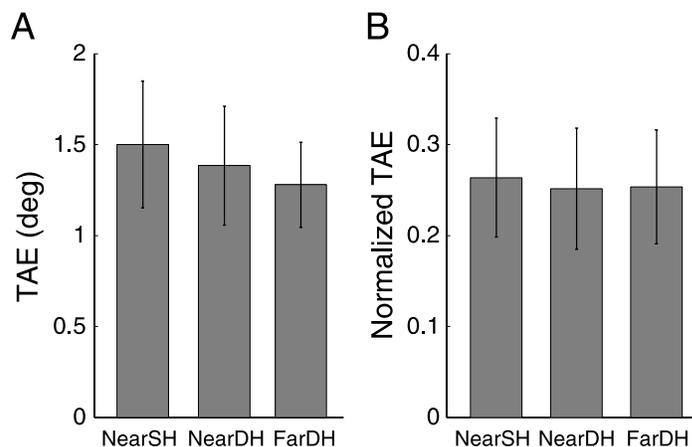


Figure 5. Average data across location pairs and observers in the attention experiment. (A) Average TAE for three sets of location pairs: same hemifield, near location (nearSH), different hemifield, near location (nearDH), and different hemifield, far location (farDH). (B) Average attentional TAE normalized by the baseline TAE for three sets of location pairs. Error bars are standard error of the mean across observers.

cantly different from 0 (t -test, all $p < 0.02$, Figure 5A). There was also no significant effect in location pairing (one-way repeated-measures ANOVA, $F(2, 8) < 1$). Finally, we normalized attention-induced TAE against the baseline TAE, by taking the ratio of the former to the latter in corresponding test locations (see Figure 3). This normalized TAE represented the proportion of attentional modulation spread from a remote location with respect to the amount of local adaptation, thus taking into account possible subtle variations in baseline adaptability across locations and participants. The normalized TAE (Figure 5B) was about 25% and significantly different from 0 (t -test, all $p < 0.02$) and showed no difference among conditions (one-way repeated-measures ANOVA, $F(2, 8) < 1$).

Discussion

In this study, we measured the spread of feature-based attention to orientation with an adaptation protocol. We found attending to one orientation in a compound stimulus modulated the tilt aftereffect in a different location. Furthermore, the magnitude of such attentional effect was constant regardless of the distance between the adapter and test stimuli or whether they resided in the same or opposite hemifield. Finally, the baseline condition showed that the four peripheral locations were equated for the amount of adaptation, making it possible to directly compare attentional modulation in these locations. These results demonstrate that attention to an orientation can spread to remote locations and such spread is more or less uniform across the visual field.

Previous work on feature-based attention has almost exclusively focused on direction of motion. These studies have shown that attending to motion modulate both psychophysical (Lankheet & Verstraten, 1995; Saenz et al., 2003) and neuronal (Saenz et al., 2002; Treue & Martinez-Trujillo, 1999) responses, and such modulation can spread to remote, unstimulated locations (Arman et al., 2006; Liu & Mance, 2011). Thus, there is strong evidence for a global modulation due to feature-based attention to motion. Beyond motion, only the color feature has received limited investigation, with one study showing an fMRI correlate (Saenz et al., 2002) and another study showing a behavioral correlate (Saenz et al., 2003) of global feature-based attention. This latter study found that it was easier to attend to the same color in two locations than to two different colors in two locations. However, the use of a dual-task paradigm might limit its conclusion due to strategic factors such as attentional switch. In any case, beyond motion and color, little is known about the global spread of attentional modulation for other features. In particular, given the inherently global nature of motion processing (see Introduction section), it is unclear whether such global

modulation can be generalized to features that are processed on a more local scale.

Our study provides evidence that attention also exert a spatially global modulation for orientation, a visual feature that is processed on a more local scale. Thus, spatially global modulation seems to be a general characteristic of feature-based attention. Such modulation suggests that attending to a feature can selectively boost the salience of that feature across the visual field. A possible neural mechanism for such an effect is described by the feature-similarity gain model in which attention selectively enhances activity in neurons that prefer the attended feature and suppresses activity in neurons that prefer very different features (Martinez-Trujillo & Treue, 2004; Treue & Martinez-Trujillo, 1999). Consistent with this model, a previous neuroimaging study showed that attention modulated orientation-selective fMRI adaptation in early visual cortex at the adapter location (Liu et al., 2007). That study also found a correlation between psychophysical and fMRI measures of adaptation only in V1, suggesting V1 as the primary site for attentional modulation. Our current psychophysical results further expand these results and imply that attention can modulate responses of orientation-selective units regardless of the location of their spatial receptive fields, possibly by modulating V1 neuronal activity in all retinotopic locations. This scenario is also supported by a computational study that quantitatively linked neuronal population responses in V1 to tilt aftereffect (Jin et al., 2005). Lastly, our results further suggest that orientation-selective modulation can occur without any direct stimulation, as the test location was never directly stimulated by the attended orientation. Such modulation could be achieved by modulating baseline neuronal activity in an orientation-selective fashion (Boynton, 2005; Chawla, Rees, & Friston, 1999) and possibly provide a neuronal mechanism for efficient deployment of spatial attention during visual search (Serences & Boynton, 2007; Wolfe & Horowitz, 2004).

Our results showed that orientation-selective modulation spread equally within and between hemifields (compare nearSH and nearDH in Figure 5); a similar result was found for the spread of feature-based attention to the direction of motion (Liu & Mance, 2011). Given the contralateral organization of the visual cortex, these results suggest that feature-based attention can spread to two hemispheres equally. At least two possible neural mechanisms can support such an outcome: either a top-down signal originates within a hemisphere and efficiently crosses the corpus callosum to the opposite hemisphere or two separate top-down signals in both hemispheres modulate their respective visual cortical activity. This latter possibility is reminiscent of the notion that the two hemispheres have independent attentional resources, based on findings from spatial selection and tracking tasks (Alvarez & Cavanagh, 2005; Awh & Pashler, 2000; Reardon, Kelly, & Matthews, 2009). Further work in

neurophysiology and neuroimaging is needed to distinguish these possibilities.

Although the spread of attentional modulation did not depend on distance (compare nearDH and farDH in Figure 5), we should note that our distance manipulation had a limited range. Due to the constraint of testing isoeccentric locations, the near and far distance has a ratio of 1:1.41, i.e., a 41% increase in distance from near to far locations. It is possible that a larger distance differential might produce a change in the attentional effect. However, testing a larger distance differential likely requires stimulus locations at different eccentricities, which are difficult to compare in terms of attentional modulation as basic visual performance varies greatly along eccentricity (see Liu & Mance, 2011, for a discussion of this issue). Furthermore, for spatial attention, a gradient of modulation can be detected with similar (and smaller) distance manipulation (e.g., Handy, Kingstone, & Mangun, 1996; Hopf et al., 2006). Thus, if there were any gradient in attention to orientation, it would be qualitatively very different from that of spatial attention. Our existing data suggest that attentional modulation to orientation spreads independently of distance.

In summary, we found that orientation-selective adaptation induced by attention can spread to distant locations across the visual field. This suggests that spatially global modulation is a general property of feature-based attention. The ability to boost feature salience across the visual field would be useful in efficiently searching for task-relevant targets and excluding distracters.

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Footnote

¹Human fMRI studies have shown that attention to motion can modulate neural responses in V1 (Saenz et al., 2002; Serences & Boynton, 2007). Thus, motion-based attention can modulate activity in small RF neurons. However, such modulation might still rely on feedback mechanism from large RF neurons in MT/MST.

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