



## Constant spread of feature-based attention across the visual field

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### ABSTRACT

Attending to a feature in one location can produce feature-specific modulation in a different location. This global feature-based attention effect has been demonstrated using two stimulus locations. Although the spread of feature-based attention is presumed to be constant across spatial locations, it has not been tested empirically. We examined the spread of feature-based attention by measuring attentional modulation of the motion aftereffect (MAE) at remote locations. Observers attended to one of two directions in a compound motion stimulus (adapter) and performed a speed-increment task. MAE was measured via a speed nulling procedure for a test stimulus at different distances from the adapter. In Experiment 1, the adapter was at fixation, while the test stimulus was located at different eccentricities. We also measured the magnitude of baseline MAE for each location in two control conditions that did not require feature-based selection necessitated by a compound stimulus. In Experiment 2, the adapter and test stimuli were all located in the periphery at the same eccentricity. Our results showed that attention induced MAE spread completely across the visual field, indicating a genuine global effect. These results add to our understanding of the deployment of feature-based attention and provide empirical constraints on theories of visual attention.

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### 0. Introduction

Our environment contains much more sensory information than we can process at any given time. Attention allows us to select relevant attributes of sensory stimuli for prioritized processing. An important question in attention research is “what is selected?” (Kahneman & Henik, 1981). For visual attention, it is known that attention can select locations, features, and objects (Maunsell & Treue, 2006; Yantis, 2000). Such flexibility is crucial for efficiently processing sensory information in order to guide adaptive behavior.

While attending to a location induces spatially-restricted changes in performance and neuronal activity (Carrasco, 2006; Reynolds & Chelazzi, 2004), attending to a feature leads to a global modulation. For example, in a seminal study, Treue and Martinez-Trujillo (1999) showed monkey subjects two apertures of moving dots, one in each hemifield. They instructed monkeys to attend to a moving dot field in the first aperture, and recorded single-unit responses from MT neurons whose receptive fields fell on the second aperture, where the dots moved in the preferred direction of the neuron. The MT neurons fired at a higher rate when dots in the first aperture moved in the neuron’s preferred direction than

when they moved in the non-preferred direction. Such an effect is purely feature-based, since spatial attention was held constant (always directed to the first aperture). Importantly, the second aperture was always in the opposite hemifield to the first aperture. Hence, attentional modulation is global; it spread from the first aperture to the second.

Subsequent human fMRI and psychophysical studies have obtained similar results, demonstrating the global nature of feature-based attention (Saenz, Buracas, & Boynton, 2002, 2003). An implicit assumption in the literature seems to be that such spread is all-or-none, i.e., independent of spatial distance. A constant level of feature-based effect has indeed been assumed in some computational models of attention (Boynton, 2005; Reynolds & Heeger, 2009). However, in all studies so far, feature-based modulation has been evaluated at one location (typically in the opposite hemifield) distant from the focus of spatial attention. Thus, although it is clear that feature-based attention does transfer to distant locations, the degree of such transfer remains an open question. The goal of the present work is to characterize the spatial gradient of the spread of feature-based attention.

Here we use an adaptation protocol to measure the spread of feature-based attention. 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). Consistent with this

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idea, attending to one motion direction in a compound stimulus produces a motion aftereffect (MAE) similar to adapting to that direction alone (Lankheet & Verstraten, 1995). Similar effects have been observed for orientation (Liu, Larsson, & Carrasco, 2007; Spivey & Spirn, 2000).

Interestingly, attention-induced adaptation can occur in a remote location which was never stimulated (Arman, Ciaramitaro, & Boynton, 2006), in accordance with the idea that feature-based attention increases gain of neuronal subpopulations across the visual field, even without sensory stimulation. Here we used a similar protocol to examine the spatial spread of such attention-induced adaptation. We presented a compound stimulus (adapter) that contained two directions of motion, and cued our observers to attend to one direction in the adapter. We then measured MAE in remote locations that were never directly stimulated, at different distances from the adapter. The adapting stimulus was held constant for different test locations, thus eliminating any differential sensory effects due to processing of the adapter. We conducted two experiments, in which the adapter was presented either at fixation (Experiment 1) or at a peripheral location (Experiment 2).

## 1. Experiment 1

Previous studies on global feature-based attention always instructed participants to attend to a peripheral location. However, during normal viewing conditions, humans tend to foveate objects they are attending to. To further explore the generalizability of feature-based attentional spread, and to mimic more ecological situations, we examined the spread of feature-based attention from the center of the visual field by presenting the adapter at fixation. One complexity for this protocol concerns possible variations in basic adaptation effects across retinal eccentricities. Such variations could reflect different motion sensitivities across retinal locations (Finlay, 1982). To assess such baseline variability, we conducted two control experiments. The first control was identical to the attention condition except that the adapter contained only a single motion direction. This control essentially measured the spread of “phantom MAE” – MAE produced at un-stimulated locations. In the second control, a single-direction adapter was presented in the same remote location as the test stimulus, which measured the magnitude of the traditional (or concrete) MAE. In order to evaluate the spatial profile of global feature-based attention, we compared the magnitude of MAE in an attention condition relative to the magnitude of MAE in two control conditions.

## 2. Methods

### 2.1. Participants

Four observers participated in the experiment; all had normal or corrected-to-normal vision. Two of the observers were authors; the other two were undergraduate students at Michigan State University. All participants gave informed consent according to the study protocol that was approved by the Institutional Review Board at Michigan State University. Observers were paid \$10/h for their participation.

### 2.2. Stimulus and display

Visual stimuli consisted of white moving dot patterns (dot size:  $0.1^\circ$ , density: 8 dots/deg<sup>2</sup>, luminance: 24 cd/m<sup>2</sup>) in a circular aperture, presented on a dark background (0.01 cd/m<sup>2</sup>). Stimuli were generated using MGL (<http://www.gru.brain.riken.jp/doku.php?id=mgl:overview>), a set of custom OpenGL libraries running in Matlab (Mathworks, Natick, MA). A 21 in. CRT monitor was used

to present stimuli (resolution: 1024 × 768, 100 Hz refresh rate), and observers viewed the screen at a distance of 57 cm; their heads were stabilized by a chinrest.

### 2.3. Task and procedure

#### 2.3.1. Attention condition

A schematic of a single trial is depicted in Fig. 1A. Each trial started with an adapter stimulus followed by a test stimulus. The adapter was comprised of overlapping fields of upward- and downward-moving dots in a circular aperture (diameter  $4.5^\circ$ ), and was always presented at the center of the screen. The adapter was presented in two 1.4 s intervals separated by a 0.3 s fixation period. The test stimulus was a single-direction dot field (diameter  $5^\circ$ ), presented for 0.7 s after a 1.1 s delay following the adapter. A small fixation cross ( $0.25^\circ$ ) was displayed in the center throughout the experiment; it was surrounded by a circular region ( $0.75^\circ$ ) of the background luminance in which dots were not drawn.

Trials were run in blocks; at the beginning of each block, a prompt indicated to participants which direction to attend in the adapter stimulus (either upward or downward motion). Participants were instructed to maintain their gaze on the fixation cross and perform two tasks during each trial.

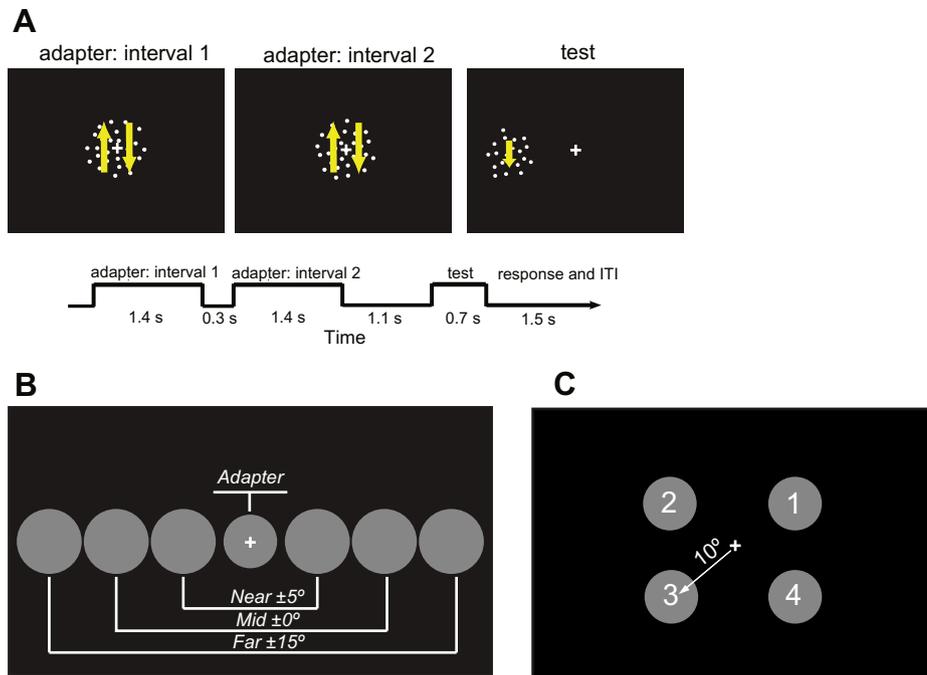
The first task was a two-interval forced choice (2IFC) speed discrimination task on the adapter. Each dot field in the adapter stimulus moved in different speeds in the two intervals, either at a baseline speed of  $4^\circ/s$  or a slightly faster speed (target). Participants reported the interval in which the attended dot field moved faster by pressing either the “1” (for interval 1) or “2” (for interval 2) keys on a standard keyboard. The speed increment was controlled via a three-down one-up staircase procedure. The target interval for the attended and unattended dot field was independently randomized. The task was attentionally demanding since participants had to ignore the threshold-level speed increments of the unattended dot fields. Participants responded on the 2IFC task during the 1.1 s interval between the adapter and test.

The test stimulus was used to measure the magnitude of MAE in a speed nulling procedure. Upon viewing the test stimulus, participants were instructed to simply report its moving direction by pressing either the “up” or “down” arrow keys on the keyboard. The speed of the test was controlled via a one-up one-down staircase procedure, which approaches the 50% threshold (point of subjective stationarity). The starting speed of the test stimulus was 0, i.e., physically stationary. Participants responded to the test stimulus during the 1.5 s inter-trial interval. To measure the spread of feature-based attentional modulation, the test stimulus was presented at one of six possible locations, at three eccentricities: near ( $\pm 5^\circ$ ), mid ( $\pm 10^\circ$ ), or far ( $\pm 15^\circ$ ). Fig. 1B depicts all six possible test locations.

Each block consisted of 40 trials, plus 7 2IFC-only trials at the beginning that served as pre-adaptation. Each session consisted of four blocks for attending one direction (e.g., upward), and four blocks attending the other direction (e.g., downward). Participants took a brief break between attending the two directions, for adaptation effect to dissipate. Test location was held constant within a session and varied between sessions. Each session took about 1 h to complete, and participants completed one session for each test location (six sessions total). The order of the test locations, as well as the order of the attended direction within a session, were all pseudo-randomized to counterbalance across participants.

#### 2.3.2. Control: phantom MAE

The phantom MAE control was identical to the attention condition (see Fig. 1), with the exception that the adapter was a single-direction dot field. Participants performed the 2IFC speed discrimination task on the adapter and the speed nulling procedure on the test stimulus. This condition measured the passive spread of



**Fig. 1.** Experimental protocol. (A) Example trial sequence. Two adapter stimuli were presented in two intervals followed by the test stimulus. (B) Schematic of the stimulus locations in Experiment 1. The size of the adapter and test was 4.5° and 5° (diameter), respectively. (C) Schematic of the stimulus locations in Experiment 2. The size of the stimulus is 5° (diameter).

the motion adaptation effect without the need to select a specific feature from the compound stimulus.

### 2.3.3. Control: concrete MAE

The concrete MAE control was identical to the phantom MAE control except that the adapter was presented in one of the six possible locations occupied by the test stimulus (see Fig. 1B). The adapter was always presented in the same location as the test in each session. This condition measured the baseline adaptation of direction-selective mechanisms without the need to select a specific feature from the compound stimulus. The order of the two control conditions and the attention condition was randomized for each participant.

### 2.4. Data analysis

No systematic differences were found between the left and right hemifield when data were analyzed separately for each test location. Hence data from the iso-eccentric locations were combined to produce near ( $\pm 5^\circ$ ), mid ( $\pm 10^\circ$ ), and far ( $\pm 15^\circ$ ) locations. Psychometric functions were fit separately for the upward and downward conditions using a cumulative Gaussian function. Fits were performed using maximum likelihood estimation as implemented in *psignifit* (Wichmann & Hill, 2001). The strength of adaptation, or motion aftereffect (MAE), was measured as the change in the point of perceived stationarity, calculated as the difference in the nulling speed between adapting (in the control conditions) and attending (in the attention condition) to the two directions.

The magnitude of the attentional effect was indexed by the ratio of the MAE in the attention vs. that in the control conditions. To evaluate the statistical reliability within subject, a non-parametric bootstrap method was used to estimate the variability of the ratios (Efron & Tibshirani, 1993). The data points (proportions) were regenerated via resampling (sampling with replacement of raw responses), and were fitted with psychometric functions in the same

manner as with the real data. Ratios were then calculated from the bootstrapped threshold estimates. This procedure was repeated 1000 times to yield a distribution for each ratio estimates. The 95% confidence intervals were determined as the range from 2.5 to 97.5 percentile values in the distribution and were plotted as error bars in data graphs.

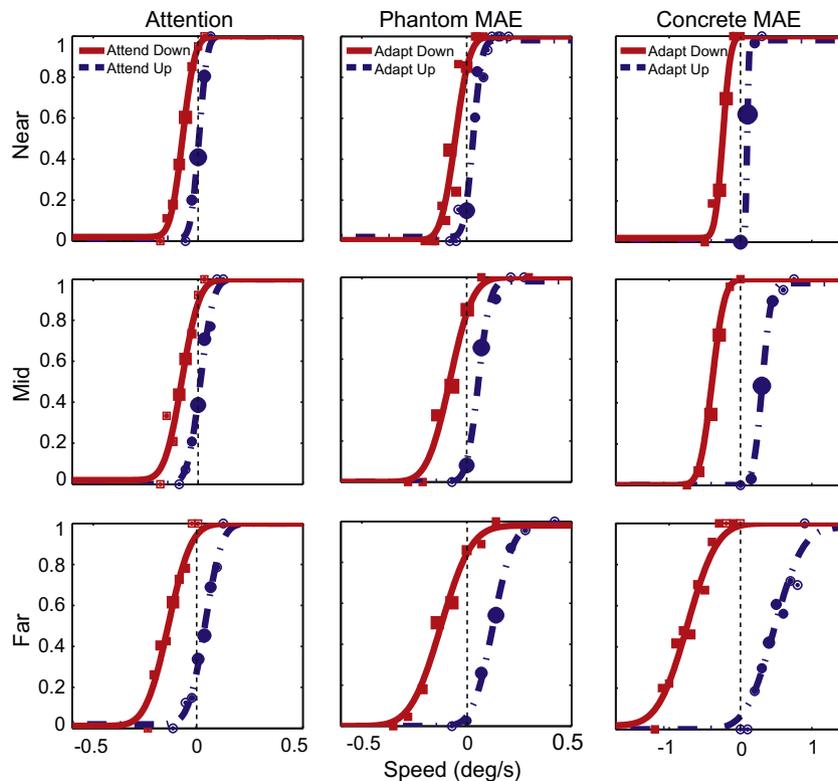
### 2.5. Eyetracking

In a subset of runs, we monitored participants' eye position with a video-based eyetracker (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  $0.5^\circ$  from fixation.

## 3. Results

### 3.1. Basic MAE measurement

Fig. 2 shows a single observer's data to illustrate how we quantified MAE with the speed nulling procedure. The graphs show the proportion of 'upward' response to the test stimulus as a function of its speed. The curves are maximum likelihood fit of a cumulative Gaussian function to the proportions. In the concrete MAE control (third column), adapting to upward motion led to a shift of the psychometric function relative to adapting to downward motion. This is the classical MAE (e.g., after adapting to upward motion, a stationary pattern appears to move downward, and vice versa). Interestingly, the psychometric functions also shifted in the phantom MAE control (second column), though to a smaller degree. This shift reflects the passive spread of MAE when the adapting and test patterns are at different locations. In the attention condition (first column), psychometric functions also showed a shift in the same direction as the controls. Such a shift is caused by attention alone,



**Fig. 2.** Data from the motion nulling procedure in a single participant in Experiment 1, plotting the proportion of reporting upward motion for the test stimulus as a function of its speed (left column: attention condition, middle column: phantom MAE control, right column: concrete MAE control). Positive speed indicates upward motion; negative speed indicates downward motion. Note the horizontal axis range is larger in the concrete MAE condition, reflecting a larger adaptation effect.

as the adapter stimulus was held constant; only the attentional state of the observer varied (attend upward vs. attend downward). We defined the magnitude of the MAE as the difference in nulling speed (50% threshold) between the upward and downward conditions (i.e., the amount of shift between the two psychometric functions).

### 3.2. Attention induced MAE varies across locations

Fig. 3 shows individual observers' data in the attention and control conditions. The graphs in the first row show the magnitude of attention induced MAE as a function of distance between the adapter and test stimulus. All observers showed MAE in all locations, although there were some individual differences in terms of absolute amount of MAE and its profile over distance. The graphs in the second row show that MAE caused by an adapter in the center (phantom MAE control) follows a similar pattern as that in the attention condition. When the adapter was presented in the peripheral test locations (concrete MAE control), MAE tend to increase as eccentricity increases (third row).

To quantify attentional effects, we normalized the attention-induced MAE against the MAE effects in the control conditions. The graphs in the fourth row show normalized attentional effect, relative to the phantom MAE control. The error bars represent 95% confidence intervals obtained from a bootstrap procedure (see Section 2). For all participants, attentional effect remained constant across locations (all confidence intervals overlapped). However, when attention induced MAE was normalized to that in the concrete MAE control (fifth row in Fig. 3), attentional effect decreased from the near location to the middle and far locations, with no difference between the latter two locations.

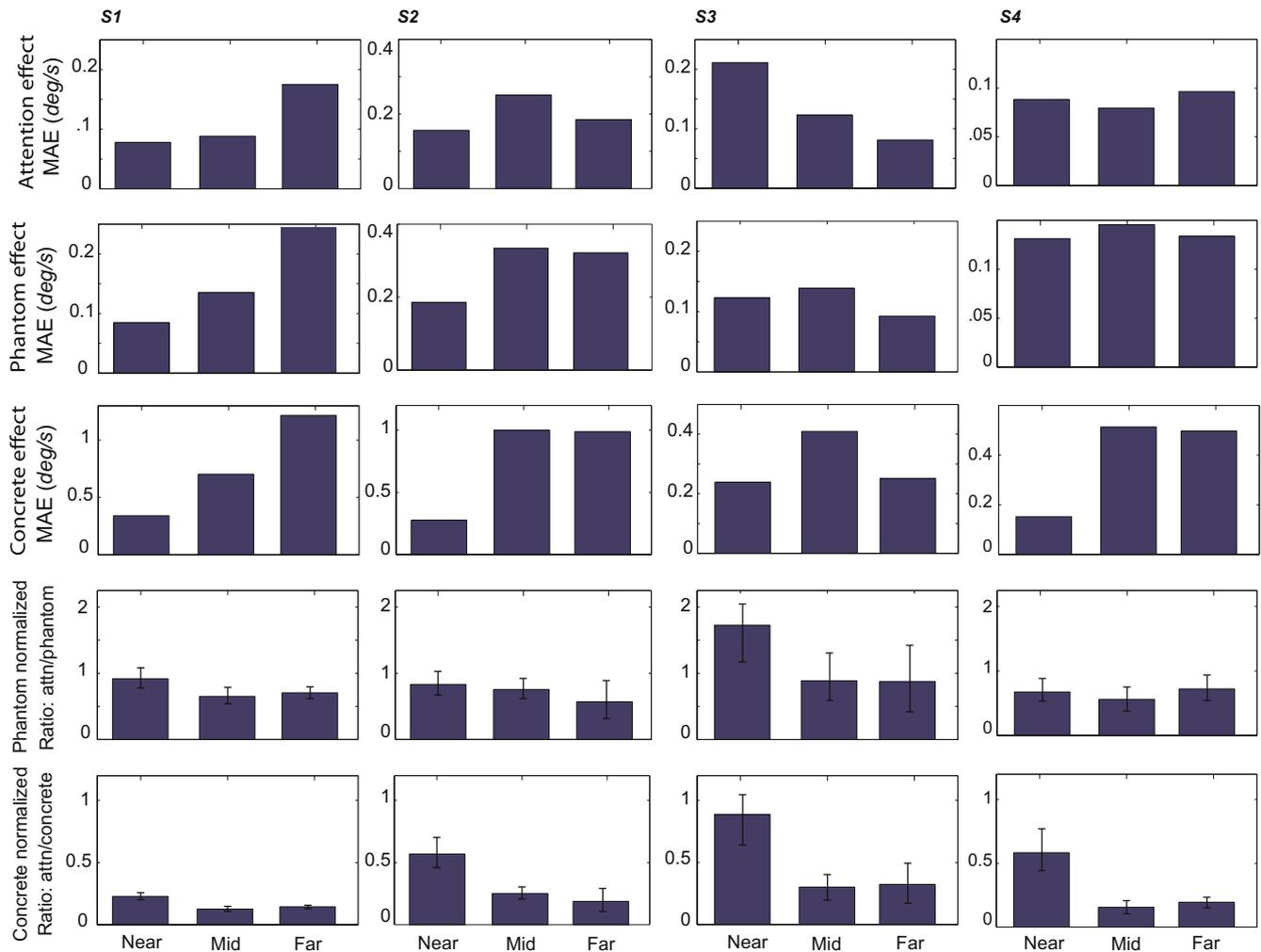
We also pooled data across participants and performed conventional statistical tests. Fig. 4 shows group-averaged MAE magni-

tude in the attention and two control conditions. There was no appreciable difference among locations for both the attention and phantom MAE. No significant effect of location was found in one-way repeated measures ANOVA (attention MAE:  $F(2, 6) < 1$ , phantom MAE:  $F(2, 6) = 1.77$ ). However, concrete MAE showed an increasing magnitude from near to far locations, which was confirmed by a significant effect of location ( $F(2, 6) = 5.63$ ,  $p < .05$ ). Finally, we performed one-way repeated measures ANOVA on the normalized attentional effects (the 4th and 5th row in Fig. 3). This analysis yielded no significant effect of distance ( $F(2, 6) = 3.25$ ,  $p > 0.1$ ) when attentional effects were normalized to phantom MAE control, however a significant effect ( $F(2, 6) = 14.3$ ,  $p < .01$ ) was present when attentional effects were normalized to the concrete MAE control.

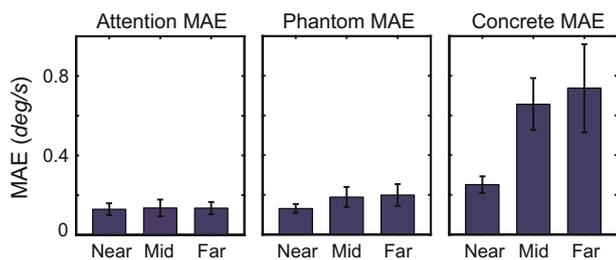
## 4. Discussion

Here we measured attention induced MAE at different distances to the central adapter. As the test locations were located at different eccentricities, we also measured baseline adaptation effect for each location, in order to take into account variations in motion processing across retinal eccentricities. We conducted two controls: one in which the adapter was always in the center (phantom MAE control), one in which the adapter and test stimuli were both in the peripheral locations (concrete MAE control).

On average, attention induced MAE and phantom MAE remained constant across distance, whereas concrete MAE increased with distance. Thus, when expressed as a proportion of the phantom MAE, normalized attentional effects stayed constant as a function of distance from the adapter (Fig. 3). However, when expressed as a proportion of the concrete MAE, normalized attentional effect decreased with larger distances from the adapter (Fig. 3). Thus, on one hand, attention seemed to spread completely



**Fig. 3.** Individual participant data in Experiment 1. Each column is a single participant. The first row plots the MAE in the attention condition; the second row plots results in the phantom MAE control condition; the third row plots results in the concrete MAE control condition. The fourth row is attentional effect normalized to the phantom MAE, and the fifth row is attentional effect normalized to the concrete MAE. Error bars indicate 95% confidence interval derived from a bootstrap procedure (see Section 2). Because there was individual variability in the MAE magnitude, and concrete MAE tended to be much larger than the other two conditions, the scale for the first three rows was not identical. The scale for the last two rows (normalized attention effect) was identical.



**Fig. 4.** Group averaged MAE magnitude for the attention condition (A), phantom MAE control (B), and concrete MAE control (C) in Experiment 1. Error bars represent  $\pm 1$  s.e.m. across participants.

across locations (compared to phantom MAE). On the other hand, such spread seemed to diminish with increasing distance (compared to concrete MAE).

However, the decrease in concrete MAE-normalized attention effect over distance occurred only between the near and mid locations, with no appreciable difference between the mid and far locations. Because the near location was adjacent to the central adapter location (Fig. 1B), there were likely small RF mechanisms responding to stimulation in both the adapter and near locations,

but not to stimulation in the mid and far locations (e.g., imagine a V1 neuron whose RF center was located between the adapter and near locations). These RFs would be actually stimulated by the adapter, potentially contributing to an increased MAE measured in the near location. Thus this apparent decrease between near and mid locations could be explained by a local process that does not reflect active long-range spread of attentional modulation.

Another caveat in this experiment concerns the use of the control conditions to index baseline neural adaptability. Even though in both conditions participants did not have to select one direction out of two competing directions in the adapter, they still performed a task on a single-direction stimulus, presumably attending to that direction. Thus, it is possible that feature-based attention was deployed in the control conditions as well. If so, they would not be appropriate measures of baseline neural adaptability without attention.

These considerations make it somewhat difficult to interpret the decrease of attentional effects when compared to the concrete MAE. Nevertheless, it should be pointed out that attention induced MAE in the mid and far locations did not differ, regardless of whether it was compared to concrete or phantom MAE control. The results from these two locations are easier to interpret than

results from the near location, given the above considerations. This observation suggests a constant spread of feature-based attention. The extent of such spread was further tested in Experiment 2.

## 5. Experiment 2

In this experiment, we measured the spread of attention induced MAE when all stimuli were presented in the periphery, at iso-eccentric locations. This avoided the complexity of measuring effects at different eccentricities in Experiment 1. Furthermore, putting the adapter in the periphery allowed us to test how feature-based attention spread within and across hemifields. Given that early visual cortical areas receive input from the contralateral hemifield, adaptation effect needs to spread across the two hemispheres of the brain when the adapter and test are located in opposite hemifields, whereas it only needs to spread within a hemisphere when they are located in the same hemifield. Thus one might expect that such spread is more complete within a hemifield than between hemifields. This possibility remains untested as previous studies on feature-based attention have always presented the test stimulus in the opposite hemifield to the attended stimulus (e.g., Saenz et al., 2003; Treue & Martinez-Trujillo, 1999). Here we explicitly test how feature-based attention spread within vs. across hemifields.

## 6. Methods

### 6.1. Participants

The two authors, plus four additional observers participated in the experiment; all had normal or corrected-to-normal vision. All participants gave informed consent according to the study protocol that was approved by the Institutional Review Board at Michigan State University. Observers were paid \$10/h for their participation.

### 6.2. Stimulus and display

The stimuli were identical to those in Experiment 1, except that the dot density was reduced to 4 dots/deg<sup>2</sup>, to accommodate reduced visual acuity in the periphery.

### 6.3. Task and procedure

The task and trial timing was identical to Experiment 1 (Fig. 1A). Again, participants viewed an adapter stimulus containing two dot fields moving in opposite directions and performed a 2IFC speed discrimination task on the attended direction. They then set their subjective stationary point on a test stimulus via a one-up one-down staircase procedure.

Unlike Experiment 1, stimuli were presented at one of four possible locations on the intercardinal axes at 10° of eccentricity (Fig. 1C). The adapter was presented in two possible locations: the upper right quadrant (location 1) and the lower right quadrant (location 4). For each adapter location, the test stimulus was presented at one of the three remaining locations. There were six possible adapter-test pairs (two adapter locations × three test locations), which were run in separate sessions in a random order for each participant. Within each session of an adapter-test pair, participants completed two blocks of trials attending to one direction and another two blocks of trials attending to the other direction, with a brief break in between. The order of attended direction (upward followed by downward or vice versa) was randomized. Each block contained seven adapter-only (pre-adaptation) trials and 40 adapter plus test trials.

To test for possible differences in baseline adaptability among test locations, we also ran a control condition. The procedure was

identical to the attention condition above, except that the adapter was a single-direction dot stimulus (i.e., similar to the concrete MAE control in Experiment 1).

## 7. Results and discussion

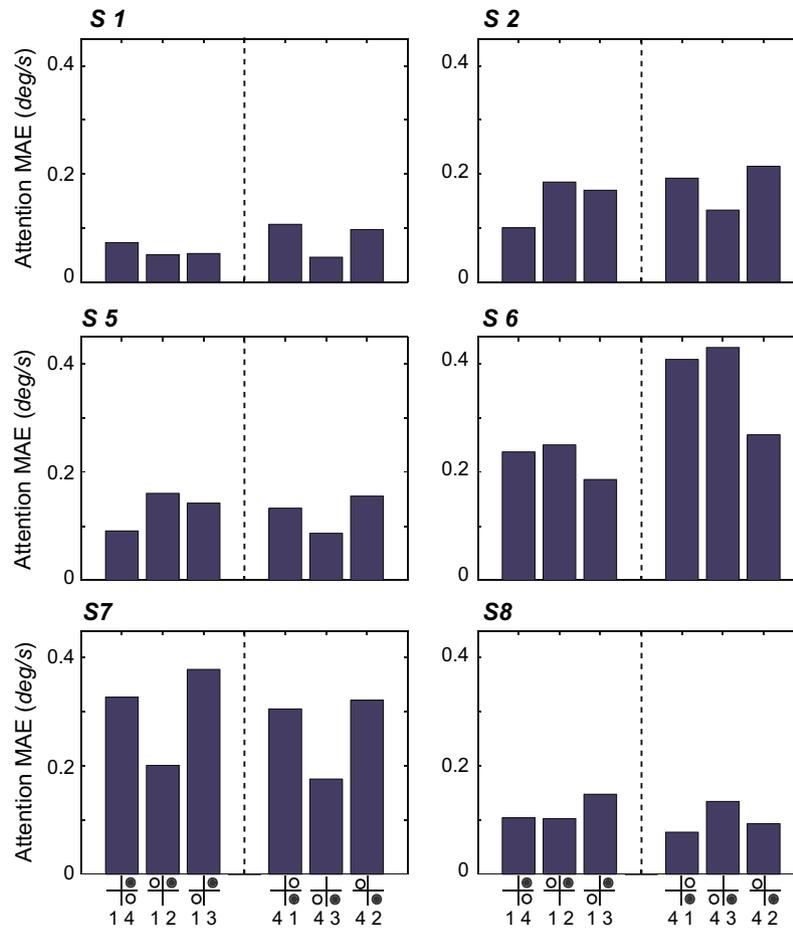
For each adapter-test pair, we fitted psychometric functions separately for attending to upward and downward motion. We then calculated the nulling speed for each condition and used the difference as a measure of attentional effects (see Fig. 2). Attention induced MAEs for each individual participant are shown in Fig. 5. Overall, there was no obvious pattern among adapter-test pairs, as was also shown in group averaged results (Fig. 6A). A one-way repeated measures ANOVA using the adapter-test location pair as the factor revealed no significant effect ( $F(5, 25) < 1$ ). Hence results were further averaged across the two adapter locations, according to the distance between the adapter-test locations and whether they resided in the same or different hemifield. This yielded three conditions: near and same hemifield (near SH), near and different hemifield (near DH), and far and different hemifield (far DH). Again, there was no significant difference among the three conditions (Fig. 6B), indicated by a one-way repeated measures ANOVA ( $F(2, 10) < 1$ ). The iso-eccentric locations on the intercardinal axis are generally equivalent in terms of visual performance (Cameron, Tai, & Carrasco, 2002; Carrasco, Talgar, & Cameron, 2001). Nevertheless, we performed a control condition to assess possible differences in motion adaptation in these locations. The control condition showed no systematic difference in MAEs elicited by a single-direction adapter (Fig. 6C, no significant effect of location in ANOVA,  $p > 0.2$ ). Thus our results cannot be explained by a difference in baseline adaptability across locations.

Results in Experiment 2 showed that when adapter and test stimuli were all located on iso-eccentric locations, attention induced MAE spread uniformly across non-stimulated locations in the visual field. First, when comparing the near SH vs. near DH location, where the physical distance was held constant but hemifield varied, there was no effect of hemifield. Second, when comparing the near DH and far DH location where hemifield was held constant but distance varied, there was no effect of distance. These results indicate that the spread of attention induced MAE is indeed complete.

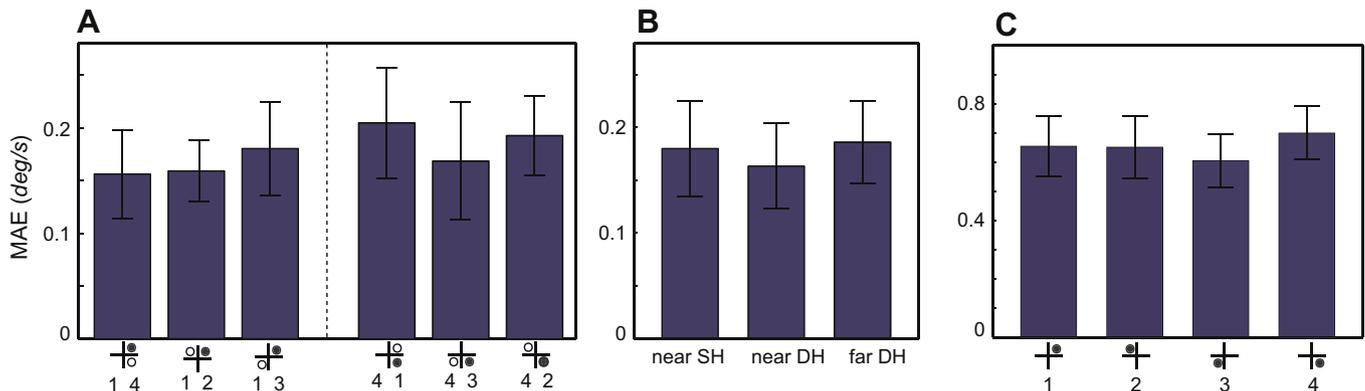
## 8. General discussion

We used an adaptation protocol to measure the spatial spread of global feature-based attention. When participants attended to one motion direction while ignoring another direction in the same location, motion aftereffect was observed in a remote location which was never stimulated (Arman et al., 2006). Thus we can hold sensory stimuli constant while assessing the spread of feature-based attention. Two main results emerged from our experiments: (1) Attention induced MAE does spread to remote locations from both foveal and peripheral adapter locations. (2) Such spread remained constant across locations, regardless of distance and hemifield factors.

Previous neurophysiological and psychophysical studies have shown that attending to a feature causes a global effect in which the processing of the attended feature is enhanced. Our finding of attention induced MAE in remote locations corroborates the global nature of feature-based attentional modulation (Martinez-Trujillo & Treue, 2004; Saenz et al., 2002, 2003; Treue & Martinez-Trujillo, 1999). Interestingly, the remote locations were never directly stimulated by the adapter in our attention experiment, replicating previous findings (Arman et al., 2006). This result suggests that when attending to a particular feature in a location, attention increases the salience of that feature across



**Fig. 5.** Individual participant data in Experiment 2. The icons below the horizontal axis depict the location of the adapter and the test stimuli (solid circle: adapter; empty circle: test). The number pairs are the labels of each adapter-test location pair (see Fig. 1C for labels of location). Dashed vertical lines separate results when the adapter was in the upper right quadrant (location 1) and when it was in the lower right quadrant (location 4).



**Fig. 6.** Group averaged data in Experiment 2. (A) Mean attention induced MAE magnitude (same axis labels as in Fig. 5). (B) Mean attention induced MAE averaged across adapter locations. (C) Mean concrete MAE for all stimulus locations. Error bars represent  $\pm 1$  s.e.m. across participants.

the visual field, which could take the form of increased firing rates for neurons preferring the attended feature. Such enhancement has been reported in monkey single-unit and human imaging studies for stimulus-evoked responses in early visual cortex (Liu et al., 2007; Martinez-Trujillo & Treue, 2004; Saenz et al., 2002; Treue & Martinez-Trujillo, 1999). Our results further suggest that such feature-based enhancement occurs even when neurons are not directly stimulated. It is not clear what physiological mechanisms are responsible for such effects. One possibility is that feature-based attention increased baseline activity in neuronal subpopula-

tions that prefer the attended feature (e.g., Chawla, Rees, & Friston, 1999).

The critical question in the current study was whether the spread of attentional modulation is constant across locations. Here we used the magnitude of MAE as a measure of attentional modulation. In Experiment 1, we measured the spread of attention induced MAE from a central adapter. To take into account the baseline variation in motion processing across eccentricities, we measured the MAE in two control conditions: one in which the adapter was always in the center (phantom MAE control), one in

which the adapter and test stimuli were both in the peripheral location (concrete MAE control). Compared to the phantom MAE, attention induced MAE remained constant across locations, whereas it showed a decrease from near to mid location when compared to concrete MAE. This latter result could be caused by local RF mechanisms receiving input from both the adapter and test stimulus, and hence might reflect a different phenomenon than the global spread of feature-based attention. Beyond this local effect, attention spread constantly through the mid and far locations, suggesting a true global effect. However, the interpretation of results from Experiment 1 is complicated by the fact that the control conditions might also involve feature-based attention.

By placing the stimuli on iso-eccentric locations in Experiment 2, we avoided complications associated with measuring attentional effects across varying eccentricities. Results showed that attention spread evenly for near and far locations in the visual field. The distance effect was also consistent with the constant level of attentional spread from the mid to far location in Experiment 1. Results from Experiment 2 further showed that when distance was held constant, attention spread evenly within and across hemifields. Assuming that MAE occurred due to adaptation of direction-selective mechanisms in retinotopic visual areas (e.g., V1-MT), this result suggests that top-down modulation is equally applied to the two hemispheres. Thus the attended feature is enhanced to a similar degree across the visual field.

Computational models of attention, such as the feature-similarity gain model (Martinez-Trujillo & Treue, 2004; Treue & Martinez-Trujillo, 1999) or the normalization model (Reynolds & Heeger, 2009), generally consider space and feature as independent dimensions. Thus spatial attention is thought to modulate retinotopically specific RF mechanisms regardless of their feature selectivity, whereas feature-based attention is thought to engender feature selective modulations regardless of the location of the RF mechanisms. While there is ample evidence for location-specific modulation of spatial attention, the present study represents the first systematic investigation of the spread of feature-based attention in space. Our results are consistent with a true global feature-based attention that modulates feature-selective mechanisms in the visual cortex to the same extent regardless of their RF location, lending empirical support to the computational models of attention. Such a mechanism would be useful in applying top-down feature-based biasing to facilitate visual processing of task relevant features.

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