

Perceptual consequences of visual performance fields: The case of the line motion illusion

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Illusory line motion (ILM) is the illusion that a line, preceded by a small dot (cue) near one end, is perceived to shoot out from the dot even though the line is physically presented at once. Does this illusion result from a low-level motion effect, a gradient of exogenous spatial attention, or both? Given that exogenous attention speeds visual processing unequally at isoecentric cardinal locations (M. Carrasco, A. M. Giordano, & B. McEree, 2004), we hypothesized that the contribution of attention to ILM would follow the same pattern. We characterized psychometric functions of perceived line motion direction, for 1.5° stimuli with varying amounts of physical line motion (8 levels) at four cardinal locations. We used three cue conditions to separate the effects of attention from low-level motion—a single cue to draw focal attention to the stimulus location, a distributed cue with elements near all four possible stimulus locations, and no visual cue. Distributed and single cues generate identical effects along the horizontal meridian, but the effect of the single cue is progressively greater along the vertical meridian, more so at the top location (“North”). We conclude that the low-level motion explanation accounts for the majority of the canonical example of the ILM (line preceded by a single dot) effect used in our study.

Keywords: motion-2D, attention, spatial vision

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Introduction

Illusory line motion

Illusory line motion (ILM) is the percept that a line, though presented all at once, appears to be drawn out from one end. It can be generated by presenting a brief visual dot (cue) at a spatial location near one end of a subsequently presented line, causing a percept that the line “grows” from the cued end. The illusion interacts with physical line motion as well, diminishing, nullifying, and even reversing the physical motion of a line growing toward the cue, depending on the speed and perceptibility of the physical motion and the distance between the cue and the line (Steinman, Steinman, & Lehmkuhle, 1995).

There is debate as to the mechanism(s) underlying the illusion. One explanation attributes the illusion to a temporal gradient of signal facilitation resulting from the allocation of spatial visual attention (Bavelier, Schneider, & Monacelli, 2002; Hikosaka, Miyauchi, & Shimojo, 1993a, 1993b, 1993c; Hikosaka, Miyauchi, Takeichi, & Shimojo, 1996; Kirschfeld & Kammer, 2000; Schmidt & Klein, 1997; Steinman et al., 1995; von Grünau, Dube, & Kwas, 1996a; von Grünau, Racette, & Kwas, 1996b). Hereafter, we refer to this as the “attention gradient” hypothesis, to signify the central role of the gradient in processing speed in this explanation. A competing explanation attributes ILM to a pre-attentive interaction between

the cue and nearby line stimulus that results in the percept that the line fills in sequentially (Baloch & Grossberg, 1997; Downing & Treisman, 1997; Kawahara & Yokosawa, 2001; Kawahara, Yokosawa, Nishida, & Sato, 1996), i.e. that it is a function of the low-level mechanisms that process motion signals and not dependent on attention.

Tse, Cavanagh, and Nakayama (1998) demonstrated that neither exogenous attention nor low-level motion energy is a necessary condition for evoking ILM. They used competing cues, placed near either end of a subsequently presented line, that remained visible throughout each experimental trial. The direction of ILM could be controlled by varying the relative contrast of the two cue elements, or by placing the line to be contiguous to one element, independent of any onset asynchronies between the two cue elements or between the cue elements and the line. ILM occurred under conditions that did not engage attention. The authors conclude that the illusion in this configuration resulted from higher level motion mechanisms, naming it “Transformational Apparent Motion.”

There are additional examples of experiments that generated ILM without low-level motion, using “reflexive orienting cues” to deploy attention, which lacked local visual input in the vicinity of the line stimulus. Bavelier et al. (2002) used a central “face” cue and found significant line motion effects, supporting the idea that attentional (not necessarily exogenous) facilitation is sufficient to generate ILM. Driver et al. (1999) pointed out that the time course of these ‘reflexive’ cues is comparable to that of endogenous

attention). Moreover, the illusion emerges when attention is directed to the relevant location cross-modally, e.g. via auditory (Shimojo, Miyauchi, & Hikosaka, 1997), and somatosensory (Hikosaka et al., 1996; Shimojo et al., 1997) spatial location cues.

The attention gradient hypothesis investigated in the present study specifically involves exogenous or transient covert attention, engaged to the location of the dot (or “cue”) by its onset. It is an automatic, involuntary orienting to a localized area of the peripheral visual field without eye movements, usually engaged by a nearby sudden luminance transient. Exogenous attention is described as “stimulus-driven” because of the automaticity of this response. Its effects, which include localized increases in contrast sensitivity and visual acuity, peak in ~100 ms and degrade quickly after. The other form of spatial covert attention, endogenous attention, is voluntary, peaking in ~300 ms and sustainable with effort (e.g. Carrasco, Giordano, & McElree, 2006; Cheal & Lyon, 1991; Nakayama & Mackeben, 1989).

Temporal acceleration by attention has been given considerable examination in the ILM literature (Hikosaka et al., 1993a, 1993b, 1993c, 1996; Kirschfeld & Kammer, 2000; Steinman et al., 1995; von Grünau et al., 1996a, 1996b). This hypothesis states that exogenous attention accelerates visual processing unevenly across a limited area of the visual field, and that the acceleration decreases with greater distance from the locus of attention. As a result, visual signals from areas nearer the cue are processed faster than those farther away, so that the latency to perception at the cued end of the line is shorter than at the farther end of the line. The resulting delay between neighboring signals within the line causes the activation of motion detectors. This hypothesis is consistent with the findings that transient attention speeds information accrual in search tasks (Carrasco, Giordano, & McElree, 2004, 2006; Carrasco & McElree, 2001), and decreases latency to perception by 20–40 ms in a temporal order judgment task (Hikosaka et al., 1993a; Shore, Spence, & Klein, 2001; Steglich & Neumann, 2000; Stelmach & Herdman, 1991).

The low-level motion hypothesis explains the illusion as the interpretation of the cue and line by the visual system as successive states of a single object in motion, in the same way that a dot or other object presented sequentially at two different spatial locations is perceived to have moved from one location to the next. By this account, the visual system responds to the discrete visual inputs of the cue and the line, which differ in spatio-temporal characteristics and shape, by interpolating between the physical inputs to create a percept of motion and shape change (Baloch & Grossberg, 1997; Downing & Treisman, 1997; Hsieh, Caplovitz, & Tse, 2005; Kawahara & Yokosawa, 2001; Kawahara et al., 1996). The system is proposed to have a “Bayesian prior” or operate on a “heuristic” that interprets such naturally uncommon visual inputs in a manner that is ecologically plausible (Hsieh et al., 2005).

The variety of studies supporting each of these two hypotheses suggests that both mechanisms are plausible explanations for ILM. Central to the experimental approaches from either side of the debate has been the need to isolate the two mechanisms. To show that one mechanism is sufficient to cause ILM, it is necessary to neutralize or significantly reduce the influence of the other.

Downing and Treisman (1997) examined both hypotheses in a series of experiments, and noted an absence of ILM in their attentional conditions. (But see Schmidt (2000) for a discussion of possible methodological issues with these attention conditions.) Kawahara and Yokosawa (2001) neutralized exogenous attention by using arrays of up to 8 dots presented simultaneously at locations spanning an area. Exogenous attention is considered to be either not engaged or so highly distributed by such cue arrays that local spatial effects are significantly reduced relative to a single peripheral cue.

Studies of focal exogenous attention have often used control conditions with highly spatially distributed cues, such as lines spanning several degrees of visual angle (e.g., Talgar & Carrasco, 2002; Yeshurun & Carrasco, 1998, 2008), and multi-element arrays of dot cues (Carrasco, Williams, & Yeshurun, 2002; Talgar, Pelli, & Carrasco, 2004), which reduce significantly the focal effects of attention at the locations of individual cue elements. Talgar et al. (2004) compared the effects of two types of “control” cues (a single, uninformative central cue at fixation, and an 8-element peripherally distributed cue) versus a single peripheral cue (that corresponded to one of the multi-element locations) in a peripheral letter identification task. Task performance was significantly better with the single peripheral cue than for either type of control cue. Of relevance to the present study, there was no performance difference in this peripheral letter task between the two control cues, the multi-element peripheral and the single central cues. This result demonstrated the usefulness of multi-element cues as a control condition in studies of the peripheral effects of exogenous attention, and shows at minimum that distributed cues significantly reduce focal attentional effects, relative to single peripheral cues of comparable eccentricity. It is important to note, however, that it does not imply that peripheral attentional effects are completely absent at the distributed cue locations. Accordingly, in this study we characterize the distributed cue as significantly reducing focal attention at the distributed cue locations compared to the single cue.

Kawahara and Yokosawa (2001) demonstrated that ILM was perceived at each of 8 locations. Moreover, the direction of perceived line motion at each location was independent of the other locations, depending solely on which end of each line was nearest its local dot cue. The authors concluded that this ILM mechanism is “preattentive,” or at least did not involve attention. In addition, their results suggest that this mechanism for ILM is the result of highly spatially localized interactions between the line-dot pairs.

von Grünau et al. (1996a) conducted a series of experiments showing that both mechanisms generate ILM and that they have different time courses. The first, which they also described as “preattentive”, was able to operate at multiple locations simultaneously across a display in which 48 inducers were presented simultaneously, and in which it is highly unlikely that focal attention would be deployed. Moreover, the effects of this mechanism were independent of the time delay between the inducer (cue) array and the target line, lending further support to the idea that the ILM effect under these display conditions was non-attentional in nature. The second mechanism, which they describe as roughly consistent with the characteristics of exogenous attention, was spatially localized and peaked in 200–300 ms. In their Experiment 2, von Grünau et al. (1996a) neutralized the effect of the low-level motion mechanism by placing their target stimulus equidistant between two cues in their array. This arrangement results in a percept that the line grows from both ends toward the center. Although this suggests that the low-level motion mechanism is not inactive, for the 2AFC motion direction task they used, it yielded chance reporting (.5) in either direction for their “non-attention” condition, neutralizing the effect of low-level motion on reporting. In focal attention trials, a single inducer in the array nearest one end of the line stimulus was oriented orthogonal to the other inducers, generating a “pop-out” attention effect that caused the reported ILM to be away from that inducer.

If, as the evidence above suggests, ILM can be induced under experimental conditions favoring the operation of low-level motion mechanisms or favoring the deployment of attention, then in the canonical example of one cue and one line, can we isolate the contributions of each mechanism? To address this question, we overcome a critical issue raised by Christie and Klein (2005), namely that for the case of a single cue the loci of attention and visual stimulation are confounded, by using a methodology in which attention and low-level motion effects are separable while maintaining the same local visual input around the stimulus location. In one cueing condition, we use a single peripheral cue with timing and spatial proximity to the line that both engages exogenous spatial attention and triggers low-level motion. Our second cueing condition adds three identical cues at disparate spatial locations to create a “distributed” cue. As discussed above, we use distributed cues for their potential to induce ILM with distributed attention at the locations of each cue element, while maintaining the same local visual conditions in the vicinity of the line stimulus favorable to low-level motion detectors. Thus, we are able to compare a condition in which both the presumed attentive and low-level motion mechanisms may operate (single cue) to one with distributed attention (distributed cue) but in which the low-level motion effect would be similar.

Visual and attentional factors: Performance fields

The term ‘performance fields’ is used to describe the fact that visual performance is not homogeneous at isoeccentric locations. Superior performance on the horizontal compared to the vertical meridian of the visual field is known as the horizontal-vertical anisotropy (HVA) and has been reported in a variety of visual tasks (e.g., Mackeben, 1999; Rovamo & Virsu, 1979). There is also evidence for a vertical meridian asymmetry (VMA) with findings that performance is better in the lower than upper regions of the vertical meridian in spatial tasks mediated by contrast sensitivity (Cameron, Tai, & Carrasco, 2002; Carrasco, Talgar, & Cameron, 2001; Fuller, Rodriguez, & Carrasco, 2008) and spatial resolution (Carrasco et al., 2002; Talgar & Carrasco, 2002). The behavioral VMA correlates with asymmetries in spatial extent and amplitude of BOLD response in V1 and V2 stimuli presented at isoeccentric locations on the upper and lower vertical meridian (Liu, Heeger, & Carrasco, 2006).

Carrasco et al. (2004) have shown the existence of temporal performance fields. Using a procedure to derive conjoint measures of response time and accuracy (Speed Accuracy Trade-off, “SAT”) in a discrimination task, they showed that the speed of visual processing for isoeccentric targets is fastest on the horizontal meridian, followed by intercardinal locations, then the lower and upper locations on the vertical meridian (East & West > intercardinal > South > North),¹ demonstrating both an HVA and a VMA. This study also examined the effects of exogenous attention on temporal performance fields. Whereas attention yields a proportional improvement in orientation discrimination at locations on the visual meridians that leaves performance fields intact (e.g. Carrasco et al., 2001), it leads to a greater increase in processing speed at more disadvantaged locations, i.e. North > South > intercardinal > East & West. The slower speed of visual processing and more pronounced attentional effect in the North suggests that exogenous attention may have a greater contribution to ILM in the North location than at the other cardinal points in the visual field.

Goals of the present study

The main goal of this study is to understand the relative contributions of low-level motion and exogenous attention to the canonical ILM induced by a single cue preceding a single line stimulus. von Grünau et al. (1996a) have proposed that the low-level motion mechanism is more fundamental than attention in this illusion, based on its ability to generate ILM at shorter cue-stimulus SOAs than exogenous attention. This view predicts that low-level motion should account for all or the majority of the effect in this simplest case of ILM. The present study proposes to test this prediction in the context of temporal performance

fields, i.e. Carrasco et al.'s (2004) evidence that the effects of exogenous attention on temporal processing speed exhibit both an HVA and a VMA. Do the contributions to ILM of low-level motion and the gradient of exogenous attention differ between isoeccentric locations on the horizontal and vertical meridians (HVA) and between the upper and lower segments of the vertical meridian (VMA)? We also examined whether these inhomogeneities are reflected in perception of physical line motion.

Experiment

In this experiment we investigate the contributions of exogenous attention and low-level motion to the canonical ILM (a line segment preceded by a single dot (or cue) at one end). We test the discriminability of radial physical line motion, i.e. toward and away from fixation, with no visual cue (control condition), and with distributed peripheral cues and single peripheral cues at four locations on the vertical and horizontal meridians.

Methods

Observers

Participants were 4 female and 3 male graduate and undergraduate students at NYU. One was an author, and six were naive to the purpose of the experiment. All had normal or corrected-to-normal vision.

Stimuli

Stimuli were presented using a Macintosh G4 computer running Matlab R7 software on a 40×30 cm gamma-corrected monitor with a refresh rate of 180 Hz and the background set to 20 cd/m^2 . All cues and stimuli were $.5 \text{ cd/m}^2$. Observers sat 57 cm from the monitor, with their heads stabilized by a chin rest. The fixation point was a cross subtending 0.4° at the center of the screen. Line stimuli ($.25^\circ \times 1.5^\circ$) were presented radially at 7° eccentricity in each of the cardinal directions (N, S, E, W).

Stimuli were presented with 8 build times that ranged from 0 ms (the line was presented all at once and had no physical motion) to 55 ms (the line was presented in 11 segments; counting from the onset of the 1st segment, the 11th segment is presented 10 screen refreshes later $10/180 \text{ Hz} = 55 \text{ ms}$), with the direction of the build either inward, toward fixation, or outward, away from fixation. At the extremes (55 ms build time), physical line motion was slow and motion direction was easily discriminable. Faster motion (shorter build times) would reduce direction discriminability. This range of stimulus presentations

allowed estimation of psychometric functions for direction discriminability versus line build time and motion direction (see Results).

Cues subtended 0.35° of visual angle, at locations 5.5° or 8.5° from fixation on the vertical and horizontal meridians. Cue locations were thus 1.5° away from the centers of the stimulus locations, or 0.75° from the ends of the line stimuli. In the distributed cues, the three dots away from the line stimulus were at a sufficient distance from the line stimulus to have no effect (Steinman et al., 1995) other than to distribute attention in the display (inside cues: lateral dots, $\sim 8^\circ$, dot in-line with the stimulus, $\sim 12^\circ$; outside cues: lateral dots, $\sim 12^\circ$, dot in-line with the stimulus, $\sim 18^\circ$).

Studies of ILM have used both “spatially coincident” cue-line configurations, in which the end of the line occludes the cue location (e.g. Hikosaka et al., 1993a, 1993b, 1993c, 1996), and “spatially offset” configurations in which there is a gap between the cue and line locations (e.g. Steinman et al., 1995; Steinman, Steinman, & Lehmkuhle, 1997; von Grünau et al., 1996a, 1996b). Neither the attentional gradient nor the low-level motion explanations of ILM are specific to one configuration or the other. We used the offset configuration and removed the cue after a brief presentation (see Procedure) because of our inclusion of physical line motion *toward* the cue. Had the cue remained onscreen, observers would have been able to discriminate direction based on whether or not they saw one or both ends of the line present at the same time, potentially biasing the results. This raises the question of whether the distance between the cue and the line is appropriate to trigger low-level motion detectors, which operate over a short distance. Aghdaee and Cavanagh (2007) measured the spatial cutoff between low-level and high-level motion detection mechanisms in terms of temporal frequency thresholds for phase alternation judgments of two dots, as a function of the spacing between the dots. Their results indicated that the transition between the two mechanisms occurred at $\sim 0.91^\circ$ of separation at 4° eccentricity, increasing to $\sim 1.75^\circ$ separation at 14° eccentricity. Interpolating from these results, low-level motion mechanisms should operate up to $\sim 1.04^\circ$ separation between the cue element and the end of the line stimulus when the cue is at 5.5° eccentricity and $\sim 1.3^\circ$ separation when the cue is at 8.5° eccentricity. Our separation of 0.75° is clearly within the limits of low-level motion detectors.

Procedure

Each trial began with 750 ms of fixation on a cross at the center of the display, which remained in place throughout the experiment. Following fixation, a brief tone indicated the start of a trial (Figure 1). As a baseline condition to assess discriminability of physical line motion, we presented only the line stimuli without a preceding visual cue (no-cue condition). In cued trials, a

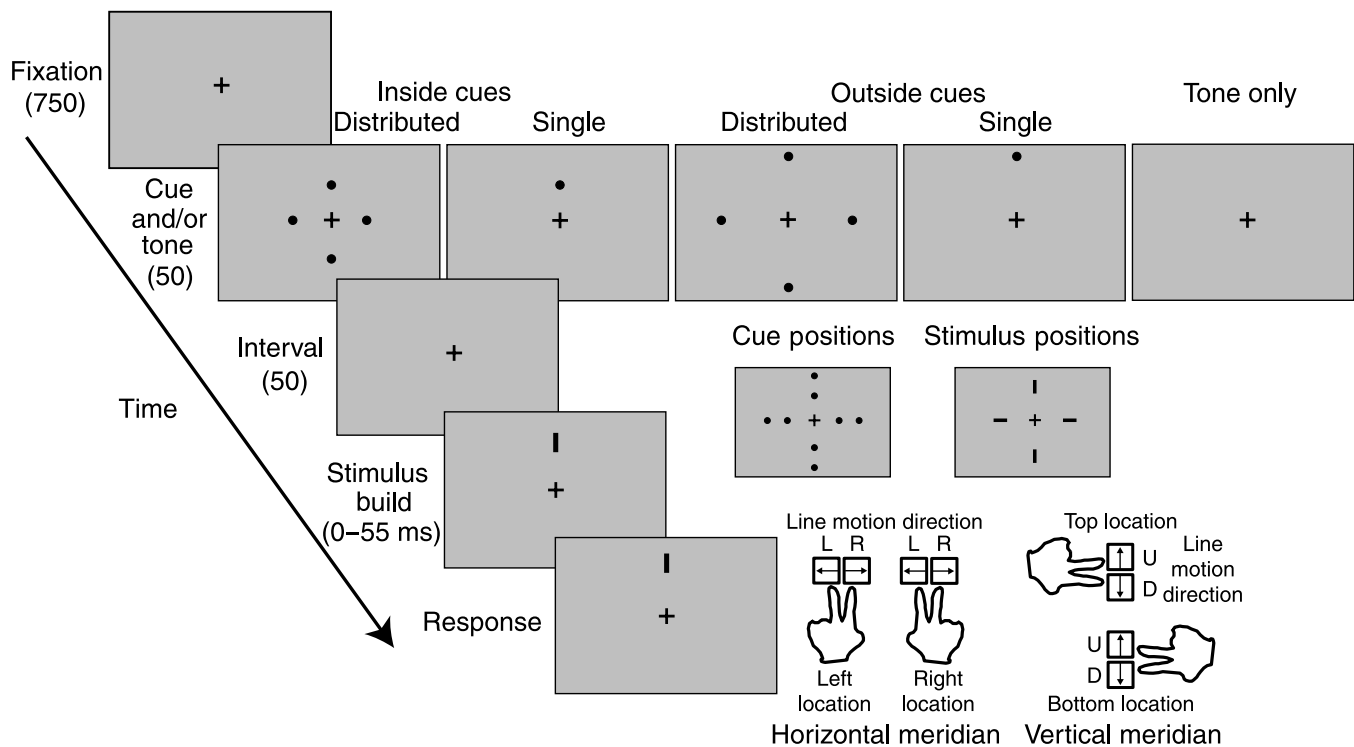


Figure 1. Trial sequence. Observers maintained fixation on the central cross. After 750 ms, a tone signals the beginning of the trial, accompanied by one of four visual cues (2 cue types \times 2 cue positions) or no visual cue (control condition) for 50 ms. Single cues were located near the stimulus location, engaging focal attention. Distributed cues appeared near all four stimulus locations, broadly distributing attention. Following a 50 ms ISI, a line stimulus was presented at one of four locations. Line stimuli were presented as a single segment or in up to 11 sequential segments, one every 5.5 ms (maximum build time 55 ms) building toward or away from fixation. The completed line remained onscreen until response. Observers reported the location of the line and the direction of line motion. Trials on the vertical and horizontal meridians are blocked (North and South locations, East and West locations).

single peripheral cue at the location of the upcoming stimulus, or a distributed cue with identical elements appearing at all four possible cue locations appeared for 50 ms (commencing with the audio tone), followed by a 50 ms fixation interval before stimulus presentation. In the no-cue condition the stimulus appeared 100 ms after the tone, such that the line was always presented at a constant delay following the tone that began each trial.

As exogenous attention peaks at about 100–120 ms after cue onset (Nakayama & Mackeben, 1989), the 100 ms interval between the visual cues and the stimulus ensured that the line stimulus presentation would occur during the temporal window of exogenous attention elicited by the visual cues; the slowest line build started at 100 ms from cue onset and was complete within 155 ms. The short time between the start of the trial and the completion of the stimulus motion precluded saccades to the stimulus while actual motion was in progress. The completed line stimulus remained visible until observer response.

Visual cues appeared at one of two possible locations relative to the line stimuli, either at the “inner” end of the line toward the fixation point or at the “outer” end away from fixation. The single cues accurately predicted the stimulus location, but were uninformative of the direction or speed of the stimulus, whereas the distributed cues

were totally uninformative except with regard to stimulus onset.

Design

The experiment was randomized across four conditions: line build time and direction (15 values ranging 55 ms toward fixation to 55 ms away from fixation and including 0 ms, i.e. simultaneous presentation of the entire line); cue condition (3); cue position relative to the line stimulus (2, on the inner (fixation) side of the stimulus or the outer (away from fixation) side), and spatial location (4, East, North, West, and South meridian at 7° from fixation). Observers were explained the task and performed a practice block of 200 trials. They were instructed to maintain gaze on the fixation cross throughout the experiment, and advised that eye movements away from fixation would impair their performance on the task. The experiment was conducted in four sessions, two in which the stimulus could appear on the right or left horizontal meridian, and two on the upper and lower vertical meridian, in counterbalanced order. Observers performed a total of 6,400 trials across the four sessions.

Observers performed a 2 AFC task, reporting the direction of motion within the line stimulus, leftward or

rightward for stimuli on the horizontal meridian, upward or downward for stimuli on the vertical meridian (Figure 1). Different keys were used for reporting direction at the two stimulus locations in a given session: ‘z’ and ‘x’ for leftward and rightward motion, respectively, when the stimulus appeared at the West location, ‘n’ and ‘m’ for the East stimulus location; for North and South locations the keyboard was rotated 90° clockwise, ‘z’ and ‘x’ corresponding to upward and downward motion at the North location, ‘n’ and ‘m’ for upward and downward at the South location. Responses were re-coded during processing to convert the original “left”, “right”, “up” and “down” direction responses into “inward” and “outward” for each of the four cardinal stimulus locations. For example, a “left” response for a stimulus in the West location was translated to “outward”, whereas a “left” response for the East location was translated to “inward.”

Results

We fitted Weibull functions to each individual observer’s data, with the probability of reporting outward line motion as the dependent variable and the combined direction and build time of the stimulus as the independent variable, for all combinations of stimulus location, inner and outer cue position, and cue condition (no cue, single cue, and distributed cue). This yielded 20 psychometric functions per observer (the cue position variable did not apply to the no-cue condition). Goodness of fit was evaluated using deviance scores (Wichmann & Hill, 2001). All scores were below the critical chi-square value ($\chi^2(15) < 25$), indicating good fits.

The pooled data for all seven observers are shown in Figure 2. The location of each panel corresponds to the stimulus location. We analyzed three aspects of the psychometric functions (Figure 3). The “Zero Point” is the probability of reporting motion when the line is presented all at once and thus there is no physical line motion. When the line is not preceded by a cue, we expect no line motion to be induced and this probability to be at chance (0.5). For trials in which a cue is presented, the probability of reporting motion at the zero point deviates from chance due to ILM elicited by the visual cue. The “point of subjective equality” (“PSE”), is the physical line build time in ms at which observers perceive no net motion, and direction reporting is at chance. In the absence of cues to induce ILM, the Zero Point and PSE are expected to coincide. The third measure is the slope parameter of the psychometric function, which represents the discriminability of the line motion direction; shallower slopes indicating poorer and steeper slopes better discriminability of the physical line motion in the stimuli.

Preliminary analysis of the four cardinal stimulus locations revealed that there were no significant differences

on any of our measures between the two locations on the horizontal meridian. We then pooled each observer’s data from the two horizontal meridian locations (HM), and from the two vertical meridian locations (VM), to test for the hypothesized horizontal-vertical anisotropies (HVA) in our various measures. We tested for vertical-meridian asymmetries (VMA) by comparing results for the upper (UVM) and lower (LVM) segments of the vertical meridian.

The results are reported here in four stages, due to the multiplicity of measures and conditions: first, the no-cue trials, in which there were no ILM inducers, to assess HVA and VMA for physical line motion as context for the ILM results; second, the single, peripheral cues; third, the distributed cues; and fourth, differences between single and distributed cues. The differences we refer to were statistically significant as revealed by ANOVAs and paired comparisons. Statistics and p values for significant differences are reported in Appendix A.

Performance fields for real line motion (no-cue condition)

We analyzed the three measures for the no-cue condition (Zero Points, PSEs, and Slopes) using within-subjects paired comparisons (HM vs. VM, UVM vs. LVM; Figure 4).

Zero Points

The Zero Points for the no-cue condition are shown in Figure 4a. There were no effects of location, and none of the meridians or meridian segments (HM, VM, UVM, LVM) differed significantly from chance (0.5). As expected, observers were equally likely to report outward and inward motion when the line was presented all at once.

PSEs

Similarly, there were no significant location effects on the PSEs. The PSEs occurred when there was no physical motion in the stimulus (Figure 4b). Absent any induced ILM, the Zero Points and the PSEs should correspond, as the data show.

Slopes

There were two significant differences in the slopes for the no-cue condition (Figure 4c). The slope for the vertical meridian was significantly shallower than that for the horizontal, indicating a HVA. Within the vertical meridian, the slope was significantly shallower in the UVM than in LVM, indicating a VMA. Line motion discrimination is poorer on the vertical meridian than the horizontal, and poorest on the upper vertical meridian. At these positions, observers require the motion to be slower to reliably discriminate its direction.

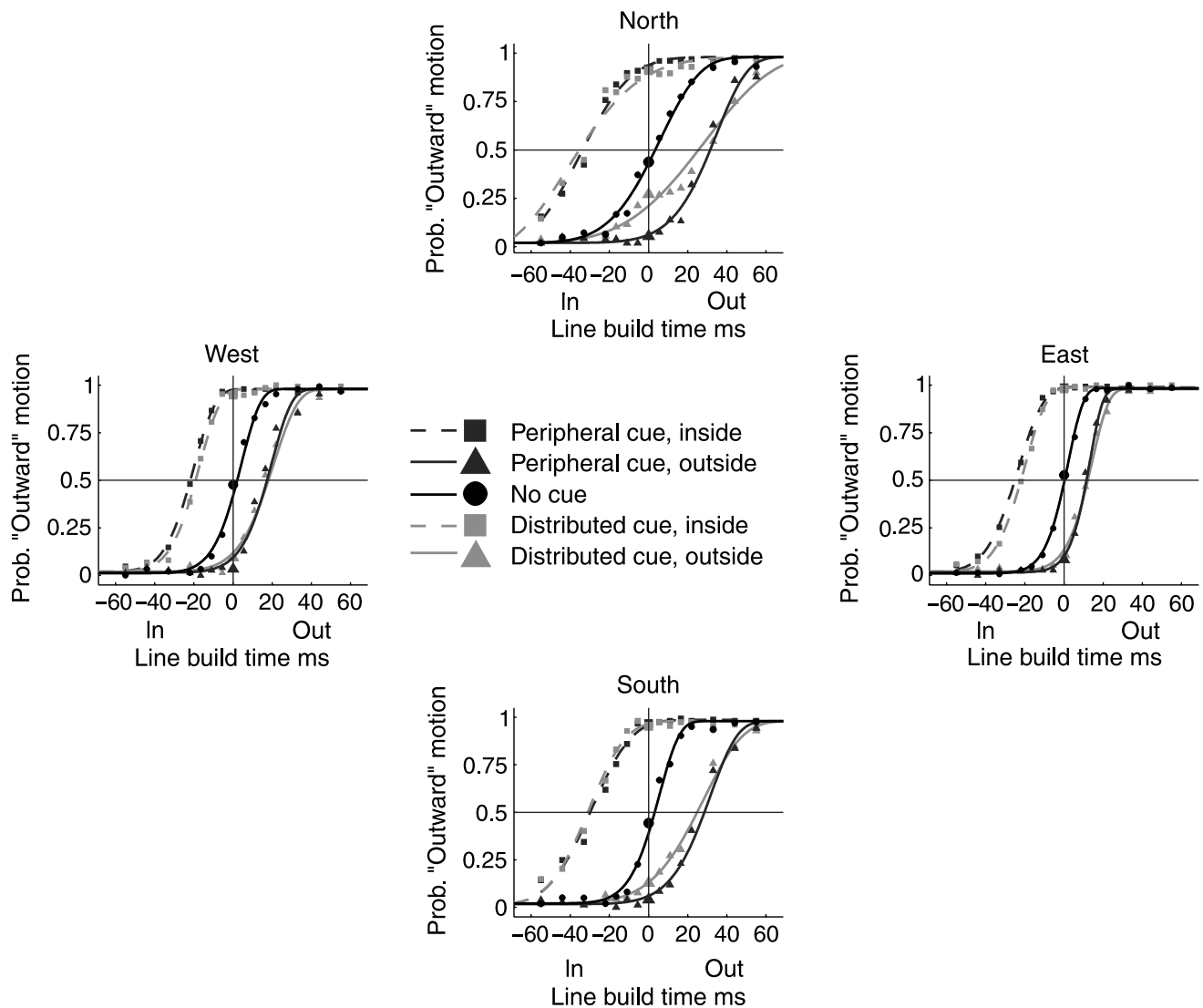


Figure 2. Pooled psychometric functions for seven observers.

Summary

Observers were equally likely to report inward and outward motion where there was no physical motion in the stimulus, at all four cardinal locations. The PSEs confirmed this result: the mean values of physical line motion that corresponded to .5 probability of reporting inward and outward motion were not significantly different from zero.

We found differences in radial motion direction discriminability (i.e. the slopes of the psychometric functions) between the vertical and horizontal meridians. This result also suggests a HVA, however our use of radial lines means that the directions of line motion were orthogonal across the meridians. The present study alone does not resolve this issue, but McColgin (1960) reported HVAs in threshold for both vertical and horizontal linear motion, in which thresholds for both directions were lower along the horizontal than the vertical meridians. The thresholds for motion in the two directions were remarkably similar, the only reported difference was that vertical motion was

slightly more discriminable than horizontal motion in regions near the horizontal meridian. The novel result here is a specific discriminability deficit on the upper vertical meridian relative to the lower vertical meridian (Figure 4c). This VMA parallels previous reports of similar UVM deficits for contrast sensitivity (Cameron et al., 2002; Carrasco et al., 2001; Fuller et al., 2008), acuity (Carrasco et al., 2002), and texture segmentation (Talgar & Carrasco, 2002).

Canonical ILM with a single cue

It is well known that a single cue generates ILM away from the cue. In our paradigm, inside cues shifted the Zero points toward outward motion, and outer cues shifted it toward inward motion. Similarly, as the ILM interacted with the physical line motion in the stimuli, the PSEs no longer corresponded to the Zero Points. Here, the PSE indicates the point at which the physical line motion and

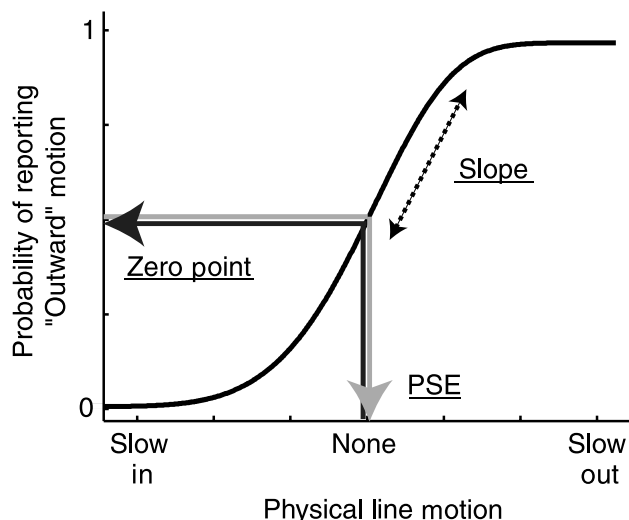


Figure 3. Analysis schematic. Psychometric functions were fitted to each observers' data (5 cue conditions \times 4 locations), probability of reporting outward motion vs. the combined line build time and direction of physical line motion. Three measures were used for analysis: 1) Zero Point: probability of reporting outward motion when no physical line motion was present (dark gray arrow); Point of subjective equality (PSE): physical line build time/direction at which the probability of reporting outward motion was chance (.5, light gray arrow); Slope parameter of the fitted psychometric function (represented by dotted line).

ILM offset each other to render direction discrimination at chance (probability .5), giving an estimate of the speed of the illusory motion generated in the line.

We analyzed each of the three measures with within-subjects ANOVAs to examine whether they differed by meridian (HM, VM) or specific location within the

vertical meridian (UVM, LVM), and position of the cue relative to the line stimulus (inside versus outside).

Zero Points

For the Zero Points (Figure 5a), the significant main effect of cue position (inside versus outside) resulted from the fact that the inside cue elicited outward ILM whereas the outside cue elicited inward ILM, reducing the proportion of “outward motion” responses. All motion direction responses were near ceiling with both inward and outward cues. The direction of ILM generated by a single peripheral cue is easily discriminable in a static line stimulus.

PSEs

The units in which we report PSEs correspond to the horizontal axes of the plots in Figure 2, a combination of line build time (55 ms for the slowest physical line motion to 0 ms for a stationary stimulus presented all at once) and direction of motion (negative sign for inward motion, positive sign for outward motion). A PSE with a large absolute value indicates that it required slow, highly perceptible physical line motion to offset or nullify the ILM induced by the cue, reducing direction reporting to chance level. PSEs can also be interpreted as estimating the speed of the ILM. The significant interaction of meridian and cue position resulted from a significant location effect for the outside cues and a trend for inside cues (Figure 5b). The PSE shifts for the outside cues were significantly greater in magnitude on the horizontal meridian than the vertical meridian. There were no significant differences between the UVM and LVM.

The magnitude of the PSE shifts was greater for inside cues than outside cues; the speed of ILM generated by the inside cues, outward from fixation, was slower than

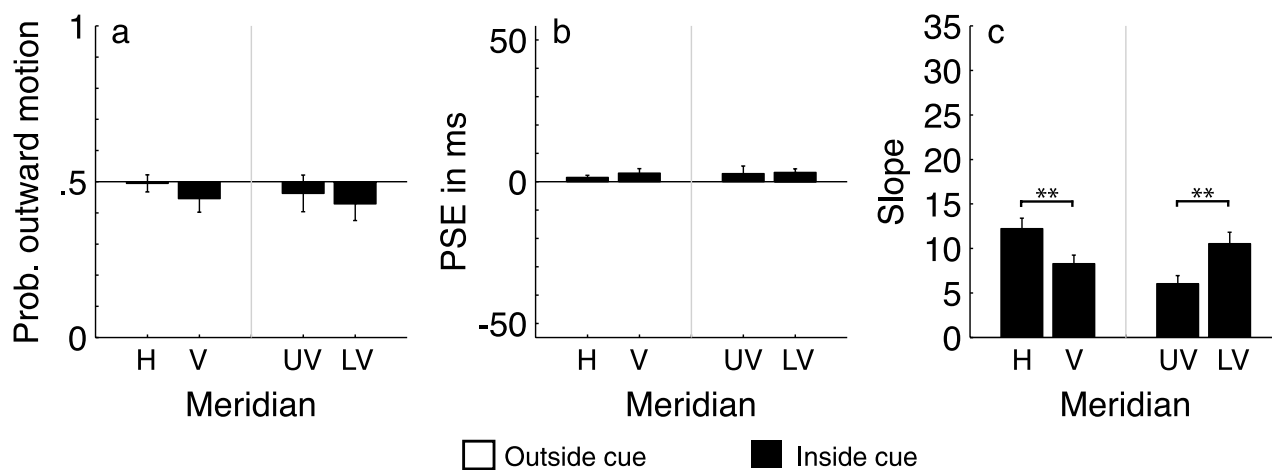


Figure 4. Mean results for no-cue (tone only) condition. (H: horizontal meridian; V: vertical meridian; UV: upper vertical meridian; LV: lower vertical meridian.) (a) Zero Points are ~.5 probability of reporting outward motion when there is no physical line motion. (b) PSEs coincide with Zero Points. (c) Slope is shallower on horizontal meridian than vertical meridian, and within vertical meridian on upper segment than lower segment. Shallower slope indicates poorer motion direction discriminability. (Error bars: 1 SE. Significance: * $p < .05$; ** $p < .01$; *** $p < .005$; **** $p < .001$.)

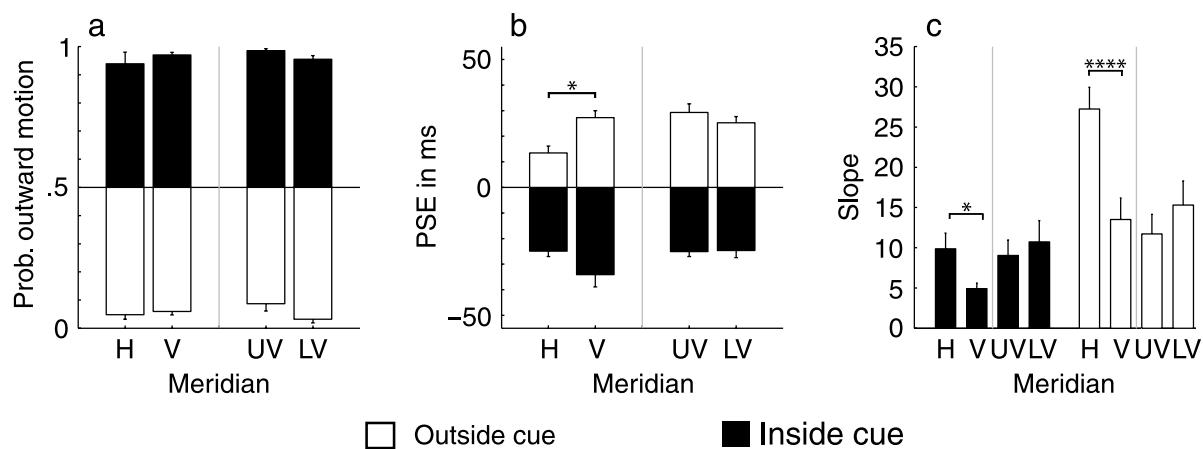


Figure 5. Mean results with single cue. (H: horizontal meridian; V: vertical meridian; UV: upper vertical meridian; LV: lower vertical meridian.) ILM is generated away from the cue. (a) Zero Points shift in opposite directions with inside cues (percept of outward motion) and outside cues (percept of inward motion); no differences by location. (b) PSEs occur at slower physical line motion on the vertical than the horizontal meridian, indicating differences in speed of ILM. Shift is greater for inside cues than outside cues at all locations. (c) Slopes for inside cues are shallower than for outside cues; direction discriminability for the net motion (ILM + physical line motion) is poorer. (Error bars: 1 SE. Significance: $*p < .05$; $**p < .01$; $***p < .005$; $****p < .001$.)

that generated by the outside cues. The progression from “faster” PSEs on the horizontal meridian to “slower” values on the vertical meridian suggested a relation with the underlying discriminability for physical line motion. Figure 6 is a scatter-plot of the single cue PSEs for all observers versus their slopes from the no-cue condition, including the original four cardinal locations for each observer. The two measures were highly correlated ($r = \pm 0.6$). For both inside and outside cues, a shallower slope in the no-cue condition correlated with a slower PSE, i.e. the PSE occurs at a longer stimulus build time. The sign difference in the correlation merely reflects the opposite direction of motion for inside and outside cues.

Slopes

With single peripheral cues, slopes were shallower when the cues are positioned on the inside than the outside of the line stimulus, indicating that the inside cues reduce the direction discriminability of the net motion percept relative to the outside cues. The main effect of meridian showed that slopes were shallower on the vertical meridian than on the horizontal meridian. The lack of an interaction effect indicated that this shallower slope on the vertical meridian was present regardless of cue position.

Summary

The percept of ILM is strong when the line stimulus is presented all at once, regardless of location in the visual field. Our observers’ direction reporting was at ceiling whether the cues were positioned on the inside (fixation side) of the line or the outside; the cue generated a clear percept of motion away from the cue.

Analysis of the PSEs revealed several interesting differences by meridian and cue position, which can be

interpreted as relating to the relative speed of the ILM percept. The PSEs occur at slower physical line motion on the vertical meridian. We note the correspondence between this and the poorer underlying motion discriminability on this meridian, demonstrated by the shallower slope in the no-cue condition. In addition, cues on the inside of the line stimulus, closer to fixation, elicited slower ILM than corresponding outside cues.

The pattern of shallower psychometric function slopes on the vertical meridian than on the horizontal that was found in the no-cue condition (Figure 4c) remained in the presence of single cues (Figure 5c). Our results also show that the inside cues further reduced the slope of the psychometric function, relative to observers’ slopes in the no-cue condition. The direction of the net motion percept was less discriminable than when there was no cue and observers are responding only to physical line motion, whereas when the cue was on the outside of the line stimulus, discriminability actually increased.

ILM with distributed cues

Zero Points

The significant meridian \times cue position interaction revealed that there was a location effect for the outside but not for the inside cues (Figure 7a). For the outside cue, the ILM generated on the vertical meridian was weaker than on the horizontal meridian.

PSEs

There was a significant main effect of cue position in which PSEs were larger with inside cues than with outside. There was a significant meridian \times cue position interaction (Figure 7b). The effect of meridian was

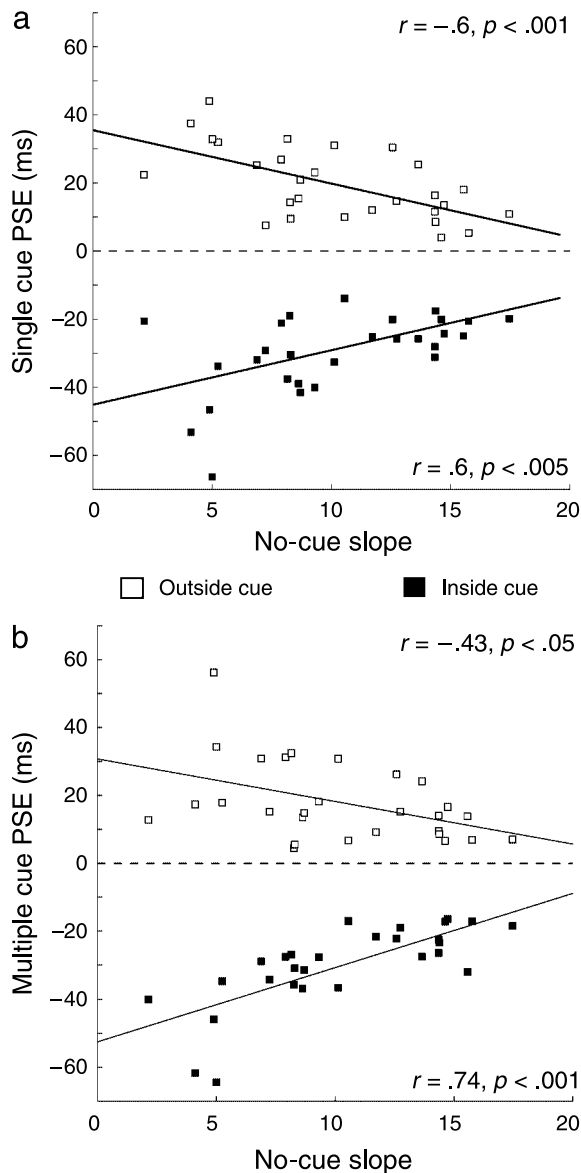


Figure 6. Scatterplots of single-cue PSEs (Panel a) and distributed-cue PSEs (Panel b) with no-cue condition slope for all observers. Speed of ILM (PSE) is correlated with discriminability of physical line motion (slope) for inside cues and outside cues. Better underlying discriminability, or sensitivity to line motion, is tied to faster ILM speed, suggesting that the speed of ILM is governed by the properties of motion detectors. Data are shown in the four cardinal locations, i.e. meridians are unpooled.

significant for the outside cues but not for the inside cues, similar to what we found for the single peripheral cue.

Slopes

Slopes were steeper on the horizontal meridian than on the vertical meridian (Figure 7c). They were also steeper for outside than for inside cues, which suggests an impairment of direction discriminability when the cues

were on the fixation side of the line, generating outward ILM, as we found with the single cues.

Summary

The results with the distributed cues followed a similar pattern as the results with the single cues regarding the PSEs and the slopes. However, there was one departure with regard to the Zero Points: the differences between the horizontal and vertical meridians for outside cues (compare Figures 5a and 7a). We address the relative effects of single versus distributed cues for Zero Points and PSEs in more detail in the next section.

ILM differences between single and distributed cues

To assess differences in the contributions to ILM from the attention gradient and low-level motion we analyzed differences in Zero Points, PSEs, and slopes by subtracting the distributed cue values from the single cue values for each observer (Figure 8). The logic of this is that the single and distributed cues are identical in the immediate local vicinity of the line stimulus, and should be equivalent in their ability to generate low-level motion between the nearest cue/dot element and the line and thus, low-level motion-generated ILM within the line. Because the single cue also engages focal spatial attention, whereas distributed cues significantly reduce focal attention, differences in our results among these types of cues indicate a separation of the contributions of these two mechanisms to ILM.

Zero Points

A within-subjects ANOVA on the difference for single cues versus distributed cues yielded significant main effects of meridian, cue position and their interaction (Figure 8a). There was no difference between cue types when the cues are positioned on the inside (fixation side) of the line stimuli, whereas there was a difference for outside cues. An ANOVA on vertical meridian locations yielded a significant main effect of cue position that was only present with outside cues (Figure 8a). On the vertical meridian, the ILM generated by the single cue is greater than that generated by the distributed cue, indicating that the focal attention engaged by the single cue provides an additional contribution to ILM beyond that of the distributed cue.

PSEs

There was a significant main effect of meridian, in which the difference between single and distributed cues was greater on the vertical meridian than on the horizontal. The ANOVA for vertical meridian location and cue position yielded a larger effect for outside than inside cues.

detection of coherently moving dot patterns, measuring signal to noise thresholds. At isoecentric locations around fixation, thresholds were higher near the vertical meridian and lower on and near the horizontal meridian. They found that thresholds were anisotropic for motion direction near the vertical meridian, with higher thresholds for vertical motion than horizontal motion. No such anisotropies were present on the horizontal meridian. A later study by Raymond (1994), using similar random dot cinematograms and measuring thresholds as % coherence of the stimuli, reported significant but small anisotropies favoring centripetal motion (inward, toward fixation) on the horizontal meridian, and heightened sensitivity for centripetal motion on the lower vertical meridian, but not on the upper vertical meridian.

Which of the visual factors known to exhibit performance fields might account for our results? Line motion discrimination differs at cardinal locations with the same pattern found for contrast sensitivity and visual acuity (Cameron et al., 2002; Carrasco et al., 2001, 2002): the slope is steeper on the HM than on the VM, and within VM it is steeper on the LVM than on the UVM. Performance in the present task would seem to depend in part on observers' ability to discriminate the size of individual line segments as they are added to the stimulus with each monitor refresh. If a particular size segment does not increase the total length of the line beyond the just noticeable difference (JND), then longer segments would have to be added for the lengthening to be perceived. However, with our fixed-length stimuli this also shortens the duration of the temporal window in which the line motion is presented, which leads to a performance impairment that exceeds the acuity benefit of the larger segments. Alternatively, whereas each longer segment may exceed the JND, this leads to fewer segments being added to the line, reducing the sampling rate of the physical motion and making direction discrimination more difficult.

With regard to eccentricity, lower threshold of motion (measured in cycles per second) for moving contrast gratings with a given spatial frequency increases with eccentricity (Johnston & Wright, 1985, 1986); more physical displacement is required per unit of time for the motion to be detectable at greater eccentricities than closer to fovea. These differences can be eliminated by applying cortical magnification factors (Rovamo & Virsu, 1979) to the data or by increasing the stimulus size at farther eccentricities (Johnston & Wright, 1985, 1986). Similarly, differential velocity detection thresholds for a moving line (of fixed length) increase with eccentricity (McKee & Nakayama, 1984). Adjusting for relative acuity by converting physical velocity to "cortical velocity," i.e. "resolution units/sec," the eccentricity differences in the data were eliminated. These authors concluded that motion is encoded relative to the cortical resolution corresponding to the relevant location in the visual field.

A second relevant aspect of visual performance fields is that the rate of visual processing is slower on the vertical

meridian, and particularly on the UVM (Carrasco et al., 2004). This suggests that temporal resolution may be poorer on the vertical meridian, particularly at the UVM. Even if the integration time were equivalent at all locations, the slower accrual of visual information on the vertical meridian would lead to a greater degree of "blurring" of the line motion. If the integration time were longer as well, this would further impair direction discrimination.

The comparison of this study, which held eccentricity constant and varied cardinal location, with studies of motion sensitivity at different eccentricities but fixed cardinal location, is difficult because the relations between visual acuity and processing speed are different across eccentricities and across isoecentric locations. As eccentricity increases, acuity is diminished (e.g. Carrasco & Frieder, 1997) but information processing is faster (Carrasco, McElree, Denisova, & Giordano, 2003). However, at isoecentric locations, moving from East to North, for example, acuity diminishes and processing speed decreases as well. Although this situation suggests an opportunity to dissociate the two effects with regard to motion sensitivity, the linkage between presentation time and line speed with our current stimuli make them impractical for addressing this issue.

ILM and performance fields

The direction of ILM generated by single cues (dots) is easily discriminable when there is no physical motion in the line stimulus. For all of our observers, reporting was at ceiling for all cardinal locations (Figures 3 and 5). Clearly, any impairment in either spatial acuity or processing speed have no measurable effect in this case, as there is no direct reporting of the speed of ILM.

However, the PSEs represent the speed of physical line motion that matches the opposing ILM, reducing direction discrimination to chance. We suggest that this is analogous to a situation in which cues (dots) are placed equidistant from both ends of a line stimulus, which generates a percept of motion from both ends (Faubert & Von Grünau, 1995): here, the physical motion is not eliminated, but the motion is countered by an equivalent ILM in the opposite direction.

The PSEs vary with cardinal location, occurring at progressively longer build times (i.e. slower physical line motion) moving from the horizontal meridian to locations on the vertical meridian. The inverse correlation with discriminability of physical line motion (the decreasing slopes from horizontal to the vertical meridian, and within the vertical meridian from LVM to UVM in the no-cue condition analysis) suggests that the speed of ILM depends on the underlying sensitivity to this type of line motion. The lower the sensitivity, the slower the ILM generated by the cue (dot). As in our discussion of physical line motion discriminability, we again point out that it is possible that the differences between the vertical

and horizontal meridians may relate to the differences in line orientation at these locations. However, this could not explain the significant slope difference between the UVM and LVM locations, at which the lines were oriented vertically (Figure 4c).

We have also found that the speed of ILM, as measured by the PSEs, is slower for outward ILM than for inward (i.e. when generated by dots on the inside than the outside of the line). This cue position effect is partially consistent with the anisotropies in radial motion reported by Raymond (1994), in which coherence thresholds for motion detection were lower for centripetal (inward) motion than centrifugal (outward) motion. Noting again that for the task and stimuli used here discrimination improves with *slower* speed/long build time, but detection performance for dot cinematograms and gratings improves with *faster* speed, Raymond's (1994) lower speed thresholds for inward motion on the horizontal meridian should correspond to our faster PSEs for inward ILM generated by outside cues on the horizontal meridian. Indeed, the correspondence is mostly consistent with our results, but Raymond (1994) reported no directional asymmetry in the on the UVM where we did find a difference in discriminability for inside and outside cues. It is possible that any asymmetry present may simply not have been apparent in Raymond's (1994) analysis: thresholds in her study were determined by % correct reporting of motion-presence trials versus "noise" trials. False alarm trials for the upper vertical meridian were 6% compared to 12% for the LVM, suggesting that observers might have used different criteria for the two locations; criterion differences for the two motion directions could have been present as well. Naito, Kaneoke, Osaka, and Kakigi (2000), however, in a study of MEG response to low-level motion, reported exactly such an asymmetry in extrastriate cortex: the amplitude of the first magnetic response to downward motion was greater than that for upward motion at locations in the upper visual field, including the UVM. The authors suggest that this difference indicates a bias in favor of downward motion.

Low-level motion and attention

To separate the low-level motion and exogenous attention gradient components of ILM, we used single dot cues and four-dot distributed cues. In the single cue condition, we used timing (100 ms before presentation of the line stimulus) and spatial proximity to the line (0.75° from the end of the line) that have been shown to engage exogenous spatial attention (e.g. Nakayama & Mackeben, 1989). Our second cueing condition adds three identical cues at isoecentric spatial locations on the cardinal meridians to create a "distributed" cue. Distributed cues at peripheral locations have been shown to significantly diminish the effects of focal attention relative to a single

peripheral cue and to be comparable to those of a neutral central cue (Carrasco et al., 2002; Talgar et al., 2004; Yeshurun & Carrasco, 2008). The single and distributed cues have identical visual input in the vicinity of the line stimulus; the second nearest dot in the distributed cue was ~10° away from the stimulus. Thus, we are able to compare a condition in which both the presumed attentive and low-level motion mechanisms are operative (single cue) to one in which low-level motion can still operate but the focal attentional effect is significantly reduced (distributed cue). For our three measures of ILM in this study, Zero Points, PSEs and slopes, differences between these two cue types would indicate different relative contributions of low-level motion and attention.

A striking overall finding is the remarkable similarity of the psychometric functions (Figure 2) for single and distributed cues. This seems to rule out a strong form of the attentional ILM hypothesis, and in this regard our results are consistent with the conclusion of Christie and Klein (2005), who investigated endogenous (voluntary) attention. We found no difference between the two cue types on the horizontal meridian, but there was a difference on the vertical meridian for our Zero Point measure, when there was no physical motion present in the line stimulus.

There are three possible explanations for this emergent difference on the vertical meridian:

1. the attentional gradient effect is stronger,
2. the low-level motion effect is weaker, or
3. both factors contribute to the difference between single and multiple cues on the vertical meridian.

We would argue in favor of the third option. First, the finding that exogenous attention yields a disproportionately large acceleration in processing speed progressing from the horizontal to the vertical meridian, and then from the LVM to the UVM (Carrasco et al., 2004), is entirely consistent with the idea that the attentional gradient contribution to ILM varies at isoecentric locations. We note that we do not interpret from these results that there is only a difference in the "strength" of attention per se between the meridians. An equally plausible interpretation is that the results represent differences in the underlying visual characteristics of the visual field locations being modulated by attention. We also believe that the reduced sensitivity to radial physical line motion that we found on the vertical meridian for the no-cue condition (i.e. the slope) and its correlation with the speed of the illusory motion, strongly supports the idea that the low-level motion mechanism is weaker on the vertical meridian.

Our results clearly show that low-level motion makes the predominant contribution to the canonical example of ILM, in which the line stimulus is preceded by a single dot. Describing the two effects in this context implies that the low-level motion contribution to ILM in this dot-stimulus configuration is more fundamental than the gradient of attention explanation.

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