

The role of speed lines in subtle direction judgments

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Abstract

Stimuli moving in slightly different directions trace trajectories that differ slightly in orientation. These different ‘speed lines’, in principle, could generate responses in orientation mechanisms, and such responses could determine how well we judge subtle direction differences. Alternatively, the ability to judge subtle direction differences could be determined by direction mechanisms rather than by orientation mechanisms. To distinguish between these possibilities we exploited the fact that opposite directions of motion share an orientation: Across trials, participants judged a constant orientation difference between trajectories having either the same or opposite motion signs. The probabilities of the motion signs were also manipulated. When the probabilities were consistent with those typically used to assess fine direction discrimination, direction mechanisms set the limit on performance. In other conditions where orientation mechanisms could have set the limit on performance, responses were neither more precise nor faster than when performance was limited by direction mechanisms.

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1. Introduction

To depict a moving object in a stationary picture, cartoonists often draw ‘speed lines’—stationary lines that are parallel to the orientation of an object’s trajectory.¹ Although speed lines are not *explicitly* present in the light from real moving objects, recent psychophysical (Burr, 2000; Geisler, 1999; Ross et al., 2000) and physiological (Geisler, Albrecht, Crane, & Stern, 2001; Jancke, 2000) data suggest that the visual system may be sensitive to the orientation *implicit* in a motion trajectory. Presumably, our sensitivity to the orientation implicit in a motion trajectory arises from the fact that

the visual system integrates light over time. This temporal integration would be somewhat analogous to a camera with a slow shutter speed, ‘blending’ together the successive positions of a moving object to record the orientation of the trajectory. In principle, then, it is possible that moving objects provide directionless orientation cues that could be used to judge direction differences (Francis & Kim, 2001). Whether the precision of direction judgments is determined by how precisely we can use implicit orientation cues (i.e., speed lines) is the issue investigated here. We will begin by considering recent work on how direction discrimination is affected by the presence of explicit orientations.

Recent studies have offered evidence that explicitly presented orientations can influence motion sensitivity. For example, Burr and Ross (2002) showed that fine direction judgments are impaired when masks comprising explicit, oriented random noise are parallel to the motion trajectory, but not impaired when the masks and the motion trajectory are perpendicular to each

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¹ Speed lines have also been referred to as ‘motion streaks’ (Geisler, 1999; Ross, Badcock, & Hayes, 2000).

other. Moreover, the effect of orientation is specific to direction judgments, as noise orientation has no effect on speed discrimination (Burr & Ross, 2002). Stimulus speed, however, does play some role in determining whether oriented noise is effective in masking motion stimuli. Specifically, Geisler (1999) showed that as stimulus speed increases, the contrast required to detect a moving target also increases when explicit noise-lines are parallel to the motion trajectory, but not when the two are perpendicular to each other.

Is it possible that motion judgments can be affected by information that is not perceptually available? Some psychophysical studies suggest that it is. One study pertains to speed discrimination for plaid stimuli, which are constructed by superimposing two differently oriented drifting gratings. Welch (1989) demonstrated that these component gratings set the limit on speed discrimination thresholds even though it is the motion of the overall pattern (i.e., the plaid), not the component-grating motion, that is perceptually available. A second psychophysical study pertains to perceptual learning in direction discrimination. Specifically, Watanabe, Nanez, and Sasaki (2001) presented a background of moving dots that were of sufficiently low contrast to render the direction of motion invisible. Nevertheless, those background dots subsequently affected motion sensitivity in a directionally specific manner.

In addition to the psychophysical evidence (Watanabe et al., 2001; Welch, 1989), there is also physiological evidence for sensitivity to perceptually unavailable motion information. For example, recordings from cat primary visual cortex (Jancke, 2000) suggest that the neuronal population response to a moving spot of light corresponds to the orientation of the dot's trajectory; That population response occurs despite the fact that the orientation is implicit, i.e., must be formed by integrating the dot positions over time. Further physiological support for implicit-orientation sensitivity can be found even at the single-cell level. Specifically, in both cats and monkeys, Geisler et al. (2001) identified individual V1 neurons whose directional selectivity, at sufficiently fast speeds, is parallel to the spatial orientation of the receptive field. Notably, those V1 neurons are positioned even earlier in the visual pathway than the well-known 'type II' (Albright, 1984) or 'pattern selective' (Movshon, Adelson, Martin, & Newsome, 1985) MT neurons, which also have parallel direction and orientation preferences.

Taken together, the above-mentioned psychophysical (Watanabe et al., 2001; Welch, 1989) and physiological (Geisler et al., 2001; Jancke, 2000) data suggest that fine direction judgments could be based on perceptually unavailable cues. Moreover, it is possible that fine direction judgments could be based on a *combination* of perceptually unavailable and perceptually available cues. Combinations of visual cues have been shown to im-

prove estimates of visual stimuli, even when the identity of each individual visual cue becomes perceptually unavailable (Hillis, Ernst, Banks, & Landy, 2002). Indeed, the possibility that cue combinations influence fine direction judgments would support recent speculation that (implicit) speed lines may add orientational precision to the output of direction mechanisms (Barlow & Olshausen, 2004).

The present study was conducted to provide new information about the role that implicit orientation cues (i.e., speed lines) play in determining the angular resolution of our direction sensitivity. Accordingly, in the first three experiments reported here, we arranged the stimulation such that, across conditions, the trajectory orientations were constant while the directional information varied. If the angular resolution of our motion system were limited by non-direction selective orientation-tuned responses, performance would be similar across conditions. By contrast, one could expect some fluctuation in performance across conditions if directionally selective responses limited the angular resolution of our motion system. In a fourth experiment, we also manipulated the *probability* of the directional signs, rendering them either consistent or inconsistent with the probabilities typically used to assess fine direction discrimination. In brief, the data support the notion that direction mechanisms set the limit on performance under the conditions most frequently used to assess fine direction sensitivity. In other conditions where orientation mechanisms could have set the limit on performance, responses were neither more precise nor faster than when performance was limited by direction mechanisms.

2. Experiment 1: Method

2.1. Apparatus, stimuli and task

The experiment was conducted on a 17 in. (43.18 cm) ViewSonic P75f+ monitor that was controlled by a Macintosh G4 computer with a 733 MHz processor and software from the psychophysics toolbox (Brainard, 1997; Pelli, 1997). The vertical refresh rate of the monitor was 120 Hz, and the spatial resolution was 1024×768 pixels. In a well-lit room, participants viewed the monitor through a circular viewing tube with an inner diameter of 15 cm. A chin rest helped to stabilize head position at 57 cm from the monitor.

The stimuli were random-dot patterns (RDPs). In each RDP, the dots (56.91 cd/m^2) appeared lighter than the dark uniform surround (5.83 cd/m^2) and were easily seen (81.42% Michelson contrast). Each dot was a 4×4 pixel square, approximately $10'$ on each side. Except for one stimulus condition that will be described below, there were 30 dots per pattern, making the dot-density 4.24 dots/deg^2 since the dots were presented within a

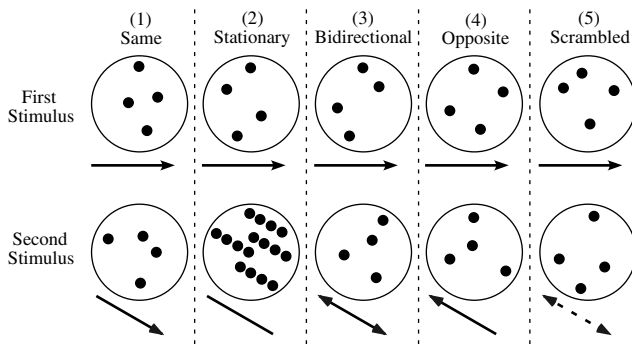


Fig. 1. Stimuli and task. Two random-dot patterns were shown on each trial. The first pattern always contained linearly moving dots. A constant orientation difference was added or subtracted from the first trajectory such that the second pattern comprised either: (1) dots moving in the *same* general direction as the first; (2) *stationary* dots, i.e., all frames of the motion sequence simultaneously; (3) dots moving coherently in *both* directions simultaneously; (4) dots moving coherently in the *opposite* direction; or (5) dots moving incoherently, i.e., the sequence of frames was *scrambled*. On each trial, participants judged whether the orientation of the second pattern was 'clockwise' or 'anti-clockwise' to the first. In the schematic above, the orientation of the second stimulus is 30 deg clockwise to the first trajectory in each condition. The actual angular differences and dot densities are detailed in the Method.

3 deg circular virtual aperture. Dots moving out of the aperture 'wrapped around' to the opposite side. Participants foveally viewed the stimuli, and a circular fixation dot (also 56.91 cd/m², 81.42% contrast) in the center of the aperture helped to stabilize eye position.

On every trial, two new and unique RDPs were generated, and presented successively. Each RDP was shown for 200 ms (24 frames), and the inter-stimulus interval varied randomly from 500 to 700 ms. Within each trial, the two stimuli always differed from each other in the orientation that the RDPs formed. Across trials, the *magnitude* of the orientation difference was held constant, but the *sign* of the orientation difference (clockwise versus anti-clockwise) varied randomly. The participant's task was to report whether the second orientation was 'clockwise' or 'anti-clockwise' to the first.

The first stimulus on each trial was a RDP that produced a compelling sense of linear motion. On any given trial, all dots in the first RDP moved at 8 deg/s (i.e., 50 image-widths/s) in the same direction.² Across trials, the direction of the first RDP was chosen randomly from the full 360 deg range. The second RDP was block-randomly chosen from five stimulus conditions that are shown schematically in Fig. 1, and are described in detail now.

Across the five stimulus conditions the orientation difference, theta, between the two RDPs was held constant while the directional information was manipulated. In the 'same' condition, dots in the second RDP moved coherently in a direction equal to that of the first RDP, plus theta. In the 'stationary' condition, the second RDP was generated by the algorithm used for the 'same' condition, but all frames of the second RDP were presented simultaneously, rather than sequentially. Therefore, the second RDP comprised 720 stationary dots (30 dots per frame \times 24 frames in the sequence) that formed straight lines at an orientation differing from the first RDP's trajectory by theta. In the 'bidirectional' condition, half of the dots in the second RDP moved coherently in one direction while the remaining dots moved coherently in the opposite direction. Computationally, half the dots moved in a direction equal to the first RDP's direction plus theta, while an additional 180 deg was added to the direction of the remaining dots. In the 'opposite' condition, all dots in the second RDP moved coherently in a direction equal to the first RDP's direction, plus theta, plus 180 deg. In the 'scrambled' condition, the second RDP was generated from the algorithm used in the 'same' condition, but the frames of the motion sequence were presented in a randomly shuffled order.³ Note that these five stimulus conditions would appear identical to an organism (or robot) with a long visual integration period, since the time-averaged orientation information was held constant.

2.2. Participants, procedure and data analysis

Denison University's Human Subject Committee approved the experiment. Twenty-three participants were recruited from the Denison University community. All had normal or corrected-to-normal vision.

We sought to establish that the limitations on our participants' performance were perceptual, rather than conceptual. Accordingly, an initial screening procedure was conducted to determine whether each participant understood the task, i.e., could perform the task at greater-than-chance levels. Of the 23 participants recruited, three were excluded from Experiment 1 because they were unable to demonstrate greater-than-chance performance during the screening. For all participants, the screening comprised a demonstration phase, practice trials, and threshold estimation. Each of these will be described in turn.

² A speed of 50 image-widths/s was sufficiently fast to generate a speed-line (or 'motion-streak') response in monkey V1 neurons, according to the physiological data in figure four of Geisler et al. (2001).

³ The second RDP in the 'same', 'bidirectional', and 'opposite' conditions moved at the same speed as the first RDP in all conditions; Each dot's speed was always 8 deg/s. In the 'scrambled' condition, however, the dot speed was 8 deg/s only *on average*, since the instantaneous frame-to-frame spatial displacement was variable. The dot speed in the 'stationary' condition was zero.

In the demonstration phase, the five stimulus conditions (see Fig. 1) were shown in random order across trials. Each trial began with a computer-generated voice announcing the correct response before the stimuli were presented. For example, the computer-generated voice would announce, ‘The correct answer will be clockwise’ prior to a trial on which the second stimulus was clockwise to the first. The difference between the first and second stimuli on each demonstration trial was ± 25 deg, which was the greatest difference from the array of differences that would be tested during threshold estimation (described below). Typically, five to 15 demonstration trials were completed before a participant proceeded to the practice trials.

Practice trials were identical to demonstration trials in all aspects, except that the correct response was not announced before each practice trial. During the practice-trial phase, each participant was required to make consecutively 10 correct responses. This performance level, which could occur by chance less than one time in a thousand, ensured that each participant understood the task before proceeding to threshold estimation.

Thresholds were estimated using the method of constant stimuli and were based, for each participant, on a 100-trial block. Each 100-trial block comprised 20 block-randomly ordered presentations of each of the five stimulus conditions shown in Fig. 1. For each of the five stimulus conditions, there were two presentations at the following 10 angular differences: ± 5 , ± 10 , ± 15 , ± 20 , and ± 25 deg. The 10 angular differences were plotted on the abscissa of a psychometric function while the ordinate reflected the proportion of ‘clockwise’ responses, combining across the five stimulus conditions. A least-squares procedure was then used to fit the data with a sigmoid of the form

$$\frac{1}{1 + \exp[-K(X - X_0)]}$$

where K and X_0 determine the slope and midpoint of the sigmoid, respectively. The correlation between the best-fitting sigmoid and the data, as indexed by the Pearson correlation coefficient (r), was statistically significant ($p < 0.05$) in each case. Because each fit was significant, it was possible to fairly interpolate from the sigmoid each participant’s 75% discrimination threshold, which was defined as half the angular difference required to alter the response rate from 0.25 to 0.75.

After completing the threshold-estimation phase, participants proceeded to the actual experiment. The actual experiment consisted of five 100-trial blocks, with each block comprising twenty randomly ordered presentations of the five stimulus conditions. The angular difference that was presented on each trial in the actual experiment was set to the participant’s 75% discrimination threshold, as measured during the threshold estimation phase. On a few occasions, the participant’s block

average exceeded 85%, or was below 65%. In these cases, we adjusted the angular difference by 25% to better approximate the desired 75% performance level. This eliminated floor and ceiling effects.

Participants were instructed to make their ‘clockwise’/‘anti-clockwise’ judgments as quickly as possible without sacrificing accuracy. To promote accuracy, participants proceeded at their own pace, initiating each trial with a button press when ready. To maintain motivation, auditory feedback informed the participant whether their response was correct or incorrect after each trial, and the computer announced the overall percentage of correct responses after each block.

Data from the actual experiment were analyzed with respect to three dependent variables. Our first dependent variable, ‘proficiency’, was operationally defined as orientation sensitivity divided by reaction time; Proficiency therefore controls for trade-offs between the precision and the speed of responding. The remaining two dependent variables are the constituents of proficiency—orientation sensitivity and reaction time. Orientation sensitivity (d') was computed using standard signal detection procedures (Green & Swets, 1966). Hits and false alarms were operationally defined as ‘clockwise’ responses made when the second RDP was, respectively, clockwise or anti-clockwise to the first. Reaction time was defined as the median duration between the offset of the second RDP and a correct response from the participant. Trials on which the participant responded incorrectly were excluded from our reaction time measure in all experiments reported in this study.

In this within-subjects experiment there was just one independent variable, stimulus condition, with five levels (see Fig. 1). We conducted separate one-way within-subject ANOVAs, for each of the three dependent variables. Additionally, for each dependent variable, we planned (*a priori*) pair-wise comparisons between the ‘same’ condition, which served as a baseline, and each of the remaining conditions.⁴ Because the pair-wise comparisons for each dependent variable were *a priori* and fewer than the number of experimental conditions (four statistical comparisons versus five experimental conditions), the alpha level was not adjusted for multiple comparisons (Keppel, Saufley, & Tokunaga, 1992).

3. Experiment 1: Results

The data from the threshold-estimation phase are shown in Fig. 2, where the participants’ mean proportion of clockwise responses (± 1 SE) is plotted as function of the orientation differences. As is clear from

⁴ We chose to have the ‘same’ condition serve as the baseline because this condition is the one most widely used by researchers who investigate fine direction discrimination.

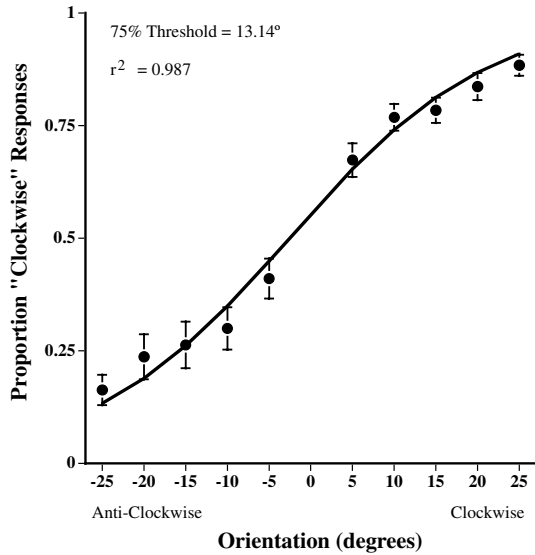


Fig. 2. Data from the threshold tracking phase. The proportion of ‘clockwise’ responses is plotted as the physical orientation difference between the first and second stimulus goes from anti-clockwise (left) to clockwise (right). Each datum represents the mean (± 1 SE) of the 20 participants, and is based on 200 trials (10 trials per condition \times 20 participants). The orderliness of the data, as indicated by the coefficient of determination ($r^2 = 0.987$) and the monotonic trend, suggests that the participants’ limitations in the threshold-tracking phase were perceptual, rather than conceptual.

visual inspection, the proportion of ‘clockwise’ responses increased monotonically as the change in physical orientation became increasingly clockwise. In fact, each datum is within one standard error of the best-fitting sigmoidal function, which accounted for approxi-

mately 99% of the response variability. The 75% threshold (see Method) associated with the best-fitting sigmoid was 13.14 deg—a value higher than those reported in some studies on random-dot direction discrimination (Liu & Weinsall, 2000; Matthews, Luber, Qian, & Lisanby, 2001; Matthews & Qian, 1999; Saffell & Matthews, 2003). Later in this report we will explore the reasons for the relatively high threshold (see Experiment 2). Nevertheless, the orderliness of the data in Fig. 1 shows that participants’ limitations during the threshold-tracking phase were perceptual, rather than conceptual.

The first dependent variable in Experiment 1 was proficiency (d'/RT). In the left panel of Fig. 3, proficiency is plotted as a function of stimulus condition, and the error bars reflect one standard error of the mean after removing consistent individual differences (Loftus, 1993). Confirming what can be readily seen in the figure, an ANOVA indicated that proficiency depended significantly on the stimulus condition ($F(4, 76) = 8.017, p < 0.001$). Specifically, although the *a priori* *t*-test showed that proficiency in the ‘stationary’ condition was statistically indistinguishable from that in the ‘same’ condition, other *a priori* pair-wise comparisons revealed that proficiency depended on direction of motion. For example, relative to the ‘same’ condition, proficiency was reduced significantly when the second stimulus contained both directions ($t(19) = 2.66, p = 0.015$), only the opposite direction ($t(19) = 2.987, p = 0.008$), or scrambled motion ($t(19) = 3.484, p = 0.002$). Indeed, when the second stimulus moved coherently in a direction opposite to the first, proficiency was no better than when the second

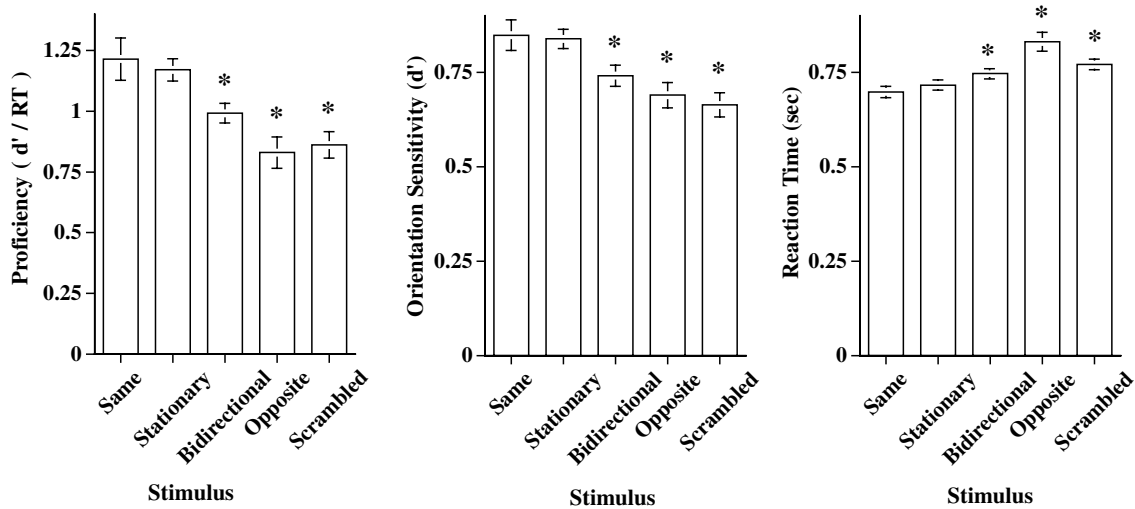


Fig. 3. Data from Experiment 1. The three dependent variables are shown in separate panels, each plotted against the five stimulus conditions described in Fig. 1. Each column represents the mean of 20 participants, and is based on 2000 trials (100 trials per condition \times 20 participants). The error bars reflect one standard error of the mean after removing consistent individual differences (Loftus, 1993). Asterisks indicate statistically significant differences from the ‘same’ condition in each panel. (Left panel) The stimulus-specific fluctuations in proficiency occurred despite the fact that the time-averaged orientations (i.e., the speed lines) were identical across stimulus conditions. Also, the fluctuations in proficiency reflect statistically significant fluctuations in both orientation sensitivity (d') (center panel), and reaction time for correct responses (right panel).

stimulus contained only randomly scrambled positions from frame to frame. This can be seen in the overlap between the ‘opposite’ and ‘scrambled’ conditions. Note that the relatively poor performance in the ‘opposite’ and ‘scrambled’ conditions is likely perceptual and not conceptual, since the performance in each of those conditions is still well above chance, i.e., well above zero. Also, we emphasize that the significant differences among the stimulus conditions occurred despite the fact that the time-averaged orientation information was held constant across all conditions. This implies that orientation mechanisms did not impose the limit on performance.

In principle, the variations in proficiency that are evident in Fig. 3 could reflect fluctuations in orientation sensitivity (d'), reaction time, or both. Visual inspection of the center panel in Fig. 3, and an omnibus ANOVA ($F(4, 76) = 5.43, p = 0.001$) confirm that fluctuations in orientation sensitivity contributed significantly to the fluctuations in proficiency. In fact, the pattern in orientation sensitivity was the same as in proficiency. Specifically, there was no statistical difference in orientation sensitivity between the ‘same’ and ‘stationary’ conditions. And, relative to the ‘same’ condition, orientation sensitivity was significantly reduced when the second stimulus contained both directions ($t(19) = 2.2, p = 0.04$), only the opposite direction ($t(19) = 2.35, p = 0.03$), or scrambled motion ($t(19) = 3.357, p = 0.003$).

Finally, consistent with what is evident in the right panel of Fig. 3, an omnibus ANOVA confirmed that the median reaction time for correct responses also depended significantly on the stimulus condition ($F(4, 76) = 8.15, p < 0.001$). Moreover, the pattern in the reaction time data was similar to the pattern in the other two dependent variables. Specifically, there was no statistical difference in reaction time between the ‘same’ and ‘stationary’ conditions. And, relative to the ‘same’ condition, reaction times became significantly worse (i.e., increased) when the second stimulus contained both directions ($t(19) = 2.857, p = 0.01$), only the opposite direction ($t(19) = 3.50, p = 0.002$), or scrambled motion ($t(19) = 4.21, p < 0.001$). Again, we emphasize that, in principle, participants could have used time-averaged orientation information as the basis for judgments in all stimulus conditions. It is therefore not obvious why reaction times would fluctuate in a stimulus dependent manner if the limiting factor on the task had been determined by orientation mechanisms.

4. Experiment 2: Training and complete stimulus certainty

Most participants in Experiment 1 had no previous experience in psychophysical studies. Although the data in Figs. 2 and 3 rule out the possibility that the participants failed to understand the task, we wondered

whether the findings from Experiment 1 would obtain after participants had further training. Accordingly, five people from Experiment 1 (participating on the basis of availability) returned for further training in Experiment 2.

An additional objective in Experiment 2 pertains to the observation that the mean angular threshold in Experiment 1 was 13.14 deg—a value larger than those reported in earlier studies on random-dot direction discrimination (Liu & Weinsall, 2000; Matthews et al., 2001; Matthews & Qian, 1999; Saffell & Matthews, 2003). The relatively high threshold might reflect that fact that there was greater stimulus uncertainty in Experiment 1 than in the earlier studies. Specifically, in Experiment 1 the stimulus conditions (i.e., ‘same’, ‘stationary’, ‘bi-directional’, ‘opposite’, or ‘scrambled’) varied randomly from trial to trial. By contrast, the stimulation in the earlier studies was constant across trials. Accordingly, in Experiment 2, separate trial blocks were run for each stimulus condition to ensure complete stimulus certainty.

5. Experiment 2: Method

Although the equipment, software, viewing conditions and luminance conditions for Experiment 2 were identical to those in Experiment 1, the procedure differed in several ways. First, in Experiment 2 the ‘stationary’, ‘bi-directional’ and ‘scrambled’ conditions from Experiment 1 were eliminated; only the ‘same’ and ‘opposite’ conditions were tested. Also, as noted in the preceding section, we eliminated stimulus uncertainty in Experiment 2 by testing the ‘same’ and ‘opposite’ conditions in *separate* trial blocks. Each block comprised 10 randomly ordered presentations at each of the 10 angular differences ranging between -7.5 and $+7.5$ deg, in 1.5 deg steps. This range of angular differences—narrower than that used in Experiment 1 (± 25 deg, in 5 deg steps)—was possible because the stimulus condition within each block was certain and participants were now well practiced. Specifically, on the day before Experiment 2 formally began, each participant completed three 100-trial blocks on the ‘same’ condition and three in the ‘opposite’ condition, in random order.

After completing the initial practice session for Experiment 2, participants returned on a different day to complete the actual trials. As in the practice session, the actual session comprised six 100-trial blocks, three on the ‘same’ condition and three in the ‘opposite’ condition, in random order. The 300 trials completed in each of those conditions were used to construct, for each participant, separate psychometric functions for the ‘same’ and ‘opposite’ conditions. For each of those conditions, each participant’s 75% discrimination threshold

was estimated using the procedure detailed in the Method for Experiment 1.

Repeated-measures ANOVAs were conducted to evaluate the null hypothesis that thresholds would be equal in the ‘same’ and ‘opposite’ conditions. Similar null hypotheses were evaluated for two other dependent variables: median reaction time; and threshold \times median reaction time, which controls for tradeoffs between precision and the speed of responding. For each dependent variable, the null hypothesis (i.e., equal performance in the ‘same’ and ‘opposite’ conditions) would be confirmed if the response of orientation-tuned mechanisms set the limit on subtle direction judgments.

6. Experiment 2: Results

The data from Experiment 2 are shown in Fig. 4. Within each of the three panels, performance in the ‘same’ (hatched bars) and ‘opposite’ (open bars) conditions is given for each of the five participants, and the mean (± 1 SE) is on the far right. In the left panel, the dependent variable is threshold \times reaction time, which directly controls for tradeoffs between precision and the speed of responding. The data indicate that each participant performed better (i.e., lower scores) in the ‘same’ condition than in the ‘opposite’ condition, and that this difference was significant ($F(1,4) = 14.675$, $p = 0.019$). An identical pattern obtained for the threshold (center panel, $F(1,4) = 14.221$, $p = 0.02$) and reaction time (right panel, $F(1,4) = 8.922$, $p = 0.04$) measures. This was also the pattern of performance observed in Experiment 1 (see Fig. 3), suggesting that the effect obtains in well-practiced participants and unpracticed participants alike.

The procedures used in the ‘same’ condition of Experiment 2 are similar to those most frequently used to investigate fine direction discrimination. That is, the two stimuli on every trial had the same directional sign, and the participant had complete certainty about that. As one might expect then, the angular thresholds (mean $4.42 \text{ deg} \pm 0.33$) in Experiment 2 are in good quantitative agreement with previous reports (Liu & Weinsall, 2000; Matthews et al., 2001; Matthews & Qian, 1999; Saffell & Matthews, 2003). Finally, we emphasize that in both Experiments 1 and 2, the difference between the ‘same’ and ‘opposite’ conditions occurred despite the fact that the speed lines in the two conditions were identical. This is contrary to what would be predicted if the response of orientation mechanisms had been the limiting factor.

7. Experiment 3: Parametric stimulus variations

Each of the five participants in Experiment 2 returned for six additional daily sessions so that performance in the ‘same’ and ‘opposite’ conditions could be assessed over a range of stimulus parameters. Specifically, *dot sizes* smaller ($2.25'$) and larger ($20'$) than that of Experiment 2 ($10'$) were assessed in separate daily sessions. Similarly, *dot densities* smaller (1 dot per frame) and larger (60 dots per frame) than that of Experiment 2 (30 dots per frame) were assessed in separate daily sessions. Finally, *dot speeds* slower (2 deg/s) and faster (16 deg/s) than that of Experiment 2 (8 deg/s) were assessed in separate daily sessions. In all cases, the stimuli in Experiment 3 differed from those in Experiment 2 only on the single feature of interest for that particular daily session. As in the earlier experiments, participants made

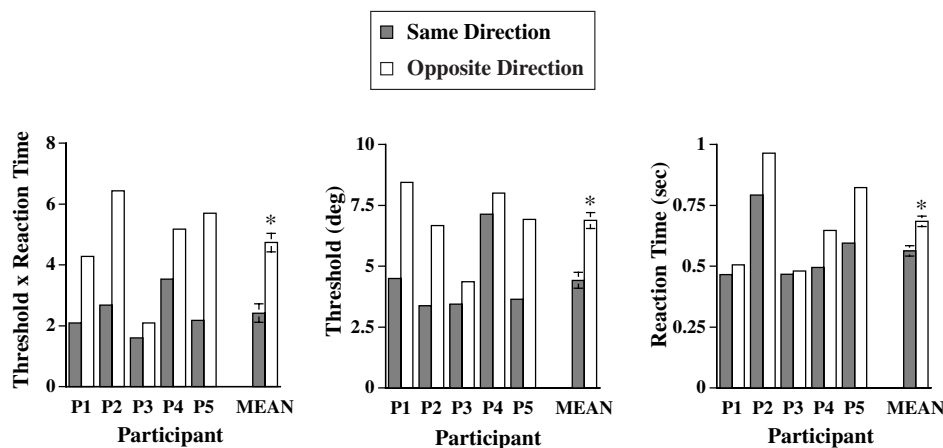


Fig. 4. Data from Experiment 2. The three dependent variables are shown in separate panels. Performance in the ‘same’ and ‘opposite’ conditions (first and fourth pairs of Fig. 1) is plotted as the parameter for each of the five well-practiced participants. The mean (± 1 SE) for each condition is plotted on the right side of each panel. As in Experiment 1, the overall performance (left panel), the precision of responding (center panel), and reaction time (right panel) are each significantly better in the ‘same’ condition (hatched bars) than in the ‘opposite’ condition (open bars). Again, this difference occurred despite the fact that the time-averaged orientations (i.e., the speed lines) were identical in the ‘same’ and ‘opposite’ conditions.

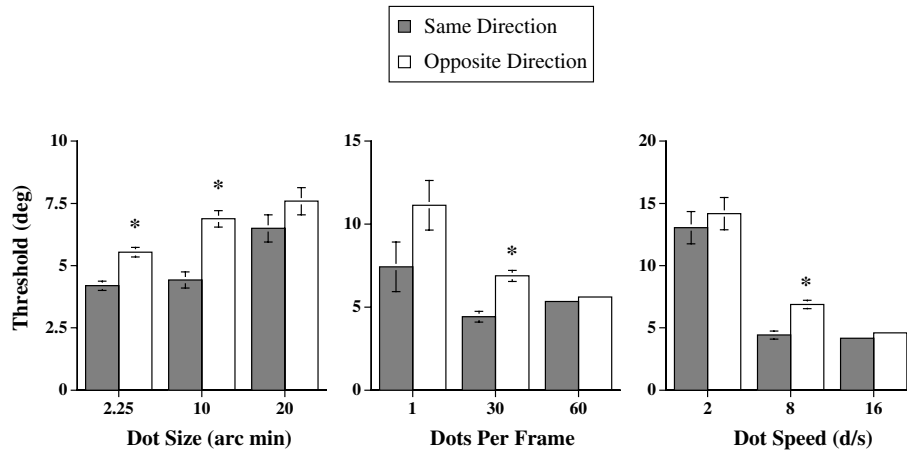


Fig. 5. Data from Experiment 3. The three stimulus features that were parametrically varied are shown in separate panels. For each panel, mean thresholds (± 1 SE) in the 'same' and 'opposite' conditions (first and fourth pairs of Fig. 1) are plotted in hatched and open bars, respectively. The center cluster in each panel indicates thresholds from the same participants in Experiment 2, re-plotted here from Fig. 4. Across sizes, densities (dots per frame), and speeds, thresholds were lower in the 'same' condition than in the 'opposite' condition, although this difference was nearly eliminated at the highest density, and at the fastest speed, where thresholds were lowest.

'clockwise'/'anti-clockwise' judgments. All other procedural details of Experiment 3 were identical to those of Experiment 2.

In Fig. 5, mean thresholds from the three stimulus features explored in Experiment 3 are shown in separate panels.⁵ In each panel, the pair of bars in the center reflects the mean thresholds from Experiment 2, which have been re-plotted here from Fig. 4. The most notable characteristic of Fig. 5 is that mean thresholds are lower in the 'same' condition than in the 'opposite' condition across all nine parametric stimulus variations. However, compared to the data from Experiment 2, the difference between the 'same' and 'opposite' conditions is reduced in some cases, and nearly zero at the highest density (60 dots per frame) and the fastest speed (16 deg/s). The fastest speed is particularly intriguing because it generated the lowest thresholds. Given that thresholds at 16 deg/s were both lowest and similar in the 'same'/'opposite' conditions, we conducted an additional experiment to further explore the mechanisms underlying performance at that speed.

8. Experiment 4: Probable direction and same/different task

Experiment 3 indicated that the previously observed (Experiments 1 and 2) performance difference between the same- and opposite-sign conditions was nearly elim-

inated at the fastest speed (16 deg/s: 100 image-widths/s). One explanation for that finding could be speed lines; That is, participants may have used a single, orientation-based strategy in both the same-sign and opposite-sign conditions, when the stimulus moved at 16 deg/s. A limitation with that explanation, however, is that it does not account for the directionally dependent findings from Experiments 1 and 2, when the speed was slower. Do participants change from a direction-based strategy to an orientation-based strategy when the speed is 16 deg/s? Given that certain V1 neurons have parallel direction and orientation preferences at sufficiently fast stimulus speeds (Geisler et al., 2001), a speed-dependent switch to an orientation-based strategy (or a combined orientation-and-direction-based strategy) would seem possible. We conducted a fourth experiment to explore this possibility.

One way to distinguish a direction-based strategy from an orientation-based strategy is to systematically manipulate the *probability* of the stimulus' direction. Consider the case in which the two stimuli on each trial are more likely to have the same- than opposite-directional signs, and the participant is using a direction-based strategy. Here, performance should be significantly better on the many trials when the directional signs are the same, than on the few randomly interleaved 'catch trials' when the directional signs are opposite to each other. The decreased performance on these catch trials could arise if the participant had assigned a lower weight to the response from the less-probable-direction channels than to the response from the more-probable-direction channels. By contrast, no such difference would be expected on the catch trials if the participant were using an orientation-based strategy, since opposite directions share an axis of orientation.

⁵ The reaction time differences between 'same' and 'opposite' conditions were modest, and tended to follow the pattern seen in the thresholds (Fig. 5). Consequently, the reaction time and threshold \times reaction-time measures have been excluded here for brevity.

9. Experiment 4: Method

Eight new, naïve Denison undergraduates were recruited for Experiment 4. Each participant completed two, 300-trial blocks. One block comprised 260 trials (86.67% of trials) on which the two RDPs had the same directional sign, and 40 randomly interleaved trials (13.33% of trials) on which the directional signs were opposite to each other. These probabilities were switched in the other block, and across participants we counterbalanced the order of these blocks. Within each block and within each directional sign (i.e., same or opposite), half the trials contained RDPs that moved along the same axis of orientation, and half contained trials on which the axes of orientation differed by 13.14 deg. The 13.14 deg difference was chosen because it was the mean angular difference-threshold in Experiment 1, empirically derived from other naïve participants from the same population. In all other ways, the stimuli in Experiment 4 were identical to those of the 16 deg/s condition in Experiment 3.

In Experiment 4, the participants judged whether the two axes (not the two physical directions) on each trial were the ‘same’ or ‘different’. Prior to each block, each participant was explicitly instructed about the probability (i.e., 86.67% versus 13.33%) of each directional sign. Additionally, each participant was explicitly instructed that an orientation-based strategy could be used correctly on all trials. For example, each participant understood that leftward and rightward are opposite directions but share an axis of orientation (horizontal), making ‘same’ the correct response. Finally, each participant completed several practice trials with angular differences that were randomly either zero or 26.28 deg i.e., twice the angle to be discriminated in the actual trials. Each participant was prohibited from proceeding to the actual experiment until s/he made 10 consecutively correct responses—a performance level that would occur by chance less than one time in one thousand. Each of the eight participants readily met this criterion, indicating that all participants understood the task before the actual trials began.

To summarize, Experiment 4 differed from Experiment 3 in two ways. First, in Experiment 4 the participants made ‘same’/‘different’ judgments (rather than clockwise/anti-clockwise) about the two axes on each trial. Second, unlike Experiment 3, Experiment 4 had a 2×2 design. Specifically, the *more probable directional sign* of the second stimulus could be the same or opposite (in separate blocks), and the *physical sign* of the second stimulus could be the same or opposite (varying across trials within each block). A direction-based strategy predicts a significant interaction between these two variables, while an orientation-based strategy predicts no interaction. We evaluated the interaction on three dependent variables—proficiency (d'/RT), orientation

sensitivity (d'), and median reaction time for correct responses—all as described in Experiment 1.

10. Experiment 4: Results

The results from Experiment 4 are shown in Fig. 6, where each of the three panels corresponds to a different dependent variable. Visual inspection readily reveals that, for each dependent variable, there is an interaction between the physical and the more-probable sign of the second direction. Indeed, ANOVAs confirmed that the interaction was statistically significant for proficiency ($F(1, 7) = 14.854, p = 0.006$), orientation sensitivity ($F(1, 7) = 15.838, p = 0.005$), and reaction time ($F(1, 7) = 13.801, p = 0.008$). Additionally, across the dependent variables, the nature of the interaction was identical. Specifically, on trials when the same directional sign was more probable (left side of each panel), performance in the same-physical-sign condition (hatched bars) significantly exceeded that in the opposite-physical-sign condition (open bars). This pattern was true for each of the eight participants. By contrast, when the opposite directional sign was more probable (right side of each panel), the performance difference between same- and opposite-physical signs was non-significant, and only four of eight participants performed better in the same-physical-sign condition.

A few features about the data in Fig. 6 should be noted. First, within each panel, the condition on the far left is most similar to the ‘same’ condition in Experiment 3, while the condition on the far right is most

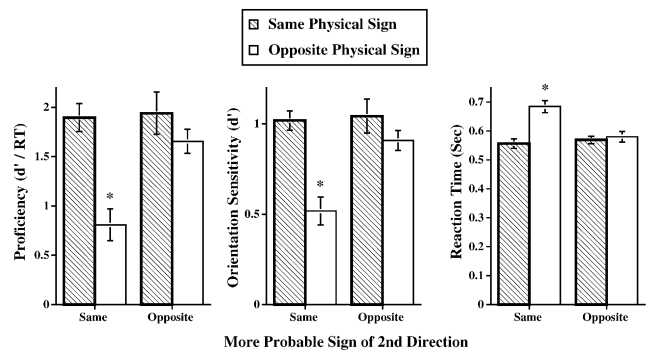


Fig. 6. Data from Experiment 4. Mean data (± 1 SE) from eight participants are shown for each of the three dependent variables—proficiency (left), d' (center panel) and reaction time (right panel). In each panel, the *more probable* sign of the second direction is on the abscissa, while the *physical sign* of the second direction is the parameter. For each dependent variable, there is a significant interaction between probable sign and physical sign. Specifically, performance was significantly better in the same-physical-sign condition (hatched bars) than in the opposite-physical-sign condition (open bars), but only when the more probable sign of the second direction was the same as the first (left side of each panel). This interaction argues against the notion that participants used a directionless, orientation-based strategy throughout the experiment.

similar to the ‘opposite’ condition in Experiment 3. As in Experiment 3, these two conditions generated statistically indistinguishable performance levels in Experiment 4. However, Experiment 4 now reveals that these statistically indistinguishable performance levels were *not* based on the same strategy; There is a clear directional dependence when same-sign motion is more probable, but not when opposite-sign motion is more probable. This directional dependence occurred despite the fact that participants were explicitly instructed that an orientation-based strategy could produce correct answers on *all* trials, before each trial block. Moreover, even if participants were using an orientation-based strategy when the oppositely signed direction was more probable, that strategy generated performance no greater than that of the direction-based strategy that was used in the same-physical/same-more-probable condition (left most bar in each graph). We believe this is a particularly important point, since the same-physical/same-more-probable condition is the one that researchers use most frequently in the study of fine direction discrimination. In other words, the data suggest that under these most frequently employed conditions, (a) participants *actually use* a direction-based strategy, and (b) that participants gain *neither* precision *nor* speed by abandoning a direction-based strategy.

11. Discussion

In the present experiments we investigated the ability to discern trajectory orientations. The ability to discern trajectory orientations is important because it could be used to judge subtle direction differences. To determine whether the limiting factor in judging subtle direction differences is more appropriately attributed to orientation mechanisms or to directional mechanisms, the stimuli were arranged to generate a constant orientation response but variable directional responses. To the extent that orientation mechanisms limited performance, one would expect constant performance across all conditions. On the other hand, performance could be expected to vary across conditions to the extent that directional mechanisms limited performance. We will begin with a summary of the findings, and then offer our inferences.

Across all four experiments in the present study, performance in the ‘same’ condition either matched or significantly exceeded performance in all other conditions. In Experiment 1, performance in the ‘same’ condition matched performance in the ‘stationary’ condition, and significantly exceeded performance in the ‘bi-directional’, ‘opposite’, and ‘scrambled’ conditions. In Experiment 2, the ‘same’ and ‘opposite’ conditions were again compared to each other, after participants were well practiced on both conditions. Here too, performance in the ‘same’ condition was statistically greater than that

in the ‘opposite’ condition, even after ensuring complete certainty about the directional sign of the second RDP. In Experiment 3, across dot sizes, dot densities, and dot speeds, mean angular thresholds were lower for ‘same’ than for ‘opposite’ directional signs—although that difference was nearly eliminated at the highest dot density, and dot speed. The fastest dot speed (16 deg/s) in Experiment 3 generated both statistically indistinguishable thresholds in the ‘same’ and ‘opposite’ conditions, and the lowest thresholds in the entire study. Accordingly, we further explored the ‘same’ and ‘opposite’ conditions at 16 deg/s in Experiment 4. We found that performance in the ‘same’ condition matched that of the ‘opposite’ condition when the two RDPs were likely to have opposite directional signs; When the two RDPs were likely to have the same directional sign, performance in the ‘same’ condition significantly exceeded that in the ‘opposite’ condition. Given these findings, we believe that two inferences can be drawn.

First, we believe that fine direction sensitivity is limited by directional mechanisms rather than orientation mechanisms, under the stimulus conditions most frequently used for measuring fine direction sensitivity. The most frequently used stimulus conditions are similar to our ‘same’ condition—where the two RDPs are likely to move with a shared directional sign along axes that differ only slightly in orientation. In principle, participants could rely on the response from orientation mechanisms for such judgments. However, an orientation-based account fails to explain why performance is better in the ‘same’ than in the ‘opposite’ condition at slower speeds (Experiments 1 and 2), and at faster speeds when the RDPs are likely to have the same directional sign (Experiment 4). Surely participants could use multiple cues, including orientation, under the unusual condition in which the speed is sufficiently fast *and* RDPs with opposite directional signs are most probable on each trial (Experiments 3 and 4). Indeed, other visual judgments, such as shape estimates, can be best made when multiple cues (e.g., binocular disparity and text gradients) are combined (Hillis et al., 2002). However, the present data indicate that even when participants are explicitly informed about how to use orientation cues, their responses are *directionally* dependent whenever the two RDPs are likely have the same directional sign—the condition most frequently used on fine direction tasks.

The notion that direction mechanisms limit performance when the two RDPs are likely to have the same directional sign is supported by three earlier studies, in addition to the present data. First, Ball and Sekuler (1987) reported that significant practice-based improvements in fine direction judgments (‘same’/‘different’) at the trained direction failed to transfer to the opposite direction. Had the practiced based improvements reflected refinements to (directionless) orientation mechanisms, one would expect complete transfer to the

opposite direction, which shares an axis of orientation with the trained direction. Second, a different perceptual learning study showed that significant practice-based improvements in orientation judgments ('clockwise'/ 'anti-clockwise') transferred neither to direction discrimination along the same axis, nor the orthogonal axis (Matthews, Liu, Geesaman, & Qian, 1999). Again, the absence of transfer argues against the notion that orientation mechanisms had set the limit on fine direction judgments. Third, the probability of 'same' versus 'opposite' directional signs was manipulated in an earlier study, where participants were required to make 'clockwise'/ 'anti-clockwise' judgments about subtle angular differences (Matthews et al., 2001). The results from that study, similar to those of the present Experiment 4 which required 'same'/ 'different' judgments, indicated that performance was significantly reduced on low-probability 'catch trials' comprising oppositely signed RDPs. This too, is contrary to an orientation-based prediction. To summarize, studies requiring 'same'/ 'different' (Ball & Sekuler, 1987; present Experiment 4) or 'clockwise'/ 'anti-clockwise' (Matthews et al., 1999, 2001) judgments have converged on the notion that direction, rather than orientation, determines performance when the two RDPs are likely to have the same sign.

In addition to our first inference—that direction, rather than orientation, determines performance when the two RDPs are likely to have the same sign—we believe the present data also warrant a second inference. Specifically, we believe the present data suggest that using an orientation-based strategy confers no advantage compared to a direction-based strategy under the conditions most often used to assess direction sensitivity. To appreciate why this point is counter-intuitive and has important implications for the study of direction sensitivity, we must first consider previous research on the comparison between orientation sensitivity and direction sensitivity.

Previous research has shown that the angular resolution for stationary lines (Vogels & Orban, 1985; Westheimer, 1998; Westheimer, Shimamura, & Mckee, 1976) and gratings (Burbeck & Regan, 1983; Heeley & Timney, 1988; Westheimer, 1998) is much finer than that for motion stimuli (Matthews et al., 1999; Matthews & Welch, 1997). Intuitively then, one might have expected *better* performance in the 'stationary' than in the 'same' condition of Experiment 1. This point can be understood by considering how orientation-tuned mechanisms would respond to the second RDP in each of those conditions.⁶ In the 'same' condition, the orientation of the second RDP's trajectory was not available in any given frame, and could be discerned only by integration *across frames*. In the 'stationary' condition, by contrast, the orientation

required for the judgment was explicitly presented in *each frame* of the second RDP. As a result, the response from orientation mechanisms would be much stronger in the 'stationary' condition than in the 'same' condition. However, an enhanced response from orientation mechanisms in the 'stationary' condition would improve performance *only* if the orientation mechanisms had been the limiting factor. The fact that performance was no better in the 'stationary' than in the 'same' condition therefore suggests that the limit was set by direction mechanisms, not orientation mechanisms. A similar line of reasoning pertains to the data from Experiment 4, where an orientation-based strategy may have been used (right side of each panel in Fig. 6), yet generated performance no greater than that when a direction-based strategy was used (left-most bar of each panel in Fig. 6). For this reason, the present findings do not confirm recent speculation that implicit speed lines (or 'motion streaks') improve performance by adding orientational precision to the output of direction mechanisms (Barlow & Olshausen, 2004). Instead, the findings from Experiments 1 and 4 suggest that, when judging angular differences between two RDPs, an orientation-based strategy is no more advantageous than a direction-based strategy—at least across the conditions tested here.

Lastly, our conclusion that direction discrimination is limited by direction-based mechanisms rather than by orientation-based mechanisms may appear to be contrary to an earlier report that explicit orientations interfere with fine direction judgments (Burr & Ross, 2002). We believe there is no contradiction. Our reasoning is based on the physiological fact that most directionally tuned cells are also orientation-tuned. Consequently, the response of the most probable direction channel could easily become 'swamped' by (directionless) explicit orientation noise. This does not imply that the orientation channel parallel to the most probable direction channel is weighted more heavily than that direction channel itself. Indeed, if the parallel orientation channel were weighted more heavily than the most probable direction channel, one would anticipate identical performance levels across all conditions in the present study—and that was not the case. The present findings instead suggest that fine direction discrimination is determined by the most probable direction channel, which is vulnerable to parallel explicit orientation noise (Burr & Ross, 2002), but not dependent on directionless orientations implicitly traced by moving stimuli.

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⁶ The characteristics of the first RDP were held constant across all conditions and therefore would not distinguish any two conditions from each other.

References

- Albright, T. D. (1984). Direction and orientation selectivity of neurons in visual area MT of the macaque. *Journal of Neurophysiology*, *52*, 1106–1130.
- Ball, K., & Sekuler, R. (1987). Direction specific improvements in motion discrimination. *Vision Research*, *27*, 953–965.
- Barlow, H. B., & Olshausen, B. A. (2004). Convergent evidence for the visual analysis of optic flow through anisotropic attenuation of high spatial frequencies. *Journal of Vision*, *4*(6), 415–426.
- Brainard, D. H. (1997). The psychophysics toolbox. *Spatial Vision*, *10*, 433–436.
- Burbeck, C. A., & Regan, D. (1983). Independence of orientation and size in spatial discriminations. *Journal of the Optical Society of America*, *73*(12), 1601–1694.
- Burr, D. C. (2000). Motion vision: are ‘speed lines’ used in human visual motion? *Current Biology*, *10*(12), R440–R443.
- Burr, D. C., & Ross, J. (2002). Direct evidence that “speedlines” influence motion mechanisms. *Journal of Neuroscience*, *22*(19), 8661–8664.
- Francis, G., & Kim, H. (2001). Perceived motion in orientational afterimages: direction and speed. *Vision Research*, *41*(2), 161–172.
- Geisler, W. S. (1999). Motion streaks provide a spatial code for motion direction. *Nature*, *400*(6739), 65–69.
- Geisler, W. S., Albrecht, G. D., Crane, A. M., & Stern, L. (2001). Motion direction signals in the primary visual cortex of cat and monkey. *Visual Neuroscience*, *18*, 501–516.
- Green, D. M., & Swets, J. W. (1966). *Signal detection theory and psychophysics*. New York: Wiley.
- Heeley, D. W., & Timney, B. (1988). Meridional anisotropies of orientation discrimination for sine wave gratings. *Vision Research*, *28*(2), 337–344.
- Hillis, J. M., Ernst, M. O., Banks, M. S., & Landy, M. S. (2002). Combining sensory information: mandatory fusion within, but not between, senses. *Science*, *298*(5598), 1627–1630.
- Jancke, D. (2000). Orientation formed by a spot’s trajectory: a two-dimensional population approach in primary visual cortex. *Journal of Neuroscience*, *20*(RC86), 1–6.
- Keppel, G., Saufley, W. H., Jr., & Tokunaga, H. (1992). *Introduction to design and analysis*. New York: W.H. Freeman and Company.
- Liu, Z., & Weinshall, D. (2000). Mechanisms of generalization in perceptual learning. *Vision Research*, *40*(1), 97–109.
- Loftus, G. R. (1993). A picture is worth a thousand *P* values: on the irrelevance of hypothesis testing in the microcomputer age. *Behavior Research Methods, Instruments and Computers*, *25*, 250–256.
- Matthews, N., Liu, Z., Geesaman, B., & Qian, N. (1999). Perceptual learning on orientation and direction discrimination. *Vision Research*, *39*(22), 3692–3701.
- Matthews, N., Luber, B., Qian, N., & Lisanby, S. H. (2001). Transcranial magnetic stimulation differentially affects speed and direction judgments. *Experimental Brain Research*, *140*(4), 397–406.
- Matthews, N., & Qian, N. (1999). Axis-of-motion affects direction discrimination, not speed discrimination. *Vision Research*, *39*(13), 2205–2211.
- Matthews, N., & Welch, L. (1997). Velocity-dependent improvements in single-dot direction discrimination. *Perception & Psychophysics*, *59*, 60–72.
- Movshon, J., Adelson, E. H., Martin, S. G., & Newsome, W. T. (1985). The analysis of moving visual patterns. In C. Chagras, R. Gatass, & C. Gross (Eds.), *Pattern recognition mechanisms* (pp. 117–151). New York: Springer Verlag.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision*, *10*, 437–442.
- Ross, J., Badcock, D. R., & Hayes, A. (2000). Coherent global motion in the absence of coherent velocity signals. *Current Biology*, *10*(11), 679–682.
- Saffell, T., & Matthews, N. (2003). Task-specific perceptual learning on speed and direction discrimination. *Vision Research*, *43*(12), 1365–1374.
- Vogels, R., & Orban, G. A. (1985). The effect of practice on the oblique effect in line orientation judgments. *Vision Research*, *25*, 1679–1687.
- Watanabe, T., Nanez, J. E., & Sasaki, Y. (2001). Perceptual learning without perception. *Nature*, *413*(6858), 844–848.
- Welch, L. (1989). The perception of moving plaids reveals two motion-processing stages. *Nature*, *337*(6209), 734–736.
- Westheimer, G. (1998). Lines and gabor functions compared as spatial visual stimuli. *Vision Research*, *38*(4), 487–491.
- Westheimer, G., Shimamura, K., & Mckee, S. P. (1976). Interference with line orientation sensitivity. *Journal of the Optical Society of America*, *66*(4), 332–338.