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Axis-of-motion affects direction discrimination, not speed discrimination

Nestor Matthews *, Ning Qian

Columbia University, Center for Neurobiology & Behavior, 722 West 168th Street, Room A738, New York, NY 10032, USA

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Abstract

The motion of an object can be described by a single velocity vector, or equivalently, by direction and speed separately. Similarly, our ability to see subtle differences in the motion of two objects could be constrained by either a velocity-based sensory response, or separate sensory responses to direction and speed. To distinguish between these possibilities we investigated whether direction discrimination and speed discrimination were differentially affected by changes in the axis-of-motion. Psychophysical data from 12 naive observers indicated that direction discrimination depended on axis-of-motion, but speed discrimination did not. The difference suggests that a velocity-based sensory response is not the limiting factor on the two tasks. Instead, the results imply that the sensory response which constrains speed discrimination is at least partially independent from the sensory response which constrains direction discrimination. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The oblique effect is the perceptual phenomenon in which visual sensitivity is greater to stimuli presented along a cardinal (i.e. horizontal or vertical) axis than to stimuli presented along a diagonal axis. This effect occurs in numerous species and has been demonstrated across many tasks relating to the perception of stationary, oriented stimuli (Apelle, 1972). There is also a strong oblique effect in human motion perception, as subtle directional differences between two sets of moving random dots (random-dot cinematograms, or RDCs) are more easily seen along cardinal than oblique axes (Ball & Sekuler, 1987; Matthews & Welch, 1997). To gain a better understanding of how the human visual system responds to moving stimuli, we sought to determine whether direction discrimination and speed discrimination are equally vulnerable to the oblique effect.

There are many reasons to expect an oblique effect in speed discrimination, given the similarities that have been found between direction and speed discrimination. It has been suggested, for instance, that both direction (Watamaniuk, Sekuler & Williams, 1989) and speed (Watamaniuk & Duchon, 1992) discrimination thresholds are determined by the pooled response of multiple band-limited neural mechanisms. Such a configuration would be expected to yield motion metamers—identical motion percepts that occur under substantially different stimulus conditions—and there is evidence for metameric directions (Williams, Tweten & Sekuler, 1991) and metameric speeds (Festa & Welch, 1998). Moreover, direction and speed discrimination are similarly affected when specific properties of RDCs are manipulated (Festa & Welch, 1997). Such properties include the number of consecutive frames over which each dot is shown, the rate at which the frames of the RDC are presented, and the signal-to-noise ratio. Moreover, both direction and speed discrimination are unaffected by high-pass spatial filtering (Smith, Snowden & Milne, 1994). These similarities are

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* Corresponding author. Tel.: + 1-212-543-5161; fax: + 1-212-543-5161; e-mail: nestor@brahms.cpmc.columbia.edu.

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consistent with the possibility that direction discrimination and speed discrimination are constrained by a unitary sensory response to stimulus velocity (i.e., the vector incorporating the direction *and* speed of motion). Indeed, physiological evidence indicates that certain neurons in the primate visual system respond maximally to specific stimulus velocities (Maunsell & Van Essen, 1983; Mikami, Newsome & Wurtz, 1986; Rodman & Albright, 1987). If the sensory response that constrains direction discrimination also constrains speed discrimination, then the oblique effect, which occurs in direction discrimination, should be evident in speed discrimination as well.

To test this possibility, we had 12 naive observers judge directional differences and speed differences between two successively presented RDCs that moved either cardinally or obliquely. In brief, the data indicated that unlike direction discrimination, speed discrimination did not depend on the axis-of-motion.

2. Method

2.1. Apparatus & stimuli

Using a chin rest to stabilize the head position, observers viewed RDCs through a circular tube having an inner diameter of 10 cm. Stimuli appeared as black dots (97% contrast) that translated across a white background (47 cd/m^2), and 'wrapped-around' the opposite side after moving out of the viewable area. Anti-aliasing software and a vertical refresh rate of 100 Hz ensured smooth apparent motion on both tasks at the 57 cm viewing distance. Each RDC comprised twenty 10 ms frames, and the interval between the two RDCs presented on each trial was 600 ms.

All trials consisted of a 'standard' RDC and a 'test' RDC, presented in random order. On each trial for both tasks, the 'standard' axis-of-motion was randomly 0, 90, 180, or 270° in the cardinal condition, and 45, 135, 225, or 315° in the oblique condition. By using four different directions within the cardinal and oblique conditions, motion aftereffects and anticipatory eye movements were minimized. 'Standard' and 'test' RDCs on the direction-discrimination task moved at 16 deg/s, which was the 'standard' speed on the speed-discrimination task. The standard speed of 16 deg/s and the 200 ms duration were chosen because performance on both tasks has been shown to be optimal under those conditions (De Bruyn & Orban, 1988). An array of ten 'test' directions or speeds was determined separately for each observer. Five of the 'tests' moved anti-clockwise to or slower than the 'standard', and five moved clockwise to or faster than the 'standard'. The method used to determine the range of 'test' directions and speeds is detailed in the Section 2.2.

Several precautions were taken to minimize cues that covary with speed. First, to reduce the effectiveness of distance cues and temporal asynchrony cues on the speed-discrimination task, the dot lifetime was randomized within each RDC. Each dot moved coherently between two and ten frames and was then replotted in a new position. This range of dot lifetimes was chosen because the resultant six-frame mean exceeded the minimum dot lifetime required for asymptotic performance on each task (Festa & Welch, 1997). Secondly, because the number of dots 'wrapping-around' would be greater at faster speeds than at slower speeds, the faster RDC on each trial would appear to have a greater number of 'new' dots. To eliminate this cue, the number of dots in each RDC was randomly varied over a $\pm 30\%$ range, with the average being 50 dots (i.e. 35–65 dots). Thirdly, any covariation between speed and apparent contrast, or between speed and apparent size was mitigated by randomizing the actual size of the dots across RDCs. All dots within a given RDC were the same size, which was randomly either 2×2, 3×3, or 4×4 pixels, with each pixel subtending 2.2 arc min. The dot lifetime, the number of dots, and the dot-size were also randomized on the direction-discrimination task to permit a fair comparison with the speed-discrimination task. Finally, we note that in the first speed-discrimination experiment reported here, all speed differences were achieved by manipulating the spatial offset (i.e. hop size) between frames. The possible use of hop-size cues was examined separately in the control experiment described later.

2.2. Procedure

Each of 12 naive observers completed either the direction-discrimination task or the speed-discrimination task on one day before beginning the other task on a different day. The order in which the tasks were practised was counterbalanced. On the direction-discrimination task, observers indicated whether the direction of the second RDC was clockwise or anti-clockwise to that of the first RDC. On the speed-discrimination task, observers indicated whether the speed of the second RDC was faster or slower than that of the first RDC.

Each daily session was conducted in two phases. During the first phase, observers were assigned, in a counterbalanced manner, to either the oblique or cardinal condition, and discrimination thresholds were measured using the method of constant stimuli. Thresholds were based on 240 directional or speed judgments made across a wide range of ten stimulus-difference values. Typically, maximum directional and speed differences were $\pm 10°$ and $\pm 15\%$, respectively, although these values had to be adjusted slightly for a few observers. For each observer in the present study, a sigmoidal function significantly ($P < 0.05$) fit the responses made to the ten stimulus differences presented in the first phase. Because each fit was significant, we were able to fairly determine each observer's threshold, which was defined as half the stimulus change required to alter the response rate from 0.25 to 0.75. Thresholds so determined corresponded to $d' = 0.67$ for each observer and task. Thus, although direction and speed discrimination are measured in different physical units (i.e., geometric degrees, and Δspeed/speed, respectively), thresholds from the first phase corresponded to identical discriminability levels ($d' = 0.67$) on the two tasks. We therefore equated task difficulty for the second phase—when the axis-of-motion was rotated 45° (from oblique to cardinal, or vice versa)—by using the thresholds obtained in the first phase. Specifically, 'test' and 'standard' RDCs in the second phase differed by 50 (the most subtle), 75, 100, 125, or 150% (the most salient) of the threshold obtained in the first phase. Since each of these five magnitudes could be presented as an increment (i.e., more clockwise or faster) or a decrement (i.e., more anti-clockwise or slower) to the 'standard' direction or speed, there were ten 'test' stimuli on each task. As an example of our procedure, an observer randomly assigned to the oblique condition during the first phase of the direction-discrimination task might have an oblique directional threshold of $\pm 5.5°$. During the second phase of the same session, that observer would judge pairs of cardinally moving RDCs in which the 'test' and 'standard' differed by ± 2.75, ± 4.125, ± 5.5, ± 6.875, or $\pm 8.25°$.

Because task difficulty had been equated for the second phase, data from the second phase could be used to fairly assess whether direction and speed discrimination were differentially affected by axis-of-motion. Accordingly, data from the second phase were analyzed via standard Signal Detection procedures (Green & Swets, 1966). During the direction-discrimination task, 'hits' and 'false alarms' were operationally defined as 'clockwise' responses made when the second stimulus in each trial moved, respectively, clockwise or anti-clockwise to the first. During the speed-discrimination task, 'hits' and 'false alarms' were operationally defined as 'faster' responses made when the second stimulus in each trial moved, respectively, faster or slower than the first. For each task, mean discriminability (d') in the oblique and cardinal conditions was calculated separately at each of the five stimulus-difference magnitudes (i.e., 50, 75, 100, 125, and 150% of threshold). If an oblique effect were present in each task, one would expect discriminability (d') in the second phase to be greater for cardinal motion than for the oblique motion.

3. Results

Data for two naive observers are shown in Fig. 1. Observer 'RS' (top) judged obliquely moving RDCs during the first phase of the direction-discrimination and speed-discrimination tasks (left and right panels, respectively). A sigmoidal function (dotted lines) was fit to these data (X's), and the threshold corresponding to $d' = 0.67$ was determined separately for each task (see Section 2). These thresholds were then used to establish the range of stimulus-differences to be presented in the second phase, which comprised cardinally moving stimuli (solid squares and solid sigmoids) for observer 'RS'.

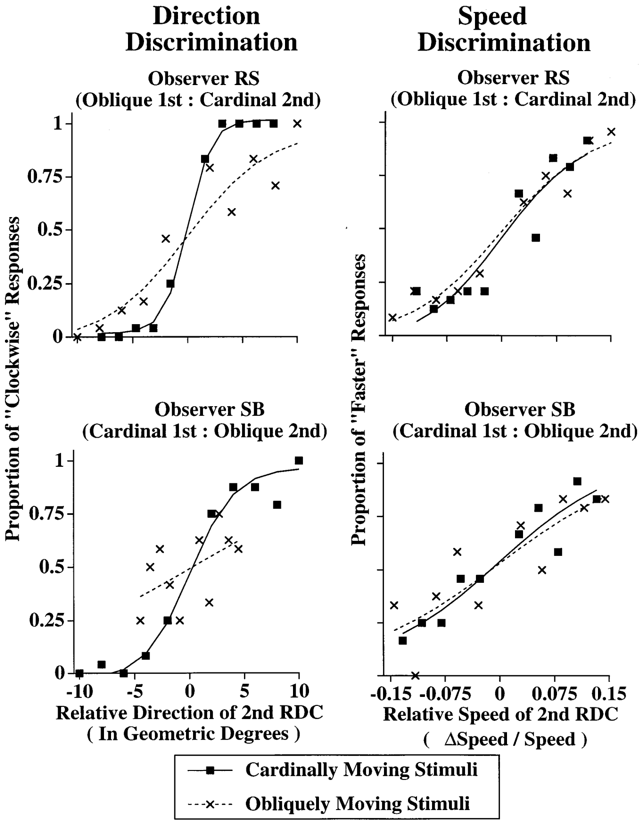

Fig. 1. The effect of axis-of-motion on two observers. Performance on the direction and speed discrimination tasks is shown separately for two observers. For the direction-discrimination task (left), negative and positive abscissal values indicate anti-clockwise and clockwise directional changes, respectively. For the speed-discrimination task (right), negative and positive abscissal values indicate that the second RDC moved slower and faster, respectively, than the first RDC. Each datum is based on 24 observations, and each psychometric function reflects 240 observations. Observer 'RS' completed the oblique ('X's' and dotted lines) and cardinal (solid squares and solid lines) conditions in the first and second phases, respectively. Observer 'SB' completed the oblique and cardinal conditions in the reverse order. A similar pattern of results was evident for both observers. The directional psychometric functions for cardinally moving stimuli are steeper than those for obliquely moving stimuli. The oblique effect is not evident, however, on the speed-discrimination task, as the psychometric functions superimpose in the cardinal and oblique conditions.

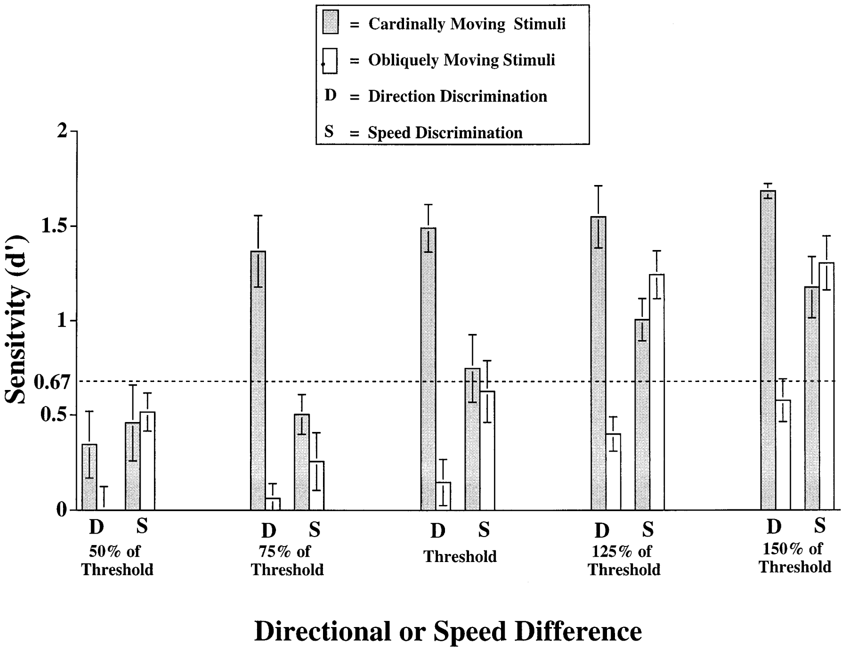

Fig. 2. The mean effect of axis-of-motion across all observers. Mean sensitivity (d') on the second phase of the direction ('*D*') and speed ('*S*') discrimination tasks is plotted separately for the cardinal (shaded columns) and oblique (open columns) conditions at each stimulus difference. The center of the abscissa represents the directional and speed thresholds determined in the first phase. On the direction task, the mean thresholds were 2.5 and 5.5° in the cardinal and oblique conditions, respectively. The mean Weber fraction in speed discrimination (Δspeed/speed) was approximately 0.13 at cardinal and oblique axes. The remaining abscissal values represent stimulus differences that were smaller (50 and 75%), and larger (125 and 150%) than threshold. Each column is based upon 288 observations (six observers * 48 observations per observer). Error bars reflect one standard error of the mean. At each of the five stimulus values, sensitivity is greater for cardinal than foroblique direction discrimination and there is no overlap between the respective error bars. For speed discrimination, however, sensitivity is not consistently greater at either axis-of-motion and the respective error bars overlap.

Observer 'SB' (bottom) completed the cardinal and oblique conditions in the opposite order. Nevertheless, a similar pattern was evident for both observers. In direction discrimination, the fitted curves for cardinal motion are steeper than those for oblique motion[1]. By contrast, the cardinal and oblique axis curves for speed discrimination do not differ from each other. The data in Fig. 1 therefore indicate that for a given observer, an oblique effect can be evident in direction discrimination without being evident in speed discrimination.

The differential effect of axis-of-motion on direction and speed discrimination was also evident in the mean data from all 12 naive observers. These data are shown in Fig. 2, where sensitivity (d') is plotted for directional and speed differences that ranged from very subtle (50% of threshold, left) to very salient (150% of threshold, right). The center-most abscissal value, labeled 'Threshold', represents the directional and speed differences that corresponded to $d' = 0.67$ in the first phase. Consider the four-column data cluster at 'Threshold'. After a directional threshold was determined for each of the six observers assigned to the oblique condition in the first phase, that same directional difference was presented cardinally in the second phase, and d' increased from 0.67 (dashed horizontal line) to 1.49 (shaded bar on the left). Conversely, for the other six observers, d' dropped from 0.67 to 0.15 (open bar on the left) when the directional threshold associated with cardinal motion in the first phase was presented along oblique axes in the second. A between-subjects t-test revealed that, at 'Threshold', directional sensitivity was significantly greater along cardinal than oblique axes ($t(10) = 7.72$, $P < 0.01$, two-tailed), with the axis-of-motion accounting for 85.6% of the variance. This contrasts sharply with the overlap in cardinal and oblique speed sensitivity (see the remaining two bars at 'Threshold'). Indeed, axis-of-motion did not significantly affect speed discrimination ($t(10) = 0.50$, $P > 0.25$, n.s.) at 'Threshold', explaining only 2.5% of the variance. Similar results were obtained when the preceding analyses were conducted on the remaining stimulus-difference magnitudes (i.e., 50, 75, 125, and 150% of threshold) shown in Fig. 2. Direction discrimination consistently depended on axis-of-motion, while speed discrimination did not.

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[1] Note that for each observer, the range of stimulus differences presented in the second phase depended entirely upon the threshold obtained in the first phase. Therefore the relatively narrow range of directional differences presented to SB in the second phase is attributable to the low directional threshold obtained from SB in the first phase.

3.1. Hop-size control experiment

In principle, it is possible that observers could have used hop size (i.e., the frame-to-frame displacement of each dot), rather than speed per se, to respond accurately on the preceding speed-discrimination task. While this seems unlikely because the anti-aliasing software made all stimuli appear to move smoothly, we nevertheless conducted a control experiment in which hop size was completely dissociated from speed.

The dissociation between hop size and speed was achieved by having the frame rate of the 'standard' on each trial differ from that of the 'test'. During half the trials, 'standard' dots were displaced on each frame (i.e., every 10 ms or 100 Hz), whereas 'test' dots were displaced on every second frame (i.e., every 20 ms or 50 Hz). These conditions were reversed on the remaining trials. In Table 1, the dissociation is exemplified in the parameters for stimulus pairs A and B (top, shaded rows). Both pairs contain a 'test' that moves 18% slower than the 'standard' speed of 8 deg/s. Yet, the 'standard' hop size is smaller than the 'test' hop size in pair A (4.8 vs. 7.872 arc min, respectively), and larger than the 'test' hop size in pair B (9.6 vs. 3.936 arc min, respectively). Since stimulus pairs were presented in random order within each trial block, observers who based speed judgments solely on hop size or frame-rate cues would perform at chance ($d' = 0$). The parameters used to achieve speed increments (pairs C and D) at 8 deg/s, and both decrements and increments (pairs E through H) at 16 deg/s are also shown in Table 1. By using two 'standard' speeds of 16 and 8 deg/s, we were able to match the 'standard' speed of the preceding experiment (i.e. 16 deg/s), and ensure that our results were not limited to one speed. The speed difference on each trial in the hop-size control experiment was ± 18%; a difference sufficiently large to avoid a 'floor effect' in naive observers, according to data from the preceding experiment.

Table 1
Stimulus parameters for the hop-size control experiment[a]

Stimulus	Speed (deg/s)	$\frac{\Delta\text{Speed}}{\text{Speed}}$	Frame Rate (Hz)	Hop Size (arc min)
A				
Standard	8	n/a	100	4.8
Test	6.56	−18%	50	7.872
B				
Standard	8	n/a	50	9.6
Test	6.56	−18%	100	3.936
C				
Standard	8	n/a	100	4.8
Test	9.44	+18%	50	11.328
D				
Standard	8	n/a	50	9.6
Test	9.44	+18%	100	5.664
E				
Standard	16	n/a	100	9.6
Test	13.12	−18%	50	15.744
F				
Standard	16	n/a	50	19.2
Test	13.12	−18%	100	7.872
G				
Standard	16	n/a	100	9.6
Test	18.88	+18%	50	22.656
H				
Standard	16	n/a	50	19.2
Test	18.88	+18%	100	11.328

[a] The spatiotemporal configuration of each pair of RDCs is shown. In the upper half of the panel, the 'standard' speed is 8 deg/s. In the lower half of the panel, the 'standard' speed is 16 deg/s. Shaded and open rows, respectively, describe RDC pairs that contained 'tests' which moved slower and faster than the 'standard' speed. At both 8 and 16 deg/s, neither the frame rate (fourth column) nor the hop size (rightmost column) was sufficient to reliably determine speed differences between 'standard' and 'test' RDCs.

Six observers participated in the hop-size control experiment. All were naive, and none had participated in the preceding experiment. As before, observers were asked to indicate whether the second RDC in each trial moved faster or slower than the first. Within each 64 trial-block, cardinally (i.e., left or right) and obliquely (i.e. 45 or 225°) moving RDC pairs were presented randomly. The two standard speeds, 8 and 16 deg/s, were tested on different days, with each daily session consisting of eight blocks per observer. All other stimulus parameters were identical to those of the preceding speed experiment.

The mean speed sensitivity (d') of the six observers is shown separately in Fig. 3 for the four stimulus conditions. Consistent with the overlap in the error bars, a within-subjects t-test indicated that the axis-of-motion did not significantly affect speed discrimination when the standard speed was 8 ($t(5) = 0.65$, $P > 0.25$, n.s.) or 16 ($t(5) = 0.35$, $P > 0.25$, n.s.) deg/s. Therefore, even after removing the possible use of hop-size cues, the data argue against an oblique effect in speed discrimination.

4. Discussion

The data from the present study suggest a dissociation between direction discrimination and speed discrimination. The observers' ability to identify subtle directional differences was altered significantly by manipulating the axis-of-motion, while the same manipulation did not affect the observers' ability to identify subtle speed differences. This finding is consistent with the possibility that the sensory response which limits speed discrimination is at least partially independent of the sensory response that limits direction discrimina-

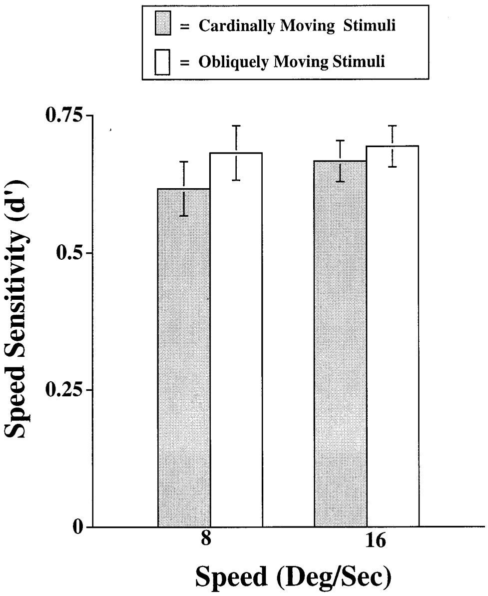

Fig. 3. Speed sensitivity in the absence of hop-size cues. Speed sensitivity (d') is plotted for the two 'standard' speeds, when the RDCs contained no usable hop-size cues. Each column represents the mean of six observers who judged a ± 18% speed change from the 'standard' speeds of 8 (left) and 16 (right) deg/s. Each observer made 256 speed judgments in each of the four conditions. The error bars reflect one standard error of the mean after consistent individual differences were removed. Contrary to what would be expected if there was an oblique effect in speed discrimination, speed sensitivity (d') is statistically indistinguishable in the cardinal (shaded bars) and oblique (open bars) conditions.

tion. For if both tasks were critically limited by a unitary velocity-based response, an oblique effect in speed discrimination would be expected to covary with the directional oblique effect. This was not the case. Thus, despite the existence of neurons that respond maximally to particular stimulus velocities (Maunsell & Van Essen, 1983; Mikami et al., 1986; Rodman & Albright, 1987) our psychophysical data imply that a unitary velocity-based sensory response is not the limiting factor in both direction discrimination and speed discrimination.

An alternative explanation for the present data might be that direction discrimination is constrained solely by *orientation* discrimination, which is also subject to an oblique effect. According to this interpretation, on each trial observers would implicitly estimate a cardinal or oblique orientation, and compare that estimate to the directional component of a velocity-based sensory response caused by the motion stimulus. Such a comparison would presumably produce an oblique effect in direction discrimination, but not in speed discrimination. Psychophysical data from other studies nevertheless pose two challenges to this account. First, orientational thresholds are typically lower than directional thresholds (Westheimer & Wehrhahn, 1994; Matthews & Welch, 1997). This implies that orientation discrimination cannot alone account for limitations in direction discrimination. Secondly, if direction discrimination were critically limited by orientation discrimination, one would expect direction discrimination to be enhanced when orientation discrimination improves significantly. In a perceptual learning study reported elsewhere (Matthews, Liu & Qian, 1998), however, we found that significant improvements in oblique orientation discrimination did not affect oblique direction discrimination. For these reasons it is unlikely that the present data can be explained by a unitary, velocity-based sensory response that is more accurately compared to cardinal than to oblique orientational estimates.

We believe that the present psychophysical finding imposes a novel constraint on neural computational models of motion perception. Specifically, complete models of motion perception must explain the dissociation between direction and speed discrimination observed across the range of stimulus conditions reported here. Our finding could be modeled by instantiating separate pooling strategies for direction discrimination and speed discrimination. Optimal direction discrimination would be achieved by pooling across all speeds and a narrow range of directions. For the best speed discrimination, on the other hand, the most effective pooling would occur across all directions (thus losing the oblique effect) and a narrow range of speeds.

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