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The effect of spatial orientation on detecting motion trajectories in noise

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ABSTRACT

A series of experiments investigated the extent to which the spatial orientation of a signal line affects discrimination of its trajectory from the random trajectories of background noise lines. The orientation of the signal line was either parallel (iso-) or orthogonal (ortho-) to its motion direction and it was identical in all respects to the noise (orientation, length and speed) except for its motion direction, rendering the signal line indistinguishable from the noise on a frame-to-frame basis. We found that discrimination of ortho-trajectories was generally better than iso-trajectories. Discrimination of ortho-trajectories was largely immune to the effects of spatial jitter in the trajectory, and to variations in step size and line-length. Discrimination of iso-trajectories was reliable provided that step-size was not too short and did not exceed line length, and that the trajectory was straight. The new result that trajectory discrimination in moving line elements is modulated by line orientation suggests that ortho- and iso-trajectory discrimination rely upon two distinct mechanisms: iso-motion discrimination involves a 'motion-streak' process that combines motion information with information about orientation parallel to the motion trajectory, while ortho-motion discrimination involves extended trajectory facilitation in a network of receptive fields with orthogonal orientation tuning.

1. Introduction

Many studies have investigated the effect of spatial orientation or configuration on motion perception. A basic question is whether motion perception is better when orientation or configuration is orthogonal to motion direction ('ortho-motion'), or parallel to motion direction ('iso-motion'). Some studies have found that ortho-motion produces the best performance (Casco, Caputo, & Grieco, 2001; Casco et al., 2006; Castet et al., 1993; Nakayama et al., 1985; Scott-Brown & Heeley, 2001; Tse & Hsieh, 2007), while others have found that iso-motion is best (Georges et al., 2002; Grzywacz, Watamaniuk, & McKee, 1995; McKee & Welch, 1985; Snowden & Braddick, 1989; van Doorn & Koenderink, 1984; Verghese et al., 1999; Watamaniuk, McKee, & Grzywacz, 1995; Werkhoven, Snippe, & Koenderink, 1990). These different results may be due to the different neural mechanisms involved, or to different responses in the same mechanism to iso- and ortho-motion, depending on stimulus conditions. To clarify the neural basis of iso- and ortho-motion effects, in the present study we investigated the interplay between them in a stimulus consisting of a single target line moving in a straight trajectory which was presented against a background of randomly moving lines of the same orientation, either parallel or orthogonal to the motion trajectory of the target.

One possible candidate mechanism was suggested by Watamaniuk, McKee, and Grzywacz (1995)'s finding that a single (non-oriented) element which moves along a straight trajectory over more than two frames can be easily detected when embedded in a background of random-direction motion noise, even though the spatial and temporal characteristics (step size and frame rate) of the target element are identical to the noise, making the target indistinguishable from the noise on the basis of a single pair of frames. It seems that an extended linear trajectory is sufficient to detect coherent motion. We refer to this mechanism as extended trajectory (ET) facilitation.

A number of studies have investigated the detectability of multi-frame motion displays and extended trajectories, and found an advantage for iso-motion (Georges et al., 2002; Grzywacz, Watamaniuk, & McKee, 1995; McKee & Welch, 1985; Snowden & Braddick, 1989; van Doorn & Koenderink, 1984; Verghese et al., 1999; Watamaniuk, McKee, & Grzywacz, 1995; Werkhoven, Snippe, & Koenderink, 1990). Verghese, McKee, and Grzywacz (2000) found

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that the linear trajectory of a group of three-dots is detected better against a dynamic noise background when the arrangement of the dots forms a line parallel rather than orthogonal to the group's trajectory. van Doorn and Koenderink (1984) also showed that thin strips of random dots were detected better when elongated in the direction of motion than when elongated in an axis perpendicular to its motion direction. This result was replicated by Fredericksen, Verstraten, and van de Grind (1994). Together, these findings indicate that iso-motion may be more salient than ortho-motion because it is more elongated in the direction of motion. However, several studies based on different stimuli have found better performance for ortho-motion. We have found that discrimination of motion direction (Casco, Caputo, & Grieco, 2001) and orientation contrast (Casco et al., 2006) in two-frame motion of line segments is highest when the motion is more orthogonal to orientation than background lines. Nakayama et al. (1985) had previously measured thresholds for detecting differential motion in random dots using configurations in which velocity varied either orthogonal to direction (shearing), or parallel to direction (compression). They concluded that spatial integration of motion signals is most efficient in a direction orthogonal to orientation. In addition, Castet et al. (1993) and Scott-Brown and Heeley (2001) have shown that the perceived speed of a line is more veridical when oriented orthogonally to its direction than when the line is tilted. Tse and Hsieh (2007) also demonstrated that the component of motion orthogonal to orientation influences perceived motion as predicted by its intrinsic terminators.

The greater efficiency of ortho-motion reported by Casco, Caputo, and Grieco (2001) and Casco et al. (2006) has been explained in terms of regions of summation along the target line, within motion sensitive receptive fields that are elongated orthogonally to their preferred direction. We refer to this model as orthogonal motion component (OMC) facilitation. There is extensive physiological evidence that the receptive fields of direction selective neurons at low levels of analysis (V1) are arranged in this manner and are able to extract the motion component orthogonal to orientation (De Valois, Yund, & Hepler, 1982; Hubel & Wiesel, 1968). Although in a two-frame display target and background lines of the same length and orientation should be indistinguishable because they have the same OMC, OMC may modulate the relative saliency of iso- and ortho-motion in a multi-frame display where the random direction of the noise makes OMC signals vary from frame to frame, whereas OMC signals for the target remain fixed.

In order to investigate the roles of ET and OMC facilitation in psychophysical performance, we have compared the relative salience of iso- and ortho-motion in different conditions using a paradigm which combines features of that used by Watamaniuk, McKee, and Grzywacz (1995), namely multi-frame displays, and features of that used by Casco, Caputo, and Grieco (2001) and Casco et al. (2006), namely oriented elements rather than dots. In particular, we tested whether the trajectory of a single target line, either vertical or horizontal, could be discriminated reliably when presented among noise lines with the same orientation, whose movements are indistinguishable from the target line on a frame-by-frame basis. The only distinguishing characteristic of the target line, both in iso- and ortho-motion conditions, is that it moves in the same direction over time while the noise lines change their motion direction from frame to frame.

2. Experiment 1: The effect of spatial jitter on motion direction discrimination

One important feature of the ET mechanism is its ability to tolerate small perturbations in dot trajectory. Watamaniuk, McKee, and Grzywacz (1995) found reliable detection when the trajectory changed its direction by a small amount. However, small perturbations in a linear trajectory do introduce motion noise; in the case of iso-oriented lines it introduces an OMC signal in a direction that is orthogonal to the trajectory. This OMC signal may impair discrimination performance for iso-motion. In order to avoid the possibility that observers could use line orientation to make their responses, trials involving iso- and ortho-motion were intermixed (Experiment 1a). Moreover, we performed a control experiment in which the two stimuli (i.e., iso- and ortho-motion trajectories) were presented in separate blocks (Experiment 1b).

2.1. Method

2.1.1. Apparatus

Stimuli were generated by a Cambridge Research System VSG graphics card with 12-bit luminance resolution and displayed on a gamma-corrected Sony monitor with a resolution of 1024 × 768 pixels. Each pixel subtended 1.9 arcmin.

2.1.2. Subjects

Six observers participated in each experiment; two of the authors participated in both Experiments 1a and 1b. Subjects sat in a dimly lit room 57 cm from the screen. Stimuli were free-viewed binocularly. At the beginning of each experiment subjects were given training to familiarize them with the stimuli and task. All subjects had normal or corrected-to-normal visual acuity.

2.1.3. Stimuli

Stimuli were random-line kinematograms in which each line moved in an eight-frame sequence. Each stimulus consisted of a background textured region made up of 180 lines oriented horizontally or vertically (see Fig. 1 for an example). The texture elements were arranged on a raster subtending 12 × 10.8 deg. Line length was 38 arcmin and width was 1.9 arcmin. The step size of both the signal and noise lines was 13.3 arcmin. Frame duration was set at 30 ms and inter-frame interval was 0 ms. Speed was 7.4 deg/s. The background lines moved in one of eight directions,

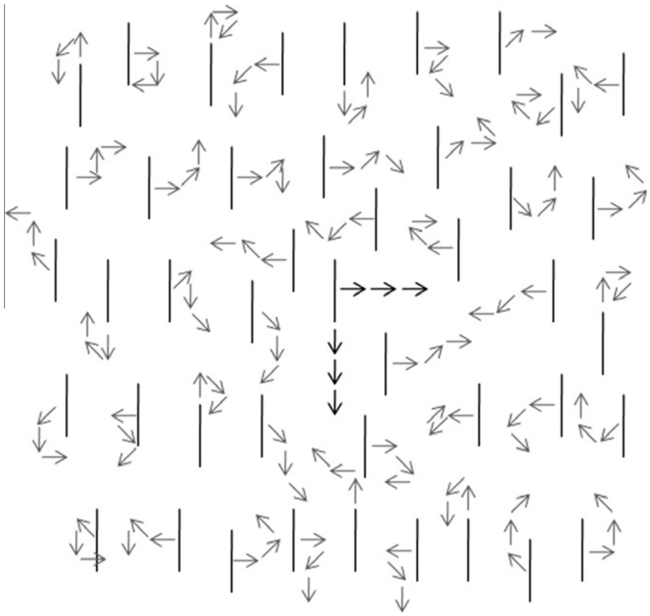

Fig. 1. A diagrammatic representation of the iso- and ortho-trajectory of a vertical signal line. For simplicity only displacements over three frames are shown (arrows). The trajectory is consistent for the target line (iso- or ortho-motion; black arrows) but not for background lines (gray arrows).

including four cardinal directions (90, 180, 270, 360 deg) and four oblique directions (45, 135, 225, 315 deg), chosen randomly in each frame. The target line moved in a fixed and coherent direction that could be horizontal (rightwards) or vertical (downwards). Note that target and background lines were allowed to overlap during their trajectory but, since they have the same orientation, cross-shape features were never formed. The starting point of the motion was the 3rd column of the raster when the target moved rightwards and among the columns of the 3rd row when the target moved downwards. Element and background luminance were 0.75 cd/m^2 and 34.29 cd/m^2 respectively.

The straightness of the target line trajectory was perturbed by jittering its spatial position from frame to frame. If the trajectory of the line was vertical, the jitter was applied along the x coordinate if the trajectory was horizontal the jitter was applied along the y coordinate. In independent blocks the amount of jitter was chosen between one of these values: 0, 7.6, 15.2 arcmin.

2.2. Procedure

In Experiment 1a there were four stimulus conditions, resulting from the factorial combination of two orientation and two direction of motion conditions: (i) vertical signal line moving vertically (iso-motion), (ii) horizontal signal line moving horizontally (iso-motion), (iii) vertical signal line moving horizontally (ortho-motion), and (iv) horizontal signal line moving vertically (ortho-motion). In each block, each of the four stimulus conditions was presented 10 times in randomized order. Observers performed two repetitions of each block to accumulate 20 trials for each stimulus condition.

Spatial jitter varied between blocks and stimulus type varied within blocks. In Experiment 1a, observers performed a two alternative forced choice task (2AFC), discriminating the motion direction of the target. That is, observers had to indicate whether the target moved horizontally or vertically. Discrimination probabilities in iso- and ortho-motion conditions were calculated from the number of correct responses out of the 20 trials. Then the iso- and ortho-discrimination probabilities were averaged across the vertical and horizontal conditions.

The procedure of Experiment 1b was the same as that of Experiment 1a with the exception that we used two stimulus conditions: (i) horizontal signal line moving horizontally (iso-motion) and (ii) vertical signal line moving horizontally (ortho-motion). Observers had to discriminate whether the signal line moved leftward or rightward.

2.3. Results

Results are shown in Fig. 2B. The abscissa plots the level of spatial jitter applied to target line trajectory, while the ordinate represents discrimination probability; results for iso- and ortho-trajectories are plotted as separate lines. Overall, results show that discrimination performance for the iso-trajectory (filled symbols) deteriorated as spatial jitter increased, whereas discrimination of ortho-trajectory (open symbols) was hardly affected at all by the level of spatial jitter.

A repeated measures ANOVA for the Experiment 1a, with Stimulus Type (iso- vs. ortho-) and Jitter (0, 7.6, 15.2 arcmin) as factors, revealed a significant effect of Stimulus Type ($F(1,5) = 25.09$; $p = 0.004$), and Jitter ($F(2,10) = 36.08$; $p = 0.0001$), indicating that discrimination worsened as the amount of jitter increased. Furthermore, the ANOVA revealed a significant interaction between Stimulus Type and Jitter ($F(2,10) = 4.37$; $p = 0.043$). Bonferroni corrected pairwise comparisons pointed out a significant difference between iso- and ortho-trajectories for the second (7.6 arcmin) ($p = 0.033$) and third (15.2 arcmin) ($p = 0.009$) levels of jitter, indicating that ortho-trajectory discrimination was better than iso-trajectory discrimination as the amount of jitter increased. For Experiment 1b a repeated measures ANOVA, with Stimulus Type (iso- vs. ortho-) and Jitter (0, 7.6, 15.2 arcmin) as factors, revealed a significant effect of Stimulus Type ($F(1,5) = 11.57$; $p = 0.019$) and a significant interaction between Stimulus Type and Jitter ($F(2,10) = 13.69$; $p = 0.001$). Bonferroni corrected pairwise comparisons pointed out a significant difference between iso- and ortho-trajectories for the third (15.2 arcmin) level of jitter ($p = 0.009$), further indicating that increasing the amount of jitter ortho-trajectory discrimination was better than iso-trajectory discrimination.

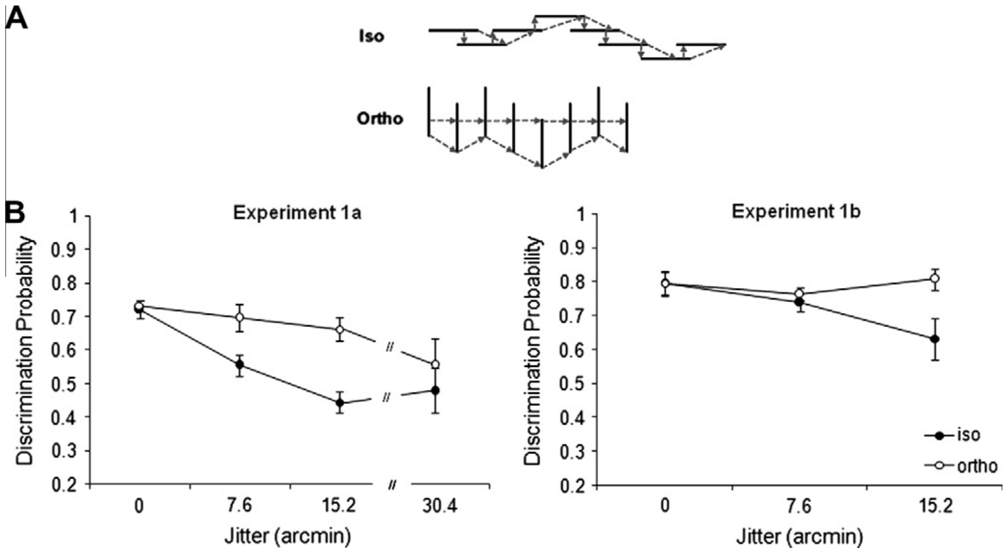

Fig. 2. (A) Motion signals at the line terminators that may allow recovery of a perturbed horizontal trajectory, and OMC signals having a congruent direction for ortho-motion but not for iso-motion. (B) Average discrimination probability as a function of spatial jitter from frame to frame, for iso- (filled circles) and ortho-trajectory (empty circles). The left panel shows discrimination probability in Experiment 1a in which iso- and ortho-motion were intermixed within each block, whereas the right panel shows discrimination in Experiment 1b in which iso- and ortho-motion were presented in separate blocks. Error bars ± *SEM*.

2.4. Discussion

Spatial jitter introduces motion noise to both iso- and ortho-stimuli, i.e., motion components that do not belong to the linear trajectory. On this basis one might expect jitter to affect performance in both conditions. However results show that only discrimination of iso-motion is impaired at high levels of spatial jitter. Although jitter alters both iso- and ortho-motion trajectories (as illustrated in Fig. 2A), there is a substantial difference between the two stimuli that may account for the differential effect of jitter. Jitter in the iso-condition produces an OMC orthogonal to the trajectory, and at the orientation given by the alternate response. For example, for a horizontal moving iso-stimulus the OMC is vertical, thus observers perceive the iso-target moving in the ortho-motion direction (i.e., upward or downward, randomly). This would greatly reduce the sensitivity to iso-motion. On the other hand, the spatial jitter could produce merely a response bias towards the ortho-motion, however, this prediction is not supported by our findings, indicating a similar effect of the jitter in the two experiments. So the poor iso-performance in both experiments, and particularly in Experiment 1a, may reflect the influence of the OMC.

On the other hand, spatial jitter that is smaller than line length would leave some overlap in the ortho-line target from frame-to-frame (see Fig. 2A). An OMC congruent with the trajectory can be extracted along this constant piece of contour. To check for this possibility we also ran a control condition with no overlap, in which the line length was 28.5 arcmin and jitter was 30.4 arcmin. Results for five subjects who did not participate in the main experiment (apart from two of the authors) are reported as isolated points in the left panel of Fig. 2B. Average discrimination probabilities were equal to 0.49 (SE: 0.06) and to 0.56 (SE: 0.07) for the iso- and ortho-conditions respectively. A one sample *t*-test revealed that iso- and ortho-discrimination probabilities did not differ from chance (iso-: $t(4) = -0.13$; $p = 0.90$; ortho-: $t(4) = 0.84$; $p = 0.44$). These results support the suggestion that ortho-motion is not affected by spatial jitter when an OMC can be extracted.

3. Experiment 2: The effect of spatial jitter on motion detection

The results of Experiment 1 showed that jitter affects iso- but not ortho-motion discrimination (except at extreme values). In Experiment 2 we asked whether the jitter effect is task-specific. Indeed, it has been shown that different populations of neurons can contribute to the detection and discrimination of visual motion (Hol & Treue, 2001; Regan & Beverley, 1985; Treue, Hol, & Rauber, 2000). Perhaps the processes underlying iso-motion effects (motion-streaks) contribute a directionally ambiguous signal while the processes mediating ortho-motion effects (OMCs) are direction specific (we are grateful to a referee for suggesting this possibility). We therefore conducted an experiment to measure signal line detection rather than trajectory discrimination of iso- and ortho-motion stimuli.

3.1. Method

The target line had either iso- or ortho-orientation and moved horizontally either leftwards or rightwards. Within each block, each stimulus condition (i.e., each combination of stimulus type and direction) was presented 10 times in randomized order. As in the previous experiments observers performed two repetitions of each block to accumulate 20 trials for each stimulus condition. Spatial jitter varied between blocks. Stimulus type was presented in separate blocks. The experiment used a detection task with a two-interval forced-choice procedure (2IFC). Six observers (including two of the authors) were instructed to indicate whether the target signal was present in the first or in the second interval. The duration of each interval was 240 ms (8 frames × 30 ms). Inter-interval duration was set at 1 s, during which the screen was uniform. Detection probabilities in iso- and ortho-motion conditions were calculated from the number of correct responses out of the 20 trials. Then iso- and ortho-data were averaged across the two motion directions. All other parameters were the same as in Experiment 1.

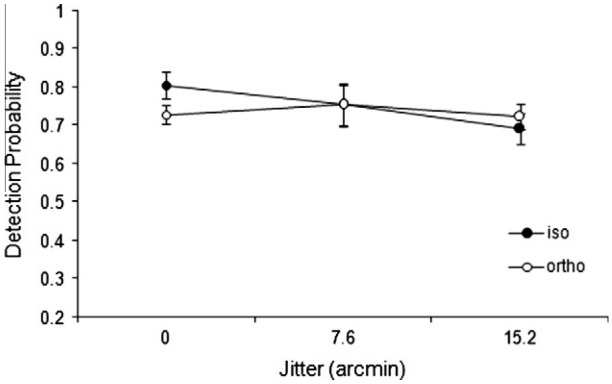

Fig. 3. Average detection probability as a function of target spatial jitter from frame to frame, for iso- (filled circles) and ortho-trajectory (empty circles). Error bars ± *SEM*.

3.2. Results

Results are shown in Fig. 3. The abscissa plots the level of spatial jitter of the target line trajectory, and the ordinate plots detection probability for iso-motion (filled symbols) and ortho-motion (open symbols). Overall, results show that iso-motion trajectory was affected by increases in spatial jitter, whereas detection of the ortho-motion trajectory was unaffected. ANOVA revealed a significant interaction between Trajectory Type (iso- vs. ortho-) and Jitter ($F(2, 10) = 5.042$; $p = 0.032$). Pairwise comparisons (Bonferroni corrected) showed that: (i) discrimination of ortho-trajectory is not significantly affected by jitter, and (ii) discrimination of iso-trajectory is impaired at the highest level of jitter. Indeed we found a significant difference between the no jitter condition and the highest level of jitter employed (i.e., 15.2) ($p = 0.001$).

3.3. Discussion

Taken together, results of Experiments 1 and 2 show that both discrimination and detection of iso-motion are impaired at high levels of spatial jitter. Although jitter introduces spurious motion components into both iso- and ortho-linear trajectories, only psychophysical performance using iso-motion is impaired. We suggest that this is due to the fact that jitter in the iso-condition produces an OMC orthogonal to the motion trajectory. Ortho-motion detection, on the other hand, is not impaired by jitter because if some overlap remains in the linear ortho-line target trajectory, an OMC congruent with the trajectory can be extracted.

4. Experiment 3: The effect of line length

Experiments 1 and 2 show different effects of jitter on iso- and ortho-trajectories. The tolerance of ortho-motion to jitter was interpreted as resulting from the preservation of OMC signals in the ortho-condition. On the other hand OMC signals disrupt the trajectory signal in the iso-condition. However there is a geometrical feature distinguishing the iso-display that may also explain the reduced saliency of iso-motion. Whereas iso-motion trajectory is parallel to background line orientation, ortho-motion trajectory is orthogonal to the orientation of background lines. It is possible that iso-trajectory is less perceivable because, having the same orientation as the background lines, it is more subject to masking by the lines. This possibility is compatible with Geisler's (1999) motion streak model (MS). Geisler (1999) found that the visual system may use orientation information to facilitate motion detection parallel to orientation. He found that below a critical speed there was no effect of mask orientation, but above a speed of about 1 dot width per 100 ms, a mask parallel to the motion direction of the dot was more effective in increasing the luminance threshold. Subsequent studies have found further psychophysical (Apthorp & Alais, 2009; Apthorp, Wenderoth, & Alais, 2009; Burr, 2000; Burr & Ross, 2002; Edwards & Crane, 2007; Ross, Badcock, & Hayes, 2000) and physiological support for the model (Geisler et al., 2001; Krekelberg et al., 2003). The MS model predicts masking of motion signals from parallel orientation signals in the iso-display. In the ortho-display, background lines are less effective in masking the motion signal because they are oriented orthogonally to it. This also could render iso-motion less salient than ortho-motion.

To test for the involvement of masking consistent with the MS mechanism, in Experiment 3 we manipulated the speed of the target by varying the step size. To increase the likelihood of background lines masking the iso-motion streak (Pack & Born, 2001) we used a longer frame duration (FD) that was still within the range of 'short-range' motion sensitivity at all velocities (see Baker & Braddick, 1985). Furthermore, we varied line length. The MS model predicts that a streak is formed at a minimum speed of 1 line length per 100 ms. Thus, minimum speed should increase with line length.

4.1. Method

Two authors and four subjects who were unaware of the purpose of the study participated in Experiment 3. Stimulus parameters were the same as in Experiment 1a unless otherwise stated. FD was 50 ms and inter-frame interval was 0 ms. We varied line length in separate experimental blocks (19, 38 and 57 arcmin). Within each experimental block we randomly varied the step size of the signal line (9.5, 19, 28.5, 38, and 47.5 arcmin, corresponding to 3.2, 6.3, 9.5, 12.7, and 15.8 deg/s). However, the step size of the noise lines was kept constant at 9.5 arcmin (3.2 deg/s), the same as the shortest step size. The procedure was the same as in Experiment 1a: each block of 40 trials consisted of 10 repetitions of the four stimuli. Subjects performed two repetitions of each block. Discrimination probabilities were calculated as in Experiment 1a.

4.2. Results

Results of Experiment 3 are shown in Fig. 4. The lower abscissa specifies the speed of the target line, whereas the upper abscissa specifies step size. The ordinate plots discrimination probability, as in Fig. 2B. Results show that discrimination performance for iso-trajectory was maximum at a specific speed (step size), and this optimal speed increased with line length. Once step size exceeded line length, iso-motion discrimination became impaired. On the other hand, discrimination performance for the ortho-trajectory depended only on target step size/speed.

A repeated measures ANOVA found a significant effect of line length ($F(2, 10) = 9.74$; $p = 0.004$), a significant effect of step size/speed ($F(4, 20) = 23.66$; $p = 0.0001$) and a significant interaction between line length and trajectory type (i.e., iso- or ortho-) ($F(2, 10) = 7.33$; $p = 0.011$). Pairwise comparisons (Bonferroni corrected) revealed that for lines of short (i.e., 19 arcmin) and intermediate length (i.e., 38 arcmin), discrimination for ortho-motion was always higher than that of iso-motion ($p = 0.034$ and $p = 0.007$ respectively). The three-way interaction was not significant.

A separate ANOVA only on the iso-condition showed a significant effect of line length ($F(2, 10) = 13.05$; $p = 0.002$), a significant effect of step size/speed ($F(4, 20) = 23.47$; $p = 0.0001$) and a significant interaction between line length and step size/speed ($F(8, 40) = 3.91$; $p = 0.002$). The optimal step size/speed increased with line length. For the shortest length (19 arcmin), discrimination dropped when step size was larger than 19 arcmin (i.e., 6.3 deg/s). At intermediate length (38 arcmin) discrimination was reduced when step size was equal or larger than 38 arcmin (i.e., 12.7 deg/s). With the longer length (57 arcmin) discrimination remained high at the largest step size used (47.5 arcmin; 15.8 deg/s). A separate ANOVA for the ortho-condition revealed only a significant effect of step size/speed ($F(4, 20) = 4.74$; $p = 0.007$).

4.3. Discussion

When lines are oriented orthogonally to their motion direction there is no effect of line length (open symbols in Fig. 4). This is compatible with the suggestion that ortho-motion discrimination involves a motion network based on interconnections between

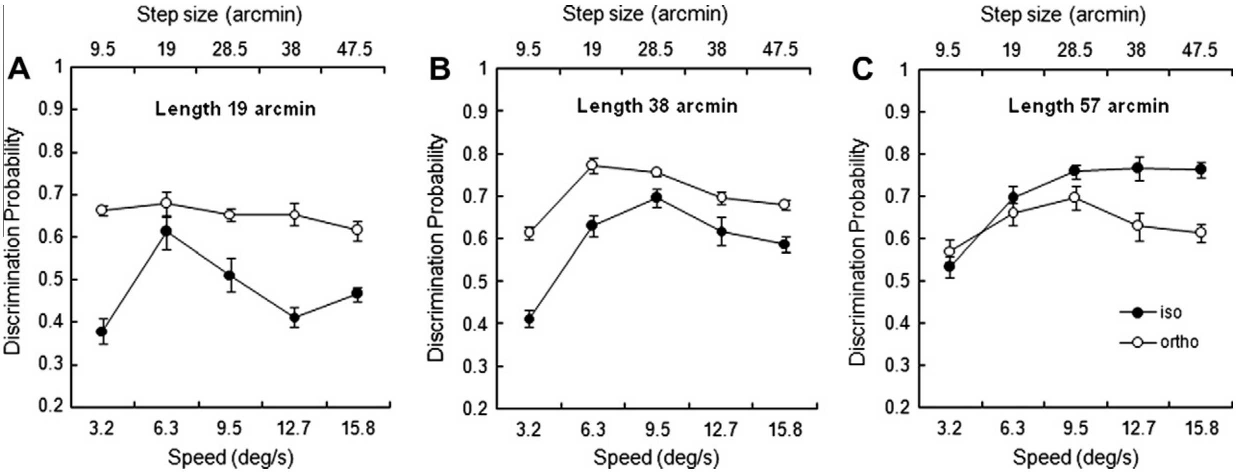

Fig. 4. Average discrimination probability as a function of step size for each of the three line-length conditions: panel (A) 19 arcmin, panel (B) 38 arcmin and panel (C) 57 arcmin, for iso- (filled circles) and ortho-trajectory (empty circles). Error bars ± *SEM*.

local motion detectors selective to the OMC. Indeed, an OMC congruent with the ortho-trajectory can be extracted equally well from short and long lines, as can been seen in Fig. 4. In the iso-condition, discrimination peaks at a specific speed (step size), and this optimal speed rises with line length. This pattern of results is consistent with a streak mechanism: as speed (step size) increases, the 'streak' produced by the iso-orientation becomes longer than the background lines and therefore more effective. However, once step size exceeds line length, iso-motion discrimination drops. It is possible that when the step size is larger than line length the response of a local motion detector with a spatial extent equal to one step is masked by the interfering local motions of background lines. This reintroduces the masking of the target streak by background lines. Experiments 1 and 2 employed a speed of 7.4 deg/s, and at zero jitter performance for iso- and ortho-motion was very similar (see Figs. 2 and 3). However, in Experiment 3 ortho-motion was more discriminable than iso-motion at similar speeds (see Fig. 4). Experiment 4 sought to examine this difference between the results of the experiments.

5. Experiment 4: The effect of stimulus duration

To investigate more thoroughly the dependency of iso-motion discrimination on target speed and so reconcile the results of the previous experiments, we compared iso- and ortho-motion discrimination over a range of speeds obtained by the factorial combination of step size and frame duration (FD).

5.1. Method

We used frame durations of 50, 30 ms and 20 ms, with 0 ms inter-stimulus interval. The target and background lines moved with a step size of 5.7, 9.5, and 13.3 arcmin corresponding to speeds of 1.9, 3.2, 4.4 deg/s at 50 ms FD, speeds of 3.2, 5.3, and 7.4 deg/s at 30 ms FD and speeds of 4.8, 7.9 and 11.1 deg/s at 20 ms FD. Line length was fixed 38 arcmin. A discrimination task was used. That is, observers had to indicate whether the target moved horizontally or vertically. As for the previous experiments, each block of 40 trials consisted of 10 repetitions of the same four stimuli used in Experiments 1a and 3. Observers performed two repetitions of each block. As before, discrimination probabilities in iso- and ortho-motion conditions were calculated from the number of correct responses out of the 20 trials. Then the iso- and ortho-data were averaged across the vertical and horizontal conditions.

5.2. Results

Results are illustrated in Fig. 5. The abscissa plots the step size of both target and background lines, and the ordinate plots discrimination probability. The left-hand graph (A) presents data for iso-motion, and the right-hand graph presents data for ortho-motion. In each graph, different lines represent different frame durations. Results show that discrimination of the iso-trajectory was improved at the highest step size and at the shortest FD (circles), whereas ortho-trajectory was generally affected very little by step size and FD.

ANOVA on results in the iso-condition showed a significant effect of FD ($F(2, 10) = 5.48$; $p = 0.025$) and a significant effect of the step size ($F(2, 10) = 20.79$; $p = 0.0001$). The interaction between FD and step size was not significant ($F(4, 20) = 0.8$; $p = 0.54$). Pairwise comparisons (Bonferroni corrected) revealed that only the difference between FD of 20 and 30 ms approached significance. Moreover, for both the smallest ($p = 0.028$) and the intermediate steps ($p = 0.004$) accuracy was lower than for the largest step. A separate ANOVA for the ortho-condition did not reveal any significant effect: FD ($F(2, 10) = 0.65$; $p = 0.54$), step size ($F(2, 10) = 1.46$; $p = 0.28$), FD × step size ($F(4, 20) = 1.4$; $p = 0.27$).

5.3. Discussion

The results of Experiment 4 clearly indicate that the detectability of iso-motion trajectory depends on step size. In particular, when the step size is not larger than the line length, discrimination performance is equivalent to that for the ortho-trajectory (across all the steps employed). In addition, when the speed is very high (i.e., with the lower FD; 20 ms) the motion streak is not masked by background lines. On the other hand, ortho-motion discrimination is relatively independent of step size/speed and FD, suggesting a lack of masking by background lines.

6. General discussion

Our results confirm and extend those of Watamaniuk, McKee, and Grzywacz (1995). A high detection rate is possible even though the spatial and temporal characteristics (step size and frame rate) of the signal are identical to the noise, making the signal indistinguishable from the noise on a frame-to-frame basis. The new result is that the spatial orientation of the local signal modulates detection of its trajectory. In particular, discrimination of signal trajectory depends on whether the spatial orientation of the signal is parallel or orthogonal to the trajectory.

Discrimination performance for iso-motion trajectories is equivalent to that for ortho-motion trajectories provided that the trajectory is straight, step size is not larger than line length, speed is high and FD is short. A possible candidate mechanism that may account for performance using iso-motion trajectories is Geisler's (1999) motion streak model (MS). According to this model, the visual system uses orientation information to facilitate motion

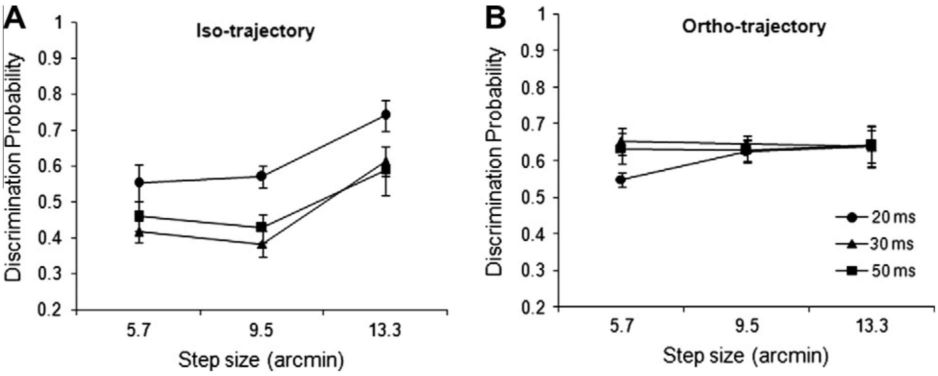

Fig. 5. Average discrimination probability ($N = 6$) in the long (50 ms), medium (30 ms) and short (20 ms) FD conditions as a function of step size, independently for iso- (A) and ortho-trajectory (B). Error bars ± *SEM*.

detection parallel to orientation. Geisler (1999) speculated that, when a localized image feature moves fast enough (more than one dot size in 100 ms), it becomes smeared in space owing to temporal integration in the visual system, creating a spatial signal – a ‘motion streak’ – oriented in the direction of motion. The streak is extracted by the static orientation system and combined with the output of perpendicularly oriented direction-selective detectors. The combined detector codes both the orientation and the direction of a motion streak. Our results show that iso-motion is more discriminable at high speed, i.e., long steps and short delays. This supports Geisler’s model that streak formation is favored at high speed. However, since in our stimuli the streak is already available in the line orientation and is masked by iso-oriented background lines, the effect of speed reported here may be due to orientation masking. Discrimination performance for ortho-motion trajectory conditions is quite constant regardless of speed, FD, line-length and whether the trajectory is straight or not. The lack of speed and FD effects suggests that the motion mechanisms underlying iso- and ortho-motion discrimination are different. Snowden and Braddick (1989) found evidence of two networks of motion-selective units, one relatively independent of delay in the range of 50–100 ms and the other responding well at shorter delays (20 ms).

We propose that ortho-motion discrimination is mediated by a combination of the response of a ET network and a local mechanism extracting the OMC component. The ET network enhances local motion in a consistent direction by combining the activity of local-motion detectors in a higher order network (Grzywacz, Watamaniuk, & McKee, 1995). Grzywacz, Watamaniuk, and McKee (1995) suggested that motion detectors may have local connections to adjacent, similarly tuned motion detectors. When a motion detector is stimulated, it sends facilitatory signals forward to other detectors positions along the motion trajectory. If the detector receiving such a facilitatory signal is also stimulated within a short time, its signal is enhanced and it sends another facilitatory signal forward, and so on. However, the ET model described above cannot account for the higher saliency of ortho-motion by itself. It could instead if we assume that ET mechanism do not rely on the motion signals at the terminators (Pack & Born, 2001; Pack, Gartland, & Born, 2004; Pack et al., 2003) when they are non-congruent with the trajectory, as when jitter is introduced (see diagram in Fig. 2); in these conditions, such a mechanism can use the OMC component to extract a trajectory direction congruent with the trajectory. The OMC is thought to affect motion perception when the terminators of the lines are not visible (Lorenceau & Shiffrar, 1992; Wallach, 1935). However, it has been shown that this component also affects the perception of unoccluded motion (Tse & Hsieh, 2007) and it contributes to the perception of the veridical speed of a moving line (Castet et al., 1993; Scott-Brown & Heeley, 2001).

A potential confound in our results is that at very low speed observers performed below chance in the iso-motion condition. This is unlikely to result from a consistent response bias at low speed, because the bias is absent in the condition involving the longest lines. Why this bias occurs could be an interesting matter of investigation in successive studies. One interesting possibility could be that, when the target signal is very weak, subjects are influenced by the overall impression of motion in the background. In fact, across all the experiments the step size of the background lines never exceeded the line length. Thus, for instance, considering a two-frame sequence, a background line that moves obliquely would leave some overlap, and similarly to a jittered ortho-target (see Fig. 2A), an OMC can be extracted along the constant piece of contour signaling ortho-motion. Thus, observers may respond to ortho-motion because the random displacement of the background lines in six of the eight directions from frame to frame is more likely to produce ortho-motion signals (signals that contain the OMC) than iso-motion signals.

In summary, we have investigated iso- and ortho-motion discrimination using a common stimulus paradigm. Results show that discrimination of iso- and ortho-motion taps distinct mechanisms with different temporal tuning properties. Discrimination of ortho-motion involves extended trajectory facilitation in a network of receptive fields with orthogonal orientation tuning, whereas iso-motion discrimination seems to rely on a motion streak process. A neural network mechanism has also been proposed to explain why the linking of disconnected elements into static contours is optimal when they are iso-oriented with the path (Bex, Simmers, & Dakin, 2001; Field, Hayes, & Hess, 1993; Ledgeway, Hess, & Geisler, 2005). Ledgeway and Hess (2002) suggested that a similar mechanism could underlie the perception of moving contours. Such an association field mechanism is thought to rely on facilitatory lateral interactions between the receptive fields of neurons tuned to similar stimuli (Fitzpatrick, 1996; Gilbert & Wiesel, 1989) as demonstrated by both physiological (Kapadia, Westheimer, & Gilbert, 2000; Kapadia et al., 1995) and psychophysical studies (Adini, Sagi, & Tsodyks, 1997).

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