

Available online at www.sciencedirect.com

SCIENCE @ DIRECT®

Vision Research 45 (2005) 2993–3003

Vision
Researchwww.elsevier.com/locate/visres

The predictive power of trajectory motion

Scott N.J. Watamaniuk

Department of Psychology, Wright State University, Dayton, OH 45435, USA

Received 3 June 2004; received in revised form 13 July 2005

Abstract

When the central region of an obliquely oriented line is bisected by a wide, vertical opaque occluder, observers misperceive the two line segments as being misaligned (the Poggendorff illusion). If the oblique line segment is replaced with a spot moving on an oblique trajectory, little if any misalignment is perceived. This accurate alignment of oblique segments depends upon the consistent motion of the dot along the oblique trajectory and not other temporal or spatial characteristics of the motion-defined segments since random plotting of the dot along each oblique segment resulted in robust misalignment. The nullification of the Poggendorff illusion was also obtained if only one of the segments was defined by a moving spot so long as the spot moved in a direction that ‘pointed’ to the static segment. Moreover, if the occluder boundary was defined by rows of vertically moving dots, was filled with vertically moving dots or was a real (cardboard) occluder, the motion-defined oblique segments were still perceived to be aligned with little error, consistent with the unimpaired detection of a trajectory dot in noise interrupted by similar occluders [Watamaniuk, S. N. J. & McKee, S. P. (1995). ‘Seeing’ motion behind occluders. *Nature*, 377, 729–730]. The results are interpreted as evidence that trajectory motion produces a cascade of activity in appropriately aligned motion detectors, in the direction of motion, that continues after the moving object has been occluded to produce a prediction of where the moving object should reappear.

© 2005 Elsevier Ltd. All rights reserved.

Keywords: Poggendorff illusion; Motion alignment; Occlusion; Perception

1. Introduction

Human observers perform remarkably well when asked to detect a single spot moving in a constant direction (trajectory) among other identical dots moving randomly from frame-to-frame (Watamaniuk, McKee, & Grzywacz, 1995). A network model, proposed by Grzywacz, Watamaniuk, and McKee (1995), posits that the trajectory gains its high detectability because the currently stimulated motion detector facilitates the next similarly tuned detector lying along the motion path when they are activated sequentially. This facilitation, cascading from one detector to the next, increases with each additional motion detector stimulated, up to some limit. In addition, this feed-forward facilitation seems to continue

for a time in the absence of stimulation because if a trajectory is obscured by opaque occluders similar to a picket fence, detectability of that trajectory is similar to that for an equivalent length but uninterrupted trajectory (Watamaniuk & McKee, 1995). This last finding suggests that the way the visual system processes trajectory motion may provide a predictive signal indicating where a temporarily occluded moving object should reappear. The present study was designed to determine if trajectory motion provides a predictive signal indicating where an object will re-emerge from behind an occluder. The stimulus was based on a traditional Poggendorff illusion configuration (Burmester, 1896): two stationary vertical lines defining an occluder and an oblique target line (see Fig. 1A). In the motion stimulus, we replaced the oblique target line with an obliquely moving target spot (see Fig. 1B). Tests were also run to determine if the way the occluder was defined (i.e., static lines, moving spots,

E-mail address: scott.watamaniuk@wright.edu.

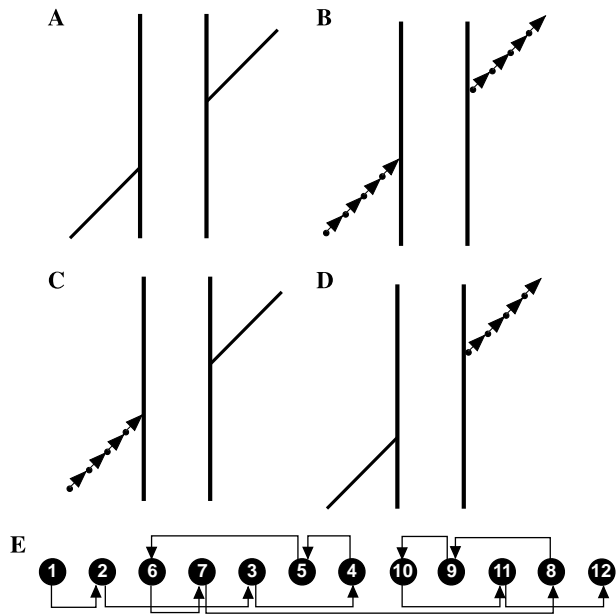


Fig. 1. Schematic representations of static, moving, and hybrid stimuli. (A) Traditional Poggendorff illusion stimulus. (B) A variant of the Poggendorff stimulus that uses a moving dot to define the oblique segments. Panels C and D show hybrid stimuli composed of a static and a motion-defined oblique segment. (C) The motion 1st configuration. (D) The motion 2nd configuration. (E) One example of an oblique segment in which the moving dot was randomly plotted along the length of the segment. The positions of the dot are identical to those if the dot had moved at a constant speed and direction along the oblique. The numbers in the dots indicate the temporal frame that the dot was plotted in that position and the arrowed lines show the motions that the dot would undergo based on the plotting sequence.

cardboard) influenced the perceived alignment of the motion-defined oblique segments (see Fig. 2).

To anticipate the results, we found that for a stimulus configuration that produced a strong static Poggendorff illusion (large perceived misalignment of the two oblique lines when they are in veridical alignment), there was no perceived misalignment for the motion stimulus. Moreover, a static segment can be perceived as correctly aligned with a segment defined by a moving spot when the spot moves in the direction that ‘points’ to the static segment. The specific way in which the occluder was represented had little influence on alignment performance.

2. Method

2.1. Observers

The author and three other experienced psychophysical observers, naïve to the purpose of the experiments, participated in the experiments. All observers had normal or corrected-to-normal visual acuity. Each observer provided informed consent prior to participating in the studies.

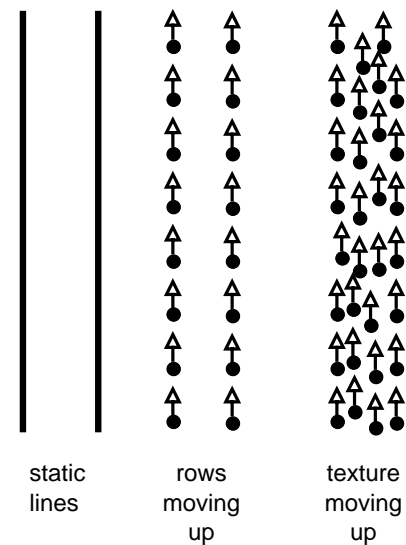


Fig. 2. Schematic representations of different occluder types. When defined or represented by moving dots (rows or texture), the direction was either up or down—both directions were tested in different trial blocks.

2.2. Stimuli

All stimuli were computer generated and presented on an X-Y CRT with P4 phosphor (50 Hz frame rate). Viewing was binocular from a distance of 57 cm, maintained through the use of a chin/headrest. Static stimuli were designed similar to typical Poggendorff illusion stimuli (i.e., Cameron & Steele, 1905); an occluder, demarcated by two vertical lines, bisected a test line oriented 45 deg counter-clockwise from horizontal. The occluder was 3.2 deg wide. The left and right segments of the oblique test were each 3 deg in length. The vertical starting point of the static or motion-defined oblique segments was jittered randomly from trial to trial up to ± 0.5 deg to make the relationship between the obliques and the ends of the vertical occluder lines an unreliable cue to alignment.

The moving stimuli were similar to the static ones except that the oblique test line was replaced with a spot moving in a direction 45 deg counter-clockwise from horizontal (see Fig. 1). The occluder was the same as in the static stimuli. The target spot moved at 10 deg/s. The duration of the static and moving stimuli was equal (960 ms) and set such that in the motion stimuli, the 1st and 2nd motion segments were both 2.8 deg in length (see Fig. 3). In addition, the 2nd (right) motion segment appeared at a time as if the spot had traveled at the same constant speed behind the occluder as it moved while visible. For both static and moving stimuli, dots subtended 4.2 min arc and had a space-averaged luminance of 40.9 cd/m², while the veiling luminance of the screen was 22.9 cd/m² (space-averaged luminance was measured using a matrix of dots, 16 × 16 dots, with a

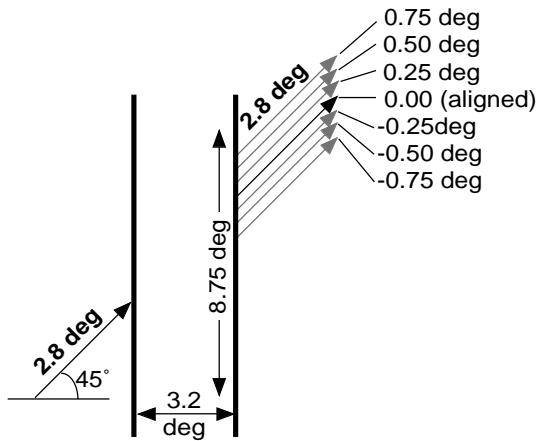


Fig. 3. Schematic representation of the motion-defined stimulus and possible positions of the rightmost segment.

center-to-center spacing of 4.8 min arc and a frame rate of 50 Hz). A control experiment used a variant of the moving stimulus in which the moving dot was plotted in random positions within each oblique segment. The positions in which the dot appeared in the oblique segment were the same as if it were moving in a constant direction but simply in a random order (see Fig. 1E). Further, the dot was constrained so that in both the left and right oblique segments: (1) the dot started and ended each segment in the positions it would have if it had moved in a constant direction, and (2) the left and right segments appeared with the same timing as if the dot had moved in a constant direction. These constraints ensured that most characteristics of this stimulus were identical to the motion stimulus in the main experiment except for a dramatic reduction in motion energy since the dot essentially moved back and forth along each oblique at a variety of speeds.

Another type of stimulus, which was a hybrid of the static and moving conditions, was also employed. This stimulus was created such that one test segment was static while the other segment was defined by a moving spot. Stimuli in which the segment on the left side of the occluder was static and the segment on the right side of the occluder was moving were used as well as the complementary configuration. In both types of stimuli, the static segment was visible the entire duration of the display. The moving spot traveled at a speed of 10 deg/s and appeared at the same time as if both segments were defined by motion; the moving spot appeared at stimulus onset if it was on the left side of the occluder (moving toward the occluder) or later in the trial if it appeared on the right side of the occluder (moving away from the occluder).

When testing the effects of occluder type on alignment of motion segments, the stimuli were similar with the following differences. The moving spot traveled at either 30 or 45 deg counter-clockwise from horizontal

at a speed of either 7.5 or 15 deg/s. The occluder was 2.5 deg wide with each visible motion segment being 3 deg in length and thus the duration of the stimuli varied from 600 to 1340 ms. The occluder was either real (a strip of cardboard affixed to the surface of the CRT) or defined by static lines, two vertically moving rows of dots, or a 2.5 deg wide strip filled with vertically moving dots.

2.3. Procedure

The experiments used the method of constant stimuli to determine the position at which the segment on the right side of the occluder appeared to be in perceptual alignment with the segment on the left side of the occluder. Seven positions of the right segment were randomly presented 20 times each during the course of a block of trials (see Fig. 3). Three different sets of offsets were used depending upon target direction and experiment (offsets for main and control experiments: 0.75, 0.50, 0.25, 0.0, -0.25, -0.50, -0.75 deg; offsets for occluder-type experiment with 30 deg obliques: 0.625, 0.313, 0.156, 0.0, -0.156, -0.313, -0.625 deg; offsets for occluder-type experiment with 45 deg obliques: 1.03, 0.625, 0.313, 0.0, -0.313, -0.625, -1.03 deg). For each trial, a random vertical offset (± 0.5 deg) was added to the position of both segments to make the position of the segments relative to the fixation spot and the ends of the vertical lines demarcating the occluder an unreliable cue to alignment. Each observer completed 2–7 blocks of trials for each experimental condition.

A typical trial started with the computer presenting a central fixation spot and indicating with a tone its readiness to present the stimulus. The observer pressed a button to start the trial—this extinguished the fixation spot and presented the stimulus. Even though the fixation spot was removed during the stimulus presentation, observers were instructed to maintain their fixation in the middle of the occluded region throughout the trial, though eye movements were not monitored. After the stimulus presentation, the observer then pressed one of two buttons to indicate whether the segment on the right side of the occluder was above or below alignment with the segment on the left side of the occluder. The number of ‘above’ responses for each of the seven right-segment positions was used to generate a psychometric function. The data were fit with a cumulative normal function using Probit analysis (Finney, 1971). The point of subjective alignment (PSA) was defined as the right-segment position necessary to generate a performance level of 50%. A PSA was determined for each block of 140 trials so that 2–7 PSAs per condition were obtained from each subject. Standard errors of the mean were computed for each subject based on the PSAs obtained for each condition.

3. Results

3.1. Testing for alignment error

3.1.1. Static configuration

Fig. 4 shows data for the two observers for the traditional static Poggendorff illusion. Data show the percent of trials for each offset value in which the observer responded that the right-hand segment was above true alignment. Each datum is the average of at least 100 trials.

Notice that under the present experimental conditions, the Poggendorff illusion was consistently strong; observers needed the right segment lowered (negative values) by about 0.3–0.6 deg from true alignment to perceive the two segments as aligned.

3.1.2. Motion-based configuration

Data shown in Fig. 5 are for the condition in which the observers judged whether two motion segments, separated by the occluder were aligned. The data are plotted in the same manner as Fig. 4 but show a decisively different pattern; in general, observers saw the motion segments as aligned when they were near true alignment. That is, for a static stimulus configuration that produced a strong classic Poggendorff illusion, little misalignment was observed when the static obliques were replaced with motion-defined segments.

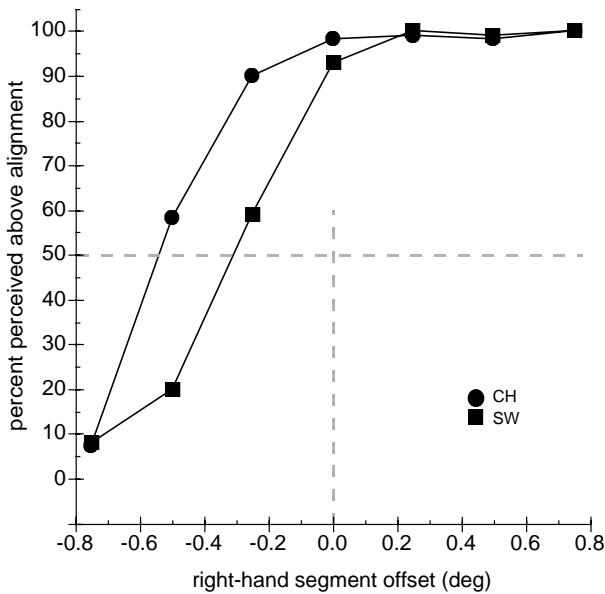


Fig. 4. Percent of trials perceived above alignment as a function of the positional offset of the right-hand segment of a traditional static Poggendorff stimulus for two observers. Each datum is the result of 100 (SW) or 120 (CH) trials. The intersection point of the dashed gray lines indicates where the psychometric functions should have crossed the 50% point if alignment of the two segments had been veridical.

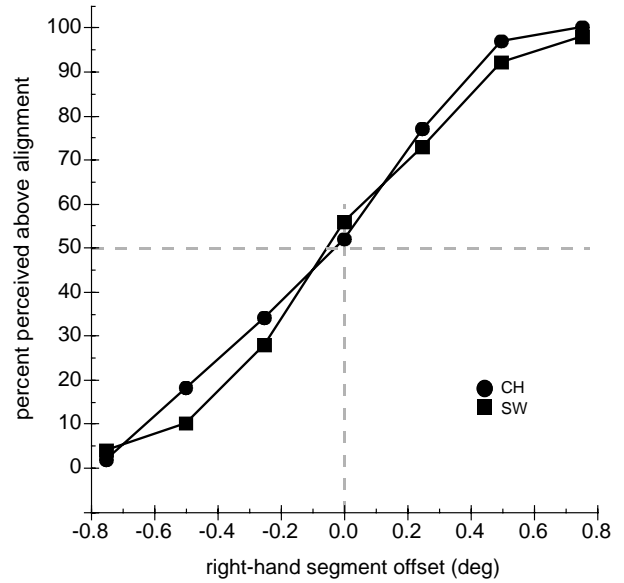


Fig. 5. Percent of trials perceived above alignment as a function of the positional offset of the right-hand segment of an obliquely moving spot bisected by an occluder for two observers. Each datum is the result of 100 trials. Both functions cross very near the intersection point of the dashed gray lines indicating that there was little error in the alignment of the two segments.

Based on these data, it seems reasonable to suspect that the *motion* used to define the oblique segments was responsible for the elimination of the illusory misalignment. However, the moving stimulus differed from the static stimulus in aspects other than just the presence of motion. Specifically, the moving spot would have less orientation energy than a static oblique line. A similar manipulation, defining the static oblique line by a pair of static dots, has been shown to reduce the magnitude of the Poggendorff illusion (Krantz & Weintraub, 1973). In addition, the moving spot defining the oblique segments is only briefly in contact with the vertical lines, while the static obliques are in constant contact with the vertical lines. This difference may also be important as previous work has shown that leaving a space between the oblique and vertical lines can reduce the magnitude of the Poggendorff illusion (Jones-Buxton & Walls, 2001). Finally, the moving segments were visible for only a brief amount of time, and thus stimulated neurons that are sensitive to transient rather than sustained stimulation. Perhaps these transient cells provide a more precise spatial signal. This idea gains some support from Mori (1981) who showed that for a traditional Poggendorff stimulus, simply moving the oblique segments perpendicular to the contours of the occluder during a trial reduced alignment error. Thus, a reasonable alternative interpretation would be that these other illusion-reducing characteristics of the motion-defined obliques acted in concert to null the misalignment rather than the motion per se. To test this idea, a control experiment

was run in which the moving spot was plotted in random positions within each oblique segment, keeping the timing of the appearance of each segment identical to that in the previous experiment. Plotting the moving spot in this way drastically reduced the amount of motion energy in each segment since the spot was moving back and forth along the oblique path but retained the other characteristics of the moving stimulus mentioned previously, namely lowered orientation energy, only brief contact with the vertical lines, and transient presentation. If misalignment was observed with this stimulus, then one could conclude that these other characteristics do not account for the absence of misalignment observed in the previous experiment. Data for this control condition were collected in alternate blocks with additional data for the constant-direction motion stimulus (as in the previous experiment) for two observers. The alignment error for the random-motion control was large, -0.42 ± 0.03 deg (SW) and -0.37 ± 0.06 deg (CH), while error for the constant-motion condition was significantly smaller [$t(20) = 9.026$, $p < 0.0001$], 0.07 ± 0.05 deg (SW) and -0.08 ± 0.02 deg (CH). As in the previous experiment, using constant-direction motion for the oblique segments virtually eliminated the alignment error while making the motion random within a segment resulted in alignment error similar to that for the static configuration.

The results of the previous experiments are consistent with previous findings that occluders did not significantly impair the detection of a trajectory target embedded within motion noise (Watamaniuk & McKee, 1995). Moreover, given the trajectory network model of Grzywacz et al. (1995), one might explain such data as indicating that the motion signal produced by a consistent-direction motion trajectory propagates for a time, in the direction of the inducing motion, even in the absence of visual input. Alternatively, the obliquely moving dots may have produced a signal that travels both in the direction of the movement and in the opposite direction. This would suggest that the reduction of the misalignment was not due to a direction-selective motion signal per se but something more akin to an orientation signal propagated by the moving target (e.g., Geisler, 1999; Jancke, 2000). The fact that randomly plotting the dot along the oblique segments resulted in consistent misalignment in the previous control experiment does not negate this alternative because the random plotting also reduced the motion energy. The orientation signal being suggested here depends upon having a strong motion signal.

3.1.3. Motion and static hybrid

Although the data in Fig. 5 are suggestive of a predictive component of motion, a hybrid stimulus com-

binning both static and moving segments was developed to test this hypothesis. The hybrid stimulus had two configurations: one had a dot moving up and to the right to create a segment on the left side of the occluder and a static segment on the right ('motion 1st' condition). The other hybrid stimulus reversed the position of the two oblique segments so that there was a static segment on the left and motion-defined segment on the right ('motion 2nd' condition). In both types of stimuli, the vertical lines defining the occluder boundaries as well as the static segment were visible for the entire duration of the display. In contrast, the moving dots defining the other segment appeared at a time consistent with the dot moving from the lower left to the upper right at a constant rate of 10 deg/s. Thus, in the motion 1st condition, the moving dot appeared at stimulus onset and disappeared at the left occluder border (after about 280 ms). In the motion 2nd condition, the moving dot appeared at the right occluder boundary approximately 700 ms after stimulus onset and moved away from the occluder until stimulus termination. Figs. 1C and D show these two configurations schematically. Notice that since both stimuli contain a static and a motion-defined oblique segment, the number of transient and sustained cells stimulated by both stimuli should be equivalent as well as the motion orientation information. Given that the static segments were constantly visible in both of these stimuli, the critical difference was whether the motion-defined oblique segment was created with a dot moving towards or away from the static segment. Why would this difference matter? If the motion segment produces a signal that propagates in the direction of motion, then these two stimuli should produce different results. When the motion is toward the occluder and the static oblique segment, the propagating motion signal should travel across the occluder and indicate the expected position of the motion continuing on the other side. If this predicted motion-reappearance location can be used to align the static segment, then observers may be able to make precise alignment judgments. Alternatively, when the motion is away from the occluder and the static oblique segment, the propagating motion signal should continue in the same direction and provide no information about the expected position of the motion on the other side of the occluder because it is traveling in the opposite direction. Observers would thus have no motion-based cue on which to judge alignment of the static segment with the motion-defined segment. Using this logic, the motion 1st condition should produce less alignment error than the motion 2nd condition.

Data for both observers for the hybrid stimuli appear in Fig. 6. The data clearly separate into two groups determined by the stimulus condition. Specifically, when the motion-defined segment appeared first, moving

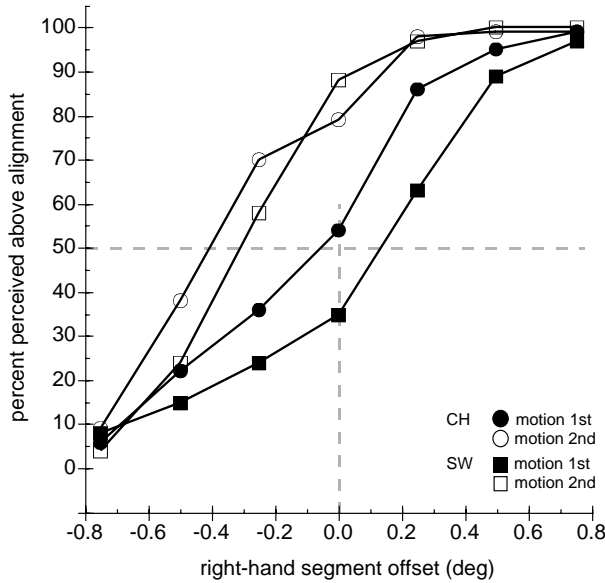


Fig. 6. Percent of trials perceived above alignment as a function of the positional offset of the right-hand segment of a hybrid Poggendorff stimulus composed of oblique segments, one static and the other defined by motion. Each datum is the result of 100 trials. Notice that for both observers, the condition in which the first segment was defined by motion produced little alignment error (filled symbols). When the motion-defined segment was presented second (open symbols), misalignment reminiscent of the static Poggendorff illusion occurred.

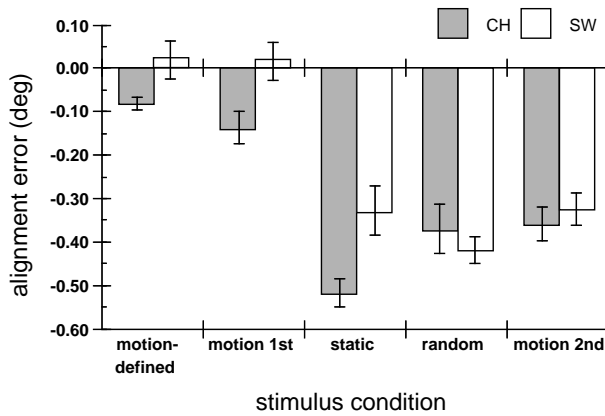


Fig. 7. Average alignment error for each condition for two observers. Each datum represents the average of 5–11 estimates, each the result of 140 trials, with error bars representing ± 1 SE of the mean.

toward the static segment (filled symbols), alignment of the two segments was accurate. However, when the motion-defined segment appeared second, moving away from the static segment (open symbols), misalignment typical of the static Poggendorff illusion was observed.

To summarize these findings, Fig. 7 shows the alignment error for all conditions for the two observers. Entering all of the PSA estimates for each condition into a one-way ANOVA showed that there was a significant difference among the five conditions [$F(4,58) = 40.411$, $p < 0.0001$]. A Fisher's posthoc pairwise comparison fur-

ther showed that there was no difference between the motion-defined and motion 1st conditions or between the static, random, and motion 2nd conditions ($p > 0.05$). However, the motion-defined and motion 1st condition were each significantly lower than the static, random, and motion 2nd conditions ($p < 0.0001$ for every comparison).

3.2. Testing occluder types

The previous results clearly indicate that observers perceive accurately the oblique path of a moving dot when it is temporarily occluded and do not show the misalignment indicative of the Poggendorff illusion. If the neural mechanism responsible for this accurate alignment is the same as that used for detection of an intermittently occluded trajectory in visual noise, then one might expect similar effects when the occluders are represented in different ways. Specifically, Watamaniuk and McKee (1995) showed that detectability of an intermittently occluded trajectory in noise was consistently high whether the occluders were simply a blank region of the screen, opaque cardboard, or filled with dots moving vertically (the trajectory dot always moved at an oblique angle). Thus, if alignment and detection rely upon a common neural substrate then one would expect alignment performance also to be unaffected by such occluder variations. Therefore, we tested alignment performance with occluders specified by static lines (as in the previous experiments), a real opaque occluder affixed to the CRT, two rows of vertically moving dots, and a strip filled with vertically moving dots (see Fig. 2). Fig. 8 shows data for four observers for the various occluder types and two dot speeds. Each panel shows data for a single observer and oblique direction. The horizontal lines surrounded by shaded bars indicate the alignment error plus and minus one standard error for a traditional static Poggendorff configuration with similar dimensions shown for 800 ms. The data show that for all occluder types, alignment of the moving dot is far superior to that for the static Poggendorff configuration. Moreover, how the occluder was represented had no consistent effect on alignment performance. A t test, using all alignment estimates for each observer and condition, was performed on the data for each oblique direction separately. The analyses showed that for both the 30 and 45 deg oblique angles, the conditions using obliques defined by a moving dot had significantly smaller alignment error than the static oblique condition [30 deg: $t(96) = 7.112$, $p < 0.0001$; 45 deg: $t(115) = 8.317$, $p < 0.0001$]. To ensure that the motion within the occluder was not responsible for the reduction in the perceived misalignment with motion-defined obliques, a control experiment measured perceived alignment for a stimulus with the occluder (width = 2.5 deg)

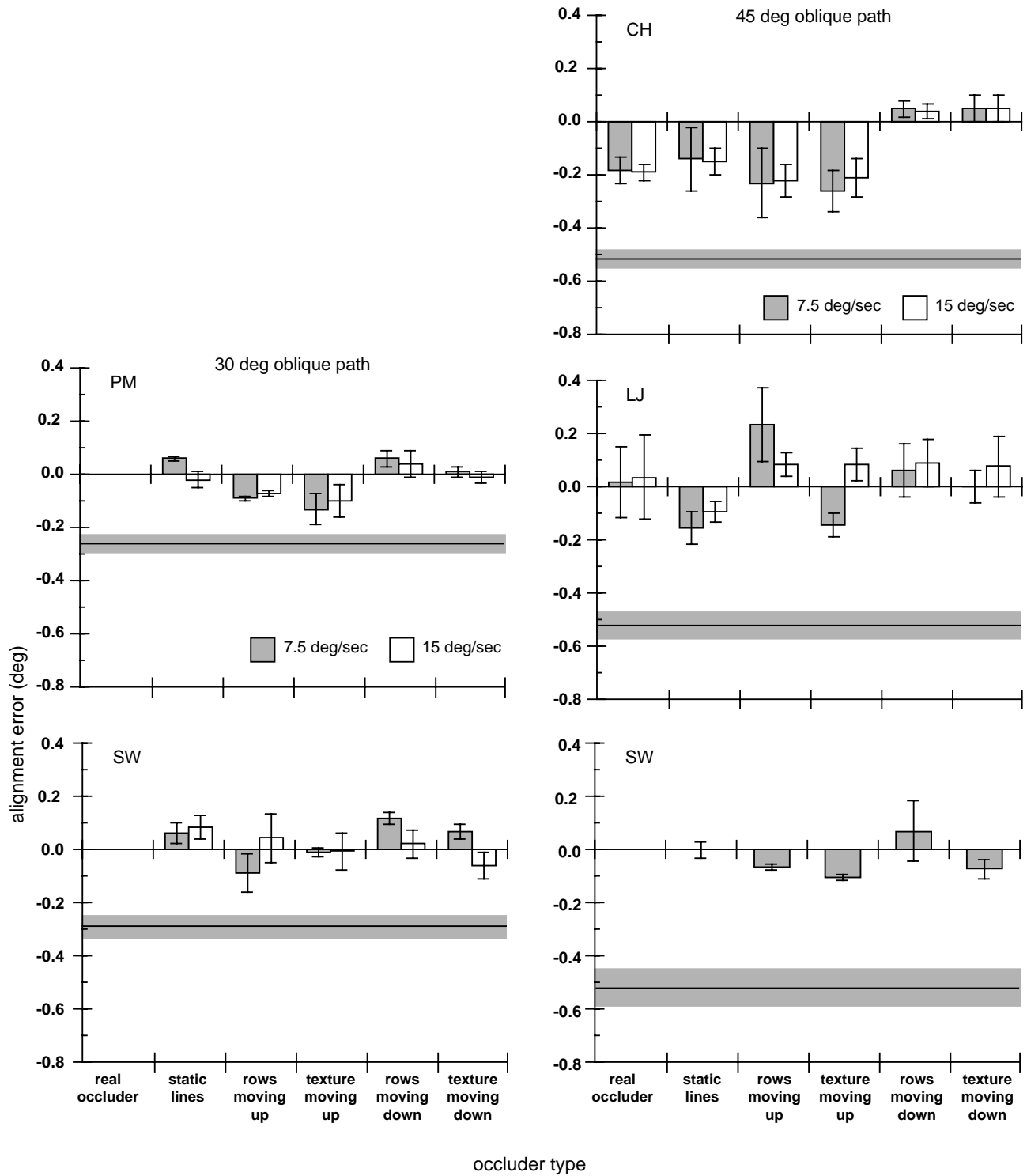


Fig. 8. Alignment error plotted as a function of occluder type. The left panels show data for an oblique direction of 30 deg and the right panels for an oblique direction of 45 deg. Shaded bars represent data for a dot speed of 7.5 deg/s and the open bars for a dot speed of 15 deg/s. Each panel shows data for one observer. In each plot, the horizontal line surrounded by a gray bar represents the alignment error (± 1 SE) measured for a static Poggendorff stimulus with comparable characteristics as the moving stimuli. Observers PM and SW did not collect data for the real occluder condition.

defined by a vertically moving texture but with static oblique lines. For two observers, this stimulus still resulted in a consistent perceived misalignment regard-

less of whether the dots filling the occluder moved upwards or downwards (SW: -0.323 ± 0.075 deg; CH: -0.163 ± 0.017 deg).

4. Discussion

The present experiments were designed to determine whether the motion of an object could help to indicate where that object would reappear after momentary occlusion. The data show that with a traditional Pogendorff stimulus configuration, whenever a motion-defined oblique segment was present in which the motion was toward the position of the other oblique segment, alignment error was negligible. However, a motion-defined oblique segment in which the motion was away from the position of a static oblique segment did not reduce the alignment error from the static condition (see Fig. 7). These results suggest that a signal propagates in the direction of the inducing motion after the motion ends or is occluded. This signal, likely generated as a consequence of motion processing, quite rigidly maintains the originating motion's trajectory and can lead to accurate alignment judgments. The propagation of this predictive signal occurs only in the inducing direction, as motion away from the occluder did not support accurate alignment judgments. Defining the occluder with various motion stimuli moving in directions considerably different from the direction of the obliques (vertically moving rows or strip of texture) also did not consistently affect alignment performance.

These results are consistent with the previous findings of Watamaniuk and McKee (1995) showing that detection of a trajectory signal embedded in random motion noise was not hampered when it was intermittently occluded by vertical opaque strips or strips filled with vertically moving dots. The trajectory network model proposed by Grzywacz et al. (1995) seems a likely candidate to explain the observed results. In their model, all motion detectors with spatially close (or overlapping) receptive fields are reciprocally inhibitory. When a motion detector is activated by a stimulus, it inhibits those detectors that are tuned to directions that are different from itself, but facilitates detectors tuned to directions similar to that of the active detector and whose receptive fields lie in the direction of the motion. This feed-forward network has been shown to account well for the detectability of a trajectory in noise, including its directional tuning (Watamaniuk et al., 1995). To account for the present data, one must also posit that the trajectory signal propagates across the occluded region without simultaneous input and that it continues for at least 450 ms and extends at least 4.5 deg, the maximum time and space separating the two oblique motion segments in the present study. Moreover, one must account for the high precision of the alignment. Previous studies measuring the detectability of a trajectory in motion noise have shown that performance was unaffected even though the trajectory dot changed direction by up to 180 deg over 160 ms, forming a circular path (Watamaniuk et al., 1995; see also Vergheze, Watamaniuk,

McKee, & Grzywacz, 1999). The present data show that alignment of the two oblique motion segments was close to veridical with an average misalignment of -0.04° (computed by averaging all thresholds across observers from Fig. 8). In fact, the largest displacement used in the experiments, 0.75° , would correspond to only a 6° change in direction of the trajectory over the occluder and observers judged this as a misalignment of the motion segments almost perfectly (see Fig. 5). How then can the trajectory network model account for these seeming inconsistent results—detectability tolerant of large direction changes but reliable discriminability of small direction changes? First, it is well known that detectability usually does not predict discriminability and thus the high precision of alignment does not necessarily conflict with the high detectability of trajectories that change direction. Even so, Watamaniuk et al. (1995) showed a monotonic falloff in trajectory detectability with increases in the directional bandwidth of the trajectory's path (these were not circular paths but wiggling paths in which a direction increment was alternately added to and subtracted from the trajectory's mean direction each frame). Their result suggests that the facilitation passed to subsequent detectors is graded as a function of the similarity of their direction-tuning to the currently active detector. When input to the trajectory network is removed, it therefore seems reasonable to expect that the strength of the signal propagated in the actual trajectory direction would be stronger than signals propagated in other similar directions. Extending this logic to the present task, if observers relied upon the position of the motion detector with the largest facilitatory signal to predict the place of motion reappearance then this would be consistent with the originating trajectory direction. The present data add to the evidence of Watamaniuk and McKee (1995) and suggest that the facilitatory signal propagated among motion detectors by the posited trajectory network continues for a period of time even when the motion stimulus is removed. Moreover, the signal is spatially localized: facilitation occurs in detectors with receptive fields lying along the direction of motion extending from the currently active motion detector. Thus, it seems that it is the directional and spatial specificity of the propagation that gives this 'motion' signal its predictive quality. The present data also imply that the spatial information of the propagated motion signal is available to the system coding spatial position of static objects because alignment error was virtually eliminated even when only one of the stimulus' oblique segments was defined by motion—so long as it moved in a direction that pointed towards the static oblique segment.

The hypothesized propagated-motion signal likely is not the same as the motion streak spatial code proposed by Geisler (1999) because he showed that static lines oriented parallel to the direction of motion impaired detec-

tion, increasing luminance detection thresholds. In the present study, if the motion segments simply produced a spatial code identical to that of static lines, then one would expect the misalignment of the motion segments to be equivalent to the static case—which it clearly was not. In addition, here it is proposed that the signal continues to propagate in the motion direction even after the motion stimulus is extinguished, an issue not addressed by Geisler. In agreement with Geisler's motion streak hypothesis, Jancke (2000) found that a moving spot will produce a wave of activity in populations of position and orientation selective cells in area 17 of cat. The population activity was such that after about 190 ms of trajectory motion, activity showed a clear peak along the motion orientation. However, activity representing position coding peaked at about 60 ms earlier and then smeared along the position axis. As with Geisler's (1999) motion streak observations, it is unclear how the orientation signals due to dot motion reported by Jancke would propagate across the occluder to allow precise alignment of the oblique motion segments since it is not known whether the smearing of activity over position extends beyond the actual region traversed by the moving spot.

As an alternative explanation, one might suggest that the classic Poggendorff illusion occurs because of an interaction among orientation cells responding to the oblique lines and occluder lines. Under this type of model, the lack of illusory misalignment may be due to the oblique motion segments failing to strongly stimulate these orientation cells thus producing little orientation energy. This type of model can be dismissed for several reasons. First, the length of the oblique motion segments was 2.8 deg, long enough to cross the receptive field of most V1 cells, which on average have a summation area of about 1 deg diameter (i.e., Sceniak, Hawken, & Shapley, 2001), within these cells' integration time of about 100 ms (i.e., Hawken, Shapley, & Grosf, 1996). Second, research has shown that the misalignment of the Poggendorff illusion remains even when the oblique line segments are replaced with dots which would have no more orientation energy than the moving spot in the present study (Krantz & Weintraub, 1973; Weintraub & Krantz, 1971; Wenderoth, 1980; Wenderoth, O'Connor, & Johnson, 1986). Finally, the stimulus in the control experiment, a dot randomly plotted along the oblique segments, should have equivalent orientation energy as a dot moving in a consistent direction along the oblique segments but yet resulted in robust misalignment. Thus, one cannot explain the reduction of the misalignment when motion-defined oblique segments are used as a result of a lack of oblique orientation energy.

The present data show that under the conditions tested, when the occluder was defined by static lines or vertical motion, perceived alignment of motion-defined oblique segments was accurate. However, it is likely that

occluders containing motion similar to the trajectory motions would influence performance since the motion signal being propagated across the occluder could be 'led astray' in the direction of the occluder motion. Thus, one might find that if the occluder contained motion at an angle slightly clockwise from the trajectory, an aligned segment on the other side of the occluder may be perceived as too high. Alternatively, if the occluder contained motion at an angle slightly counter-clockwise from the trajectory, an aligned segment on the other side of the occluder may be perceived as too low. Even if the occluders contained brownian motion, directions similar to the trajectory falling in the vicinity of the trajectory could reduce the trajectory's propagated signal because the weak signals due to the brownian motion would be integrated with the trajectory signal thus reducing the predictive power of the propagated signal (see Watamaniuk & McKee, 1995). These predictions have yet to be tested.

Several previous studies, other than those already cited, have also suggested that the visual system may extrapolate motion signals. Nijhawan (1994) suggested that the flash-lag effect (the perceived spatial misalignment between aligned moving and flashed objects originally reported by MacKay, 1958) occurs because the visual system extrapolates the position of moving objects to compensate for the approximate 100 ms delay in transmission of motion information from the retina to visual areas of the brain (DeValois & DeValois, 1991). Whitney and Murakami (1998) tested Nijhawan's hypothesis by measuring the perceived position of a flashed line relative to a moving bar that would suddenly reverse its direction at a random time. They found that for trials in which the moving bar disappeared before it reversed direction, the perceived position of the moving stimulus never 'overshot' the reversal point. Whitney and Murakami suggested that there was no spatial extrapolation of the motion signal but rather that people perceive objects in the position they were at before any neural delays but the delays can be shorter for moving stimuli. They further suggest that the shorter transmission delay for moving stimuli might be due to an anticipatory response where active motion detectors facilitate the response of other motion detectors along the expected path of motion, consistent with the view of Grzywacz and Amthor (1993). Such anticipatory activity reducing transmission latency for moving stimuli has been observed in population responses of cells in cat primary visual cortex (Jancke, Erlhagen, Schöner, & Dinse, 2004), and even in population responses of retinal ganglion cells in salamander and rabbit (Berry, Brivanlou, Jordan, & Meister, 1999). Further, this anticipatory activity and resultant latency reduction have been incorporated into a model of speed processing by (Seriès, Georges, Lorenceau, & Frégnac (2002)) to account for psychophysical results showing that the perceived speed of motion can be

influenced by the orientation of the moving object (Georges, Serié, Frégnac, & Lorenceau, 2002). In their model, the perception of speed is mediated by the spatio-temporal correlation of V1 inputs to MT cells. Thus, a reduction in the latency of V1 cell responses due to anticipatory feed-forward connections would lead to an increase in the perceived speed. The present study adds to this literature and suggests that, at least under the conditions tested, this anticipatory facilitation may do more than just reduce cell latency but actually provide a persisting signal that can be used to accurately predict the position of motion after brief occlusion. This suggestion is consistent with the results of Verghese and McKee (2002) who showed that a contrast increment of a moving spot, presented in dense motion noise, was more easily detected at the end of a 200 ms trajectory rather than at the beginning. They proposed that the initial motion of the trajectory spot acted as a cue to identify the most likely direction and future location of the moving spot on which the contrast increment was to be applied. The present study extends these previous findings by demonstrating that this predictive signal can extend an even greater distance in both space and time when stimulus noise is absent.

Although this study employed a stimulus designed around the traditional Poggendorff stimulus, the goal was not to try to explain the Poggendorff illusion. However, there are a couple of points in regards to the Poggendorff illusion that deserve mention. First, the present data are completely opposite that reported by Fineman and Melingonis (1977). They found that moving a spot of light behind obliquely oriented slots on either side of an occluder increased the error in alignment of the obliques (though not significantly) from the static condition. Their explanation, to be consistent with explanations of the Poggendorff illusion based on the interactions of the component line segments, was that lines in the stimulus may be defined in several ways, even by the motion of a single spot. The reason for the different result likely stems from the procedure used to create the stimuli in the two studies. In their study, Fineman and Melingonis (1977) created the stimulus by cutting out strips from light cardboard, covering the openings with translucent white paper, and illuminating the stimulus from behind with an incandescent light. The oblique segments were constructed in the same way but the right oblique was on a vertical slide and could be moved up and down by an attached nylon string. To create their moving spot condition, a disk with a narrow slit was put in front of the incandescent source and rotated so that a bar of light repeatedly traversed the oblique slits producing a light moving along the oblique segments. It is likely that the outlines of the oblique segment slits were visible even in the moving spot condition because of scattered light. The visibility of the oriented lines may have

been responsible for the alignment error. In contrast, since the present stimuli were created on a CRT, no ‘lines’ were visible when the oblique segments were defined by motion. Interestingly, Mori (1981) showed that moving the oblique segments perpendicular to the occluder verticals reduced the alignment error by about 60%. The conclusion was that this motion may have segregated the oblique from the vertical lines, and that this separation (like a figure/ground segregation) may have reduced the illusion. While the same type of descriptive explanation could be offered to account for the present data, the reduction in error found here was larger than what Mori observed and was on average near 90%. In addition, the motion-signal propagation hypothesis provides a potential mechanistic explanation and is consistent with past results on trajectory detection (e.g., Grzywacz et al., 1995; Watamaniuk & McKee, 1995; Watamaniuk et al., 1995).

More recently, Fermüller and Malm (2004) proposed that uncertainty in the visual processes involved in the perception of images is responsible for many geometrical illusions such as the Poggendorff illusion. Specifically, it was suggested that the estimate of the intersection point of the oblique and vertical line segments is biased due to the processes of smoothing and edge detection, a suggestion similar to that proposed by others (e.g., Ginsburg, 1986; Morgan, 1999). Moreover, Fermüller and Malm suggest eye movements are a relevant source of noise as well. This type of explanation does not seem to account for the present data because under viewing conditions that produced a robust static Poggendorff illusion, replacing the oblique line segments with a moving spot significantly reduced or eliminated the perceived misalignment. Although the sources of noise identified by Fermüller and Malm should be ubiquitous to the visual system, the motion processing system clearly is not subject to the same biases or overcomes them in some way.

Finally, Olson, Gatenby, Leung, Skudlarski, and Gore (2003) recorded brain activation (functional magnetic resonance imaging) while observers viewed a moving ball on a CRT that either became occluded as it traveled ‘behind’ a black rectangle in the middle of its traverse or stopped, and suddenly disappeared at one edge and then suddenly reappeared at the other edge of the occluder. They found that activation in MT/MST and the intraparietal sulcus was larger under the ‘occluder’ condition versus the ‘disappear’ condition, though not significantly so. They suggest that the regions in the brain that process occluded motion are similar to regions that process real motion. In contrast, the putative trajectory network model (Grzywacz et al., 1995) suggests that the *same* mechanisms that process visual motion generate predictive motion signals when the moving object becomes occluded.

5. Conclusions

The present data show that for a static stimulus configuration that produced a robust Poggendorff illusion, replacing the oblique segments with segments defined by a moving spot essentially eliminated the perceived misalignment. Perceiving the veridical alignment of motion segments separated by an occluder suggests that the mechanism that processes trajectory motion creates a cascade of activity in similarly tuned motion detectors that are aligned with the inducing motion (Grzywacz et al., 1995). This cascade of activity among aligned, similarly tuned motion detectors can propagate for a period of time without visual stimulation (during occlusion of the motion signal) and provide an estimate or prediction of where the occluded moving object should reappear. Future studies will systematically test relevant stimulus parameters and include simulations of the trajectory network model using stimuli like those in the present study.

Acknowledgment

This research was supported by National Science Foundation Grant IBN-9983563.

References

- Berry, M. J., II., Brivanlou, I. H., Jordan, T. A., & Meister, M. (1999). Anticipation of moving stimuli by the retina. *Nature*, *398*, 334–338.
- Burmester, E. (1896). Beiträge zur experimentellen Bestimmung geometrisch-optischer Täuschungen. *Zeitschrift für Psychologie*, *12*, 355–394.
- Cameron, E. H., & Steele, W. M. (1905). The Poggendorff illusion. *Psychological Monographs*, *7*, 83–111.
- DeValois, R. L., & DeValois, K. K. (1991). Vernier acuity with stationary moving Gabors. *Vision Research*, *31*, 1619–1626.
- Fineman, M. B., & Melingonis, M. P. (1977). The effect of a moving dot traversal on the Poggendorff illusion. *Perception & Psychophysics*, *21*, 153–156.
- Finney, D. J. (1971). *Probit analysis*. Cambridge: Cambridge University Press.
- Fermüller, C., & Malm, H. (2004). Uncertainty in visual processes predicts geometrical optical illusions. *Vision Research*, *44*, 727–749.
- Geisler, W. S. (1999). Motion streaks provide a spatial code for motion direction. *Nature*, *400*, 65–69.
- Georges, S., Seriès, P., Frégnac, Y., & Lorenceau, J. (2002). Orientation dependent modulation of apparent speed: Psychophysical evidence. *Vision Research*, *42*, 2757–2772.
- Ginsburg, A. P. (1986). Spatial filtering and visual form perception. In K. Boff (Ed.), *Handbook of perception and human performance* (Vol. 2). New York: John Wiley & Sons, Chapter 34.
- Grzywacz, N. M., & Amthor, F. R. (1993). Facilitation in on-off directionally selective ganglion cells in the rabbit retina. *Journal of Neurophysiology*, *69*, 2188–2199.
- Grzywacz, N. M., Watamaniuk, S. N. J., & McKee, S. P. (1995). Temporal coherence theory for the detection and measurement of visual motion. *Vision Research*, *35*, 3183–3203.
- Hawken, M. J., Shapley, R. M., & Grosz, D. H. (1996). Temporal-frequency selectivity in monkey visual cortex. *Visual Neuroscience*, *13*, 477–492.
- Jancke, D. (2000). Orientation formed by a spot's trajectory: A two-dimensional population approach in primary visual cortex. *The Journal of Neuroscience*, *20*, 1–6, RC86.
- Jancke, D., Erlhagen, W., Schöner, G., & Dinse, H. R. (2004). Shorter latencies for motion trajectories than for flashes in population responses of cat primary visual cortex. *Journal of Physiology*, *556*, 971–982.
- Jones-Buxton, R. A., & Walls, H. M. (2001). The Poggendorff illusion: Effect of distance between the parallel lines. *Perceptual and Motor Skills*, *92*, 706–710.
- Krantz, D. H., & Weintraub, D. J. (1973). Factors affecting perceived orientation of the Poggendorff traversal. *Perception & Psychophysics*, *14*, 511–517.
- MacKay, D. M. (1958). Perceptual stability of a stroboscopically lit visual field containing self-luminous objects. *Nature*, *181*, 507–508.
- Morgan, M. J. (1999). The Poggendorff illusion: A bias in the estimation of the orientation of virtual lines by second-stage filters. *Vision Research*, *39*, 2361–2380.
- Mori, T. (1981). Reduction of the Poggendorff effect by motion of oblique lines. *Perception & Psychophysics*, *29*, 15–20.
- Nijhawan, R. (1994). Motion extrapolation in catching. *Nature*, *370*, 256–257.
- Olson, I. R., Gatenby, J. C., Leung, H., Skudlarski, P., & Gore, J. C. (2003). Neuronal representation of occluded objects in the human brain. *Neuropsychologia*, *42*, 95–104.
- Sceniak, M. P., Hawken, M. J., & Shapley, R. (2001). Visual spatial characterization of macaque V1 neurons. *Journal of Neurophysiology*, *85*, 1873–1887.
- Seriès, P., Georges, S., Lorenceau, J., & Frégnac, Y. (2002). Orientation dependent modulation of apparent speed: A model based on the dynamics of feed-forward and horizontal connectivity in V1 cortex. *Vision Research*, *42*, 2781–2797.
- Verghese, P., & McKee, S. P. (2002). Predicting future motion. *Journal of Vision*, *2*, 413–423.
- Verghese, P., Watamaniuk, S. N. J., McKee, S. P., & Grzywacz, N. M. (1999). Local motion detectors cannot account for the detectability of an extended trajectory in noise. *Vision Research*, *39*, 19–30.
- Watamaniuk, S. N. J., & McKee, S. P. (1995). 'Seeing' motion behind occluders. *Nature*, *377*, 729–730.
- Watamaniuk, S. N. J., McKee, S. P., & Grzywacz, N. M. (1995). Detecting a trajectory embedded in random-direction motion noise. *Vision Research*, *35*, 65–77.
- Weintraub, D. J., & Krantz, D. H. (1971). The Poggendorff illusion: Amputations, rotations, and other perturbations. *Perception & Psychophysics*, *10*, 257–264.
- Wenderoth, P. (1980). Alignment errors in Poggendorff-like displays when the variable segment is a dot, a dot series, or a line. *Perception & Psychophysics*, *27*, 505–518.
- Wenderoth, P., O'Connor, T., & Johnson, M. (1986). Evidence for a significant contribution of interactions between oriented line segments in the Tolansky version of the Poggendorff illusion. *Perception & Psychophysics*, *39*, 334–338.
- Whitney, D., & Murakami, I. (1998). Latency difference, not spatial extrapolation. *Nature Neuroscience*, *1*, 656–657.