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Direction-specific changes of sensitivity after brief apparent motion stimuli☆

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Abstract

Direction-specific losses in sensitivity were found for a test grating which was superimposed on a stationary contrast pedestal and which moved either in the same or opposite direction as a prior biasing stimulus. Three types of biasing stimuli were employed: a grating swept through 270° in 45° steps, a single 90° step of a grating, and a single 90° step of a grating which contained a blank IFI and whose perceived direction was reversed. For the biasing sweep and the single 90° step, the response of directionally selective mechanisms (directional motion energy) is greatest for the direction which corresponds to the actual physical displacement of the stimulus. For the biasing step with an IFI, the response is maximum for the opposite direction. For all three types of biasing stimuli, directional sensitivity for a test stimulus was reduced most when it moved in the biasing direction, i.e. the direction which produced the strongest signal in directionally selective mechanisms. Unlike the effects of the same types of biasing stimuli on the perceived direction of a suprathreshold 180° step of a grating [Pinkus, A., & Pantle, A. (1997). Probing motion signals with a priming paradigm. *Vision Research*, *37*, 541–52; Pantle, A., Gallogly, D.P., & Piehler, O.C. (2000). Direction biasing by brief apparent motion stimuli. *Vision Research*, *40*, 1979–91], all the direction-specific losses of sensitivity can be explained by changes in the response characteristics of directionally selective mechanisms. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The existence of directionally selective motion mechanisms in the visual system has been demonstrated by physiological and psychophysical studies (e.g. Barlow & Hill, 1963; Sekuler & Ganz, 1963). It has been proposed that the perceived direction of a stimulus is at least in part determined by the relative responses among such mechanisms (e.g. Sekuler & Pantle, 1967; Moulden, 1980). For the purpose of making more specific predictions in psychophysical experiments, directionally selective mechanisms have been modeled as elaborated Reichardt detectors (van Santen & Sperling, 1984), motion energy analyzers (Adelson & Bergen, 1985; Watson & Ahumada, 1985) or spatial/temporal gradient detectors (e.g. Marr, 1982). Past studies (e.g. Pinkus & Pantle, 1997; Pantle, Gallogly, & Piehler, 2000) made use of a biasing paradigm to investigate relative responses of putative directionally selective mechanisms to a motion stimulus. They attempted to determine whether exposure to a brief motion step, a biasing stimulus, could produce an imbalance among directionally selective mechanisms and lead to the resolution of the direction ambiguity of a later occurring motion step, a test stimulus.

A single 180° phase shift of a sine-wave grating by itself is a physically ambiguous motion step (e.g. McCarthy, 1993; Pinkus & Pantle, 1997). Consequently, its perceived direction would not be resolved unless somehow the mechanisms responding to it and signaling its direction of motion was unbalanced. The perceived direction would correspond to the one favored by the imbalance. Pinkus and Pantle (1997) used a biasing paradigm (which they referred to as visual motion

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priming, VMP) in which an ambiguous 180° shift of a sine-wave grating followed an unambiguous 90° shift. They found that the 180° step of the test grating could be disambiguated by the prior unambiguous step. Specifically, their results showed that the 90° biasing step caused the 180° test step to appear to move in the same direction as the biasing step. Pinkus and Pantle assumed that the resolution of the ambiguous 180° stimulus was a consequence of the ability of the 90° single-step biasing stimulus to upset the balance in favor of the biasing direction. That is, they interpreted these results as an indication of the increased relative sensitivity of mechanisms tuned to the direction of the biasing motion.

In later experiments, Pantle et al. (2000) used multiple-step motion sequences (motion sweeps) as biasing stimuli. One might expect that motion sweeps would be more effective motion stimuli than single-step stimuli (e.g. McKee & Welch, 1985; Snowden & Braddick, 1989), and that they would create stronger biasing in a biasing paradigm (Anstis & Ramachandran, 1987). Consequently, the sweeps might be expected to be more effective at creating a directional imbalance which favors the same direction of motion as the biasing stimulus. However, this was found not to be the case. When a directionally unambiguous motion sweep (about 100 ms) was used as the biasing stimulus, a 180° test step appeared to move in a direction opposite that of a biasing sweep (Pantle et al., 2000). These results are suggestive of a system imbalance in which there was a decreased relative sensitivity for the direction of the biasing motion.

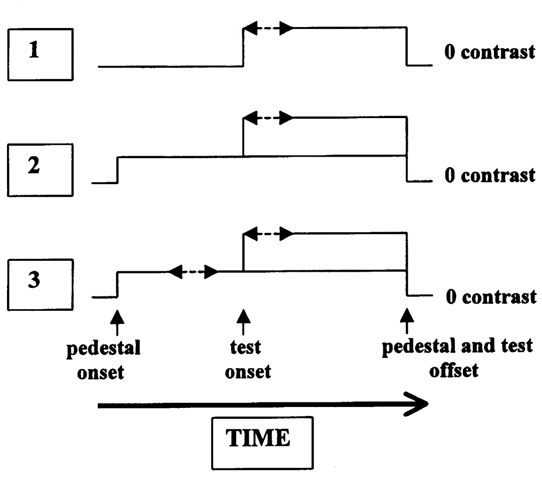

Fig. 1. Time-line diagrams (not to scale) of the stimulus events for trials in the three conditions of experiment 1. (1) No pedestal condition; (2) stationary pedestal condition; (3) directional pedestal condition. Arrows enclosing the dashed lines define intervals in which the pedestal or test stimulus moved.

In summary, past studies indicate that a one-step biasing stimulus increases the sensitivity of directionally selective mechanisms tuned to the same direction of motion as the biasing stimulus, whereas multiple-step stimuli appear to decrease the sensitivity of mechanisms tuned to the same direction of motion. In the following series of experiments, a new paradigm was developed from a combination of the biasing procedures with brief apparent motion stimuli and the pedestal procedure of Lu and Sperling (1995, 1996). The new paradigm permitted us not only to investigate more closely the apparent differences between the biasing effects of one-step and multiple-step stimuli, but also to isolate the role of first-order mechanisms (Lu & Sperling, 1995, 1996) in the motion biasing phenomenon.

2. Experiment 1

The present experiment was designed to measure contrast thresholds for discriminating the direction of test stimuli moving in the same and opposite directions as a biasing sweep. Consistent with the suprathreshold results obtained with a biasing sweep and an ambiguous 180° test step, we expected higher discrimination thresholds for trials in which the test stimulus moved in the same direction as the biasing sweep. Higher thresholds for the same direction would correspond to a greater likelihood of seeing the ambiguous 180° test step move in an opposite direction.

In the current direction discrimination experiment, the biasing stimulus was swept in a rightward or leftward direction, and then it remained stationary while a directional test stimulus was superimposed on it. The stationary biasing stimulus after the sweep acted as a static pedestal.[1] For control purposes, we used trials (1) in which there was no biasing stimulus (pedestal) either prior to or during the presentation of the directional test stimulus and (2) in which the biasing stimulus was present, but never moved. The latter condition resembles one in Lu and Sperling's (1995, 1996) pedestal paradigm in which they superimposed a directional test stimulus on a static pedestal. With Lu and Sperling's paradigm one would not expect to find a threshold difference in sensitivity for different test directions because their pedestal would not have generated a directional motion signal, and indeed they did not find a threshold difference dependent upon test direction. We used pedestals which contained motion sweeps prior to the addition of the test stimulus because we wanted to look specifically for differential changes of sensitivity for different directions of test motion.

[1] The biasing stimulus remained on as a pedestal so that there was no temporal contrast transient produced by its onset/offset.

2.1. Methods

2.1.1. Experimental design

The time-line diagrams in Fig. 1 illustrate the three different conditions used in the experiment.

1. No-pedestal condition: this condition provided baseline motion discrimination thresholds for the directional test stimuli used in this series of experiments. A vertical sine-wave test grating appeared in the center of a spatially uniform surround. It was presented 1716 ms after the offset of a tone signaling the beginning of a trial. It moved in a rightward or leftward direction for 143 ms, stopped, and terminated 1358 ms later at the end of a trial. Test grating contrast was varied in order to obtain thresholds for discriminating direction of motion.
2. Stationary pedestal condition: this condition provided a control for any changes in discrimination thresholds due to the mere presence of a stationary pedestal grating. The onset of the stationary pedestal grating was coincident with the offset of the tone, and directional test stimuli were superimposed on the pedestal 1716 ms later. The test stimulus moved for 143 ms, stopped, and terminated with the stationary pedestal 1358 ms later. Direction discrimination thresholds for the superimposed test stimuli were measured by varying test contrast. Changes of contrast thresholds for discriminating motion direction obtained with this condition, compared with the no-pedestal condition, would be the result of a non-direction-specific change in sensitivity because the stationary pedestal could not differentially activate directionally selective motion mechanisms.
3. Directional pedestal condition: this condition was designed to reveal potential differences in motion discrimination thresholds produced by a difference of sensitivity in directionally selective mechanisms after exposure to a brief biasing sweep. This condition was similar to the stationary pedestal condition in that a directional test stimulus was superimposed on a stationary pedestal 1716 ms after the offset of a tone signaling the beginning of a trial and the pedestal onset. The only difference was that in this condition the pedestal was swept either rightward or leftward. The sweep began 1387 ms after the pedestal onset, continued for 100 ms, and then remained stationary for the 229 ms (ISI) before test onset. Again, direction discrimination thresholds for the superimposed test stimuli were measured by varying test contrast.

2.1.2. Stimulus generation

The apparent motion stimuli were made up of image sequences constructed from uniform blank fields and sine-wave gratings in a uniform surround. The gratings were patterns whose luminance was modulated sinusoidally along the horizontal axis, and they were displayed on a Nec MultiSync monitor (model no. XP17) with a 70-Hz refresh rate. Prior to each experimental session, images were generated with the use of C-language Genus graphics libraries and stored in the virtual memory of a Pentium Gateway 2000 P5-75 computer. During an experimental trial, each successive image of a sequence was transferred to graphics memory from virtual memory and displayed at the refresh rate of the monitor. Individual images could be as short as one screen refresh (14.3 ms), or held as long as needed with multiple refreshes. Intensities of each point in each image were obtained with a mixing circuit which provided a linear sum of the red, green, and blue signals from the graphics board of the computer. The appropriate weights for the different signals were achieved by differential attenuation of the three signals. All three of the attenuated signals were fed to the green electron gun of the monitor. The full red signal plus one half the green signal set the mean luminance level. Adding a greater or lower number of green steps ($2^6 = 64$ possible steps) provided coarse linear changes of luminance after gamma correction via a look-up table. Finer modulation of the luminance level around the mean was obtained by varying the blue signal; it required 2^5 (32) steps of the blue signal to equal one step of the green signal. Therefore, we had 2^{11} (2048) linear steps of intensity resolution. Grating contrast (C) was expressed as the difference between the peak and trough luminances divided by their sum; i.e. $(L_{\mathrm{MAX}} - L_{\mathrm{MIN}})/(L_{\mathrm{MAX}} + L_{\mathrm{MIN}})$. The mean luminance of all blank frames, of all pedestal and test gratings or their combination, and of the surrounds of the gratings was constant throughout the experiment at 20.7 cd/m^2. All luminance values were calibrated with a Pritchard Photometer (model no. 1980A) equipped with PD Spectar lens.

2.1.3. Stimulus sequences

The directional test stimulus can be described by its spatial-temporal contrast:

$$L_{\mathrm{m}} * (1.0 + C_{\mathrm{t}} * \sin((360° * \alpha * x + \beta_{\mathrm{t}}) + \theta_{\mathrm{t}})) \tag{1}$$

where L_{m}, C_{t}, α, x, β_{t} and θ_{t} are the mean luminance, contrast, spatial frequency, horizontal position, temporally changing phase, and initial phase of the test grating, respectively. Movement of the test stimulus is represented by 90° phase shifts of β_{t} from 0° through 360° for each sequence (five successive phases of β_{t}). Phase shifts were positive ($+90°$) for leftward motion and negative ($-90°$) for rightward motion. Each frame was presented for 28.6 ms (two screen refreshes). The θ_{t} for each trial was randomly selected. In the no-pedestal condition, there were a total of four C_{t} levels used for each of the two test directions of motion (rightward vs. leftward): 0.19, 0.29, 0.38 and 0.58%. In the stationary pedestal condition, five C_t levels were used for each of the two test directions of motion: 1.54, 2.31, 3.08, 3.85 and 4.62%. Finally, in the directional pedestal condition, the four C_t levels used for each of the two tests directions of motion were 2.31, 3.85, 5.38 and 6.92%. The C_t levels were chosen on the basis of pilot data so as to bracket the threshold level for each condition.

The biasing stimulus (pedestal) can be described by its spatial-temporal contrast in the same manner as the test contrast, except that the subscript p denotes pedestal values instead of test stimulus values:

$$L_m * (1.0 + C_p * \sin((360° * \alpha * x + \beta_p) + \theta_p)) \quad (2)$$

For the directional pedestal trials, movement of the pedestal is represented by 45° phase shifts of β_p from 0° through 270° for each sweep in a sequence (seven successive phases of β_p). After the sweep was over, the pedestal grating remained in the 270° phase for the rest of the sequence. Again, phase shifts were positive (+45°) for leftward motion and negative (−45°) for rightward motion. Each frame was presented for 14.3 msec (1 screen refresh). For stationary pedestal trials, β_p was 0° (producing no movement of the pedestal) for the entire trial. The θ_p for each trial was randomly selected. C_p is the contrast of the pedestal stimulus. In the no-pedestal condition, C_p was always equal to zero. For both the stationary pedestal and the directional pedestal conditions, C_p was equal to 15.4%.

In order to superimpose a test stimulus on a static pedestal, the two spatial-temporal contrasts described above were added:

$$L_m * (1.0 + C_p * \sin((360° * \alpha * x + \beta_p) + \theta_p) + C_t * \sin((360° * \alpha * x + \beta_t) + \theta_t)) \quad (3)$$

with β_p constant when the test stimulus was superimposed on it, and with β_t varying for each successive image, the test stimulus appeared to slide across the pedestal. The starting relative phase relationship between the pedestal and test gratings was varied randomly across trials as a consequence of the random independent selection of θ_p and θ_t for each trial. The pedestal and test gratings were 4.4° wide by 3.6° high with a surround whose outside dimensions were 9.5° wide by 7.2° high. The spatial frequency of the gratings was 1.37 c/deg.

2.1.4. Procedure

For each trial in the experiment, an observer saw the test stimulus in one of the three biasing conditions. An observer was instructed to look towards the center of the display and to attend globally to it. At the end of each trial an observer reported the direction (right or left) of motion of the test stimulus. No feedback was provided at any time during the experiment.

The trials for each experimental condition (no-pedestal, stationary pedestal, and directional pedestal) were run in blocks, where each block contained trials with both directions and all contrast levels. Each block was presented 30 times over the course of the experiment. Five blocks for a single experimental condition were presented during one session. Test direction and contrast levels were randomized within each block, and an observer completed an entire block before starting a new one. The order of experimental conditions across sessions was pseudo-random and different for each observer.

Observers supported their heads with a chin rest and viewed the display binocularly with natural pupils from a viewing distance of 183 cm. The experimental room was dark except for a small amount of ambient light produced by the apparatus.

2.1.5. Observers

A Miami University undergraduate student (M.D.D.), naïve about the purpose of the experiment, and the two authors (A.J.P. and O.C.P.) were the observers. All observers had normal or corrected-to-normal vision.

2.2. Results and discussion

Results for experiment 1 are shown in the different panels of Fig. 2. Each panel shows four psychometric functions for percent correct (ordinate) as a function of test grating contrast (abscissa). Trials in which there was no pedestal stimulus are represented by open circles (no-pedestal condition); trials in which there was a pedestal stimulus which had not undergone any motion prior to the presentation of the test are represented by open squares (stationary pedestal condition); and trials in which there was a pedestal stimulus that was swept prior to the presentation of the test comprise the remaining two psychometric functions (directional pedestal condition). Open diamonds are used to represent those trials in which the test stimulus moved in the same direction as the pedestal (same-direction pedestal trials), and the 'X' symbol represents those trials in which the test moved in a direction opposite the pedestal (opposite-direction pedestal trials). Panels A–C show data for individual observers, and panel D shows the group data for the three observers.

The curves for no-pedestal and stationary pedestal trials were obtained by collapsing across both right (R) and left (L) directions of test motion. Each point on either curve is a percentage based upon 60 trials (30 R + 30 L trials). The curve for opposite-direction pedestal trials was obtained by collapsing across trials in which the biasing stimulus moved to the right and the test stimulus moved to the left (R–L trials) and trials in which the biasing stimulus moved to the left

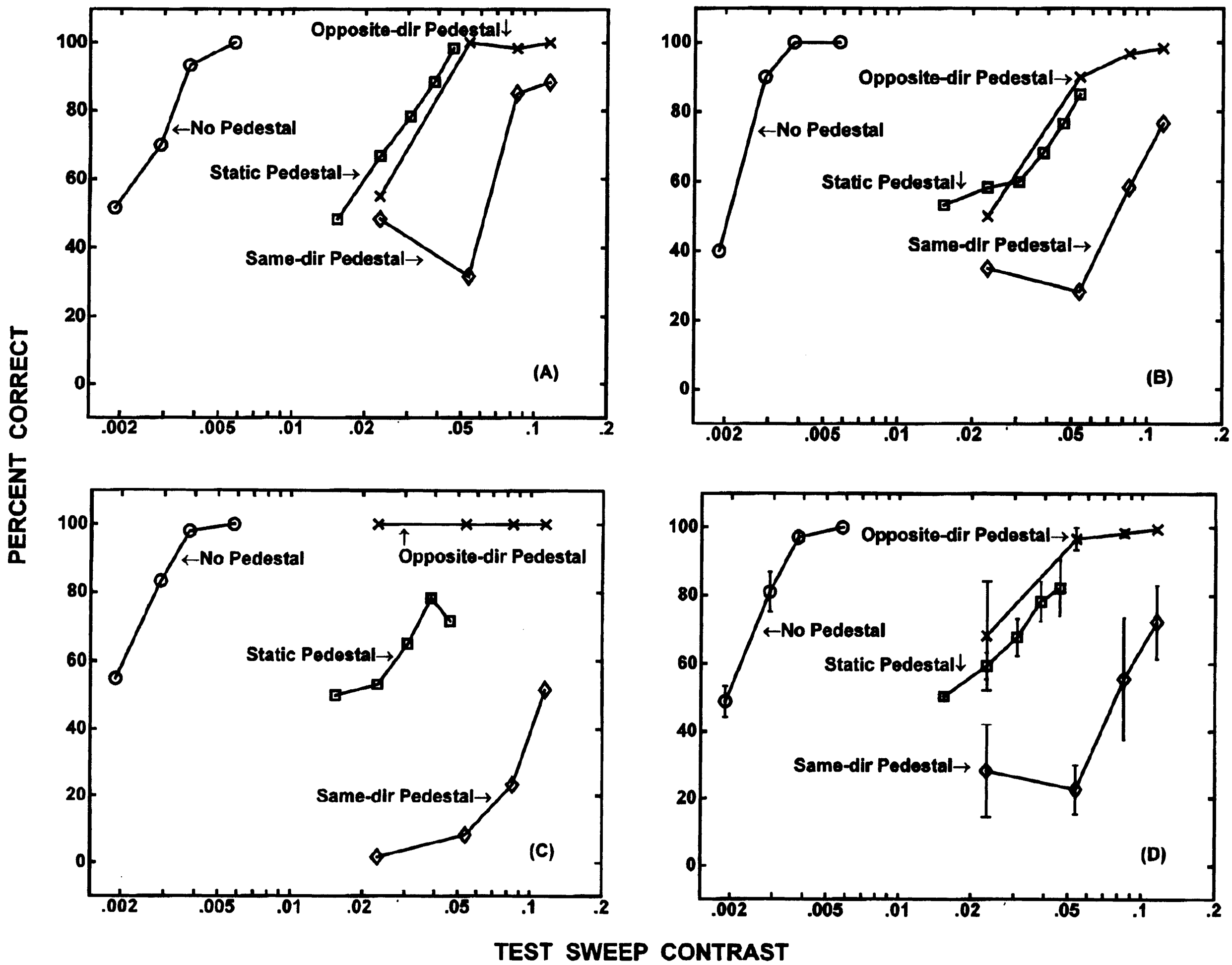

Fig. 2. Psychometric functions for percent correct responses (ordinate) as a function of test grating contrast (abscissa) for four different stimulus conditions. No pedestal condition (open circles); stationary pedestal condition (open squares); same-direction pedestal condition (open diamonds); opposite-direction pedestal condition ('X' symbols). Panels A–C show the data for individual observers, AJP, OCP and MDD, respectively; panel D shows group (mean) data with $\pm$ one standard error bars. Data for no-, stationary, and sweep biasing pedestals: experiment 1.

and the test moved to the right (L–R trials). Each point on the curve is a percentage based upon 60 trials (30 R–L + 30 L–R trials). The curve for same-direction pedestal trials was obtained by collapsing across trials in which the biasing and test stimuli moved to the right (R–R trials) and trials in which the biasing and test stimuli moved to the left (L–L trials). Each point on the curve is a percentage based upon 60 trials (30 R–R + 30 L–L trials). Each point in panel D is the mean of the corresponding three percentages of the individual observers, and the vertical bars represent $\pm$ one standard error of the mean.

A downward or rightward shift of one function relative to another in Fig. 2 is evidence of poorer performance and reduced sensitivity. A downward shift would represent reduced sensitivity by showing poorer performance at a given test contrast. A rightward shift would represent reduced sensitivity by showing that a higher test contrast was required to meet some arbitrary level of performance (percent correct).

For each observer, the psychometric function for the stationary pedestal condition is shifted rightward to higher contrasts away from the psychometric function for the no-pedestal condition. That is, to obtain an arbitrary level of performance, more contrast was required in the stationary pedestal condition than in the no-pedestal condition. This shift reflects a non-direction-specific loss of contrast sensitivity. The result is not surprising. Consistent with the results of Lu and Sperling (1995, 1996), one would expect discrimination thresholds obtained for the stationary pedestal condition to be higher than for those for the no-pedestal condition because, in the former condition, the pedestal would reduce overall sensitivity to the test stimulus. However, for both conditions there was no reason to expect a difference in discrimination thresholds for the two test directions (rightward vs. leftward) because in neither condition was there any directional signal of the pedestal capable of differentially influencing sensitivity to test stimulus direction.

The psychometric functions for trials in which the pedestal was swept prior to the presentation of the test stimulus are also shifted to higher contrast levels, away from the function for the no-pedestal trials, again showing a reduction in contrast sensitivity as a result of the presence of the pedestal prior to the presentation of the test grating. For observer M.D.D. the opposite-direction curve lies above the stationary curve, and for observers A.J.P. and O.C.P. the curves overlap. Performance for trials in which the test stimulus moved in a direction opposite that of the pedestal was no worse on average than performance for stationary pedestal trials (panel D). It can be concluded that a pedestal which is swept in a direction opposite the test stimulus produces no further reduction of contrast sensitivity beyond that produced by a stationary pedestal. However, the psychometric function for trials in which the test grating moved in the same direction as the pedestal is shifted to higher contrast levels away from those for the opposite direction and stationary pedestal trials. There was a further reduction in contrast sensitivity by a pedestal swept in the same direction as the test stimulus. The difference in threshold levels for opposite-direction and same-direction pedestal trials demonstrates a direction-specific reduction in contrast sensitivity. That is, it took more contrast to discriminate the direction of a test stimulus when it moved in the same direction as the pedestal than when it moved in the opposite direction.

It should be apparent from the pattern of results in Fig. 2 that the performance difference in the two sweep biasing conditions is not simply a consequence of the adoption of different criteria for reporting motion in different directions. For observers A.J.P. and O.C.P. the percentage of responses for the two test directions is approximately equal (near 50%) at the lowest test contrast used (weak signals) for each sweep biasing condition. Also, for the same two observers the curve for the opposite-direction pedestal trials coincides with the curve for the stationary pedestal trials, i.e. when no directional bias can be introduced by the biasing stimulus.

In order to provide further evidence that the sweep biasing stimuli not only resulted in direction-specific changes in sensitivity for observers A.J.P. and O.C.P., but also for observer M.D.D., a supplementary signal detection analysis was conducted (Macmillan & Creelman, 1991). For each of the stationary and sweep biasing conditions, the number of rightward and leftward test stimuli was the same during any given block of trials at a given test contrast. Each leftward test stimulus was treated as a 'noise' trial; each rightward test stimulus, as a 'signal' trial within a signal detection framework. Therefore, a rightward response to a rightward test stimulus would constitute a 'hit'; a rightward response to a leftward test stimulus, a 'false alarm.' In the stationary biasing condition, the highest test contrasts used were 3.85, 5.38 and 4.62% for observers A.J.P., O.C.P. and M.D.D., respectively. The corresponding d'-values were 2.47, 2.12 and 1.22 for the three observers. Averaged across the two sweep biasing conditions, interpolated test contrasts (derived from d' vs. test contrast functions) which yielded the same d'-values were 8.47, 9.06 and 8.76% for A.J.P., O.C.P. and M.D.D., respectively. That is, in order to obtain equivalent d'-values, the mean test contrast for the sweep biasing conditions had to be 1.93 (S.E.M. = 0.15) times higher than the mean test contrast for the stationary biasing condition. In the context of signal detection theory our results imply that the distributions of sensory signals evoked by rightward and leftward test stimuli overlap more in the sweep biasing conditions than in the stationary biasing condition. In other words, a significant component of the reduction of the correct direction discriminations for all observers after sweep biasing stimuli was a change of sensitivity of directional mechanisms, not simply a change of response (decision) bias. A similar analysis applies to experiments 2 and 3, although for the sake of brevity the further analyses are not presented. Also, it should be emphasized that our analysis specifically deals with sensitivity to direction of motion (left vs. right), not detection sensitivity (presence or absence) of the test stimulus. The former analysis is more important to the issues in this paper because the latter sensitivity may be mediated by cues other than direction of motion (e.g. a simple change in appearance of the pedestal during a test presentation or presence of flicker during a test interval).

The results of experiment 1 are consistent with those of Pantle et al. (2000). In their studies, an ambiguous stimulus was seen to move in a direction opposite that of a brief biasing sweep. That is, an imbalance in directionally selective mechanisms, as inferred by the perceptual resolution of the ambiguous test grating, favored motion in the opposite direction. The results of experiment 1 show that motion discrimination thresholds for directional test stimuli moving in the same direction as a brief biasing sweep are higher than those for trials in which the test stimulus moved in the opposite direction, indicating a reduction in sensitivity to the same direction of motion.

3. Experiment 2

Experiment 2 was designed to measure contrast discrimination thresholds for test stimuli moving in the same and opposite directions as a single biasing step. Results using a biasing step and an ambiguous 180° test step have shown that one-step biasing stimuli cause a 180° test step to appear to move in the same direction, indicating an increased relative sensitivity of mechanisms tuned to the same direction of motion as the biasing step. In the present experiment, one would expect to find higher contrast discrimination thresholds for trials in which a test stimulus moves in a direction opposite a biasing step. Higher thresholds for the opposite direction would reflect a greater likelihood of seeing the 180° test step move in the same direction.

3.1. Methods

The methods for experiment 2 were the same as those for experiment 1 with the following exceptions. Experiment 2 contained only trials with a directional pedestal. The directional pedestal condition was similar to that used in experiment 1 in that a directional test stimulus was superimposed on a static pedestal that had undergone previous motion. The difference was that in the current experiment the directional pedestal motion is represented by a single 90° phase shift, β_p. As in experiment 1, phase shifts were positive (+90°) for leftward motion and negative (−90°) for rightward motion. The directional test stimulus was superimposed on the pedestal 1630 ms after the offset of the tone signaling the beginning of the trial and pedestal onset.

3.2. Results and discussion

Results for experiment 2 are shown in Fig. 3. Each panel shows two psychometric functions for percent correct as a function of test grating contrast. One of the psychometric functions is for trials in which the test stimulus moved in a direction opposite the pedestal (shown as the 'X' symbol); and the other function, for trials in which the test stimulus moved in the same

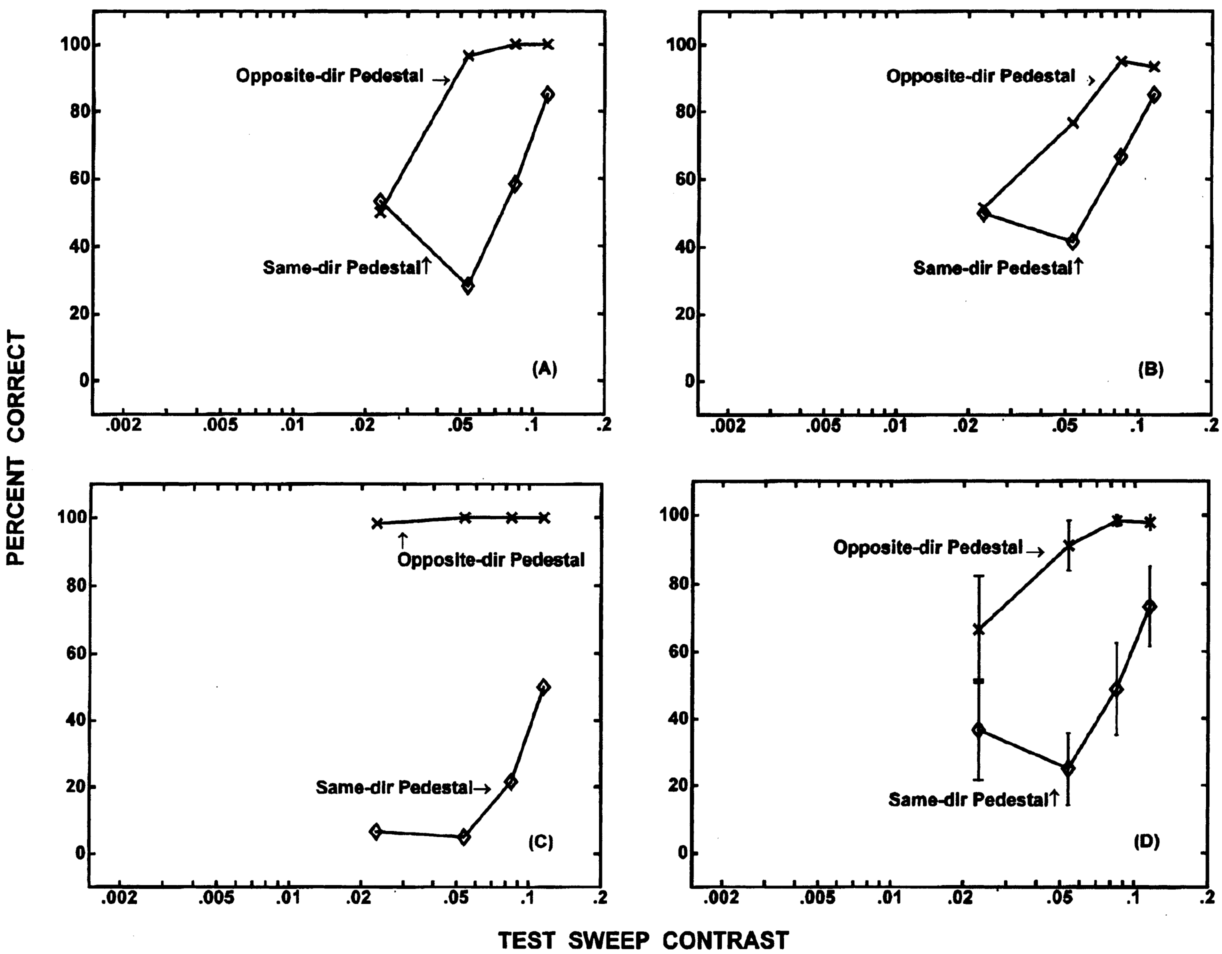

Fig. 3. Psychometric functions for percent correct responses (ordinate) as a function of test grating contrast (abscissa) for two different stimulus conditions. Same-direction pedestal trials (open diamonds); opposite-direction pedestal trials ('X' symbols). Panels A–C show the data for individual observers, AJP, OCP and MDD, respectively; panel D shows group (mean) data with ± one standard error bars. Data for single-step biasing pedestals: experiment 2.

direction as the pedestal (shown as open diamonds). Panels A–C show the data for individual observers, and panel D shows group data for the three observers.

As in experiment 1, the curve for opposite-direction pedestal trials was obtained by collapsing across trials in which the biasing stimulus moved to the right and the test stimulus moved to the left (R–L trials) and trials in which the biasing stimulus moved to the left and the test moved to the right (L–R trials). Each point on the curve is a percentage based upon 60 trials (30 R–L + 30 L–R trials). The curve for same-direction pedestal trials was obtained by collapsing across trials in which the biasing and test stimuli moved to the right (R–R trials) and trials in which the biasing and test stimuli moved to the left (L–L trials). Each point on the curve is a percentage based upon 60 trials (30 R–R + 30 L–L trials). Each point in panel D is the mean of the corresponding three percentages of the individual observers, and the vertical bars represent ± one standard error of the mean.

For each observer, performance was poorer for trials in which the test and pedestal stimuli moved in the same direction (same-dir pedestal curve) than it was for the opposite-dir pedestal trials. Analogous to experiment 1 with sweep pedestals, there was a reduced sensitivity for the test grating when it moved in the same direction as a single-step pedestal.

The results of experiment 2 are not consistent with the conclusions of Pinkus and Pantle (1997). In their study, an ambiguous test grating was seen to move in the same direction as a prior unambiguous single motion step. They inferred that an imbalance in directionally selective mechanisms favored motion in the same direction as the biasing step, as shown by the greater likelihood of seeing the ambiguous test stimulus move in the biasing direction.

4. Experiment 3

The present experiment was designed to measure motion thresholds for test stimuli moving in the same and opposite directions as a single biasing step that contained a blank frame (IFI-biasing step). In suprathreshold experiments Pantle and Turano (1992), as well as Strout, Pantle, and Mills (1994), showed that the insertion of a blank frame between the 90° phase-shifted positions of a single motion step reversed the perceived direction of the step. That is, a rightward 90° step was perceived as a large 270° leftward jump, and a leftward step was perceived as a large rightward jump. In the present experiment, we wanted to determine whether discrimination thresholds for directional test stimuli following an IFI-biasing step would be reversed compared with those found in experiment 2. In other words, would the reversal of the perceived direction of the IFI-biasing stimulus also cause the direction discrimination thresholds for test stimuli after the IFI-biasing step to reverse?

4.1. Methods

The methods for experiment 3 were the same as those for experiment 2 with the following exceptions. The biasing stimuli used in experiment 3 were similar to those used in experiment 2 in that the directional pedestal movement was a single 90° phase shift, β_p. The difference was that in the current experiment the biasing stimuli contained one added blank frame (14.3 ms, 20.7 cd/m^2) between the 90° phase-shifted positions that made up the biasing step.

4.2. Results and discussion

The results for experiment 3 are shown in Fig. 4. The format of each panel of Fig. 4 is the same as that of Fig. 3.

As in experiments 1 and 2, the curve for opposite-direction pedestal trials was obtained by collapsing across trials in which the biasing stimulus physically shifted to the right and the test stimulus moved to the left (R–L trials), and trials in which the biasing stimulus moved to the left and the test stimulus moved to the right (L–R trials). Each point on the curve is a percentage based upon 60 trials (30 R–L + 30 L–R trials). The curve for same-direction pedestal trials was obtained by collapsing across trials in which the biasing and test stimuli moved to the right (R–R trials) and trials in which the biasing and test stimuli moved to the left (L–L trials). Each point on the curve is a percentage based upon 60 trials (30 R–R + 30 L–L trials). Each point in panel D is the mean of the corresponding three percentages for the individual observers, and the vertical bars represent ± one standard error of the mean.

For each observer, performance was poorer for trials in which the test and pedestal stimuli moved in the opposite direction (opposite-dir pedestal curve) than it was for the same-dir pedestal trials. There was a reduced sensitivity for the test grating when it moved in a direction opposite a single-step pedestal which contained a blank frame.

For each observer, the psychometric functions for same- and opposite-dir pedestal trials in experiment 3 were reversed relative to those obtained for experiments 1 and 2. Not only did the blank frame in the biasing step reverse the perceived direction of the biasing stimulus, it also reversed the direction discrimination thresholds for a later test stimulus.

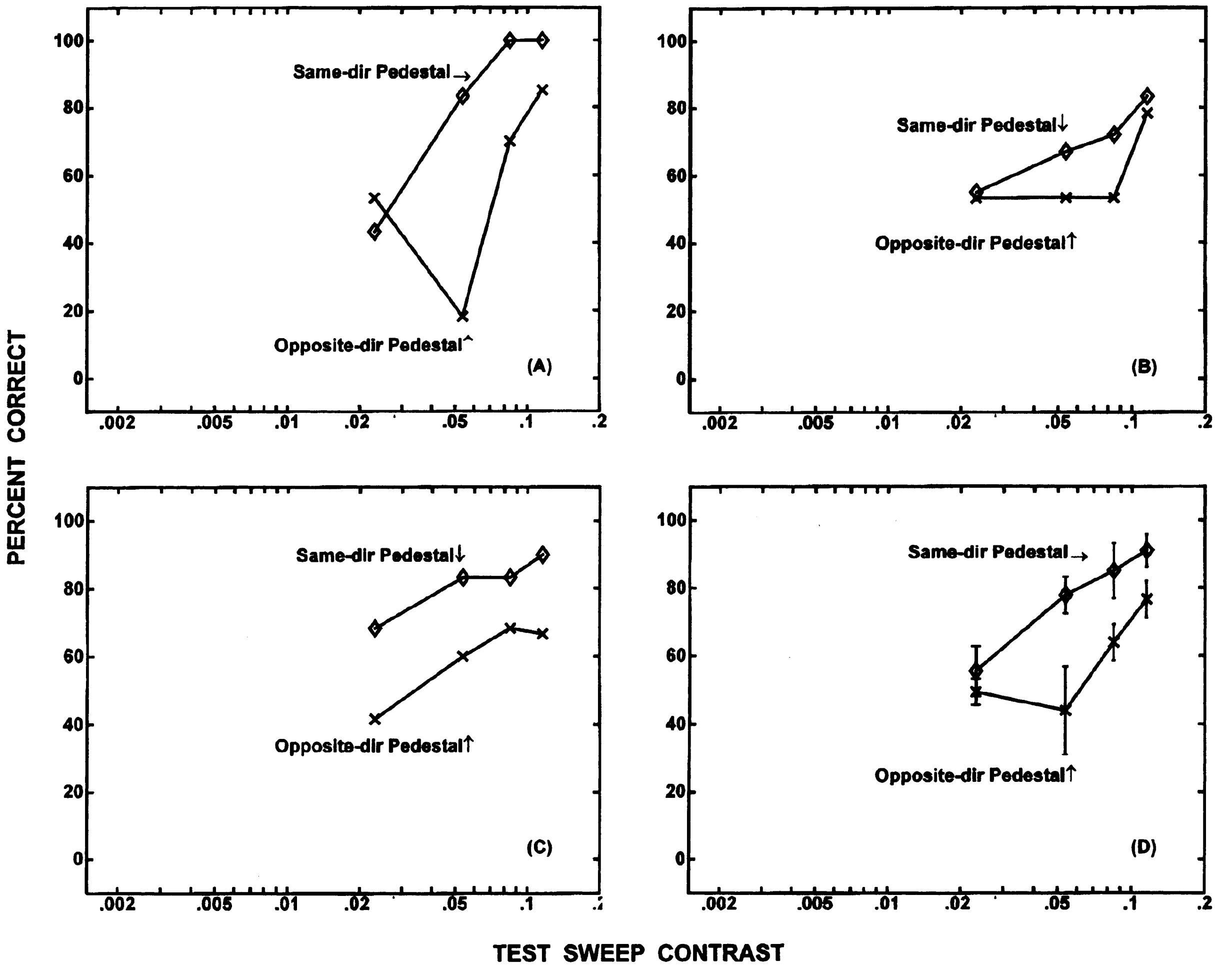

Fig. 4. Psychometric functions for percent correct responses (ordinate) as a function of test grating contrast (abscissa) for two different stimulus conditions. Same-direction pedestal trials (open diamonds); opposite-direction pedestal trials ('X' symbols). Panels A–C show the data for individual observers, AJP, OCP and MDD, respectively; panel D shows group (mean) data with $\pm$ one standard error bars. Data for IFI-biasing pedestals: Experiment 3.

5. Discussion

In all experiments there was a direction-specific reduction of sensitivity after a brief apparent motion stimulus. Thresholds for discriminating direction of motion were found to be higher for test stimuli that moved in the same direction as a sweep biasing stimulus (experiment 1), in the same direction as a single-step biasing stimulus (experiment 2), and in a direction opposite an IFI-biasing stimulus (experiment 3).

The sensitivity losses can be explained in terms of directionally selective motion mechanisms; that is, mechanisms which can be modeled as elaborated Reichardt detectors (van Santen & Sperling, 1984) or motion energy analyzers (Adelson & Bergen, 1985). In general, all one needs to assume is that, after a brief biasing stimulus, directionally selective mechanisms which responded most to the biasing stimulus are rendered least sensitive. In experiments 1 and 2, the biasing stimuli contained most directional energy in the sweep direction and in the direction which corresponded to the 90° step, respectively. Mechanisms most sensitive to those directions would have been rendered least sensitive, and performance with test stimuli which moved in those directions (same-dir pedestal trials) was found to be poorest. In experiment 3, due to the insertion of a blank frame, the IFI-biasing stimuli contained most directional energy in a direction opposite the 90° phase shift. Mechanisms most sensitive to that direction would have been rendered least sensitive, and performance with test stimuli which moved in that direction (opposite-dir pedestal trials) was found to be poorest.

Lu and Sperling (1995, 1996) have claimed that superimposing a moving sine-wave on a static pedestal is a procedure which isolates spatio-temporal filters which respond to luminance-defined stimuli. Superimposing a moving sine-wave grating on a static pedestal produces a back-and-forth pattern of oscillating features. Consequently, a feature-tracking system which responds to the changing positions of the features in the stimulus is not capable of eliciting an unequivocal directional signal. Following Lu and Sperling's lead, it seems reasonable to assume that our current experiments isolated individual sensitivities of spatio-temporal filters to different directions of test motion by measuring motion discrimination thresholds in the presence of contrast pedestals.

5.1. Extension of results to studies with suprathreshold ambiguous test stimuli

Two factors must be born in mind when extending the threshold results to past suprathreshold studies on direction biasing. (1) Within directionally selective filters, the perceived direction of an ambiguous, suprathreshold test stimulus would be determined by any imbalance among the filters. Consequently, the perceived direction would correspond to the direction whose sensitivity was not reduced by a biasing stimulus. (2) It is possible that mechanisms other than directionally selective filters come into play when simple sine-wave stimuli are used in suprathreshold studies without a pedestal. Table 1 summarizes relationships among empirical results and hypothetical signals in biasing experiments with threshold directional test stimuli and with suprathreshold ambiguous test stimuli.

In Table 1 the rows represent the three different types of biasing stimuli (sweep, single-step, and IFI) used in the present and past studies (Pinkus & Pantle, 1997; Pantle et al., 2000), and the columns represent different directional responses, both empirical and hypothetical. With the physical biasing directions given in column 1, poorer performance was obtained in the present experiments with test stimuli moving in the directions given in column 2. Under the simple assumption that performance with threshold test stimuli reflects the individual sensitivities of underlying directionally selective mechanisms, column 3 gives the directional signals which would be weakest after exposure to a biasing stimulus. In accordance with point (1) above, the predicted direction (column 4) of a 180° test step should be opposite the direction shown in column 3 for each of the different types of biasing stimuli. Empirically, the perceived directions, as shown by past research, appear in column 5. The empirical and hypothetical directions agree for sweep and IFI-biasing stimuli, but not for single 90° step stimuli. The lack of agreement suggests that some mechanism other than directionally selective filters is at least in part responsible for the biasing of an ambiguous suprathreshold test stimulus after a single 90° step biasing stimulus, a possibility consistent with point (2) above. We are currently exploring the possibility that a feature-tracking mechanism might be involved by using dichoptic biasing stimuli.

5.2. Apparent conflicts with other past studies

Our finding of a direction-specific loss of sensitivity for the same direction as a brief biasing stimulus might be considered surprising given some past research on the temporal interaction of motion signals. Examples of visual inertia with dot biasing stimuli (Ramachandran & Anstis, 1983) and enhancement of trajectory perception in random noise patterns (Grzywacz, Watamaniuk, & McKee 1995; Snowden & Braddick, 1989; Fredericksen, Verstraten, & van de Grind, 1994) would predict an increased sensitivity to the direction of a prior unambiguous motion. However, the discrepancy in conclusions between the present and earlier results may only be apparent. Unlike the present set of experiments where the biasing and test steps overlapped completely in space, past studies explored interactions between motion signals for conditions in which the motion steps were presented in spatially adjacent positions along trajectory paths. It is possible that a brief motion stimulus produces direction-specific losses of sensitivity only within the local areas it stimulates. Only a later occurring test stimulus that overlaps the prior motion stimulus in space will stimulate the same local areas and will suffer a loss of sensitivity. With trajectory studies, Grzywacz et al., (1995) hypothesized that facilitatory effects would occur only ahead of a moving bar along

Table 1
Summary table of empirical and hypothetical directional signals for threshold experiments[a]

Type of biasing stimulus	Direction of biasing stimulus	Direction with lowest measured sensitivity	Weakest directional signals	Predicted direction of 180° test step based upon threshold results	Perceived direction of 180° test step
SWEEP	Right (left)	Right (left)	Right (left)	Left (right)	Left (right)
STEP	Right (left)	Right (left)	Right (left)	Left (right)	Right (left)
IFI-STEP	Right (left)	Left (right)	Left (right)	Right (left)	Right (left)

[a] Rows represent the three different types of biasing stimuli (sweep, single step and IFI), and columns represent different kinds of directional signals.

a trajectory path, and not at other spatial locations relative to the moving bar. In any event, other studies using biasing stimuli surrounding an ambiguous test stimulus (Gallogly, 1997; Ido, Ohtani, & Ejima, 1997) found results similar to those of Pinkus and Pantle (1997) and Pantle et al. (2000), and therefore, they suggest that direction-specific losses of sensitivity can originate outside a local area.

Still other studies have explored motion temporal interactions between motion steps within the same local areas and found facilitatory, but not inhibitory effects. Simpson (1994) found summation of two threshold-level motion pulses. He presented a threshold-level motion pulse (equivalent to our biasing stimulus) and measured its temporal interaction with a later occurring threshold motion pulse (equivalent to our test stimulus). Unlike our experiments, in the sequences of Simpson, the first threshold-level motion pulse might not have generated a strong enough signal to generate any changes of sensitivity in underlying mechanisms.

Further implications of the present and past biasing experiments (Pinkus & Pantle, 1997; Pantle et al., 2000) for other motion phenomena have been explored in Pantle et al. For the sake of brevity, they are not repeated here. Suffice it to say that direction-specific losses of sensitivity after brief biasing stimuli have not been previously reported and that the losses are as large in magnitude (a factor of two, 0.3 log units) as has been found for long periods of adaptation (Pantle, Lehmkuhle, & Caudill, 1978). Moreover, the pedestal procedure employed permitted us to rule out the role of feature-tracking mechanisms in the direction-specific losses of sensitivity. Our results can be viewed as a significant step in disentangling the mechanisms involved in direction biasing with brief stimuli. Undoubtedly, it will take more steps with substantially different converging operations (e.g. the interocular method alluded to above) to achieve a full understanding of direction biasing with brief stimuli.

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References

Adelson, E. H., & Bergen, J. K. (1985). Spatio-temporal energy models for the perception of apparent motion. *Journal of the Optical Society of America A*, *2*, 284–299.

Anstis, S., & Ramachandran, V. (1987). Visual inertia in apparent motion. *Vision Research*, *27*, 755–764.

Barlow, H. B., & Hill, R. M. (1963). Selective sensitivity to direction of movement in ganglion cells of the rabbit retina. *Science*, *139*, 412–414.

Fredericksen, R., Verstraten, A., & van de Grind, W. (1994). An analysis of the temporal integration mechanism in human motion. *Vision Research*, *34*, 3153–3170.

Gallogly, D. (1997). The interaction of motion-signals: space-time asymmetries. PhD dissertation, Miami University, OH.

Grzywacz, N., Watamaniuk, S., & McKee, S. (1995). Temporal coherence theory for the detection and measurement of visual motion. *Vision Research*, *35*, 3183–3203.

Ido, K., Ohtani, Y., & Ejima, Y. (1997). Dependencies of motion assimilation and motion contrast on spatial properties of stimuli: spatial-frequency nonselective and selective interactions between local motion detectors. *Vision Research*, *37*, 1565–1574.

Lu, Z. L., & Sperling, G. (1995). The functional architecture of human visual motion perception. *Vision Research*, *35*, 2697–2722.

Lu, Z. L., & Sperling, G. (1996). Contrast gain control in first- and second-order motion perception. *Journal of the Optical Society of America A*, *13*, 2305–2318.

Macmillan, N., & Creelman, C. D. (1991). *Detection theory: a user's guide*. New York: Cambridge University Press.

Marr, D. (1982). *Vision* (pp. 167–169). San Francisco: W.H. Freeman and Company.

McCarthy, J. E. (1993). Directional adaptation effects with contrast modulated stimuli. *Vision Research*, *33*, 2653–2662.

McKee, S., & Welch, L. (1985). Sequential recruitment in the discrimination of velocity. *Journal of the Optical Society of America A*, *2*, 243–251.

Moulden, B. (1980). After-effects and the integration of patterns of neural activity within a channel. *Philosphical Transactions of the Royal Society of London*, *290*, 39–55.

Pantle, A., Gallogly, D. P., & Piehler, O. C. (2000). Direction biasing by brief apparent motion stimuli. *Vision Research*, *40*, 1979–1991.

Pantle, A., Lehmkuhle, S., & Caudill, M. (1978). On the capacity of directionally selective mechanisms to encode different dimensions of moving stimuli. *Perception*, *7*, 261–267.

Pantle, A., & Turano, K. (1992). Visual resolution of motion ambiguity with periodic luminance- and contrast-domain stimuli. *Vision Research*, *32*, 2093–2106.

Pinkus, A., & Pantle, A. (1997). Probing motion signals with a priming paradigm. *Vision Research*, *37*, 541–552.

Ramachandran, V. S., & Anstis, S. (1983). Extrapolation of motion path in human visual perception. *Vision Research*, *23*, 83–85.

Sekuler, R., & Ganz, L. (1963). Aftereffect of seen motion with a stabilized retinal image. *Science*, *139*, 419–420.

Sekuler, R., & Pantle, A. (1967). A models for after-effects of seen movement. *Vision Research*, *7*, 427–439.

Simpson, W. A. (1994). Temporal summation of visual motion. *Vision Research*, *34*, 2547–2559.

Snowden, R., & Braddick, O. (1989). The combination of motion signals over time. *Vision Research*, *29*, 1621–1630.

Strout, J., Pantle, A., & Mills, S. (1994). An energy model of interframe interval effects in single-step apparent motion. *Vision Research*, *34*, 3223–3240.

van Santen, J. P. H., & Sperling, G. (1984). Temporal covariance model of human motion perception. *Journal of the Optical Society of America A*, *1*, 451–473.

Watson, A., & Ahumada, A. (1985). Model of human visual-motion sensing. *Journal of the Optical Society of America A*, *2*, 322–342.