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Direction biasing by brief apparent motion stimuli☆

Allan J. Pantle [a,*], Donald P. Gallogly [b], Olga C. Piehler [a]

[a] *Department of Psychology, Miami University, Oxford, OH 45056, USA*

[b] *Department of Electronics and Computer Science — UCEH, University of the Algarve, Campus de Gambelas, 8000 Faro, Portugal*

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Abstract

The perceived direction of a motion step (probe stimulus) can be influenced by an earlier motion step or a brief motion sweep containing a series of steps (biasing stimulus). Depending upon experimental conditions, the biasing of the direction of the probe step (a phase shift of 180° $\pm \Phi$) by a biasing stimulus which precedes it by approximately 250 ms can either increase (positive filter biasing) or decrease (negative filter biasing) the tendency to see the probe move in the biasing direction as computed with a motion filter with a biphasic temporal impulse response. In a series of experiments it was found that biasing motions traversing 90° of phase angle in fewer than six steps in less than 100 ms produced positive filter biasing. Also, biasing of the probe direction could be dissociated from the consciously reported direction of the biasing stimulus, and it did not occur when the probe preceded rather than followed the biasing stimulus. A biasing sweep containing more than six steps traversing 90° or a sweep traversing 270° produced negative filter biasing. Perceptual fusion of the steps of the sweep was not a necessary condition for obtaining negative filter biasing. In general, the negative filter biasing effects were found to be the most pervasive for the conditions investigated, and they are suggestive of a direction-specific, adaptation-like (gain-control) process in first-order motion filters. The exception to the negative biasing rule was found only with biasing stimuli which were short in duration or distance spanned.

Keywords: Apparent motion; Motion biasing; Direction specificity; Spatio-temporal integration; Motion signal interactions

1. Introduction

Pinkus and Pantle (1997) described a visual phenomenon which they called motion priming. They found that an unambiguous 90° abrupt phase shift (step) of a sine-wave grating constrained a subsequent ambiguous 180° test step to be in the same direction. Their results could be interpreted in a relatively straightforward manner. Simply put, the unambiguous biasing step generated a directional signal which put the system in a state of readiness for the same direction of motion. The bias, in turn, upset the normal balance of directional signals produced by the ambiguous motion step at a later time. The motion priming phenomenon of Pinkus and Pantle (1997) can be viewed as an extension of earlier observations on 'visual inertia' of dot stimuli by Anstis and Ramachandran (1987). In the present paper we employed the priming (hereafter, biasing) paradigm of Pinkus and Pantle (1997), but expanded their single two-frame biasing steps to include: (1) single-step stimuli with a blank frame between grating frames; and (2) multi-frame motion sweeps. In addition, in one experiment, the single 180° test (probe) stimulus was expanded to include multiple probe measurements with a set of weakly directional stimuli whose step sizes were near 180° in order to obtain a whole psychometric function for evaluating biasing effects. What emerges from the new experiments is a web of biasing effects which are more complex than either Pinkus and Pantle (1997) or Anstis and Ramachandran (1987) had envisioned with their explanations of simple priming or visual inertia. To anticipate the results, it was found that biasing stimuli could both increase and decrease the tendency to see a test stimulus move in the same direction, with the decrease being the more prevalent effect.

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* Corresponding author. Fax: +1-513-5292420.

E-mail address: pantleaj@muohio.edu (A.J. Pantle)

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2. General methods: experiments 1–3

2.1. Stimuli

The apparent motion stimuli for experiments 1–3 were image sequences constructed from spatially uniform blank fields and vertical sine-wave gratings. Each image was generated ahead of time and stored in graphics memory for later display as part of the motion sequence for a trial by a machine-language program. An IBM-PC AT computer equipped with a Number Nine graphics controller (Revolution 1024) connected to a Mitsubishi monitor (Model #6479A) was used to generate and display the images. Each image was 384 pixels wide × 320 pixels high with 8-bits/pixel to control the green gun of the monitor. An appropriate color look-up table insured that the monitor luminance was a linear function of the color indices used for image generation. Luminances were calibrated with a Pritchard Photometer (Model #1980A) equipped with a PD Spectar lens. The luminance of a blank image and the space-average luminance of the gratings was 17.1 cd/m^2. The Michelson contrast of the gratings was 40% and their spatial frequency was 1.4 c/deg at a viewing distance of 137 cm.

There were two major types of apparent motion sequences, one-step control sequences and one-step biasing sequences. The control sequences are not important in the present context and will not be discussed further.

One-step biasing sequences contained a single biasing step and a probe step. In the basic paradigm, the biasing step preceded the probe step, except in some conditions of experiment 2 where the order of the steps was reversed (described later). Each biasing sequence contained three successive grating images, with the transition from the first to second image comprising the first motion step (biasing step) and the transition from the second to third image forming the second step (probe step). The duration of the first, second and third grating images was 1728 (96), 288 (16) and 1728 (96) ms (screen refreshes), respectively. Each biasing sequence was seen as two *discrete* apparent motion jumps in rapid succession (288 ms between jumps). With the exception of some conditions of experiment 3 (described later), there was no interstimulus interval between the successive grating images, and the monitor screen was returned to a uniform blank field immediately following the motion sequence for a trial. The blank field stayed on until the motion sequence for the following trial was presented. The luminance of the blank field (17.1 cd/m^2) matched the space-average luminance of the sine-wave gratings.

The motion stimuli were viewed through a 3.7° circular hole in a cardboard mask. The outside dimensions of the surrounding mask were 21° high × 12.7° wide. The luminance of the mask was 3.1 cd/m^2, and it was the result of the low ambient room lighting provided by incandescent bulbs.

2.2. Procedure

For each trial of the experiment, an observer viewed one biasing sequence. No fixation point was provided at any time, but an observer looked toward the center of each grating stimulus during a trial and attended globally to it. The absence of a fixation point and the instruction for viewing encouraged an observer to judge the motion of a grating directly rather than to infer its direction of motion from changes of its position relative to a fixation point. In the experiments of Pinkus and Pantle (1997) control measurements demonstrated that, even without a fixation point, eye movements were not responsible for results in the biasing paradigm. At the end of a trial, an observer reported the direction of each motion stimulus, one response (right or left) for the biasing stimulus and one response (right or left) for the probe stimulus.

2.3. Observers

Observers were undergraduate students at Miami University who participated in an experiment for course credit, experienced psychophysical observers who worked in the lab, and two of the authors. Only the authors were aware of the goals of the experiments. There were no essential differences between the results of the authors and those of the other observers. Observers were not given feedback about their responses during practice trials or during the actual trials of an experiment. All observers had normal or corrected-to-normal visual acuity.

2.4. Terminology

Sb: unfiltered motion energy of a biasing stimulus or shortest phase shift between the consecutive frames of a grating step or sweep.
Fb: filtered motion energy of a biasing stimulus computed with a first-order, biphasic temporal impulse response (Strout, Pantle & Mills, 1994).
Pb: perceived direction of a biasing stimulus.
Pp: perceived direction of a test (probe) stimulus.
Filter biasing: Pp is constrained by (correlated with) Fb irrespective of Pb.
- *Positive filter biasing:* Pp–Fb directions matched or positively related.
- *Negative filter biasing:* Pp–Fb directions not matched or negatively related.

Perceptual biasing: Pp is constrained by (correlated with) Pb irrespective of Fb.

Positive perceptual biasing: Pp–Pb directions matched or positively related.
Negative perceptual biasing: Pp–Pb directions not matched or negatively related.

3. Experiment 1

Experiment 1 was a partial replication of the findings of Pinkus and Pantle (1997). The new results could be compared directly with those of other new experiments with the same observers. More importantly, the data of experiment 1 were analyzed more completely. Pinkus and Pantle (1997) only looked for positive filter biasing of a probe stimulus by a biasing stimulus. In this, and our remaining experiments, we looked for both forms (positive and negative) of filter and perceptual biasing. The phase shift of the probe stimulus was always 180°. The physical magnitude (Sb) of the biasing step was either a +90° (leftward), 180°, −90° (rightward) phase shift, producing three different biasing sequences (+90°/180°, 180°/180°, −90°/180°, respectively), one for each of three experimental conditions. For the +90° and −90° biasing steps, Fb matches Sb.

3.1. Methods

In this and all other experiments, the experimental conditions made up one block of trials. The order of trials (conditions) within a block was random, and each observer completed one entire block of conditions before beginning the next block. Each experimental session began with a set of practice trials in which an observer saw a number of biasing sequences to familiarize him\her with the stimuli. In this experiment eight observers completed ten blocks of trials.

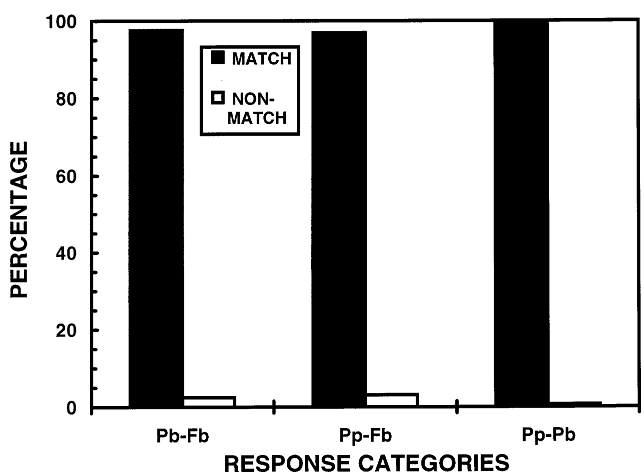

Fig. 1. Matching and non-matching percentages for three different response categories. Pb–Fb, perceived direction of the biasing stimulus (Pb) compared with the filtered directional energy of the biasing stimulus (Fb); Pp–Fb, perceived direction of the probe stimulus (Pp) compared with the filtered directional energy of the biasing stimulus (Fb); and Pp–Pb, perceived direction of the probe stimulus (Pp) compared with the perceived direction of the biasing stimulus (Pb). Data for the ±90°, single-step, biasing sequences without an IFI. Experiment 1.

3.2. Results and discussion

There were four pairs of possible responses to the biasing and probe stimuli for a single trial. The response pairs were grouped in different ways to evaluate various hypotheses about the effects of the biasing stimulus. The different data combinations appear under different category labels along the abscissa of Fig. 1. Each vertical bar represents a mean of the individual percentages for the eight observers.

Data for the +90° and −90° biasing conditions are discussed first (see Fig. 1); data for the 180° biasing condition, second. Pb matched Fb on 97.5% of the trials with +90° and −90° biasing sequences. On only 2.5% of the trials did Pb not match Fb. It can be concluded that the ±90° steps, as the first steps in the biasing sequences, were perceived in accordance with their filtered direction.[1]

With respect to Pp, it is possible to ask whether its direction was constrained by Fb and/or Pb, and if it were, whether in either case the biasing effect was positive or negative. First, consider the possibility of a filter biasing effect. As shown in the center of Fig. 1, the percentage of matching Pp–Fb responses (96.9%) was significantly larger than the percentage of non-matching Pp–Fb responses (3.1% of trials when Pp was opposite Fb). Thus, the data demonstrate positive filter biasing of a test stimulus by a two-frame 90° biasing step. Moreover, the percentage (96.9%) of matching Pp–Fb responses is not significantly different from the percentage (97.5%) of matching Pb–Fb responses, indicating that the perceived directions of both the biasing and probe steps followed the filtered directional energy of the biasing step, and they both followed it to the same degree ($t(7) = 1.00$, $P > 0.2$). Second, consider the possibility of a perceptual biasing effect. As shown on the right of Fig. 1, the percentage of matching Pp–Pb responses (99.4%) was significantly larger than the percentage of non-matching Pp–Pb responses (0.6%). The results are consistent with the hypothesis of positive perceptual biasing. Thus, the 90° biasing step disambiguated the direction of the probe stimulus, and its influence can be explained by either filter or perceptual biasing. The relative merits of the filter and perceptual hypotheses are examined in experiments 3–6.

[1] Whenever comparisons between matching and non-matching percentages yielded differences which were statistically significant at the $P < 0.001$ and one of the percentages exceeded 90%, values of t-tests were omitted for the sake of brevity.

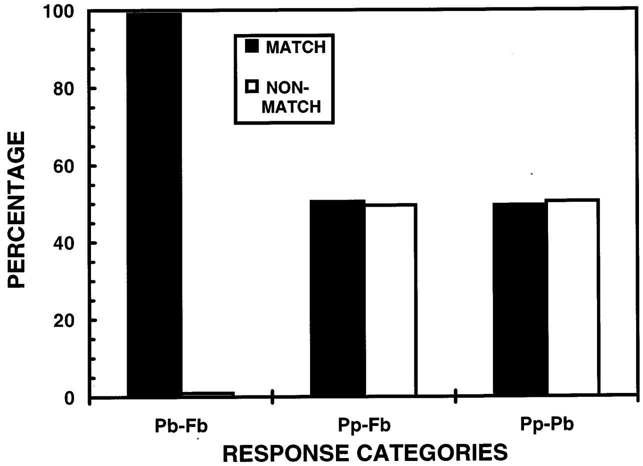

Fig. 2. Matching and non-matching percentages for three different response categories. Pb–Fb, perceived direction of the biasing stimulus (Pb) compared with the filtered directional energy of the biasing stimulus (Fb); Pp–Sb, perceived direction of the probe stimulus (Pp) compared with the filtered directional energy of the biasing stimulus (Fb); and Pp–Pb, perceived direction of the probe stimulus (Pp) compared with the perceived direction of the biasing stimulus (Pb). Data for the backward biasing sequences. Experiment 2.

For the 180°/180° biasing sequence, responses to the biasing step were exactly equally divided between left and right, and on average observers perceived the probe step jump more often (86.2% of trials) in the same direction as the biasing step rather than in the opposite direction (13.8% of trials). The non-independence of the successive 180° steps of a sine-wave grating is contrary to the findings of Pinkus and Pantle (1997) under almost identical conditions, and it is not replicated in experiment 3 of this paper. Considering all results, perceptual biasing with a 180°/180° biasing sequence is weak and unreliable.

The next experiment was designed to determine whether the direction of a probe step can be influenced by a biasing step which follows it, analogous to cases in which the detection of a test stimulus is influenced by a masking stimulus which comes after it (the phenomena of backward masking and metacontrast) (Breitmeyer, 1984).

4. Experiment 2

The present experiment contained biasing sequences in which a probe stimulus preceded (backward biasing), rather than followed (forward biasing), a $\pm 90°$ biasing stimulus.

4.1. Methods

The methods of experiment 2 were the same as those in experiment 1 with the following exceptions. Experiment 2 contained only two conditions, each condition with a different backward biasing sequence. Each backward biasing sequence contained three successive grating images, with the transition from the first to the second image comprising the 180° probe step and the transition from the second to the third image forming the biasing step. The biasing step was 90° in one condition; $-90°$, in the other condition. As in experiment 1 the duration of the second grating image was 288 ms, and it served to divide the biasing sequence into two discrete apparent motion jumps; in this case, a physically ambiguous step followed by a physically unambiguous one. Each of the two backward biasing conditions was viewed ten times by each of ten observers. An observer reported the perceived direction of the biasing step and the probe step on each trial.

4.2. Results and discussion

The data for experiment 2 were reduced in the same way as those for experiment 1 and are presented in the same figure format (see Fig. 2). Despite the fact that the biasing step was second in the biasing sequences, Pb nonetheless matched Fb on 99% of the trials (left of Fig. 2).

However, neither Pb nor Fb had an influence on the test stimulus which preceded it. As shown on the right of Fig. 2, the percentage of Pp–Pb matches across the two biasing conditions was 50.5%, and it was 49.5% for Pp–Pb non-matches. The percentages are not significantly different ($t(9) = 0.16$, $P > 0.2$). Also, as shown in the center of Fig. 2, the percentage of Pp–Fb matches (49.5%) was slightly less than the percentage of Pp–Fb non-matches (50.5%), and the percentages are not significantly different from each other ($t(9) = -0.16$, $P > 0.2$). The lack of a difference between the percentages of Pp–Pb matches and non-matches and the lack of a difference between the percentages of Pp–Fb matches and non-matches rules out the possibility that the biasing step acted retroactively and controlled the perceived direction of the probe in any way. The complete lack of a relationship between the perceived direction of the probe step and the direction of the biasing step, filtered or perceived, in this experiment contrasts sharply with the strong influence of the biasing step in the forward biasing conditions of experiment 1. Interactions between two discrete motion steps are asymmetric, acting forward in time.

Our forward biasing results are consistent with other demonstrations of 'visual inertia' and with some models of motion facilitation and integration. Such models or theories take a number of different forms, inclusive of simple filtering (e.g. Regan & Beverley, 1984), leaky integration (Fredericksen, Verstraten & van de Grind, 1994), cooperative processes (e.g. Snowden & Braddick, 1989), motion trajectory mechanisms (Grzywacz, Watamaniuk & McKee, 1995), and feedback processes (e.g. Marshall & Hubbard, 1994). In sum, temporal biasing based upon the filtered directional energy of a biasing stimulus, temporal perceptual biasing, and any straightforward application of the above-mentioned class of models all lead one to expect that a biasing step and a later occurring 180° probe step will be reported to move in the same direction. Yet, the consciously perceived direction of motion of a biasing step and its measured effect on the perceived direction of a later probe step can be dissociated, as the next experiment demonstrates.

5. Experiment 3

As found in experiment 1 and earlier experiments (e.g. Pantle & Turano, 1992; Strout et al., 1994) the perceived direction of motion of a 90° grating step without an IFI corresponds to the smallest phase shift (shortest motion path) between the grating images. A leftward 90° shift (+90°) is seen as a leftward jump; a rightward 90° shift (−90°), as a rightward jump. However, when a blank stimulus (spatially uniform interframe interval) of sufficient duration is inserted between the two grating images which comprise a 90° motion step, the perceived direction of motion is reversed, i.e. the grating appears to move in the direction of the largest phase shift between the grating images (Pantle & Turano, 1992). A leftward 90° shift (+90°) is seen as a large rightward jump (−270°); a rightward 90° shift (−90°), as a large leftward jump (+270°). The perceptually reversed motion can be explained by the observation that the output of a motion filter with a biphasic temporal impulse response, Fb, is opposite Sb (Strout et al., 1994).

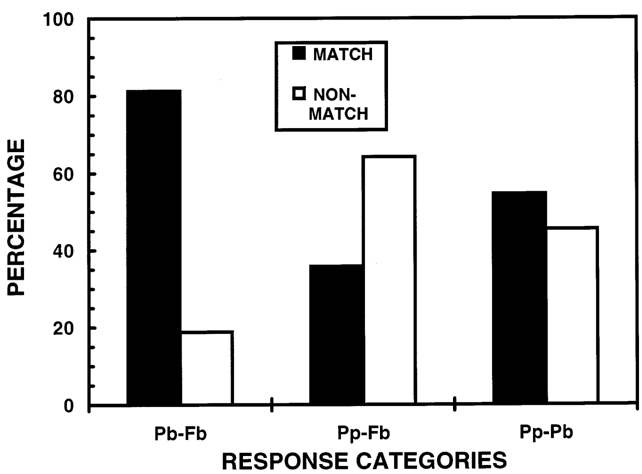

Fig. 3. Matching and non-matching percentages for three different response categories. Pb–Fb, perceived direction of the biasing stimulus (Pb) compared with the filtered directional energy of the biasing stimulus (Fb); Pp–Fb, perceived direction of the probe stimulus (Pp) compared with the filtered directional energy of the biasing stimulus (Fb); and Pp–Pb, perceived direction of the probe stimulus (Pp) compared with the perceived direction of the biasing stimulus (Pb). Data for the IFI biasing sequences. Experiment 3.

Experiment 3 was identical to experiment 1 except that a blank (spatially uniform) interframe interval (IFI) was inserted between the two grating images which comprised the biasing step of the motion sequences. Because the insertion of an IFI in the biasing step reversed Fb and Pb, it seemed interesting to know whether the IFI biasing step would also reverse Pp, and still produce positive filter biasing.

5.1. Methods

The methods of experiment 3 were the same as those in experiment 1 with the following exceptions. Blank IFIs of 18-ms duration were added between the two successive images which made up the biasing step (+90°, −90° and 180°) of the motion sequences of experiment 1. The probe step was unchanged. Hereafter, a biasing sequence with an IFI in the biasing step is called an IFI biasing sequence. The luminance of the blank IFI was 17.1 cd/m^2. Each condition was presented ten times to each of 12 observers.

5.2. Results and discussion

The data for experiment 3 were reduced in the same way as those for experiment 1. Consider first the results for the 180°/180° IFI biasing. The perception of the second 180° step (probe) was independent of the IFI biasing step. After an observer perceived the biasing step to jump in a specific direction (either left or right), he/she was about equally likely to perceive the probe step jump in the same direction as in the opposite direction. The percentage of Pp–Pb matching trials (55%) was not significantly different from the percentage of Pp–Pb non-matching trials (45%) ($t(11) = 0.44$, $P > 0.2$). The independence of the successive 180° steps is consistent with Pinkus and Pantle (1997), and it shows that the non-independence found in experiment 1 for the 180°/180° biasing sequence is not reliable. In sum, the weight of the evidence is against any strong perceptual biasing for 180°/180° biasing sequences, and it makes it less likely that perceptual biasing plays a role in observed biasing effects with +90° or −90° biasing steps to which we now turn.

Fig. 3 shows the same type of reduced data as Fig. 1. It gives the mean percentages of Pb–Fb, Pp–Fb, and Pp–Pb matches and non-matches for the ±90° IFI biasing sequences. Observers most often perceived the +90° or the −90° IFI biasing step jump in a direction opposite Sb, but consistent with Fb. The perceptually reversed motion of the IFI biasing step is apparent in the data of Fig. 3 where the percentage of Pb–Fb matches (81.2%) significantly exceeded the percentage of Pb–Fb non-matches (18.8%) ($t(11) = 7.32$, $P < 0.001$).

Pp–Pb matches and non-matches with $\pm 90°$ biasing sequences provide the necessary data for testing the perceptual biasing hypothesis. As shown on the right side of Fig. 3, the percentage of Pp–Pb matches (45.4%) did not differ significantly from the percentage of Pp–Pb non-matches (54.6%) ($t(11) = -0.45$, $P > 0.2$). It can be concluded that the Pp was not linked to Pb.

The results did, however, provide some evidence of an unexpected negative relationship between Pp and Fb. The number of Pp–Fb non-matches exceeded the number of Pp–Fb matches for nine of 12 observers. The probability of the obtained result is not likely under the null hypothesis as evaluated with a binomial test ($P = 0.073$). In addition, weak corroborative evidence for negative filter biasing is provided by a t-test. The P-value for a t-test comparing the larger mean percentage of Pp–Fb non-matches (64%) with the mean percentage of Pp–Fb matches (36%) is 0.15 ($t(11) = 1.53$) (center of Fig. 3). Both statistical results suggest that the perceived direction of the probe was opposite the filtered directional energy of the IFI biasing step. Experiment 4 revisits this relationship and provides strong evidence for it.

In experiment 1 the perceived directions of the biasing and probe steps both followed Fb, and they were equally influenced by it. However, in experiment 3, the separate analyses above revealed a differential effect of Fb on the perceived directions of the IFI biasing and probe steps. The percentage of Pp–Fb non-matches was 64.2%, whereas the percentage of Pb–Fb non-matches was 18.8%; that is, most were Pb–Fb matches (81.2%). The differential effect of Fb on Pb and Pp is statistically significant ($t(11) = 5.04$, $P < 0.001$).

In sum, the important empirical conclusions of experiment 3 are: (1) that there is no biasing of Pp by Pb; and (2) that the biasing of Pp by Fb is negative, a relationship which stands in stark contrast to the positive biasing of Pp by Fb obtained in experiment 1. Experiment 4 used three-frame biasing stimuli (motion sweeps) with no IFI in an effort to shed more light on the biasing effects. Like IFI biasing stimuli, the sweeps produce motion with three frames. Unlike IFI biasing stimuli, the filtered directional energy of a motion sweep in a biphasic channel corresponds to its unfiltered directional energy, i.e. Fb corresponds to Sb.

6. General methods: experiments 4–6

The stimuli, procedure, and classes of observers were the same as in experiments 1–3, with the exception of those changes described here and in the context of each of the individual experiments 4–6. Each image in a motion sequence was generated ahead of time and stored in memory for later display as part of the motion sequence for a trial by a C-language program and a Genus graphics library. An IBM-30386 computer equipped with a Number Nine graphics controller (#9GX) connected to a Mitsubishi monitor (Model #FL/HL6615K) was used to generate and display the images. Each image was 1024 pixels wide × 768 pixels high with 8-bits/pixel to control the green gun of the monitor. The luminance of a blank image and the space-average luminance of the gratings was 34.3 cd/m^2. The Michelson contrast of the gratings was 30%. The luminance of the cardboard mask surrounding the grating stimuli was 27.4 cd/m^2.

In contrast to experiments 1–3 which examined the effects of single-step biasing stimuli, experiments 4–6 focused on the effects of multi-frame biasing stimuli on subsequent probe stimuli. The multiple frames produced a series of motion steps which appeared perceptually fused and smooth. Hereafter, the multi-frame stimuli are called motion sweeps, or simply sweeps. With the sweeps as biasing stimuli, a biasing sequence comprised a sweep followed by a probe stimulus (hereafter, a sweep biasing sequence).

Each sweep biasing sequence contained four or more successive grating images, with the transition from the penultimate to the last image always forming the probe stimulus. The duration of the first, penultimate, and last grating images was 1536 (96), 256 (16) and 1536 (96) ms (screen refreshes), respectively. In different experimental conditions, a different number of grating images was inserted between the first and penultimate images of a biasing sequence to produce different biasing sweeps. Each image (one screen refresh long, 16.7 ms) added a motion step to a biasing sweep. Thus, each sweep began with the first image of a biasing sequence and ended with the penultimate image. The 256-ms duration of the penultimate image separated the biasing sequence into two discrete motions, a biasing sweep and a probe.

In experiment 5, the simple 180° probe step was replaced with a probe step whose magnitude was varied in 20° steps from $180° - 60°$ (physically leftward steps) to $180° + 60°$ (physically rightward steps) across trials. The spatio-temporal Fourier spectrum of a 180° phase shift contains equal power for motion in right and left directions. Phase shifts of less than 180° contain relatively more power in a leftward direction; phase shifts of more than 180°, relatively more power in a rightward direction. Additionally, the greater the extent of the phase shift difference from 180°, the greater is the relative directional energy. For example, a 160° phase shift ($180° - 20°$) has more leftward energy than rightward energy, but not as much leftward energy as a 140° phase shift ($180° - 40°$). Psychometric functions were

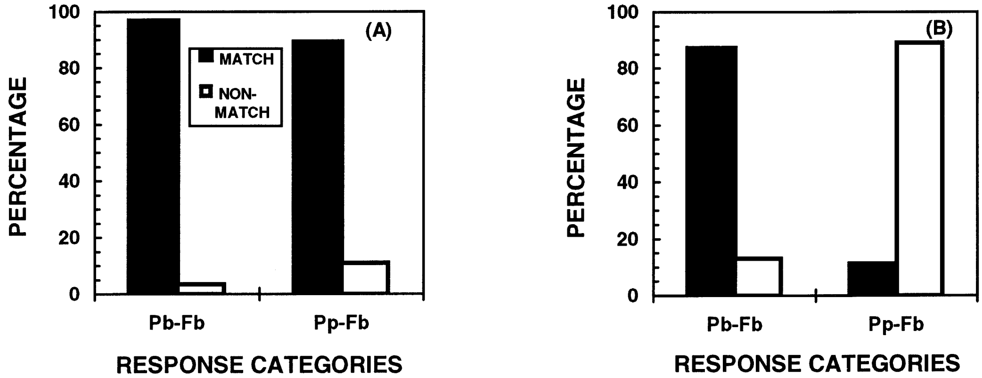

Fig. 4. Matching and non-matching percentages for two different response categories. Pb–Fb, perceived direction of the biasing stimulus (Pb) compared with the filtered directional energy of the biasing stimulus (Fb); Pp–Fb, perceived direction of the probe stimulus (Pp) compared with the filtered directional energy of the biasing stimulus (Fb). Left panel (A): data for the ±90°, single-step, biasing sequences; right panel (B): data for the IFI biasing sequences. Experiment 4.

constructed from the directional responses to the probe stimuli of different phase shift magnitudes. The functions provide a more complete description of the effects of biasing stimuli than does the directional response to the single-valued (180°) probe stimulus used in other experiments.

7. Experiment 4

Four new biasing stimuli, ±90° and ±270° sweeps, were introduced in experiment 4. The sweep biasing stimuli had one frame inserted between the first and last frames creating two-step biasing stimuli which appeared perceptually fused. The middle frame was always half the magnitude of the phase shift between the first and last frames, +45°, −45°, +135°, and −135° for the +90°, −90°, +270°, and −270° biasing sweeps, respectively. The +90° and +270° sweeps contain more motion energy in a leftward direction; the −90° and −270° sweeps, more motion energy in a rightward direction. This is true for unfiltered energy (Watson, 1990) or filtered energy computed for a biphasic temporal channel as in the Strout, Pantle and Mills model (1994). Single-step ±90° biasing stimuli and IFI biasing stimuli were included in the experiment so that their biasing effects could be directly compared with the sweep results.

Of particular interest in experiment 4 was the question whether biasing sweeps would produce positive filter biasing like the single-step ±90° stimuli in experiment 1 or negative filter biasing like the IFI stimuli in experiment 3.

7.1. Methods

All sequences in this experiment created the impression of two discrete apparent motions. As described above, the first apparent motion was the biasing stimulus which was either: (1) a single ±90° step; (2) an IFI ±90° step; (3) a ±90° sweep produced by two integrated steps of 45° each; or (4) a ±270° sweep produced by two integrated steps of 135° each. The second apparent motion was the 180° test probe, formed by the transition from the penultimate to the last grating image of a biasing sequence. Each condition was presented ten times to each of ten observers.

7.2. Results and discussion

Figs. 4 and 5 show the same type of reduced data as those in Fig. 1, except that the Pp–Pb category has been omitted. The data in an individual panel of each figure give the results for a single biasing condition.

The data in Fig. 4A replicate the results of experiment 1 for the single-step ±90° biasing sequences. Pb–Fb matches occurred more often than Pb–Fb non-matches. The percentage of Pp–Fb matches was significantly greater than the percentage of Pp–Fb non-matches ($t(9) = 13.1$, $P < 0.001$), again supporting the positive filter biasing hypothesis. It can be concluded that the perceived directions of both the biasing stimulus and the probe stimulus coincided with filtered directional energy of the biasing stimulus. The data in Fig. 4B replicate the results of experiment 3 for the IFI biasing sequences. As in experiment 3 the biasing stimulus was perceptually reversed. Its direction matched Fb as evidenced by the predominance of Pb–Fb matches over Pb–Fb non-matches ($t(9) = 11.9$, $P < 0.001$). Moreover, as in experiment 3 the filter biasing effect of IFI stimuli was negative as shown by the significantly greater percentage of Pp–Fb non-matches compared with Pp–Fb matches ($t(9) = 7.52$, $P < 0.001$).

The results for sweep biasing sequences are given in Fig. 5. They provide evidence for both positive and negative filter biasing with sweeps whose filtered and perceived directions are not reversed. Pb matched Fb significantly more often than not for both the 90° ($t(9) = 104$, $P < 0.001$) and 270° ($t(9) = 104$, $P < 0.001$) sweeps.

For 90° sweep biasing sequences, the percentage of Pp–Fb matches was greater than the percentage of Pp–Fb non-matches ($t(9) = 12.7$, $P < 0.001$). The biasing effect was positive. For the 270° sweep biasing sequences, the percentage of Pp–Fb non-matches exceeded the percentage of Pp–Fb matches ($t(9) = 9.47$, $P < 0.001$). The biasing effect was negative.

To summarize the results of experiments 1–4, (1) Pp was negatively related to Fb for IFI and 270°-sweep biasing stimuli, and (2) Pp was positively related to Fb for 90° single-step and sweep biasing stimuli. Because biasing stimuli with larger phase shifts and with more steps produced negative biasing in our experiments, whereas those with smaller phase shifts and fewer steps produced positive biasing, biasing effects were explored more exhaustively in experiment 5 by systematically varying the sweep phase shift magnitude and number of steps. Of particular interest was the question whether it is possible to obtain instances of negative filter biasing with sweeps moving through less than 270°. Also, in order to obtain a more sensitive measure of any differences among various biasing sweeps, we employed the phase test described earlier instead of a single 180° probe step.

8. Experiment 5

Experiment 5 extended the sweep biasing conditions of experiment 4 in order to better understand the source of the differences between positive and negative filter biasing effects of sweep stimuli.

8.1. Methods

Experiment 5 was divided into two parts. The methods of each part were identical to those of experiment 4 with the following exceptions. Experiment 5A: In order to construct 1-, 2-, 6-, or 12-step biasing sweeps to be used in different conditions, 0, 1, 5, or 11 frames, in equal phase shift increments, were inserted between the first and the penultimate frames of a biasing sequence. There were two sweep directions (left and right) for each of the four multi-step biasing sequences, giving eight biasing sequences in all. There was also a control condition in which there was no biasing stimulus. The control condition provided baseline directional responses to which the data obtained with biasing stimuli could be compared. The distance covered by the biasing sweeps was 90°. There were five shift magnitudes for the phase test. Experiment 5B: (1) The biasing sweeps covered a distance of 270°; (2) there were sweep biasing stimuli with 2-, 6- or 12-steps; and (3) there were seven possible shift magnitudes in the phase test. In experiments 5A and 5B, four measurements were obtained for each shift magnitude of the phase test for each sweep biasing condition; eight measurements, for each shift magnitude of the phase test for the control condition. The order of the entire set of measurements was random and different for each observer. The same 6 observers completed both experiments 5A and 5B.

8.2. Results and discussion

There were only occasional Pb–Fb non-matches (19 out of approximately 1800 trials), distributed randomly across the different biasing sweeps. The perceived direction of the biasing sweeps corresponded to their unfiltered and/or filtered directional energy, irrespective

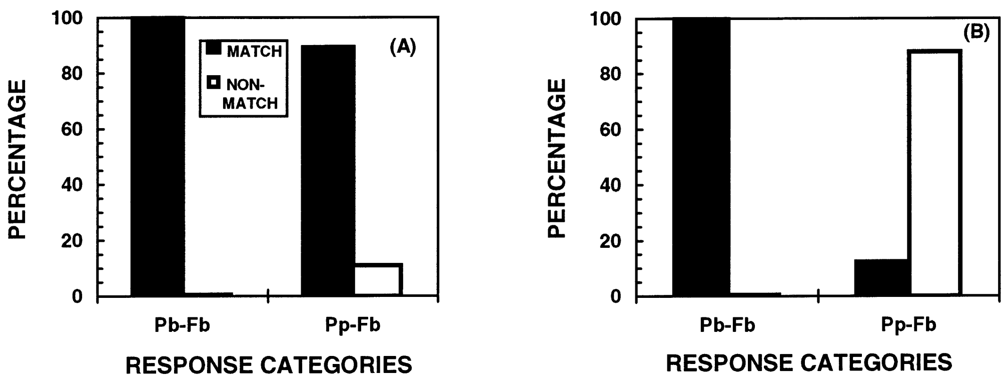

Fig. 5. Matching and non-matching percentages for two different response categories. Pb–Fb, perceived direction of the biasing stimulus (Pb) compared with the filtered directional energy of the biasing stimulus (Fb); Pp–Fb, perceived direction of the probe stimulus (Pp) compared with the filtered directional energy of the biasing stimulus (Fb). Left panel (A): data for the ±90°, two-step, sweep sequences; right panel (B): data for the ±270°, two-step, sweep sequences. Experiment 4.

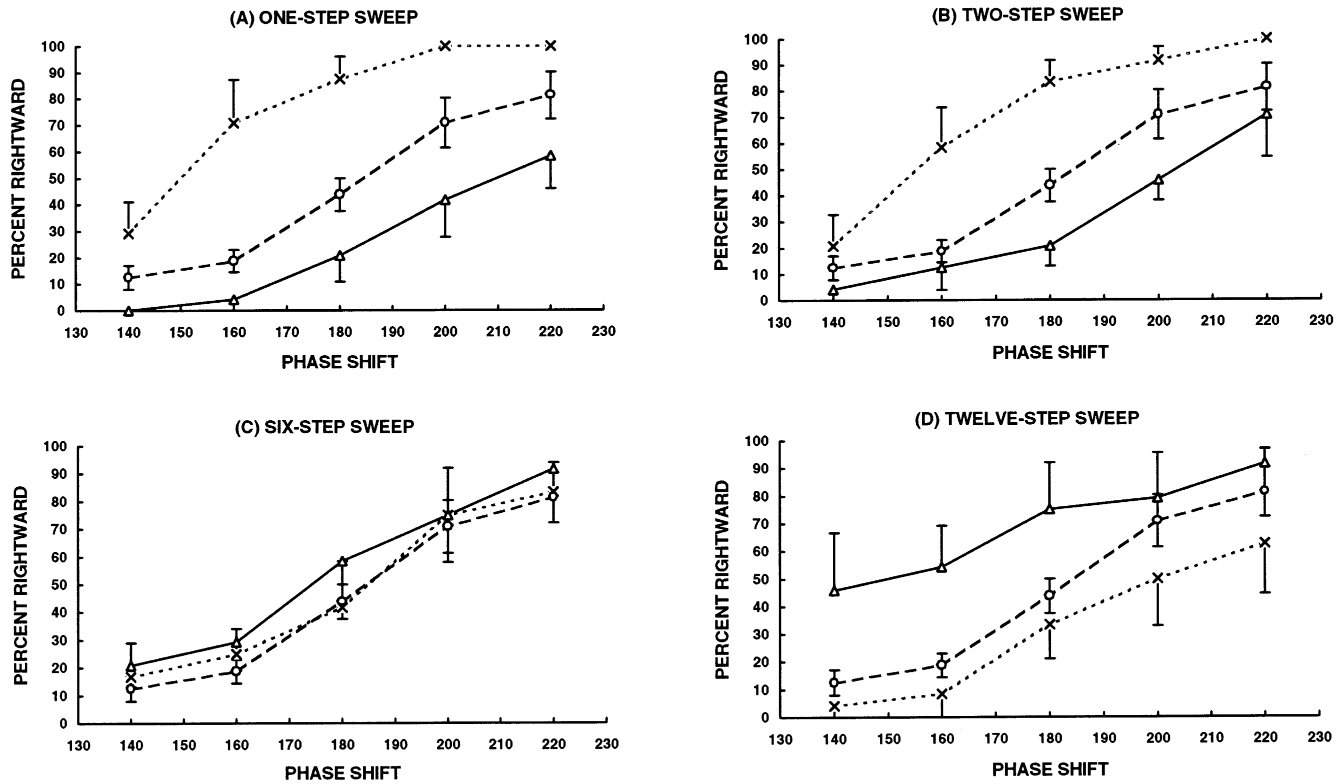

Fig. 6. Percent rightward responses to the probe stimulus as a function of its phase shift. The separate curves in each panel represent different biasing conditions. No biasing sweep (control): long-dashed curve; +90° (leftward) biasing sweep: solid curve. −90° (rightward) biasing sweep: short-dashed curve. The data for the ±90° biasing sweeps with 1-, 2-, 6- and 12-steps are given in the panels A–D, respectively. Experiment 5.

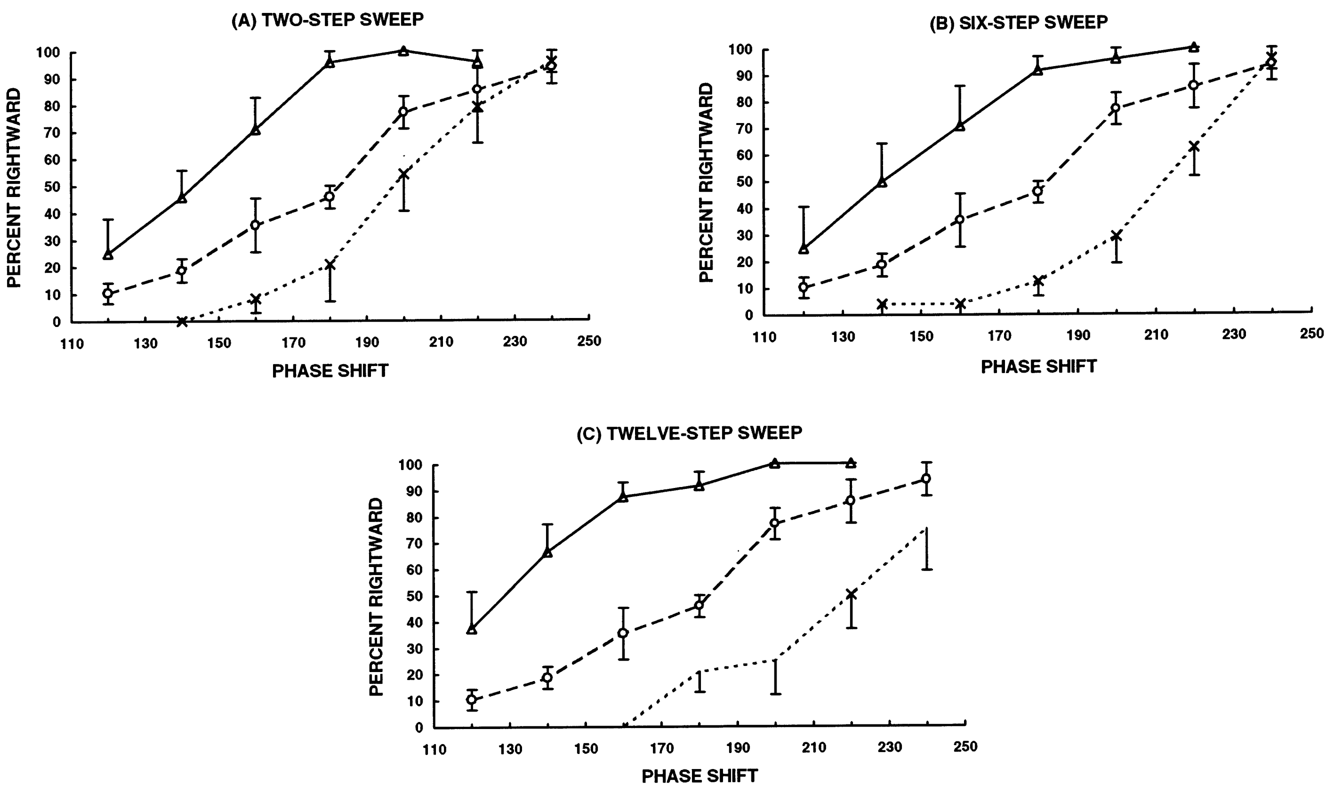

Fig. 7. Percent rightward responses to the probe stimulus as a function of its phase shift. The separate curves in each panel represent different biasing conditions. No biasing sweep (control): long-dashed curve; +270° (leftward) biasing sweep: solid curve. −270° (rightward) biasing sweep: short-dashed curve. The data for the ±270° biasing sweeps with 2-, 6- and 12-steps are given in the panels A–C, respectively. Experiment 5.

of the number of steps comprising a sweep and irrespective of the distance covered by a sweep.

Biasing effects in experiment 5 are revealed by the data in Figs. 6 and 7. Each panel shows the percentage of rightward responses to a probe stimulus as a function of its phase shift for a biasing sweep with a specific number of steps. Psychometric functions for the leftward and the rightward biasing conditions, as well as the control conditions, are shown in each panel. Each point in the figures is a mean percentage computed for the six observers. The vertical bars represent ± 1 SEM.

The long-dash curve in the upper left panel of Fig. 6 represents the responses for the control condition. The curve is reproduced in each of the other panels of Fig. 6 for easy comparison with the results of the leftward (solid curve) and rightward (short-dash) 90° sweep biasing conditions. The percentage of rightward responses in the control condition increases as a function of the shift magnitude of the phase test, i.e. as the relative rightward energy of the phase step increased. As expected, the control curve crosses the 50% rightward point near a phase test magnitude of about 180°, where rightward and leftward energies are equal.

In panel A, the short-dash curve represents responses for the condition which contained single-step, 90° rightward biasing sweeps. A comparison of the short-dash curve to the long-dash curve shows that, for each shift magnitude of the phase test, the percentage of rightward responses for trials in which the probe followed a rightward sweep was greater than that for corresponding trials in which the probe was presented alone. A comparison of the solid curve to the long-dash curve shows that, for each shift magnitude of the phase test, the percentage of rightward responses for trials in which the probe followed a 90° leftward sweep was less than that for corresponding trials in which the probe was presented alone. The displacements of the sweep biasing curves from the control curve reflect the tendency of the perceived direction of the probe to follow the directional energy of a biasing sweep. The remaining panels show that the displacements were only slightly smaller for a two-step 90° biasing sweep (panel B), essentially disappeared for a six-step sweep (panel C), and reversed for a 12-step sweep (panel D). That is, as the number of steps in a biasing sweep increased, the tendency of the perceived direction of the probe to follow the directional energy of the sweep gradually became a tendency to be opposite its directional energy; that is, a changeover from positive filter biasing to negative filter biasing.

The format for Fig. 7 is identical to that of Fig. 6. New data were obtained for the control condition and are plotted as the long-dash function in each panel of Fig. 7. Irrespective of the number of frames comprising a 270° biasing sweep, there was a tendency for the perceived direction of the probe to be opposite the directional energy of the sweep. That is, rightward sweeps resulted in more leftward responses (fewer rightward responses) than in the control condition, and leftward sweeps resulted in more rightward responses. The results conform to negative filter biasing.

In general experiment 5 demonstrates that it is possible to push the visual system towards a state whose direction is positively related to the filtered motion energy of a biasing sweep, or to push it towards a directional state which is negatively related to the filtered motion energy of a biasing sweep. The former outcome is the result of biasing sweeps which are short in time and distance covered; the latter outcome, the result of biasing sweeps which are long in time or distance covered.

The last experiment focuses on timing requirements for the steps of biasing stimuli which result in positive or negative filter biasing, and the relationship of those timing requirements to those required for perceptual fusion of the steps.

9. Experiment 6

In experiment 6 we employed two-step biasing sweeps. Each step on its own was known to produce positive filter biasing (Pinkus & Pantle, 1997), but taken together as one temporally integrated sweep, the steps produced negative filter biasing (experiment 4). Across different conditions of the experiments, the individual steps of the two-step biasing sweep were gradually separated in time until they appeared as two discrete motion steps. The question asked was whether or not negative filter biasing would break down at the point at which the two motion steps were no longer perceptually fused.

9.1. Methods

The methods of experiment 6 were the same as those in experiment 4 with the following exceptions. Only $\pm 270°$ two-step sweep biasing sequences were used. Each step advanced the phase position by 135°. The duration of the second frame of the three frames comprising the biasing sweep was systematically varied across different conditions of the experiment. The duration corresponds to the interval between the first and second steps of the biasing stimulus. The range of durations was 16–1024 ms. The probe stimulus was a single 180° motion step.

The experiment was divided into two parts, dependent upon the nature of the judgment made by an observer on each trial. On each trial of experiment 6A an observer reported the direction (right or left) of the probe stimulus which followed the biasing stimulus. In experiment 6B an observer reported the number (one or

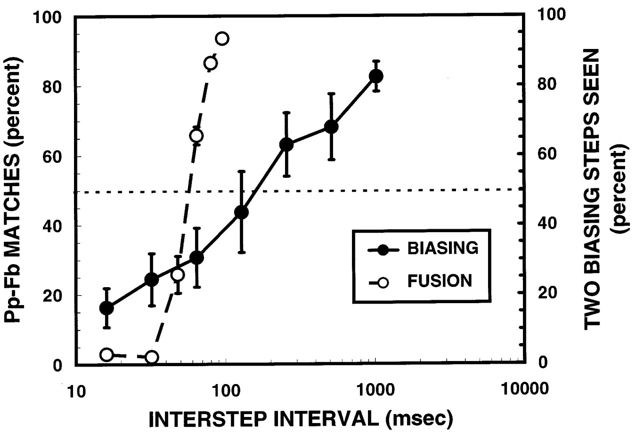

Fig. 8. Percentage of trials in which the perceived direction of the probe stimulus (Pp) matched the filtered directional energy of the biasing stimulus (Fb) (left ordinate, solid curve), and percentage of trials in which the two steps of the biasing stimulus were resolved (right ordinate, dashed curve) as a function of the interval between the steps comprising the biasing stimulus. Experiment 6.

two) of discrete motions which appeared to make up the biasing stimulus. Experiment 6B followed experiment 6A for each observer. For both parts of experiment 6, each biasing condition appeared once in a block of experimental trials, and each block was presented eight times to each of ten observers.

9.2. Results and discussion

The results of experiment 6 are shown in Fig. 8. The solid (biasing) curve summarizes the judgments of the direction of the probe stimulus. Specifically, the mean percentage of Pp–Fb matches is plotted as a function of the duration between the steps of the biasing stimulus (inter-step interval). The percentage of matches starts well below 50% for short inter-step intervals and increases with the inter-step interval, reaching a percentage well above 50% for long inter-step intervals. The change in the percentage of matches corresponds to a transition from negative filter biasing at short inter-step intervals to positive filter biasing at long inter-step intervals. The point at which the biasing transition occurs is approximately 200 ms.

The dashed (fusion) curve in Fig. 8 summarizes the judgments of the number of apparent steps reported for the biasing stimulus. In particular, the mean percentage of times two steps were seen is plotted as a function of the inter-step interval. At short intervals, one step was seen; at long intervals, two steps were seen. The point at which the two steps of the biasing stimulus appeared to be fused (appeared as one motion) 50% of the time corresponded to an inter-step interval of approximately 56 ms. The fusion curve crosses the 50% point at a shorter inter-step interval than does the biasing curve (200-ms cross-over), and it has a steeper slope. The difference of cross-over points reflects the fact that, at intermediate inter-step intervals, observers often saw the biasing stimulus as two discrete steps, yet still saw the probe stimulus move in a direction opposite the biasing steps. Perceptual fusion was not a necessary condition for negative filter biasing. What this means is that the temporal integration of motion steps required for negative biasing is longer than the integration time for perceptual fusion. A difference of the time constants of integration for fusion and biasing is also suggested by the difference of slopes of the fusion and biasing curves.

10. General discussion

10.1. Theoretical implications of motion biasing effects

Even though no unitary mechanism or process seems capable of explaining the entire set of motion biasing effects, the pattern of effects itself can be described relatively succinctly. All biasing effects are compatible with the concept of negative filter biasing, except those obtained with single-step biasing stimuli or with sweep biasing stimuli which spanned a short distance (90°) *and* contained only a few frames (less than six). The negative filter biasing effects produced by IFI or biasing sweeps long in time or space are suggestive of an adaptation-like, normalizing, and /or gain-control process (Heeger, 1993; Cannon & Fullenkamp, 1996; Thomas & Olzak, 1997; Wilson & Kim, 1998). The biasing effects which prevailed with biasing stimuli short in time and distance covered must be explained in some other way. Two alternatives come immediately to mind. (1) A temporally short 90° sweep or step might produce positive biasing due to the persistence of a filtered directional signal as computed by a first-order motion energy mechanism (Pinkus & Pantle, 1997). A compensatory adaptation-like, gain-control process may simply not be engaged with biasing stimuli short in time or space. (2) Some other motion mechanism (e.g. third-order; Lu & Sperling, 1995) may be responsible for positive biasing when biasing stimuli are short in time and space. If the first alternative were correct, differences of individual sensitivities of first-order spatio-temporal filters to different directions of probe motion after a biasing stimulus ought to be revealed by measurements of direction discrimination thresholds in the presence of contrast pedestals (Lu & Sperling, 1995). If the second alternative were correct, positive biasing for biasing stimuli short in time and space via a third-order mechanism should also be observable with interocular biasing and probe stimuli. Both of the above alternatives are being evaluated in ongoing research.

10.2. Relationship of biasing effects to other empirical studies

Given past research on the temporal interaction of motion signals like motion biasing with single-step, sine-wave biasing stimuli (Pinkus & Pantle, 1997), visual inertia with multi-frame, non-periodic (dot) biasing stimuli (Ramachandran & Anstis, 1983), enhanced perception of motion trajectories in random noise patterns (Snowden & Braddick, 1989; Fredericksen et al., 1994; Grzywacz et al., 1995), it was somewhat surprising to find negative biasing. In the past studies, ambiguous motions were resolved in favor of prior, brief, unambiguous motions, and multiple motion steps in a uniform direction constituted a more effective stimulus than a single step. All of these phenomena are consistent with finding positive biasing in the current experiments. Upon deeper examination, it may not have been all that surprising to find negative biasing in our long, sweep biasing conditions. The biasing and probe sine-wave stimuli generate motion signals which overlap completely in space, and for the sweep biasing stimuli with multiple frames, local areas were stimulated multiple times before the probe impinged upon the same local areas. By contrast in past studies, the methods were such that interactions between motion steps were explored for steps in spatially adjacent positions along trajectories.

Still other studies in which biasing stimuli surround probe (test) stimuli or in which broad-band random-dot stimuli were employed have also demonstrated negative biasing (motion contrast) effects (Gallogly, 1997; Ido, Ohtani & Ejima, 1997; Raymond & Isaak, 1998). Negative surround biasing effects would be consistent with contrast gain control (or normalization) which is reliant on spatial pooling (Heeger, 1993; Cannon & Fullenkamp, 1996; Thomas & Olzak, 1997; Wilson & Kim, 1998), but psychophysical studies of gain-control in pools of motion mechanisms have yet to be conducted. Negative biasing with random-dot stimuli may be due to the ability of random-dot stimuli to at least partially thwart third-order motion mechanisms. With a diminished ability to attentionally track individual dots or groups of dots, negative biasing based upon gain control in first-order motion mechanisms would be more evident. The difficulty with this interpretation is that inattention (explicit task intended to divert attention from the biasing stimulus) during biasing with random-dot stimuli should reinforce negative biasing, but it has actually been shown to produce less negative biasing (Raymond, O'Donnell & Tipper, 1998).

In the realm of empirical phenomena, it is difficult to resist the temptation to compare negative filter biasing with the motion aftereffect (MAE). The classic MAE is the apparent motion of a stationary pattern in a direction opposite the uniform motion of a pattern seen beforehand for a prolonged period of time, of the order of seconds or minutes. If the long biasing sweeps of the present experiments simply end with the grating being stationary, no further motion of the grating is observed. The lack of visible motion suggests that different mechanisms underlie negative biasing and the MAE. However, negative biasing may just be a weaker form of the MAE, requiring a test stimulus with motion energy (e.g. 180° step) to be manifest (e.g. McCarthy, 1993).

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