Centrifugal bias for second-order but not first-order motion

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Limited-lifetime Gabor stimuli were used to assess both first- and second-order motion in peripheral vision. Both first- and second-order motion mechanisms were present at a 20-deg eccentricity. Second-order motion, unlike first-order, exhibits a bias for centrifugal motion, suggesting a role for the second-order mechanism in optic flow processing. © 2001 Optical Society of America

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1. INTRODUCTION

First-order motion consists of moving luminance-defined attributes. Second-order motion, on the other hand, consists of moving patterns whose motion attributes are not luminance defined, e.g., moving contrast or texture borders.[1,2] The detection of first- and second-order motion is thought to be mediated by different mechanisms, i.e., a quasi-linear (first-order) and a nonlinear (second-order) mechanism.[3,4] A variety of different patterns are considered to be second-order stimuli, and further distinctions in stimuli and mechanisms have been suggested.[5–7]

Psychophysical evidence suggests that first- and second-order motion are processed, at least initially, by distinct visual pathways and different mechanisms. Early nonlinearities in visual processing introduce significant artifacts only at high contrasts and at higher temporal frequencies, as shown by Scott-Samuel and Georgeson[8] and by Holiday and Anderson.[9] Dissociation between first- and second-order motion has been shown by several studies. For instance, Landy *et al.*[10] found that even though second-order motion could provide depth clues, first-order motion detectors are the primary input to the kinetic depth system. Harris and Smith[11] found that only first-order and not second-order motion elicits optokinetic nystagmus. Further evidence for separate mechanisms is provided by the studies of Mather and West[12] and by Ledgeway and Smith,[13] which showed that direction discrimination fails when first- and second-order frames have to be integrated to detect motion. Nishida *et al.*[14] found no cross adaptation between first- and second-order motion, and Scott-Samuel and Smith[15] found a lack of cancellation between directionally opposed first- and second-order motion signals. First- and second-order motion also differ in their ability to induce motion aftereffects (MAEs). Second-order motion stimuli produce no MAEs on a static background but may induce MAEs on a flickering background.[16–19] Furthermore, aging has been shown to have a different effect on first- and second-order processing.[20] Brain lesion studies indicate that each kind of motion can be affected separately while leaving the other intact,[21–24] providing a neuropsychological "double dissociation." With electrophysiological techniques, neurons have been found to respond to second-order stimuli in cat areas 17 and 18,[25–30] with spatial and temporal frequency tuning that was different for first- and second-order stimuli. Neurons in primate extrastriate cortex have also been shown to respond to second-order motion.[31–34]

With a single stimulus constructed of Gabor micropattern arrays, first- and second-order motion mechanisms can be dissociated by varying several stimulus parameters. The behavior of the first-order motion mechanism can be described by a spatiotemporal energy model,[35] which for Gabor stimuli produces motion signals related to the carrier, rather than the envelope, of the micropatterns.[36–38] The envelope of the Gabor micropatterns drives the second-order motion mechanism. Consequently, changing the orientation, phase, or frequency of the carrier on alternate frames leaves second-order motion intact but eliminates first-order direction discrimination.[7,38,39] Furthermore, temporal intervals,[6,39,40] micropattern density,[37,39,41] percentage of distractor elements,[38,42] and displacement[7,38] can be used to dissociate the two kinds of motion.

Previous studies have differed over the presence of second-order motion processing in the periphery. Pantle[43] reported immobility for a range of second-order stimuli in peripheral but not central vision. Similar re-

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sults were reported by McCarthy *et al.*[44] and Zanker[45] for two specific kinds of second-order motion, i.e., flicker gratings and form-from-motion (θ motion), respectively. Even though the direction of motion could not be perceived, these stimuli could be detected in the periphery.[43–45] Studies using contrast-defined second-order motion, however, suggest that second-order motion can be perceived in peripheral vision under the appropriate spatiotemporal conditions.[19,46–49]

Owing to forward movement of ourselves relative to the world, we are more exposed to expanding patterns.[50] These optic flow patterns have been implicated in the guiding and regulation of the organism's own motion in relation to the environment.[51] Therefore a higher sensitivity to expanding optic flow patterns would not be unexpected. Thus in peripheral vision the sensitivity of motion perception in different directions does not necessarily have to be equal. Indeed, several studies, using a variety of techniques, have indicated anisotropies and inhomogeneities of the detection of the direction of motion.[52–62] These studies have revealed several anisotropies in the peripheral field, one of which is a difference in the perception of centrifugal (away from the center, expanding) and centripetal (toward the center, contracting) motion.

Using reaction times to motion onset of an 8-deg-diameter random dot field, Ball and Sekuler[53] found faster reaction times for the onset of centrifugal motion. Mateeff and colleagues[54,56,57] reported shorter reaction times for a moving single dot if it moved toward the fovea (centripetal). However, they confirmed the results of Ball and Sekuler[53] when using larger, textured stimuli. Thus the bias found may depend on the stimulus, suggesting different underlying mechanisms.

Van de Grind *et al.*,[58] who measured signal-to-noise ratio thresholds of random pixel arrays, found inhomogeneities and anisotropies throughout the visual field but did not report a strong centripetal or centrifugal preference. Measuring motion-detection coherence thresholds using radially expanding or contracting global-dot-motion stimuli (size 0 to 12 deg), Edwards and Badcock[59] found lower thresholds for centripetal motion. An increase in eccentricity (16 to 24 deg), however, resulted in either a reduction or a loss of the observed centripetal bias. Raymond[60] also found lower thresholds for centripetal motion when measuring the detection of global motion in random dot kinematograms (up to 12.5 deg). However, she did not find a reduced centripetal bias with increasing eccentricity.

Anisotropies have also been indicated with use of MAEs, which may have a similar basis. Larger motion aftereffects were found for apparent centrifugal motion, after adaptation to centripetal motion, than for apparent centripetal motion.[63,64]

Georgeson and Harris[52] reported an apparent centrifugal drift with counterphase gratings. This result suggests that even in incoherently moving patterns with no net motion, e.g., random dot patterns, an apparent bias might be present.

Albright[65] showed that more neurons in macaque middle temporal area (MT or V5) prefer motion in directions away from the center of gaze (centrifugal) than toward it (centripetal). This bias increased as a function of eccentricity.

The studies described above do not distinguish between different motion mechanisms, i.e., first- and second-order, that might underlie the perceptual judgments or the responses of neurons. Different mechanisms might have different functions, and processes involved in optic flow processing might mediate a centrifugal bias, whereas other processes might not. Investigating a centrifugal or centripetal bias of different motions might shed some light on the heterogeneity of previous results and on the functions of the mechanisms involved.

Researchers using stimuli constructed of arrays of Gabor patterns have identified distinct first- and second-order mechanisms underlying the processing of motion stimuli in central vision.[7,37–42] The purpose of the current study was (1) to identify and characterize both first- and second-order mechanisms in peripheral vision with use of a paradigm identical to that of Baker and Hess[38] and (2) to identify anisotropies related to centrifugal/centripetal biases in the detection of first- and second-order motion.

2. EXPERIMENT 1

The purpose of the first experiment was to assess the relative contributions of first- and second-order motion for a stochastic Gabor kinomatogram stimulus presented in the peripheral visual field.

A. Methods

For a more detailed description of the stimuli see Baker and Hess.[38] The visual stimuli were generated with a VSG 2/2 graphics card (Cambridge Research Systems) and were displayed on a NEC XP17 monitor refreshed at 160 Hz. The raster consisted of 512 × 379 pixels with a pixel size of 0.6 mm. At a viewing distance of 57 cm the pixels subtended 0.06 deg and the field size was 30.72 × 22.74 deg. The monitor intensity nonlinearity was measured with a photometer (United Detector Technology, S370) and was corrected by a method of Pelli and Zhang[66] with use of appropriate functions from the VideoToolBox software package.[67] An ISR Video Attenuator (Institute for Sensory Research, Syracuse University, New York) was used to resistively add the red, green, and blue video signals to produce a monochrome signal having a higher intensity resolution.[66] The monitor was operated with its green video input only.

The stimuli consisted of linearly added Gabor patterns each consisting of a one-dimensional sine-wave carrier enclosed by a two-dimensional Gaussian envelope [see Eq. (1)]:

$$L(x, y) = L_0\left[1 + C^{-(x^2/2\sigma_x^2\ +\ y^2/2\sigma_y^2)}\sin\left(\frac{2\pi x}{\lambda}\right)\right]. \quad (1)$$

The whole stimuli were spatially scaled by a factor of 2 when presented in peripheral vision to compensate for the difference in central and peripheral acuity. Unless stated otherwise, the orientation of the Gabor stimuli was perpendicular to their direction of motion, the spatial wavelength λ was 1.43 deg (0.715 deg for central vision), the envelope size σ was 3/4λ, the contrast C was 30%, and the mean luminance L_0 was 28.6 cd/m^2.

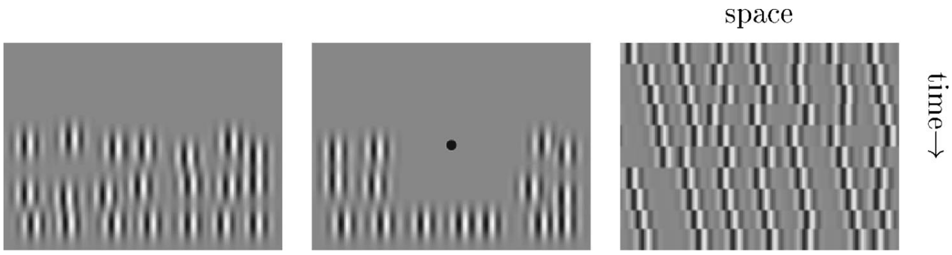
The Gabors were placed with respect to a grid with each Gabor having an (x and y) offset by a random amount with respect to their respective grid positions. This method provided a good density uniformity and prevented overlap between the Gabor patterns, which could cause intensity saturation.

A Gabor position was maintained for 100 ms (16 frames) before being replotted. Each stimulus presentation was 1000 ms. Two kinds of Gabor micropatterns were used, which differed only in their motion trajectories. One set of micropatterns moved coherently by a fixed amount; the others were randomly jittered around their respective grid positions. The average probability of a micropattern moving coherently was determined by the coherence level. The Gabors had a limited lifetime (400 ms or four exposures), after which they were replotted at their respective grid positions, and it was freshly determined whether each would move coherently for the next set of displacements.

The stimulus [see Fig. 1(a)] was presented in the lower visual field with the center of the micropattern grid at a 20-deg eccentricity (eccentricity range 14–26 deg). The stimulus used for central stimulation is depicted in Fig. 1(b); micropatterns falling in a central circular zone of 3.8-deg radius were not plotted to avoid attentional tracking, which has been shown to operate in the fovea.[68] The direction of motion of the Gabor patterns was either to the left or to the right. Percent errors in a forced-choice direction-discrimination task were measured as a function of spatial displacement.

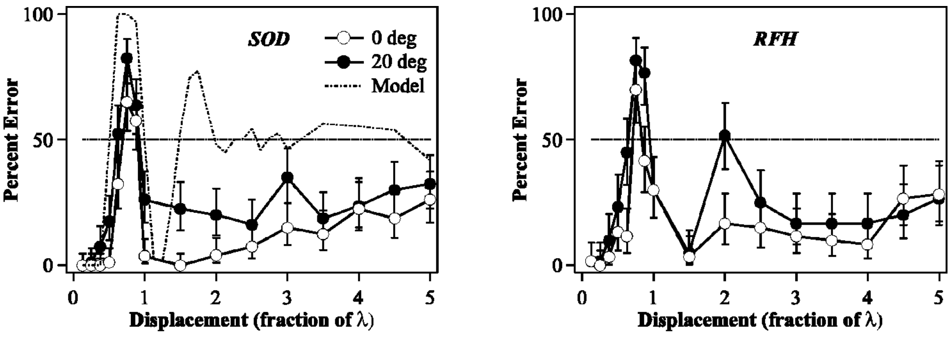
B. Results

The resulting psychometric functions (see Fig. 2) showed an errorless performance at small displacements (~1/4λ), rising steeply to a reversal, i.e., high error percentages at 3/4λ and then falling back to a relatively stable percent error level for a large range of displacements. The cyclic performance at smaller displacements (<λ) is predicted by a spatiotemporal energy model,[35] which produces responses to the carrier, rather than the envelope, of the micropatterns. At larger displacements (>λ) the model fails to predict motion detection (see Fig. 2). Baker and Hess[38] suggested that the performance of the subjects at these larger displacements is mediated by a second-order



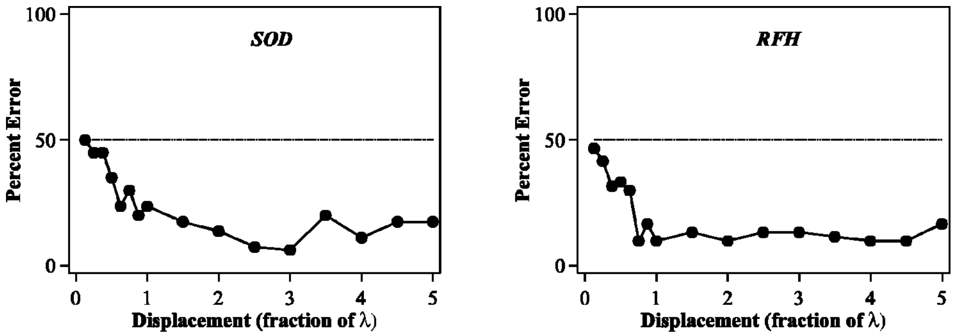
(a) (b) (c)

Fig. 1. Spatial layouts (a) and (b) and a space–time diagram (c) of the visual stimuli. (a) Stimulus configuration for the periphery; the viewing distance was 57 cm. (b) Stimulus used for central vision. The viewing distance was 114 cm; i.e., the size of the stimulus was 50% of the stimulus presented in peripheral vision [(a)]. (c) Space–time diagram along a horizontal transect of the stimulus. In this example the coherence was 50%, the lifetime 4, and the spatial displacement 1/4λ rightward.



(a) (b)

Fig. 2. Psychometric functions for central vision (open circles) and at a 20-deg eccentricity (solid circles) for two subjects. For subject SOD the results of a linear filter model (Adelson and Bergen[35]) are also shown (dashed-dotted curve). The percentage errors in direction discrimination are plotted as a function of the spatial displacement of the Gabor micropatterns. The error bars indicate 95% confidence limits: $n = 80$ (SOD) and $n = 60$ (RFH). For smaller displacements the data follow the prediction of the model; however, at larger displacements the model fails to predict motion detection. Baker and Hess[38] suggested that motion perception in this stimulus is carried out by a first-order mechanism responding to the carrier frequency at small displacements and a second-order mechanism responding to the contrast envelopes at large displacements.



(a) (b)

Fig. 3. Psychometric functions at a 20-deg eccentricity for two subjects. The percent errors in direction discrimination are plotted as a function of the spatial displacements of the Gabor patterns: $n = 80$ (SOD) and $n = 60$ (RFH). The carrier orientation of the Gabors was flipped by 90 deg on alternate exposures, thus eliminating the contribution of the first-order mechanism.

mechanism responding to the contrast envelopes of the micropatterns. Further evidence that these distinct first- and second-order mechanisms are underlying the perceptual judgments of this stimulus was presented by previous studies.[7,38]

The psychometric function for peripheral vision [Fig. 2, solid symbols] is similar to that of central vision (open symbols) except for larger error rates at larger displacements. The larger error percentages suggest that at this eccentricity there is a significant although weaker contribution of the second-order mechanism.

To further test the idea that a second-order mechanism is underlying the perceptual judgments at larger displacements, the carrier orientation was changed by 90 deg on alternate exposures. Changing orientations eliminates the perception of the direction of first-order motion, thus isolating the second-order motion.[7,38,39] The results are plotted in Fig. 3. The cyclic performance at smaller displacements is abolished, although the performance at larger displacements remains similar to that of Fig. 2, supporting the idea that changing the carrier orientation isolates the second-order mechanism. These data further illustrate the presence of a second-order mechanism in peripheral vision. Other manipulations of the stimulus variables verified the findings of Baker and Hess[38] and are not reported.

C. Conclusion

Both first- and second-order motion can be processed in peripheral vision with use of limited-lifetime random Gabor patterns. This supports the results of previous studies indicating that contrast-defined second-order motion can be perceived in peripheral vision,[19,46–49] with use of a different kind of stimulus.

3. EXPERIMENT 2

Initial pilot experiments indicated large perceptual differences between centrifugal and centripetal direction of motion for second-order motion. Whereas centrifugal motion was perceived as “normal” motion, centripetal motion, on the other hand, seemed perceptually similar to incoherent motion with no net directional component. The purpose of the second experiment was to assess centrifugal/centripetal directional anisotropies for both first- and second-order motion in peripheral vision.

A. Methods

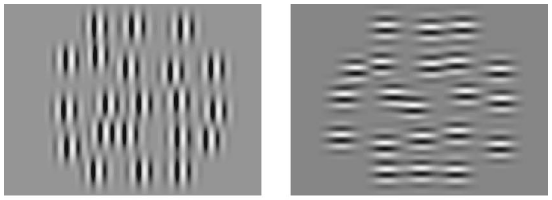
The methods were similar to those for the first experiment. The stimuli (see Fig. 4) were presented at a nominal 20-deg eccentricity in the left, right, upper, or lower visual field. The stimulus area was changed to allow for equal motion trajectories in all four directions. Two displacements were used, 1/4λ and 3.5λ, to isolate the first- and the second-order mechanism, respectively. Previous results (see Figs. 2 and 3 here, Baker and Hess,[38] and Ledgeway and Hess[7]) show that the responses at these displacements are dominated by the first- and the second-order mechanism, respectively.

In pilot studies at this eccentricity centrifugal motion was vividly perceived, but centripetal motion appeared incoherent with no net motion-direction component. This anisotropy provided a cue in a direction-discrimination task; i.e., when subjects did not perceive any motion away from the center, they could conclude that it was going in the other direction. To eliminate this possibility, a two-interval two-alternative forced-choice task was designed; i.e., two judgments were required from the subject. Each trial consisted of two intervals. One of these intervals contained the actual stimulus of a given coherence, the other a 0% coherent stimulus. The coherent stimulus could contain any of seven coherence levels (including 0% coherence, providing “catch trials” to reveal any internal or observer bias). In the first forced-choice judgment, subjects indicated which interval contained the coherent moving stimulus. In each session the direction of motion was either vertical (up–down) or horizontal (left–right). In the second forced-choice judgment, subjects indicated the direction of motion; i.e., in a session in which the direction of motion was vertical, an up–down discrimination was required, and in a session where the direction of motion was horizontal, a left–right discrimination was required. Two displacements, each varying across the seven coherence levels, were interleaved in each session. Because two judgments were required in each trial, chance level was at 75% error.

Two experienced psychophysical observers were used as subjects, one of whom was naïve to the purpose of the study. The subjects used their dominant (right) eyes, and they were instructed to fixate at a provided fixation point. Both observers had normal or corrected-to-normal visual acuity.

B. Results

First-order (1/4λ) and second-order (3.5λ) motion stimuli were interleaved in the same session. Furthermore, a 0% coherence trial was interleaved to assess any internal, or observer, bias. In the 0% coherence trial, both first- and second-order motion were present without a net motion direction. For the coherence judgment no bias was found [see Figs. 5(a) and 5(b)]. In Figs. 5(c) and 5(d) the judged directions, averaged over all four positions, for centrifugal, centripetal and clockwise (90-deg) and counterclockwise (270-deg) motion, are plotted just for the 0% coherence trials. Both observers chose centrifugal motion significantly more than centripetal motion, even though no net motion was present. This result is consistent with the study of Georgeson and Harris,[52] who reported an apparent centrifugal drift with counterphase gratings.

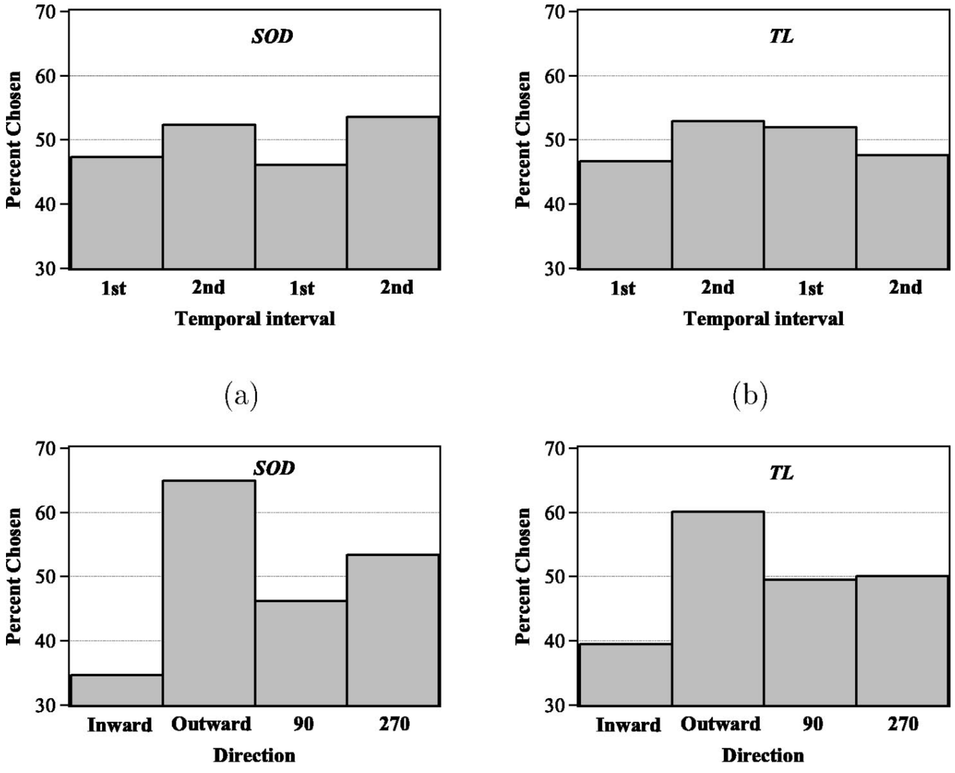


(a) (b)

Fig. 4. Spatial layout of the visual stimuli. Stimulus configuration for (a) horizontal motion and (b) vertical motion The stimuli were presented with the center at a 20-deg eccentricity from the fixation point (ranging from 11 to 29 deg) in the left, right, upper, and lower visual fields.

The internal bias found in Fig. 5 predicts anisotropies in motion-direction judgments that would be a function of observer performance. Thus on the basis of the internal bias alone, anisotropies in either motion mechanism would be predicted as observer performance decreased. These anisotropies would be a function of observer performance: No anisotropies would be found at 0% error, and a maximal anisotropy reflecting the internal bias would be found at 75% error (chance level). The relationship between the internal bias and observer performance relates to the signal-to-noise ratio within the observer. Therefore we assume a linear relationship between the internal bias and the subject's performance:

$$PE_b = C_b \frac{PE}{C}, \tag{2}$$



(a) (b)

(c) (d)

Fig. 5. 0%-coherence trial was intermixed in the trials; i.e., both presentations were of 0% coherence. The data shown here are the average of all four positions. (a), (b) Relative intervals judged to contain the coherent stimulus for two subjects. The plots are for the first or second interval when the stimulus was moving centrifugal/centripetal (first two bars) or clockwise/counterclockwise (last two bars). No clear preference is present. (c), (d) Judgments of direction of motion, revealing internal biases for centrifugal versus centripetal motion for two subjects: SOD, $n = 640$; TL, $n = 320$.

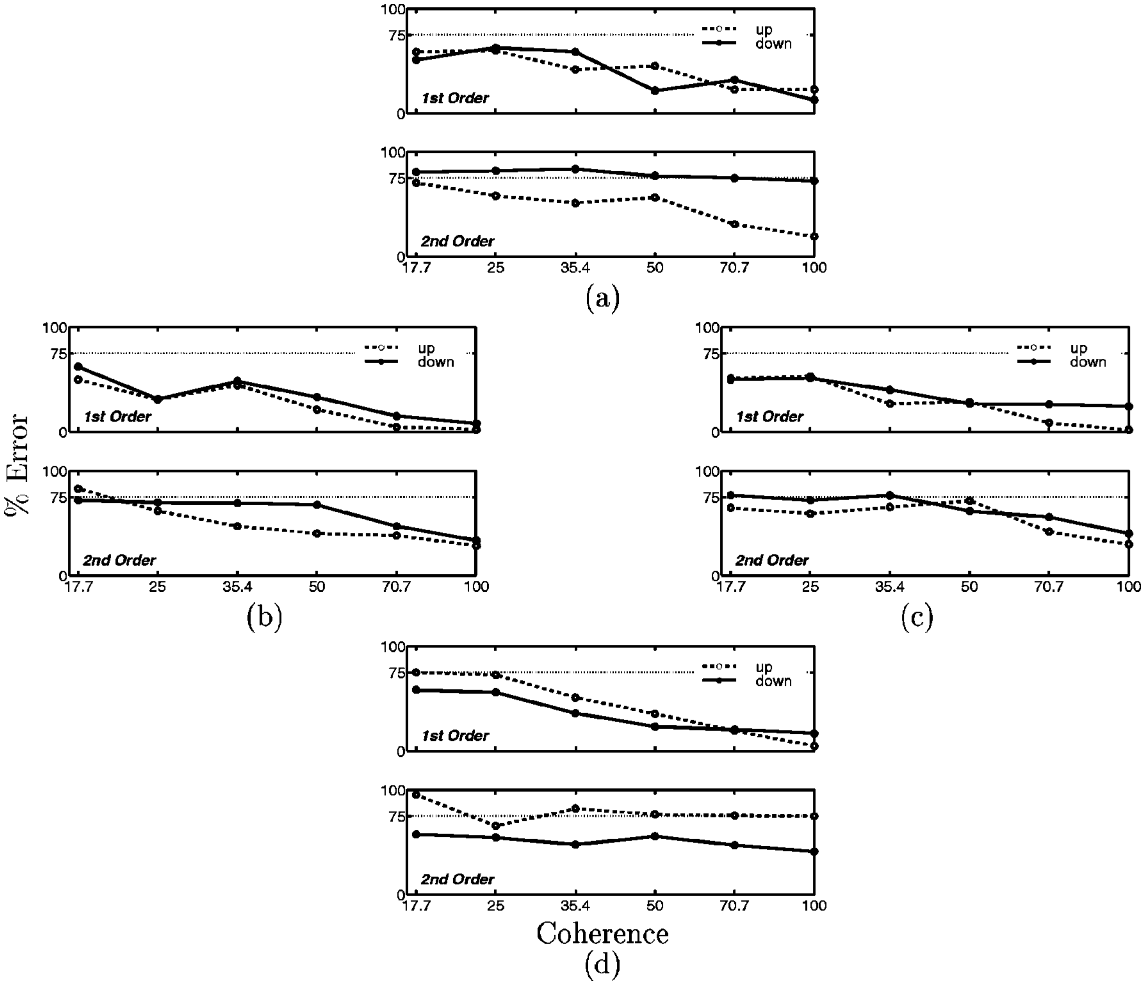


Fig. 6. (a) Upper visual field, (b) left visual field, (c) right visual field, (d) lower visual field: psychometric functions for vertical motion at four different positions in the visual field for one subject ($n = 40$). Percentage errors in a coherence and direction-discrimination task are plotted as a function of coherence for both first- (top graph parts) and second-order (bottom graph parts) motion. Open circles and dashed curves, motion in the upward direction; solid circles and solid curves, downward motion.

where PE is what the percent error should be if no bias were present. PE_b represents the percent error predicted on the basis of the internal bias, C is chance level (75% in this case) and C_b is the error rate that which is produced by the subject on the basis of internal preference, as measured in Fig. 5. The chance level is 75% because the percent errors are a combination of the detection and the discrimination tasks.

The data collected in each of the four positions in the visual field are shown in Fig. 6 (vertical motion) and Fig. 7 (horizontal motion). All these figures show a rising error rate with declining coherences. The data of perceptual judgments to the second-order motion stimuli show higher error percentages than to the first-order stimuli at comparable coherences, consistent with the data in Fig. 2.

For vertical motion (Fig. 6), the second-order data show different error rates measured in the upper and lower visual fields [Figs. 6(a) and 6(d)] but not for the left and right fields [Figs. 6(b) and 6(c)]. A similar result is present for the horizontal motion directions in the left and right fields [Figs. 7(b) and 7(c)] but not for the upper and lower fields [Figs. 7(a) and 7(d)]. In both cases no similar systematic differences are seen for first-order motion. All these differences for second-order motion are consistent with a common centrifugal/centripetal organization. To reveal any centripetal/centrifugal anisotropies, the data from the different parts of the visual field (see Figs. 6 and 7) were selectively averaged on the basis of their directions relative to the fixation point; e.g., data for centrifugal motion directions in the four visual positions were averaged. Similarly, the data in the four positions for centripetal, clockwise, and counterclockwise motion were averaged. The data shown in Fig. 8 are the results of different parts of the visual field, averaged on the basis of their directions relative to the fixation point, and thus they depict more clearly the data of Figs. 6 and 7.

The left and the middle columns of the resulting Fig. 8 shows the percent error as a function of coherence for first-order [Figs. 8(a) and 8(b)] and second-order [Figs. 8(d) and 8(e)] motion. In each graph the data for four different directions relative to the fixation point are plotted separately, i.e., centripetal, centrifugal, clockwise (90 deg), and counterclockwise (270 deg) around the fixation point. The latter two directions served as a control, since they would be unlikely to show a difference. In this figure [Figs. 8(c) and 8(f)] are also plotted the anisotropies predicted purely from the internal bias [Eq. (2)]. The input to the equation, *PE*, was the measured value of average percent error for clockwise and counterclockwise motion for both observers. C_b was estimated from Fig. 5; C was 75%.

All figures show a rising error rate with declining coherence. The data of the second-order motion stimuli show higher error rates than for the first-order stimuli at comparable coherences, consistent with the data in Fig. 2. The perceptual judgments to the first-order stimuli reach error rates at lower coherence levels, similar to the error rates of the detection of second-order motion at higher coherence levels.

Figures 8(a) and 8(b) do not show any large or systematic differences between the different motion directions for first-order motion or a large deviation from the anisotropies predicted by the internal bias [Fig. 8(c)]. Thus we conclude that no measurable first-order anisotropies or bias was evident.

For perceptual judgments to second-order motion [Figs. 8(d) and 8(e)], however, a centrifugal bias was found across a range of coherence levels. It could be argued that this anisotropy is mediated by the internal bias revealed in Fig. 5. However, this anisotropy was larger than predicted by the internal bias alone [Fig. 8(f)]. Furthermore, if the second-order anisotropy were due purely to the internal bias, then the anisotropies should vary as a function of subjects' performance (and thus also with coherence). Figures 8(d) and 8(e) show that the anisotropies are present over a large range of coherences, and the anisotropies do not seem to vary as a function of the coherence. Therefore we would argue that the internal bias cannot explain the second-order anisotropy. Together with the absence of an anisotropy in the responses to first-order stimuli even at comparable error rates, Fig. 8 suggests rather the opposite: that the internal bias found at 0% coherence could be mediated largely by an anisotropy of the second-order motion mechanism.

The first- and second-order mechanisms were selectively activated by the same stimulus but with different displacements. Motion at these displacements with the same temporal properties is thus at different effective velocities. The difference between first- and second-order motion might be due to this velocity difference rather than to the two types of motion *per se*. If this is so, then the bias found would be expected to disappear if the two velocities were similar.

Figures 9(a) and 9(b) show the perceptual judgments to second-order motion at a large range of displacements. The orientation of the Gabors were changed by 90 deg on

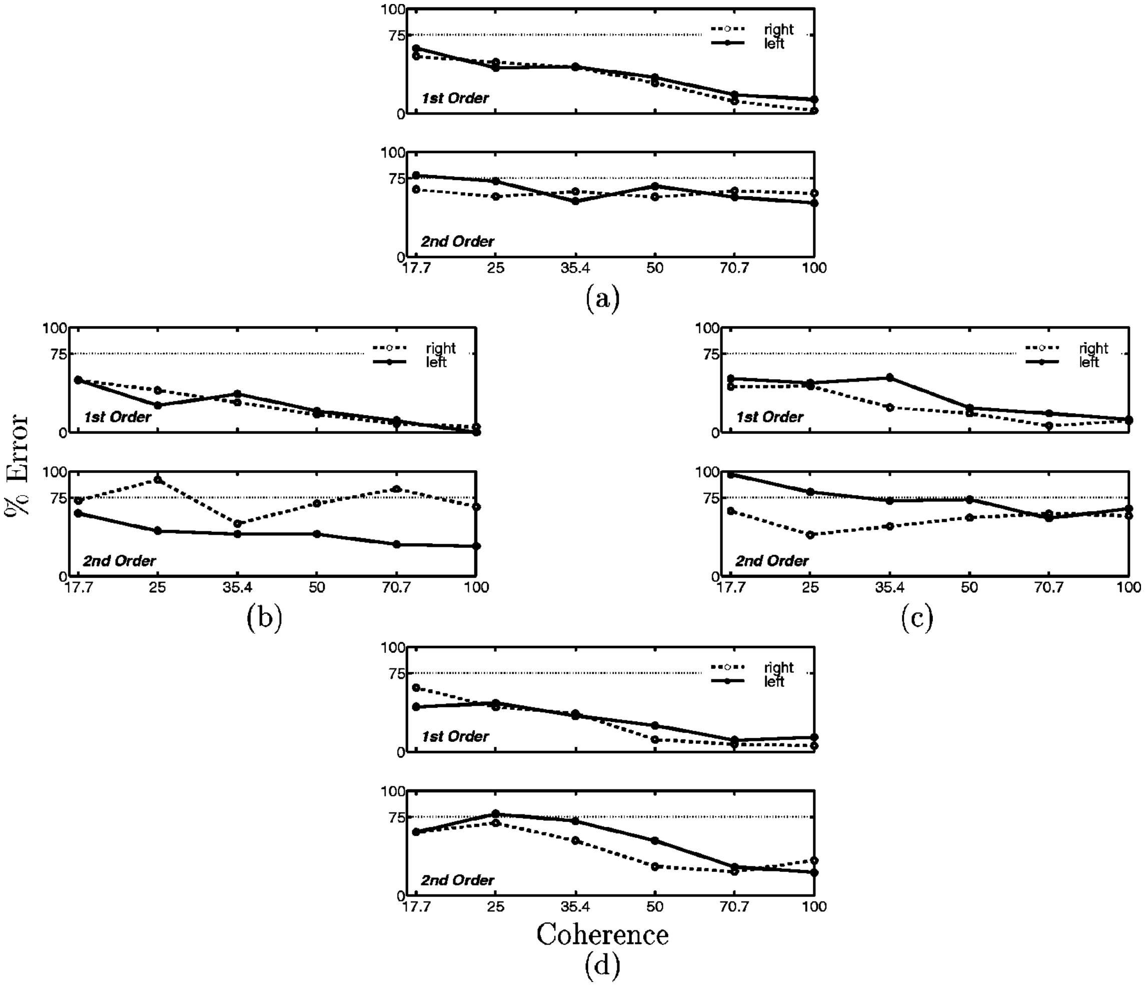


Fig. 7. Same as Fig. 6, but for horizontal motion.

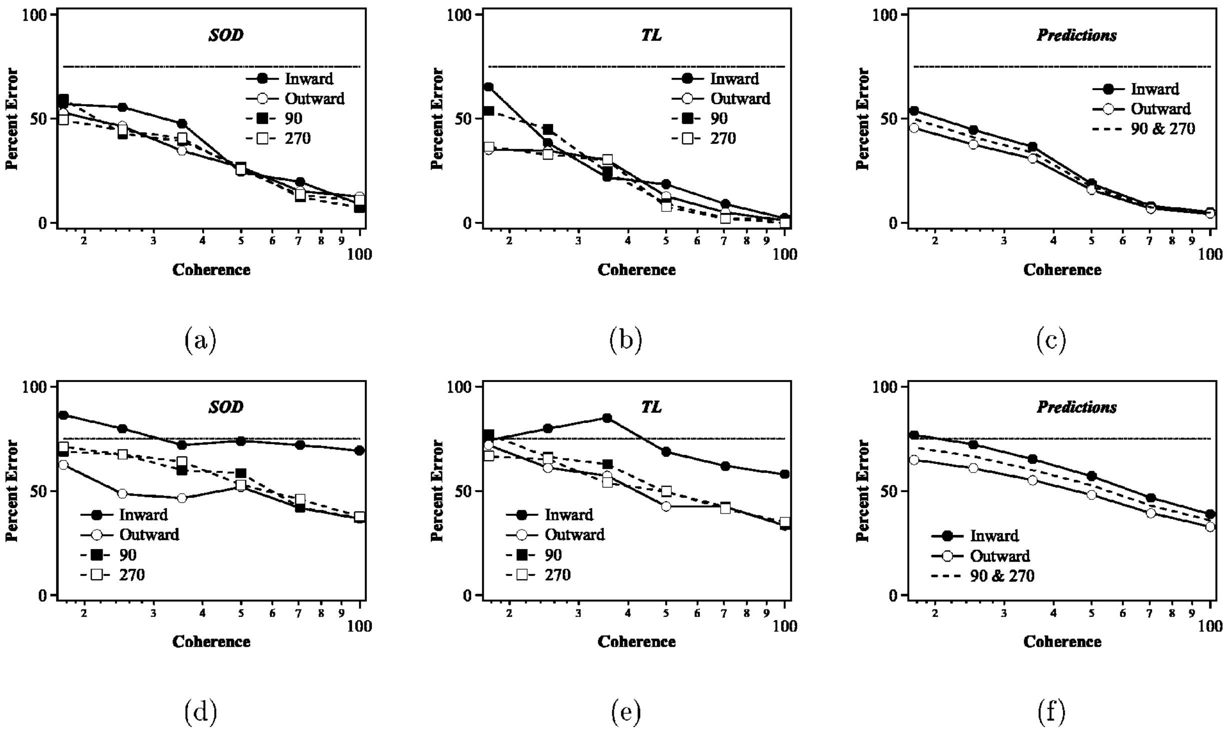


Fig. 8. Psychometric functions at a 20-deg eccentricity for two subjects and predictions based on the internal bias. Percent errors in a coherence and direction-discrimination task are plotted as a function of coherence for first-order motion, (a)–(c), and second-order motion, (d)–(f). Standard error of the mean of each point was smaller than the size of the symbols ($n = 160$ and $n = 80$ for observers SOD and TL, respectively). Solid curves and open circles, centrifugal motion; solid curves and solid circles, centripetal motion; dashed curves with open and solid squares, clockwise and counterclockwise motion, respectively. In (c) and (f) the dashed curve represents the average of the clockwise and the counterclockwise percent errors of observers TL and SOD. The percent errors in (c) and (f) for centripetal and centrifugal motion are calculated according to Eq. (2). The thin line represents chance performance (75%).

alternative exposures to eliminate the contribution of first-order motion to the perceptual judgments.[7,38,39] The total displacements between alternative (like orientations) exposures were multiples of 1/2λ, so the direction of motion could not be determined by a first-order mechanism that correlated every other exposure. The centrifugal bias is present at all displacements, suggesting that the anisotropies of the second-order mechanism are not velocity dependent. At the velocity of the first-order motion stimuli, i.e., a displacement of 1/4λ, the responses to second-order motion reaches $D_{\min}$, i.e., the minimal displacement needed for detecting motion.[69–71] To bring the first-order motion into the velocity range of the second-order stimuli, we performed a control experiment at a lower spatial frequency (λ of 3 deg) and with exposure times of 50 ms [Figs. 9(c) and 9(d)]. This manipulation increased the velocity fourfold. The σ-to-λ ratio of the micropatterns and the relative density of the micropattern distribution were kept constant. The coherence was decreased to 50% to achieve comparable performance (percent errors). Two displacements were used, 1/4 and 3/8λ. These displacements are plotted in Fig. 9(b) at their corresponding velocities (displacements of 1 and 1.5λ). No anisotropies were seen similar in size to those for the second-order mechanism. Therefore we conclude that the difference between first- and second-order motion and the anisotropies of the second-order stimuli are not velocity dependent.

C. Conclusion

Second-order motion, unlike first-order, exhibits a bias for centrifugal directions, suggesting a role for the second-order mechanism in optic flow processing and providing a dissociation between first- and second-order motion processing.

4. GENERAL DISCUSSION

A variety of studies that use contrast-defined second-order motion suggest that second-order motion can be perceived in peripheral vision under appropriate spatiotemporal conditions.[19,46–49] In our first experiment we confirmed these findings, using limited-lifetime Gabor patterns that allowed a comparison of first- and second-order motion with the same stimulus. A significant though weaker contribution of the second-order motion mechanism was found.

In the second experiment a centrifugal bias was found for second-order but not first-order motion mechanisms. Since the performance with centrifugal motion is similar to rotational motion directions, this centrifugal bias seems to be mediated by a reduced sensitivity to centripetal motion rather than to an elevated sensitivity to centrifugal motion. Optic flow patterns due to self-motion with independent head and eye movement contain both translational and rotational components.[72–74] The second-order mechanism is best at detecting the centrifugal and rotational components, and thus the anisotropies described would suggest a role for the second-order system in optic flow processing. This result is in agreement with the results of Gurnsey *et al.*[19] who found a contribution of first-and second-order motion mechanisms to vection (illusory self-motion induced by image flow).

The trials at 0% coherence indicate that a centrifugal bias exists when no net first- or second-order motion is present. This is consistent with the results of Georgeson and Harris,[52] although they used a pure first-order stimulus. The intrinsic bias implies that a centrifugal bias would be more prominent at lower coherence levels. At similar coherence levels the first-order motion mechanism does not show such a bias, whereas the second-order one does. Therefore the result indicates that the intrinsic bias may be mediated largely by the second-order motion mechanism.

Edwards and Badcock[59] and Raymond[60] both found a centripetal preference using random dot stimuli, a result opposite to the one described here. Raymond[60] collected data at smaller eccentricities (up to 12.5 deg). Edwards and Badcock[59] collected data at eccentricities similar to those used in this study (16 to 24 deg) and reported a decline or loss of the observed centripetal bias. Thus the difference between their results and the data described here might be related to the eccentricity at which the data were collected. Neither study distinguishes between first- and second-order motion; however, that does not explain the opposite bias found. The difference in results might be explained on the basis of the internal bias described by Georgeson and Harris[52] and this study. Edwards and Badcock[59] and Raymond[60] measured detection thresholds in a temporal-coherence-judgment two-alternative forced-choice method, i.e., the minimal amount of motion needed to detect global motion in 79% and 71%, respectively, of the cases. The control interval contained incoherent motion. The internal centrifugal bias described by Georgeson and Harris[52] and in this paper is present in incoherent motion. Therefore the difference in perceived motion of low-coherence centrifugal movement and incoherent motion with centrifugal bias is less than the difference between centripetal motion and incoherent motion. Thus the difference in perceived motion, or motion energy, would result in lower thresholds for identifying coherent centripetal motion. Therefore lower-threshold centripetal motion might be elicited by a centrifugal bias. Thus even though they describe lower thresholds for centripetal motion, these results do not necessarily disagree with our data.

Seiffert and Cavanagh[75] suggested that for their stimulus, second-order motion is detected by a mechanism

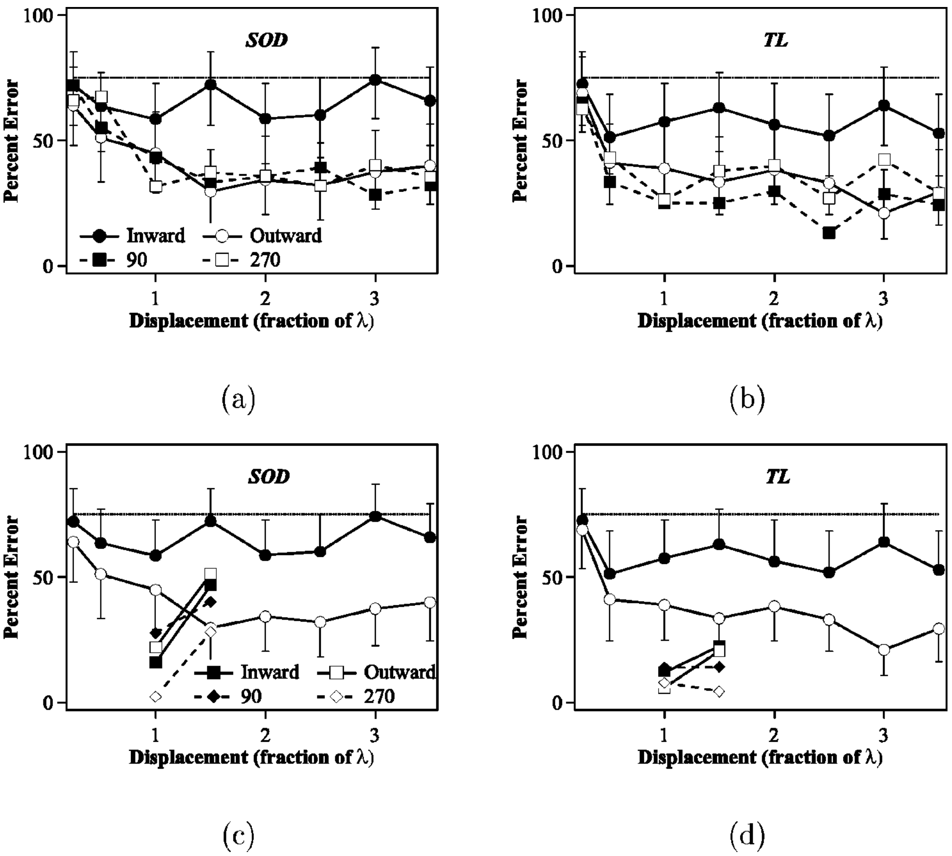


Fig. 9. Percent error in a coherence and direction-discrimination task plotted as a function of the displacement size for two subjects ($n = 40$ for observers SOD and TL). (a), (b) The orientation of the Gabors was changed by 90 deg on alternate exposures thus eliminating contributions from the first-order mechanism. Solid curves and open circles, centrifugal motion; solid curves and solid circles, centripetal motion; dashed curves with open and solid squares, clockwise and counterclockwise motion, respectively. The error bars indicate the upper or lower part of the 95% confidence interval for centripetal and centrifugal motion. The dotted line represents chance performance (75%). (c), (d) Same data as in (a) and (b) are plotted for centripetal and centrifugal motion as well as results of a first-order control experiment at comparable velocities. Solid lines with open and solid squares, centrifugal and centripetal motion, respectively. Dashed lines with open and solid diamonds, clockwise and counterclockwise motion, respectively.

tracking the change of position of features over time. Ledgeway and Hess[7] demonstrated that two mechanisms underlie the perception of the kind of second-order motion described here. They implied that both low-level and high-level second-order mechanisms, such as feature tracking, mediate the perceptual judgments. We cannot say at present which of these two second-order mechanisms is responsible for the reported bias.

To conclude, we have used limited-lifetime Gabor stimuli to identify both first- and second-order mechanisms in peripheral vision. Anistropies in motion directions were found for second- but not first-order motion. The second-order motion mechanism, but not the first-order one, mediates a bias for centrifugal motion. In ecological conditions we are more exposed to centrifugal (expanding) flow patterns owing to our forward motion relative to the world. The second-order centrifugal bias suggests a role for the second-order mechanism in optic flow processing.

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