Pergamon

PII: S0042-6989(97)00088-6

Vision Res., Vol. 37, No. 23, pp. 3399–3405, 1997
© 1997 Elsevier Science Ltd. All rights reserved
Printed in Great Britain
0042-6989/97 $17.00 + 0.00

Radial Motion Looks Faster

PETER J. BEX,*† WALTER MAKOUS*

Received 29 October 1996; in revised form 7 January 1997

Current models of motion perception depend on unidirectional motion-sensitive mechanisms that provide local inputs for complex pattern motion, such as optic flow. To test the generality of such models, we asked observers to compare the speed of radial gratings with the translational speed of vertical gratings. The speed of the radial gratings was consistently overestimated by 20–60% relative to that of translating gratings that were identical in all other respects. The speed bias was not associated with a general spatial or temporal processing bias, nor with the high *relative* speed of points about the center of expansion/contraction. The bias increased non-linearly with the size of sectors of the radiating pattern exposed. As the motion of the two patterns was locally identical but judged differently, the apparent speed of both kinds of motion cannot be served by any mechanism, nor described by any model, that is based entirely on local motion signals. We speculate that the greater apparent speed of the radial motion has to do with apparent motion in depth. © 1997 Elsevier Science Ltd

Motion Speed Optic flow Depth

INTRODUCTION

In recent years, much has been learned about the mechanisms involved in the detection of motion by human observers. Several models are now available to account for local detection of translational motion (for review see Nakayama, 1985). From the known spatial (e.g. De Valois and Switkes, 1980) and temporal (Foster *et al.*, 1985) selectivity of cells in primate visual cortex, an estimate of local velocity can, in principle, be encoded by variants of such models (e.g. Heeger, 1987; Grzywacz & Yuille, 1990; Smith & Edgar, 1994). Speed can be determined from these spatio-temporal properties according to the identity:

$$V = \omega_t/\omega_s \qquad (1)$$

where V is speed in deg/sec, ω_t is temporal frequency in Hz and ω_s is spatial frequency in c/deg.

Recently, attention has turned to higher level optic flow mechanisms that might use local motion signals to encode ego motion and three-dimensional image structure. Several hierarchical models of optic flow have been proposed in which higher level mechanisms combine local direction and speed (i.e., velocity) signals to determine the focus of expansion and the direction of heading (Zhang *et al.*, 1993; Lappe & Rauschecker, 1994, 1995). This hierarchical approach is supported by a number of electrophysiological studies in primate visual cortex showing sensitivity to more complex patterns of motion at higher stages of visual processing (Van Essen & Maunsell, 1983). Simple translational motion is first encoded in area V1, where many cells show directionally selective responses. Selectivity for translational motion is maintained in area MT (Saito *et al.*, 1986), but receptive fields are larger. Higher areas (MSTd) show selectivity for more complex forms of pattern movement, such as radial or spiral motion (Tanaka & Saito, 1989; Duffy & Wurtz, 1991; Orban *et al.*, 1992; Graziano *et al.*, 1994). Similar selectivity for complex patterns of motion has also been reported from recordings of inter-neurons in the third visual neurophile of the blowfly (Krapp & Hengstenberg, 1996), where cells with large receptive fields respond selectively to optic flow components.

Psychophysical studies also support the hierarchical arrangement of motion detection mechanisms. Freeman & Harris (1992) found that detection thresholds for coherently expanding and rotating groups of dots were lower than for coherently translating groups or incoherent groups containing the same distribution of local motions. Morrone *et al.* (1995) reported that detection thresholds for random dot patterns undergoing radial and rotational motion fell predictably with the visible extent of the patterns. These studies suggest that the local motions in rotating and expanding images are combined by specialized higher level mechanisms that integrate across large spatial scales. Freeman & Harris (1992) also found that the detection of rotation was unaffected by the presence of expansion and *vice versa*, and Regan & Beverly (1978) argued that expansion is encoded independently of contraction, suggesting separate mechanisms may exist for each class of global motion.

Little is known about how local motion signals

---

*Center for Visual Science, University of Rochester, 274 Meliora Hall, Rochester, NY 14627-0268, U.S.A.

†To whom all correspondence should be addressed [*Fax*: +1-716 271 3043; *Email*: bex@cvs.rochester.edu].

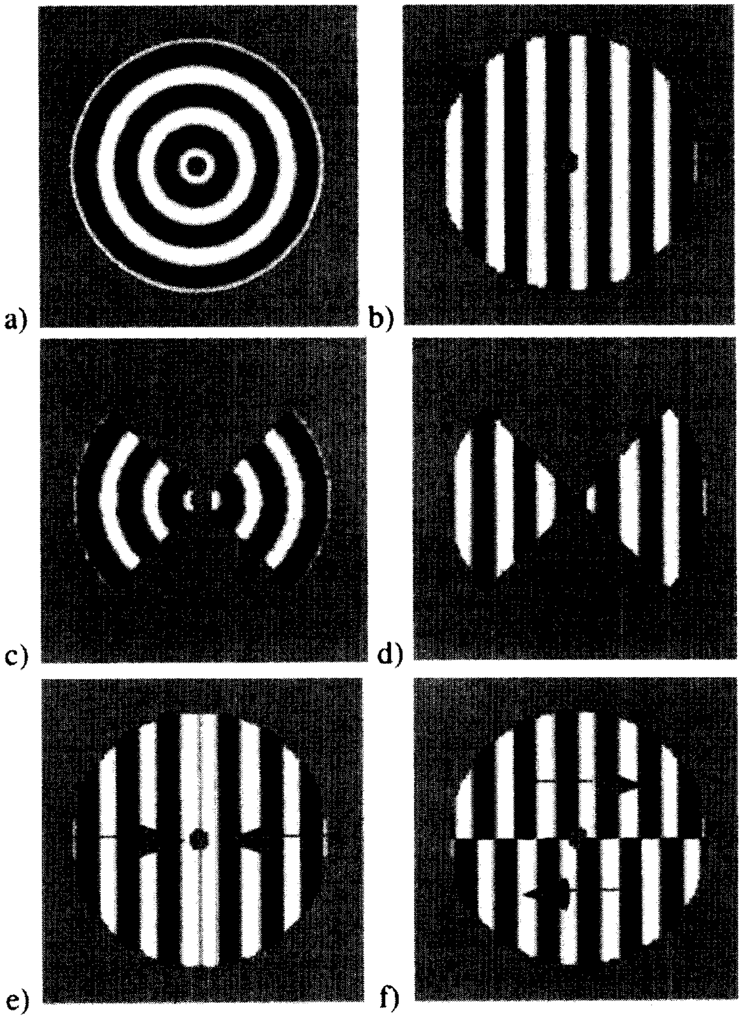

FIGURE 1. Schematic illustrations of the stimuli. (a) radial sinusoidal grating; (b) vertical sinusoidal grating. In (c) and (d) upper and lower segments of the patterns have been masked by uniform sectors at the mean luminance; illustrated here is a 180 deg visible pattern, masked by two 90 deg sectors. In (e) and (f) the vertical sinusoidal grating field has been halved through the fixation point, either vertically (e) or horizontally (f). Gratings in each hemi-field drifted in opposite directions, illustrated here are one of each combination of directions. The gratings were presented at 50% contrast in a circular aperture that subtended 8 deg, surrounded by a blank field of mean luminance extending 18 deg horizontally and 13.8 deg vertically. Initial starting phase of all gratings [including separate hemi-fields, for (e) and (f)] was randomized. Observers compared the apparent speed of pairs of gratings in two intervals.

combine to yield information about global pattern speed. We report here observations showing that the rule of combination depends on the spatial configuration of the motion. We asked observers to compare the apparent speed of drifting radial gratings (rings) to that of drifting translating gratings of the same spatial frequency [see Fig. 1(a) and (b)]. Along any radius of the radial grating, the spatial and temporal structure is identical to a horizontal radius of the translating grating. For any local area of either pattern (that might correspond to a simple cell receptive field in visual cortex (e.g. Field & Tolhurst, 1986) the spatial and temporal structure of the two patterns is identical, except for a possible difference in orientation. Locally, therefore the speed of both radial and vertical gratings is the same. Simple rules for combining local motion signals dictate that the apparent speed of the two patterns should be equal. However, the results showed that the apparent speed of a ringed pattern was faster (by as much as 60%) than that of a translating grating of the same spatial and temporal frequency. The bias was not related to a general spatial or temporal frequency bias because the apparent spatial frequency and flicker rate of the two patterns was the same. The bias was not associated with the relative speed of points about fixation because the speed of a vertical grating containing relative motion was not overestimated unless it represented radial motion in one dimension. This result also rules out the possibility that smooth pursuit eye movements reduced the retinal velocity of translating gratings but not radial gratings. We speculate that the speed bias can be interpreted in terms of a simple geometrical principle, such that for radial motion, local motion is misperceived as motion in depth at a correspondingly greater speed.

METHODS

Stimuli were generated by a Power Macintosh 7100/80 AV and were presented on a Nanao Flexscan 6500 gray-scale monitor at a frame rate of 75 Hz. The mean luminance of the display was 55 cd/m^2. The luminance of the display was linearized to pseudo-12 bit resolution by combining the output of three 8 bit DACs (Pelli & Zhang, 1991) and calibrated with a Minolta Chromameter. Pseudo 12 bit resolution in this case allowed the use of 2^8 luminance levels from a possible range of 2^{12} levels. The display was 18 deg horizontally (1152 pixels) by 13.8 deg vertically (870 pixels) and was viewed in a dark room from a distance of 115 cm. Observers had normal or corrected vision and viewed the screen binocularly.

A standard and match grating were presented in temporal forced choice. In the main experiment, the standard stimulus was a radial sinusoidal grating [Fig. 1(a)]; the match was a horizontal grating of the same contrast and spatial frequency [Fig. 1(b). In the center of each pattern was a prominent fixation point consisting of a 0.5 deg uniform patch held constant at the mean luminance of 55 cd/m^2. Both patterns were presented at 50% contrast in a circular aperture that subtended 8 deg. The gratings were drifting or flickering; the initial spatial and temporal phase was randomized. We considered and tested alternative standard stimuli with velocity and size gradients more closely mimicking optic flow patterns. However, such patterns required changes in velocity and spatial frequency with eccentricity that made speed matching impossible. Although the radial grating does not have the true velocity gradient of an optic flow field, its spatial and temporal structure approximates optic flow accompanying ego motion or expansion/contraction of an object moving in depth. The principle advantage of a radial sine grating however is that it has constant velocity along any radius, allowing facile speed comparison with the match sine grating. Matches of three different stimulus properties were made: drift speed, spatial frequency and flicker rate. In each case the spatial and temporal frequency of the standard radial grating was fixed for a particular run, and the relevant parameter of the match vertical grating was varied from trial to trial according to the method of constant stimuli. In Experiment 1, drift speed was matched: the spatial frequency of both gratings was equal, and the drift speed of the match grating was varied. The spatial frequency of the standard (radial) grating was 1, 2 or 4 c/deg, and for each spatial frequency the temporal frequency of the standard grating was 1, 2, 4 or 8 Hz. In pilot experiments, we ascertained that the apparent speed of translation was independent of direction and that expanding radial motion was equal to that of contracting radial motion. Therefore, the direction of motion of test and match gratings was randomized from trial to trial to minimize the build-up of motion aftereffects.

Experiment 2 was the same as Experiment 1 for a subset of conditions (2 c/deg and 8 Hz), except that a blank sector was introduced above and below fixation, and the perceived speed of the radial grating was measured as a function of the angle of the sector [see Fig. 1(c) and (d)]. In Experiment 3, spatial frequency was matched. The spatial frequency of the standard (radial) grating was 1, 2 or 4 c/deg, and the spatial frequency of the match grating was varied. Both gratings were flickered at 2 Hz to minimize after-images. In Experiment 4, flicker rate was matched: the spatial frequencies of both gratings were equal (1, 2 or 4 c/deg), and the flicker rate of the match grating was varied to match an 8 Hz standard. In a final experiment, speed matches were performed as in the main experiment for two control patterns designed to determine how much relative motion and pursuit eye movements contributed to the estimates of apparent speed. In each case, the standard stimulus was a pair of drifting sinusoidal gratings presented in the circular aperture. The field was split either horizontally or vertically and the gratings drifted in opposite directions in each hemi-field, as illustrated in Fig. 1(e) and (f). The match grating was a simple grating as before [Fig. 1(b)].

In the two-alternative forced-choice, the sequence of presentation of standard and match grating was random. Each interval lasted 1 sec and was separated by 0.5 sec, during which the screen was a blank field at the mean luminance of the gratings. The observer initiated each trial and maintained steady fixation. The observers' task was to indicate whether the pattern in the first or second interval was faster (or of higher spatial frequency in Experiment 3 or higher flicker rate in Experiment 4), ignoring other differences between the patterns. A Weibull function (Weibull, 1951) was fitted to the data, from which the point of subjective equality was estimated at the 50% level. The presentation sequence for the various conditions was randomized, and each data point is based on at least 200 discriminations.

RESULTS

In Experiment 1, observers compared the speed of expanding or contracting patterns of radial gratings to that of vertical translating gratings presented in two time intervals. The match speed was the speed of the vertical grating at which the observers judged the apparent speed of the two patterns to be equal. Figure 5 (circles) shows typical psychometric functions for two observers, showing the proportion the match grating was judged faster at each of the speeds illustrated on the x-axis when compared with a 2 c/deg radial grating drifting at 4 c/sec. From these data, equal apparent speed was determined from the 50% point of a Weibull function fitted to the data. Figure 2 shows the relative perceived speed of the patterns for different spatial and temporal frequencies: the perceived speed of the rings was overestimated relative to that of the grating by approximately 20–60%.

A blank sector was introduced in Experiment 2, and the speed matches were repeated for a 2 c/deg standard ringed pattern drifting at 4 c/sec. Figure 3 shows the relative perceived speed of the radial and vertical sine wave grating as a function of the visible extent of the stimuli. The results show that the estimated speed of the

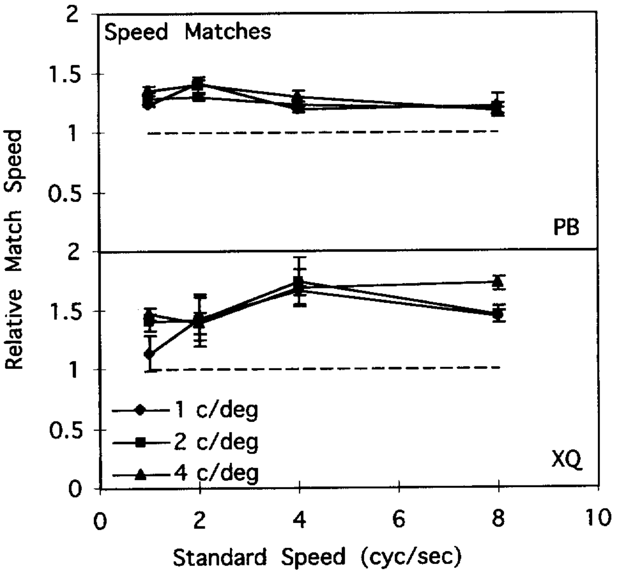

FIGURE 2. Perceived speed of the rings for a range of spatial and temporal frequencies for two observers (PB and XQ). The x-axis shows the speed of the rings in cycles per second; the y-axis shows the relative speed of the grating at which the apparent speeds of the patterns were equal. The broken line illustrates equal speed: points above the line indicate that the rings pattern appeared faster than the grating; below the line, the rings appeared slower. For a range of spatial and temporal frequencies, the perceived speed of the rings was overestimated by about 30% for PB and between 20 and 60% for XQ.

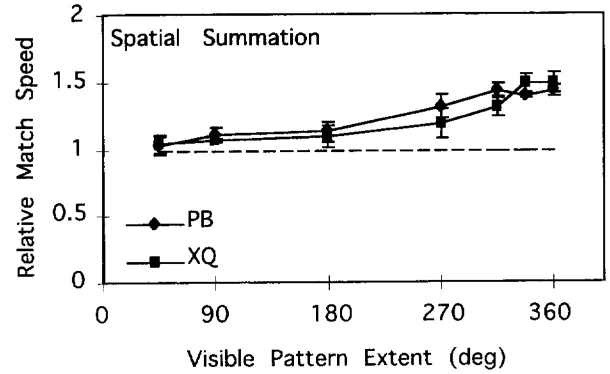

FIGURE 3. Perceived speed of the rings as a function of the visible extent of the pattern. The spatial frequency of the rings and grating was 2 c/deg, and the drift speed of the rings was 4 c/sec. The data show a non-linear increase in perceived speed of the rings with increasing pattern area. This suggests that mechanisms that detect the radial motion of the rings sum local translational motion signals non-linearly.

rings was within 10% of the correct speed as long as the area of the visible sector of the rings was restricted to 180 deg or less. However, perceived speed increased rapidly and non-linearly with further increases of the visible extent of the pattern.

In Experiments 3 and 4, observers compared the spatial frequencies and counterphase flicker rates of radial and vertical gratings. Figure 4 shows that both spatial frequency and counterphase flicker rate of radial and vertical gratings were perceived as approximately equal. This confirms that the overestimation of radial speed is not the result of a general bias of spatial or temporal frequency in the radial motion pattern.

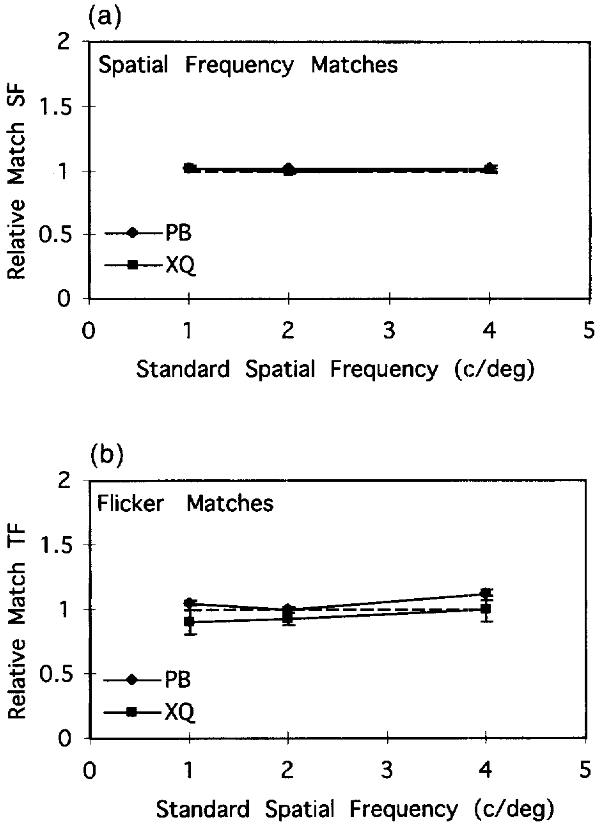

FIGURE 4. For two observers (PB and XQ): (a) spatial frequency matches between a ringed pattern and a vertical grating. Both patterns were counterphase flickered at 2 Hz; (b) temporal frequency matches between counterphase flickering rings and a vertical grating. The rings were flickered at 8 Hz, which was too fast for observers to count the temporal modulations. The spatial frequency of both patterns was 2 c/deg. The results show that the spatial and temporal frequency of the patterns was perceived as equal, even though their perceived speed differed.

One potential source of bias in speed estimates of radial motion is the relative speed of points on opposite sides of the center of expansion/contraction. Thus, a point moving towards or away from the center of motion at a given speed moves at twice the speed relative to a corresponding point beyond the center of motion. There is no such bias in simple translating patterns. Alternatively, a difference in apparent speed might arise if the retinal speed of translational motion is reduced by smooth pursuit eye movements. Figure 5 shows psychometric functions for three conditions that test these possibilities: circles show speed judgments for radial patterns [Fig. 1(a)]; squares show 1-D expansion/contraction [Fig. 1(e)]; triangles show shear [Fig. 1(f)]. It can be seen that the apparent speed of shearing motion is approximately equal to that of translation; 1-D radial motion appeared faster and 2-D radial motion appeared even faster still.

DISCUSSION

Implications for motion detection models

The results of Experiments 1 and 2 show that the apparent speed of radial motion is greater than that of

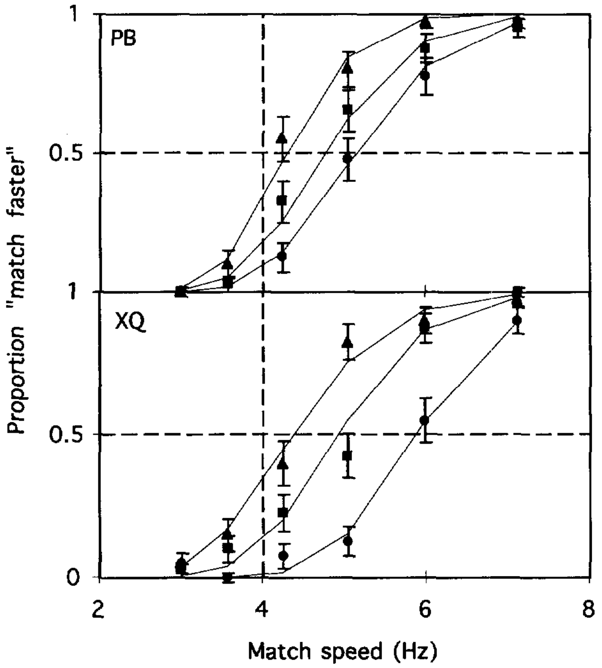

FIGURE 5. Psychometric functions for two observers (PB and XQ) who matched the speed of a drifting sine grating to that of a 2 c/deg test grating drifting at 4 c/sec. The test gratings were: radial gratings [circles—Fig. 1(b)], one-dimensional expansion/contraction [squares—Fig. 1(e)] or shearing [triangles—Fig. 1(f)]. The *x*-axis shows the speed of a match sine grating [Fig. 1(a)], the *y*-axis shows the proportion of times the match grating was judged faster than the test pattern. Error bars show the binomial standard deviation, based on a minimum of 40 observations per data point. The data have been fitted by psychometric functions (Weibull, 1951) by least Chi-squares fit, from which subjective speed equalities were estimated at the 50% point, with the 95% confidence intervals as follows:

	XQ	95% c. i.	PB	95% c. i.
2-D radiation	5.88	0.22	5.14	0.21
1-D radiation	4.92	0.21	4.78	0.19
Shear	4.36	0.20	4.30	0.17

translational motion of the same actual speed. Eq. (1) shows that an increase in the apparent speed of radial motion could arise from either an overestimation of the temporal frequency of the radial grating or an underestimation of its spatial frequency. Experiments 3 and 4 showed that both the spatial and temporal frequency of radial and vertical gratings were perceived as equal, ruling out this possibility.

Models of motion detection that are based on spatial and temporal frequency analysis such as motion energy models (e.g. Adelson & Bergen, 1985; Watson & Ahumada, 1985) or correlation models (e.g. van Santen & Sperling, 1985) yield the same local output for both radial and translational patterns and so, in themselves cannot account for these results. Gradient motion detection models, which compare the responses of filters tuned to flickering and static patterns by calculating the ratio of flicker to pattern responses, and compute velocity from the quotient of the filter outputs, again compute the same local speed for radial and vertical gratings. Another approach to motion detection is based on matching spatial primitives between successive image locations (e.g. Morgan, 1992; Eagle & Rogers, 1996). Although speed encoding has not been incorporated into such models as yet, the rate of displacement of spatial primitives (zero crossings or peaks) is the same for both radial and translating patterns, and so their apparent speed should be the same.

No current model of motion detection can account for these results without hypothesizing a meta-stage that combines local signals differently, depending on the relative orientation of the local motion. It was mentioned above that the receptive field sizes of motion-sensitive cells increase at higher stages of processing (Saito *et al.*, 1986). Note, however, that for the drifting radial grating, motion is equal and opposite in all directions, so simple integration over a larger area would tend to decrease the overall speed estimate, opposite to the effect observed here (Fig. 2).

Role of relative motion or pursuit eye movements

The subjects were experienced psychophysical observers (although one was naïve with respect to the purposes of the experiment), and generally could be expected to maintain fixation as instructed; nevertheless, it is inherently more difficult to fixate steadily in the presence of a translating grating than a radial grating. Any eye movements in pursuit of a moving grating reduce its retinal speed, and this could account for its slower apparent speed. However, in the control experiments, steady fixation was facilitated by shearing and 1-D radial motion, and slowing the retinal motion of one grating by pursuit eye movements correspondingly increases the retinal motion of the grating moving in the opposite direction. Shearing gratings, which contain no components of radial motion but do have a form of motion contrast, appeared to move with the same speed as unidirectional translating gratings, showing that neither pursuit eye movements nor motion contrast are sufficient to cause an overestimation of speed. The 1-D radial patterns appeared faster than the translating gratings, but not as fast as the 2-D radial gratings, which is qualitatively consistent with the sector experiment (Fig. 3).

Taken together, the results of these two control conditions suggest that relative motion or smooth pursuit eye movements cannot account for the speed bias. However, one of the controls did appear faster than translational motion, but in this case the pattern contained radiation along one dimension of motion, supporting the general finding that radial motion looks faster, even if represented by a single dimension of motion.

Relation to previous research

Verghese & Stone (1995, 1996) have shown that speed discrimination decreases as multiple drifting micropatches combine to form a single patch of coherent motion. This shows that sensitivity to motion depends on the relative direction of motion at different loci. The authors argue that higher level pattern analysis, such as segregation and grouping, can affect processes that have previously been assumed to occur at the earliest stages of processing, such as speed encoding. However, the changes in pattern configuration were accompanied by local changes in spatial frequency and orientation bandwidth that may have contributed to speed discrimination thresholds at a local rather than global stage of motion processing. Our results confirm their suggestion by showing that apparent speed depends on the relative direction of motion at different loci, a result that requires a mechanism such as they hypothesized.

Regan & Beverly (1978) demonstrated that radial and translational motion depend on separate mechanisms, for adaptation to one pattern of motion does not affect sensitivity to the other. The present results represent a second line of evidence for separate mechanisms.

Sekuler (1992) showed that speed discriminations for looming and rotating dot patterns are the same, and pointed out that as these results require nothing more than linear summation of local motion signals, there is no need to invoke higher level mechanisms to explain them. However, quite aside from the differences between experiments (Sekuler compared radial to rotational motion of dots, and we compared radial motion to translational motion of gratings), there is no conflict between their results and ours, for their results do not exclude the existence of the higher level mechanisms we find necessary, and our results simply mean that the discriminations of radial motion are performed on gratings appearing to move faster than the corresponding rotational gratings: no difference in discriminability necessarily follows.

After the present paper had been submitted, Geesaman & Qian (1996) published a paper showing, like the present one, that the apparent speed of radiating random dot patterns appears faster than rotating dot patterns, and that the magnitude of the illusion increases with increases of signal/noise and, like the present study, with the visible extent of the pattern. The two papers, taken together, show that the overestimation of radial gratings is not due to: any peculiarity of dot patterns, such as dot lifetime (e.g., Treue *et al.*, 1993) or curvature of path, in their case, or of gratings in ours; nor to cyclo-rotation of the eye in their case, or to pursuit eye movements in ours (see Fig. 5 also). Perhaps, however, the differences in technique account for the fact that in Geesaman and Qian's paper, apparent speed increases with a negatively accelerated function of sector size, whereas ours is positively accelerated.

Geesaman and Qian attributed the illusory speed increase to a supposed difference in relative number of cells sensitive to expansion as opposed to rotation, based on the relative numbers of such cells sampled and studied by neurophysiologists. Instead, we suggest that the phenomenology of radial motion may offer a clue to the reason for the apparent speed difference. When in motion, the radial grating tends to resemble a concave cone rather than a flat grating on the surface of the display. Such radial motion is frequently encountered naturalistically as part of the optical flow associated with motion with respect to the environment (ego-motion) under conditions rather different from those most often associated with translational motion across the point of fixation. It is not implausible that different mechanisms might have evolved to handle the two kinds of motion. To be sure, the radial grating is not identical to the pattern of optic flow associated with ego-motion, and that may be why the illusion is not stronger than it is, but presumably the radially moving rings are similar enough to optic flow to excite the same mechanisms. If so, the radial grating may appear to be moving in depth with respect to the observer and must travel a further distance in the same time (i.e., move faster), as shown in Fig. 6. If this were the case, the speed bias would be consistent with an orientation (θ) of 30–50 deg with respect to the screen.

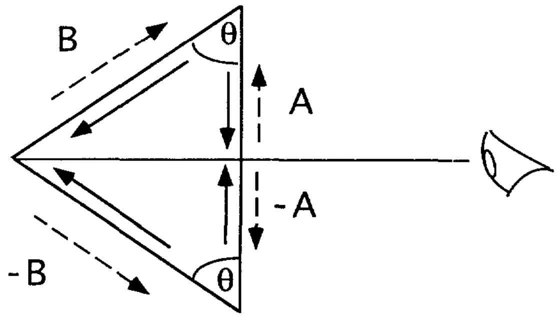

FIGURE 6. Perceived speed and direction of radial motion. An eye on the right of the figure observes local translational motion of speed A but motion is perceived in direction θ at speed B. The angle θ calculated from the data in Fig. 2(a) is between 34 and 51 deg.

CONCLUSIONS

These results show that, although local spatial and temporal coding is equivalent for translational and radial motion, the corresponding perceived speeds differ. Hence, they confute any model in which the *same* rules for integrating local velocity signals are used in assembling higher level receptive fields sensitive to *different* global patterns of motion.

REFERENCES

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

De Valois, K. K. & Switkes, E. (1980). Spatial frequency specific interaction of dot patterns and gratings. *Proceedings of the National Academy of Sciences USA, 77*, 662–665.

Duffy, C. J. & Wurtz, R. H. (1991). Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli. *Journal of Neurophysiology, 65*, 1329–1345.

Eagle, R. A. & Rogers, B. J. (1996). Motion detection is limited by element density not spatial frequency. *Vision Research, 36*, 545–558.

Field, D. J. & Tolhurst, D. J. (1986). The structure and symmetry of simple-cell receptive-field profiles in the cat's visual cortex. *Proceedings of the Royal Society of London B , 228*, 379–400.

Foster, K. H., Gaska, J. P., Nagler, M. & Pollen, D. A. (1985). Spatial and temporal frequency selectivity of neurones in visual cortical areas V1 and V2 of the macaque monkey. *Journal of Physiology, 365*, 331–363.

Freeman, T. C. A. & Harris, M. G. (1992). Human sensitivity to expanding and rotating motion: effects of complementary masking and directional structure. *Vision Research, 32*, 81–87.

Geesaman, B. J. & Qian, N. (1996). A novel speed illusion involving expansion and rotation patterns. *Vision Research, 36*, 3281–3292.

Graziano, M. S., Andersen, R. A. & Snowden, R. J. (1994). Tuning of MST neurons to spiral motions. *Journal of Neuroscience, 14*, 54–67.

Grzywacz, N. M. & Yuille, A. L. (1990). A model for the estimation of local image velocity by cells in the visual cortex. *Proceedings of the Royal Society of London B, 239*, 129–161.

Heeger, D. J. (1987). Model for the extraction of image flow. *Journal of the Optical Society of America A, 4*, 1455–1471.

Krapp, H. G. & Hengstenberg, R. (1996). Estimation of self motion by optic flow processing in single visual interneurons. *Nature, 384*, 463–466.

Lappe, M. & Rauschecker, J. P. (1994). Heading detection from optic flow. *Nature, 369*, 712–713.

Lappe, M. & Rauschecker, J. P. (1995). An illusory transformation in a model of optic flow processing. *Vision Research, 35*, 1619–1631.

Morgan, M. J. (1992). Spatial filtering precedes motion detection. *Nature, 355*, 344–346.

Morrone, M. C., Burr, D. C. & Vaina, L. M. (1995). Two stages of visual processing for radial and circular motion. *Nature, 376*, 507–509.

Nakayama, K. (1985). Biological image motion processing: a review. *Vision Research, 25*, 625–660.

Orban, G. A. (1992). First-order analysis of optical flow in monkey brain. *Proceedings of the National Academy of Science USA, 89*, 2595–2599.

Pelli, D. G. & Zhang, L. (1991). Accurate control of contrast on microcomputer displays. *Vision Research, 31*, 1337–1350.

Regan, D. & Beverly, K. I. (1978). Looming detectors in the human visual pathway. *Vision Research, 18*, 415–421.

Saito, H. A. (1986). Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. *Journal of Neuroscience, 6*, 145–157.

Sekuler, A. B. (1992). Simple-pooling of unidirectional motion predicts speed discrimination for looming stimuli. *Vision Research, 32*, 2277–2288.

Smith, A. T. & Edgar, G. K. (1994). Antagonistic comparison of temporal frequency filter outputs as a basis for speed perception. *Vision Research, 34*, 253–265.

Tanaka, K. & Saito, H. (1989). Analysis of motion of the visual field by direction, expansion/contraction, and rotation cells clustered in the dorsal part of the medial superior temporal area of the macaque monkey. *Journal of Neurophysiology, 62*, 626–641.

Treue, S., Snowden, R. J. & Andersen, R. A. (1993). The effect of transiency on perceived velocity of visual patterns: a case of "temporal capture". *Vision Research, 33*, 791–798.

Van Essen, D. C. & Maunsell, J. H. R. (1983). Hierarchical organization and functional streams in the visual cortex. *Trends in Neurosciences, 6*, 370–375.

van Santen, J. P. & Sperling, G. (1985). Elaborated Reichardt detectors. *Journal of the Optical Society of America A, 2*, 300–321.

Verghese, P. & Stone, L. S. (1995). Combining speed information across space. *Vision Research, 15*, 2811–2823.

Verghese, P. & Stone, L. S. (1996). Perceived visual speed constrained by image segmentation. *Nature, 381*, 161–163.

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

Weibull, W. (1951). A statistical distribution function of wide applicability. *Journal of Applied Mechanics, 18*, 292–297.

Zhang, K. & Sereno, M. I. (1993). Emergence of position-independent detectors of sense of rotation and dilation with Hebbian learning: an analysis. *Neural Comp., 5*, 597–612.

Acknowledgements—This research was supported by U.S. Public Health Service Grants EY-4885 and EY-1319. We are grateful to Xiaofeng Qi for observing.