

# Psychophysical evidence for a functional hierarchy of motion processing mechanisms

Peter J. Bex,\* Andrew B. Metha, and Walter Makous

*Center for Visual Science, University of Rochester, 274 Meliora Hall, Rochester, New York 14627-0268*

Received June 20, 1997; revised manuscript received November 25, 1997; accepted December 1, 1997

Current models of motion perception typically describe mechanisms that operate locally to extract direction and speed information. To deal with the movement of self or objects with respect to the environment, higher-level receptive fields are presumably assembled from the outputs of such local analyzers. We find that the apparent speed of gratings viewed through four spatial apertures depends on the interaction of motion directions among the apertures, even when the motion within each aperture is identical except for direction. Specifically, local motion consistent with a global pattern of radial motion appears 32% faster than that consistent with translational or rotational motion. The enhancement of speed is not reflected in detection thresholds and persists in spite of instructions to fixate a single local aperture and ignore the global configuration. We also find that a two-dimensional pattern of motion is necessary to elicit the effect and that motion contrast alone does not produce the enhancement. These results implicate at least two serial stages of motion-information processing: a mechanism to code the local direction and speed of motion, followed by a global mechanism that integrates such signals to represent meaningful patterns of movement, depending on the configuration of the local motions. © 1998 Optical Society of America [S0740-3232(98)01804-3]

*OCIS codes:* 330.4150, 330.4270, 330.5510, 330.6790.

## 1. INTRODUCTION

Contemporary modelers of motion perception typically postulate local mechanisms that are selective for the direction of motion and spatiotemporal frequency of moving patterns.<sup>1-3</sup> Little is known about how such motion signals combine to provide information about the movement of objects in the real world, but some models of higher-level motion processing depend on local estimates of velocity that might be encoded by such mechanisms.<sup>4-6</sup> There is a growing body of behavioral evidence to support such hierarchical organization. The first evidence was reported by Regan and Beverley,<sup>7</sup> who measured detection thresholds following adaptation to the motion of the edges of square patterns. Out-of-phase oscillation of opposite edges resulted in looming motion about a central point, but in-phase oscillation resulted in diagonal translation of the square, with no change in size. Out-of-phase adaptation raised thresholds for detecting looming motion much more than equivalent in-phase adaptation, despite the fact that the only difference in motion was the relative phase of motion at opposite sides. The results were initially taken as evidence of separate pathways for the detection of looming and translational motion but are easily interpreted within the hierarchical approach. In this case, both adapting patterns adapt local detectors, but only the out-of-phase oscillations adapt looming detectors at a higher level. In more-recent studies, Regan and Beverley<sup>8</sup> measured thresholds for detecting rotational movement formed by four patches of drifting noise. The directions of the noise patches for the adapting patterns either were arranged to form a global pattern of rotation or were jumbled so as to give no coherent global motion. Once again, thresholds were higher when the local directions of the noise patches formed global rotation,

even though the local motion signals were the same in all cases but in different combinations.

Studies of the motion aftereffect also yield evidence of higher-order motion analyzers. After prolonged adaptation to a moving image, a static image appears to move in the opposite direction: This is the motion aftereffect (MAE; for a review, see Wade<sup>9</sup>).

Most studies of the MAE have concentrated on simple translational motion of gratings or random dot patterns in the frontoparallel plane, but several researchers have studied the MAE's elicited by complex patterns of motion. For example, Cavanagh and Favreau<sup>10</sup> measured MAE duration after adaptation to spiral motion. One test pattern was a mirror image of the adapting spiral, with all its contours at 90 deg to those of the adapting spiral. Local motion detectors tuned to the directions of the mirror image spiral should fail to respond, and therefore not adapt, to the adapting spiral. Nevertheless, MAE's were present when the patterns were tested with the mirror image spiral and lasted one third as long as the MAE's measured with a test figure that was the same as the adapting spiral. More recently, Snowden and Milne<sup>11</sup> studied the MAE's elicited by adaptation to noise patterns undergoing radial, rotational, or spiral motions. Following adaptation to a large patch of motion, a smaller test patch was placed in a region of the display where the local motion during adaptation was exclusively translational. Some observers reported a MAE in this subregion that had the characteristics of the MAE expected for the global pattern; e.g., during adaptation to expansion, adapting dots in the region to the left of fixation translated to the left, but a test patch placed at this location sometimes appeared to contract. Also, adaptation to a large field of expansion selectively raised thresholds for detecting expansion

sion on the local field where the dots underwent only translational motion. The same was true for contraction, spiral, and rotational motions, indicating adaptation of specialized mechanisms beyond the stage where local motion vectors are encoded. The results suggest not only that there are higher-level mechanisms that are selective for complex configurations of motion but that these specialized detectors are relatively insensitive to the location of the center of radiation or rotation—an insensitivity termed position invariance. Note, however, that Regan and Beverley<sup>8</sup> also examined the MAE following adaptation to expansion but observed no such position invariance: The aftereffect disappeared when fixation shifted by approximately half of the length of the square edge.

Freeman and Harris<sup>12</sup> found that direction-discrimination thresholds for coherently expanding and rotating groups of dots were lower than for coherently translating groups or incoherent groups containing the same local motions, suggesting pooling of local motion signals by higher-level mechanisms sensitive to expansion and rotation. However, Sekuler<sup>13</sup> showed that speed-discrimination thresholds for looming, rotating, and translating dot patterns were the same and argued that the results required simple pooling of local motion signals without any need to invoke higher-level mechanisms selective for particular configurations of motion in depth. Freeman and Harris<sup>12</sup> also found that the detection of rotation was unaffected by the presence of expansion and vice versa, and Regan and Beverley<sup>7</sup> argued that expansion is encoded independently of translation, suggesting that a separate mechanism may exist for each class of global motion.

Evidence that sensitivities for the different tasks of detecting the presence of grating patterns and for identifying their movement depend differently on the spatial extent of the pattern have been interpreted in terms of a hierarchical organization,<sup>6</sup> but alternative explanations based on separate processing by parallel mechanisms with different spatial properties have not been excluded. Verghese and Stone<sup>14,15</sup> showed that speed-discrimination thresholds decreased as the arrangement of component drifting Gabor elements became more widely separated or their number increased (total stimulus area was held constant). Those authors argued that the increased sensitivity reflected image segmentation processes at higher stages of visual analysis, although it is not immediately clear why speed-discrimination thresholds should be higher for a single large object than for multiple small objects. Their manipulations of pattern configuration (by shifting the location or number and size of the component Gabor patches) were accompanied by changes in the local spatial frequency or orientation bandwidth or both, which could affect speed-discrimination thresholds at a local rather than a global stage of motion processing.

Two recent papers have shown that radial motion appears faster than rotational<sup>16</sup> and translational<sup>17</sup> motion, in spite of equal local motion signals. However, one, by Geesaman and Qian,<sup>16</sup> compared radial motion only with rotational motion and tested only expanding and anticlockwise motion, omitting observations with contracting or clockwise motion; and although the other, by Bex and

Makous,<sup>17</sup> used both directions of radial motion, they compared it only with translational motion (both directions). Moreover, in both experiments the stimuli differed in ways other than that being tested, so the effects of global motion cannot be separated from any effects of the other stimulus differences. In the experiment of Bex and Makous, the shapes of the grating stimuli differed (curved versus straight bars). In the experiment of Geesaman and Qian, the method used to generate the random dot pattern produced a shearing jitter, present only in the radial pattern, so adjacent dots moved at different speeds. Moreover, with random dot patterns it is possible to equalize the speeds of all the dots in Cartesian coordinates, which leaves a radial gradient of angular speeds, or to equalize all the angular speeds, which leaves a radial gradient of Cartesian speeds.

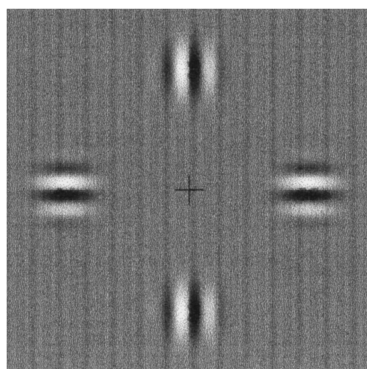
The present study extends this work on the effects of local velocity on the apparent speed of a global pattern in the following ways: (1) all stimuli were locally identical except for direction of motion, so the spatial frequency and orientation bandwidths were constant; (2) we compared the apparent speed of both radial and rotation motion with translation motion under identical conditions and in both directions; (3) we tested whether one dimension of movement was sufficient to elicit a speed bias; (4) we tested whether the enhanced apparent speed of a radial grating is related to sensitivity or (5) to apparent contrast; and (6) we tested the effects of efforts to attend solely to the local elements and to ignore the global movement of the complex pattern.

## 2. METHODS

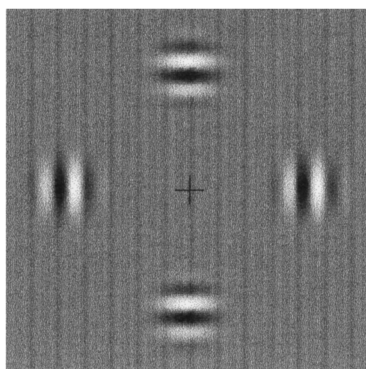
Two of the authors (PB and AM) served as observers, and the main findings were reproduced with a naïve observer (JB). All had normal or corrected visual acuity. Stimuli were generated on a Macintosh 7600/120 computer and displayed on a Nanao Flexscan 6500 gray-scale monitor at a frame rate of 75 Hz and a mean luminance of 55 cd/m<sup>2</sup>. The luminance of the display was linearized with pseudo-12 bit resolution<sup>18</sup> and calibrated with a Minolta chromameter. Pseudo-12 bit resolution in this case permitted the presentation of 2<sup>8</sup> gray levels from a possible range of 2<sup>12</sup> levels. The display measured 36.0 cm horizontally (1152 pixels) and 27.2 cm vertically (870 pixels) and was 115 cm from the observer, in a dark room.

Three stimulus configurations were presented, each consisting of four windows, 2 deg from fixation, containing a moving grating with a 2 cycles/deg sinusoidal luminance profile, as illustrated in Fig. 1. The contrast of the gratings was 40%, multiplied by a stationary spatiotemporal Gaussian envelope with a radially symmetrical space constant,  $\sigma_s = 0.4$  deg, and a time constant,  $\sigma_t = 213$  ms. The location of the windows was fixed, but the orientation of the gratings varied, forming three patterns of complex motion: radiation, rotation, and translation (see Fig. 1). As preliminary observations showed that the apparent speed of each pattern was independent of direction (i.e., left/right, up/down, expansion/contraction, and clockwise/counterclockwise), direction was randomized from trial to trial to minimize the buildup of directionally specific aftereffects. A stimulus

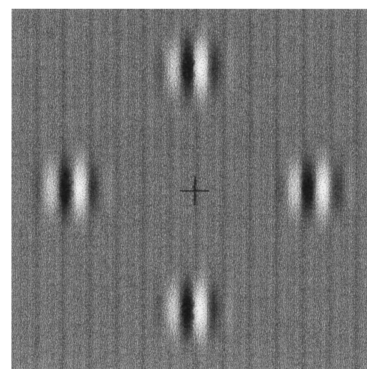
## (a) Rotation



## (b) Radiation

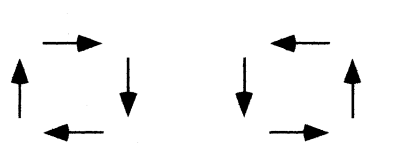


## (c) Translation



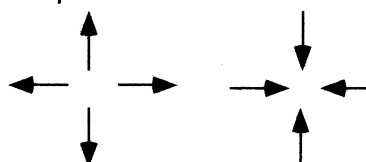
clockwise

anti-clockwise



expansion

contraction



right

left

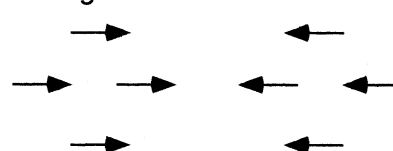


Fig. 1. Examples of the stimuli. Observers compared the speed of three stimulus configurations, each consisting of four windows containing a moving grating with a 2-cycle/deg sinusoidal luminance profile. The locations of the windows were fixed, but the orientation of the gratings was varied to form three compound patterns forming (a) rotational, (b) radial, and (c) translational motion. The arrows beneath each illustration show the directions of motion within the windows. The crosses are for fixation.

containing either radial or rotational motion was presented immediately before or after one containing translational motion, with 1 s between peak contrasts. Observers fixated the central cross and reported whether the first or the second pattern appeared to move faster. The speeds of rotational and radial motion were set on a particular run at 2 or 4 cycles/s, while the speed of the translational motion varied from trial to trial according to an adaptive procedure designed to concentrate observations near the point of subjective speed equality.<sup>19</sup> Initial phases were randomized. At least four but typically 8 runs of 32 trials each were made for each condition, and all trials were randomly interleaved.

### 3. RESULTS

#### A. Experiment 1: Apparent Speed Estimates

Figure 2(a) shows how often a naïve observer judged translational motion as faster than rotational (open symbols) and radial (filled symbols) motion at various speeds of the translational motion. The data have been fitted with a psychometric function<sup>20</sup> by a least- $\chi^2$  fit, from which the point of subjective equality and 95% confidence intervals were estimated at the 50% point. We define the point of subjective equality (the speed at which translation appeared faster on half of the trials) as the match speed of the rotational or radial motion. The ratios of match speed to physical speed, where the physical speeds were 2 and 4 cycles/s, are shown in Fig. 2(b) for three observers; error bars show 95% confidence intervals. Apparent rotational speed was approximately equal to that of translation speed (mean difference,  $1\% \pm 2\%$ ), but radial motion appeared faster by  $32\% \pm 8\%$ . In no case

was the absolute direction of motion significant, whether translation (left or right), rotation (clockwise or counter-clockwise), or radiation (contraction or expansion).

#### B. Experiment 2: Speed-Discrimination Thresholds

Verghese and Stone<sup>14,15</sup> have proposed that changes in speed-discrimination thresholds with changes in pattern configuration implicate high-level image segmentation processes in speed encoding. To test whether both sets of results were manifestations of the same high-level integration process, we measured speed-discrimination thresholds for each of our classes of pattern. Experiment 2 was similar to Experiment 1, except that each trial contained the same configuration of local patterns and the observer was required to indicate the interval containing the faster pattern. The speed of the standard pattern was fixed (2, 4, or 6 cycles/s), and the speed of the test pattern was varied to concentrate observations near a threshold of 75% correct.<sup>19</sup> Auditory feedback identified incorrect responses.

Figure 3 shows that speed-discrimination thresholds were approximately equal for all three patterns at three drift speeds for two observers. The Weber fractions are in line with earlier estimates of  $\sim 0.09$  at 1 deg/s, falling to  $\sim 0.03$  at 3 deg/s for drifting bar stimuli.<sup>21</sup> Note that speed-discrimination thresholds for radiating patterns were the same as for translating patterns even though the apparent speed was much faster.

#### C. Experiment 3: One-Dimensional Apparent Speed Estimates

It is possible that the increased apparent speed of the radial pattern in Experiment 1 was based simply on the

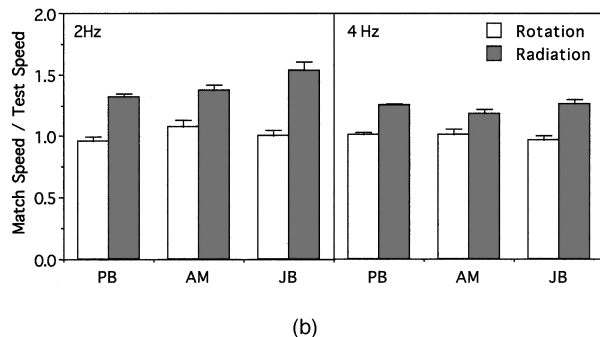
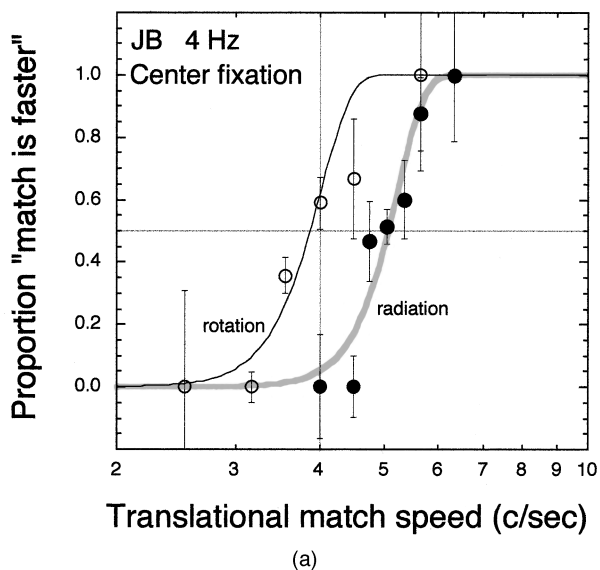


Fig. 2. (a) Typical psychometric functions for naïve observer JB, showing the proportion of trials in which the translational motion at the speed shown on the x axis was judged faster than rotational (open symbols) or radial (filled symbols) motion at 4 cycles/s (c/sec). The data are fitted by Weibull functions with a least- $\chi^2$  algorithm. Error bars represent the standard deviation of each point according to the binomial distribution. (b) Apparent/physical speed ratios for three observers at two physical speeds (2 and 4 cycles/s) for rotational (open bars) and radial (filled bars) patterns of motion. A value of 1 indicates equal apparent speed; values above 1 indicate that the pattern appeared to move faster than a translating pattern. Error bars show 95% confidence limits.

relative speeds of points around fixation. Thus a point moving in one direction on the left of fixation moves with respect to a similar point to the right of fixation faster in a radial pattern than it does in a translating pattern (i.e., there is motion contrast in radial patterns). Militating against this hypothesis is the fact that rotational motion also contains motion contrast but shows no increase in apparent speed. Nevertheless, we evaluated directly the contribution of motion contrast to the apparent speed of radial patterns. In a third experiment, the four Gabor patches were arranged to present expansion or contraction along a single spatial dimension of motion (see the inset of Fig. 4), thereby preserving an equal amount of motion contrast but removing one of the two dimensions of expansion/contraction. Speed matches were made as in Experiment 1 for translating and expanding/contracting groups of gratings (but this time, the radial motion was along a single dimension). Four patches were presented to maintain the same stimulus area as in Experiment 1,

but the results (not shown) were also the same when only two patterns were presented, one on each side of fixation.

Figure 4 is plotted in the same way as Fig. 2(b). The data show the ratios of match speed (of the translating pattern) to physical speed (of the radial pattern), where the physical speed of the radial pattern was 2 or 4 cycles/s. It can be seen that the apparent speed of one-dimensional patterns of radial motion is approximately equal to that of translational motion patterns in all cases.

This result addresses a possible concern that a translating pattern might elicit a greater tendency for an observer to make pursuit eye movements that would reduce the retinal velocity of translating patterns and possibly could affect their apparent speed. As radial gratings produce no such tendency for pursuit eye movements, eye movement could be the cause of the differences in apparent motion. However, if that were so, it should affect measurement of the apparent speed of opposing one-dimensional movement in the same way that it affects that of radial motion, but the results are not the same: There was no difference between the apparent speed of opposing one-dimensional motion and that of translational motion, so eye movements cannot be the cause of the difference between the apparent motion of radial and translational gratings. Note also that rotating patterns, which are like radial gratings in their inability to elicit pursuit eye movements, appear to move at the same speed as translating patterns.

**D. Experiment 4: Contrast-Detection Thresholds**

Apparent speed increases with the contrast of moving grating patterns,<sup>22</sup> so it is possible that the overestima-

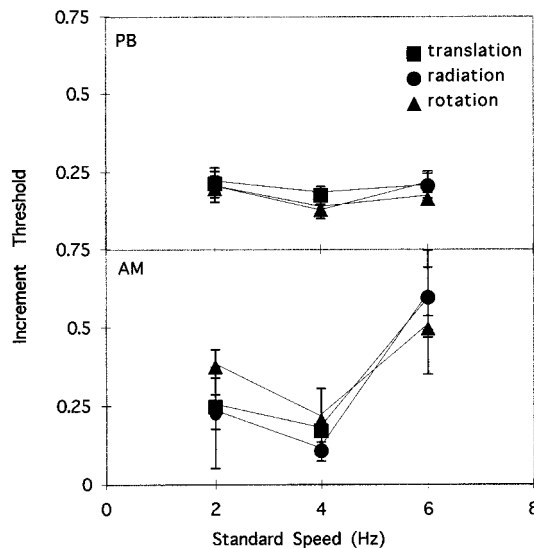


Fig. 3. Speed-discrimination thresholds: speed increment and 95% confidence intervals at which observers correctly identified the interval containing the faster pattern on 75% of trials. The corresponding Weber fractions on the mean threshold for each speed are as follows:

Standard Speed	Fraction for Observer AM	Fraction for Observer PB
2	0.106	0.147
4	0.037	0.043
6	0.032	0.095

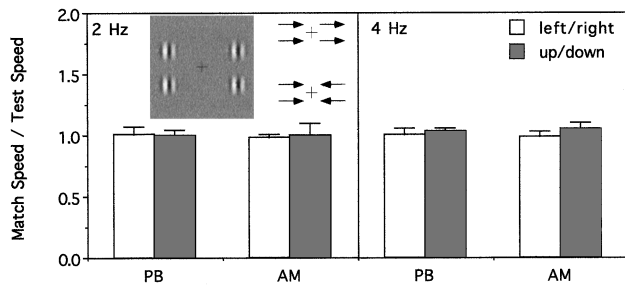


Fig. 4. Motion contrast control and test of configuration of Gaussian windows: Apparent/physical speed ratios of radial motion at 2 and 4 cycles/s were measured (for two observers) in a more-linear array of windows, as illustrated in the inset. Data are plotted as in Fig. 2(b).

tion of speed produced by radial motion could be a by-product of some enhancement of apparent contrast for this particular configuration. However, we calculate that the contrast differences necessary to produce even a detectable difference in apparent speed would be easily noticed, yet the observers all reported that the apparent contrasts of the three motion patterns were equal.

To test objectively whether radial motion enhances the contrast of the moving gratings, we conducted a fourth experiment to measure contrast-detection thresholds for each class of pattern. Stimuli identical to those in the 2-Hz speed-matching experiments were interleaved in a detection paradigm, in which observers identified which of two intervals contained a stimulus rather than a homogenous field of mean luminance. Auditory feedback identified incorrect responses. The contrast of the component gratings varied from trial to trial according to an adaptive procedure, and the resulting psychometric functions were fitted with Weibull functions. This procedure yielded the contrast required for 75% detection performance level (and corresponding 95% confidence interval) for each motion configuration, as shown in Fig. 4.

Even after accounting for absolute difference between the two observers by normalizing the individual average thresholds, an analysis of variance failed to show any reliable differences between thresholds ( $p > 0.15$ ). We also completed suprathreshold contrast matches. The procedure was as in Experiment 1, except that the speed of all patterns was fixed (2 or 4 Hz) and contrast of the translating patterns was varied from trial to trial to converge on the 50% match contrast. Figure 5(b) shows that the apparent contrast of all patterns was approximately equal. As the data in Fig. 5 give no evidence for an increased apparent contrast or increased sensitivity to patterns in radial motion, the overestimation cannot be attributed to an enhancement of contrast.

### E. Experiment 5: Apparent Speed of the Local Components

In a final experiment, we measured whether the greater apparent speeds of global patterns of radial motion were accompanied by changes in the apparent speed of each of the local component elements. The basic procedure was the same as in Experiment 1, except that the spatial locations of the Gaussian windows were changed so a single, vertical, drifting grating always appeared in the

center of the screen. Three additional gratings were placed around this grating, so the four grating elements (including the central, vertical grating) formed radial, rotational, or translational patterns of motion but the central grating was always vertical and drifted either leftward or rightward (Fig. 6). Observers fixated the central grating element, aided by cross-hairs around the patch, and compared its speed in two intervals, with instructions to ignore the motion of the remaining gratings. The four grating elements occupied the same locations in both intervals, but the configuration in one interval was consistent with translational motion, whereas the configuration in the other interval was of radial or rotational motion. We measured speed matches for rotating and radial patterns as in Experiment 1 by varying the speed of the translating pattern. The locations and relative direction of motion were changed randomly (while the three basic configurations were maintained) between trials to discourage formation of any particular expectation or habit.

Figure 7 shows that the change of fixation and instructions for selective attention had little effect on the overestimation of the speed of radial motion. Single elements forming part of a radial group appeared to move faster than single elements forming part of either a translational or a rotational group, but the enhanced speed effect was slightly smaller ( $25\% \pm 2\%$ ) for these two observers than when they were fixating the center of the group ( $28\% \pm 6\%$ ).

Although one cannot prove that observers would also be unable to ignore the global pattern under all other con-

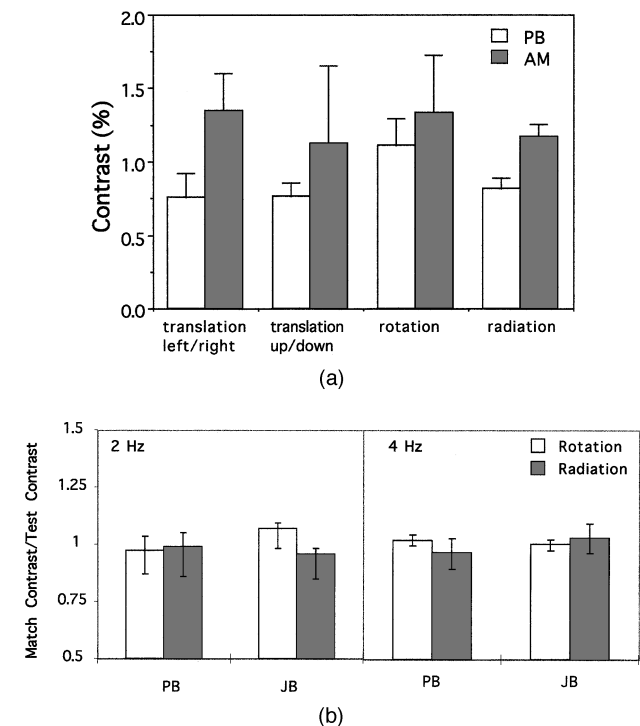


Fig. 5. (a) Contrast thresholds: contrasts and 95% confidence intervals at which two observers correctly identified the interval containing a stimulus on 75% of the trials. (b) Contrast matches: contrast of a translating grating that matched the apparent contrast of radiating or rotating patterns of 40% contrast. The match contrast is the contrast at which observers reported that the translating grating was of higher contrast on 50% of trials, inferred from the psychometric function.

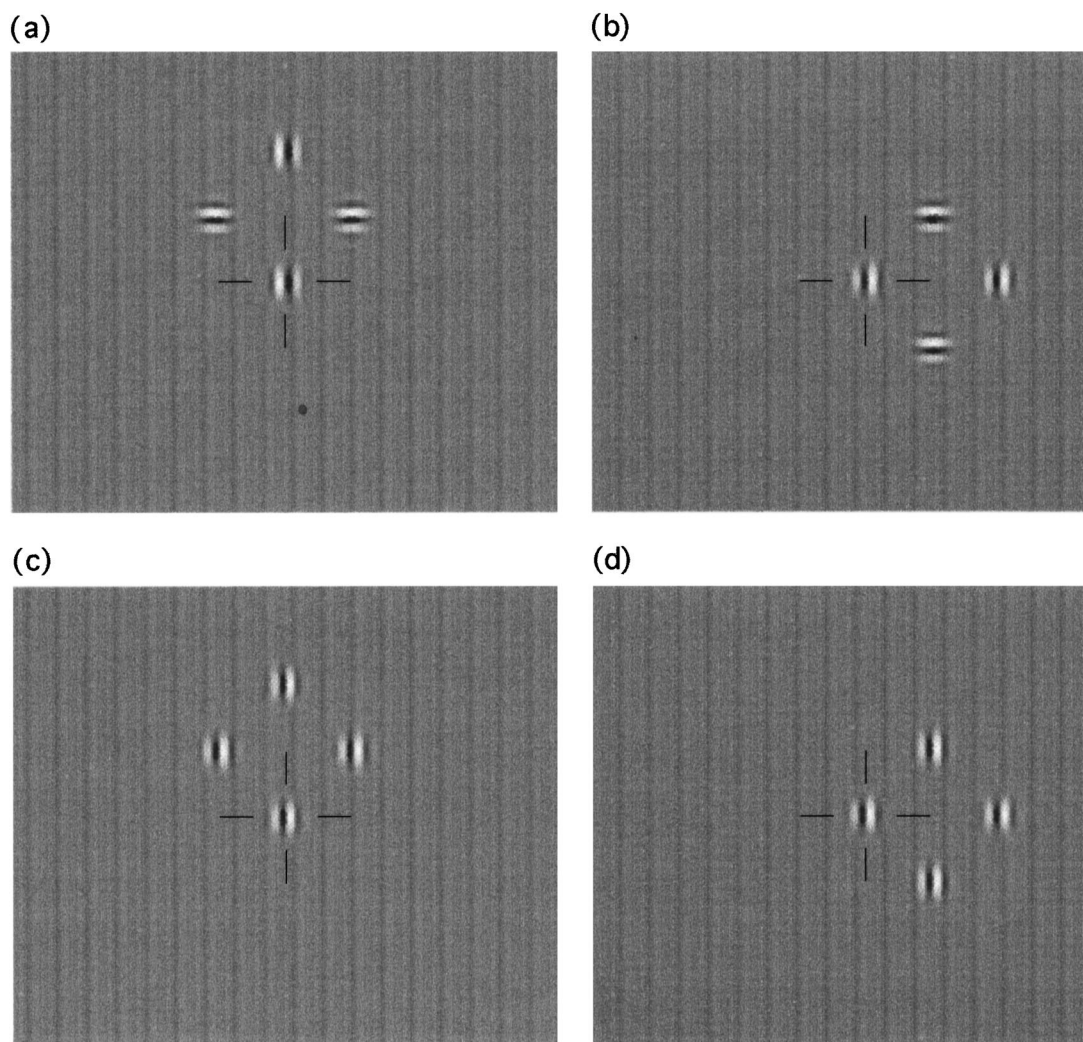


Fig. 6. Examples of the stimuli used in Experiment 4. The apparent speed within a single centrally fixated window containing a vertical grating moving left or right was compared in two intervals. In one interval the single patch formed either part of (a) a rotational or (b) a radial pattern; in the other interval, it formed part of (c), (d) a translating pattern. Cross-hairs were provided around the target pattern to facilitate steady fixation. The sequence and direction of motion were randomized from trial to trial. The four windows were at the same location on a given trial, but on different trials the paracentral windows were presented above or below fixation (for rotation) or left or right of fixation (for radial motion). Only one example of each configuration is illustrated here.

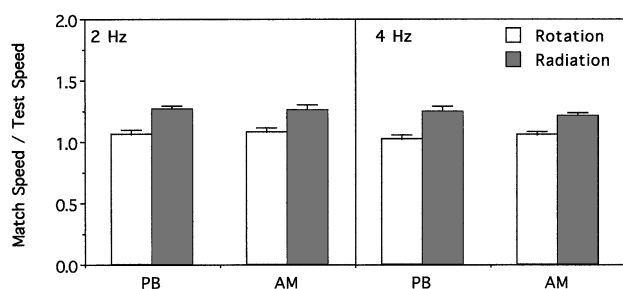


Fig. 7. Relative apparent speed of grating elements within centrally fixated windows (two observers), plotted as in Fig. 2(b). Open bars, elements that constituted part of rotational motion configurations; filled bars, radial configurations. Error bars show 95% confidence limits.

ditions, we are encouraged to speculate that the operations responsible for overestimation of the speed of radial motion are preattentive and influence perception of the individual elements of the global configuration.

## 4. DISCUSSION

These results show that the apparent speed of a pattern depends on the configuration of the local motions that form the pattern. Specifically, radial patterns and their components appear to move approximately one third faster than either translating or rotating patterns, which appear to move at approximately the same speeds. The results show that the speed bias requires two dimensions of motion. The equivalence of contrast sensitivities and suprathreshold apparent contrasts of the patterns rules out any effects of contrast as the basis of the speed enhancement for radial patterns of motion.

### A. Motion Contrast

One might attribute the overestimation of the speed of radial motion to differences in relative speeds with respect to nearby movement: gratings on opposite sides of the center of expansion or contraction have relative speeds that are twice their absolute speeds, whereas the points

in translating patterns all have the same relative speed. Neurons selective for such motion contrast have been observed in area MT of macaque brains.<sup>23</sup> However, this cannot cause the overestimation of speed, for the rotational motion configuration produces the same doubling of relative speeds between opposite windows, albeit along parallel trajectories, but produces no overestimation of speed. The results also rule out the proposal that the apparent speed of translation is slower (rather than radiation faster) because of a reduction in retinal velocity accompanying pursuit eye movements. In any case this explanation would require that rotation also look faster, which we did not record.

Geesaman and Qian<sup>16</sup> likewise observed no enhancement of perceived speed when two windows containing motion in opposite directions were juxtaposed, although, paradoxically, the effect returned when the windows were separated by 1.83 deg, approximately half of the separation of our windows (4 deg).

### B. One versus Two Dimensions of Motion

We also found that although radial motion is necessary for the overestimation of speed, it is not sufficient, for no noticeable overestimation of speed occurred when the windows were arranged to form a more nearly one-dimensional array (Fig. 3). This result is further evidence against motion contrast or pursuit eye movements as the basis for the enhancement of apparent speed of radial motion. The only difference between the pattern that does produce the overestimation of speed [Fig. 1(b)] and those that fail (Fig. 3) lies in the representation of motion in two dimensions. Therefore, within the stimulus domain tested, two conditions are necessary to produce the overestimation of speed: (1) an expanding or contracting pattern, (2) of which two dimensions of motion are visible.

Bex and Makous<sup>17</sup> found that reducing the area of their radial grating also reduced the speed bias. The area of their radial grating was reduced by a mask of mean luminance that left a bow-tie-shaped area of grating, under some conditions approximating a one-dimensional pattern. They attributed the loss of speed bias to a loss of stimulus area. Here we find that reducing the motion to a single dimension eliminates the speed enhancement, even when area is held constant; hence the dimensionality of motion, not the stimulus area, affects the apparent speed of a grating.

### C. Comparison with Psychophysical Literature

Sekuler's findings<sup>13</sup> may seem to conflict with these, for she showed that speed discriminations for looming, rotating, and translating dot patterns were the same and pointed out that these results require nothing more than linear summation of local motion signals and require no higher level mechanisms. However, neither do her results exclude the existence of the higher-level mechanisms that we find necessary. Our results simply mean that the discriminations of radial speed are performed on gratings that appear to move faster than the corresponding rotating or translating gratings: no difference in discriminability necessarily follows.

The results support the conclusions of Verghese and Stone,<sup>14,15</sup> who proposed that changes in speed-discrimination thresholds with changes in pattern configuration implicate high-level image segmentation processes in speed encoding. However, we failed to find differences in speed-discrimination thresholds among the pattern classes. To be consistent with their interpretation, all our stimuli would have to be parsed in the same way: either as four separate objects or as a single object moving behind four apertures. Separating the two experimentally poses a challenge.

### D. Comparison with Physiological Literature

Neurophysiological observations in macaques suggest that local motion analyzers lie at the bottom of a hierarchical arrangement of motion-sensitive mechanisms.<sup>24</sup> Simple translational motion is encoded in the first stage of cortical processing (V1), where many cells respond selectively to direction of motion. Such uncomplicated directional selectivity is maintained in neurons throughout the next four levels in the hierarchy (up to area MT) with a concomitant sharpening of speed tuning and a large increase in receptive field area.<sup>25-27</sup> At the next level (MSTd), cells become selective for more-complex forms of pattern movement, such as the radial or the rotational motion associated with optic flow.<sup>28-31</sup> Specialization of response selectivity at later stages of visual processing is not unique to primate visual systems; selectivity for complex patterns of motion has also been reported for cells in the lateral suprasylvian area of the cat<sup>32,33</sup> and for interneurons in the third visual neuropile of the blowfly,<sup>34</sup> where cells with large receptive fields respond selectively to optic flow components. The increasing selectivity for particular configurations of motion at larger spatial scales implies a functional hierarchy that integrates local motion signals into a representation of the movement of real objects and optic flow.

None of the current models of motion perception can account for the enhancement of apparent speed reported here without modification. In these models, local motion detectors are directionally selective within a limited spatial area. Therefore, to take into account motion from nearby locations, such detectors must integrate over larger areas, but this tends to decrease rather than to increase the motion signal for radial and rotational patterns because the direction of motion within each window is balanced by opposite motion in another window. It might be possible to develop a model with complex interaction between local motion analyzers that could account for the selective speed enhancement of radial patterns. However, the model would have to recognize that adjacent speeds in orthogonal directions may sometimes be part of a radial and sometimes part of a rotational group and must deal with each differently. The present results show that the integration rules depend on the configurations of the local motion signals and that the same rules cannot be applied for different configurations of local motions. A simpler interpretation, consistent with physiological evidence and growing psychophysical data, places local motion analyzers at the first stage of a motion-processing hierarchy in which local speed and direction are encoded; subsequent receptive fields could be as-

sembled from local velocity estimates projected from the first stage. The ubiquitousness of recurrent feedback in the visual system frustrates efforts to identify the neural level at which the global pattern affects the local neural signals for speed. Nevertheless, it is clear that analysis of the relative directions of local motion requires complex integration at some level higher than that at which local motion is analyzed.

Under natural conditions, radial motion is presented to the eye most often by the surroundings as the viewer moves through them, i.e., by what has come to be known as optic flow. In such situations, any radial component of such optic flow is reduced by geometric foreshortening. The overestimation of such radial motion may result from a tendency of the visual system to interpret such image motion in terms of the actual speed of the observer relative to the surroundings or of a rigid body moving in depth relative to the observer. The interpreted speed is faster than its two-dimensional representation on the retina (see Bex and Makous<sup>17</sup> for more discussion). The increase in the apparent speed of radial patterns, then, suggests that the bias may serve to represent the speed of movement in depth.

## ACKNOWLEDGMENTS

This research was supported by U.S. Public Health Service grants EY-4885, EY-1319, and EY-04440. We thank Peter Lennie, Jacob Nachmias, Tatiana Pasternak, David Williams, and two anonymous reviewers for helpful comments.

\*Present address, Department of Psychology, University of Glasgow, Florentine House, 53 Hillhead Street, Glasgow G12 8QF, Scotland.

## REFERENCES

1. E. H. Adelson and J. R. Bergen, "Spatiotemporal energy models for the perception of motion," *J. Opt. Soc. Am. A* **2**, 284–299 (1985).
2. J. P. van Santen and G. Sperling, "Elaborated Reichardt detectors," *J. Opt. Soc. Am. A* **2**, 300–321 (1985).
3. A. B. Watson and A. J. Ahumada, "Model of human visual-motion sensing," *J. Opt. Soc. Am. A* **2**, 322–342 (1985).
4. K. Zhang, M. I. Sereno, and M. E. Sereno, "Emergence of position-independent detectors of sense of rotation and dilation with Hebbian learning: an analysis," *Neural Comput.* **5**, 597–612 (1993).
5. M. Lappe and J. P. Rauschecker, "Heading detection from optic flow," *Nature (London)* **369**, 712–713 (1994).
6. M. C. Morrone, D. C. Burr, and L. M. Vaina, "Two stages of visual processing for radial and circular motion," *Nature (London)* **376**, 507–509 (1995).
7. D. Regan and K. I. Beverly, "Looming detectors in the human visual pathway," *Vision Res.* **18**, 415–412 (1978).
8. D. Regan and K. I. Beverly, "Visual responses to vorticity and the neural analysis of optic flow," *J. Opt. Soc. Am. A* **2**, 280–283 (1985).
9. N. J. Wade, "A selective history of the study of visual motion aftereffects," *Perception* **23**, 1111–1134 (1994).
10. P. Cavanagh and O. E. Favreau, "Motion aftereffect: a global mechanism for the perception of rotation," *Perception* **9**, 175–182 (1980).
11. R. J. Snowden and A. B. Milne, "The effects of adapting to complex motions: Position invariance and tuning to spiral motions," *J. Cogn. Neurosci.* **8**, 435–452 (1996).
12. T. C. A. Freeman and M. G. Harris, "Human sensitivity to expanding and rotating motion: effects of complementary masking and directional structure," *Vision Res.* **32**, 81–87 (1992).
13. A. B. Sekuler, "Simple-pooling of unidirectional motion predicts speed discrimination for looming stimuli," *Vision Res.* **32**, 2277–2288 (1992).
14. P. Verghese and L. S. Stone, "Combining speed information across space," *Vision Res.* **15**, 2811–2823 (1995).
15. P. Verghese and L. S. Stone, "Perceived visual speed constrained by image segmentation," *Nature (London)* **381**, 161–163 (1996).
16. B. J. Geesaman and N. Qian, "A novel speed illusion involving expansion and rotation patterns," *Vision Res.* **36**, 3281–3292 (1996).
17. P. J. Bex and W. Makous, "Radial motion looks faster," *Vision Res.* **37**, 3399–3405 (1997).
18. D. G. Pelli and L. Zhang, "Accurate control of contrast on microcomputer displays," *Vision Res.* **31**, 1337–1350 (1991).
19. A. B. Watson and D. G. Pelli, "QUEST: a Bayesian adaptive psychometric method," *Percept. Psychophys.* **33**, 113–120 (1983).
20. W. Weibull, "A statistical distribution function of wide applicability," *J. Appl. Mech.* **18**, 292–297 (1951).
21. S. P. McKee, "A local mechanism for differential velocity detection," *Vision Res.* **21**, 491–500 (1981).
22. L. S. Stone and P. Thompson, "Human speed perception is contrast dependent," *Vision Res.* **32**, 1535–1549 (1992).
23. J. Allman, F. Miezin, and E. McGuinness, "Stimulus specific responses from beyond the classical receptive field: neurophysiological mechanisms for local-global comparisons in visual neurons," *Annu. Rev. Neurosci.* **8**, 407–430 (1985).
24. D. C. Van Essen, C. H. Anderson, and D. J. Felleman, "Information processing in the primate visual system: an integrated systems perspective," *Science* **255**, 419–423 (1992).
25. H. A. Saito, M. Yukei, K. Tanaka, K. Hikosaka, Y. Fukada, and E. Iwai, "Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey," *J. Neurosci.* **6**, 145–157 (1986).
26. J. H. R. Maunsell and D. C. Van Essen, "The connections of the middle temporal visual area (MT) and their relationship to a cortical hierarchy in the macaque monkey," *J. Neurosci.* **3**, 2563–2586 (1983).
27. T. Pasternak and W. H. Merigan, "Motion perception following lesions of the superior temporal sulcus in the monkey," *Cereb. Cortex* **4**, 247–259 (1994).
28. K. Tanaka and H. Saito, "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," *J. Neurophysiol.* **62**, 626–641 (1989).
29. C. J. Duffy and R. H. Wurtz, "Sensitivity of MST neurons to optic flow stimuli. I. A continuum of response selectivity to large-field stimuli," *J. Neurophysiol.* **65**, 1329–1345 (1991).
30. G. A. Orban, L. Lagae, A. Verri, S. Raiguel, D. Xiao, H. Maes, and V. Torre, "First-order analysis of optical flow in monkey brain," *Proc. Natl. Acad. Sci. USA* **89**, 2595–2599 (1992).
31. M. S. Graziano, R. A. Andersen, and R. J. Snowden, "Tuning of MST neurons to spiral motions," *J. Neurosci.* **14**, 54–67 (1994).
32. J. Kim, K. Mulligan, and H. Sherk, "Stimulated optic flow and extrastriate cortex. I. Optic flow versus texture," *J. Neurophysiol.* **77**, 554–561 (1997).
33. K. Mulligan, J. Kim, and H. Sherk, "Stimulated optic flow and extrastriate cortex. II. Responses to bar versus large-field stimuli," *J. Neurophysiol.* **77**, 562–570 (1997).
34. H. G. Krapp and R. Hengstenberg, "Estimation of self motion by optic flow processing in single visual interneurons," *Nature (London)* **384**, 463–466 (1996).