

Available online at www.sciencedirect.com

Vision Research xxx (2006) xxx–xxx

**Vision
Research**

www.elsevier.com/locate/visres

Motion in depth from interocular velocity differences revealed by differential motion aftereffect

Julian Martin Fernandez, Bart Farell *

Institute for Sensory Research, Syracuse University, Syracuse, New York 13244-5290, USA

Received 7 January 2005; received in revised form 21 October 2005

Abstract

There are two possible binocular mechanisms for the detection of motion in depth. One is based on disparity changes over time and the other is based on interocular velocity differences. It has previously been shown that disparity changes over time can produce the perception of motion in depth. However, existing psychophysical and physiological data are inconclusive as to whether interocular velocity differences play a role in motion in depth perception. We studied this issue using the motion aftereffect, the illusory motion of static patterns that follows adaptation to real motion. We induced a differential motion aftereffect to the two eyes and then tested for motion in depth in a stationary random-dot pattern seen with both eyes. It has been shown previously that a differential translational motion aftereffect produces a strong perception of motion in depth. We show here that a rotational motion aftereffect inhibits this perception of motion in depth, even though a real rotation induces motion in depth. A non-horizontal translational motion aftereffect did not inhibit motion in depth. Together, our results strongly suggest that (1) pure interocular velocity differences can produce motion in depth, and (2) the illusory changes in position from the motion aftereffect are generated relatively late in the visual hierarchy, after binocular combination.

© 2005 Elsevier Ltd. All rights reserved.

Keywords: Motion in depth; Motion aftereffect; Interocular velocity differences; Motion adaptation

1. Introduction

A stimulus whose retinal images move with different velocities in the two eyes cannot maintain the same relative image positions in both eyes. Therefore, any velocity difference between the eyes, as results from viewing motion in depth, is tied to a change in binocular disparity. There are two parts to unraveling the contributions to the perception of a stimulus moving in depth. One part is to isolate the contribution of disparity change over time. This is easily done using temporally uncorrelated dynamic random-dot stereograms, which lack any monocular motion cues. With this technique Julesz (1971) showed that disparity change over time could by itself produce the perception of MID.

This indicates that interocular velocity differences (IOVDs) are not necessary for the perception of MID. The second part, determining if IOVD is sufficient to generate the perception of MID, is harder, for IOVD cannot be isolated from an interocular disparity difference. Because of this, most previous attempts to answer this question have relied on indirect measurements (Brooks, 2002; Brooks & Mather, 2000; Cumming & Parker, 1994; Shioiri, Saisho, & Yaguchi, 2000; Sumnall & Harris, 2002). Thus far, the results have been inconclusive (for a review, see Howard & Rogers, 2002, vol. 2, pp. 527–540).

There are two studies that have attempted rather directly to isolate a pure IOVD signal. The first one used binocularly uncorrelated random-dot kinematograms (Shioiri et al., 2000). This study found that subjects could detect MID direction, at a level above chance, when the two eyes were shown different random-dot stereograms moving in opposite directions (horizontal left and right). They

* Corresponding author.

E-mail address: bart_farell@isr.syr.edu (B. Farell).

concluded that the perception of MID in this kind of stimulus is based on IOVD because the stimulus images in the two eyes were uncorrelated and there was no real binocular moving object that could have provided a disparity signal. However, these conclusions should be treated cautiously because of one methodological issue: even if the authors tried some manipulations to minimize it, random pairing of dots between the images in the two eyes could have provided a changing disparity signal.

The second study, by Shioiri, Kakehi, and Yaguchi (2002); Shioiri, Kakehi, Tashiro, and Yaguchi (2003), made use of the motion aftereffect (MAE) (Mather, Verstraten, & Anstis, 1998; Wohlgenuth, 1911). Shioiri et al. showed that a differential MAE to left and right eyes could result in the perception of MID. They adapted one eye to a moving grating, and this differential adaptation produced an IOVD when stationary test patterns were subsequently presented binocularly. They called this monocular-adaptation binocular-testing procedure "monocular MAE". Shioiri et al. (2002, 2003) found that the monocular MAE procedure could result in the perception of MID and concluded that IOVD was what produced the perception. The justification for this conclusion is that the MAE produces a motion signal uncontaminated by changes in stimulus position. This is the traditional view of MAE as a pure case of perception of motion without displacement.

However, recent studies have shown that the MAE also produces shifts in perceived stimulus position (Fang & He, 2004; Nishida & Johnston, 1999; Snowden, 1998). These changes in position are about 8% of the displacement of a real motion that matches the MAE in velocity. Though relatively small, these illusory shifts can be well above threshold for disparity detection and would contaminate the IOVD signal that Shioiri et al. (2002, 2003) concluded was responsible for the MID perceived in their experiment.

In this article, we study the monocular MAE to determine whether the MID perception arising from it are due to IOVDs or can be attributed to illusory shifts in position. We find that translational and rotational MAEs are very different in their effectiveness in eliciting the perception of MID, but no such difference occurs between physical translations and rotations. We use these indirect findings to evaluate two hypotheses about the perception of MID, one assuming that MID perception arises only from changing disparity over time, and the other assuming that MID perception arises both from changing disparity over time and from IOVD. This analysis allows us to conclude that pure interocular velocity differences can produce motion in depth, and also to suggest that the illusory changes in position from the motion aftereffect are generated relatively late in the visual hierarchy, after binocular combination.

2. Experiment 1

Both motion and stereo are subject to aperture effects (Farell, 1998, 2003; Morgan & Castet, 1997; Wohlgenuth, 1911) and signals of both kinds can be detected by mecha-

nisms tuned to directions other than that of stimulus motion or disparity (Adelson & Movshon, 1982, 1984; Bischof & Di Lollo, 1990; Farell, 1998). As a result, the effectiveness of a translational MAE in producing the perception of MID may depend jointly on the direction of motion of the adapting stimulus and the orientation of the adapting and test stimuli.

In the first experiment, we sought to verify that the method did in fact work and to identify the types of stimulus that might be best at supporting the perception of motion in depth from differential motion adaptation. Previous work on the monocular MAE (Shioiri et al., 2002, 2003) used as testing stimuli oblique (45°) gratings of opposite orientation in each eye. Here, we examined three stimuli: random dots, an obliquely oriented grating, and a vertically oriented grating. The motion of all three stimuli was horizontal. The stimuli differed in the orientation of their Fourier components relative to this horizontal direction of motion. We developed a hypothesis about how, given non-linearities in the adaptation process, this relation would contribute to differences between perception of adapter motion and perception of aftereffect motion. Such differences could affect the likelihood of perceiving motion in depth from monocular adaptation. Our hypothesis led us to predict that vertical gratings would produce the most robust post-adaptation perception of motion in depth. However, while large differences in MID perception were observed between our three stimulus types, these differences were not those predicted by our hypothesis, which therefore will not be discussed further. The differences found among the stimuli of this experiment form the basis for the subsequent experiments.

2.1. Methods

2.1.1. Stimuli

The three stimuli used in the experiment are shown in Fig. 1. The first pattern consists of a square composed of light and dark random dots, the second is a vertical square-wave grating and the third an oblique (45°) squarewave grating. Thus, the first and second pattern differ in orientation and frequency bandwidth (among other parameters), and the second and third differ in orientation relative to the direction of perceived motion.

During adaptation the upper and lower halves of each pattern moved horizontally but in opposite directions. Stimuli wrapped around at the border of the pattern, appearing on the opposite (left or right) side. Speed was constant at 10°/s. Movies were shown at half the refresh rate of the monitor (which was 75 Hz), this is, at 37.5 Hz. During adaptation a 60-frame movie was presented cyclically for the duration of the adapting period.

Luminances of the patterns inside the windows (randomly-positioned black and white dots or squarewave gratings, see Fig. 1) were 2 cd m^{-2} (black) and 85 cd m^{-2} (white). Background luminance was 34 cd m^{-2} . Dots were square and $7.5'$ on a side. The spatial frequency of the

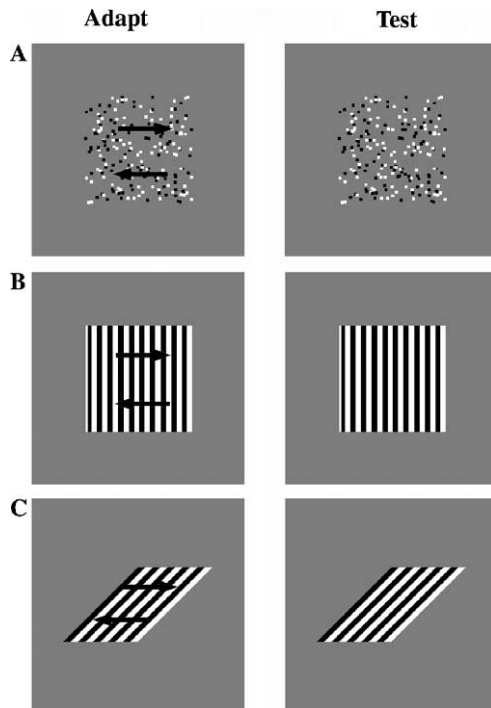


Fig. 1. Patterns used in Experiment 1. Each pattern was adapted in one eye and then tested binocularly. In the adapting phase the dots or stripes inside the upper and lower halves of each pattern moved in opposite horizontal directions and wrapped around at the border of the pattern. In the testing phase, the pattern was static but otherwise the same. As an example, when stimulus (a) was adapted in the left eye with the upper half moving towards the right, in the testing phase a motion aftereffect in the opposite direction was seen, and this aftereffect was stronger in the left (adapted) eye than in the right eye. Because of this differential motion aftereffect, subjects perceived the upper half receding from them and the lower half approaching them.

gratings was $2.5c/d$. The oblique (45°) squarewave of pattern **c** had a horizontal and vertical extent of 2.66° measured at the center of the pattern. The patterns **a** and **b** were square, 4° on a side.

In all cases subjects viewed the patterns through a mirror stereoscope at an optical distance of 94 cm. The square windows in which the patterns were presented had an extent of 8° on a side. The screen outside the windows was black (2cd m^{-2}). A white square, 6 min on a side, was continually present at the center of each window, as a zero-disparity fixation point. The random-dot pattern **a** had a total of 190 dots, the vertical squarewave pattern **b** a total of 10 cycles, and the oblique squarewave pattern **c** a total of 5 cycles.

2.1.2. Procedure

2.1.2.1. Motion-in-depth experiments. On each trial subjects viewed the adapting stimulus with one eye. Both the eye and the stimulus class were chosen at random.

The duration of the adapting phase was 60 s. During the test period immediately following adaptation, the static pattern was presented binocularly. Because of incomplete interocular transfer, measurements of which are described below, the MAE was greater in the adapted eye than in the

unadapted eye. This provided an IOVD signal during the testing phase that could in principle induce perception of MID in the test stimulus.

Subjects were permitted to inspect the test stimulus as long as they wanted. At the end of the inspection period they had to indicate with the click of a mouse whether the stimulus was in the “target” configuration (the upper half of the stimulus was approaching and the lower half was receding) or in the opposite “non-target” configuration. The categories “target” and “non-target” were used merely as shorthand designations for complementary stimulus configurations.

The procedure was repeated 20 times for each stimulus class, with no less than 5 min separating the subject’s response and the beginning of the next trial, to wash out effects of prior adaptation. The experiment sessions extended over several days. No feedback was provided, to prevent learning from hidden cues. During both the adapting and the testing phases, subjects were instructed to maintain fixation on the fixation point.

Subjects were not made aware of which eye was being adapted, although they could obtain this information if they wished. However, the possibility that subjects made a judgment of the eye of origin is ruled out by two facts. First, knowing the eye of origin does not make evident which response is consistent with the motion that a real object would have. To get the right answer it is necessary to know about and reason through the problem, something a typical naïve subject could not do. Pilot experiments with three additional naïve subjects viewing the random-dot stimuli gave data very similar to those reported here. Moreover, judgments based on the eye of origin would be similar for all stimuli, which is not what we found.

2.1.2.2. MAE measures. To measure interocular transfer of the MAE, the standard adaptation procedure was followed by a test stimulus that was presented to one eye only. The tested eye could be same as or different from the adapted eye. Subjects pressed the mouse button when the illusory motion stopped, so that the duration of the MAE could be measured. The procedure was repeated using the same adapted eye but alternating the tested eye between trials. After a series of 10 measurements for each eye and a recovery period of at least 2 h, the other eye was adapted and the procedure was repeated. The index of interocular transfer was the duration of the MAE for the non-adapted eye divided by that for the adapted eye. MAE strength was assumed to be proportional to its duration, and the duration of the MAE in the adapted eye was used as an index of MAE strength. Measure of the MAE strength agreed well with the subjective rating of MAE intensities described below.

To gauge the subjective intensity of the motion aftereffect, we used the same stimuli and procedure as in the MID experiment, but altered the subject’s task. We asked subjects in these runs to rate between trials the intensity of the perceived MAE on a scale from 1 to 10. This method

for assessing MAE intensity yielded results comparable to the method using MAE duration described above.

Two experienced subjects, S1 and S2, and one inexperienced subject, S3, all with normal or corrected-to-normal acuity and normal stereo vision, participated in the motion-in-depth experiments. Two subjects, S1 and S2, participated in the MAE measures.

2.2. Results

The oblique grating produced a very robust MAE (Fig. 2C), with a mean duration 2–3 times those for random dots (Fig. 2A) and the vertical grating (Fig. 2B). The interocular-transfer index, measured in the same control experiment, was about the same for the three patterns, averaging 52%, 63%, and 59% for random dots (Fig. 2A), the vertical squarewave grating (Fig. 2B), and the oblique squarewave grating (Fig. 2C), respectively. These interocular-transfer values are consistent with previous results (Raymond, 1993). MAE strength (as assessed by adapted-eye MAE duration) is shown in the right-most column of Fig. 2 for the three types of pattern. Subjective ratings of MAE intensities gave very nearly proportional results.

For the random-dot pattern, the less-than-complete interocular transfer resulted in a compelling perception of both motion in depth and lateral motion. In a two-alternative forced-choice “target”–“non-target” discriminations, subjects judged whether the top half-surface was approaching or receding. As shown in Fig. 2A, the perceived direction of MID was consistent with the IOVD generated by monocular motion adaptation on 95.8% of trials averaged across subjects (in the two experienced subjects the value reached 100%).¹

In contrast to the random-dot stimuli, the squarewave gratings did not consistently yield the perception of MID. Figs. 2B and C show that forced-choice judgments of MID direction were only slightly, though significantly, above chance (60.6% and 59.1% for the vertical and oblique gratings, respectively, averaged across subjects). This is well below the near-perfect performance obtained with the random-dot stimulus. High interocular transfer cannot explain this low level of discrimination because, as we have seen, the transfer index was about the same for gratings and random dots. Even the very strong MAE following adaptation to the oblique grating resulted in a weak perception of motion in depth.

The similarity of MID discrimination levels for vertical and oblique gratings shows that grating orientation relative to direction of motion was irrelevant. The superiority of MID discrimination for random dots shows that a broad orientation bandwidth does not interfere with post-adaptation MID perception. Both of these results contradicted our

¹ After these experiments were performed, we discovered that Shioiri et al. (2002, 2003) had reported in conference papers finding similar results using as test stimuli gratings of opposite orientation in the two eyes. We mentioned their work in more detail in the Section 1.

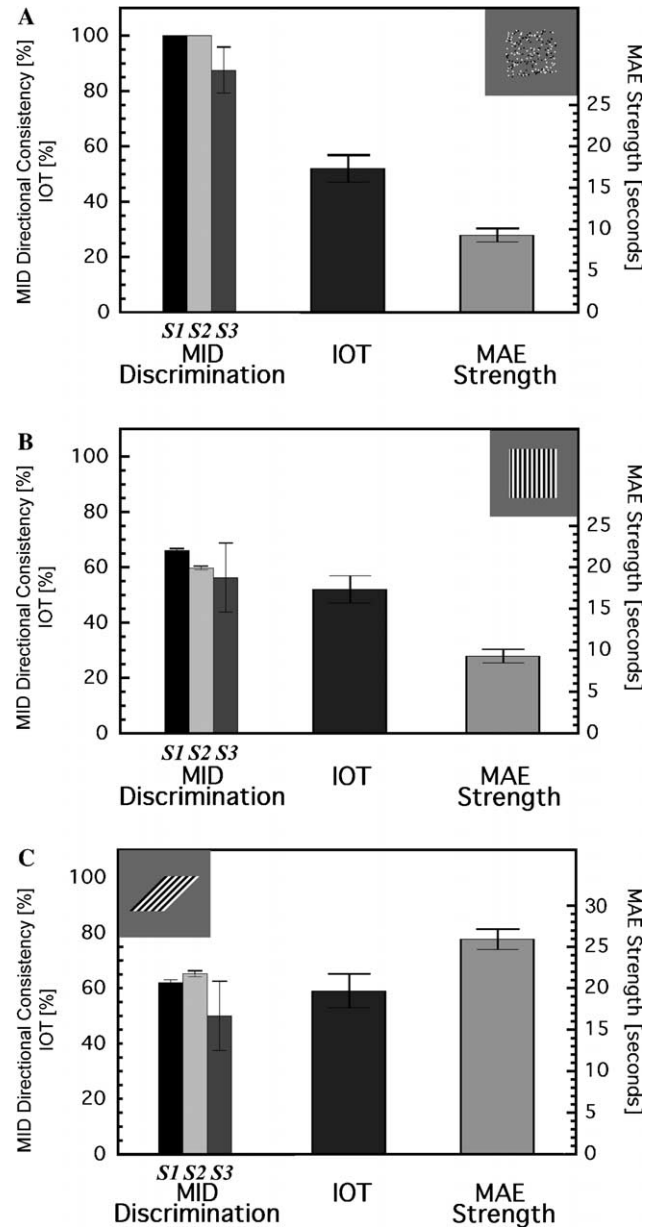


Fig. 2. Results for the three patterns of Experiment 1. Left bars: proportion of consistent responses for direction of MID, for each of the three subjects. Fifty percent corresponds to chance level. Error bars are standard error of the proportion. Central bar: interocular transfer (IOT) of MAE, averaged for the two subjects. IOT is computed as the ratio between the duration of the MAE for the non-adapted eye and that of the adapted eye. The bar shows the averaged interocular transfer after separately adapting the left eye and right eye. Error bars equal ± 1 SEM. Right bar: MAE intensity (averaged across two subjects), computed as the mean MAE duration for the adapted eye. Error bars equal ± 1 SEM.

initial hypothesis and led us to follow up the clues provided by test-stimulus appearance as a means to understand the difference in the perceived motion in depth of random dots and gratings.

2.2.1. Stimulus appearance

It was noticed that the stimuli differed in terms of the appearance of their motion in depth. These adventitiously

noted differences in stimulus appearance suggest hypotheses to account for the differences in the discriminability of motion in depth. For random-dots, the two components of the motion aftereffect (lateral motion and motion in depth) are superimposed. This creates the appearance of surfaces moving obliquely (for example, leftward and receding in the upper half of the pattern, and rightward and approaching in the lower half). But this did not generally result in the appearance of two separate random-dot surfaces, one above the other, each with a distinct trajectory. Instead, subjects perceived a single surface slanted in depth and undergoing a stretching deformation. Specifically, stimulus velocity, both in depth and laterally, was seen to be greater at distances further from the horizontal midline. This percept is readily understood. Near the horizontal midline the upper and lower surfaces abut with opposite motion directions. In this region, adaptation is attenuated by eye movements and neural integration over space, which combine the opposing direction signals. The MAE will be weakest where the two stimuli abut and will strengthen above and below this line. Thus, the intensity variation of the MAE along the vertical axis resembles a gradient more than a step. This applies both to the MAE and the MID it induces, and accounts for the perceived deformation.

For the gratings, the resulting MAE was qualitatively different. The bars appeared to rotate around the center of the figure, rather than moving in horizontally opposite directions in the top and bottom of the pattern. Thus, the perceived MAE in the grating's case was rotational, as opposed to translational as in the random-dot case. In a 2AFC paradigm where subjects were asked to classify the MAE they perceived as translational vs. rotational, they classified the random-dot pattern as translational 95.8% of the trials, and the gratings as rotational on 100% of the trials, averaged across the three subjects. Presumably, this rotational percept results from the same mixing process that gives rise to the stretching deformation in random dots. Unlike dots, the bars of the gratings are extended stimuli. Therefore, a gradient in MAE speeds, with speeds increasing with distance from the midline, is partially consistent with rigid-body rotation.

Following monocular adaptation, motion-in-depth discrimination was excellent for our random-dot pattern, yet poor for gratings. Two questions arise from these results. First, is the difference in MID discrimination between random dots and gratings connected to the difference in their motion aftereffects—translational for dots and rotational for gratings? The second question is, What is the mechanism by which random dots are perceived as moving in depth? Motion in depth might result from the interocular velocity difference produced by the monocular MAE or it might result from an illusory change in disparity, which could also accompany the monocular MAE. This disparity change would result from a perceived shift in stimulus position (Fang & He, 2004; Nishida & Johnston, 1999; Snowden, 1998).

The perceived position shift following adaptation to motion could have a high-level origin (e.g., the predictive mechanism of Nijhawan, 1994), but in this case it presumably would not provide input to primary disparity detectors, which are located early in cortical processing (Barlow, Blakemore, & Pettigrew, 1967; Cumming & Parker, 1994; Ohzawa, DeAngelis, & Freeman, 1990; Poggio & Fischer, 1977). However, if the shift originated in early vision—and in principle it could be as early as the retina (Berry, Brivanlou, Jordan, & Meister, 1999)—it could supply direct input to disparity detectors. Though the perceived position shifts resulting from adaptation to motion are small (Nishida & Johnston, 1999; Snowden, 1998), and their binocular differences after monocular adaptation are smaller still, they could be well above threshold for detecting disparity in stimuli with high-spatial-frequency components, such as random dots (Coutant & Westheimer, 1993; Schor & Wood, 1983; Smallman & MacLeod, 1994). We estimated that the disparity arising from differential illusory positional shifts should be about 12' based on Snowden (1998) results, and 3.6' based on Nishida and Johnston (1999) results. Even the smaller of these values represents a large fraction of the 7.5' dot width and a highly suprathreshold phase shift of even the fundamental component of the 2.5 c/d squarewave grating (e.g., Schor & Wood, 1983).

Experiments 2 and 3 examined the first of the two questions posed above: whether the global pattern of the motion aftereffect, translational or rotational, accounts for the difference in the MID perceived for these two stimulus types. The results of these experiments bear on the second question: by what mechanism does the aftereffect drive the perception of motion in depth? Experiment 2 examined random-dot patterns to determine the conditions under which a rotational aftereffect could support the perception of motion in depth. Experiment 3 used a discontinuous grating to shift the perceived MAE from rotational to translational and to determine whether MID perception changed accordingly, from absence to presence. Finally, Experiment 4 studied real differential rotational motion to compare the effectiveness of MAE and physical motion in eliciting the perception of motion in depth.

3. Experiment 2

Experiment 1 showed that for gratings, a MAE yields a perception of MID that is weak or absent. We surmise that it was not the gratings themselves that produced this result, but rather the rotational MAE that gratings induced. To test this notion, we sought to extend rotational aftereffects to random-dot stimuli. To do this we compared rotational vs. translational adapting motion. We also determined whether rotational and translational MAEs produce differing perceived motion in depth because of local or global motion cues.

We adapted the subjects to a ring of moving dots, as shown in Fig. 3. The ring was divided in four quadrants: top, bottom, left, and right. In one condition all the dots

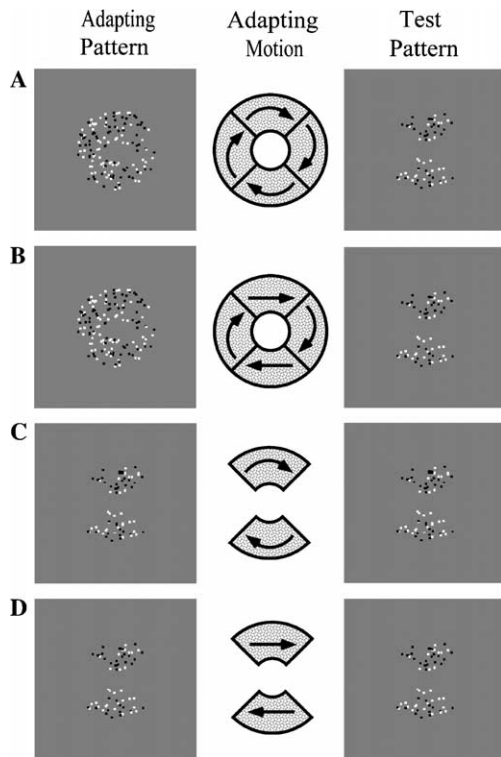


Fig. 3. Stimuli used in Experiment 2. The four conditions differ only in the adaptation phase. Adaptation to the moving pattern was monocular; testing with the static patterns was binocular.

409 had circular motion in the adaptation phase. In a second
 410 condition, only the dots in the left and right quadrants had
 411 circular motion in the adaptation phase, while dots in the
 412 top and bottom quadrants had constant linear horizontal
 413 velocity (equal to the average of the modulus of the circular
 414 velocities present in the left and right quadrants, and
 415 opposite in direction between top and bottom). Tests of
 416 MAE-induced MID were in all cases confined to the top
 417 and bottom quadrants, as shown in the right-most column
 418 of Fig. 3.

419 3.1. Methods

420 Random dots were arranged in an annulus with internal
 421 and external radii of 0.5° and 2° , respectively. The annulus
 422 was segmented into top, bottom, left, and right quadrants.
 423 During adaptation all the quadrants were presented
 424 together or only the top and bottom quadrants were pre-
 425 sented. There were a total of 130 dots in the four quadrants.
 426 Dots were square and $7.5'$ on a side. The four adapting con-
 427 ditions are shown in Fig. 3. During adaptation the motion
 428 was either rotational or translational in the upper and
 429 lower quadrants. In the rotational-motion condition, upper
 430 and lower quadrant dots in the adapting annulus moved in
 431 a circular path. The rotational frequency was 0.5 Hz, which
 432 corresponds to a retinal speed of $3.93^\circ/s$ at midradius (1.25°
 433 from the center). In the translational-motion condition, the
 434 dots in the upper and lower quadrants moved in opposite
 435 directions at a constant horizontal linear velocity of $3.93^\circ/s$.

In all cases dots wrapped around at the quadrant bound- 436
 437

Each adaptation motion type, rotational and transla- 438
 439 tional, could be presented in isolation in the upper and
 440 lower quadrants (Figs. 3C and D) or could be presented
 441 along with the left and right quadrants (Figs. 3A and B).
 442 Dots in these latter quadrants always followed a circular
 443 trajectory with the same clockwise or counter-clockwise
 444 sense as the dots in the upper and lower quadrants. In all
 445 cases the stationary test dots were confined to the upper
 446 and lower quadrants (see Fig. 3). Thus, adaptation in the
 447 test quadrants was either translational or rotational,
 448 regardless of the global adapting pattern. In all other
 449 respects the adaptation and test procedures were identical
 450 to those of the previous experiment.

On a subset of trials, subjects were asked to classify the 451
 452 movement they perceived in the test pattern as translational
 453 vs. rotational, instead of indicating the direction of motion
 454 in depth.

455 3.2. Results

Results widely varied across the three subjects. After 456
 457 adapting to four-quadrant circular motion (Fig. 3A), sub-
 458 jects S1 and S2 classified the test stimulus as rotational on
 459 100% of the trials and subject S3 on 75% of the trials. As
 460 shown in Fig. 4, MID direction discrimination was just
 461 above the chance level of 50% for the three subjects. The
 462 average across the three subjects was 59.2%, well below the

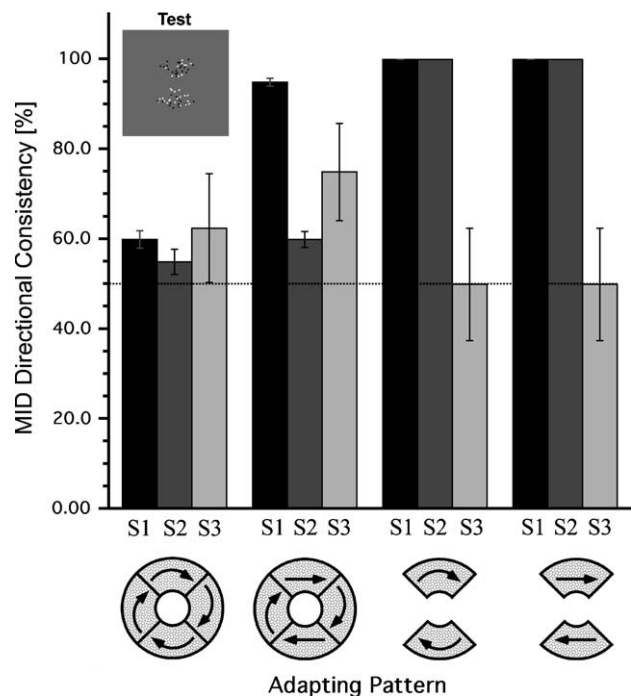


Fig. 4. Proportion of consistent responses for MID direction discrimina-
 463 tion for the four conditions of Experiment 2. The dotted line at a propor-
 464 tion of 0.5 corresponds to chance level. Error bars show ± 1 standard error
 465 of the proportion.

near-perfect performance obtained after adapting to translating random dots in Experiment 1. When the motion in upper and lower quadrants was changed to linear (Fig. 3B), subject S1 classified the stimuli as translational on 100% of the trials and, as seen in Fig. 4, discriminated MID direction almost perfectly (95% consistent). Subject S2, by contrast, classified the stimuli as rotational on 100% of the trials and discriminated MID direction only slightly above chance (60% consistent). Finally, subject S3 fell between the extremes represented by the other two subjects, classifying the stimuli as translational on a slight majority (62.5%) of the trials and discriminating MID direction with moderate reliability, at 75% consistent.

After adapting to only the top and bottom quadrants (Figs. 3C and D), subjects S1 and S2 classified the MAE as translational on 100% of the trials and discriminated MID direction perfectly in both cases (Fig. 4). Subject S3, by contrast, classified the MAE as rotational on 87.5% and 75% of the trials, respectively, and discriminated MID direction at chance level in both cases (Fig. 4). These results are consistent with the hypothesis that humans see motion in depth from translational motion aftereffects, and that motion in depth is not supported by rotational motion aftereffects. This consistency is evident for subjects S1 and S2, whose performance levels are near chance or maximal consistency with the IOVD generated by monocular motion adaptation, according to their perception of a rotational or translational aftereffect. Data for subject S3 are not as consistent as for the other two subjects, yet motion classification (perceiving translation vs. rotation) also predicts MID direction discrimination levels in this case.² For the four conditions shown in Figs. 3A and B, the predicted values are 62.5%, 81.25%, 56.25%, and 62.5%, respectively. These values correlate well ($r=0.904$) with the observed values of 62.5%, 75%, 50%, and 50%, respectively.

Thus, intersubject variability in directional discrimination is high in this experiment, especially for the top- and bottom-quadrant adaptation conditions of Fig. 4, yet this appears largely due to variability in the type of MAE perceived. Reasons why one subject should perceive rotational aftereffect in upper and lower quadrants while others perceive translational motion are obscure and presumably idiosyncratic. Whatever its source, though, this variation is predictive of performance in discriminating MID direction.

If illusory positional shifts stimulate disparity mechanisms and were thus responsible for the MAE-induced motion in depth, then there exists the possibility that rotational motion disrupted MID perception due to interference from vertical disparities generated by the differential rotation. To rule out this possibility, we used a random-dot pattern that was identical to that in Fig. 1A except for a rotation of the entire

pattern in the frontoparallel plane. Both the adapting pattern and its direction of motion were rotated by a given angle, so the motion had both horizontal and vertical components. The static test pattern was rotated similarly. Angles between 10° and 80° were tested, at 10° intervals (vertical is 90°), and no response feedback was provided.

Discrimination of motion in depth for the two subjects was correct on all trials following adaptation to horizontal motion and at chance level (45% and 55%, respectively) following adaptation to vertical motion. For inclinations of 50° the two subjects still consistently discriminated MID direction (75% and 95%, respectively). One of the subjects even could reliably discriminate (80% correct) MID at angles departing as much as 70° from horizontal. Thus, MAE-induced vertical disparities, even when they are large relative to the magnitude of the horizontal component of the disparity, are compatible with the perception of MID. This result also holds for real physical motion and real physical disparities, as confirmed in Experiment 4. (It should be noted that MID discrimination is expected to fail for strictly vertical motion. IOVDs for physical motion in depth are primarily horizontal; the vertical component of IOVD is much smaller than the horizontal component, except at large retinal eccentricities. Thus, a purely vertical IOVD is not consistent with a MID interpretation.)

The next two experiments complement each other and further assess the relation between the appearance of the stimulus and the perception of motion in depth. The purpose of Experiment 3 is to isolate the translational component of the grating MAE studied in Experiment 1 and to determine if it can induce the perception of MID. Experiment 4 examines the contribution to MID perception of interocular differences of physical, rather than MAE-induced, rotational motion.

4. Experiment 3

The results of Experiments 1 and 2 suggest that differential translations support the perception of motion in depth, whereas differential rotations do not. The boundary conditions of this translation/rotation difference were investigated in Experiment 3 by modifying the gratings used previously. In this case an attempt was made to eliminate the rotational component of the grating motion aftereffect to determine whether MID could be perceived on the basis of the remaining translational component, as hypothesized. This was done by using a discontinuous test grating, each half of which was seen as moving in a horizontal direction opposite that of its adapting pattern.

4.1. Methods

The vertical squarewave adapting stimulus (Fig. 1B, left) and the adaptation procedure were the same as those used in Experiment 1. The test pattern (Fig. 5A, right) was identical to the vertical grating used in Experiment 1 except for an abrupt phase shift of 90° between the top and bottom halves.

² Assuming that perceiving the motion as a translation results in perfect MID direction discrimination and perceiving it as a rotation results in chance levels, then the expected proportion of consistent responses for MID direction discrimination is $(1+p)/2$, where p is the proportion of trials in which a motion is perceived as a translation.

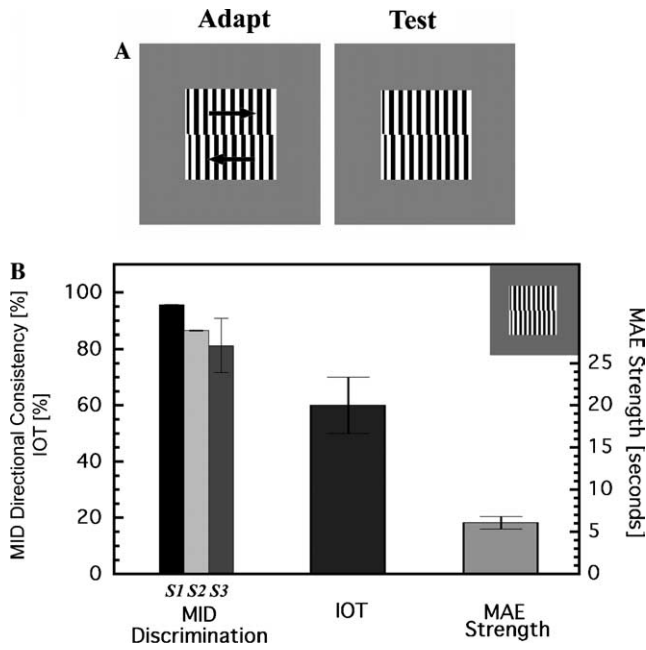


Fig. 5. (A) Stimuli used in Experiment 3. Adaptation to the moving pattern was monocular and testing with the static pattern was binocular. (B) Results for Experiment 3. Left bars: proportion of consistent responses for MID direction discrimination, for each of the three subjects. Fifty percent corresponds to chance performance. Error bars are ± 1 standard error of the proportion. Central bar: interocular transfer (IOT) of MAE, averaged for the two subjects. IOT is computed as the ratio between the duration of the MAE for the non-adapted and that of the adapted eye. The plotted value is the average IOT after separately adapting the left eye and right eye. Error bars equal ± 1 SEM. Right bar: MAE intensity (averaged across two subjects), computed as the mean duration of MAE for the adapted eye. Error bars equal ± 1 SEM.

than a rotational aftereffect. The large intersubject variability in directional discrimination performance, especially evident in Experiment 2, appears to stem from variability in translational vs. rotational aftereffects. Fig. 6 shows the relation between the probability of a translational aftereffect and the probability of directionally consistent MID discrimination. Data for the three subjects and for all the stimuli used in Experiments 1–3 are plotted. The regression fit shows a correlation between these measures that is high and significant ($r = 0.9437$, $t = 13.38$, $df = 22$, $p < 0.0001$). Thus, subjects respond diversely to adaptation, in the type of motion aftereffect they experienced—rotations vs. translations—and whether they classified the aftereffect categorically (subjects S1 and S2) or in graded fashion (S3). Yet across subjects and stimuli MID direction discrimination performance nevertheless is strongly related to the perception of translational aftereffects.

5. Experiment 4

Experiment 4 examined differential physical rotation of gratings seen by the left and right eyes to assess its contribution to the perception of motion in depth. Two subjects, S1 and S2, participated in the experiment.

5.1. Methods

On each trial, an oblique grating identical to that used in Experiment 1 was presented to one eye as a static pattern and to the other eye as a rotating pattern (Fig. 7). Rotational speeds were tested in the range of 1–10°/s (1°/s, 3.5°/s, 7°/s, and 10°/s), consistent with previous rotational MAE speed measurements (Nishida & Johnston, 1999). Stimulus

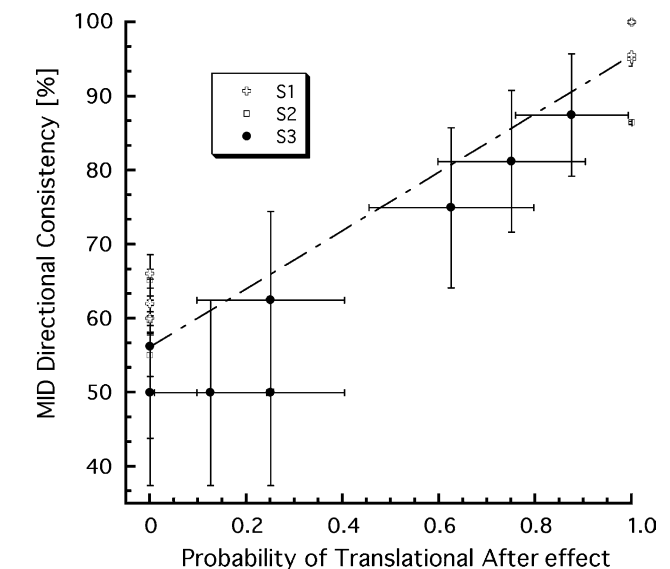


Fig. 6. Proportion of consistent responses for MID direction discrimination as a function of the probability stimulus motion was seen as translational. Data points are from all the stimulus types used in Experiments 1–3. Data from each subject are represented by a different symbol. Dashed line: linear regression fit to the data ($r = 0.94$).

4.2. Results

MAE strength for the bisected test grating (Fig. 5B) was very similar to that found earlier for the continuous test grating (Fig. 2B). However, the two test stimuli differed qualitatively in their perceived motion trajectories. As intended, the discontinuity at the center of the bisected test pattern (Fig. 5A) led to a perceived segregation between the upper and lower portions of the moving grating and to a translational MAE. Subjects classified the stimuli as translational (as opposed to rotational) on 91.6% of trials, averaged across the three subjects. This translational motion aftereffect was accompanied by a perception of motion in depth. Depth discriminations, shown in Fig. 5B, were highly accurate (87.8% correct, averaged across the three subjects) and significantly above the levels of chance and of the continuous test grating of the previous experiment (Fig. 2B). Thus, gratings do appear capable of supporting the perception of motion in depth following monocular adaptation, provided that adaptation produces a translational aftereffect on the test stimulus, rather than a rotation aftereffect.

The first three experiments show that the discriminability of the direction of MAE-induced motion in depth correlates highly with the likelihood of a translational rather

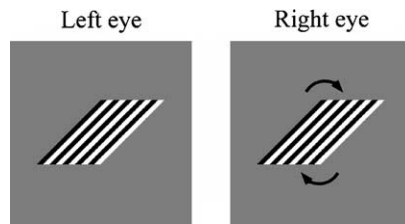


Fig. 7. Pattern used in Experiment 4. One eye was presented with a static oblique grating (left eye in this example) and the other eye with a rotating oblique grating.

619 duration was 2 s. The direction of rotation (i.e., clockwise or
620 counter-clockwise) and the eye to which the rotation was
621 applied were chosen at random. The starting angle of inclina-
622 tion of the moving pattern was such that midway
623 through the path its inclination was 45° (i.e., the same as
624 that of the static pattern).

625 Subjects indicated whether the upper half of the stimulus
626 was approaching and the bottom half was receding (“tar-
627 get” configuration) or vice versa (“non-target” configura-
628 tion). Two experienced subjects participated in this
629 experiment. Subjects were not made aware which eye was
630 presented the rotation. Each subject was tested in a single
631 run of 20 trials.

632 5.2. Results

633 A grating presented to one eye as a static pattern and to
634 the other eye as a rotating pattern (Fig. 7) yielded the
635 perception of a surface slanting in depth, as expected. Yet
636 subjects discriminated the correct direction of motion in
637 depth on 100% of the trials.

638 The continuous grating of Experiment 1 induced a
639 rotational motion aftereffect, with the grating perceived as
640 deviating from vertical in the direction of apparent rota-
641 tion. This rotational MAE was confined to or near the
642 frontoparallel plane, supporting only weak discrimination
643 of the direction of motion in depth. By contrast, the transla-
644 tional MAE seen with random dots in Experiment 1, and
645 the discontinuous grating in Experiment 3 deviated
646 strongly from the frontoparallel plane, yielding accurate
647 discrimination of the direction of motion in depth. One
648 might infer from these results that differential rotation
649 across the two eyes does not support the perception of
650 motion in depth. However, as shown in this experiment, a
651 differential *physical* rotation between the two eyes does
652 result in the perception of motion in depth. It is surprising,
653 indeed, that the differential rotation induced by monocular
654 MAE failed to generate a robust perception of MID. Since
655 interocular transfer is approximately the same for all the
656 grating patterns (Figs. 2B and C and 5B), complete interoc-
657 ular transfer of the aftereffect cannot be the reason for the
658 lack of MID from a rotational MAE.

659 Why, then, does a differential physical rotation lead to
660 the perception of MID while a differential perceived rota-
661 tion produced by adaptation to translational motion does

not? In an attempt to resolve this question, we hypothesize
that physical rotation leads to the perception of MID
because the grating’s horizontal disparities change over
time (Arditi, 1982; Arditi, Kaufman, & Movshon, 1981).
We propose that this disparity signal is not generated by
the motion aftereffect because the illusory change in posi-
tion from MAE has a high-level origin. The primary dispar-
ity detectors, located early in the visual processing
hierarchy, would not respond to illusory position signals
arising later in the processing sequence. This hypothesis is
discussed in more detail below.

6. General discussion

Our data show that conditions of local motion adaptation
and the degree of interocular transfer of the motion after-
effect are not sufficient to predict whether observers will per-
ceive motion in depth after adaptation. Our data show that
post-adaptation perception of MID depends on whether
adaptation induced a translational motion aftereffect or a
rotational motion aftereffect. The results of the four experi-
ments can be broadly summarized in two points: (1) The per-
ception of motion in depth can result from differential
binocular translation, both when the translation is a physical
motion and when it derives from a motion aftereffect. (2) The
perception of motion in depth can result from differential
binocular rotation when the rotation is a physical motion but
not when it derives from a motion aftereffect.

We argue that these results imply that motion in depth
induced by adaptation is based on interocular velocity
differences rather than changes in binocular disparity. To
see this, let us examine the results in light of two alternative
hypotheses. The first hypothesis is that only changing dis-
parity over time (CDOT) results in the perception of MID.
The second hypothesis is that both CDOT and IOVD can
result in the perception of MID. Table 1a and b show the
mechanisms that would generate the perception of MID for
the two motion sources (real vs. MAE) and the two motion
types (translation vs. rotation). Table 1a is based on the first
hypothesis, which assumes that only CDOT can result in
MID. Table 1b is based on the second hypothesis, which
assumes that both CDOT and IOVD can result in MID.

Table 1
Mechanisms that would be involved in MID perception of four possible kinds of stimuli

	Rotation	Translation
(a) CDOT→MID		
Real	CDOT	CDOT
MAE	No MID	CDOT
(b) CDOT + IOVD→MID		
Real	CDOT	CDOT + IOVD
MAE	No MID	IOVD

(a) It assumes that only CDOT plays a role in perception of MID and (b) assumes that both CDOT and IOVD play a role. In the former case, only a combination of both MAE and rotation inhibits CDOT. In the later case, MAE inhibits CDOT, and rotation inhibits IOVD.

The first hypothesis (Table 1a) requires that in the case of differential rotational motion, CDOT produces MID when the stimulus is physically rotating but not when its rotation is the result of an aftereffect. The problem that arises from this is that the specific combination of rotation and aftereffect would have to inhibit the perception of motion in depth from CDOT, even though neither a physical rotation nor a translational aftereffect alone inhibits it. We know of no reasonable mechanism for generating this particular combination of effects. In addition, illusory shifts in position from MAE should be sufficient by large to yield MID through CDOT, being above threshold for disparity detection in both translational (Snowden, 1998) and rotational (Nishida & Johnston, 1999) aftereffects. Therefore, for the purpose of processing disparity, any difference between physical and induced motion should apply equally to both translations and rotations; MID should be either perceived from both translational and rotational motion or not perceived from both translational and rotational motion. However, as we have found, MID from MAE is only perceived from translations and not from rotations.

The second hypothesis is that both CDOT and IOVD play a role in the perception of MID. Table 1b shows the conditions needed to generate MID under this hypothesis. Even though each combination of motion source (physical or aftereffect) and motion type (rotation or translation) gives rise to a unique generating condition, there are just two requirements needed to justify these conditions: (i) differential rotations do not activate the IOVD mechanism; (ii) MAEs do not activate the CDOT mechanism.

Both of these requirements appear reasonable. If IOVD detectors were based in a global rather than local signal, then the fact that rotational motion provides poor input to IOVD detectors would be understandable. Naturalistic viewing conditions lack sources of differential rotational velocities, so the interpretation of such stimuli would be problematic. If, on the other hand, CDOT were based on local rather than global computations, it would not suffer from this limitation; the difference between translation and rotation would not be important.

The second requirement is that MAEs do not activate the CDOT mechanism. A simple reason for this was previously mentioned: the illusory changes in position associated with MAE may occur after disparity detection. Disparity detectors, located as early in visual processing as area V1, would not be stimulated.

A third but more complex possibility, suggested by an anonymous reviewer, also argues in favor of IOVD participation in MID. In this scenario, the IOVD signal that provides input to motion in depth is early and local rather than global, but then the MID signal interacts with the differential-rotation signal in a high-level module. At this high level a coherent interpretation for both motion in depth and differential rotation may not exist. For real motion, the signal for MID is strong because both IOVD and CDOT contribute to it, and so the MID signal is not suppressed. But for adaptation-induced motion, the CDOT signal provided

by the illusory positional shifts is weaker or qualitatively different from a real CDOT signal, causing a suppression of the MID interpretation.

This explanation cannot be ruled out by the data, yet it is unclear how a suppressive mechanism for motion in depth could have come into existence if it does not work for real stimuli. We believe that the explanation we proposed based on Table 1b has the advantages of simplicity and logical soundness, and it should be chosen over a more complicated and ad hoc option.

The experiments, under either of these explanations, imply that the perception of MID can be induced by IOVD alone. For IOVD-driven MID, whether the adapting stimulus is rotational or translational is less important than the global MAE perceived in the testing phase—in particular, whether it is rotational or translational. In addition, the simplest interpretation of the results suggest that (1) the MID mechanism uses as input a global rather than local IOVD signal, and (2) that this input signal is specifically a linear, non-rotational, motion signal. The results further suggest that the MAE produces illusory changes in position relatively late in the visual hierarchy, after binocular combination, preventing these position changes from stimulating disparity-sensitive neurons.

7. Uncited references

Brown (1931); Cumming and DeAngelis (2001); Reagan and Beverly (1973); Whitney (2002).

Acknowledgments

This research was supported by NEI Grants F32 EY015673 (J.M.F.) and EY012286 (B.F.).

References

- Adelson, E. H., & Movshon, J. A. (1982). Phenomenal coherence of moving visual patterns. *Nature*, *300*, 523–525.
- Adelson, E. H., & Movshon, J. A. (1984). Binocular disparity and the computation of two-dimensional motion. *Journal of the Optical Society of America*, *1A*, 1266.
- Arditi, A. (1982). The dependence of the induced effect on orientation and a hypothesis concerning disparity computations in general. *Vision Research*, *22*, 247–256.
- Arditi, A., Kaufman, L., & Movshon, J. A. (1981). A simple explanation of the induced size effect. *Vision Research*, *21*, 755–764.
- Barlow, H. B., Blakemore, C., & Pettigrew, J. D. (1967). The neural mechanism of binocular depth discrimination. *Journal of Physiology*, *193*, 327–342.
- Berry, M. J., II, Brivanlou, I. H., Jordan, T. A., & Meister, M. (1999). Anticipation of moving stimuli by the retina. *Nature*, *398*, 334–338.
- Bischof, W. F., & Di Lollo, V. (1990). Perception of directional sampled motion in relation to displacement and spatial frequency: Evidence for a unitary motion system. *Vision Research*, *30*, 1341–1362.
- Brooks, K. R. (2002). Interocular velocity difference contributes to stereomotion speed perception. *Journal of Vision*, *2*, 218–231.
- Brooks, K., & Mather, G. (2000). Perceived speed of motion in depth is reduced in the periphery. *Vision Research*, *40*, 3507–3516.
- Brown, J. F. (1931). The visual perception of velocity. *Psychologische Forschung*, *14*, 199–232.

- 814 Coutant, B. E., & Westheimer, G. (1993). Population distribution of stereo- 842
 815 scopic ability. *Ophthalmic and Physiological Optics*, 13, 3–7. 843
 816 Cumming, B. G., & DeAngelis, G. (2001). The physiology of stereopsis. 844
 817 *Annual Review of Neuroscience*, 24, 203–238. 845
 818 Cumming, B. G., & Parker, A. J. (1994). Binocular mechanisms for detect- 846
 819 ing motion-in-depth. *Vision Research*, 34, 483–495. 847
 820 Fang, F., & He, S. (2004). Strong influence of test patterns on the percep- 848
 821 tion of motion aftereffect and position. *Journal of Vision*, 4, 637–642. 849
 822 Farell, B. (1998). Two-dimensional matches from one-dimensional stimu- 850
 823 lus components in human stereopsis. *Nature*, 395, 689–693. 851
 824 Farell, B. (2003). Detecting disparity in two-dimensional patterns. *Vision* 852
 825 *Research*, 43, 1009–1026. 853
 826 Howard, I. P., & Rogers, B. J. (2002). *Seeing in depth*. Toronto: I: Porteus. 854
 827 Julesz, B. (1971). *Foundations of cyclopean perception*. Chicago: Chicago 855
 828 University Press. 856
 829 Mather, G., Verstraten, F. A. J., & Anstis, S. M. (1998). *The motion after-* 857
 830 *effect: A modern perspective*. Cambridge, Massachusetts: MIT Press. 858
 831 Morgan, M. J., & Castet, E. (1997). The aperture problem in stereopsis. 859
 832 *Vision Research*, 39, 2737–2744. 860
 833 Nijhawan, R. (1994). Motion extrapolation in catching. *Nature*, 370, 256–257. 861
 834 Nishida, S., & Johnston, A. (1999). Influence of motion signals on the per- 862
 835 ceived position of spatial pattern. *Nature*, 397, 610–612. 863
 836 Ohzawa, I., DeAngelis, G. C., & Freeman, R. D. (1990). Stereoscopic depth 864
 837 discrimination in the visual cortex: Neurons ideally suited as disparity 865
 838 detectors. *Science*, 249, 1037–1041. 866
 839 Poggio, G. F., & Fischer, B. (1977). Binocular interaction and depth sensi- 867
 840 tivity in striate and prestriate cortex of behaving rhesus monkey. *Jour-* 868
 841 *nal of Neurophysiology*, 40, 1392–1405. 869
- Raymond, J. E. (1993). Complete interocular transfer of motion adapta- 842
 tion effects on motion coherence thresholds. *Vision Research*, 33, 1865– 843
 1870. 844
 Reagan, D., & Beverly, K. I. (1973). Some dynamic features of depth per- 845
 ception. *Vision Research*, 13, 2369–2378. 846
 Schor, C. M., & Wood, I. (1983). Disparity range for local stereopsis as a 847
 function of luminance spatial frequency. *Vision Research*, 23, 1649– 848
 1654. 849
 Shioiri, S., Saisho, H., & Yaguchi, H. (2000). Motion in depth based on 850
 inter-ocular velocity differences. *Vision Research*, 40, 2565–2572. 851
 Shioiri, S., Kakehi, D., Yaguchi, H. (2002). Motion in depth perception 852
 based on monocular motion aftereffect. *Proceedings of the second asian* 853
conference on vision (p.10). Gyeongju, Korea. 854
 Shioiri, S., Kakehi, D., Tashiro, T., & Yaguchi, H. (2003). Investigating 855
 perception of motion in depth using monocular motion aftereffect. VSS 856
 abstracts. *Journal of Vision*, 3(9), 856a. 857
 Smallman, H. S., & MacLeod, D. I. A. (1994). Size-disparity correlation in 858
 stereopsis at contrast threshold. *Journal of the Optical Society of Amer-* 859
ica A, 11, 2169–2183. 860
 Snowden, R. J. (1998). Shifts in perceived position following adaptation to 861
 visual motion. *Current Biology*, 8, 1343–1345. 862
 Sumnall, J. H., & Harris, J. M. (2002). Minimum displacement thresh- 863
 olds for binocular three-dimensional motion. *Vision Research*, 42, 864
 715–724. 865
 Whitney, D. (2002). The influence of visual motion on perceived position. 866
Trends in Cognitive Sciences, 6, 211–216. 867
 Wohlgenuth, A. (1911). On the aftereffect of seen movement. *British Jour-* 868
nal of Psychology Monographs, Suppl. 1, 1–117. 869