Motion adaptation shifts apparent position without the motion aftereffect

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Adaptation to motion can produce effects on both the perceived motion (the motion aftereffect) and the position (McGraw, Whitaker, Skillen, & Chung, 2002; Nishida & Johnston, 1999; Snowden, 1998; Whitaker, McGraw, & Pearson, 1999) of a subsequently viewed test stimulus. The position shift can be interpreted as a consequence of the motion aftereffect. For example, as the motion within a stationary aperture creates the impression that the aperture is shifted in position (De Valois & De Valois, 1991; Hayes, 2000; Ramachandran & Anstis, 1990), the motion aftereffect may generate a shift in perceived position of the test pattern simply because of the illusory motion it generates on the pattern. However, here we show a different aftereffect of motion adaptation that causes a shift in the apparent position of an object even when the object appears stationary and is located several degrees from the adapted region. This position aftereffect of motion reveals a new form of motion adaptation—one that does not result in a motion aftereffect—and suggests that motion and position signals are processed independently but then interact at a higher stage of processing.

Most historical observations of the motion aftereffect (MAE) have supported the idea that the illusion is due to an adaptation mechanism that is retinotopically specific and generates an illusory motion without an accompanying displacement in the apparent position of the test stimulus (Mather, Verstraten, & Anstis, 1998; Wohlgemuth, 1911). This is often cited as evidence that motion information and position information are analyzed independently, since a change in an object's location is not necessary to perceive motion.

More recent research has qualified this conclusion. Snowden (1998), Nishida and Johnston (1999), and Whitaker, McGraw, and Pearson (1999) have demonstrated that the perceived position of a static test pattern can appear to be displaced in the direction of an MAE. For example, Snowden adapted subjects to a moving grating that was immediately followed by a stationary test grating at the same location. The test grating appeared to move in the direction of the MAE. Adjacent to the test grating was another grating that was physically stationary for comparison. Observers reported that the test grating not only appeared to move, but also appeared to be phase-shifted in position, relative to the adjacent comparison grating.

This could be interpreted as evidence against the segregation of motion and position information; units that

code an object's location could, theoretically, also code its motion. However, the time course of the position shift was not found to follow that of the MAE (Nishida & Johnston, 1999). Furthermore, the perceived position shift need not be accompanied by a concurrent illusory motion, which suggests that, to some degree, there is a separation of motion from position coding (McGraw, Whitaker, Skillen, & Chung, 2002; Nishida & Johnston, 1999). It is, therefore, clear that although object location cannot be coded by the *same* mechanism that registers motion, motion signals can directly *influence* units that code object location.

The other principal characteristic of the MAE, in the belief of early researchers, was that motion adaptation was thought to be retinotopically specific. After adapting to a moving stimulus, for example, only test stimuli presented in roughly the same location invoke the MAE (Masland, 1969; Mather et al., 1998; Wohlgemuth, 1911).

In this case, as above, recent research has raised some qualifications. For example, von Grünau and Dubé (1992) have shown that the MAE can be perceived in nonadapted regions. In their study, subjects adapted to a moving stimulus that was followed by a dynamic, or flickering, pattern in a region adjacent to the adapted site. Surprisingly, an MAE was observed in the dynamic pattern presented in the unadapted region. Snowden and Milne (1997) have reported a remote MAE in one location produced by adaptation to remote complex patterns of motion, such as rotation and expansion. Another type of remote MAE has been shown more recently by Culham, Verstraten, Ashida, and Cavanagh (2000). After attentively tracking motion in one region of space, an MAE was observed in another

area of the visual field. Because these remote MAEs have been observed only with flickering or dynamic test patterns, they might be due to a different mechanism than that which causes the static MAE. Setting aside the difference between static and dynamic MAEs and whether this reflects distinct stages of processing (Nishida & Sato, 1995; Verstraten, Fredericksen, van Wezel, Lankheet, & van de Grind, 1996), there is evidence that at least some forms of motion adaptation are not specified retinotopically but can spread to adjacent regions.

The remote MAE and the position shifts that occur after adaptation to motion are, in some respects, similar to other illusions that occur with visible motion (see Whitney, 2002, for a review). For example, a stationary aperture filled with moving texture not only appears to move, but also can appear to be displaced in the direction of its illusory motion (De Valois & De Valois, 1991; Hayes, 2000; Ramachandran & Anstis, 1990). This could imply that the perceived illusory motion, as opposed to the actual motion in the scene, causes the perceived displacement in position. However, we recently found that the perceived position of a stationary object can be shifted in position by nearby motion, even when the object appears stationary (Whitney & Cavanagh, 2000). When there is real motion present in the scene, it is not necessary to perceive motion of the test item for a shift in its apparent location to be seen.

The position shift that follows motion adaptation (Nishida & Johnston, 1999; Snowden, 1998; Whitaker et al., 1999), however, presents a slightly different case: In this situation, there are no physical motion signals present in the scene, and yet the position of the test pattern still appears shifted. There remains a possibility that, when there are no physical motion signals present, perceived motion of the stimulus (an MAE in this case) could be necessary to cause a displacement in its perceived position.

In this study, we report that motion adaptation in one region of the visual field can influence the apparent position of another object, even when this object is a substantial distance from the adapted region. Surprisingly, although the shift is due to motion adaptation, the object does not have to appear to move for it to appear to be displaced in position. Motion adaptation can, therefore, shift the apparent position of a stimulus without an MAE being visible on that stimulus. This suggests that motion information is selectively incorporated into the position coding of stimuli throughout the visual field but that the motion and location of an object are coded by separate, independent mechanisms.

EXPERIMENT 1
Position Shifts of Remote Objects After Adaptation to Motion

Method

Three subjects participated in the experiment. Each had normal or corrected-to-normal vision. The subjects were seated in a darkened experimental booth with a chinrest 28 cm from an NEC Mul-

tisync P1150 CRT, which had a refresh rate of 75 Hz. A rotating radial grating (14.4° diameter, 3.2 Hz) was presented for 33 sec during the first adaptation period. A 4.3° circle with a fixation point was provided at the center of the rotating radial grating at all times. The grating had a sinusoidal luminance modulation of eight cycles per rotation at 84.9% contrast on a dark (0.01 cd/m²) background. After the first adaptation period, test periods were alternated with 3-sec readaptation periods (see Figure 1A). During each test period, the radial grating was removed (the screen was completely blank, aside from the visible fixation point), and after an interstimulus interval (ISI) of 135 msec, two horizontal lines were flashed for 200 msec. Each flash (34.5 cd/m²) was 0.36° × 3.6°. The flashes were vertically misaligned in one of six positions, and subjects were asked to judge the relative alignment of the two flashes (vernier) in a two-alternative forced-choice (2AFC) method of constant stimuli task (Figure 1B). The subjects were instructed to respond as quickly as possible during the test period. The readaptation period began immediately following the subject's response.

During each test period, there were five possible eccentricities at which the flashes could be presented. For each of these five conditions, there were six possible vertical misalignments between the flashes and 20 trials for each of these positions. In each of these conditions, psychometric functions were fitted to the data from the logistic function $y = \{1+\exp[a(x-b)]\}^{-1}$, where b estimates the physical misalignment between the flashes that creates an apparent alignment. For example, when the flashes were physically aligned, they appeared shifted in a direction consistent with that of the MAE; in order to offset this apparent misalignment, the flashes would have to be physically misaligned in a direction opposite that of the MAE. In separate experimental sessions, the radial grating
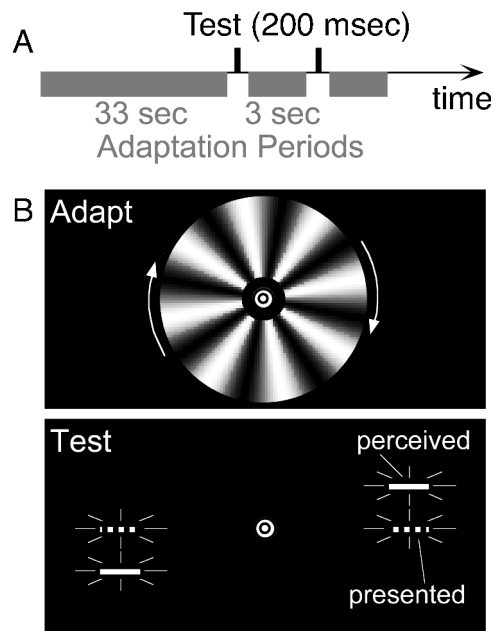

Figure 1. (A) The procedure used in Experiment 1. An initial 33-sec adaptation period was followed by interleaved test and 3-sec adaptation periods. During the adaptation period, a rotating radial grating was presented. During the test period, two flashed lines were presented (nothing else was visible during the test period except the fixation point). (B) Experiment 1 stimulus and percept. After adaptation to a rotating grating, two physically aligned flashes appeared misaligned in a direction opposite that of the previous motion; that is, in a direction consistent with that of the motion aftereffect.

rotated counterclockwise and clockwise. Data for the two directions were not different and were, therefore, flipped and merged.

Results

Figure 1B shows that after adaptation to a rotating grating, a pair of flashed lines appear to be misaligned in a direction consistent with that of the MAE. That is, the flashes appear to be misaligned in a direction opposite that of the previous motion. Note that during the test period, when the flashes are presented, the grating is not present; the flashes are the only visible stimuli.

Figure 2B shows the perceived misalignment between the two flashes as a function of the flash eccentricity. The gray region on the left of the graph shows where the rotating grating was presented during the adaptation period; no grating was presented during the test period. There was a significant misalignment between the two flashes at each eccentricity tested. A misalignment was

still perceived even when the flashes were separated from the adapted region by over 10°. The misalignment increased slightly with increasing eccentricity, which is consistent with the fact that the perceived speed of the MAE increased with eccentricity (Wright & Johnston, 1985).

Perhaps the most interesting aspect of the data is that there was virtually no difference in the misalignment whether the flashes were presented inside or outside the adapted region. This shows that motion adaptation in one retinal location can influence the perceived positions of remote objects.

The effect of the flash's duration on its apparent shift is graphed in Figure 3. There is a misalignment between the flashes when they are presented for less than ~5 sec. At longer durations, the apparent misalignment falls off.

EXPERIMENT 2
Are Eye Movements Responsible for the Misalignment?

The first experiment showed that adapting to motion in one region of space can shift the apparent positions of objects located in unadapted regions. Because a rotating grating was used, however, torsional eye movements could have been induced and, thus, could have caused the phenomenon. For example, while the grating was presented, the eyes could have rotated in one direction. After the grating was removed, the eyes could have reflexively rotated in the opposite direction. This might have caused an apparent tilt in a frame of reference, such as the monitor; in turn, the flashed stimuli, which were presented on a physically horizontal plane, might have appeared to be slightly oblique. The second experiment tested the eye movement and frame-of-reference explanations.

Method

The method in the second experiment was similar to that in the first experiment. Three subjects were seated in a room with ambient light, with a chinrest 31.5 cm from a Sony G520 CRT (85-Hz refresh). Two horizontally adjacent radial gratings (rather than one) rotated at 4 Hz in opposite directions during the adaptation period (Figure 4; sinusoidal luminance modulation, eight cycles per rotation, 82% contrast on a dark background). The diameter of each grating was 22°, and each was horizontally separated from the fixation point by 13°. During the test period, three flashes (47-msec duration, 32 cd/m²) were presented—two straddling the outer edges of the two gratings and one superimposed on the fixation point (each of the flashes was 0.44° × 4.4°). The procedure and the 2AFC task were identical to those in the first experiment. The two outer flashes were vertically offset relative to the central flash by varying degrees, and the subjects were asked to respond whether the flashes were misaligned, as in Figure 4. When fitted to the data, the psychometric function described above reveals the degree to which the flashes needed to be physically misaligned in order to cancel the apparent shift shown in Figure 4.

Results

Figure 5 shows that after the subjects adapted to the two radial gratings rotating in opposite directions, the outer two flashes appeared to be shifted in a direction consistent with that of the nearest site of adaptation—
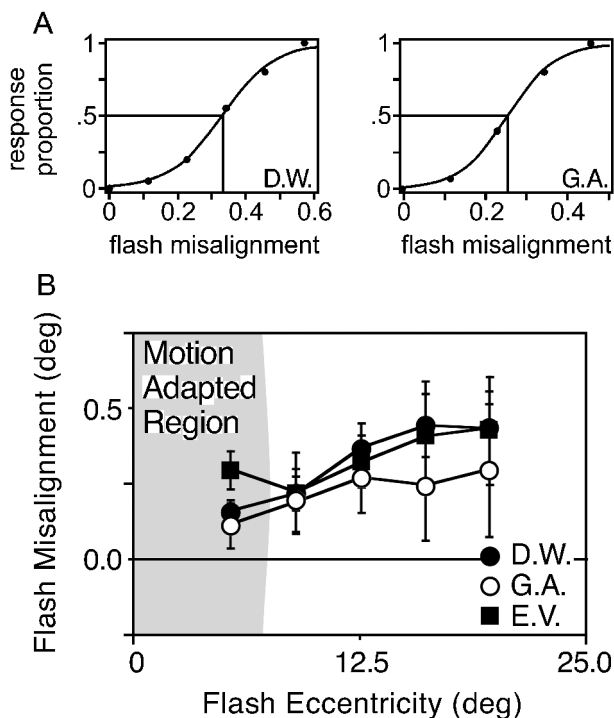

Figure 2. Results of Experiment 1 for 3 subjects. (A) Example psychometric functions for 2 subjects (for the condition in which the flashes were presented at ~12.5°). The points of subjective equality on the psychometric functions (indicated by the line at .5 along the ordinate) show that the subjects perceived a substantial misalignment between the flashes. That is, the flashes had to be physically misaligned in a direction opposite that of the MAE in order for the flashes to appear to be aligned. (B) The perceived misalignment between the flashes is plotted as a function of the eccentricity of each flash. The shaded area shows the location of motion adaptation (where the rotating grating was presented). Note that a misalignment was perceived between flashes whether they were presented inside or outside the motion-adapted (shaded) region. The perceived misalignment between the flashes increased slightly with eccentricity. The error bars show 95% confidence intervals (Finney, 1971).
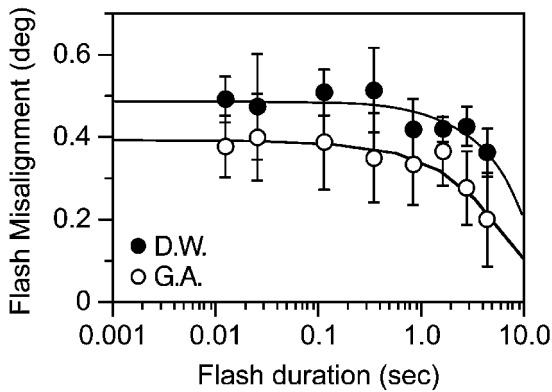
Figure 3. The apparent misalignment is plotted as a function of the duration of the flashes. The magnitude of the illusion begins to decrease for flashes presented longer than about 2 sec. The error bars show 95% confidence intervals. The best linear fit lines are $[f(x) = -0.00004*x + 0.38]$ for G.A. and $[f(x) = -0.00003*x + 0.48]$ for D.W.

that is, consistent with the nearest direction of MAE. Since the eye cannot rotate in two directions simultaneously and two oppositely rotating gratings produced misalignments in opposite directions, the flash misalignment must not be due to eye movements.

Likewise, if there were a frame of reference, or major axis, that was tilted by the motion of the grating, we would expect two gratings rotating in opposite directions to cancel or reduce any induced tilt and, therefore, reduce the flash misalignment, because a single frame of reference (such as the monitor) could not tilt in two directions simultaneously. Since the flash misalignment remained unchanged in this condition, a shifted frame of reference is not responsible for the effect.

Considering that the position aftereffect of motion spreads well beyond the adapted site (as was seen in Experiment 1), it may seem surprising that the effect does not cancel itself when produced by two oppositely rotating gratings. However, in the first experiment, adaptation to the rotating grating produced both upward and downward motion energy and yet still produced a misalignment between the two flashes, rather than canceling itself out. Similarly, the flashes in the present experiment simply appeared to be displaced in a direction opposite that of the *nearest* motion-adapted region, just as they had in the first experiment.

EXPERIMENT 3
Perceived Motion of the Mislocalized Flashes

The results of the first experiment showed that the influence of motion adaptation on the perceived locations of the flashes increased with eccentricity: At increasing eccentricity, the flashes appeared to be more misaligned. It is known that the perceived speed of the MAE grows with increasing eccentricity (Wright & Johnston, 1985), so the question arises as to whether the misalignment is caused by the same mechanism that causes the MAE.

One way to test this relationship is to examine whether the flashes appear to move. If the flash shift is mediated by an illusory motion, an MAE of the flashes themselves, then they should appear to move.

Method

The subjects and stimulus in the third experiment were similar to those in the first experiment, except that during the test period, the two flashed lines were moved vertically in opposite directions to cancel any illusory motion that they might exhibit. Since MAEs are generally perceived to be slow, we physically moved the flashes at extremely slow speeds. To do this, each flash was presented as a traveling Gaussian luminance distribution, thereby creating sub-pixel motion (Morgan, 1980). This creates an apparently smooth motion that can be slower than the pixel resolution of the monitor would normally allow.

Just as in the previous experiments, a 2AFC task was used; the subjects were asked to judge whether the flashes moved in one direction or the other. The physical motion required to null any illusory flash motion was measured. The duration of the flashes was initially fixed at 200 msec (identical to the first experiment), whereas the eccentricity of the flashes was varied randomly across trials between one of five values. In subsequent experimental sessions, the eccentricity was fixed at 7.4°, and the duration of the flashes was varied between one of four values. The radius of the rotating adaptation grating was 7.2°. All other aspects of the data collection and analysis were identical to those in Experiment 1.

Results

Figure 6A shows the perceived speed of the flashes as a function of their eccentricity. The perceived motion of the flashes was biased in the direction of the MAE (positive speed), but the perceived speed of the flashes was consistently below threshold (which is calculated as half the distance between the 25th and the 75th percentiles on the psychometric function). The perceived speed of the flashes did not increase with eccentricity, contrary to traditional measures of the MAE (Wright & Johnston, 1985).

Figure 6B shows the perceived speed of the flashes as a function of the flash duration. The illusory motion of
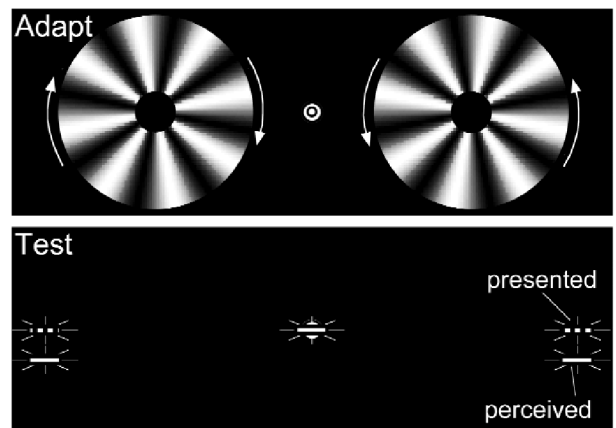

Figure 4. Stimulus and percept in Experiment 2. Two radial gratings rotated in opposite directions during the adaptation period. Three flashes were presented straddling the gratings in the test period. The flashes appeared to be misaligned in a direction consistent with that of the nearest motion aftereffect.
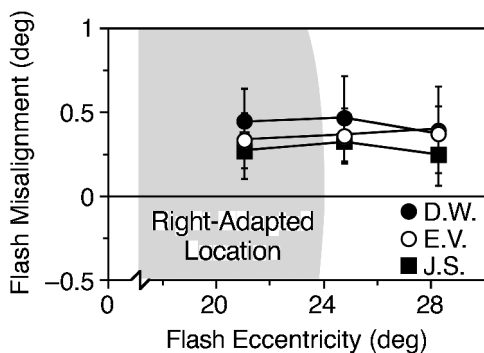
Figure 5. Results of Experiment 2. The perceived misalignment is plotted as a function of the flash eccentricity. The shaded region shows the location of the right-hand side rotating radial grating that was presented during the adaptation period (the grating was not visible during the test period). The error bars show 95% confidence intervals.

the flashes depended on their duration. For example, flashes presented for ~50 msec appeared to move, consistent with the fact that briefly presented stimuli have high velocity thresholds (Cropper, 1994). So, to cancel any perceived motion of the flash, even very little, the flash was rapidly moved in the opposite direction. At longer durations, on the other hand, the flashes did not appear to move as fast. In fact, flashes presented for over ~300 msec appeared stationary when they were presented as stationary (data points on far right of Figure 6B). Interestingly, as Figure 3 shows, flashes presented for longer than 300 msec did appear shifted in position. Therefore, even when the flashes were *perceived* to be stationary, they still appeared to be shifted in position by motion adaptation in a remote region of the visual field.

To confirm this result further, we tested a variation of this experiment. We presented a pair of flashes (of a particular duration) that moved just enough so that they appeared stationary and then measured the misalignment between the flashes. For example, on the basis of the results shown in Figure 6A, a pair of flashes that are presented for 200 msec appear to move at ~0.1 deg/sec. We therefore physically moved the flashes at this speed, to cancel their illusory motion, and then measured how misaligned they appeared to be. The result was that when the flashes were physically moved, therefore appearing stationary, they nonetheless appeared to be shifted in position. This suggests that illusory motion (e.g., an MAE) does not mediate the position displacement. Obviously a motion-adapted site is responsible for the effect in some manner, but this must not be identified with the mechanism that assigns positions to the flashes.

EXPERIMENT 4
Is the Site of Motion Adaptation Binocular?

The traditional static-test MAE does not transfer completely between the eyes (Moulden, 1980; see Wade, Swan-

ston, & de Weert, 1993, for a review.) Using dynamic or flickering test stimuli, however, it has been shown that some types of MAE do exhibit complete interocular transfer (Nishida, Ashida, & Sato, 1994). If the influence of motion-adapted units on apparent position is mediated by a mechanism that is binocularly driven, we might expect the perceived flash misalignment from the first experiment to occur even if the motion adaptation stimulus were presented to one eye while the test flashes were presented to the other eye.

Method

The method in the fourth experiment was identical to that in the first experiment, except that the stimulus was presented in a dichoptic display: The adaptation stimulus (the rotating radial grating) was presented to one eye, while the test flashes were presented to the other eye. A fixation point was presented at the center of each image. A haploscope was provided to aid subjects in fusing the two images. All other stimulus parameters and procedures were identical to those in the first experiment.
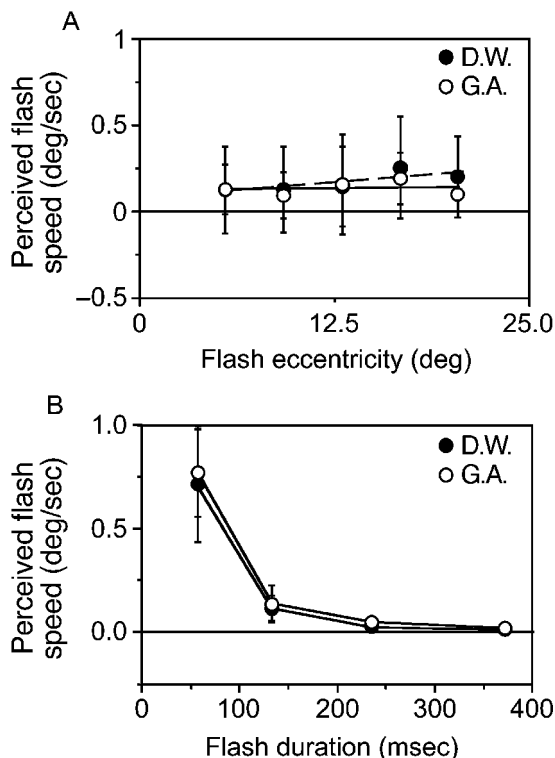

Figure 6. Results of Experiment 3. (A) The perceived speed of the (physically stationary) flashes is plotted as a function of their eccentricity. Flashes presented for 200 msec did not appear to move significantly. The error bars show 95% confidence intervals. The lines through the data show best linear fits for G.A. [$f(x) = 0.001 * x + 0.11$] and D.W. [$f(x) = 0.007 * x + 0.07$]. (B) The perceived flash speed is plotted as a function of the flash duration. The longer the flash was presented, the slower it appeared to move. Note that although flashes presented for longer than 300 msec appeared stationary when they were physically stationary, they still appear to be misaligned, as is shown in Figure 3. The error bars show 95% confidence intervals.
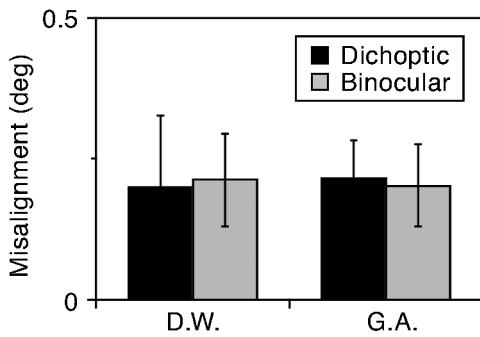
Figure 7. Results of Experiment 4. The misalignment exhibits complete interocular transfer; the illusion is comparable for both binocular and dichoptic stimulus presentations. The error bars show 95% confidence intervals.

Results

Figure 7 shows that when the rotating grating is presented to one eye, the flashes presented to the other eye appear substantially misaligned. This clearly shows that the flash displacement must be produced by motion adaptation at a site that is binocularly driven.

EXPERIMENT 5
The Effect of Storage on the Misalignment

The MAE is well known to exhibit an effect called storage—if there is an interval of time between the adaptation and the test periods in which no visual stimulation is present, the MAE can still be observed in the test pattern (Spigel, 1960, 1962, 1964; Thompson & Wright, 1994; Verstraten, Fredericksen, Grüsser, & van de Grind, 1994; Wohlgemuth, 1911). Even if a textured pattern is presented during the storage period, there can still be a strong residual MAE (Thompson & Wright, 1994; Verstraten et al., 1994).

In this experiment, we investigated whether the misalignment observed in the first experiment exhibits storage. If storage is a characteristic of both the flash misalignment and the MAE, this would raise the possibility that the flash shift might be due to motion adaptation of units that also give rise to the MAE.

Method

Initially, the subjects adapted to a rotating radial grating (identical to that used in Experiment 1) for 30 sec. Test flashes, presented at ±12.6° eccentricity, were presented on either side of the grating. Subsequently, adaptation (6.7 sec) and test periods were alternated. After each adaptation period, there was a variable delay (ISI) before the presentation of the test flashes. During this ISI, or storage period, nothing was presented on the monitor aside from the fixation point. There was minimal illumination in the room, so the monitor itself was dark (0.05 cd/m²). In the first experiment, the ISI was 135 msec, whereas in this experiment the ISI was 1 of 11 durations between 135 and 7,650 msec, each presented in different blocks of trials.

During the first test period (within each block), the test flashes were misaligned by a random degree (within a range of ±0.3°). In a method of adjustment task, the subjects were asked to respond as to

which of the two flashes appeared above the other or whether the flashes appeared to be aligned (there were three possible responses—two for reporting the direction of misalignment and one for reporting that the flashes looked aligned). In the subsequent test period, the flashes were shifted (by 0.07°) in a direction that partially nulled the misalignment reported by the subject; if, in the previous test period, the subject had responded that the flashes looked aligned, the flashes were not shifted at all, and the trial was simply repeated. Additional trials continued to be presented until the subject was satisfied that the misalignment was entirely canceled. Once satisfied of this, the subject pressed an escape key (different from the three used by the subject during the experiment), and the final nulled
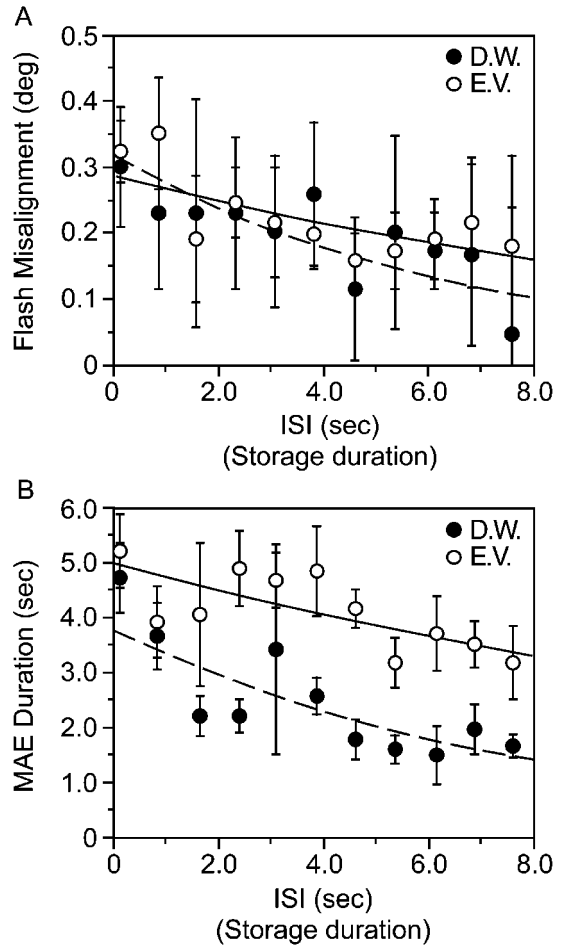

Figure 8. Results of Experiment 5. (A) The flash misalignment is plotted as a function of the storage duration. There is an exponential decrease in the magnitude of the illusion with an increasing storage period between the adaptation and the test periods. The solid and dashed lines through the data show the best fit exponential curves for Subjects E.V. [$f(x) = 0.28 * \exp(-0.07 * x)$] and D.W. [$f(x) = 0.31 * \exp(-0.14 * x)$], respectively. (B) For purposes of comparison, the motion aftereffect (MAE) strength (duration; see Wade, 1994) is also plotted as a function of storage duration. Like the flash misalignment, the MAE falls off with increasing storage duration. The solid and dashed lines through the data show the best fit exponential curves for Subjects E.V. [$f(x) = 4.94 * \exp(-0.05 * x)$] and D.W. [$f(x) = 3.74 * \exp(-0.12 * x)$], respectively. The error bars show 95% confidence intervals.

misalignment was recorded. Perceived misalignments were measured in this way for each of the five storage (ISI) periods.

In a subsequent experiment, we measured the duration of the traditional MAE, using the same adaptation stimulus. In this case, rather than presenting two flashed lines during the test period, a stationary version of the adaptation grating was presented. The adaptation and test gratings occupied the same location. The subjects judged the duration of the MAE by pressing a key when the static test no longer appeared to move.

Results

Figure 8A shows that even after storage periods of greater than 3 sec, there is still a misalignment perceived between the flashes. The illusion falls off exponentially with increasing storage duration.

For purposes of comparison, Figure 8B also shows the strength of the MAE as a function of the storage duration. It is clear that there is an MAE after storage and that the effect falls off with increasing storage duration. Interestingly, the MAE and the misalignment both follow similar decay functions (see the figure caption).

GENERAL DISCUSSION

The experiments above showed that after adaptation to motion in one region of the visual field, a briefly presented stimulus in a remote, nonadapted region appeared to be shifted in position. This position aftereffect of motion was not caused by eye movements or a single frame of reference, and even when the flashes were perceived to be stationary, they still appeared to be misaligned. The effect exhibited complete interocular transfer and must, therefore, be binocularly driven, since motion adaptation in one eye influenced the perceived positions of the flashes presented to the other eye.

Although certainly due to motion adaptation in some way, there are significant differences between this illusion and traditional aftereffects of motion adaptation. The most obvious of these differences is that the illusion can be seen even when there is no perceived motion of the test stimulus; the flashes appeared shifted in position even when they appeared stationary. In addition, the apparent positions of the flashes did not depend on the retinotopic location of the previously viewed motion; whether a flash was presented in an adapted region or not made no difference on its illusory position shift. This is contrary to previously reported MAEs, where the aftereffect was strongest in the adapted region. Finally, the position aftereffect of motion showed complete interocular transfer, whereas the classic motion aftereffect showed only partial transfer (Moulden, 1980).

The position aftereffect of motion is, therefore, not a secondary consequence of the illusory motion of an MAE. It demonstrates a previously unknown relationship between an object's perceived position and the current and prior history of motion in the visual field. The independence of the illusory position shift and the MAE suggests that separate units must underlie the perception of position and motion (as is generally thought; Mather et al., 1998).

Nevertheless, the position-coding units must receive input from the motion-coding units to create the interaction between motion and position that we measured here.

How and why does the position-coding mechanism respond to motion signals? At least two broad hypothetical mechanisms are possible. First, a single, motion-adapted site could subsequently cause both the MAE and apparent shifts in position (i.e., the MAE and the position shifts are caused by independent mechanisms, but both receive input from a common motion-adapted site). Alternatively, motion could cause distinct kinds of adaptation in separate motion- and position-coding units. The issue is whether the adaptation itself occurs at a single site or in separate ways for different kinds of information.

Relation to Dynamic and Static MAEs

MAEs are frequently categorized as either static or dynamic, depending on whether the illusion is perceived on a static or a flickering/dynamic-noise test pattern. For example, adaptation to second-order (contrast-defined) motion generally produces an MAE on a dynamic or flickering test (Ledgeway & Smith, 1994; McCarthy, 1993), but not on a static test pattern (Derrington & Badcock, 1985). In the present article, the test pattern comprised only brief flashes that appeared just once, rather than flickering continuously. The flashes were usually stationary but did have temporal frequency components in all directions because they were abruptly presented. For these reasons, it is difficult to classify the flashes as either static or dynamic.

Although the position aftereffect of motion does not involve visible motion of the test flashes, its properties show some similarities to those of the dynamic MAE. For example, the flashes appear to be displaced even when they are not presented in the adapted region, which shows that the effect is not spatially specific. This property is inconsistent with the static MAE (Mather et al., 1998; because no motion is perceived in surrounding regions during adaptation; previously reported phantom or relative MAEs involve overlapping adaptation and test regions, or at least perceived motion in the test region; cf. Anstis & Reinhardt-Rutland, 1976; Ashida, Susami, & Osaka, 1996; Bonnet & Pouthas, 1972; Swanston & Wade, 1992; Wade, Spillmann, & Swanston, 1996; Weisstein, Maguire, & Berbaum, 1977; Zaidi & Sachtler, 1991). But this property is consistent with the remote MAE found with dynamic test patterns (Culham et al., 2000; Snowden & Milne, 1997; von Grünau & Dubé, 1992). Also, the position aftereffect of motion showed complete interocular transfer, similar to the dynamic MAE (Nishida et al., 1994). However, unlike the dynamic MAE (Verstraten et al., 1996), the results in the fifth experiment demonstrated that the misalignment can be stored for a substantial period of time, whereas only the static MAE has shown storage (Thompson & Wright, 1994). The illusion presented here cannot be easily classified as either a static or a dynamic MAE, and the conflicting evidence strongly suggests that another process is at work.

CONCLUSIONS

After adaptation to motion, the apparent positions of briefly presented objects can appear to be shifted in a direction consistent with that of the MAE. This position aftereffect of motion is not simply a secondary, local effect of the classic MAE, since the effect works equally well in adapted and nonadapted regions of the visual field, is completely transferred between the two eyes, and occurs even when the test flashes appear stationary—that is, when there is no perceived motion of the test. The illusion is, therefore, a new aftereffect of motion and shows that the perception of an object's location (even a stationary one) is influenced by nearby and distant motion signals that have occurred over the past several seconds.

REFERENCES

ANSTIS, S. M., & REINHARDT-RUTLAND, A. H. (1976). Interactions between motion aftereffects and induced movement. *Vision Research*, **16**, 1391-1394.

ASHIDA, H., SUSAMI, K., & OSAKA, N. (1996). Re-evaluation of local adaptation for motion aftereffect. *Perception*, **25**, 1065-1072.

BONNET, C., & POUTHAS, V. (1972). Apparent size and duration of a movement after-effect. *Quarterly Journal of Experimental Psychology*, **24**, 275-281.

CROPPER, S. J. (1994). Velocity discrimination in chromatic gratings and beats. *Vision Research*, **34**, 41-48.

CULHAM, J. C., VERSTRATEN, F. A. J., ASHIDA, H., & CAVANAGH, P. (2000). Independent aftereffects of attention and motion. *Neuron*, **28**, 607-615.

DERRINGTON, A. M., & BADCOCK, D. R. (1985). Separate detectors for simple and complex grating patterns? *Vision Research*, **25**, 1869-1878.

DE VALOIS, R. L., & DE VALOIS, K. K. (1991). Vernier acuity with stationary moving Gabors. *Vision Research*, **31**, 1619-1626.

FINNEY, D. J. (1971). *Probit analysis* (3rd ed.). Cambridge: Cambridge University Press.

HAYES, A. (2000). Apparent position governs contour-element binding by the visual system. *Proceedings of the Royal Society of London: Series B*, **267**, 1341-1345.

LEDGEWAY, T., & SMITH, A. T. (1994). The duration of the motion aftereffect following adaptation to first-order and second-order motion. *Perception*, **23**, 1211-1219.

MASLAND, R. (1969). Visual motion perception: Experimental modification. *Science*, **165**, 819-821.

MATHER, G., VERSTRATEN, F. [A. J.], & ANSTIS, S. [M.] (EDS.) (1998). *The motion after-effect: A modern perspective*. Cambridge, MA: MIT Press.

MCCARTHY, J. E. (1993). Directional adaptation effects with contrast modulated stimuli. *Vision Research*, **33**, 2653-2662.

MCGRAW, P. V., WHITAKER, D., SKILLEN, J., & CHUNG, S. T. (2002). Motion adaptation distorts perceived visual position. *Current Biology*, **12**, 2042-2047.

MORGAN, M. J. (1980). Spatiotemporal filtering and the interpolation effect in apparent motion. *Perception*, **9**, 161-174.

MOULDEN, B. (1980). After-effects and the integration of patterns of neural activity within a channel. *Philosophical Transactions of the Royal Society of London: Series B*, **290**, 39-55.

NISHIDA, S., ASHIDA, H., & SATO, T. (1994). Complete interocular transfer of motion aftereffect with flickering test. *Vision Research*, **34**, 2707-2716.

NISHIDA, S., & JOHNSTON, A. (1999). Influence of motion signals on the perceived position of spatial pattern. *Nature*, **397**, 610-612.

NISHIDA, S., & SATO, T. (1995). Motion aftereffect with flickering test patterns reveals higher stages of motion processing. *Vision Research*, **35**, 477-490.

RAMACHANDRAN, V. S., & ANSTIS, S. M. (1990). Illusory displacement of equiluminous kinetic edges. *Perception*, **19**, 611-616.

SNOWDEN, R. J. (1998). Shifts in perceived position following adaptation to visual motion. *Current Biology*, **8**, 1343-1345.

SNOWDEN, R. J., & MILNE, A. B. (1997). Phantom motion aftereffects—evidence of detectors for the analysis of optic flow. *Current Biology*, **7**, 717-722.

SPIGEL, I. M. (1960). The effects of differential post-exposure illumination on the decay of a movement after-effect. *Journal of Psychology*, **50**, 209-210.

SPIGEL, I. M. (1962). Contour absence as a critical factor in the inhibition of the decay of a movement aftereffect. *Journal of Psychology*, **54**, 221-228.

SPIGEL, I. M. (1964). The use of decay inhibition in an examination of central mediation in movement aftereffects. *Journal of General Psychology*, **70**, 241-247.

SWANSTON, M. T., & WADE, N. J. (1992). Motion over the retina and the motion aftereffect. *Perception*, **21**, 569-582.

THOMPSON, P., & WRIGHT, J. (1994). The role of intervening patterns in the storage of the movement aftereffect. *Perception*, **23**, 1233-1240.

VERSTRATEN, F. A. J., FREDERICKSEN, R. E., GRÜSSER, O. J., & VAN DE GRIND, W. A. (1994). Recovery from motion adaptation is delayed by successively presented orthogonal motion. *Vision Research*, **34**, 1149-1155.

VERSTRATEN, F. A. J., FREDERICKSEN, R. E., VAN WEZEL, R. J. A., LANKHEET, M. J. M., & VAN DE GRIND, W. A. (1996). Recovery from adaptation for dynamic and static motion aftereffects: Evidence for two mechanisms. *Vision Research*, **36**, 421-424.

VON GRÜNAU, M., & DUBÉ, S. (1992). Comparing local and remote motion aftereffects. *Spatial Vision*, **6**, 303-314.

WADE, N. J. (1994). A selective history of the study of visual motion aftereffects. *Perception*, **23**, 1111-1134.

WADE, N. J., SPILLMANN, L., & SWANSTON, M. T. (1996). Visual motion aftereffects: Critical adaptation and test conditions. *Vision Research*, **36**, 2167-2175.

WADE, N. J., SWANSTON, M. T., & DE WEERT, C. M. (1993). On interocular transfer of motion aftereffects. *Perception*, **22**, 1365-1380.

WEISSTEIN, N., MAGUIRE, W., & BERBAUM, K. (1977). A phantom-motion aftereffect. *Science*, **198**, 955-958.

WHITAKER, D., MCGRAW, P. V., & PEARSON, S. (1999). Non-veridical size perception of expanding and contracting objects. *Vision Research*, **39**, 2999-3009.

WHITNEY, D. (2002). The influence of visual motion on perceived position. *Trends in Cognitive Sciences*, **6**, 211-216.

WHITNEY, D., & CAVANAGH, P. (2000). Motion distorts visual space: Shifting the perceived position of remote stationary objects. *Nature Neuroscience*, **3**, 954-959.

WOHLGEMUTH, A. (1911). On the after-effect of seen movement. *British Journal of Psychology*, **1**(Supp.), 1-117.

WRIGHT, M. J., & JOHNSTON, A. (1985). Invariant tuning of motion aftereffect. *Vision Research*, **25**, 1947-1955.

ZAIDI, Q., & SACHTLER, W. L. (1991). Motion adaptation from surrounding stimuli. *Perception*, **20**, 703-714.