

Independent Aftereffects of Attention and Motion

Jody C. Culham,*†# Frans A. J. Verstraten,‡||
Hiroshi Ashida,‡§ and Patrick Cavanagh*

*Vision Sciences Lab
Department of Psychology
Harvard University
Cambridge, Massachusetts 02138

†Vision and Motor Control Lab
Department of Psychology
University of Western Ontario
London, Ontario N6A 5C2
Canada

‡ATR Human Information Processing
Research Laboratories
Kyoto 619-0288

§College of Letters
Ritsumeikan University
Kyoto 603-8577
Japan

||Utrecht University
Utrecht NL-3584 CS
The Netherlands

Summary

In the motion aftereffect (MAE), a stationary pattern appears to move in the opposite direction to previously viewed motion. Here we report an MAE that is observed for a putatively high level of visual analysis—attentive tracking. These high-level MAEs, visible on dynamic (but not static) tests, suggest that attentive tracking does not simply enhance low-level motion signals but, rather, acts at a subsequent stage. MAEs from tracking (1) can overrule competing MAEs from adaptation to low-level motion, (2) can be established opposite to low-level MAEs seen on static tests at the same location, and (3), most striking, are specific to the overall direction of object motion, even at nonadapted locations. These distinctive properties suggest MAEs from attentive tracking can serve as valuable probes for understanding the mechanisms of high-level vision and attention.

Introduction

Attention plays several roles in visual perception, with selection among input signals being the most extensively studied (Broadbent, 1958). However, attention also serves a tracking function that is central to many visual tasks, particularly when there are multiple targets, up to four or five, that cannot all be followed with eye movements (Pylyshyn and Storm, 1988; Cavanagh, 1992; Kahneman et al., 1992; Yantis, 1992). Some common examples include negotiating a busy intersection, attending to teammates and opponents in sports, or managing an air-traffic control display. Some have pro-

posed that this tracking function of attention constitutes a high-level motion system (Cavanagh and Mather, 1990; Cavanagh, 1991; Lu and Sperling, 1995a; although, see Lu and Sperling, 1995b, for an alternative mechanism), subsuming the function attributed to the long-range process of Braddick (1980) or the high-level system of Julesz (1971). This second motion system complements the more automatic, low-level system based on motion detectors that signal spatiotemporal changes in luminance energy, even in the absence of attention to the stimulus. Although the two motion systems should typically operate in tandem in natural scenes, it is the high-level system that imposes the ultimate limit on our ability to keep track of objects as they move. We now report a phenomenon that can probe this high-level aspect of motion and visual attention.

One hallmark of automatic, low-level motion perception is the motion aftereffect (MAE; Wohlgenuth, 1911; Mather et al., 1998); prolonged exposure to a moving stimulus makes a subsequently viewed stationary stimulus appear to move in the opposite direction. Traditionally, MAEs have been attributed to the fatigue or adaptation of the directionally selective units in visual cortex. Direction-selective neurons have been reported in both striate (Hubel and Wiesel, 1962) and extrastriate cortex, particularly visual area MT (named for its homology with the monkey middle temporal area or, alternatively, visual area 5, V5; Zeki, 1974). Neural correlates of the MAE have been observed across a range of regions, from retinal ganglion cells in the rabbit (Barlow and Hill, 1963) to the MT complex in humans (Tootell et al., 1995). A characteristic property of low-level MAEs is that their effect is limited to the receptive fields of the adapted units; a unit is adapted only if exposed to motion within its receptive field, and the effect of the adaptation is only seen if the static test pattern also falls in the receptive field (Anstis and Gregory, 1965).

In addition to the local MAEs produced by adaptation to low-level motion energy, we now show that global MAEs can be produced when attention is used to track moving features and that these global MAEs are independent of low-level MAEs. These higher-order MAEs can only be revealed with dynamic (flickering or counterphasing) tests and are visible even at nonadapted locations (far from the adapting stimulus). However, these same dynamic tests are also sensitive to low-level MAEs, so that we can use them to evaluate the relative strength of the low- and high-level motion signals. We find that attention-based aftereffects can be strong enough to overcome opposing motion energy-based aftereffects.

We have been able to identify several novel aspects of the high-level motion system with these tracking MAEs and, moreover, we have demonstrated their effectiveness as probes of high-level vision and attention.

Results

Experiment 1: Aftereffects of Attentive Tracking

First, we demonstrate that attentive tracking on its own can generate an MAE. To invoke attentive tracking in

To whom correspondence should be addressed (e-mail: culham@irus.rrri.on.ca).

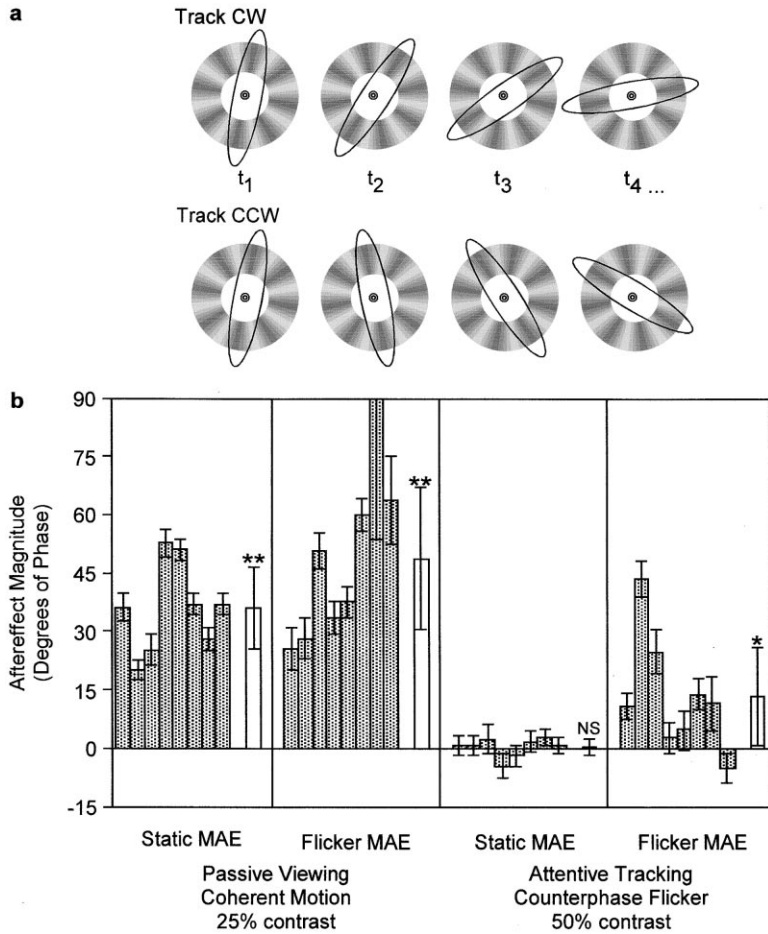


Figure 1. Stimulus and Results of Experiment 1

(A) Schematic of the attentive tracking task used during adaptation. A radial grating counterphase flickered over time, such that equal motion energy was present in two opposite directions (CW and CCW). Although the retinal stimulus itself was identical for both conditions, as shown in the upper and lower panels, attention was used to disambiguate the perceived direction of motion. Observers attended to a particular pair of bars on opposite sides of the grating (indicated by an ellipse but not actually present in the display) and followed the pair's position in either the clockwise (upper panel) or counterclockwise (lower panel) direction. Only the first four frames in time (t_1 , t_2 , t_3 , and t_4) are shown. Observers maintained fixation on the central bull's-eye throughout the tracking, such that attention shifted without eye movements. Following 30 s of adaptation, either a static or flicker MAE was measured.

(B) Results of experiment 1, showing motion aftereffects following attentive tracking of a counterphase grating, as described in (A), as well as following passive viewing of a coherently drifting grating. Static and flicker MAEs for eight observers (gray bars) and for the group average (white bars) are quantified by the phase shift necessary to null the MAE, where a positive magnitude indicates a negative MAE (a bias to report motion opposite to the adapted direction). The asterisk and double asterisks indicate group average values that were statistically significant, $p < 0.05$ or $p < 0.001$, two-tailed, respectively; NS indicates nonsignificant average values. Error bars show 95% confidence intervals.

the absence of any net low-level motion signals, we presented a radial counterphasing grating, a stimulus constructed by superimposing two identical sine wave gratings moving in opposite directions. This stimulus has equal motion energy in the clockwise (CW) and counterclockwise (CCW) directions. As shown in Figure 1A, observers were instructed to use attention to mentally track (Wertheimer, 1961) the bars of a radial grating in one of the two ambiguous directions while keeping their gaze fixed on a central bull's-eye. Thus, the actual stimulus was identical for all attentive tracking conditions; only the observer's instructions differed. All observers were able to attentively track the grating accurately without moving their eyes (see Experimental Procedures). As a comparison, we also examined MAEs following passive viewing of a single-grating component rotating unambiguously in one direction.

In the adaptation period, the grating either counterphase flickered for attentive tracking conditions or smoothly drifted for passive viewing conditions. The stimulus was presented for an initial 30 s adaptation period, followed by 5 s top-up intervals interleaved with test trials to maintain adaptation.

MAEs demonstrate different properties depending on whether the test pattern is static (static MAE; Wohlge-muth, 1911) or dynamic (e.g., flicker MAE; von Grünau, 1986; von Grünau and Dubé, 1992; Nishida and Sato,

1995). When a static test grating is employed, observers report that the grating drifts slowly opposite to the adaptation direction, although they are often simultaneously aware that it is not really moving with respect to local landmarks. When an ambiguously flickering test grating is employed, it is perceived as moving rapidly (depending on the test temporal frequency), opposite to the adaptation direction, in a manner easily confused with real motion (as with other dynamic test stimuli; Hiris and Blake, 1992). Static and flicker MAEs are believed to have different underlying substrates (see Culham et al., 1998b, for a review). For example, the static MAE has only partial interocular transfer, suggesting that at least some of the underlying processing occurs at an early stage before input from the two eyes has been combined (at or before striate cortex), whereas the flicker MAE can have complete interocular transfer, suggesting that it taps a later stage (at or beyond striate cortex) (Raymond, 1993; Nishida et al., 1994; Nishida and Ashida, 2000). We measured both the static and flicker MAEs using a nulling procedure. In both cases, eight observers judged the perceived direction of motion (CW or CCW) on each trial, and MAEs were quantified by the phase shift necessary to null the perceived illusion (see Experimental Procedures).

As shown in Figure 1B, attentive tracking produced a significant flicker MAE but with a negligible static MAE.

As expected, passive viewing of coherent motion produced both a static MAE and a flicker MAE. Thus, it appears that the flicker MAE but not the static MAE can be adapted by attentive tracking. It may be that the flicker MAE is simply a more sensitive test of motion adaptation than the static MAE (von Grünau, 1986) and thus is better able to detect a relative enhancement of adaptation in the attended direction. If so, static and flicker MAEs should differ only in magnitude but should always occur in the same direction. However, as the next two experiments show, static and flicker MAEs can be induced in opposite directions, indicating qualitative rather than just quantitative differences.

Experiment 2: Attention versus Motion Energy

To dissociate the relative contributions of attentive tracking and motion energy mechanisms to MAEs, we pitted the two against one another in a second experiment. To do so, we manipulated motion within the radial grating by changing the relative contrast of the two component gratings. In the two conditions we tested, either the motion energy was balanced and the direction was inherently ambiguous (counterphase flicker, as in experiment 1; see Figure 2A) or one of the two directional components was slightly stronger than the other, producing a bias in one direction (counterclockwise; see Experimental Procedures; Figure 2B). Although the stimulus appeared to move in the direction of the bias when passively viewed, attention could reverse the perceived direction when observers mentally tracked a pair of bars in the direction opposite to the bias. Observers (five) were instructed to track the grating clockwise in all cases, including the biased condition, in which attentive tracking went against the direction of the energy bias (Figure 2C). Both static and flicker MAEs were measured by their direction and a duration index. We compared the MAEs following attentive tracking of unbiased and biased gratings to the MAEs following passive viewing of each type.

Attentive tracking reversed the direction of the flicker MAE, compared to passive viewing. As shown in Figure 2D, following passive viewing of the biased grating, the aftereffect was opposite to the direction of the motion energy. However, when subjects attentively tracked the bars of the grating, the MAE was opposite to the tracked direction not only for the unbiased gratings (as in experiment 1) but for the biased gratings as well (the biased flicker MAE was significantly different between passive viewing and attentive tracking conditions, $t = 3.32$, $df = 4$, $p < 0.05$, two-tailed). That is, the flicker MAE was always opposite to the direction of motion that was perceived during adaptation, regardless of whether the percept arose from a bias within the stimulus or from attentive feature tracking. This reversal suggests that attentional MAE effects were strong enough to override energy-based MAE effects. However, the power of attentive tracking is limited. If the motion energy bias was increased much above the levels used here (see Experimental Procedures), tracking against the motion energy simply became too difficult, and the MAE always opposed the energy direction, regardless of attentive tracking efforts.

The reversal of MAE direction for a biased grating with

attentive tracking was not observed for the static MAE. As illustrated in Figure 2E, the static MAE was opposite to the biased direction whether the subjects had attentively tracked the grating or not. That is, the biased condition could produce an aftereffect specific to a direction that had never been perceived during adaptation. As in experiment 1, attention had negligible effects on the magnitude of the static MAE, even in the case of the unbiased grating. This result is important because it implies that the responses of the early motion detectors remained the same, regardless of the state of attention, and are therefore stimulus driven. Given the reversal of flicker MAE with attentive tracking described above, attention must act at a later stage of motion processing. Several articles have shown that attention can modulate the static MAE (Chaudhuri, 1990; Rees et al., 1997); however, in these articles, attention was modulated by directing it to a different retinal location. In our stimuli, attention was always directed to the location of the low-level motion; it was only the motion path within that area that was affected by attention. Perhaps the static MAE is modulated not by the selection of the adapting motion for awareness but only by the presence of attention in the adapting area.

Two separate controls were run to determine whether eye movements might have contributed to the effects we measured. First, eye movements during adaptation and test were monitored in three observers, with a variety of monitoring devices (including scleral eye coils; see Experimental Procedures). No systematic eye movements were detected other than microsaccades. In these conditions, with verified absence of tracking eye movements, the flicker MAE was seen at its usual strength. To demonstrate that the monitoring was sufficient to detect tracking eye movements, we asked the observers to pursue the target bar with their eyes; the large-amplitude pursuit was then easily seen in the traces. Second, we also measured MAEs when two observers were instructed to overtly track a single bar of the grating as it moved around the test annulus (smooth-pursuit eye movements). They tracked the target for the same adaptation period as in the main experiment and then made direction judgements of the static and flickering tests while fixating the center of the test displays (Figure 2F). Eye tracking produced negligible effects on the static MAE. Small aftereffects were observed with eye tracking for the flicker MAE; however, these were not statistically significant and were significantly less than those produced by attentive tracking ($p < 0.05$, one-tailed, for attentive tracking compared to all three flicker MAE controls). Therefore, even if the maximum possible tracking eye movements did occur, they could not produce the strength of flicker MAE that we see with attentive tracking.

Thus, we have demonstrated that, although static and flicker MAEs occur in the same direction following passive viewing, attentive tracking can reverse the direction of the flicker MAE but not the static MAE. This qualitative difference in attentional impact between flicker and static MAEs cannot be attributed solely to sensitivity differences between the two types of tests. The third experiment corroborates this finding and further suggests that the attentional- and energy-based MAEs occur at different processing stages.

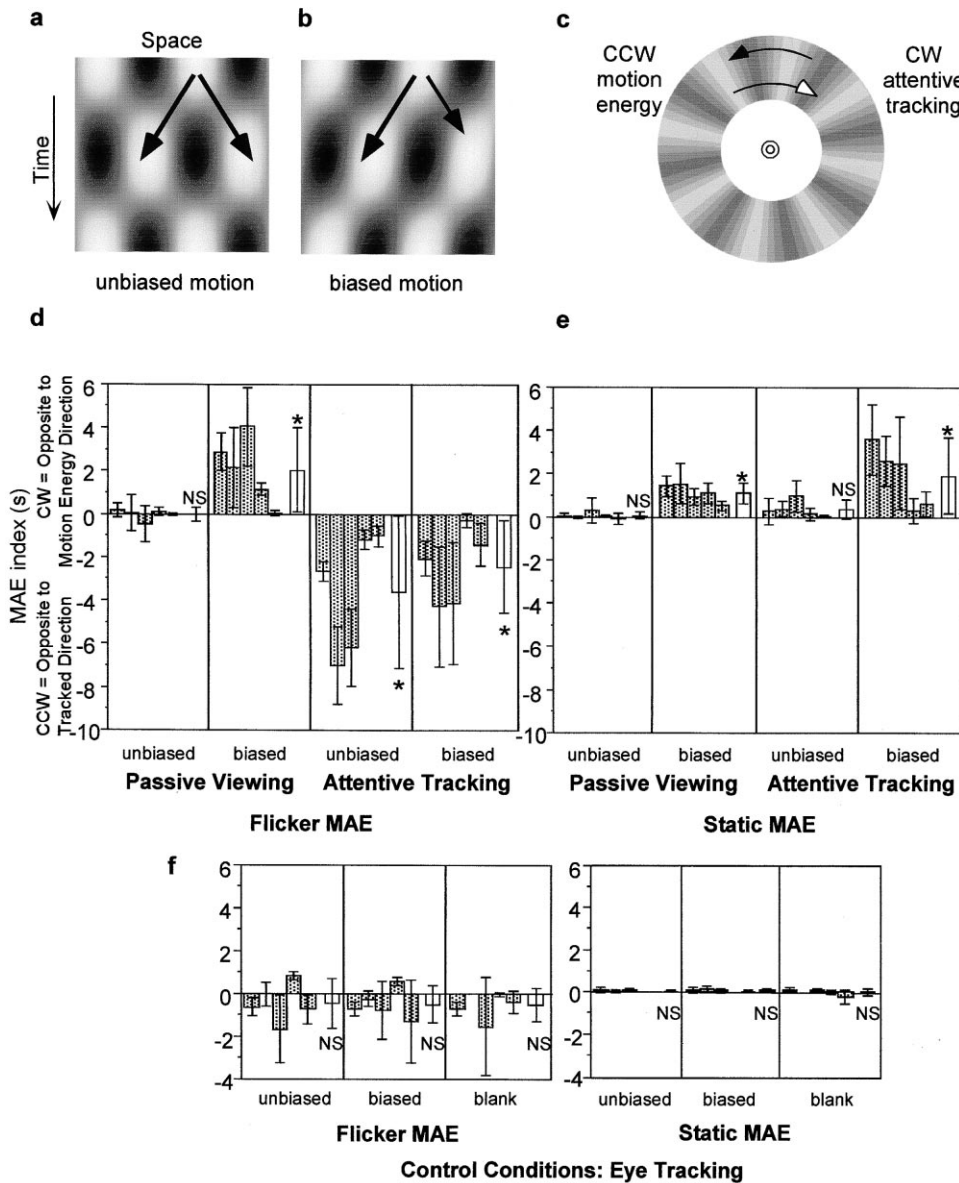


Figure 2. Stimulus and Results of Experiment 2

(A) Space–time plot for an unbiased grating, demonstrating equal motion energy in each of two opposite directions, as indicated by two same-size arrows.

(B) Space–time plot for a biased grating, demonstrating stronger motion in one direction than the other, as indicated by two arrows of different sizes. Although motion energy is stronger in the leftward direction, the position of a feature, such as the white bar, can still be seen to move in either direction.

(C) With small bias levels, observers are able to attentively track a radial grating in the direction opposite to the energy bias. For all conditions of experiment 2, the grating was biased to move CCW, and observers were cued to attentively track CW.

(D) Results of the main conditions in experiment 2, showing flicker MAEs for five observers (gray bars) who passively viewed or attentively tracked unbiased and biased radial gratings, along with the group averages (white bars). The asterisk indicates group average values that were statistically significant, $p < 0.05$, two-tailed; NS indicates nonsignificant average values. Error bars show 95% confidence intervals.

(E) Results of the control conditions in experiment 2, showing static MAEs for passive viewing and attentive tracking of unbiased or biased gratings.

(F) Results of control conditions in experiment 2, showing static and flicker MAEs when observers used smooth-pursuit eye movements to visually track cues that rotated in synchrony with the grating, which was unbiased, biased, or absent.

Experiment 3: Retinotopic Specificity of MAEs

Finally, we demonstrate that MAEs to attentive tracking are global—opposite in direction to the adapting tracking even at nonadapted locations. To examine the retinotopic specificity (Weisstein et al., 1977; Cavanagh and

Favreau, 1980; von Grünau and Dubé, 1992; Snowden and Milne, 1996, 1997) of energy-based and attention-based MAEs, we had five subjects adapt to a radial grating surrounding a central bull's-eye (Figure 3A). Following adaptation, a radial test grating appeared in the

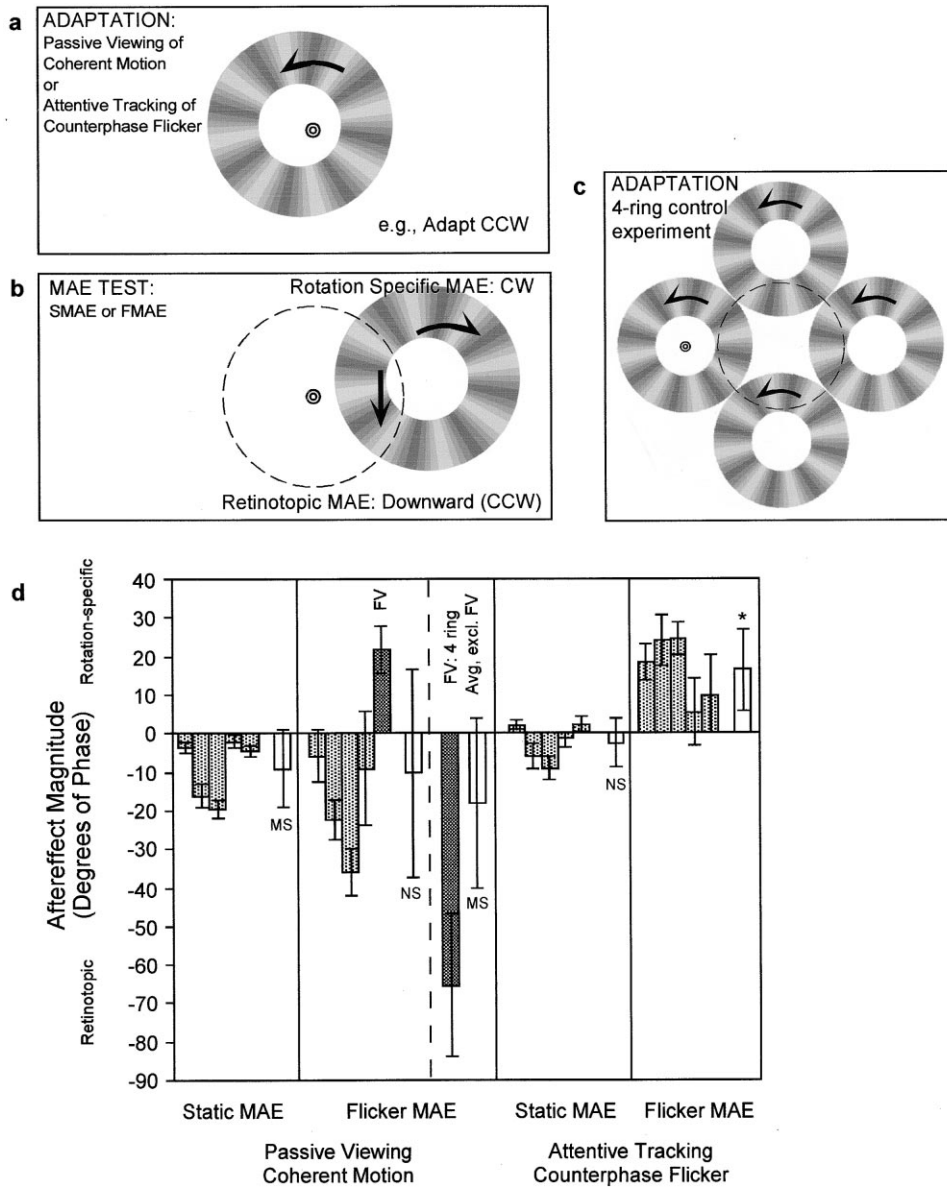


Figure 3. Stimulus and Results of Experiment 3

(A) The adaptation grating appeared concentric with a fixation point in the middle of the display.

(B) The test grating appeared peripheral to the fixation point to produce a region of overlap that yields two potential outcomes. First, local MAEs could result from the adaptation of neurons early in the motion processing stream, which have relatively small receptive fields specific to the local direction of linear motion. These effects could only occur in the region where adapt and test gratings overlap. For example, CCW adaptation would affect neurons in the region of overlap that are selective to approximately upward motion. Upon presentation of a test with no net motion signal, these neurons would signal the opposite, downward motion, biasing the observer to CCW responses (i.e., the same direction as the adapting grating). Second, global MAEs could arise from the adaptation of rotation-selective mechanisms, in which case units active for one direction of motion, CCW, would signal the opposite direction of rotation during the test phase, CW, independent of the location of the test grating.

(C) Stimulus configuration for the four-ring control experiment performed by subject FV. Four adaptation gratings were used, making it difficult to attend to any one grating during adaptation and producing four times the overlap between the four adapt gratings (grayscale rings) and the test grating (dashed circle).

(D) Results of experiment 3, showing motion aftereffects following attentive tracking of a counterphase grating, as described in (A), and following passive viewing of a coherently drifting grating. Static and flicker MAEs for five observers (gray bars) and the group averages (white bars) are quantified by the phase shift necessary to null the MAE. Positive values indicate outcomes consistent with a rotation-specific MAE, and negative values indicate the local MAE. The asterisk indicates group average values that were statistically significant, $p < 0.05$, two-tailed; MS indicates marginally significant values, $p < 0.05$, one-tailed ($p < 0.10$, two-tailed); NS indicates nonsignificant average values. Error bars show 95% confidence intervals. In the flicker MAE condition, the result from the four-ring condition from FV is shown. Given that FV shows a clear local MAE under these more powerful conditions, the group average for the single-ring condition has been replotted with his data excluded.

periphery, while the subjects maintained fixation on the central bull's-eye. The overlap between adaptation and test gratings yielded opposite predictions for models of motion perception based on retinotopic and nonretinotopic mechanisms (Figure 3B). That is, retinotopic motion mechanisms based on linear motion direction would predict only regional MAEs that would bias the observer to report MAEs in the same rotational direction as the adaptation, whereas nonretinotopic rotation-specific mechanisms would yield MAEs opposite to the direction of adaptation, regardless of the placement of the test.

Following attentive tracking, flicker MAEs were observed opposite to the overall direction of the ring's rotation, even when the adapt and test gratings were spatially separated. For example, adaptation to CCW motion yielded a CW flicker MAE (Figure 3D) at test locations to the right or left of the adaptation ring. In comparison, without attentive tracking, both static and flicker MAEs (with the striking exception of one observer) were retinotopically specific. That is, aftereffects opposed the local direction of motion within the region of overlap for both static and flicker MAEs.

How do we explain the anomalous result of one observer (FV) who showed a rotation-specific flicker MAE in the "passive" viewing condition? We believe that, despite the instructions, this observer was unable to avoid attentively tracking the motion of the rotating adapting grating. To verify our supposition, FV was retested with a stimulus composed of four peripheral adapting rings placed to overlap with one central test ring (Figure 3C). This configuration provides a more powerful stimulus (with four times the retinal overlap), and the crowding makes it difficult to attend to and track even one adapting ring (He et al., 1996), let alone all four. When adapted to passive viewing of smooth motion in the four peripheral rings, FV demonstrated a robust local flicker MAE. We conclude that instructions alone were not enough to stop FV from tracking and that, had he been able to stop tracking on his own in the passive case of the main experiment, he would have also shown the local as opposed to global MAE. Under passive viewing, static and flicker MAEs only reached marginal significance in the one-ring case; however, casual duration tests with FV and two additional observers found highly robust retinotopic MAEs with the four-ring configuration. Because of the crowding effects and difficulty in attentively tracking any one ring, we were forced to use the less effective single-ring configuration for comparisons with attentive tracking conditions.

Discussion

We have discovered a motion aftereffect of attentive tracking that taps a high level of visual representation. It is nonlocal, revealed only by a dynamic test, and its motion can compete with and override low-level motion aftereffects. We picked an ambiguous motion stimulus to induce the tracking aftereffect, as it has no net low-level motion. Observers overcome the ambiguity by using attention to track a specific feature in one direction or the other, as requested (both directions were equally "trackable" in the ambiguous stimulus). Whereas previous studies have examined aftereffects of the motion

of "first-order" features, namely luminance, or "second-order" features, such as texture or depth, we have shown that aftereffects can also arise purely from a mentally imposed trajectory (attentive tracking in a direction of the subject's choice) in the absence of any net motion in the stimulus. The aftereffects of attentive feature tracking are qualitatively different from traditional motion aftereffects arising from adaptation to motion energy.

We have shown that attentional aftereffects occur only when a flicker test is employed. Given past comparisons of static and dynamic/flicker MAEs, such as complete interocular transfer of dynamic but not static MAEs (Raymond, 1993; Nishida et al., 1994; Nishida and Ashida, 2000), it has been proposed that the flicker MAE taps later stages of motion processing than the conventional static MAE (Culham et al., 1998b). Although some have suggested that the flicker MAE is simply a more sensitive test of motion adaptation than the static MAE (von Grünau, 1986), this hypothesis is not supported by the two directional dissociations that we have demonstrated here.

Our results show that, for the flicker MAE, attention can overrule stimulus motion energy. When a grating biased to move in one direction is attentively tracked in the opposite direction, the direction of the subsequent flicker MAE can be reversed. No such reversal is observed for the static MAE, however, implying that attention does not just enhance processing at the initial stages of motion processing. Our results dissociate two stages of MAEs: (1) the static MAE, which is always specific to motion energy within the stimulus, regardless of whether or not it reaches perceptual awareness, and (2) the flicker MAE, which responds to both local, low-level motion and global, high-level motion based on the conscious perception of an object's direction, as determined by attention to its visual features.

Attentional aftereffects are selective for the overall direction of object rotation, independent of the location in the visual field, whereas MAEs produced by stimulus motion energy are selective for the local linear motion direction. Although it has been previously shown that the flicker MAE is nonlocal (von Grünau, 1986; von Grünau and Dubé, 1992), we have further shown that it can be rotation specific and highly dependent on the attended and perceived direction. Physiological evidence shows that cortical motion area MT has relatively small receptive fields that respond to local, linear motion signals, whereas, at the next stage of processing in area MST (named for its homology with the monkey middle superior temporal area), receptive fields are much larger and can be integrated into complex motion patterns such as rotation and expansion/contraction (Saito et al., 1986). Thus, these results suggest MST as the earliest possible stage at which attentional aftereffects could be mediated. However, it is also possible that such effects could occur at a substantially later stage. Physiological evidence has shown that extraretinal effects such as attention are progressively stronger at later stages of motion processing, with larger influences in MST than MT (Treue and Maunsell, 1996) and still larger influences in parietal cortex (Ferrera et al., 1994). Furthermore, human neuroimaging results show relatively weak effects of attentive tracking in the MT/MST complex, compared

to later parietal motion areas (Sunaert et al., 1999), which are strongly enhanced by attentive tracking (Culham et al., 1998a).

Taken together, these dissociations argue that attention does not merely modulate input to the motion system at the initial stages of processing. This is not to say that attention cannot do so nor that attentive tracking accounts for all attentional modulation of MAEs. Indeed, attentional effects on MAEs have been demonstrated in situations where attentive tracking is unlikely to be involved. These cases include attentional modulation of static MAEs (Chaudhuri, 1990; Rees et al., 1997), which do not appear to be influenced by attentive tracking in our data, as well as the modulation of dynamic MAEs for limited-lifetime random dot patterns, which are not conducive to the tracking of single elements (Lankheet and Verstraten, 1995). However, modulatory influences by themselves cannot account for the effects found here, as they would have been visible in the static MAEs where no influence of attentive tracking was found. The absence of an effect of attentive tracking on the static MAEs may result from the fact that attention was always allocated to the region of the ambiguous low-level motion. It was never directed elsewhere, as was the case for previous modulatory effects of attention on static MAEs (Chaudhuri, 1990).

Although one potential explanation for our results is that attention modulates motion processing but only at a relatively late stage of processing (in area MST or beyond), an intriguing alternative is that these effects result from a cognitive process in which attention selects one among competing motion trajectories and suppresses the alternatives. The aftereffect of extended selection of one trajectory appears to be a bias in favor of the suppressed trajectory. Raymond has reported that motion adaptation-like effects can be observed with fleetingly brief presentations (Raymond and Isaak, 1998) and that attention to one direction enhances these adaptation effects (Raymond et al., 1998). She has suggested that attending to and selecting the direction of motion of an object decreases sensitivity to subsequent objects moving in the same direction, making changes in trajectory more salient, operating in a manner similar to other cognitive effects such as priming (Tipper, 1985), repetition blindness (Kanwisher, 1987), or inhibition of return (Posner and Cohen, 1982), but for direction rather than location or identity. Our results show definitively that the effects of attentionally selecting a motion direction are not only independent of low-level sensory adaptation but that they can overpower it. Furthermore, they suggest that, like other high-level attentional effects (Kanwisher and Driver, 1992), the aftereffect of attentional tracking is clearly object-based, specific to the direction of motion of the object rather than motion of the local contours. Thus, just as aftereffect of low-level motion has been an invaluable tool for the study of early motion mechanisms, the aftereffect of attentional motion may also be a powerful means to understand high-level vision, motion, and attention.

Experimental Procedures

General Methods

All observers who participated were trained psychophysical observers with normal or corrected-to-normal acuity. Three of the authors

participated in the experiments (subjects JC, FV, and HA), but all other observers were naive as to the purpose and hypotheses. Data from three subjects were discarded: one subject (experiment 1) subsequently received a diagnosis of glaucoma and may have had abnormal motion perception, another subject (experiment 1) had data that was too noisy to perform Probit analysis (though duration measures showed effects consistent with the other observers), and a third subject (experiment 2) had difficulties in accurately maintaining attentive tracking.

Stimuli were generated on Macintosh computers using custom software (Vision Shell, Micro ML) and presented on calibrated monitors. The display, shown in Figure 1A, consisted of an eight-cycle radial grating within an annulus on a gray background with a central black-and-white bull's-eye. In attentive tracking conditions, the grating was presented in smooth counterphase flicker (except for the biased condition in experiment 2) at 2 Hz. Note that in a counterphasing grating, the net motion energy is equal in the two directions, clockwise and counterclockwise, such that, without attentive tracking, observers alternately perceive one direction and the other in equal proportions. With attentional effort, however, the motion can be disambiguated, such that the attended direction dominates the perception, although reversals may still occur occasionally, especially with fatigue. During adaptation, observers maintained fixation and used attention without eye movements to select a pair of bars on opposite sides of the grating and actively follow their changing positions in one direction, clockwise or counterclockwise, rather than the other. In passive viewing conditions, observers maintained fixation and made no special efforts to track the grating.

Test conditions examined both static and flicker MAEs. Experiments 1 and 3 used a nulling measure to quantify the magnitude of the MAE; experiment 2 used a duration index to quantify the effect. Different methods were employed because the experiments originated in two independent labs. Subjects (five) from experiment 1 (which used the nulling method) were also tested with the duration index measure and showed qualitatively similar results. At least 1 min was allowed between sessions, to allow the observer to recover from adaptation before the next session.

We were careful to verify that subjects could accurately maintain fixation during attentive tracking and its MAE. Recently, one of us (Verstraten et al., 2000) recorded eye movements during attentive tracking, using a search coil, the most accurate technique currently available. During attentive tracking, observers showed only microsaccades that did not differ from those during fixation alone and that were uncorrelated with the stimulus. In addition, we verified accurate fixation in one author/subject, JC, who participated in all experiments of this paper and showed robust effects in all three. JC's eye movements were recorded using a binocular infrared eye tracker (Ober2, Permobil; 50 Hz sampling rate). No differences in fixation were detected between attentive tracking, the attentive tracking MAE, or fixation, although smooth pursuit of target rings was easily detected (for four repetitions, with each condition lasting 8–16 s). Accurate fixation was also verified in one other subject (SS) who participated in experiments 1 and 3. Although radial gratings prevent linear eye movements, torsional eye movements are possible during motion and MAEs; however, they do not appear to account for standard MAEs (Seidman et al., 1992). Because eye trackers cannot reliably detect torsional rotations, we used a video camera placed very close to subject JC's eye to record the iris during attentive tracking, a technique that has been previously used to quantify torsion (Balliet and Nakayama, 1978a, 1978b). No torsional movements were evident. Concerned readers can view all eye movement data on the world wide web (see supplemental data at <http://www.neuron.org/cgi/content/full/28/2/607/DC1>).

Observers in experiments 1 and 3 were also prescreened to ensure they could maintain accurate tracking, as indicated by a screening test in which a pair of bars was cued by flanking dots and the subjects continued to track over an interval of 10 s. After tracking, a pair of bars was marked, and subjects indicated whether they were the ones that had been initially cued or not (with a 50% probability of the marked bars being cued or uncued).

Experiment 1

The adaptation stimulus was either a counterphasing grating that was attentively tracked, as described above, or a single-radial grat-

ing (one of the two components of the counterphase grating), rotating unambiguously in one direction, while it was passively viewed. The adaptation pattern appeared for an initial 30 s period and, to maintain adaptation, during 5 s top-up intervals interleaved with test trials. The stimulus had an inner radius of 3.5°, an outer radius of 8.2°, a fixation bull's-eye of 1°, a contrast of 50% for the counterphase grating or 25% for the single component, and a screen luminance of 45 cd/m².

MAEs were measured using a nulling method over a series of trials of variable phase shift presented with the method of constant stimuli. Probit analysis (Finney, 1971) was used to determine the null point, that is, the phase shift at which there were equal CW and CCW responses. Each test stimulus was preceded by a tone and a blanking of the annulus to the mean luminance for 495 ms. This indicated that the observer should stop tracking and passively view the test stimulus, which was presented for 510 ms. In test blocks measuring the static MAE over the 510 ms, the test grating underwent a smooth, continuous displacement of variable phase shift (in a range around 0° of phase). In blocks measuring the flicker MAE, the grating underwent a discrete phase shift of variable size (in a range around 180° of phase) between two frames (255 ms each). In both cases, observers judged the perceived direction of motion (two-alternative forced choice: CW or CCW). For example, if a static MAE test grating smoothly moved 10° CW, an unadapted subject would accurately report CW motion. Similarly, if a flicker MAE test grating abruptly shifted by 170° CW, he would accurately report that the grating moved in the direction with the smallest phase jump (170° CW rather than 190° CCW; i.e., the shortest distance between corresponding bars). However, following adaptation to CW motion, the observer would be biased to see CCW motion (smooth CCW motion on the static MAE test example or a phase jump of 190° CCW rather than 170° CW on a flicker test example). Thus, it could take a relatively large CW jump (e.g., 44° in the case of subject SS) in order for the subject to report CW jumps half of the time; that is the threshold. The subject would then be said to have an MAE magnitude of 44°, where (in Figure 1) that corresponds to the typical negative MAE (a bias to report motion in the direction opposite to adaptation). Conditions were blocked by adaptation type, adaptation direction, and test type and then presented in counterbalanced order. Each subject participated in four blocks of 60 trials for each condition. Adaptation direction alternated between blocks to prevent the long-term buildup of an MAE in one direction.

Experiment 2

A flickering grating can be decomposed into two sinusoids drifting in opposite directions. We manipulated the amplitude of these two components, resulting in a bias favoring the larger component. Modulation of the grating was expressed as:

$$m(\theta) = \frac{C_0}{2} [c_{cw} \cos(w\theta + 2\pi ut) + c_{ccw} \cos(w\theta - 2\pi ut)]$$

$$c_{cw} = \frac{1}{1+b} \text{ and } c_{ccw} = 1 - c_{cw} = \frac{b}{1+b}$$

where θ = spatial position (radians), t = time (s), w = spatial frequency = 8 cycles/annulus, u = temporal frequency = 2 Hz, C_0 = maximum contrast = 0.6 for the adaptation stimulus and 0.3 for the test stimulus, and C_{cw} and C_{ccw} are the biases in the CW and CCW directions. Stimulus size was as in experiment 1, with a screen luminance of 69 cd/m². The unbiased grating had a ratio value of $b = 1$ (i.e., equal motion energy in both directions or counterphase flicker). The biased grating had a ratio value of $b = 0.90$ for observer HA and MT or $b = 0.93$ for JC and FV, indicating the energy in the CCW direction was stronger than that in the CW direction.

For both unbiased and biased adaptation conditions in the main experiment, observers attentively tracked the grating in the CW direction (opposite to the motion energy in the biased condition). To assist the observer in initiating attentive tracking, the adapting stimulus initially appeared with no bias, and then the bias gradually increased to the appropriate level over 1 s. In addition, as soon as the adaptation stimulus appeared, two guide dots just outside the grating followed the bars to be tracked for 2 s and then disappeared for the remainder of adaptation.

With prolonged adaptation, attentive tracking can fail, such that

the perceived direction reverses. To prevent the perception of motion in the energy direction from contributing to the MAEs, the adaptation stimulus disappeared as soon as the observer reported the first perceptual reversal by releasing a key. The test grating appeared 250 ms later and either remained static or counterphase flickered (with no bias). Following adaptation, observers pressed one of two keys to indicate the perceived direction over a 15 s test period (or pressed no key if neither direction predominated). The MAE index was taken as the difference in the total durations of CW and CCW responses over the test period.

Three control conditions were also included. The duration over which subjects had maintained attentive tracking against the biased stimulus during the previous main condition was used as the adaptation duration for all subsequent control measures. In a passive viewing control condition, subjects looked at the adaptation stimuli while fixating and without any effort at attentive tracking. In one eye movement control condition, subjects used smooth-pursuit eye movements rather than attention alone to track a cued bar of the grating. In a second eye movement control condition, no grating was present; however, subjects used eye tracking to follow the peripheral guide dots, which moved in synchrony with the (invisible) bars.

Experiment 3

The third experiment used similar methods as the first, except that the adapt and test stimuli were smaller (inner radius, 1.8°; outer radius, 4.4°; 25% contrast) and spatially separated by 6.2°, as shown in Figure 3A. In half of the sessions, the test grating was to the right of the central adaptation ring; in the other half, it was to the left.

Acknowledgments

This research was supported by grants from the National Eye Institute (NEI EY09258) to P. C., from the McDonnell Pew Program in Cognitive Neuroscience to J. C. C., from the Royal Netherlands Academy of Arts and Sciences to F. A. J. V., and from the Japanese Ministry of Education, Science, Sports, and Culture (GA-EY A10710026) to H. A. We thank our subjects for their participation in experiments and pilot testing, Satoru Suzuki for helpful discussions, Julian Joseph and Preeti Verghese for assistance with Probit analysis, Fiona James and Stacey Woodward for assistance with eye movement recording, and Ken Nakayama, Ron Rensink, Keith Humphrey, and Titis Vilis for comments on earlier drafts of the manuscript.

Received May 15, 2000; revised September 11, 2000.

References

- Anstis, S.M., and Gregory, R.L. (1965). The after-effect of seen motion: the role of retinal stimulation and eye movements. *Q. J. Exp. Psychol.* 17, 173–174.
- Balliet, R., and Nakayama, K. (1978a). Egocentric orientation is influenced by trained voluntary cyclorotary eye movements. *Nature* 275, 214–216.
- Balliet, R., and Nakayama, K. (1978b). Training of voluntary torsion. *Invest. Ophthalmol. Vis. Sci.* 17, 303–314.
- Barlow, H.B., and Hill, R.M. (1963). Evidence for a physiological explanation for the waterfall phenomenon and figural aftereffects. *Nature* 200, 1345–1347.
- Braddick, O.J. (1980). Low-level and high-level processes in apparent motion. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 290, 137–151.
- Broadbent, D.E. (1958). *Perception and Communication* (London: Pergamon).
- Cavanagh, P. (1991). Short-range vs. long-range motion: not a valid distinction. *Spat. Vis.* 5, 303–309.
- Cavanagh, P. (1992). Attention-based motion perception. *Science* 257, 1563–1565.
- Cavanagh, P., and Favreau, O.E. (1980). Motion aftereffect: a global mechanism for the perception of rotation. *Perception* 9, 175–182.
- Cavanagh, P., and Mather, G. (1990). Motion: the long and short of it. *Spat. Vis.* 4, 103–129.

- Chaudhuri, A. (1990). Modulation of the motion aftereffect by selective attention. *Nature* 344, 60–62.
- Culham, J.C., Brandt, S.A., Cavanagh, P., Kanwisher, N.G., Dale, A.M., and Tootell, R.B.H. (1998a). Cortical fMRI activation produced by attentive tracking of moving targets. *J. Neurophysiol.* 80, 2657–2670.
- Culham, J.C., Nishida, S., Ledgeway, T., Cavanagh, P., von Grünau, M.W., Kwas, M., Alais, D., and Raymond, J.E. (1998b). Higher order motion aftereffects. In *The Motion Aftereffect: A Modern Perspective*, G. Mather, F. Verstraten, and S. Anstis, eds. (Cambridge, MA: MIT Press), pp. 85–124.
- Ferrera, V.P., Rudolph, K.K., and Maunsell, J.H.R. (1994). Responses of neurons in the parietal and temporal visual pathways during a motion task. *J. Neurosci.* 14, 6171–6186.
- Finney, D.J. (1971). *Probit Analysis* (Cambridge, UK: Cambridge University).
- He, S., Cavanagh, P., and Intriligator, J. (1996). Attentional resolution and the locus of visual awareness. *Nature* 383, 334–337.
- Hiris, E., and Blake, R. (1992). Another perspective on the visual motion aftereffect. *Proc. Natl. Acad. Sci. USA* 89, 9025–9028.
- Hubel, D.H., and Wiesel, T.N. (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J. Physiol.* 160, 106–154.
- Julesz, B. (1971). *Foundations of Cyclopean Perception* (Chicago, IL: University of Chicago Press).
- Kahneman, D., Treisman, A., and Gibbs, D.J. (1992). The reviewing of object files: object-specific integration of information. *Cog. Psych.* 24, 175–219.
- Kanwisher, N.G. (1987). Repetition blindness: type recognition without token individuation. *Cognition* 27, 117–143.
- Kanwisher, N.G., and Driver, J. (1992). Objects, attributes, and visual attention: which, what and where. *Curr. Dir. Psychol. Sci.* 1, 26–31.
- Lankheet, M.J.M., and Verstraten, F.A.J. (1995). Attentional modulation of adaptation to two-component transparent motion. *Vision Res.* 35, 1401–1412.
- Lu, Z.L., and Sperling, G. (1995a). Attention-generated apparent motion. *Nature* 377, 237–239.
- Lu, Z.L., and Sperling, G. (1995b). The functional architecture of human motion perception. *Vision Res.* 35, 2697–2772.
- Mather, G., Verstraten, F., and Anstis, S. (1998). *The Motion Aftereffect: A Modern Perspective* (Cambridge, MA: MIT Press).
- Nishida, S., and Ashida, H. (2000). A hierarchical structure of motion system revealed by interocular transfer of motion aftereffects. *Vision Res.* 40, 265–278.
- Nishida, S., and Sato, T. (1995). Motion aftereffect with flickering test patterns reveals higher stages of motion processing. *Vision Res.* 35, 477–490.
- Nishida, S., Ashida, H., and Sato, T. (1994). Complete interocular transfer of motion aftereffect with flickering test. *Vision Res.* 34, 2707–2716.
- Posner, M.I., and Cohen, Y. (1982). Components of visual orienting. In *Attention and Performance X: Control of Language Processes*, H. Bouma and D.G. Bouwhuis, eds. (Hillsdale, NJ: Erlbaum), pp. 531–556.
- Pylyshyn, Z.W., and Storm, R.W. (1988). Tracking multiple independent targets: evidence for a parallel tracking mechanism. *Spat. Vis.* 3, 179–197.
- Raymond, J.E. (1993). Complete interocular transfer of motion adaptation effects on motion coherence thresholds. *Vision Res.* 33, 1865–1870.
- Raymond, J.E., and Isaak, M. (1998). Successive episodes produce direction contrast effects in motion perception. *Vision Res.* 38, 579–589.
- Raymond, J.E., O'Donnell, H.L., and Tipper, S.P. (1998). Priming reveals attentional modulation of human motion sensitivity. *Vision Res.* 38, 2863–2867.
- Rees, G., Frith, C.D., and Lavie, N. (1997). Modulating irrelevant motion perception by varying attentional load in an unrelated task. *Science* 278, 1616–1619.
- Saito, H., Yukie, M., Tanaka, K., Hikosaka, K., Fukada, Y., and Iwai, E. (1986). Integration of direction signals of image motion in the superior temporal sulcus of the macaque monkey. *J. Neurosci.* 6, 145–157.
- Seidman, S.H., Leigh, R.J., and Thomas, C.W. (1992). Eye movements during motion after-effect. *Vision Res.* 32, 167–171.
- Snowden, R.J., and Milne, A.B. (1996). The effects of adapting to complex motions: position invariance and tuning to spiral motions. *J. Cogn. Neurosci.* 8, 435–452.
- Snowden, R.J., and Milne, A.B. (1997). Phantom motion aftereffects: evidence of detectors for the analysis of optic flow. *Curr. Biol.* 7, 717–722.
- Sunaert, S., Van Hecke, P., Marchal, G., and Orban, G.A. (1999). Motion-responsive regions of the human brain. *Exp. Brain Res.* 127, 355–370.
- Tipper, S.P. (1985). The negative priming effect: inhibitory effects of ignored primes. *Q. J. Exp. Psychol. A* 37, 571–590.
- Tootell, R.B., Reppas, J.B., Dale, A.M., Look, R.B., Sereno, M.I., Malach, R., Brady, T.J., and Rosen, B.R. (1995). Visual motion aftereffect in human cortical area MT revealed by functional magnetic resonance imaging. *Nature* 375, 139–141.
- Treue, S., and Maunsell, J.H.R. (1996). Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature* 382, 539–541.
- Verstraten, F.A.J., Hooge, I.T.C., and van Wezel, R.J.A. (2000). Question: do (small) eye movements explain the percept of motion under attentive tracking conditions? Answer: no! *Invest. Ophthalmol. Vis. Sci.* 41, S46.
- von Grünau, M.W. (1986). A motion aftereffect for long-range stroboscopic apparent motion. *Percept. Psychophys.* 40, 31–38.
- von Grünau, M.W., and Dubé, S. (1992). Comparing local and remote aftereffects. *Spat. Vis.* 6, 303–314.
- Weisstein, N., Maguire, W., and Berbaum, K. (1977). A phantom-motion aftereffect. *Science* 198, 955–958.
- Wertheimer, M. (1961). Experimental studies on the seeing of motion. In *Classics in Psychology*, T. Shipley, ed. (New York: Philosophical Library), pp. 1032–1089.
- Wohlgemuth, A. (1911). On the after-effect of seen movement. *Br. J. Psychol.* 7, 1–117.
- Yantis, S. (1992). Multielement visual tracking: attention and perceptual organization. *Cog. Psych.* 24, 295–340.
- Zeki, S.M. (1974). Functional organization of a visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey. *J. Physiol.* 236, 549–573.