A moving stimulus is normally required to elicit smooth pursuit eye movements that serve to keep the retinal image of moving objects on the fovea. Recent experiments have shown that in cases where motion cues are ambiguous, pursuit eye movements tend to agree in direction and speed with the percept of motion. Here, we exploit the motion aftereffect (MAE) to show for the first time that smooth pursuit eye movements can also be elicited by the illusory motion of a stationary stimulus. After prolonged exposure to a moving stimulus, subjects show reliable pursuit of a physically stationary stimulus that is perceived to be moving. Conversely, the eyes remain stationary when viewing a physically moving stimulus that is perceived to be stationary. The MAE biases smooth eye movements in a way that agrees with the constant offset that is required to null the MAE perceptually. The agreement between perception and pursuit holds over a variety of stimulus conditions that modulate the magnitude of the MAE.

Keywords: motion aftereffect, adaptation, pursuit eye movements, motion perception

Introduction

The motion aftereffect (MAE) is one of the earliest described visual illusions. It was mentioned by Aristotle as early as 330 B.C. (Wade, 1999). In the 19th century, Purkinje (1820) and Addams (1834) rediscovered it. Addams noticed that prolonged viewing of the downward motion of a waterfall led to a subsequent percept of upward motion when viewing nearby rocks and trees. In subsequent quantitative investigations of the phenomenon, it was found that the MAE is strongest when fixation is maintained during adaptation (Wohlgemuth, 1911) and when low temporal and medium spatial frequencies are used (Cameron, Baker, & Boulton, 1992; Pantle, 1974; Thompson, 1998). The “positive” percept (Van Wezel & Britten, 2002) of the movement of stationary objects in the opposite direction or the perceptual slowing for movement in directions close to that of the adaptor after motion adaptation has been explained in different models by mutual inhibition among opposite motion directions (Adelson & Bergen, 1985; Barlow & Hill, 1963; Mather, 1980). It is generally assumed that prolonged exposure to a moving stimulus leads to a change in the responsiveness of motion-sensitive neurons in the visual system (Barlow & Hill, 1963; Hammond, Mouat, & Smith, 1985; Kohn & Movshon, 2003; Petersen, Baker, & Allman, 1985; Van Wezel & Britten, 2002; von der Heydt, Hanny, & Adorjani, 1978). Thus, after motion adaptation, neurons selective to the adapting direction give a weaker response to subsequent stimuli than neurons selective to the opposite direction. This imbalance leads to a net motion signal opposite to the adapting direction, which makes a stationary or flickering stimulus seem to move in that direction.

For V1 neurons, Hammond et al. (1985) reported a direction-specific effect of visual adaptation with a reduction of neuronal responses in the adapted direction. For responses in the opposite direction, sometimes, an enhancement was found (Hammond et al., 1985; von der Heydt et al., 1978). At the next stage of motion analysis in the middle temporal area (MT or V5), adaptation effects have also been reported as being very selective (Newsome, Britten, & Movshon, 1989; Salzman, Britten, & Newsome, 1990). Only neurons representing the adaptation direction had attenuated extracellular responses, but no effect was found after adaptation in the opposite (null) direction (Van Wezel & Britten, 2002). More recently, Kohn and Movshon (2003) showed that adaptation in the preferred direction reduces the direction tuning bandwidth of MT neurons by changing their contrast gain. Unlike in V1, prolonged adaptation to drifting gratings reduced the responsiveness of MT neurons least, when the direction of the test stimulus was similar to that of the adaptation stimulus. Adaptation to a nearby direction caused both a narrowing and a shift in tuning toward the preferred direction, which might explain the repulsive shift in perceived direction. In general, the neuronal responses in area MT seem to correspond quite well with the MAE and other psychophysical observations, indicating motion opponency (Stromeyer, Kronauer, Madsen, & Klein, 1984). For humans, the study of Heeger, Boynton, Demb, Seidemann, and Newsome (1999) provides evidence for direction-selective interactions in area MT+.
These authors measured responses to paired and unpaired dot displays, which were introduced by Qian and Andersen (1994) to study the physiological basis of motion opponency in V1 and MT. Qian and Andersen found that MT cells were more direction selective than V1 cells and that the most direction-selective MT cells showed the strongest motion opponency effect. In addition, several neuroimaging experiments have reported that motion adaptation increased human MT+ responses (He, Cohen, & Hu, 1998; Tootell et al., 1995) or caused a direction-selective imbalance in human MT+ and earlier visual areas (Huk, Ress, & Heeger, 2001).

Here, we use the MAE to determine the relationship between the signals that drive smooth pursuit eye movements and the signals that determine the perception of motion. Because area MT is important not only for the perception of motion but also for the generation of signals that are used to initiate smooth pursuit eye movements (Dürsteler, Wurtz, & Newsome, 1987; Lisberger & Movshon, 1999; Newsome & Pare, 1988; Newsome, Wurtz, & Komatsu, 1988; Pasternak & Merigan, 1994; Tychsen & Lisberger, 1986), we hypothesized that the perceived motion of stationary stimuli after prolonged motion adaptation might persist and drive smooth pursuit eye movements. Recently, it has been shown that there is a close connection between motion perception and smooth pursuit. If there is ambiguity in terms of direction of motion, then the perceived direction of motion and the direction of eye movements tend to agree (Beutter & Stone, 1998, 2000; Krauzlis & Stone, 1999; Stone, Beutter, & Lorenceau, 2000; Stone & Krauzlis, 2003). It has even been shown that smooth eye movements are possible without any net retinal motion signal under certain circumstances. This is the case when following the motion of illusory edges (Steinbach, 1976; Wyatt, Pola, Fortune, & Posner, 1994), when pursuing an object behind an occluding surface (Becker & Fuchs, 1985; Churchland, Chou, & Lisberger, 2003; Morris & Lisberger, 1987), when viewing objects behind narrow slits (Fendrich, Rieger, & Heinze, 2005), or when following second-order motion stimuli defined by flicker (Butzer, Ilg, & Zanker, 1997; Guo & Benson, 1998; Hawken & Gegenfurtner, 2001; Lindner & Ilg, 2000). However, there are several previous reports indicating that smooth eye movements are not possible when viewing a stimulus that is physically stationary. In these studies (Mack, Fendrich, & Pleune, 1979; Mack, Fendrich, & Wong, 1987; Seidman, Leigh, & Thomas, 1992; Watamaniuk, Velisar, Badler, & Heinen, 2004), high-contrast test stimuli with sharp edges were used to measure the MAE. Our results show that smooth eye movements are indeed not elicited when stimuli with sharp edges and high contrast are used but that medium-contrast and isoluminant gratings can reliably elicit the MAE as well as smooth pursuit of a similar magnitude. Although we were unable to find any significant trial-by-trial covariation between eye movements and perception, we did observe a close agreement between eye movements and perception over a variety of different stimulus conditions that modulated the perceptual effect.

## Methods

### Equipment

Subjects were seated in a dimly lit room facing a Sony Trinitron F-900 23-in. monitor with a refresh rate of 100 Hz. At a viewing distance of 92 cm, the active screen area subtended 26.5 deg of visual angle in the horizontal direction and 14 deg vertical on the subject’s retina. The screen was viewed binocularly. The subject’s head was fixed in place using a bite bar made of dental medical material and two support points at the forehead.

### Subjects

The age of the 12 subjects was between 21 and 47 years. Eight of them were female. All subjects had normal visual acuity or were slightly myopic. The myopes performed the experiments without their optical corrections. Two of the authors (D.B. and K.G.) served as subjects. The other 10 subjects were naive with respect to the experiment.

### Visual stimuli

At the beginning of each session, the subjects viewed an adapting stimulus for 30 s, which consisted of a vertical sine-wave grating of 0.25 cycles/deg and 40% contrast. The adapting stimulus moved constantly either left- or rightward at a constant speed of 8.31 deg/s. During the adaptation period, gaze fixation was aided by a bright red dot at the monitor’s center and controlled by the experimenter. Preliminary experiments indicated that the MAE decreases at slower adapting speeds and at lower contrasts of the adapting stimulus. At higher contrasts, the MAE also decreases and maintaining fixation during adaptation becomes increasingly difficult for the subjects. After the adaptation period, the fixation point disappeared and, simultaneously, the test stimulus appeared. The test stimulus was also a vertical sine-wave grating of the same contrast and spatial frequency as the adapting stimulus, but it either moved at three different speeds (0.35, 0.69, and 1.73 deg/s) in the same or in the opposite direction of the adaptation stimulus or it was stationary. Here, and throughout the article, we will use positive speeds to refer to motion of the test grating or the eyes in the direction of adaptation and negative speeds to refer to motion in the direction opposite to adaptation. The test grating appeared for 1 s. After the test, a uniform gray screen was presented with a luminance of 40 cd/m², matching the mean luminance of the grating stimuli.

The subject was asked to indicate the perceived direction of motion of the test grating by pressing either a left or a right button. In the case of a stationary percept, the subject was requested not to press either button.
used the additional “stationary” category rather than a traditional 2AFC procedure because we were particularly interested in determining what the eyes do on exactly these trials. During the adaptation period, subjects were instructed to maintain fixation, but during the test phase, they were told to let their eyes follow the percept. The next trial started with a brief 5-s presentation of the initial adaptation stimulus to “top up” adaptation (see, e.g., Kohn & Movshon, 2003). Initially, we collected data using a more lengthy procedure, in which the subjects were adapted for 30 s at the start of each trial. This turned out to be rather time consuming and tiring for the subjects. We obtained data from several subjects under both conditions, and after ensuring that the data were not different in any respect, we switched to the faster top-up procedure. Data obtained with the original, lengthier procedure are shown in some of the figures and are labeled as such.

Further experiments were designed to manipulate the magnitude of the MAE. In one set of experiments, high-contrast (100%) square-wave gratings were used as adapting and test stimuli. In another experiment, isoluminant red-green adapting and test gratings were used. The spatiotemporal characteristics remained the same, and the mean luminance of the display was as before (40 cd/m²). However, the grating was modulated between red (CIE xY0.381, 0.310, 40) and green (0.226, 0.388, 40) to isolate the red-green color opponent mechanism. We ensured that all observers were reasonably close to their individual point of isoluminance by confirming that slowly moving test gratings showed the slowing that is typical under these conditions (Cavanagh, Tyler, & Favreau, 1984; for a review, see Gegenfurtner & Hawken, 1996).

As a control condition, we made the same measurements without prior adaptation to a moving stimulus. In this case, the adapting grating was stationary and lasted for 1 s only. Six of our 12 subjects participated in these additional experiments. For these 6 observers, the top-up adaptation procedure was used in all four experiments (luminance gratings, square-wave gratings, isoluminant gratings, and no-motion-adaptation control). The experiments were run in two sessions on different days, and the sessions for all four conditions were interleaved in a pseudorandom order.

**Eye-movement recording**

Eye movements of the right eye were recorded using a Dual Purkinje Image Eye Tracker, Generation 6.x from Fourward Optical Technologies, Inc. The analog eye position signal was sampled at a frequency of 500 Hz. For saccades, which did not occur frequently, we omitted an interval, starting 20 ms before the saccade and ending 50 ms after the saccade in the computation of the velocity of smooth eye movements. During the 1-s test phase, eye-movement speed was averaged in an interval of 500 ms, starting 500 ms after the end of the adaptation phase (see Figure 1, shaded area). Different analysis intervals were used to investigate the time course of the adaptation effects.
Oculometric analysis

We followed the procedure detailed in Gegenfurtner, Xing, Scott, and Hawken (2003). On each trial, eye speeds were converted into oculometric judgments. When the eye moved in the same direction as the adapting stimulus on a given trial, we marked that trial as indicating an ocular judgment in the direction of adaptation. We used these responses to fit oculometric functions in the same manner as for the standard psychometric functions (Wichmann & Hill, 2001). The psychometric and oculometric functions give estimates of the point where the stimulus is subjectively stationary (here, the observer has the impression that the grating is not moving at all) and where the eyes move left- or rightward equally often. The deviation of the point of subjective stationarity from zero indicates the magnitude of the MAE for perception and for pursuit. Note that the use of a third response category (stationary) in the psychometric judgments potentially introduces a bias into our results. Therefore, we analyzed the psychophysical data in three different ways. Firstly, those trials in which the observer responded with stationary were evenly split among the “same” and “opposite” trials in the psychometric functions. Second, we simply omitted these trials from the analysis. And third, we estimated the perceptual effect as the mean of all stimulus speeds that led to stationary judgments. As stated in the Results section, there was a near-perfect agreement between these three different methods of analysis.

Results

Figure 1 shows average eye-movement traces of two representative subjects for all test conditions during the last 200 ms of the adaptation period and the test phase. At Time 0, the test grating appeared and moved as indicated on the right-hand side with three different speeds in the same direction as the adaptation stimulus (plotted upward) or in the opposite direction. The gray area indicates the analysis period of 500 ms. After adaptation, the eyes of both subjects started to move away from the former fixation position after a latency of about 300 ms. This latency might seem long compared with pursuit latencies as low as 100 ms under optimal conditions, but it does fall within the range observed under conditions of medium contrast and extremely slow speeds (Carl & Gellman, 1987; Spering, Kerzel, Braun, Hawken, & Gegenfurtner, 2005; Tychsen & Lisberger, 1986). The blue traces indicate trials in which a stationary test grating was used. Although no motion is present, both subjects move their eyes with an average speed of 0.3 deg/s during the analysis interval. Thus, smooth pursuit eye movements can be initiated by the illusory motion caused by motion adaptation in the presence of a stationary stimulus. The red traces indicate trials where the test stimulus was moving in the direction of adaptation at a speed of 0.35 deg/s. Under these conditions, the eyes remained stationary and no pursuit was elicited, although there was retinal stimulus motion. Thus, a slowly moving test stimulus moving in the same direction as the adaptor basically nulls the effect of adaptation.

The MAE on smooth pursuit is further illustrated in Figure 2. Here, the blue curve represents a histogram of the eye-movement speeds of 456 trials from 12 subjects when the test stimulus was physically stationary. The average eye speed was $-0.29$ deg/s, which was highly significantly different from 0 ($t_{11} = -11.497, p < .001$). The subjects judged the same stimulus to be moving opposite to the adapting stimulus in 72%, to be stationary in 26%, and to be moving in the same direction as the adapting stimulus in 2% of all 456 trials. The red curve of Figure 2 shows the histogram of eye-movement speeds of 597 trials judged as being stationary by the same observers. Average eye speed on these trials was $-0.01$ deg/s, which was not significantly different from 0 ($t_{11} = -0.61, p > .05$), although the average physical speed of the corresponding test stimuli was 0.37 deg/s ($t_{11} = 8.99, p < .001$). Note that there is ample variability in the eye speeds. The standard deviation of eye speeds for these two cases is 0.37 and 0.42 deg/s, respectively.

Until now, we have exclusively looked at extremely slow eye movements, elicited by the MAE alone or by stimuli that effectively null the MAE. It is interesting to see whether motion adaptation also affects test stimuli that move at higher speeds. In Figure 1, eye position traces are shown for the three test speeds ranging from 0.35 to 1.73 deg/s. There is a marked asymmetry in the eye speeds depending on the direction relative to adaptation: The eyes move faster for test stimuli moving in the opposite direction of the adaptor, and they move slower for test stimuli in the adaptation direction.

![Figure 2](https://jov.arvojournals.org/pdfaccess.ashx?url=/data/journals/jov/932840/)
In Figure 3, eye-movement speed is plotted after adaptation (red line) as a function of test speed for three typical subjects and for the population average. Eye speed during the analysis interval varied linearly ($r > .99$) with the speed of the test stimulus. The adaptation effect resulted mainly in a downward shift of the red line from the diagonal. The magnitude of this shift, which was on average 0.29 deg/s, is another indicator of the magnitude of the MAE for smooth pursuit. Furthermore, the slope of the red line is not equal to 1. This could be due to the fact that the gain for smooth pursuit eye movements without adaptation (blue line) is typically smaller than 1 at these slow test speeds (Collewijn & Tamminga, 1984; Ilg, 1997). We therefore compared the gain of smooth pursuit eye movements with and without previous motion adaptation. The average gain without adaptation was 0.86, which was significantly higher than the average gain of 0.73 after motion adaptation ($t_5 = -4.9610, p < .01$). Thus, motion adaptation not only biases the smooth pursuit eye movements in the direction opposite of adaptation but also reduces the gain. As a consequence, for stimuli moving in the adaptation direction, the MAE and gain change sum up to produce a larger effect of adaptation. In the opposite direction (left parts of the graphs in Figure 3), MAE and gain change nearly cancel, leading to eye movements with the exact same speed as the test stimulus.

This asymmetry in the effects of adaptation in the two directions of motion can also be seen in the average traces for observer C.A. shown in Figure 4. The red position traces are without prior motion adaptation, and the blue traces are with motion adaptation. Note that the blue traces in this figure are identical to the traces shown in Figure 1. In Panel A, average eye position traces are shown, when a physically stationary test stimulus was presented. The red trace stays close to zero, whereas the blue trace indicates that the eyes move smoothly in the direction opposite to adaptation. Panels B and C illustrate cases in which the test stimulus moved in the direction of adaptation. After adaptation, pursuit has a slightly longer latency and acceleration is slower as well. As expected from the leftmost data points in Figure 3, motion adaptation has no effect when the test stimulus moves opposite to the adaptor at 1.73 deg/s. In this case, the red and blue traces overlap completely as can be seen in Panel D of Figure 4. This
could be due to either the absence of an effect of adaptation or the combined effects of adaptation on gain and offset (see Figure 3), which might perfectly cancel each other. We cannot resolve these two possibilities with the data at hand.

The data presented in Figures 1 and 2 suggest a good agreement in the magnitude of the adaptation effect on pursuit and perception. For a more precise comparison of psychophysical judgements and SPEMs, we obtained ocularmetric functions from hypothetical judgments based on the eye-movement speed for each subject. Figure 5 shows psychometric and ocularmetric functions (Gegenfurtner et al., 2003; Kowler & McKee, 1987; Stone & Krauzlis, 2003) for three representative observers and for the average of all 12 observers. The red curve is based on the psychophysical judgments of the subjects, and the blue curve represents the ocularmetric functions based on the SPEMs. The magnitude of the MAE is indicated by a rightward shift of the 50% point of the psychometric and ocularmetric functions toward positive test speeds. For some observers, the MAE was larger for smooth pursuit eye movements than for perception, and for some observers, it was the other way around. Overall, there was no significant

Figure 4. Average eye-movement traces with adaptation (blue curves) and without adaptation (red curves) for observer C.A. at four different test stimulus speeds: (A) stationary, (B) 0.69 deg/s and (C) 1.73 deg/s in the direction of adaptation, and (D) −1.73 deg/s in the direction opposite to adaptation. The vertical line indicates test stimulus onset.
difference in the magnitude of the MAE between perception and eye movements for our 12 observers ($t_{11} = 0.6652$, $p > .05$). This can also be seen in the average psychometric and oculometric functions, shown in Figure 5 (lower right panel). There is indeed a remarkable agreement between the perception of motion and SPEMs in this adaptation task.

In Figure 5, the psychometric curves were constructed by assigning stationary judgments evenly to the same and opposite categories. This could introduce a bias to the results, unless the distribution of stationary judgments is centered at the point where same and opposite judgments are equally likely. We therefore also calculated psychometric functions based on same and opposite judgments alone. This led to nearly identical results. The mean difference across all 12 subjects in the magnitude of the perceptual MAE was less than 0.05 deg/s for the two different methods, and the correlation of MAE magnitude across all 12 observers was .97 ($t_{10} = 12.65$, $p < .001$). Therefore, we can exclude the possibility of any bias due to the stationary judgments.

Several other problems complicate comparing perception and pursuit data. For instance, we obtained a single perceptual judgment for each trial. However, it is not clear which interval of the stimulus presentation the visual system used to arrive at this judgment. We chose to perform our analyses for an interval starting 500 ms after motion offset and lasting for another 500 ms. At this point in time, pursuit has reached a steady state and is being driven not only by visual signals but also by internal signals of eye speed (Lisberger, Morris, & Tychsen, 1987; Morris & Lisberger, 1987). Thus, the response of the oculomotor system could affect perceptual judgments. However, we do not think that this is likely because, presumably, the internal eye-movement signal and the retinal error signal would simply cancel. That is, when viewing a stationary test stimulus after motion adaptation, the internal signal would indicate motion opposite to the direction of adaptation, whereas the retinal motion would be in the direction of adaptation. Nevertheless, it is important to investigate how robust our analysis is with respect to the particular time interval used to calculate eye speed.

We investigated the dynamics of the MAE for pursuit by using a sequence of short analysis intervals (200 ms), beginning at motion offset and ending 1 s after motion offset. Figure 6 shows how the MAE for pursuit develops during that period. In Figure 6A, the blue symbols indicate the average shift of the oculometric function for all observers. It can be seen that the oculometric functions on average start out slightly negative, indicating that the eyes

Figure 5. Results of the oculometric analysis. Psychometric (red curve) and oculometric (blue curve) functions for three representative observers, D.B., N.Z., and A.S., and for the average of all 12 observers (lower right panel). Eye speeds on each trial were converted into oculometric “judgments” following the procedure described in the Methods section. For each test stimulus speed, the proportion of trials is plotted where the observer judged the test stimulus to move in the same direction as the adapting stimulus (red squares) or where the eye movement was in the direction of adaptation (blue squares).
indicates the magnitude of the MAE. During the interval centered around 100 ms, the gain is still zero. It rises steadily until about 500 ms. As in Figure 6A, the MAE is initially positive; that is, the eyes keep moving in the direction of adaptation. This was not the case for all the individual observers. Figure 1 shows that subject D.B. mostly drifted in the adapting direction right after the fixation point went off, whereas subject C.A. drifted in the opposite direction. This initial drift is probably an after-nystagmus that emerges when subjects are not perfectly able to hold fixation. It is not related to the test stimulus and is no longer visible when the effect of motion adaptation and the motion of the test stimulus appear after about 200–300 ms. In Figure 6B, the MAE for pursuit emerges within 500 ms. This is the same interval during which the gain of the eye movements increases steadily. Thus, as soon as the eye movements show a clear dependence on the stimulus speed, they also exhibit an effect of adaptation. This means that our analysis is fairly robust with respect to the particular choice of analysis interval.

The close agreement that we observed between perception and pursuit could be due to a single mechanism responsible for the computation of motion, the signals of which are used to drive pursuit and to determine our percept. If this were the case, then we would expect a significant degree of correlation between perception and pursuit across different observers. In Figure 7A, the magnitudes of the perceptual and pursuit MAEs are plotted for the above experiments. Although they agree on average, there was no correlation ($\rho = -0.067$, $t_{10} = -0.2126$, $p > 0.05$) in the magnitudes of the MAE across different observers.

There is an alternative way to test for a correlation between perception and pursuit. We analyzed the correlation between judgment and eye speed over individual trials. Because both judgment and eye speed are closely linked to the physical speed of the test stimulus, there is a highly significant correlation between the two ($\rho = 0.45 < 0.83$ for the 12 observers). It is possible, however, to account for the influence of the physical test speed by either looking at the correlation between eye speed and judgment for each test speed separately or computing a partial correlation between eye speed and judgment. These partial correlations varied between $-0.22$ and $0.11$, with a mean of $-0.0027$. Despite the relatively large number of trials (at least 400) for each observer, only 2 of 12 partial correlation coefficients reached significance. If the proper Bonferroni correction for multiple tests is applied, none of the correlations are significant.

We repeated this partial correlation analysis for the very early pursuit analysis intervals because the first 100 ms of pursuit is determined by visual inputs exclusively. Therefore, one might expect a higher correlation with visual perception for these intervals. There was no difference, however, and the partial correlations between eye speed and psychophysical judgments remained close to zero throughout. Further statistical tests also failed to show any association between pursuit and perception across intervals, which were 200 ms in length. Error bars indicate time. After 200 low slopes of the oculometric function at this point in stimulus. The large variability stems from the very shallow slopes of the oculometric function at this point in time. After 200–300 ms, the oculometric functions become well defined and the effect of adaptation becomes visible in the oculometric functions as a shift. After 500 ms, most of the variability between observers is gone, as can be seen by the much smaller error bars ($\pm 1$ SE) in Figure 6A, and the oculometric MAE reaches an asymptote at the same speed as the perceptual MAE, indicated by the red shaded area.

In Figure 6B, another representation of the MAE for pursuit was used. Here, the parameters of the regression lines shown in Figure 3 are plotted for the different time intervals. The slope of these lines is a measure of the gain of the pursuit eye movements, whereas the intercept initially tend to move in the direction of the adapting stimulus. The large variability stems from the very shallow slopes of the oculometric function at this point in time. After 200–300 ms, the oculometric functions become well defined and the effect of adaptation becomes visible in the oculometric functions as a shift. After 500 ms, most of the variability between observers is gone, as can be seen by the much smaller error bars (± SE) in Figure 6A, and the oculometric MAE reaches an asymptote at the same speed as the perceptual MAE, indicated by the red shaded area.

In Figure 6B, another representation of the MAE for pursuit was used. Here, the parameters of the regression lines shown in Figure 3 are plotted for the different time intervals. The slope of these lines is a measure of the gain of the pursuit eye movements, whereas the intercept
individual trials. To achieve more statistical power, we computed $\chi^2$ coefficients (Hays, 1973) as a measure of the contingency between eye direction and psychophysical judgment for a fixed test speed of 0.35 deg/s and for two observers, D.B. and C.A. (for whom we had collected 400 individual trials). (Typically, the largest variability in judgments was observed at the test speed of 0.35 deg/s, with all three judgments frequently occurring.) The observed frequencies of psychophysical judgments were nearly identical, irrespective of whether the eyes moved in the direction of adaptation or opposite to it. The $\chi^2$ test was not significant for either observer ($\chi^2 = 0.71, df = 2, p > .05$ for C.A. and $\chi^2 = 0.19, df = 2, p > .05$ for D.B.). An analysis of the eye speed as a function of the psychophysical judgment also failed to reveal any significant differences. The lack of an association between pursuit and perception could be due to one of two things: The mechanisms might indeed be independent, or the noise that determines trial-by-trial variability might be quite large relative to the noise in any shared visual-motion substrate.

Therefore, a more promising way to answer the question about the independence of the mechanisms for pursuit and perception is to vary the experimental parameters. The magnitude of the MAE has been shown to vary with stimulus conditions in a number of times (for a review, see Thompson, 1998). In fact, it certainly seems possible to abolish the MAE for eye movements because other studies (Mack et al., 1987; Seidman et al., 1992) have failed to find motion adaptation effects on smooth pursuit eye movements. In these studies, high-contrast adapting stimuli were used in conjunction with test stimuli that had sharp edges. During the adaptation phase, high-contrast stimuli make it more difficult to fixate by inducing a stronger nystagmus in the direction of adaptation. In the test phase, this can lead to an after-nystagmus (Brandt, Dichgans, & Büchele, 1974; Kudo, Yoshida, & Makishima, 2002; Schor & Westall, 1986), which drives the eyes in the direction of adaptation and, therefore, opposes the MAE. More important, the edges of the stationary test stimuli will allow the fixation system to keep the eyes stationary. At the same time, high-contrast stimuli, in combination with large sizes, can lead to smaller aftereffects even in perception (Tadin, Lappin, Gilroy, & Blake, 2003).

We therefore repeated our experiment using high-contrast square-wave gratings as the adapting and test stimuli. In Figure 7, we compare the effect of motion adaptation on SPEMs elicited by sine-wave gratings (filled [black] and open circles) and square-wave gratings (blue circles) for six subjects. As expected, there is no MAE for the pursuit of square-wave gratings. However, an analysis of the psychometric functions reveals that these were also not shifted away from zero. This means that the perceptual effect also tends to vanish under these conditions. In fact, only one subject exhibited a significant perceptual MAE with the high-contrast square-wave gratings.

Another potential way to dissociate perception and pursuit is through the use of isoluminant stimuli. These stimuli appear to move slower under some conditions (Cavanagh et al., 1984), and neurons in cortical area MT respond at a lower rate to these stimuli (Gegenfurtner et al., 1984), and neurons in cortical area MT respond at a lower rate to these stimuli (Gegenfurtner et al., 1984). Furthermore, it has been shown that isoluminant stimuli can elicit a perceptual MAE (Cavanagh & Favreau, 1985; Derrington & Badcock, 1985; Mullen & Baker, 1985). It seems possible, therefore, that isoluminant stimuli could cause only a perceptual but not an oculomotor effect of motion adaptation. We therefore repeated our experiments with red–green sine-wave gratings as the adapting and test stimuli. The results of the corresponding analysis of oculometric and psychometric functions are shown by the red circles in Figure 7B. There was an effect of motion adaptation on both perception ($t_5 = 5.76; p < .01$) and pursuit ($t_5 = 3.99; p < .01$). The magnitude of the perceptual effect is quite similar to the 0.3 deg/s that was reported by Cavanagh and
Favreau (1985). Similar to these authors, we also observed that it was quite difficult to null the MAE with isoluminant test gratings. This was the case for both perception and pursuit and resulted in a flattening of the psychometric and oculometric functions for test stimuli that moved in the direction of adaptation. We also observed that the eye-speed responses were extremely low to isoluminant gratings in the direction of adaptation. These stimuli resulted in eye-movement gains as low as 0.2.

The more interesting aspect of these results is that isoluminant stimuli led to a massive increase in the variability between observers. Along with this variability we found an enormous increase in the correlation between pursuit and perception ($\rho = .84$), which was significant ($p < .05$) despite the small number of observers ($n = 6$). Isoluminant gratings, thus, increase variability mostly for those stages of motion processing that are common to perception and pursuit. For the luminance gratings, the common variance was smaller and presumably masked by variance in mechanisms separate for pursuit and perception.

**Discussion**

Our data show that smooth pursuit eye movements can be elicited by a purely illusory motion percept that is caused by motion adaptation. The magnitude of the effect is about equal for perception and pursuit. On average, the same physically moving stimulus is able to null not only the MAE perceptually but also smooth pursuit eye movements. The close link between pursuit and perception is also found when the magnitude of the MAE is modulated by using different types of stimuli that either increase the effect or abolish it altogether.

We explored the relationship between the MAE for pursuit eye movements and perception using low-contrast luminance and isoluminant stimuli. In contrast to earlier studies, in which no effect of motion adaptation on pursuit was found for high-contrast stimuli with sharp edges (Mack et al., 1987; Watamaniuk et al., 2004), we found reliable eye-movement responses after motion adaptation in the presence of stationary pursuit targets. We were also able to replicate the earlier negative findings when we used square-wave adapting and test gratings.

Several factors seem to contribute to the eye response after adaptation. First of all, the physically stationary test stimulus engages the fixation system, whose function is to keep the eyes on the stationary target. Of course, sharp edges and high-contrast test stimuli are stronger stimuli for fixation than the low-frequency, medium-contrast sine-wave gratings we used. A second factor is optokinetic eye responses. High-contrast adapting stimuli lead to imperfect fixation during the adaptation phase. The eyes exhibit a residual optokinetic nystagmus, which might result in an optokinetic after-nystagmus during the test phase. This after-nystagmus is in the direction of adaptation (Brandt et al., 1974), opposite to the direction of the MAE. The third factor contributing to the eye response after adaptation is the MAE, which drives the eyes in the direction opposite to adaptation. Stimuli that strengthen the MAE have to be used while keeping the other two forces small to obtain a large and significant MAE for pursuit. Our exact stimulus conditions were chosen in preliminary experiments in which we varied spatial frequency, speed, and contrast of the adapting and test stimuli to maximize the MAE for pursuit. It turns out that a medium-contrast stimulus can even be better for eliciting the MAE than a high-contrast stimulus through surround interactions (Tadin et al., 2003).

All these factors may have affected earlier studies that failed to find an MAE for pursuit, at least for stationary test stimuli, and may have served to obscure any trial-by-trial correlation in our experiments.

In one of the earlier studies, Watamaniuk et al. (2004) observed an effect of motion adaptation with dynamic random dot displays on test stimuli that moved in the direction of adaptation but not for test stimuli that moved in the opposite direction. Gardner, Tokiyama, and Lisberger (2004) present similar results for monkey observers. Our results, using a variety of test speeds in both directions, indicate that this asymmetry is caused by the combined effects of motion adaptation on eye-movement gain and directional bias. For test stimuli moving opposite to the adapting direction, the two effects seem to cancel, resulting in smooth pursuit eye movements with a perfect gain of 1. For test stimuli in the direction of adaptation, the effects add up, resulting in extremely slow smooth pursuit eye movements. This has important consequences for computational models of perception and pursuit, which need to disambiguate these two effects.

In the past, smooth pursuit eye movements have been shown to be closely linked to the perception of motion. In cases where the physical motion and the perceived motion are different, the oculomotor system mostly follows the percept rather than the physical stimulus (Beutter & Stone, 1998, 2000; Dobkins, Stoner, & Albright, 1998; Madelain & Krauzlis, 2003; Ringach, Hawken, & Shapley, 1996; Steinbach, 1976; Stone et al., 2000; Wyatt & Pola, 1979; Yasi & Young, 1975). Furthermore, several studies have established that the variance of the eye-movement signals is of the same magnitude as the variance of perception when performing the same task (Gegenfurtner et al., 2003; Kowler & McKee, 1987; Osborne, Lisberger, & Bialek, 2005; Stone & Krauzlis, 2003). Our results strengthen this point. Even when viewing a stationary stimulus, pursuit can be elicited in the case when the stimulus appears to be moving after adaptation.

In our present study, perception and pursuit of the MAE were tightly linked across a variety of different stimulus conditions. However, no correlation across observers or across trials was found for luminance stimuli. This is somewhat surprising because recent work by Newsome et al. (1989), Gardner et al. (2004), and Priebe, Churchland, and Lisberger (2001) indicates that there is likely a common
and central analysis of visual motion in MT that is responsible for both driving smooth pursuit and perceptual judgments of speed. However, the results of psychophysical experiments have been ambiguous. One study that compared the perceived direction of motion with the direction of smooth pursuit eye movements observed a significant correlation between the two systems (Stone & Krauzlis, 2003). Another study linking perceived speed and pursuit speed (Gegenfurtner et al., 2003) also found that speed discrimination by perception and pursuit had similar thresholds but that there was no correlation on a trial-by-trial basis, as in this study. Because trial-by-trial correlations are typically rather small, even when neuronal responses are linked to behavior (Newsome et al., 1989), this issue might be difficult to settle in psychophysical experiments, in which there are many additional sources of variability.

In our experiments, a significant correlation across observers emerged for isoluminant stimuli. These stimuli are known to be less efficient in driving neurons in MT (Gegenfurtner et al., 1994). Less reliable performance of MT neurons would in turn generate additional variance in the motion analysis stage. Because the added variance is highly correlated, this stage must be common to perception and pursuit. We, therefore, conclude that the neuronal mechanisms that generate the MAE for perception and pursuit are tightly linked.

Acknowledgments

We would like to thank Frank Bremmer, Dirk Kerzel, and Miriam Spering for helpful comments. Brian White and Ted Sharpe helped a lot to improve the English. This work was supported by the DFG-Graduiertenkolleg NeuroAct (L.P.) and the DFG Forschergruppe 560 “Perception and action” (D.I.B. and K.R.G.).

Commercial relationships: none.
Corresponding author: Karl R. Gegenfurtner.
Email: karl.gegenfurtner@psychol.uni-giessen.de.
Address: Abteilung Allgemeine Psychologie, Justus-Liebig-Universität, Otto-Behaghel-Str. 10F, 35394 Giessen, Germany.

References


