MOTION AFTEREFFECTS ASSOCIATED WITH PURSUIT EYE MOVEMENTS

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Abstract—Contrary to an earlier report [Anstis and Gregory, Q. Jl exp. Psychol. 17, 173–174 (1965)], we find that the sustained retinal motion caused by tracking a moving target over a stationary grating does not result in a motion aftereffect (MAE) which is equivalent to that resulting from comparable retinal motion caused by actual motion of a grating. The MAE associated with tracking generally occurs in elements falling on areas not previously exposed to retinal motion. It is in the same direction as the previous retinal motion in the display and is apparently an induced MAE caused by a weak, below threshold MAE in the elements stimulating areas that were previously exposed to retinal motion. Based on an analysis of eye movement records, we do not believe that the weakness of the tracking MAE is primarily a function of the poor quality of the tracking eye movements. Other possible reasons for the weakness of the MAE are suggested.

INTRODUCTION

Prolonged exposure to the sustained undirectional motion of contours causes a motion aftereffect (MAE). A subsequently viewed pattern appears to move in the opposite direction. In a widely cited study, Anstis and Gregory (1965) assert that this effect is a function of the retinal, rather than the perceived motion of contours. This assertion is based on two parallel findings. When observers tracked a moving point over a stationary set of vertical bars, a condition which causes retinal but not perceived motion, a MAE was subsequently perceived. Conversely, if the observers tracked the moving vertical bars, a condition which eliminates their retinal but not their perceived motion, no MAE was perceived. According to Anstis and Gregory the MAE produced by tracking over a stationary pattern is, in fact, indistuinguishable from that caused by fixating while observing an actually moving pattern.

Support for the Anstis and Gregory assertion is provided by a report of findings by Tolhurst and Hart (1972). They found that there were no differences between the adaptation produced by an actually moving grating and a grating whose motion was produced by tracking a moving point across it when it was stationary. In their study the measure of adaptation was the elevation of the contrast threshold for the moving pattern. Contradictory evidence has also been reported, however. Morgan *et al.* (1976) found that when observers tracked moving stripes across a superimposed stationary or oppositely moving set of stripes, and then looked at a motionless version of this display, a MAE was perceived which was in the *same* direction as the previous retinal motion of the nontracked stripes. In other words, the MAE was opposite in direction to that reported by Anstis and Gregory.

Morgan and his collaborators attribute their effect to induced motion (Duncker, 1929). To summarize their analysis: when observers track a moving stimulus, it is stable on the retina while all other visible contours displace. A normal MAE develops in the area of the retina stimulated by the displacing edges, which then induces an opposite motion in the area of the retina previously exposed to retinally stable stimuli. In one condition, observers tracked moving stripes visible to only one eye, while the other eye viewed only the surrounding stationary background. Since the resulting MAE was equally strong in each eye, they concluded that the effect did not depend on sight of the moving bars but rather on stimulation by the displacing background which induced a MAE in the previously tracked pattern. Morgan et al. attributed their failure to replicate Anstis and Gregory to the nature of their test stimulus. Anstis and Gregory had used a photograph of sandpaper as their test pattern whereas Morgan *et al.* used the adapting pattern itself. This explanation seems unlikely, however, particularly since Tolhurst and Hart also used the adapting pattern as the test pattern and found results which were consistent with those reported by Antis and Gregory.

Because of the importance of the Anstis and Gregory finding for our understanding of MAEs and motion perception more generally, it seemed important to re-examine the comparability of MAEs following an observation interval in which the adapting motion was produced either by the actual motion of a grating pattern or only retinal motion produced by tracking. The experiment designed to do this had two comparable conditions. In one condition the observer tracked a set of moving bars and a superimposed tracking target as they moved between two rows of flanking, stationary bars. Thus the tracked bars were essentially stationary on the retina while the flanking bars moved. In the other condition which is considered a control condition, the observer fixated a stationary point centered on the stationary row of inner bars while the upper and lower rows of flanking bars moved. In both cases, assuming accurate tracking, the image of outer bars displaced and therefore if there is a MAE, they should subsequently appear to move. The inner bars in both cases were stationary on the retina and therefore any subsequent perceived motion in these bars must be induced. Were tracking perfect, fixation and tracking would yield equivalent amounts of both absolute and relative motion. This may be important since there is evidence that MAEs are negligible or nonexistent if there is no relative motion (Wohlgemuth, 1911; Day and Strelow, 1971).

EXPERIMENT 1

Method

Subjects. Two separate groups of eight observers were paid for their participation. One group was tested in the tracking condition while the other served in the control condition. A total of 16 subjects were tested.

Apparatus and stimuli. The visual display pictured in Fig. 1 was presented on Tektronix 5110 oscilloscope with a fast phosphor CRT. The phosphor (P15) decays to 10% of its initial luminance in less than $3 \mu sec$. Wavetek function generators and a Tekronix Type 4701 multiplexer were used to generate the displays. A dense raster produced by the function generators formed a horizontal band of luminance which crossed the CRT screen. This band of luminance was multiplexed on to 3 vertical positions on the screen and converted to a square wave grating by a square wave signal from a third function generator. The output of the third function generator was synchronized with the horizontal raster forming signal and applied to the oscilloscope's Z axis input. A fourth function generator was used to display the fixation point. The 3 square wave gratings (with contrast levels approaching 1) and the fixation point could be independently swept across the screen by a ramp wave form produced by a fourth function generator. Since the effective length of the gratings was several times the width of the screen, the gratings remained continuous across the 12.7 cm width of the screen as they were swept across it. Finally, a logic signal tripped by the ramp generator retrace blanked the gratings during the retrace interval. The resulting dislays were stable and free of visible flicker with the individual stimulus elements being refreshed at rates in excess of 250 Hz.

The visual display was viewed from a distance of 34.5 cm. It consisted of three rows of light grey, vertical bars vertically separated by 1.06° and a centered fixation point. The background was black and all testing was in the dark, so only the pattern itself was visible. The alternating light and dark bars in the outer flanking rows each subtended a horizontal extent of 2.12° , and a vertical extent of 5.3° . The bars in the inner center row had the same horizontal dimension as the flanking bars but were 3.18° vertically. The bars in each row formed a square wave grating with a spatial frequency of 0.236 c/deg. When they moved, they covered a distance of 21.18° .

During the adaptation period in the tracking condition, the fixation point was initially 1.27° to the left of the right edge of the virtual viewing window and moved to the left covering a visual extent of 19°. It moved in tandem with the middle row of bars and thus maintained its position in the center of a bar as it moved across the screen. When the fixation point reached the left edge of the screen, the entire display vanished for 700 msec providing the observer with time to saccade back to the right. The display reappeared with the tracking target in its initial position again moving leftward with the bars.

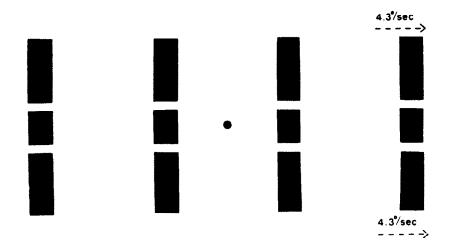


Fig. 1. Adaptation and test display.

The velocity of the tracking target and inner bars was 4.4°/sec. The upper and lower flanking rows of bars were stationary.

In the fixation control condition, the inner bars and centered fixation point remained stationary during the adaptation period. The upper and lower flanking rows of bars moved rightward at 4.4° /sec. Every 4.32 sec the display blanked (the fixation point remained visible) for 700 msec simulating the tracking conditions. In both conditions the stationary adapting pattern with centered fixation point was the test stimulus. Eye movements were monitored by an SRI eye tracker (Crane and Steele, 1978).

Procedure. In the tracking condition calibration of the eye tracker and a practice tracking trial preceded actual testing. In the tracking practice trial the observers tracked the moving fixation point to the left and saccaded back to the right just as they would during the actual adaptation period, but no bars were visible. During the actual adaptation period, but no bars were visible. During the actual adaptation period the observers tracked the moving point superimposed on the moving middle row of bars. The flanking bars were stationary. A trial lasted 90 sec during which time the bars and fixation point made 18 sweeps across the field. Following the 18th sweep, the display blanked and reappeared with the fixation point centered and nothing moving.

In the control condition the observer maintained fixation on the centered point throughout the adaptation and test period. In both conditions the observer reported any apparent motion in the middle and/or flanking rows of bars and its duration and direction. Observers viewed binocularly with their heads held in position by a dental impression bite plate. If no MAE was reported in the first trial up to three additional trials were run. Testing was terminated either on the trial in which the observer reorted a MAE or after the fourth trial.

Observer's task. On actual display motion trials, subjects were asked to carefully maintain fixation on the stationary point. On tracking trials they were asked to fixate the center point and track it carefully as it moved to the left. When it reached the edge of the display window where it disappeared, they were instructed to close their eyes, saccade back to the right edge of the display aperture where the point reappeared, and begin tracking once again. The instruction to shut the eyes during the saccade was, of course, meant to eliminate the remote possibility of visual stimulation by oppositely moving contours that might interfere with the adaptation.

Subjects were told that immediately following the 90 sec period in which they either tracked or fixated while the pattern moved, the display would briefly disappear and reappear with a centered fixation point. They were instructed to fixate this point when it became visible and report any motion in the center and/or flanking bars. Prior to testing they were told that sometimes it was possible to have a sense of motion without seeing objects actually change their positions and that this might be the character of the motion they perceived. If any motion was perceived, they were asked to verbally report its direction and its duration. The experimenter kept track of whether or not a MAE was reported, the trial on which it occurred, its direction and duration. The principle evidence of a MAE is therefore the number of times it was reported following the first, second, third or fourth trial in the center and flanking bars. It is simple frequency data.

Results

If Anstis and Gregory's results are to be confirmed, we should find equivalent MAEs in the 2 conditions, since, assuming adequate tracking, the retinal adapting motions are largely equivalent. In both conditions the outer, flanking bars displaced rightward which means that they should appear to displace to the left during the test. Since in both conditions the center bars were retinally stable, they should not appear to move. In the fixation condition in which the outer bars moved and the observers fixated a stationary center point, 5 of the 8 subjects reported a MAE to the left in the outer bars by the fourth adaptation trial. Seven of these 8 subjects also reported a MAE to the right in the center bars by the fourth trial, which we take to be an induced MAE generated by the primary MAE in the outer bars. In sharp contrast to these results, only one of the 8 subjects in the tracking condition ever reported any MAE in the outer bars and the one subject who did, did so on the third trial. However, as in the fixation condition, 7 of the 8 subjects reported an induced MAE to the right in the center bars by the fourth adaptation trial. There was no clear difference in the duration of the MAE in the 2 conditions. In the control condition its mean duration was 10.8 sec (SD 6.5), while in the tracking condition it was 15.9 sec (SD 12.1). Thus the difference between the results from the 2 conditions resides in the frequency of reports of the primary MAE in the outer bars. In the control condition 63% of the subjects reported it, while in the tracking condition, only one subject (13%) reported it.

Eye movements. Although there were no differences between the results of the two conditions with respect to the frequency of reports of the induced MAE in the center bars, there was a sharp difference with respect to reports of the primary MAE in the outer, flanking bars. What might account for this difference? One obvious source of the difference might be the quality of the smooth eye motions in the tracking condition. If tracking were poor, periods of smooth image motion would have been less frequent. If the duration of the exposure to smooth image motion is important in the production of MAEs, then perhaps the differences in results

were a function of the quality of these eye movements.

The description of the eye movement data from the tracking condition is based on averaged results from four typical sweeps of the eye across the field from the trial in which the observer reported a MAE. (Data from the one observer who failed to report any MAE was taken from the fourth trial.) If we include data from this subject in our calculations, then an average of 86.6% (16.7) of the distance covered by the eye in any single 19 sweep can be attributed to smooth pursuit eye movements. (If we exclude the subject who failed to report any MAE, this mean is increased to 90%.) The average velocity of pursuit movement for the 7 subjects who reported MAEs was 40/sec which was somewhat less than the target velocity of 4.4° /sec. The mean number of saccades on a single sweep was 6.67 and the mean extent of these saccades was 41.6'. For the seven subjects who reported a MAE, smooth motion accounted for between 59 and 76 sec ($\overline{X} = 69$ sec) of the 77.4 sec of the adaptation period in which the pattern was visible. (A trial actually lasted for 90 sec but the pattern was blanked for 12.6 sec of that period.) For the one subject who failed to report a MAE, smooth pursuit accounted for an average of 53 of the 77.4 sec.

The analysis of the eye records indicates that on any single adaptation trial, tracking was likely to provide an average of about 10 sec (13%) less of smooth motion than actual pattern motion observed while fixating. However, there were 4 subjects in the tracking condition who reported the induced MAE on the first trial and for these subjects smooth pursuit accounted for an average of 95% of the trial. (The mean tracking velocity for these subjects was 4.2° /sec.) Nevertheless, none of these subjects reported a primary MAE in the outer bars. While in contrast, 3 subjects in the control condition reported the primary MAE on the first trial. Certainly in the case of these subjects the difference in the perceived MAE does not seem to be largely a function of differences in exposure to smooth motion. Furthermore, if we assume that the adaptation of the mechanism underlying MAEs is cumulative, increasing with exposure to the adapting stimulus, then certainly by the third or fourth tracking trial, the amount of exposure to smooth pattern motion was at least as great, and probably greater, than that provided by the first 2 fixation trials. Yet, by the second fixation trial, 50% of the subjects in the control condition had reported the primary MAE, while there was only *one* report of a primary MAE by the fourth trial in the tracking condition. For these reasons we think it unlikely that much of the difference between the 2 conditions can be attributed to the quality of the tracking.

Discussion

These results which fail to confirm Anstis and Gregory (1969) raise related questions. The first question is why does the retinal motion caused by tracking eye movements rather than actual stimulus motion fail to elicit reports of a primary MAE in the elements of the pattern which displaced over the retina during the adaptation period? In asking this question it is necessary to remember that the adapting retinal motion produced by tracking was as effective as that produced by actual stimulus motion in eliciting reports of a secondary or induced MAEs in the elements of the pattern which had been retinally stable during the adaptation period. This necessarily would seem to imply that a primary MAE was in fact produced in the flanking elements in both conditions but, with one exception, was perceived and reported only in the condition involving actual stimulus motion. This must mean that for some reason the MAE produced in the tracking condition was weaker than that in the control condition and therefore (except for the one subject who reports it in the tracking condition) is below threshold.

We know from Duncker (1929) that when motion is below threshold and occurs in a stimulus which surrounds another stationary stimulus, it is only the stationary surrounded stimulus which appears to move and does so in the opposite direction. Since the flanking bars which had displaced retinally during adaptation surround the bars which had been stationary during adaptation, an undetected, below threshold, primary MAE in the flanking bars could induce an opposite motion in the center bars. Moreover, if Rock et al. (1980) are correct in arguing that induced motion is motion subtracted from the motion of the inducing stimulus, then on this account as well, a weaker primary MAE which induced motion in a surrounded stimulus would be less likely to be perceived.

The next experiment examines the proposition that a weak MAE, even if produced by actually moving bars which are observed while fixating a stationary stimulus will generally only induce an opposite MAE in a previously stationary surrounded stimulus rather than elicit a primary MAE in the stimulus that previously displaced. Evidence that this is so would lend credibility to the argument that the reason why tracking produces an induced MAE is because the primary MAE produced by image motion associated with tracking is weak. Of course, if this is true, we are still left with the question, why this should be.

EXPERIMENT 2

Method

Subjects. Fourteen observers were paid for their participation.

Apparatus and stimuli. The display was identical to that used in the control condition of the first experiment.

Procedure. In order to try to produce a weak MAE, the period of adaptation was severely abbreviated. During adaptation the observer fixated the central stationary point which was superimposed on the center row of stationary bars. As in Experiment 1, the 2 outer sets of flanking bars moved rightward but now only for 4 cycles. Each cycle was again 4.32 sec followed by a 700 msec blank period. Adaptation time in a single trial was 17.28 sec. Following the adaptation period, the observer reported whether all or any part of the display which was now stationary, appeared to move and if so the direction and duration of the motion. If an observer failed to report any MAE after the first trial, a second trial was run.

Results

Of the 14 subjects tested, only 2 reported a primary MAE in the outer bars which had moved during adaptation. These 2 subjects reported a MAE to the left, opposite the direction of the adapting motion. Twelve of the 14 subjects, however, reported an *induced* MAE in the center bars to the right. Nine of the subjects reported this effect following the first adaptation trial and the remaining 3 reported the induced MAE following the second adaptation trial. The mean duration of the MAE was 5.3 sec (SD 2.8 sec).

Discussion

As predicted, brief exposure to actual pattern motion leads to a general failure to report a primary MAE in the elements of the pattern which had displaced during adaptation, but does cause the perception of an induced MAE in the pattern elements which had been stationary during adaptation and which are surrounded by the previously moving elements. These results appear to lend direct support to the view that a weak MAE, itself below the detection threshold, will induce an opposite motion in a surrounded stimulus. They therefore lend indirect support to the hypothesis that the induced MAE associated with tracking is the consequence of the fact that tracking causes a weak MAE unlike that caused by an equivalent amount of retinal motion produced by actual pattern motion.

Finding an induced MAE following tracking is consistent with the report of Morgan et al. but, because it failed to confirm the Anstis and Gregory results, seemed to demand further exploration. As noted in the introduction, Morgan et al. attributed their failure to confirm Anstis and Gregory to the difference in test pattern. Anstis and Gregory tested for a MAE with a photograph of sandpaper while we, like Morgan et al., used the adaptation pattern itself as the test stimulus. Although this did not seem to us the reason for the difference in outcome, we nevertheless thought it reasonable to attempt to replicate Anstis and Gregory under conditions which more closely resembled the ones they used. Thus in Experiment 3 observers tracked across a pattern of stationary bars for 45 sec, the adaptation interval used by Anstis and Gregory and then looked at a photograph of sandpaper, which served as the test pattern.

EXPERIMENT 3

Method

Subjects. Five subjects were tested and paid for their participation.

Apparatus and stimuli. The apparatus and stimuli used for the adaptation display were a version of that used in the earlier experiments. A single set of vertical bars were displayed on the oscilloscope. These were actually the center set of bars from the previous displays. The photograph which served as the test stimulus was of coarse sandpaper (No. 36) which was magnified $2\frac{1}{2}$ times. The photograph was placed on a wall at right angles to the oscilloscope screen so that the subject had to turn 90° in order to see it. It measured 23.5 by 20.9 cm and subtended a visual angle of 10.4° vertically and 11.7° horizontally at the viewing distance of 114.3 cm. The photograph was lit by a lamp

which was turned on immediately after the adaptation period.

Procedure. Since eye movements were again recorded in this experiment, the eye calibration procedure was undertaken prior to actual testing. Once this was completed, the subject was instructed to fixate and track the central point as it displaced to the left over the stationary vertical bars. As in the earlier experiment when the tracking target reached the edge of the display, it and the bar elements blanked for 700 msec and reappeared with the tracking target again 1.27° from the right edge of the display and moved leftward at 4.4°/sec. A 45 sec adaptation period was used. Following the tracking interval, the subject was instructed to turn immediately to the illuminated photograph of the sandpaper and to report any appearance of motion, its direction and duration.

Results

None of the subjects reported seeing any motion in the test stimulus. In other words we found no evidence of any MAE under these conditions. The eye movement records verified that tracking was reasonably accurate and therefore could not account for this complete failure to elicit a MAE.

Discussion

This failure once again to confirm the Anstis and Gregory findings led us to make one final attempt to do so. However, instead of testing with the photograph of sandpaper which we found to be a poor stimulus for eliciting a MAE even if the retinal motion was produced by actual bar motion, we chose to test for a MAE using the adaptation pattern itself as we had done in the earlier experiments. Since monitoring eye movements required our adaptation and testing to occur in the dark, whereas Anstis and Gregory adapted and tested their subjects in a lit environment in which the display aperture and other things as well were visible, we added a luminous frame to the oscilloscope screen. We did this despite the fact that we did not believe that the absence of a visible surround would make a difference when the subjects tracked. Relative motion is known to be important for MAEs and therefore the presence of a visible stationary surround is important when a set of moving elements serve as the adapting stimulus. With tracking, however, the adapting elements are physically stationary and caused to displace retinally by pursuit eye movements which, of course, also cause all other visible, stationary stimuli to displace in the same way. Thus, a visible stationary surround fails to provide any relative motion stimulation. In fact, when tracking a moving target over a stationary grating, the only relative motion is that between tracking target and everything else that is visible. From the description of the Anstis and Gregory report it would seem that relative motion in their tracking condition was also restricted to that between tracking point and whatever else was visible. Thus in this respect too, the experiment more closely duplicates the conditions present in the Anstis and Gregory testing situation.

EXPERIMENT 4

Method

Subjects. Ten observers were paid for their participation.

Apparatus and stimuli. The display was again presented on the oscilloscope and was identical to that of the first experiment. A luminous frame 10.5° by 11.7° surrounded the display.

Procedure. During the adaptation period which was 45 sec the subject tracked the moving fixation point leftward over the static array of bars. All 3 sets of bars were visible during both adaptation and test. When the adaptation period ended, the pattern froze with the fixation point at its center. The subject then reported whether any part of the display appeared to move and its direction and duration.

Results

Only one of the 10 subjects reported a MAE in the bars. This subject reported motion as leftward which is opposite the adapting motion. In contrast, 7 of the 10 subjects reported an induced MAE to the right in the fixation point. The mean duration of this effect was 7.11 sec (SD 6.07 sec). Two subjects failed to report any MAE.

Again our results fail to support those of Anstis and Gregory.* To make perfectly certain that the stimuli we were using would produce a typical MAE when the adaptation occurred under more normal conditions, that is where the adapting motion was caused by grating motion, we ran one final control experiment in which the inner set of bars displaced between the set of outer flanking bars which were stationary.

EXPERIMENT 5

Method

Subjects. Ten observers were tested.

Apparatus, stimuli and procedure. The apparatus and stimuli were identical to those used in the first experiment. In this experiment, however, the inner bars displaced to the right and the outer bars were stationary. Adaptation lasted 45 sec during which time the observer fixated the centered fixation stimulus.

Results

All ten subjects reported a MAE to the left in the center bars. Its mean duration was 6.05 sec (SD 2.3 sec). These results, like those in the fixation-control condition of the first experiment, thus demonstrate that the stimuli were appropriate for producing a standard MAE when adapting motion was a function of actual pattern motion.

Discussion

Contrary to prior reports, our results indicate that the retinal motion produced by actual pattern motion and that produced by tracking over an identical stationary display are not equally effective in causing a MAE. Tracking rarely causes the perception of a primary MAE in the elements which previously displaced over the retina, although it frequently causes the perception of an induced MAE in stimulus elements falling on areas of the retina not peviously exposed to motion. This seems to be because the MAE associated with retinal motion produced by tracking is weaker than that produced by an equivalent interval of actual pattern motion. In fact, the aftereffect associated with tracking appears to be sufficiently weak so that its presence is generally apparent only indirectly, through the induced motion of stimuli falling in areas not previously exposed to moving edges.

There may be several reasons why this is so. The first and least interesting reason concerns the availability of relative motion information. In Experiment 4 where the adapting motion was

^{*}We continue to be extremely puzzled by our failure to replicate the Anstis and Gregory tracking results. Perhaps a lit environment is the critical difference. However, we have run a series of related MAE experiments which did not involve monitoring of eye movements and were carried out in dim ambient illumination and still failed to obtain their tracking results.

produced by tracking, the only relative motion was between the retinally stable tracking target and all other visible elements of the display (the physically stationary bars and the luminous viewing frame). This only caused an induced MAE in the fixation point that must have been induced by an unreported, weak MAE in the stimulus elements which had displaced during tracking. In Experiment 5 in which the inner bars displaced between flanking stationary bars every subject reported a primary MAE in the center bars. Clearly some of the difference between these two sets of results depend on the difference in the availability of relative motion.

In Experiment 1, however, where we did not attempt to closely duplicate the testing conditions used by Anstis and Gregory, and every effort was made to equate the amounts of relative as well as absolute retinal motion in the two conditions, the MAEs elicited in the 2 conditions were still not comparable. The MAE produced by tracking was much weaker than that produced by actual pattern motion. Tracking produced only a single report of a primary MAE although it did elicit reports of induced MAEs. In contrast actual pattern motion was far more likely to elcit reports of primary MAEs as well as induced effects. Since, for the reason given earlier, we do not think that these differences can be largely or primarily attributed to the quality of the tracking eye movements, some other explanation must be sought.

Although we have no independent evidence, we would like to suggest that at least some of the difference between tracking and fixation may be due to the damping of the motion signal by the compensation process which operates during tracking (Mack and Herman, 1978) and which accounts for the phenomenon of position constancy. If this is correct, it would mean that the compensation process which matches the retinal motion signal against the eye movement signal, nulling it when a match is found, has an impact on the mechanism underlying MAEs.

We suggest that there also may be another possible reason why tracking may cause a weaker MAE. It is, at least possible, that some of the diffrence between tracking and fixation might be due to differences in perceived motion. During tracking the retinal motion of the physically stationary elements is associated with little or no perception of motion. This is an instance of position constancy. On the other hand, the retinal motion caused by actual element motion in the fixation condition is accompanied by the perception of pattern motion. It is therefore possible that this difference contributes to the difference in outcomes.

However, even if neither of these factors are responsible for, or even contribute to the difference between the MAEs caused by tracking and actual pattern motion, these experiments demonstrate that the retinal motion caused by tracking generates a distinctly weaker MAE and is therefore not comparable to that caused by actual stimulus motion.

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