Chapter 18

Motion Aftereffects and Retinal Motion

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Introduction

Observation of a pattern moving in one direction will, after a period of time, cause a subsequently viewed stationary pattern to appear to move in the opposite direction. This motion aftereffect (MAE) has been intensively studied. Nevertheless, there remains a question about the nature of the adaptation process which underlies the effect. Is the adaptation a response to retinal motion or is it rather a response to motion processes which occur at later stages in the processing of visual information? An answer to this question may be of importance because the motion signal which accounts for the aftereffect is likely to be the basic signal to which the visual system responds.

The evidence is conflicting. Data reported by Anstis and Gregory (1965) and Tolhurst and Hart (1972) are consistent with a strictly retinal motion account of the aftereffect. Both sets of investigators found that retinal motion produced by the tracking of a moving point over a stationary grating caused an MAE that was indistinguishable from that which followed fixation of a stationary point while a moving grating drifted across the visual field. Furthermore, Anstis and Gregory found no MAE in subjects after a period in which the moving grating itself was tracked, apparently ruling out the possibility that perceived motion or the motion signal issued from the compensation process believed to match eye movement information (corollary discharge) against the image motion signal is the cause of the aftereffect (Holst and Mittelstadt 1950). This signal is frequently, but not invariably, the basis of perceived motion. For example, it is the basis for the perceived motion of a smoothly tracked target but cannot account for the perception of induced motion.[1]

In contrast, results reported by Morgan et al. (1976), Weisstein et al. (1977), and Mack et al. (1987) are incompatible with a retinal motion account of MAEs but are consistent with the view that the aftereffect entails adaptation to a motion signal which occurs at a later stage in the

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information processing chain. Weisstein et al. found MAEs in subjects who had observed drifting phantom contours. Since these cannot be based on adaptation to retinal motion the involvement of some higher level process is implicated. Morgan et al. (1976) and Mack et al. (1987) have also reported results which are incompatible with a retinal motion account of MAEs. Unlike Anstis and Gregory (1965), both groups of investigators failed to find normal MAEs from the retinal motion of a physically stationary grating caused by the tracking of a moving point across it. In one experiment (Mack et al. 1987), observers tracked a moving grating which displaced between flanking stationary gratings. The MAE produced by this condition was compared with the effect obtained after steady fixation of a point centered on the stationary middle grating while the flanking bars moved together across the field. The retinal motion in the two conditions was virtually identical. Nevertheless, during testing when all three sets of bars were stationary, the MAE associated with tracking appeared in the middle set of bars that fell on an area of the retina not previously exposed to motion. Moreover, it was in the *same* rather than the opposite direction to the adapting retinal motion and was apparently induced by a very weak below-threshold MAE in the flanking gratings which had displaced over the retina by virtue of the pursuit eye movements. (A similar induced MAE obtained under similar conditions was reported earlier by Morgan et al. 1976.) In contrast, observation of the moving flanking gratings during steady fixation of the middle stationary grating led to a normal MAE in the flanking gratings.[2]

The principal question posed by the Mack et al. (1987) and the Morgan et al. (1976) results is why retinal motion caused by tracking yields an aftereffect that is so much weaker than that produced by the equivalent retinal motion caused by actual pattern motion. Why is the tracking MAE below threshold and therefore only evident by virtue of the aftereffect it induces in a surrounded pattern?[3] Mack et al. (1987) proposed the tentative answer that MAEs may be based on the motion signal issued from the comparator which sums eye movement and image motion information (Holst and Mittelstadt 1950). It is this mechanism which is believed to account for position constancy and, under the tracking conditions of the Mack et al. (1987) experiment, would have signalled that the retinally moving, physically stationary flanking gratings were either not moving or moving only slightly (Mack and Herman 1978). Moreover, since there is sometimes a small loss of position constancy during tracking which is associated with a signal indicating some stimulus motion, this could account for the slight below-threshold aftereffect which did occur. It is also possible that at least some of the difference between MAEs that occur after tracking and fixation might be due to a difference in *perceived* motion. During tracking, the retinal motion of physically stationary elements causes little or no perception of motion. In contrast, the retinal motion caused by actual stimulus motion normally produces a clear perception of motion. Therefore this difference must be considered a potential source of the difference in the strengths of the MAEs.

The present research was designed to provide independent evidence for these speculations. The principal question is whether retinal motion alone or the motion signal derived from the compensation process is the basis of the MAE. We did not attempt to evaluate independently the role of perceived motion in these experiments, and the predictions from the two hypotheses were the same.

The stimulus conditions permitted a direct comparison of the efficacy of the retinal motion signal and that of the signal issuing from the compensation process in generating MAEs. The stimulus conditions were such that if the MAE were a direct function of retinal motion, its direction would differ from an MAE based on the comparator motion signal. Each observer tracked a vertically moving point while an adapting pattern drifted horizontally across the field. The vertical motion of the eye caused the adapting pattern to drift obliquely over the retina so that if the MAE were based on retinal motion, a subsequently viewed stationary pattern should appear to move obliquely in the opposite direction. However, if the aftereffect were based on the comparator motion signal, then the subsequently viewed stationary pattern should appear to move horizontally in the opposite direction to the adapting motion, because during adaptation the comparator which matches the vertical eye motion signal against the oblique image motion should signal horizontal pattern motion (see figure 18.1).

Experiment 1

Method

Subjects. Ten observers with normal or corrected-to-normal vision were paid for their participation.

Apparatus and Stimuli. The adapting display consisted of a tripartite square-wave grating and a fixation point (see figure 18.1a). The display was the same as one that has been used previously (see Mack et al. 1987, for a complete description). It was presented on a fast phosphor (P15) cathode ray tube. The three square-wave gratings and fixation point could be swept independently across the screen. The display appeared as three rows of light grey vertical bars (with contrast levels approaching 1) vertically separated by 1.06 deg, and a horizontally centered fixation point. The background was black. The alternating light and dark bars each subtended a horizontal extent of 2.12 deg. The outer flanking bars subtended

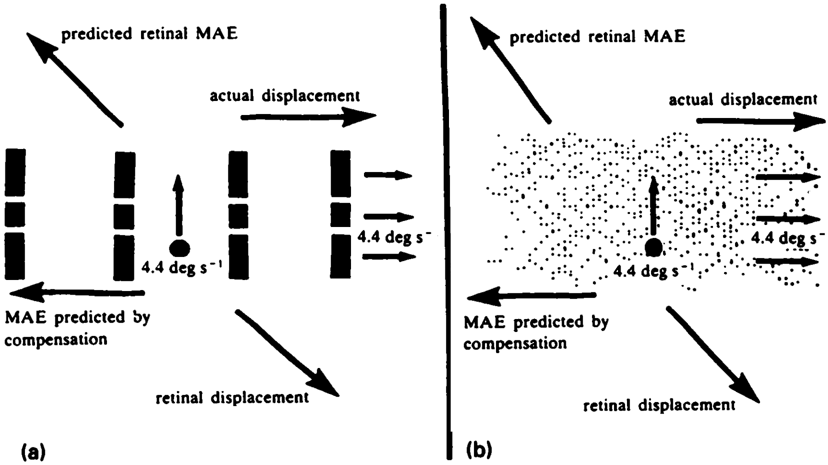

Figure 18.1
The adapting displays used in (a) experiment 1 (grating) and (b) experiment 2 (random-dot pattern) to induce motion aftereffects (MAEs).

a vertical extent of 5.30 deg, and the center row of bars subtended a vertical extent of 3.18 deg. The bars in each row formed a square-wave grating with a spatial frequency of 0.236 cycle deg^{-1}. When they moved, they covered a distance of 21.18 deg. Their motion was rightward at 4.4 deg s^{-1}. On trials in which the fixation point also moved, it travelled vertically upward at the same rate as the bars, starting from a position at the bottom of the screen. When it reached the upper edge of the screen the entire display vanished for 700 ms. It then reappeared, with the fixation point again centered at the bottom of the screen, drifting upwards while the bars drifted rightward. (This blank interval allowed the observer more than enough time to saccade back to the bottom of the screen and refixate the moving point when it appeared, without the possibility of undesirable retinal stimulation.)

Procedure. There were two adaptation conditions: one involved tracking the vertically moving fixation point while the bars drifted rightward (tracking condition); the other involved fixation of the stationary point centered in the display as the bars drifted rightward (fixation condition). The tracking condition always preceded the fixation condition. The display was viewed from a distance of 34.5 cm and an adaptation trial lasted 90 s, during which time the fixation point and/or the bars swept across the screen eighteen times. In the fixation condition the display blanked every 4.42 s during adaptation (the fixation point remained visible), simulating the blanking that was necessary in the tracking condition. In both conditions, after the eighteenth sweep the display blanked for 700 ms and

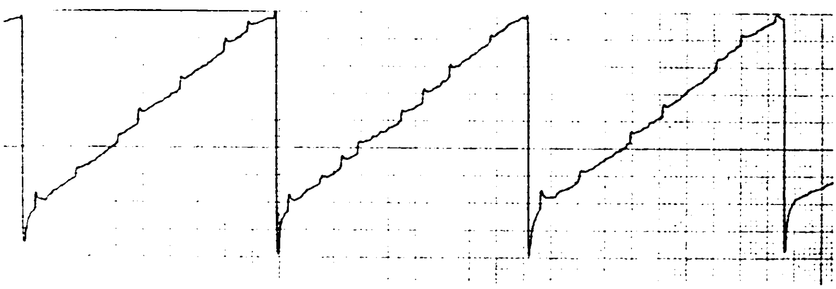

Figure 18.2
A sample segment of an eye movement record.

reappeared centered and stationary. This marked the start of the test period.

During the test period, the observer fixated the stationary centered point and reported any apparent motion (and its direction) of the now stationary bars. The observer then reported when the test pattern no longer appeared to drift. The interval between the appearance of the stationary test pattern and the observer's verbal statement served as the index of MAE duration. The observer indicated the direction of the aftereffect by noting the number towards which the pattern appeared to drift on a circular clocklike figure. If an observer failed to report an MAE after the first adaptation period, a second trial was provided. Prior to actual testing observers were given practice in repetitively tracking the vertically moving fixation point. During this training period, the vertical bars were absent.

Eye movements were monitored in three randomly selected observers to rule out the possibility that results in the tracking condition might reasonably be attributed to the failure to track vertical motion adequately. An SRI Purkinje Image tracker was used as the monitoring device (Crane and Steele 1978) and yielded an analogue eye movement record.

Results

The eye movement records indicated that the three observers whose eye movements were monitored tracked the vertical motion adequately, thus ruling out the likelihood that the tracking results were caused by faulty pursuit motions. A sample segment of an eye movement record appears in figure 18.2. All observers perceived the horizontal adapting motion as horizontal, although the point which was tracked appeared to move obliquely. The perceived oblique motion was, of course, due to the motion induced by the horizontally drifting adapting pattern. In the tracking condition, eight of the ten observers reported a leftward horizontal MAE (mean duration 11.1 s, standard deviation 3.8) after the first adaptation trial. The remaining two observers reported a leftward horizontal MAE after the second adaptation trial. No observer reported an oblique MAE. In the fixation control condition all ten observers reported an MAE after the first adaptation trial (mean duration 12.8 s, standard deviation 2.12). It was, of course, leftward.

The absence of any directional difference between the MAEs reported in the fixation and tracking conditions seems strong evidence for the hypothesis that the adaptation on which MAEs are based is a response to the motion signal derived from the compensation process (bearing in mind a possible role for perceived motion). There was, however, another possible explanation of these results which we examined.

It was possible that the horizontal MAE in the tracking condition was an instance of the operation of a rule, first stated by Wallach (1976, page 203), that "a line in a homogeneous field is always seen to move in a direction perpendicular to the line itself." Since the test pattern consisted of vertical bars, this rule predicts a horizontal MAE. Although there appeared to be good and sufficient reasons for thinking this rule was not operative, e.g. the ends of the bars were visible, as were the edges of the screen, and therefore the field was not homogeneous, it, nevertheless, seemed advisable to be certain that this was so.

To this end, we used adapting and test patterns which comprised a field of random dots which, in the adaptation period, drifted rightward across the field. Since there were no visible lines, there could be no line effect. Everything else remained the same, so if tracking of the vertically moving point again produced a horizontal MAE, it could not be attributed to the line effect.

Experiment 2

Method

Subjects. Ten new observers were tested in both the tracking and the fixation conditions. The tracking condition again preceded the fixation condition.

Apparatus, stimuli, and procedure. The adapting and test patterns comprised a field of random dots which, in the adaptation period, drifted rightward across the display at 4.4 deg s^{-1} (see figure 18.1b). Position and movement of the fixation point were as in experiment 1. All other details and procedures were also as in experiment 1.

Results

All ten observers reported a horizontal leftward MAE after the first tracking trial (mean duration 11.03 s, standard deviation 2.82). Identical results were obtained in the fixation condition, where the mean duration of the MAE was 12.14 s (standard deviation 3.19).

Discussion

The results of experiment 2 eliminated the possibility that the direction of the MAE could be explained in terms of the Wallach line effect, therefore increasing the likelihood that MAEs are based on the signal derived from the compensation process rather than on the retinal motion signal alone. These results are consistent with those reported earlier (Mack et al. 1987). Together they make a case for the critical role in the adaptation of the motion signal derived from the compensation process. Since in animals with moving eyes it is this signal which disambiguates image motion due to object motion from image motion due to eye motion, it is not surprising that it may be this signal, rather than "raw" retinal motion, to which the visual system is primarily attuned. Distinguishing between these two sources of retinal motion is frequently critical to an organism's survival.

There is at least one other possible explanation for these results which was suggested to us after these experiments had been completed.[4] It is based on the fact that relative motion is more effective in generating MAEs than is absolute motion (Day and Strelow 1974). This explanation accounts for the failure to obtain an oblique MAE by assuming that the vertical motion vector of the adapting motion is only weakly relational. The reasoning is as follows. When the observer is tracking the vertically moving point, the oblique retinal motion of the adapting pattern is a conjoint function of the actual horizontal motion of the pattern and the vertical motion caused by the tracking. The horizontal vector of this motion is relative with respect to all the visible stationary references in the field, such as the screen frame. The vertical vector, however, is relative with respect to the tracking point only, which is assumed to mean that its relative aspect is minimal. Given the established importance of relative motion for MAEs, a paucity of relative motion associated with the vertical motion vector might account for the fact that the subsequent MAE is horizontal rather than oblique. Were this correct, it would not be necessary to invoke the compensation process to account for the results. Although a direct test of this alternative explanation is in order, there are reasons for doubting its applicability. In earlier work (Mack et al. 1987), where the subject tracked a moving grating centered between two flanking stationary gratings, the relative displacement of the retinal motion of the flanking gratings caused by the eye movements was completely equivalent to that in the fixation control condition.[5] Nevertheless, the tracking condition produced an MAE that was below threshold whereas the fixation condition produced a normal MAE. Since in those experiments the tracking condition produced a very weak MAE despite ample availability of relative motion, it seems unlikely that the paucity of relative vertical motion in the present experiments accounts for the failure to find an oblique MAE. Moreover, it might be noted that there is no published evidence suggesting that relative motion with respect to one point is weaker than relative motion with respect to many contours. Only if this were true, would the alternative ingenious explanation offered by Anstis be tenable.

Notes

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1. For example, in the classic case of induced motion the observer fixates a stationary point while a surrounding frame moves, inducing the opposite motion in the enclosed point. Only if the eye movement command to fixate were captured by the perceived induced motion, or if the oculomotor command to fixate entailed countering a tendency to track the moving frame, would it be possible to consider the signal from the eye movement compensation process the basis of the induced motion. There is evidence that no such oculomotor visual capture occurs (Mack et al. 1985).
2. Anstis and Reinhardt-Rutland (1976) reported that an MAE can induce motion. However, the conditions in which this was demonstrated were quite different from those used by Mack et al. (1987) and Morgan et al. (1976).
3. Duncker (1929) established that a motion which is below threshold can induce motion in a neighboring stationary stimulus.
4. This alternative explanation of our data was suggested by Stuart Anstis in a personal communication.
5. This is why observers tracked a moving grating flanked by stationary gratings rather than simply a moving point over a stationary grating as in Anstis and Gregory (1965).

References

Anstis S. M., Gregory R. L., 1965. "The aftereffect of seen motion: the role of retinal stimulation and of eye movement" *Quarterly Journal of Experimental Psychology* **17** 173–174.

Anstis S. M., Reinhardt-Rutland A. H., 1976. "Interactions between motion aftereffects and induced motion" *Vision Research* **16** 1391–1394.

Crane H., Steele C. H., 1978. "Accurate three dimensional eye tracker" *Applied Ophthalmology* **17** 691–704.

Duncker K., 1929. "Uber induzierte Bewegung" *Psychologische Forschung* **12** 180–259.

Day R. H., Strelow C. H., 1974. "Reduction or disappearance of visual aftereffect of movement in the absence of patterned surround" *Nature (London)* **230** 55–56.

Holst E. von, Mittelstadt H., 1950. "Das Reafferenz-prinzip" *Die Naturwissenschaften* **20** 464–467.

Mack A., Goodwin J. H., Thordarsen H., Palumbo D., Hill J., 1987. "Motion aftereffects with pursuit eye movements" *Vision Research* **27** 529–536.

Mack A., Herman E., 1978. "The loss of position constancy during pursuit eye movements" *Vision Research* **18** 55–62.

Mack A., Heuer F., Fendrich R., Vilardi K., Chambers D., 1985. "Induced motion and oculomotor capture" *Journal of Experimental Psychology: Human Perception and Performance* **11** 329–345.

Morgan M., Ward R., Brussell E., 1976. "The aftereffect of tracking eye movements" *Perception* **5** 307–317.

Tolhurst D. J., Hart G., 1972. "A psychophysical investigation of the effects of controlled eye movements on the movement detectors of the human visual system" *Vision Research* **12** 1441–1446.

Wallach H., 1976. "The direction of motion of straight lines" in *On Perception* Ed. H. Wallach (New York: Quadrangle Press) pp 201–216.

Weisstein N., Maguire W., Berbaum K., 1977. "A phantom motion aftereffect" *Science* **198** 955–958.