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Motion aftereffect: a global mechanism for the perception of rotation

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Abstract. Observers adapted to motion by looking at rotating logarithmic spirals. They were tested with a stationary mirror image of the adapting spiral in which all contours were at 90° to those of the first spiral. Motion aftereffects were reported in the contrarotational direction—that is, observers who had seen clockwise rotating motion reported seeing counterclockwise aftereffects. These aftereffects lasted one-third as long as the aftereffects obtained when the adapting spiral was used as the test figure. These two aftereffects were shown to have different storage properties, thereby indexing the operation of at least two different mechanisms. We interpret the motion aftereffect that is obtained with the mirror-image stimulus as indicative of the existence of global rotation detectors.

1 Introduction

After one has looked at steadily moving contours for a period of time, stationary contours will appear for a while to move in the opposite direction. Originally called the waterfall effect because of the circumstances in which it was first noted, the phenomenon is today known as the motion aftereffect (MAE). Theoretical explanations of the MAE have often invoked the properties of neural units which are sensitive to a particular direction of motion. Thus, Sutherland (1961) proposed that the MAE could be caused by neural fatigue in complex cortical cells of the kind that were identified by Hubel and Wiesel (1959). These units are sensitive to lines of a given orientation moving in a direction perpendicular to their orientation. Subsequent to adaptation, a lower than normal level of firing in such units could lead to perception of motion in the opposite direction when an appropriate stationary stimulus is viewed. An alternate proposal has been that the MAE may be due to release from inhibition of cells sensitive to the unadapted direction of motion (Erke and Graser 1972). In either case, whether an imbalance of activity between units sensitive to opposite directions of motion is due to fatigue or to inhibition, the reversed direction of the aftereffect could be accounted for by the greater contribution of the unadapted neurons to the total percept.

One of the most popular stimuli for studying the MAE has been a rotating spiral for this makes it possible to rule out eye movements as an artifactual cause of the aftereffect, since the motion in a spiral involves all directions equally. After one has viewed a rotating spiral, motion can be seen in the same spiral when it is stationary, and also, but less strongly, in other patterned or textured surfaces. Spiral motion may be described in terms of either expansion or contraction, since the contours can appear to move away from or towards the center. Another dimension for describing spiral motion is in terms of clockwise or counterclockwise rotation. The dimension which predominates is determined by the specific configurational properties of the spiral, such as the slope of the arms or speed of rotation. In either case the spiral aftereffect can be conceptualized as being the sum of many locally generated MAEs produced by the direction of contour motion of line segments at each retinal location. Note that the direction of motion at any given location always remains

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constant as the spiral turns. An alternative explanation of the spiral aftereffect is that it may be the result of activity in detectors which are specialized for more global properties—units whose action is not so closely bound to the specific contours of the inducing stimulus. Thus, for example, Regan and Cynader (1979) have reported that there are units in the cat's prestriate cortex which respond to changes in the size of an object; and Beverley and Regan (1979) have reported decreased sensitivity to change in a pattern's size following exposure to a radially flowing pattern of annular line segments.

The generalization of the motion aftereffect to test patterns other than the adapting spiral (e.g. random dots or squares) may thus be the result of either or both of these two processes. First, if the aftereffect is due to local adaptation of orientation-specific motion detectors, the presence of any contours in the test pattern that are colinear with those of the adapting spiral should produce some aftereffect. Thus, even in a random dot pattern, the observed aftereffect could be produced by those pairs of dots which are aligned with the spiral's arms. Second, if global motion detectors such as those mentioned above are involved in the motion aftereffect, some aftereffect should be observed even in test stimuli which have no contours aligned with the contours of the adapting spiral.

In order to test whether any component of the spiral aftereffect may be due to adaptation of global detectors, we exposed observers to rotating logarithmic spirals and tested them with stationary mirror images of the same spirals. The logarithmic spiral used was defined by $r = \exp(\theta)$, where r is the radius and θ is the angle about the origin in radians. When the center of this spiral is superimposed on that of its mirror image, all of the contours intersect at 90°. The orientation selectivity of monkey cortical cell response to moving lines is about ± 20° [half-width at half maximum response, derived from data reported by Schiller et al (1976)], and that of a number of human visual aftereffects is ±6° to ±15° (Campbell and Kulikowski 1966; Blakemore and Nachmias 1971). These data suggest that few if any cells would be sensitive to both the contours of the adapting spiral and those of its mirror image. Thus if an MAE is obtained with the mirror image as the test figure, it is unlikely that any orientation-specific motion-sensitive cells are involved as none of the adapted cells of this type would be among those responding to the stimulus. It would seem likely that detectors of global, rather than local, motion properties would be mediating the aftereffect. As a control for the cognitive similarity of the mirror-image spirals, we also used as a test stimulus a pattern of radial lines—the contours of the logarithmic spiral intersect the radial lines at 45°.

We were also interested in the time course of the decay of the aftereffect. Masland (1969) has observed that the spiral aftereffect persists much longer when the adapting spiral is used as the test stimulus than when other patterns are used. Favreau (1976) has suggested that these different storage times may reflect the operation of two different motion-sensitive systems. To evaluate the persistence of the MAE with the standard, mirror-image, and radial test figures, two experiments were run: one with both immediate and delayed tests of the aftereffect, and another with only delayed tests. The delayed test of the first experiment will reflect the effects of both time and test exposure, while the delayed test of the second experiment will reflect only the effect of time.

2 Method

2.1 *Experiment 1*

The eighty observers in this experiment were recruited from among students, faculty, and staff at the University of Montréal. All had normal or corrected vision and were paid $2.50 for their participation.

Two different kinds of logarithmic spirals, both 20 cm in diameter, were used for adaptation and testing. For half of the experimental group the spiral segments were alternate black and white sections; for the remainder the spiral contours were indicated by black outlines against a white ground. They are referred to, respectively, as the 'filled' and 'outline' spirals (see figure 1 for diagrams of all the stimuli). The filled and outline spirals were used in order to determine whether there were differences attributable to the low-spatial-frequency content of the filled spirals. The radial-line test stimuli were drawn on discs 20 cm in diameter and similarly came in two versions—filled and outline.

The observers were divided into eight groups according to the adapting spirals, test figures, and order of testing. Four of the groups were adapted and tested with filled figures and four with outline figures. The same test conditions were repeated within each of these groupings in the following way. Any one observer was tested with two stationary figures: the standard adapting spiral and either its mirror image or the radial lines. The groups were further divided according to order of testing: in two of the four groups the first test was with the standard adapting spiral followed by the mirror image or by the radial lines, and in the other two groups this order was reversed.

An experimental session proceeded as follows. Observers were seated 1·6 m from the adapting spiral which thus subtended 7 deg of visual angle. The spiral was rotated at 23 rpm for 7·5 min. The observers were instructed to fixate the center of the spiral while it rotated, as well as the center of the stationary test stimuli when they were presented. At the end of the adaptation period the adapting spiral was hidden by a screen and the motor driving it was stopped. The first test with a stationary stimulus was then presented. This stimulus appeared in the same place in which the rotating spiral had appeared. Observers were asked to indicate the duration of the MAE, if any, by depressing a timer switch for as long as the aftereffect remained apparent. They were also asked to state the direction of the aftereffect, using two

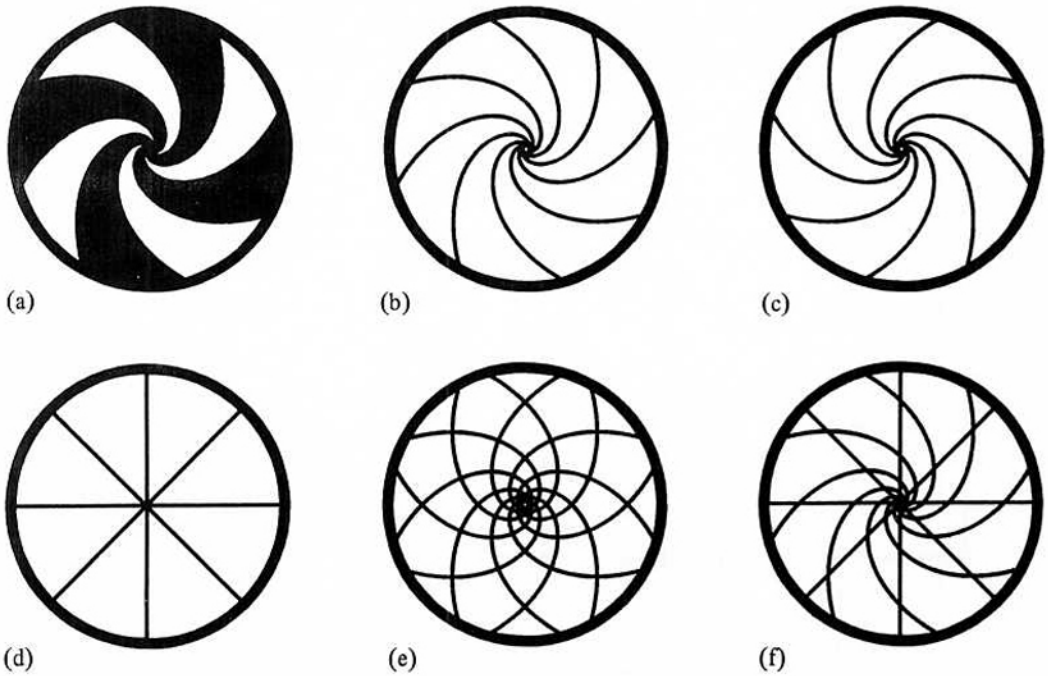

Figure 1. The filled logarithmic spiral (a), the outline logarithmic spiral (b), and its mirror image (c), the outline radial figure (d), the intersection of the log outline spiral with its mirror image (e) and with the outline radial figure (f).

criteria: direction of rotation (clockwise or counterclockwise) and expansion or contraction. For both of these response categories observers were required to make forced-choice guesses—that is, even if they felt that they had seen no recordable aftereffect, they were nevertheless asked to guess (a) in which direction the spiral seemed to be rotating and (b) whether it was expanding or contracting. In this way three response measures were obtained on each test—duration, rotation, and centripetal versus centrifugal motion. (The requirement for the latter category was dispensed with for the radial lines.)

The first test was followed immediately by the second test with the other test stimulus. Seven minutes later the two tests were again administered in the same order.

2.2 *Experiment 2*

Experiment 2 was identical in all respects to experiment 1 except that the eighty observers who participated in this experiment were given only the two 7 min delay tests, and were not tested immediately after adaptation.

3 Results

There was little or no consistency in the observers' reports of expansion or contraction of the test figure following adaptation. In fact, few observers were comfortable in describing the aftereffect as either expansion or contraction. On the other hand, observers practically always reported that the direction of rotation of the aftereffect was opposite to that of the adapting spiral—over 98% of the responses in both experiments. Furthermore, it is interesting to note that, of the observers who were asked, none noticed that the mirror-image spiral had been substituted for the standard. This reflects a high degree of cognitive similarity between these two stimuli.

The mean durations of the aftereffects are shown in figure 2. For purposes of the analysis of variance a $\log(x+1)$ transform was used to remove the dependence of standard error on the means in the duration data. A simple log transform was not possible owing to the many zero values in the data. In addition, the logic of the forced-choice procedure requires that wrong directional responses cancel equivalent appropriate directional responses. Therefore the eight durations where observers

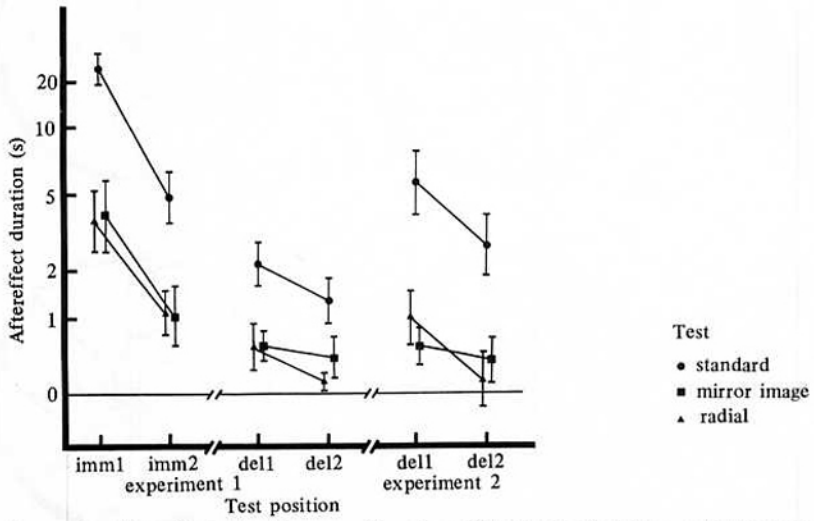

Figure 2. Aftereffect duration as a function of test type (circles—test same as adapt; square—test mirror image of adapting spiral; triangle—radial figure) and test position in experiment 1 and 2 (imm1, imm2: first and second test immediately after adaptation; del1, del2: first and second test 7 min after adaptation). Vertical lines are ±1 standard error, the durations are plotted on a $\log(x+1)$ scale and are the averages of transformed data.

reported rotation in the same direction as that of the adapting spirals (owing perhaps to random forced-choice guesses or to response confusion) were coded as $-\log(|x|+1)$. Because these eight negative responses constitute less than 2% of the data, their effect on the analysis of variance is negligible.

No difference in the duration of aftereffect was observed between filled and outline spiral tests and no interactions were found involving filled versus outline figures; therefore the data for both types of figures are combined. Aftereffect durations for mirror-image and radial-line tests do not differ from each other but the duration when the test figure is the standard spiral is significantly greater than that for both mirror-image and radial-line tests ($F_{1,240} = 73{\cdot}06$; $p < 0{\cdot}0001$, experiment 1; $F_{1,80} = 33{\cdot}13$; $p < 0{\cdot}0001$, experiment 2).

There is a significant transfer of the MAE to both mirror-image and radial-line tests in experiment 1 (mirror image: $t_{39} = 5{\cdot}22$; radial lines: $t_{39} = 5{\cdot}51$; $p < 0{\cdot}0001$) and especially for the initial test (mirror $t_{19} = 5{\cdot}15$; radial $t_{19} = 5{\cdot}43$; $p < 0{\cdot}001$, Bonferroni statistic). The transfer in experiment 2 does not reach significance, however. A direct comparison of the delayed tests of experiment 1 with those of experiment 2 shows an interaction between test type and experiment ($F_{1,160} = 4{\cdot}91$; $p < 0{\cdot}05$). That is, although the durations of the MAEs observed with mirror-image and radial-line tests are similar in the two experiments, the aftereffect duration for the standard test is longer in experiment 2 than in the delayed condition of experiment 1.

4 Discussion

The foremost finding in the present research is that the MAE does transfer to the mirror-image spiral as well as to radial lines, even though the contours of these test stimuli are at 90° and at 45°, respectively, from the contours of the standard adapting spiral. There is another possible source for this transfer, however. If the observers did not maintain fixation at the center of the test figures, then a shift of fixation might have brought the test figure's contours into near alignment with the contours of the adapting figure. Within retinal areas where, owing to misfixation, the orientations of adapting and test contours differ by less than 20°, we can assume that a significant number of cells adapted by the rotating spiral will be among the population normally responding to the test and therefore capable of producing a local MAE. In order to determine to what extent inaccurate fixation might have contributed to the overall transfer of the MAE, we calculated the percentage of test surface for which test and adapting contours are aligned to within 20° of each other for the three test figures at various eccentricities of fixation.

The results of these calculations show that for the mirror-image spiral this alignment never exceeds 10%, and that value is attained only when fixating at the periphery of the spiral, an unlikely point for erroneous fixation. With fixation off as much as 50%, the percentage of alignment is only 3%. The amount of alignment with eccentric fixation is greater in the case of the radial lines but is still only 10% at 30% misfixation. Moreover, the geometry of these overlapping figures is such that there are always two areas of alignment for misfixated tests and these two areas will generate aftereffects in opposing directions. In particular, for the mirror-image test the two opposing areas are always of equal importance, whatever the eccentricity. If fixation offset was a significant factor, then it should tend to produce frequent reports of inconsistent or no motion in the case of the mirror-image test. On the contrary, however, the observed direction of rotation for the mirror-image test was highly stable. In any case, it seems unlikely that observers would be more than about 10% or 20% off fixation, and so we feel confident in rejecting the possibility that the transfer of the MAE to the mirror-image spiral and to the radial lines was due to faulty fixation.

It seems fairly clear, then, that MAEs were obtained with contours that are perpendicular to the inducing contours. For convenience we shall distinguish between the MAE which was obtained with the standard spiral and the MAE that was transferred to the mirror image and to the radial lines, by calling the first the 'standard' MAE and the second the 'global' MAE, global because it is obtained when the specific local features that could be responsible for the transfer are removed. Because of the occurrence of this global MAE it is not valid to postulate that the standard MAE depends entirely on the activity of motion detectors which are finely tuned for orientation. Rather, it would seem more plausible to postulate that it depends in part on the functioning of such local units and partly on the functioning of more global movement detectors which are not sensitive to the local properties of a stimulus.

Before we examine the arguments in favor of a global detection mechanism, let us first reject two alternative explanations, namely that our results may simply be demonstrating that some motion detectors have very wide angular tuning or may have been due to random textures on the test figure. The first possibility can be rejected on a number of grounds. Were we to describe our data in terms of local effects of oriented motion-detecting units, we would say that, after having seen a line segment move in a direction orthogonal to its orientation, observers see an MAE in line segments perpendicular to the original segment. In this connection, consider a grating. Our data are equivalent to reporting that following adaptation to vertical bars moving from left to right an aftereffect is observed in which stationary horizontal bars appear to be moving upwards (or downwards). Notice first that this aftereffect is at 90° from the adapting motion rather than the 180° typically observed; second, notice that even if there were some local explanation for this transfer to an orthogonal direction, there would always be two equally available orthogonal directions. For our spiral tests these two orthogonal directions are equivalent to opposite directions of rotation. As we have seen, however, the overwhelming majority of observers reported seeing the MAE as rotation in the direction opposite to the adapting rotation, thereby consistently selecting one of the two possible orthogonal directions over the other. In terms of a local level of explanation there is no logical source for this consistent choice.

Second, any local effect dependent on a wide orientation tuning of motion detectors would predict a greater transfer to radial lines, whose contours differ from those of the adapting spiral by only 45%, than to the mirror-image spiral where the deviation is 90°. The data, however, show a virtually identical pattern of transfer for both radial-line and mirror-image test figures, implying that the transfer in both instances is based on a common mechanism which is insensitive to contour orientation.

Finally, it is well known that had our subjects merely closed their eyes following adaptation or fixated a totally blank screen, they would have seen an MAE. Some readers may wish to argue that our effect is an instance of this phenomenon; that is, some nonspecific MAE is being seen within the white or black areas of our mirror-image tests. We believe, however, that the aftereffects seen in a blank field are due to the random internal or external textures seen in these fields, some portions of which fall into alignment with the contours of the adapting stimulus. We would argue, in addition, that when actual contours are present in the test figure, these contours will dominate the organization of the MAE. To test this, we adapted five subjects to a rotating figure of radial lines and tested on a stationary figure of concentric circles. No MAE was observable on the test disk even though a very strong strong effect was seen on the inducing disk when it was stationary; a weaker MAE was also visible when subjects fixated the blank wall above the test stimulus. That is, the presence of strong contours perpendicular to those in the inducing figure appears to suppress the MAE that might otherwise have been observed on the random

textures of the blank areas between the contours. Thus we find no transfer of MAE over 90° (which would here have been an expansion or contraction of the concentric circles following adaptation to rotating radial lines) and no nonspecific MAE visible in the blank areas of the test figure when its contours are orthogonal to those of the inducing figure. Note that adapting to a vertical grating moving horizontally might produce an MAE at 180° to the inducing motion when a stationary horizontal grating is viewed but only due to the endpoints of the grating's bars; the concentric circles test figure used here avoided this artifact.

To reiterate, then, the aftereffect seen in the mirror-image log spiral test is a transfer over 90°, not the typical 180°; the transfer is equally strong for an orientation difference of 90° as for an orientation difference of 45° (radial test figure); and no evidence is seen of a nonspecific MAE in blank areas of a test figure whose contours are at 90° to those of the inducing figure. For these reasons, we believe that the transfer to the mirror-image test is attributable neither to random textures in the test figure nor to broadly tuned local motion detectors but rather is mediated by global rotation detectors.

Thus we must ask what kinds of units these could be. Let us first rule out the global size detectors that have been discussed by Regan and Cynader (1979) and Beverley and Regan (1979). The observers in our research were not able to use expansion–contraction as a reliable dimension for describing the MAE. They were able, however, to use direction of rotation in a consistent manner. Our results may be explained by the presence of global rotation detectors in the visual system, that is, units which are sensitive to overall rotation regardless of specific local properties of the rotating stimulus.

From an evolutionary point of view it is conceivable that rotation detectors could have evolved in conjunction with tilting movements of the head, possibly as a means of compensating for such movements so that the world maintains a stationary appearance in spite of head motion.

Neural units which are sensitive both to moving visual stimuli and to body rotation have been identified in the superior colliculus (Bisti et al 1971). Moreover, other researchers have found that motion-sensitive cells in this structure tend to respond to the motion of a wide range of different edge configurations (e.g. Cynader and Berman 1972; Sterling and Wickelgren 1969). On the basis of a congruency between certain psychophysical properties of the MAE and electrophysiological properties of collicular cells, Richards (1971) has suggested that the superior colliculus is the site of the spiral aftereffect. It seems not implausible that cells with properties like those in the superior colliculus may underlie the residual MAE obtained in the present research. While the conditions under which single cells in the superior colliculus have been examined have not been entirely appropriate as direct tests of whether these cells are responsive to global aspects of stimulus movement, nevertheless some of the properties they have exhibited are consistent with global detection. Specifically, the extreme lack of precision for contour and direction of motion may be indicative of units with global characteristics. In addition, the sensitivity of some of these units to body rotation makes them particularly appealing in the present context.

The 'global' MAE has another interesting characteristic when compared with the standard MAE. We noted above that there was an interaction between test type and experiment. We interpret this interaction as evidence that the two MAEs have different storage properties. Consider experiment 1. In this experiment when we tested both immediately after adaptation and again after a 7 min delay, both aftereffects had decayed substantially.

However, in experiment 2, when the MAE tests were given only at the 7 min delay, the standard MAE was greater than it had been when it had also had an earlier test, as in experiment 1, but there was no such difference for the 'global' MAE, which

was quite low on both occasions. This would seem to indicate that the occurrence or nonoccurrence of the 'global' MAE depends solely on the passage of time, whereas the standard MAE appears to be affected by previous tests as well as by the passage of time, implying possibly that not only do different detectors underlie these aftereffects, but also that they function according to different principles. Elsewhere, Favreau (1976) has suggested that the MAE depends on at least two parallel motion-detecting systems which are distinguished in part by the persistence of the aftereffects they sustain.

The results of the present experiment again point to the involvement of two distinct motion-detecting systems distinguishable on the basis of the rate of recovery from adaptation. Furthermore, the present data allow us to identify the rapidly recovering system as a system sensitive to global stimulus attributes. We have also speculated that cells in the superior colliculus such as those described by Bisti et al (1971) may be responsible for the global characteristics of this system.

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