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What Goes Up Need Not Come Down: Moving Flicker Edges Give Positive Motion Aftereffects

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ABSTRACT

Motion aftereffects (MAEs) are usually negative (i.e., opposite to the direction of the stimulating motion). However, we report a positive MAE, in the same direction as the stimulating motion. A special horizontal flickering edge made small jumps downward, changing in polarity between black/white and white/black on each jump. Apparent motion (AM) downward was perceived, but it was followed by an MAE downward (not upward). So an invisible feature of the stimulus produced a visible aftereffect. This is interpreted as evidence for two separate systems for seeing visual motion (Braddick, 1974): A long-range system correctly perceived the change of location downward, but a short-range system sensed an illusory reversed apparent motion upward, caused by the changes in edge polarity from positive to negative (Anstis, 1970, 1978). The short-range signal was not consciously seen, but it is thought to adapt motion detectors to give a motion aftereffect.

respond to "cyclopean" edges that are defined not by luminance but by higher-order properties such as spatial phase, stereo depth, textural properties, or flicker (Anstis, 1980).

The experiment to be reported here was designed to test Braddick's hypothesis of the two motion systems. We used flickering moving edges, and we believe that these stimulated both motion systems simultaneously in opposite directions: The temporal phase of the flicker defined an edge moving in one direction for the long-range system, while at the same time a step luminance edge defined an edge moving in the opposite direction for the short-range system.

3. Normal Apparent Movement (AM) and Reversed Apparent Movement (RAM). For normal apparent movement, two projectors can be arranged to project the same picture onto a single screen. Let the two pictures be overlapping but displaced out of perfect register by a few minutes arc. Now, if one picture replaces the other via a slow fade or dissolve, apparent motion will be seen. Moreover, adaptation to such fading apparent motion can give a motion aftereffect.

A new illusion of visual motion was reported by Anstis (1970) and further described by Anstis and Rogers (1975) and by Rogers and Anstis (1975). Suppose that one of the two projected pictures is now the photographic negative of the other. A fade or dissolve will now produce an apparent motion in a direction opposite to the direction of stimulus displacement. For instance, if a white disc is gradually replaced by an overlapping black disc that is shifted a few minutes arc downward, a strong upward apparent motion is seen. Moreover, exposure to this reversed apparent movement leads to motion aftereffects that are appropriate to (opposite to) the direction of the perceived illusory motion, not of the physical displacement (Anstis, 1978, 1980; Anstis & Rogers, 1975; Rogers & Anstis, 1975). In our example, a downward displacement of the disc would give an apparent motion upward, followed by a motion aftereffect downward. This would suggest that reversed apparent motion stimulated motion-sensitive neurons, and Blakemore and Anstis have confirmed this with some unpublished results. A pair of white spots was exposed in sequence on a screen, with the second spot lower than the first, to give a percept of downward apparent motion to human observers. They also produced firing of a motion-sensitive neuron, tuned to downward motion, in the cortex of an anesthetized cat that was looking at the same screen. When a negative (black) spot was substituted for one of the white spots, the apparent direction of motion reversed, and now an upward (not downward) physical displacement was necessary, both to give a sensation of downward motion to the two human observers and to produce firing of the downward-sensitive neuron in the cat's cortex.

These properties of reversed apparent movement, which we have just described, suggest that it occurs only in the short-range and not in the long-range system. To summarize the evidence: Reversed AM occurs only for small spatial shifts, say of 15' or less; it can give motion aftereffects in a direction appropriate

to (opposite to) the illusory reversed direction and not to the direction of physical displacement; and it can directly stimulate neural motion detectors. It is probably caused by spatial brightness summation, either in or before the neural motion detectors. This summation effectively shifts the apparent positions of the positive/negative composites, in a direction opposite to the physical displacement.

Consider a white dot or picture element (pixel) as it gradually fades away and is replaced by a negative, black dot that is slightly displaced to the right (see Fig. 4.1). In our theory, each pixel is neurally blurred by a point-spread function,

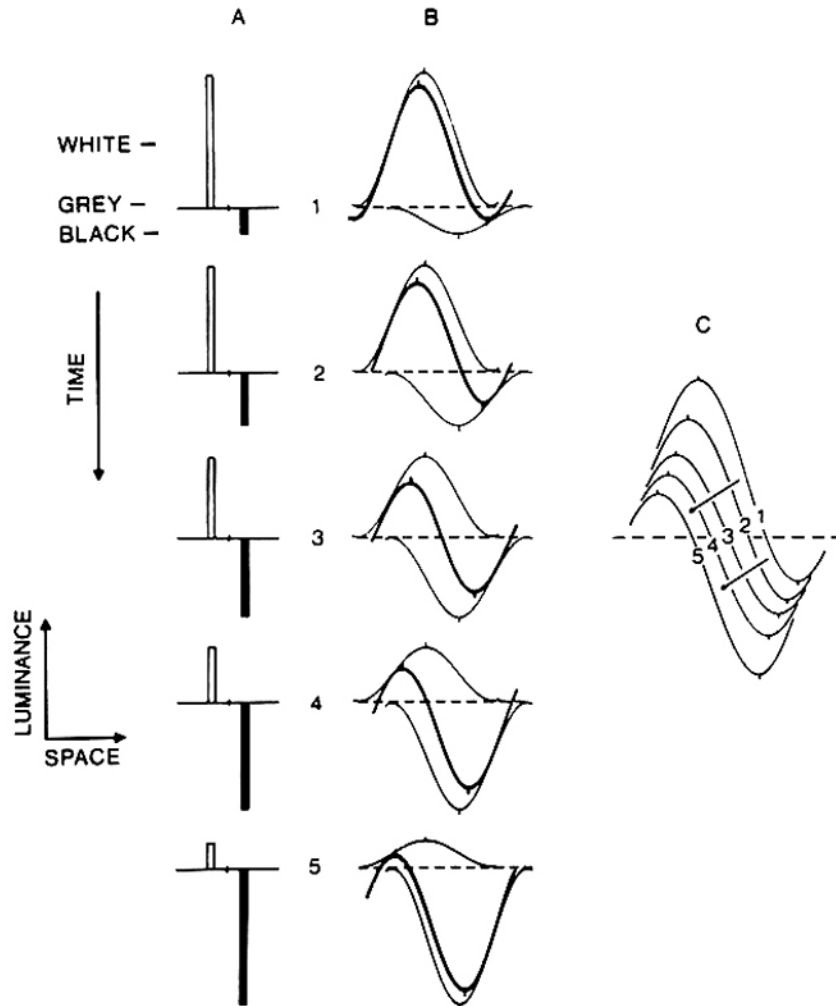


FIG. 4.1. Reversed apparent movement is explained by spatial summation. (a) Luminance profiles of white pixel as it fades over time and is gradually replaced by a black pixel that is displaced a few minutes arc to the right. (b) Spatial summation turns each pixel into a Gaussian point-spread function, which sum together to give an S-shaped curve (difference between displaced Gaussians). This combined point-spread function shifts gradually to the left. (c) Combined point-spread functions shown in (b) are superimposed. Shift to the left over time gives percept of reversed apparent movement to the left.

whose exact shape is not critical but may conveniently be taken as Gaussian. The point-spread function of an isolated white pixel will be exactly centered on the pixel. But when a black pixel is added, shifted slightly to the right, and the two pixel image profiles are convolved with the point-spread function, the combined luminance profile of the two pixels together will have its peak shifted slightly to the left (Fig. 4.1b). As the black pixel is gradually made more intense and the white pixel less so, the peak is shifted progressively farther and farther to the left. The point-spread function becomes S-shaped, like a sine wave that is being phase-shifted progressively to the left. What is true for a single pixel is also true for an edge or indeed for any complex picture. As a positive picture gradually dissolves to a negative picture that is displaced slightly to the right, reversed apparent movement will be seen apparently to the left.

There is no reason why this hypothetical spatial summation should be confined to dynamic moving stimuli. Rogers (1976) measured the spatial summation when an overlapping positive-negative pair was presented as a static vernier acuity target or else was embodied in a stereogram. He measured reversed apparent shifts in three conditions, using vernier, stereo, and AM targets. Consider the two stimuli shown in Fig. 4.1a (1) and (2), which would be blurred by spatial summation into Fig. 4.1b (1) and (2). In Roger's vernier condition, these two stimuli were presented one above the other and the subject was asked to set them into vernier alignment. Result: Figure 4.1a (2), which contains a negative image shifted to the right, appeared shifted slightly to the left, compared to Fig. 4.1a (1). In his stereo condition, the two stimuli were presented one to each eye. Result: The perceived depth was reversed (i.e., opposite to the direction of the physical disparity). Finally, in his apparent movement condition, the set of stimuli in Fig. 4.1 were presented dynamically, as a positive picture faded away and was replaced by a shifted negative. Result: reversed apparent movement.

Rogers found that the magnitude of reversed apparent vernier offset, depth, and AM, respectively, was an inverse function of the spatial displacement between positive and negative. Thus, as the spatial displacement was progressively increased, the extent of reversed vernier offset, depth, or AM was progressively reduced and finally disappeared. However, the space constants found for the three tasks were different. The maximum physical displacements at which illusory reversed vernier, stereo, and AM could still just be seen were, respectively, 3', 6', and 10' arc.

Rogers attributed these findings to spatial summation and inhibition. Computer simulations of various hypothetical point-spread functions predicted the following:

1. Reversed apparent motion shifts only when the width of the hypothetical summatory region exceeded the displacement between positive and negative. This gave estimated foveal summatory zones of 3' arc for static vernier targets, 6' arc in the stereo disparity domain, and 10' arc for the short-range motion system.

2. Summatory point-spread functions without inhibition would give reversed shifts of contours that were relatively independent of the size of the displacement between positive and negative. This prediction was not supported by the data. The inverse relationship actually observed between physical displacement and amount of illusory shift could be predicted from a summatory zone surrounded by an inhibitory zone.

Rogers concluded that the visual pathways that respond, respectively, to static vernier targets, stereo, and apparent movement have point-spread functions consisting of summatory zones, respectively, 3', 6', and 10' arc wide, flanked in each case by inhibitory zones.

On this theory, reversed apparent movement will be seen only if the point-spread function is wider than the shift between positive and negative. In practice, the shift must be less than about 10–15' arc. (Larger shifts give indeterminate percepts of movement.) This gives a rough estimate of the size of foveal receptive fields. We have confirmed informally that larger shifts between pictures can still give RAM in two conditions: (1) peripheral vision, where the size of receptive fields is known to increase progressively with retinal eccentricity; and (2) when the stimulus pictures are optically blurred by defocusing the projectors. In this case, the optical blurring outside the head simply adds to the neural blurring inside the head.

These two phenomena—reversed apparent movement and the motion aftereffect—were combined in a special moving pattern whose movement, by design, could not be perceived exclusively by neural motion detectors. A moving, flickering edge was devised that was correctly perceived as moving downward. However, this moving edge contained a hidden, unseen component of reversed (upward) apparent motion, which adapted upward-specific neural motion detectors and subsequently gave a downward aftereffect of motion. We argue that the visible stimulus motion and the invisible motion that led to a subsequent aftereffect must have stimulated two different and independent motion-sensing systems. If the two opposite directions had been coded in separate motion detectors, say in the short-range system, such that the perceived output was some kind of vector sum of the two activities, then whichever direction was perceived during adaptation would have determined the direction of any subsequent—negative—aftereffect. However, we predicted that the moving step luminance change would stimulate the short-range system and give an aftereffect, whereas the temporal phase of the flicker would stimulate the long-range system, which would register the successive positional changes of the flicker edge but not lead to a subsequent aftereffect. A gradual fade or dissolve between a pair of pictures gives the best reversed AM, as in Fig. 4.1. A rapid cut or switch between two pictures comprises only the first and last stages of such a dissolve, and this gives less effective reversed AM. We once demonstrated this with a TV set in which alternate TV frames were successively positive–negative–positive–negative–. . . . We presented on the screen a moving real-life scene

from a TV camera (Anstis, 1970). The result was a perceptual conflict between forward and reversed movement, in which the moving objects were seen moving in their true direction, with an overlaid effect of reversed AM that looked rather like sand streaming in the opposite direction.

In the present experiment, a horizontal edge was made to flicker or alternate in polarity between black/white and white/black at 15 Hz, which is well below flicker fusion frequency. When stationary, its position could be seen perfectly clearly; and when it made a series of small step movements downward, it gave a good, clear percept of movement, perhaps not as salient as a moving black/white edge that was not flickering but subjectively clear nonetheless. Adaptation to the apparent downward movement was followed by an upward (negative) motion aftereffect. This is just what one would expect if neural motion detectors responded to, and were adapted by, the apparent motion. But we devised a second, totally new flickering edge stimulus that was also correctly seen as moving downward but that introduced a hidden, unseen reversed apparent motion upward. Adaptation to this modified flickering edge gave a positive (upward) motion aftereffect. In the second case, the perception of motion cannot be mediated by motion detecting neurons.

Method

The horizontal edge, flickering at 15 Hz, was presented on a TV screen. On each flicker cycle the edge alternated in polarity between black/white and white/black and made a small jump downward.

The basis of the experiment is shown in Fig. 4.2. We manipulated the temporal phase relationships between the flicker and the movements. In the control condition, the edge alternately flickered and then moved; first it changed polarity (without moving), then moved (without changing polarity), and so on. This gave a series of movements, all downward. It was also true, but (we believe) irrelevant, that the moving edges were alternately black/white and white/black and were interspersed with static flickers or polarity changes.

In the experimental condition, a small but crucial change was made: the flicker and movement were now synchronized instead of being alternated, so that the edge jumped downward and simultaneously switched polarity, from black/white to white/black or vice versa. The purpose of this was to produce reversed AM, because the stimulus was now a positive edge being replaced by a displaced negative, which as we found in earlier papers (Anstis, *op. cit.*) would give a percept of apparent motion upward, followed by an MAE downward. However, the stimulus was different from the reversed AM stimulus in our earlier papers. We now had a flickering edge making a series of small discontinuous jumps, instead of a single pair of pictures making a slow fade. It was found that the experimental flickering edge was correctly perceived as jumping downward: There was no visible reversed AM effect of apparent motion upward.

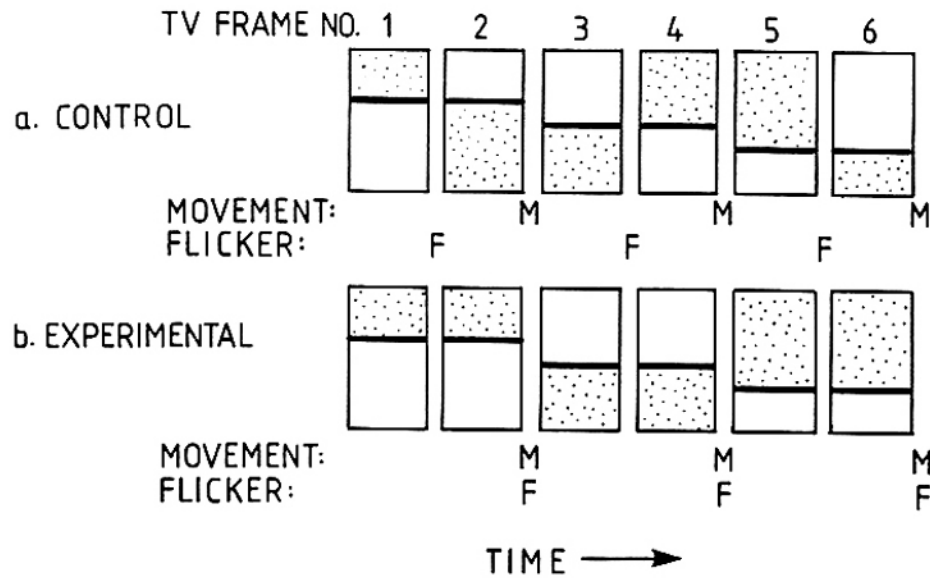


FIG. 4.2. Moving, flickering edges used as adapting stimuli in (a) control condition; (b) experimental condition. Edges were congruent in position in the two conditions. (a) Flicker and motion were out of phase. Edge alternately flickered or changed polarity without moving (frames 1-2, 3-4) and moved down without changing polarity (frames 2-3, 4-5). The flickers had no particular effect. The movements led to a negative motion aftereffect upward. (b) Flicker and motion were in phase. Nothing happened on frames 1-2, 3-4. The edge simultaneously changed polarity and jumped down on frames 2-3, 4-5. These jumps were correctly seen as being downward, but because the edge also changed from positive to negative on each jump, a hidden reversed apparent movement upward stimulated the neural motion detectors, leading to a downward motion aftereffect. The upward reversed apparent motion was not consciously seen. Conclusion: What the observer sees is not decided entirely by his neural motion detectors.

In the control condition, both the short-range and long-range motion signals were downward. In the experimental condition, the long-range motion signal was still downward, because the overall position of the flickering edge was being steadily displaced downward; however, the short-range signal was not upward, because the contrast reversal on each jump was giving a reversed apparent movement stimulus.

Why was the long-range downward motion seen and the short-range upward reversed AM not seen? The answer is that the stimulus time constants were carefully chosen to make the reversed AM suboptimal: strong enough to build up an aftereffect, but not strong enough to mask out the conflicting long-range movement signal. The moving flicker edges also gave a perceptual conflict, in which the downward displacement of the flicker edges completely masked out the reversed AM during the adaptation period. The reversed AM was able to reveal its presence only indirectly in the guise of an aftereffect.

Notice that the velocities, and the positions of the edges over time, were congruent in the two conditions: The only differences lay in the brightness

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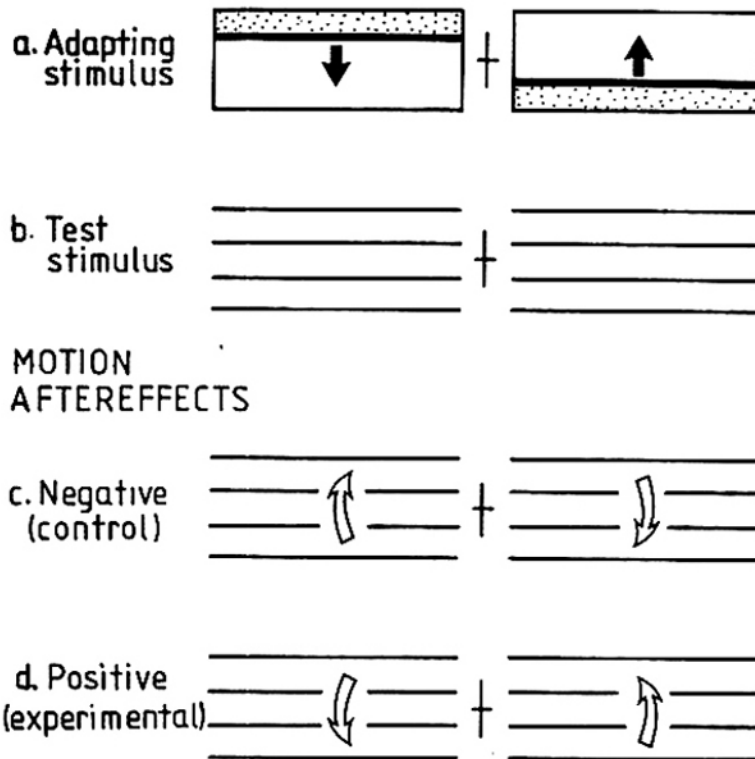


FIG. 4.3. (a) Adapting stimulus: left-hand flickering edge moved downward; right-hand edge moved upward. (b) Test stimulus. (c) Apparent direction of a negative motion aftereffect (opposite to the adapting direction). This MAE was observed in the control condition. (d) Apparent direction of a positive motion aftereffect (same as the adapting direction). This MAE was observed in the experimental condition.

polarities of the edges. So the opposite aftereffects found in the two conditions were not determined by the actual positions of the adapting edges of the retina, because these were always the same. One confounding factor must be conceded: The flicker frequency in the zone adjacent to the experimental edge was half that at the control edge (Fig. 4.2), because the effective flicker rate was necessarily confounded with the phase of the movement/flicker combination. However, we do not feel that this confounding factor is important. Although the reduced flicker rate might alter the magnitude of the subsequent motion aftereffect, there is no clear theory, other than ours, that could predict the observed reversal in the direction of the aftereffect.

The moving flickering edge was generated by a program in an APPLE II microcomputer (Cavanagh & Anstis, 1980) and displayed on the screen of a good quality black and white TV monitor. The display, which was viewed from a distance of 2.1 m, is shown in Fig. 4.3. Two rectangles 1.3° wide and 0.5° high were placed on either side of a fixation cross, with their inner edges 0.17° apart. During the adapting phase, a moving, flickering edge scanned repetitively down the left-hand rectangle and a similar edge scanned up the right-hand rectangle,

moving in a series of jumps of $3.8'$ arc. Each scan took 1.1 sec, so the effective velocity of the edges was $0.46^\circ/\text{sec}$. The double display presenting step motions in opposite directions was intended to enhance any motion aftereffects.

During the test phase the moving edges were replaced by a field of four stationary horizontal lines, spaced $10'$ arc apart, within each rectangle. A trial run consisted of 10 adapting periods each lasting 9 sec (eight scans of the rectangle), interspersed with 10 brief test periods. As soon as the test lines appeared, subjects reported any apparent motion aftereffects by pressing appropriate keys on the APPLE keyboard, whereupon the adapting scans resumed. Subjects were instructed to press a key on the left of the keyboard (A) if they saw a positive MAE and to press a key on the right of the keyboard (;) if they saw a negative

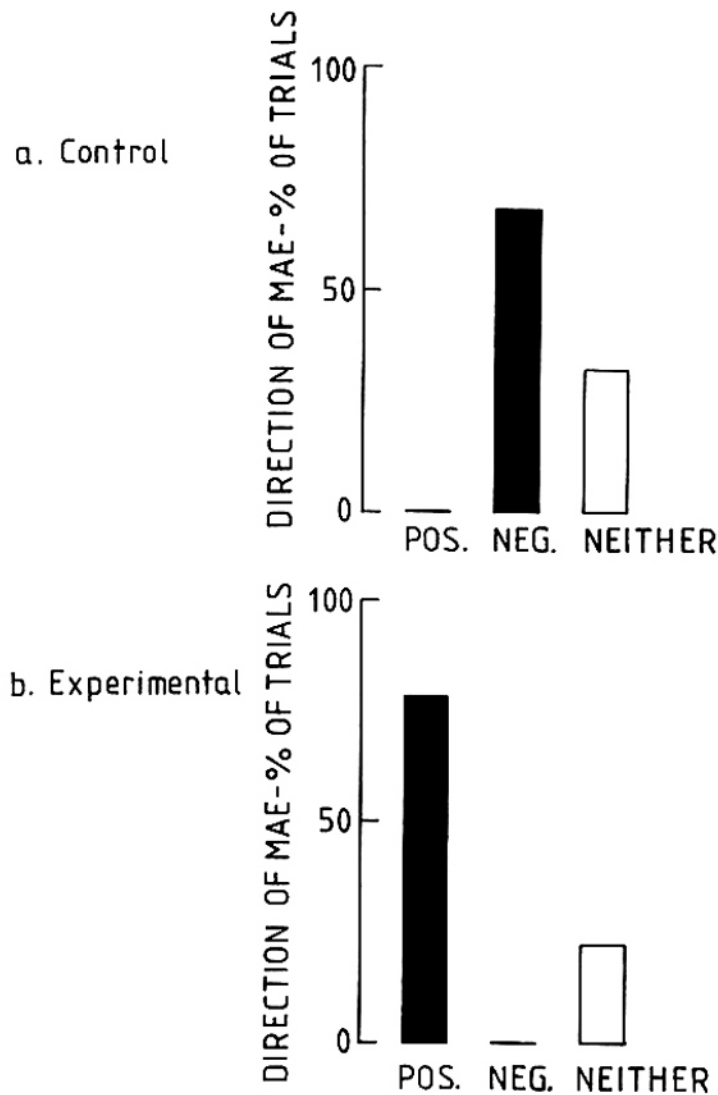


FIG. 4.4. (a) Control condition: 68% of trials gave negative MAEs, no trials at all gave positive MAEs, and 32% gave no MAEs (or ambiguous ones). (b) Experimental condition: no trials negative MAEs, 78% gave positive MAEs, and 22% gave no MAEs (or ambiguous ones). See text.

MAE. They were told to press the spacebar if they saw any other direction of MAE or no MAE. After 10 test periods the computer printed out the total reports of positive and negative MAEs or otherwise, and these were recorded. Eight subjects were tested, including the two authors. Five subjects were naive about the purposes of the experiment.

Results

Results are shown in Fig. 4.4. They fulfil our predictions. In the experimental condition the motion aftereffects were positive (i.e., in the same direction as the adapting moving edges) in 78% of the trials; 22% of trials gave no MAE, but there were no (0%) reports of negative MAEs. In the control condition, on the other hand, the aftereffects were negative (i.e., in the opposite direction to the moving edges) in 68% of the trials; 32% of trials gave no MAE, and there were no (0%) reports of positive MAEs.

It should be noted that several subjects commented on how weak the MAEs in this experiment were. The experimental design constrained us to use small, flickering edges, so the MAEs were always brief and transitory, never lasting more than a second or two; a far cry from the robust, long-lasting motion aftereffects that are commonplace with an optimally chosen large, slowly moving, textured surface. Nevertheless, the MAEs, although small, were in the directions predicted by our theory.

DISCUSSION

We have argued that the flickering edges stimulated the long-range system in one direction and at the same time stimulated the short-range system in the opposite direction. These results support the idea that motion can be perceived in two ways: The short-range system does have a substrate of neural motion detectors that can be adapted, the alternative way is more central and is mediated by still unknown neural mechanisms that show little or no adaptation (Braddick, 1974, 1980; Braddick & Adlard, 1978). These ideas have been elaborated by Ramachandran (1977) and Anstis (1978, 1980). See also Ullman (1980).

When we pitted the long-range against the short-range system, the long-range system determined the perceived direction of the adapting motion, but the short-range system determined the direction of the motion aftereffect. This suggests that MAEs are much stronger in the short-range than in the long-range system. We cannot entirely rule out long-range MAEs; in fact, there have been reports of very brief long-range MAEs, lasting for 1 sec or less, following adaptation to long-range motion stimuli such as drifting cyclopean stereo gratings (Papert, 1964) and dichoptic AM of isolated spots that jumped through a few degrees (Anstis & Moulden, 1970). So the long-range system may show a very limited

amount of adaptation. But it is undoubtedly much "stiffer" and less prone to adaptation than the short-range system.

Why should there be two separate systems for seeing movement, instead of just one? It may be economical to change visual strategy according to the size of the visual jump. An object in real movement makes infinitely small jumps. Larger jumps are very rare in the real world, perhaps occurring only for occluded motion when an object disappears behind an obstruction and reappears on the other side. Detecting these rare, large jumps would slow the system down considerably; in the worst case of a random-dot textured field, the number of comparisons needed to keep track of jumps through n dot diameters would increase according to n^2 . In a serial processor, such as a modern computer, increasing the spatial range would impose an increased search time; in a parallel processor, which the visual system seems to be, it would increase the number of neural channels needed. So it may be efficient to restrict the spatial range of hard-wired motion detectors, say to $1/4^\circ$, for the following reasons: (1) Receptive fields (or their subunits) cannot be made infinitely small; (2) time constants in the nervous system cannot be made infinitely small either, so to detect a useful range of velocities would require samples to be taken at certain spatial intervals; (3) even if the spatial distances could be made very small, a prohibitively large number of motion-detecting regions would then be needed to cover the visual field, each served by a different cell or subunit; and (4) it is useful to detect the motion of targets of finite size that move as wholes, and this would require some spatial integration for this region (Nakayama & Tyler, in press).

The psychophysics of the short-range system can be compared with the physiology of the motion detectors that are thought to underlie it. Barlow and Levick (1965) found evidence that a neural motion detector compares inputs from two nearby retinal regions, A and B. Michael (1968) showed that a single small jump by a spot across any small subregion of a motion detector's receptive field could make the cell respond. The receptive field seems to be built up of many subunits, each containing an A region and a B region, and the jumping spot need stimulate only one subunit to make the cell fire.

We can speculatively equate short-range perceptual phenomena with the properties of neural motion detectors. The spatial integration range over which luminance is summated for an AM stimulus is about $10'$ arc (Rogers, 1976). (This will set an upper bound on dynamic visual acuity for moving targets.) It may correspond to the diameter of each A or B region within a subunit. The spatial range, or largest jump over which random-dot AM can be seen, is about $15'$ arc (Braddick, 1974). This may correspond to the mean separation between each A region and its corresponding B region. The largest region over which a field of uniformly moving random dots can be summated has been estimated to be about 2° arc (Nakayama & Tyler, in press). We conclude that the foveal units underlying the short-range system may have receptive fields as large as 2° in diameter. Each receptive field may be composed of many pairs of subregions, about $10'$ arc in diameter and separated by about $15'$ arc.

The short-range system will respond adequately to nearly all moving objects. Larger jumps can be detected by a backup system with a longer spatial range. It is not known whether this second, more global system has a fixed neural structure of higher-order cortical motion detectors or whether it is a set of perceptual strategies or procedures—a form of neural “software.”

ACKNOWLEDGMENTS

This research was supported by Grant A 0260 to SMA and by Grant A 8606 to JPC, both from the Natural Science and Engineering Research Council of Canada (NSERC).

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