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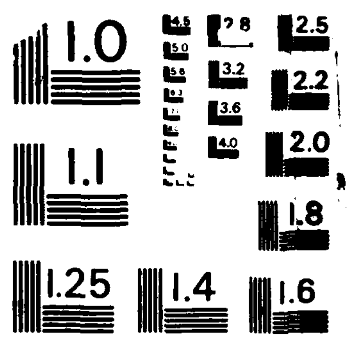

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This final report provides a brief overview of work conducted prior to the final year of this project, as more complete descriptions have been published. The overview covers work done on the sensitivity of the perceptual system to changing speed. The stimuli were sinusoidal gratings drifting normal to the lengths of their bars, and speed was modulated. Threshold modulation of speed was about 12% of average speed, although performance was better for higher spatial frequencies and higher average speeds. To avoid effects of contour change, we adopted a random dot approach in which threshold for motion of dots was determined as a function of the proportion of dots exihibiting correlated motion. Thus, threshold is expressed as a signal to noise ratio.

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For the detection of uniform motion of moderate speed, the percent correlation was about 5.7, i.e., 5 or 6 dots out of 100 had to move together, with all the other dots in random motion. There was approximately a 47% increase in threshold for change in direction of motion where the change in direction was about 30 deg. However, in a parametric experiment it was found that there was a monotonic decrease in threshold with amount of change in direction. Where the change in direction was only 2 deg, it could not be detected even with 100% correlation. At 3 deg 96% correlation was required. Only 14% correlation required at 30 deg. There are individual differences in these values. Motion after effects (MAEs) were studied for changes in direction of motion. All MAEs were observed in static fields of random dots, as they could not be seen in dynamic noise. Also, the speed of the MAE was matched to real motion and found to be less than 0.5 deg/sec. Circulatory motion gave no MAE at all. Zig zag motion gave MAE, but it was unidirectional and coincided with the direction of vector sum of motions of legs of zig zag. This was true even for 130 deg change of direction, suggesting very broad tuning of motion detecting elements. Interposing periods of static display or random motion between the legs of zig zag motion inhibits the MAE. We conclude that perception of change of direction of motion is a high order process as compared with perception of motion per se. Also, considering stimulus as a vector field, it appears that property of curl produces no MAE while divergence does. Gradient of speed would probably produce no MAE, since MAE is apparently insensitive to speed per se, and is predominated by direction of motion and the simple retinal flow produced by motion.

FINAL REPORT
THE PERCEPTION OF THE HIGHER DERIVATIVES OF VISUAL MOTION

by L. Kaufman
Professor of Psychology
Professor of Physiology and Biophysics

INTRODUCTION

Over the past several years (under Grant No. AFOSR 85-0329) we have been investigating the basic problem of visual sensitivity to the acceleration of moving targets. An image formed at different places on the retina at different times may be identified as belonging to the same object which is perceived as moving through space. Explanations of this class of motion perception, which has been described as representative of the "image-retina system", (Gregory, 1966) usually incorporate the operation of cross-correlation (see Regan, Kaufman and Lincoln, 1986 for an overview of this approach). However, while such theories can account for the perception of uniform motion across the retina, they do not of themselves explain how it is that observers can detect changes in speed or changes in direction. Either of these changes the velocity of the moving target, so we refer to such a detection as the perception of acceleration.

Nonuniformities in motion of the stimulus, e.g., acceleration and, perhaps, higher derivatives of motion, have very distinctive effects on how the motion is perceived. Thus, for example, Michotte (1946), in his classic work on the perception of causality, describes situations in which two moving targets change speed and direction. Under certain conditions these changes can lead to the perception of one of one of the targets as "causing" the other to change its velocity, while under other conditions the perception has an entirely different quality. Similarly, changing velocity in the image plane is a necessary condition for the occurrence of the kinetic depth effect (Wallach and O'Connell, 1953; Ullman, 1979). While such examples illustrate how changing velocity may affect other perceptions, e.g., of depth, they are not instances of the perception of acceleration per se. Even so, the changing velocity of a target must be registered by the nervous system if it is to affect other perceptions, and existing models of the mechanisms underlying (image-retina) motion perception make no explicit provision for such a capability.

Work done prior to this final year was based on earlier work which was described in previous Annual Reports submitted to AFOSR. Much of this work on the perception of changing speed is also reviewed in the chapter by Regan, Kaufman and Lincoln (1986), the writing of which was partly supported by this project. Since the chapter is available, for the purposes of this report we shall touch only on a few of the more salient points.

Changing speed (acceleration) was the subject of only a very few studies (e.g., Gottsdanker, 1952; Runeson, 1975), and led to the conclusion that humans do not perceive changes in speed with any great degree of sensitivity. Thus, for example, Gottsdanker (1952) had subjects manually track a target that moved with either an increasing speed or a decreasing speed. At some point during the tracking session the target was made to disappear, but the subject continued to track along the path and with the speed of the now invisible target. The tracks made by the subject indicated that they tended to follow the tangent to the target's motion (its velocity) at or near the point in time of its disappearance. These subjects were unable to project the targets acceleration into the future, thus suggesting that tracking itself is based on sampling velocity from time-to-time while tracking, or, perhaps, simply minimizing a positional error between the stylus used to track the target and the target itself and then simply keeping to the same speed of tracking after the target had disappeared. At any rate, these subjects were unable to store and use information about target acceleration. Despite this negative finding, changing velocity is utilized by the perceptual system in many ordinary tasks, such as positioning one's self to catch a ball, anticipating the amount of pressure needed on the brake pedal to stop a car, and so on. Unfortunately, in many such activities it is not possible to separate the perception of acceleration from the perception of relatively abrupt changes in size, or from other possible concomitants of changing speed. Kaufman and Williamson (1987) found that gratings moving with some average speed in a direction normal to the bars of the grating have to change speed by about 12% in order for the change to be detectable 50% of the time. This is consistent with earlier results, but there are systematic tendencies for this sensitivity to become greater with the spatial frequency of the grating, and also to improve with the average speed of the grating (see Regan et al. for a review). Thus, the detection of changes in speed are more or less consistent with Weber's law, but the Weber fraction is rather large - indicating that humans lack a high degree of sensitivity to changing speed as such.

This conclusion is consistent with the notion that single units respond preferentially to speed in a particular direction (velocity), and apparently are not "tuned" to respond to acceleration. Therefore, the perception of acceleration must be a higher order process involving neurons with differential tuning. In fact, we might make the claim (along with Gottsdanker and his colleagues), that humans are capable of responding to velocity directly, but employ inferential strategies, e.g., comparing average velocity at one point in time with average velocity at a later point in time. The latter point has a bearing on the single neuron doctrine of Barlow (1972). It is fairly obvious that there are no single units designed to detect changes in velocity. Thus, acceleration may well be perceived because of higher order (cognitive or computational) processes. This does not imply that such processes are outside the domains of contemporary neuroscience and psychology. Rather, it suggests a role for complicated computational networks of neurons. Clearly, it is of some importance to develop our understanding of the perception of acceleration, since it might deepen our knowledge of such higher order processes.

During the last year of work on this project we shifted emphasis from the perception of changing speed to that of the perception of changes in the direction of motion. This too is a relatively neglected area of visual psychophysics. While investigators such as Michotte (1963) and Johanssen (1974) employed stimuli in which the direction of motion changed, they were more concerned with the resulting phenomena rather than with the sensitivity of the observer to changes in direction. Moreover, there is virtually no work at all on the possible effects of changing direction on perceptual adaptation. Hence, this is a particularly rich area for research.

To be more concrete, a target that moves along a circular path is perceived as changing its direction of motion. Is the detection of such changes in direction of motion explicable in terms of the tuning characteristics of specialized neurons in the visual system? If so, the selective adaptation to a repeated change in the direction of motion would be likely to have very specific after effects. Moreover, the failure to find such after effects would be suggestive of a different level of processing. One of our first goals, therefore, is to provide a measure of sensitivity to changing direction of motion, and then go on to examine the effects of adaptation on this sensitivity.

PROFESSIONAL PERSONNEL

The work to be described in this report was the result of a joint effort by L. Kaufman, B.J. Schwartz, J.A. Movshon, and S.J. Williamson.

METHOD

1. Instrumentation

As already indicated, the earlier studies that led to this work employed sinusoidal gratings drifting across a display in a direction normal to the lengths of the bars. This type of display is unsuitable for the present project, because changes in the direction of such motion would involve confounding changes in the orientations of the gratings. Consequently, the display was composed of dots placed at random positions in the display. The position of each dot was changed to produce the impression of motion. If each dot moved by the same amount and in the same direction, their motion was referred to as being correlated. When the motion of each dot was independent of that of each other dot (random), then it was described as being uncorrelated. Various degrees of correlation were introduced, depending upon the proportion of the dots exhibiting correlated motion.

The random dot displays were generated with a DEC PDP 11/23 Q-Bus computer (running under RT-11), employing a custom made random number generator, all linked to a Tektronix 606 display scope, via Data Translation D/A converters, and a voltage divider. The display was a square random texture pattern 6 cm on a side.

The random number board, based on a design by Morgan and Ward (1980) and Williams and Sekuler (1982), was constructed by Robert Picardi, the senior engineer in the Psychology Department at NYU. The board puts out a different 32 bit random number per cycle, and runs at 6 Megahertz. The random number pattern does not recycle or repeat itself until about 4,000,000,000 numbers are generated. The numbers stand for X Y coordinates on the display, and a third number whose function is described below.

2. Software

Macro-11 assembler language code (provided by J.A.Movshon and extended by B.J. Schwartz) displays the dots in random X Y locations on a screen with a resolution of 2048 x 2048 dots. The software paints dots on the display scope in the order in which they are generated by the random number board. Thus, the display is similar to pseudorandom dot scan television rather than the conventional raster scan. One dot is painted every 30 microsec.

Although dots are being displayed and are decaying continuously, persistence of vision and that of the phosphor combine to give the visual result of about 500 dots on the screen in apparently continuous motion.

Each dot is characterized by three numbers: X location, Y location, and a third number which places all dots in one of two lists: to be remembered and to be discarded. Remembered dots are then saved and offset by dX and dY increments, at a particular delay time, T. dX, dY and T are all passed as parameters to the Macro-11 routine along with a parameter C%, which is the per centage of dots to be correlated from one display to the next. Finally, the whole motion sequence remains on for a duration D, (5 msec < D < 3000 msec). dX,dY,T,D, and C are all parameters passed from a FOCAL program (running under RT-11 on the DEC 11/23) to the Macro-11 program generating the display.

In our software, we can create sequences of motion intervals each with its own direction, speed, correlation percentage, and duration. For example, we can change dX and dY from one interval to the next and get a "two frame random dot movie" which repeats itself until a subject responds with a button press.

To collect thresholds for changing direction, we create a a two interval display with a constant correlation of moving dots (C%). The display repeats itself until the subject presses one of 8 buttons telling the program to increase or decrease the C%, at which time, the display is recreated (after a 2 sec delay) with the new correlation. This is repeated until the subjective threshold is indicated by another button. The program then records the value indicated as the threshold.

The result is a randomly moving texture containing a fixed percentage of dots which move in one direction for 100 msec, and then move in a different direction and/or speed for the next 500 msec, after which the sequence of intervals is displayed again. This movement can be placed in a central square area surrounded by a randomly moving texture which contains no correlated motion at all.

THRESHOLD EXPERIMENTS

The following experiments were designed to determine the sensitivity of unadapted observers to both change in speed and the change in direction of correlated random dots in a random dot noise background. Firstly, however it was necessary to determine the absolute threshold for the detection of motion *per se* to compare sensitivity to changing motion with sensitivity for motion itself. Thresholds are given in terms of the minimum amount of correlation (expressed as a per centage) needed to just detect the change in speed or direction of the correlated dots.

1. Experiment #1:

1.1. Procedure

Thresholds were obtained using a method of adjustment in which the subject increased and decreased correlation until motion was just detectable. Pilot experiments were run with speeds that ranged from 3 to 10 deg/sec, and since no large differences resulted, a moderate speed of 4.8 deg/sec was used. The screen was viewed at a distance of 30 cm. Thresholds were taken for different directions of motion, to determine whether there was any directional anisotropy in sensitivity. This in turn would enable us to generalize results of later motion change experiments.

1.2. Subjects

Although three subjects were employed, one undergraduate volunteer was investigated most fully. Data are consistent with the partial data obtained from the other subjects.

1.3. Results

The mean threshold across all directions of motion was 5.7% correlation, i.e. 5 or 6 out of every 100 dots had to exhibit correlated motion if coherent motion was to be detected. The overall data, based on 10 trials per direction, are summarized in Table 1. The 0 deg direction was chosen by convention to be horizontally to the right.

Table 1. Thresholds for Detecting Motion in Different Directions

DIRECTION in Deg	MEAN % CORRELATION at THRESHOLD
0	5.75
45	6.00
90	5.25
135	5.00
180	6.00
225	6.00
270	5.33
315	6.33

1.4. Conclusions

Overall, the threshold for detecting motion is approximately 5.7 deg/sec. Also absolute motion thresholds reveal no anisotropy with direction.

2. Experiment #2: Large Changes in Direction of Motion and Speed

2.1. Procedure

Five different combinations of speed and motion change were investigated, combining two different. In each condition of this experiment, dots moved in one direction at one speed for 300 msec, and then the direction and/or speed changed abruptly to another set of values for the next 300 msec. This two interval pattern immediately repeated itself. Again, method of adjustment was employed to determine the minimum correlation required for detecting a *change* of speed or direction at several different magnitudes of change. The subject showed a rapid "learning curve" for thresholds, from correlations of .25 down to .10 and less during the first two sessions. The results of these sessions were deleted, leaving 16 trials per condition, totalling 176 for one subject.

The following list describes the conditions under which the experiment was conducted:

I. Change of Speed only from 1.6 deg/sec to 4.9 deg/sec

II. Change of Direction only (30 degree change)

III. Change of both speed and direction 1.6 deg/sec to 4.9 deg/sec
30 degree change in direction

IV. Reversal of direction -- 180 deg change
speed = 1.6 deg or 4.9 deg

V. One direction of Motion alternating with uncorrelated motion interval

2.2. Subjects

The subjects were the same as in the preceding experiment.

2.3. Results Overall, there was a 47 per cent increase in the correlation threshold value needed to detect changes in motion, in comparison with the detection of coherent motion itself. Results are summarized in Table 2.

Table 2. Threshold Correlations for Change in Motion

STIMULUS	THRESHOLD CORRELATION
I. Change of Speed only 1.6 deg/sec to 4.9 deg/sec	8.65
II. Change of Direction only 30 degree change	8.25
III. Change of both speed and direction 1.6 deg/sec to 4.9 deg/sec 30 degree change in direction	7.75
IV. Reversal of direction 180 deg change speed = 1.6 deg or 4.9 deg	7.75
V. One direction of Motion alternating with uncorrelated motion interval	9.25

Standard deviations about the values in the table fall between +/- 1.2 and 1.8 per cent correlation.

2.4. Conclusions

Thresholds for changes in motion are at least 47% higher than thresholds for motion itself. Moreover, changes of direction and/or speed are detected more easily if anything than thresholds for cessation and resumption of motion (condition V above). Of course, these results hold for rather large magnitudes of changes in direction and speed. It is to be noted that our minimum change in direction of 30 deg is itself rather large. It may well be true that very tiny changes in direction (.e.g. on the order of 1 or 2 deg) would require a correlation threshold near 100 per cent. This is a subject for further study. Furthermore, the high values for these thresholds are consistent with the notion that the detection of changes in motion require several complicated stages of processing that are not required in the simple detection of motion. The worst performance was obtained when coherent motion was succeeded by random motion (condition V above). This seemed somewhat surprising and it is not fully understood. Again, more research is needed.

3. Experiment #3: Thresholds as Function of Magnitude of Direction Change"

In this experiment we measured the degree of correlation needed to just detect a change in the direction of motion as a function of the magnitude of the change in direction.

3.1. Procedure

A designated proportion of the dots moved in one of several directions for a period of 500 msec at a speed of 5 deg/sec from the 30 cm viewing distance. The direction of motion was changed abruptly by one of several designated amounts, ranging from 2 deg to 180 deg, and this new direction maintained for another 500 msec. This was repeated many times and the subject adjusted the degree of correlation (the proportion of dots having a common direction of motion) until the change in direction was just detectable.

3.2. Results

For one subject the results were quite straightforward. The subject could not detect a 2 deg change in direction even with 100% correlation. At 3 deg, however, the change in direction could be detected with 96% correlation. There was a monotonic decline in threshold correlation with increasing magnitude of change in direction up to about 90 deg, with 180 deg change in direction being virtually the same as 90 deg. The results with a 30 deg change in direction (14% correlation) differed from those obtained for the other subject of Experiment #2 who was exposed to a similar condition, but this is probably due to intersubject variability, as well as the inherent variability of the method of adjustment. The main point, however, is that the degree of correlation needed to detect a change in direction increases as the change in direction decreases. The amount of this change in correlation seems to begin to asymptote between 10 and 15 deg.

AFTER EFFECTS OF ALTERNATING DIRECTIONS OF MOTION

In the following experiments a random dot pattern was made to change directions periodically and the observer watched the display for a period of time ranging from 1 - 5 minutes. After adapting to this pattern of dots whose motion changed direction, a different stationary random-dot pattern served as a test field. When the adapting field had a zig zag motion trajectory, then the observed motion aftereffect (MAE) was seen in a direction opposite the average of the two directions comprising the alternating adapting field. More importantly, the motion after effect (MAE) did not appear to change direction over time, but was smooth and unidirectional. A variety of zig zag trajectories were tested as adapting fields.

1. General Procedure

Pilot experiments revealed that the strongest after effects were obtained with close in viewing and with bright dots in the adapting field, followed by a dim stationary test field. Therefore, viewing distance was maintained at 20 cm, and the adapting field had a mean luminance of roughly 30 candelas per square meter, while the test field had a mean luminance of about 4 candelas per square meter.

In all the experiments below adaptation times were 5 minutes in duration. The dots of the adapting field moved at moderate speeds, in a range between 3.5 to 10.1 deg/sec seen at the 20 cm viewing distance. The test field was displayed on the same CRT as the adapting field, but it appeared about 2 sec after the cessation of the adapting field, and lasted until the subject pressed a button indicating end of trial. All test fields were observed for at least 1 minute.

MAE's were measured by subjective strength on a scale of 0 to 10, with 10 representing vivid motion indistinguishable from real motion, and 0 indicating no motion. Duration of the aftereffect was noted by having the subject report when the motion was gone. Thirdly, the direction of the MAE was noted.

2. Perceptual appearance of zig zag adapting field

At high rates of alternation (50 - 200 msec per motion interval, 10 to .25 Hz), observers report that the pattern exhibited a jittering motion with a speed and direction corresponding to the vector average of the zig and zag components. The superimposed jitter seemed to be a motion at right angles to the average direction of travel.

At lower rates of alternation where the period of one direction of motion was more than 300 msec (e.g., where the oscillation frequency ranged from about 2 to 2.5 Hz) observers report two distinct motion paths, as though the alternating zig and zag motions were temporally distinct. Between 200 and 300 msec per interval, either of the two modes of perception can be seen. This ambiguity of interpretation is analogous to a variety of ambiguities of motion, notably Johannsen's two point motion displays (Johannsen 1950) in which the observer is able to separate the vector components of complicated patterns of motion

Threshold elevation methods and MAEs are both after effects, and both are used in identifying mechanisms that might underly perceptual processes. An example is the use of threshold elevation for motion in a given direction to verify the existence of direction-specific channels in the visual system. MAEs, e.g., the waterfall illusion, have been put to similar use. At issue here is whether similar methods can be used to detect signs of mechanisms that mediate detection of changing direction of motion.

2.1. An illusion of time perception

One alternating sequence was constructed such that a random dot texture was displaced by equal distances but in two different directions. One sequence was brief (300 msec), and the pattern travelled at about 6 deg/sec; the other was twice as long (600 msec), but the pattern travelled at 3 deg/sec. With all dots correlated, (moving in the same directions), observers tended to experience the durations of each interval as equal, even though they differed by 300 msec, a ratio of 2 to 1. This *time illusion* was diminished but not entirely eliminated by lowering the degree of correlation from 100% to 50%.

3. Results: MAE's from zig zag adaptating fields

The adapting field consisted of two motion intervals equal in speed and duration, with direction changing by angles of which from 10 to 160 deg. direction was 180 deg away from the average of the two component motions. The strength of the MAE did not depend strongly upon the rate of alternation, where interval durations ranged from 50 msec (10 Hz zig zag cycle) to 1000 ms (0.5 Hz cycle). The aftereffect did not depend upon the subjective impression of the motion of the adapting field. It was the same whether the adaptation was seen as jittery motion in one direction, or as two alternating and separate motions.

3.1. Comparison with simple motion adapting fields

After 5 minutes of adaptation to a zig zag pattern, the MAE appeared to be nearly as vivid and long lasting as MAE's for simple, continuous motion at a speed equivalent to the net displacement of the stimulus pattern over time. Using 50% correlation rather than 100% correlation caused the apparent strength and duration of the MAE to diminish by about half.

3.2. Apparent Speed of the Aftereffect

As with linear motion adapting fields, the perceived speed of the MAE from zig zag motions is constant and slow in relation to the motion of the adapting field. Only the direction of the aftereffect and its duration and vividness were affected by the properties of the adapting field.

Subjects typically judged the speed of the MAE to be approximately the same as a pattern drifting with a speed of no more than 0.5 deg/sec. This estimate could be estimated by use of a slowly drifting random dot test field (below).

3.3. MAE's with different test fields

No MAE's were ever observed in purely random motion (uncorrelated) test fields. On test fields with very high correlation (C% > 90%) only the objectively stationary dots were seen with MAE. MAE's could be seen, however with 100% correlated test fields whose dot texture moved very slowly (.3 deg/sec) in one direction. The direction of the MAE was superimposed on the objective direction of the test field. This permitted us to obtain an index of the apparent speed of the MAE as follows: A field of dots moving steadily North at 5 deg/sec was adapted to for 5 min, producing a strong MAE, which was seen against at test field moving East (objectively) at .3 deg/sec. The result was an MAE that began SSE, then slowed slightly over 1 minute, changing direction to due East. Therefore we can estimate the MAE for this strong adapting field condition as having an apparent speed of between .3 and .6 deg/sec. This was judged by both our Ss to be subjectively similar to the speeds of the other MAEs obtained with a variety of speeds, direction changes in adapting fields.

3.4. Long zig zag periods do not cancel the MAE

3.4.1. Procedure

As described earlier, when each of the two directions of motion is presented in alternating manner with a duration of from 200 to 300 ms per direction, the resulting perception is bistable in character, that is, it can be seen as a jittery motion switch from one diagonal direction to another in rapid sequence, or it can be seen as a unidirectional motion with a side-to-side jitter added to it. In this experiment we employed 1000 msec per direction (0.5 Hz zig zag), so that there was a clear long-term motion in one direction that alternated with an equally clear motion in another quite different direction.

3.4.2. **Results** The resulting MAE was judged to be as strong as that obtained with periods of less than 300 msec per direction (about 8 on a scale of 10), had about the same duration (45 - 60 sec), regardless of the presentation rate of the adapting field. The direction of the MAE was consistent across subjects and trials, and always corresponded to the direction opposite to the vector average, even in the .5 Hz case in which the vector average could never be perceived in the adapting field.

4. Variations on the zig zag adapting field

4.1. Unequal speeds and durations in zigs and zags

One question that emerged in the course of these experiments concerned the dependency of the MAE on speed, duration and direction of motion. Pilot observations suggested that at least over some range of these parameters duration and speed could not be traded off against each other. That is, increasing the duration of flow in one direction did not appear to bias the MAE away from the mean of the two directions of the zig zag adaptation stimulus. Keeping duration constant did not but varying speed of motion in one direction and not the other also seemed to have no effect. This led to the speculation that perhaps within limits, direction of motion and its speed have independent effects on the MAE.

4.1.1. Procedure

In this experiment a zig zag motion similar to that employed in the earlier experiments was used except that motion in one direction (at about 6 deg/sec) had a duration of only 300 ms while motion in the other direction was twice as long (600 msec), and at half the speed. The two directions differed from each other by 45 deg. In both intervals 100% of the dots were correlated. In this first case, the product of speed and duration is constant for each direction of motion.

In a second condition intervals of the same speed were used, but with one motion lesting 300 msec and the other 600 msec.

In a third condition the two directions of motion had equal durations of 300 msec but differed in direction (45 deg, as in the other conditions) and speed (3 and 6 deg/sec, respectively). Finally, one direction of motion was maintained for 300 msec, but instead of presenting motion in the other direction, the flow suddenly stopped, or it lasted for less than 100 msec and was perceived as a near stop.

4.1.2. Results

Where the duration of motion differed in the two intervals and the speed also differed so that the products of speed and duration were the same, for two subjects MAEs were much weaker than for the equal speed and duration zig zag stimuli. However, a third subject estimated an equally strong MAE, and its direction was unaffected by differences in either speed or duration. Direction of the MAE was somewhat variable for the other two subjects. In any event, neither higher speed nor longer duration by themselves seemed to exert a dominating influence on the direction of MAE.

In the condition where one of the two alternating intervals was very brief relative to the other (.e.g less than 100 msec), or when the speed in one direction was slow enough to be perceived as a sudden stop in the motion (i.e. speed less than 1 deg/sec), the MAE was greatly reduced in strength and duration. The faint MAEs were more variable in perceived direction of motion.

4.2. Zig zag motions interruped by intervals of 0 correlation

4.2.1. Procedure

Four-interval sequences were constructed by adding an extra interval of short duration between the two zig zag motion interval components. In one case, the alternating directions were interrupted by brief random motion texture ("brownian motion", 0% correlation). Viewing conditions are the same as described above, with 5 minute adaptation periods.

4.2.2. Results

The following observations pertain to 3 repetitions of each type of adapting field for two different subjects.

One direction of motion, for example vertical (90 deg), with 100% correlation and with dots moving at 3.5 deg/sec for 500 msec, followed by a 100 msec field of 0 correlation followed by another direction of motion, horizontal (0 deg), with 100% correlation, at 3.5 deg/sec for 500 msec, followed by another 100 msec field of 0 correlation.

The MAE lasted 30 sec, moving slowly (about 0.5 deg/sec) in the direction approximately 225 deg, The subjective rating of the vividness of the MAE was about 4 on the scale of 1 to 10.

In the following set of observations the duration of the brownian motion intervals was varied on each trial. The results are summarized as follows: (D= duration of brownian motion).

for D = 0 msec --- MAE is average of directions of two components
duration= 45 - 60 sec, rated strength @ 8

for D = 20 msec --- no diminution of MAE
duration= 45 - 60 sec, rated strength @ 8

for D = 100 msec --- weaker MAE's, less consistency of direction
duration= 20 - 30 sec, rated strength @ 4

for D = 500 msec --- MAE is cancelled completely

4.2.3. Conclusions

At 500 msec ISI, the subject observes equal alternating intervals of 100% correlatred and 0% correlated motion. Yet, the MAE is much weaker than corresponding MAE for two-interval zig zags with 50% correlation, which has a roughly similar effect as the 100 msec ISI in the present condition. It seems that total number and duration of dots in motion averaged across frames is not a good predictor of MAE.

4.3. *Intervening intervals with static patterns*

4.3.1. Procedure

Four-frame motion sequences were displayed, as above, except that the zig zag motion intervals was followed by a duration in which the random dot pattern remained static, rather than breaking up into 0 correlation brownian motion. In these stopped motion sequences, a static interval follows each of the component zig zag intervals.

4.3.2. Results

In two-interval zig zag stimuli, the motion is interpreted as a "jerky" sideways motion superimposed on a single direction of travel. The jerkiness and the motion are seen as orthogonal to one another. In the stopped motion displays, however sudden changes in speed occur, not orthogonal to, but along the common vector average direction of motion for the zig zag components.

Stopping between frames, even for 50 msec, and even in the single direction case, eliminates the MAE completely. For four-frame sequences, where zig zag components are separated in time by brief (100 msec) static intervals, the MAE was never observed by any of 4 subjects tested so far.

4.3.3. Conclusions

In the two conditions above 100 msec of stationary texture interposed between 500 msec motion frames is much more effective in cancelling the MAE than stimuli with longer (up to 500 msec) durations of brownian motion intervals interposed between motion components.

While we have no explanation for this effect of intervening static displays, the decceleration which occurs whenever a static display is abruptly introduced may play a role. This, however, requires further study.

5. Circulatory Motion

We add this section for the sake of completeness, even though it describes an essentially negative result. It is well known that the waterfall illusion produces a strong MAE, as does the Plateau Spiral. The latter involves a rotating stimulus, but the direction of the after effect is radial and not rotatory. In view of the fact that circular motion is perceptible, and that it involves continuing changes in direction, hypothesized that long term viewing of circular motion would produce a circulatory MAE. Toward this end we had the random dots move in a circular path with 100% correlation and two of us viewed this pattern for various periods of time, some longer than 5 minutes. Afterwards we viewed a static random dot pattern of lower luminance. In no case could either of us discern any after effect at all. Therefore, we rejected our initial hypothesis and concluded that changing direction per se does not produce an after effect of its own.

6. Discussion: MAE and Motion Detection Models

Perhaps the simplest class of models for the MAE involves Reichardt type detectors, broadly tuned to velocity (Braddick, 1980, Nakayama, 1986). Each component of motion causes activity in a subset of these detectors. During the test condition, when no motion is present in the display, the detectors tuned to respond to all other directions of motion exhibit a greater degree of spontaneous activity than do those that had become adapted. This results in a net flow in the direction opposite to that present during adaptation. When two different directions of motion are present in a given trial, as in the zig zag stimulus, the detectors must be so broadly tuned that the two directions of motion affect a common subset of them. It is adaptation of this common subset that leads to perception of a unidirectional after effect, even though two different directions were present in the adapting stimulus. Furthermore, the directional tuning of the detectors must be very broad indeed, as a median direction MAE will occur even when the two alternating directions of motion are as far apart as 130 deg.

It is not at all clear that the results we have obtained are consistent with the after effect being a vector sum or average of the two velocities. The reason for this is rather straightforward. Within constraints, the magnitude of the after effect is independent of the speed of the adapting stimulus. *Rather, it is affected* by the duration of exposure to each "leg" of a zig zag stimulus. Since velocity is a vector defining both speed and direction, and since direction alone seems to determine the direction of the MAE, it seems likely that direction of motion per se is the predominant parameter determining the MAE. Any appreciable retinal flow at all in one direction is sufficient to produce an MAE. With extremely short exposure intervals there is less retinal flow, and, consequently, less time of exposure to motion. This reduces the MAE, at least for the shorter exposure times we used. This did not always result in a bias in direction of the MAE toward the direction opposite to that of the leg of longer duration but led to inconsistent results instead. This may have occurred because a very short interruption of motion in one direction with random motion or with a stopped display tends to inhibit the MAE. Again, the possible role of abruptness of change in velocity needs additional exploration. Finally, the lack of an MAE for circulatory motion is strong evidence that there are no neurons specially tuned to respond to changes in visual direction.

Recent investigations have begun to focus on the means by which simple motion detection mechanisms combine to allow more complex interpretations of complex and natural motion (Sperling & van Santen, 1984; Watson & Ahumada, 1984; Adelson & Bergen, 1985). It is clear that these more complicated networks do not exhibit the kind of adaptation typical of more primitive levels of sensory processing.

A zig zag motion with 50% correlation, and a smooth linear motion with 50% correlation each create a stronger aftereffect than a sequence of alternating frames as follows (a) linear motion with 100% correlation, 500 msec long, interrupted by (b) stationary frame with either 0 correlation, or stationary dots, lasting 100 msec. It does not appear that the adaptation that governs the aftereffect is a multiple of total time of stimulation and the amount of correlation in the stimulus.

It is tantalizing to note that in the language of vector calculus, when the vector field has the property of divergence a negative MAE can occur. However, where divergence is zero and the vector field has the property of curl, the curl is not sufficient to produce a MAE, even though the circulatory motion is visible. Hence, perceiving changes of direction occurs, but it is evidently a higher order process than that involved in perceiving divergence. Of course, future work will address the issue of gradients of motion and any possible selective adaptation to this property of vector fields. It is quite likely that gradients of speed will not be associated by negative gradients of the MAE since the MAE is unnaffected by rather large differences in speed. This is a topic for future research.

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