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# The movement aftereffect and a distribution-shift model for coding the direction of visual movement

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**Abstract.** At present the only widely accepted explanation for the movement aftereffect is Sutherland's so-called ratio model, which states that motion is coded by taking the ratio between the outputs of detectors tuned to opposite directions. However, as yet there have been few attempts to derive predictions from the model in the context of movement aftereffects and test them experimentally. This paper reports experiments which attempt to determine whether such a simple model is sufficient, or requires additional assumptions which recast it in a form more akin to the distribution-shift models used in other domains (which assume comparisons between outputs in the whole population of direction detectors, rather than just those tuned to opposite directions). These experiments examined the interactive effects of two simultaneous directions on subsequent aftereffect durations and directions. The results obtained are difficult to explain in terms of a simple ratio model but can be incorporated into a more complex distribution-shift type model.

## 1 Introduction

The movement aftereffect (MAE) is conventionally defined as follows. After prolonged exposure to a stimulus moving in one direction, a subsequently viewed stationary stimulus appears to move in the opposite direction. The phenomenon has a very long recorded history (dating back at least to Aristotle) and is a robust one, lending itself readily to a wide range of experimental manipulations. Not surprisingly, it has been a primary consideration in attempts to describe the way in which the visual system codes direction of movement. (The MAE has also been applied to problems of *velocity* coding in the visual system, but the models to be presented here are relevant only to the way in which the system codes direction with velocity held constant.) Only one widely accepted model exists to explain the MAE, the so-called ratio model. According to this model, first proposed by Sutherland (1961), the direction in which a stimulus is seen to move depends upon the ratio of the firing rates of motion detectors tuned to opposite directions. Firing rates in detectors tuned to one direction must exceed firing rates in detectors tuned to the opposite direction by a certain minimum ratio before movement in that direction is seen. Thus after unidirectional adaptation, one set of detectors will be suffering reduced levels of firing, allowing detectors tuned to the opposite direction to exceed the minimum ratio even in the presence of a stationary stimulus, and thus produce an erroneous motion signal. [See Moulden and Mather (1978) for a formal description of the model; the essentials of the model are preserved if it is couched in terms of differences rather than ratios, so strict ratio comparisons are not crucial.]

Paradoxically, although the ratio model has gained widespread acceptance as a working hypothesis, it has not yet been tested empirically in the context of MAEs, not least because there is a lack of plausible alternatives against which it can be pitted in an experiment. Its widespread acceptance is thus largely based on its intuitive appeal and powerful simplicity. However, recent reports of shifts in apparent direction when two moving stimulus fields are presented either successively (Levinson and Sekuler 1976), or simultaneously (Marshak and Sekuler 1979; Mather and Moulden 1980) have implicated another model for direction perception. Levinson

Levinson and Sekuler (1976, p 780) suggested that

“Perceived direction may therefore depend upon the response distribution among direction-selective neurons, and an adaptation-induced shift in perceived direction may be caused by alteration of this distribution”,

while Marshak and Sekuler (1979, p 1400) stated,

“Several lines of psychophysical evidence indicate that human motion perception involves the product of activity in an array of mechanisms each sensitive to a different but partially overlapping range of directions.”

The aims of the present paper are: firstly, to provide a more explicit statement of the ‘distribution-of-activity’ model than those offered by Levinson and Sekuler (1976) and Marshak and Sekuler (1979) in the above extracts; and, secondly, to determine empirically whether such a model can accommodate the MAE as well as shifts in apparent direction, and therefore replace the ratio model (as suggested by Mather and Moulden 1980).

The ‘distribution-of-activity’ model as presented here deals separately with the two problems of direction perception—detecting the presence of a moving stimulus, and assigning a direction to that movement. Detection seems to involve a ratio-like process (Moulden and Mather 1978) which can be conceptualised as a comparison between a target signal (provided by detectors sensitive to the stimulus present) and some general level of background noise (provided by activity in the remainder of the population). Threshold for the target signal is attained when the signal-to-noise (S/N) ratio reaches some critical value, which remains constant.

To deal with the assignment of perceived direction, a notion can be employed which has already proved useful in the orientation domain (see e.g. Coltheart 1971); perceived direction is given by taking some weighted average of all direction detectors whose outputs exceed the critical S/N ratio. The weighted average should also be correlated with the magnitude or strength of the suprathreshold signal. This may be made apparent by identifying the weighted average as the ‘centre of gravity’ of the distribution [mathematically the two concepts are identical, see Bajpai et al (1973, p 2:84)]: the stronger the input stimulus (in terms of contrast or perhaps velocity) the more ‘lopsided’ will be the accompanying distribution of activity (owing to greater levels of firing in the detectors sensitive to the stimulus); hence the further will the distribution’s centre of gravity shift from its location in the absence of stimulation.

This model could account for the MAE as follows: adaptation to a particular direction will desensitise a large section of the population. So, in the presence of a stationary stimulus the distribution of activity will be depressed in the region of the adapting direction. The weighted average of this adapted distribution would yield a signal corresponding to a direction opposite to the adapting direction. For a MAE to be present, it must be assumed that the adaptation-induced reduction in ‘noise’ level in the presence of the stationary stimulus is sufficient to allow unadapted detectors to exceed the critical S/N ratio, just as the ratio model must assume a sufficient reduction in the activity of the adapted detector of the opponent process pair. The proposed distribution-of-activity model can thus account for the MAE as convincingly as the ratio model—which is not surprising since the former is simply a more detailed extension of the latter.

The question now is: which of these models presents the more appropriate description of the way in which the visual system codes movement when signalling MAEs? The two models are similar in that they both involve ratio-like comparisons across the outputs of direction-specific (DS) detectors. However, they differ crucially in respect of the detectors which are assumed to participate in the comparisons. On the one hand, the ratio model proposes that only *oppositely tuned* detectors are

involved; on the other hand, the distribution-of-activity model proposes that detectors tuned to *all* stimulus directions are involved. This difference between the two theories will be used to attempt a decisive distinction between them. A new paradigm will be employed which involves adapting the subject not to one direction of motion, in the classical way, but rather to *two* directions presented simultaneously. The different integrative processes proposed by the two models generate contrasting predictions about changes in resultant MAEs with changes in the angular separation between the two directions.

Both models propose that individual stimulus directions are integrated or compared in one way or another to generate a resultant motion signal. The different integrative processes can be used to convert the MAEs generated by each direction presented individually into the integrated MAEs generated by the two directions when presented simultaneously, thus yielding testable predictions. Such predictions on integrated MAEs should be derived from data on the known effects of adapting to each stimulus direction when presented individually. Strangely, although data on many aspects of the MAE are plentiful, there are none available on MAE magnitude as a function of stimulus direction. The one-dimensional gratings conventionally used in modern research obviously confound the effects of stimulus direction with those of orientation, so the three experiments reported here used isotropic random-dot patterns to isolate stimulus direction from stimulus orientation. Experiment 1 measured MAE duration as a function of adapting direction, which could vary from vertically upwards to vertically downwards.

## 2 Experiment 1

### 2.1 Methods

2.1.2 *Subjects.* Four subjects took part in the experiment, two males and two females. All were members of Reading University, aged between twenty-one and thirty-three. None of them were aware of the experimental predictions.

2.1.1 *Stimuli and apparatus.* The stimuli used in all three experiments were computer-generated fields of random dynamic visual noise, which had the appearance of dots 'twinkling' against a dark background. Each dot had a lifetime of 288 ms before being replaced by another dot in a different, randomly plotted, location. Onsets of individual dots were staggered so that the display was in a state of constant flux. The field of dots could be given an overall direction of drift, either upwards or downwards, by changing the position of each dot in a vertical direction by a certain amount during its lifetime. Fields of dynamic noise have several distinct advantages over the vertical gratings conventionally used: they contain no orientation information orthogonal to any direction of motion, thus the possibility is avoided that any specificity in measured effects is due to the intrusion of orientation specificity rather than direction specificity; and their dynamism means that MAEs viewed on such noise fields possess no paradoxical qualities resulting from the presence of permanent 'landmarks' undergoing no change in location. Nor can the fields generate intrusive afterimages when left without an overall direction of drift.

The noise field was viewed monocularly through a Dove prism, thus an adapting stimulus of variable direction was provided. A circular aperture restricted the field to a diameter of 4.2 deg of visual angle and allowed approximately thirty dots to be visible, each having a luminance of 10.2 cd m<sup>-2</sup>. The velocity of the dots when moving was 2.5 deg s<sup>-1</sup>. A small fixation lamp and a homogeneously illuminated background (0.88 cd m<sup>-2</sup>, also 4.2 deg of visual angle in diameter) were viewed via narrow-gauge Perspex acting as a half-silvered mirror.

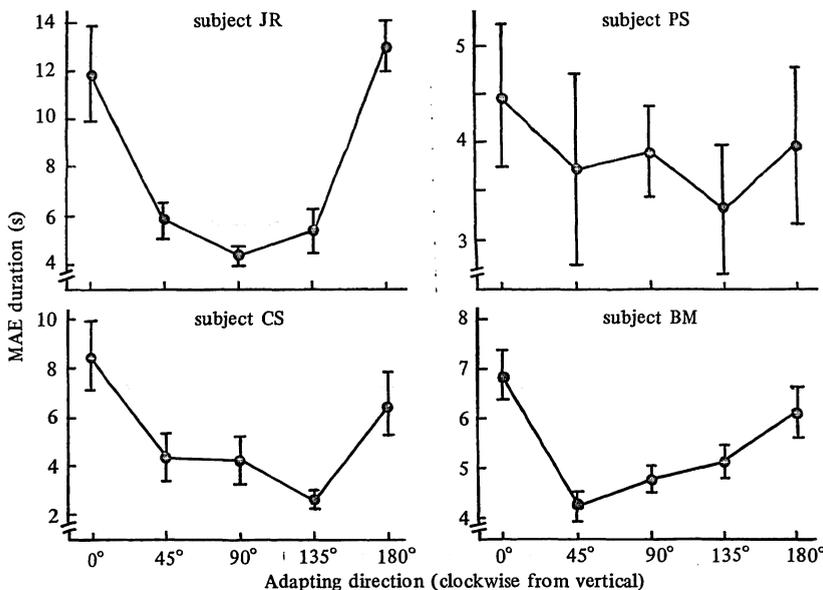
### 2.1.3 Design and procedure

The independent variable was the direction of the adapting stimulus. For the four subjects there were five possible adapting directions, namely 0, 45, 90, 135, and 180° clockwise from vertically upwards.

The dependent variable was the duration of the resultant MAE on the stationary test field. Each trial consisted of two phases; the first consisted of an 80 s exposure to the adapting direction, and in the second phase the field was made stationary (and doubled in dot density to ensure comparability with later experiments). A timer-counter started automatically at the end of the 80 s adaptation period. Subjects were instructed to press a button, which stopped the clock, as soon as any motion in the test field ceased. Three such trials were performed in succession for each condition, separated by a break of 1–2 s (while the experimenter recorded the time elapsed on the counter). The total of five conditions was completed in a single session. Their order of presentation was randomised, and a break of at least 80 s separated successive conditions. This whole procedure was then repeated for each subject in a second session, in which a different random order of conditions was used. Each session began with an unrecorded practice condition comprising three trials. Thus each subject provided a total of six duration estimations in each condition, sufficient to allow confident location of the data point for each condition. However, there was a total of only five possible adapting directions, spanning 180°. Thus a slightly different design was also used, on just one subject; only three duration estimations were made for each condition, but there was a total of ten possible adapting directions (0, 20, 40, 60, 80, 100, 120, 140, 160, and 180° clockwise from vertically upwards). The ten conditions were done in two sessions and in random order. Data from this second design could determine whether extrapolation between the five data points of the first design was justified.

### 2.2 Results

Figure 1 shows the mean of each subject's settings in each condition ( $\pm 1$  S.E.). As can be seen, every subject shows a similar change in MAE duration as a function of adapting direction. Longest aftereffects occurred for adapting stimuli moving



**Figure 1.** MAE duration as a function of adapting direction: four subjects. Vertical bars represent 1 S.E. about each mean.

vertically, either upwards or downwards, while the shortest aftereffects are produced by adapting stimuli moving horizontally rightwards. Aftereffects from oblique adapting stimuli are usually intermediate. Data for the one subject who performed in more conditions but supplied fewer observations for each data point are shown in figure 2. Exactly the same trend is shown in this data as is shown in the data of figure 1. It should be said that the subject who provided the data in figure 2 (BM) also provided one of the functions in figure 1. There is a difference in the overall level of the durations shown in each. The two sets of data were gathered in sessions several weeks apart: it is well known (see Thompson 1976) that small shifts in criterion result in large shifts in duration, and the shift in level observed here is probably attributable to this effect.

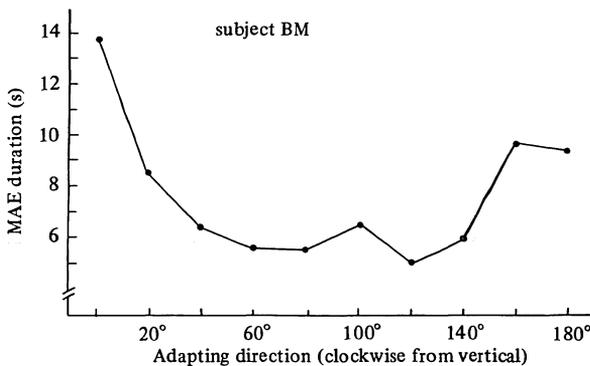


Figure 2. MAE duration as a function of adapting direction: one subject.

### 2.3 Discussion

The results show that MAE durations from different directions of adaptation vary in a 'U'-shaped function as one progresses from vertically upwards to vertically downwards. Other data on possible anisotropies in human DS mechanisms are scarce indeed, but there are at least two sources: Scott et al (1966) reported that centrifugally moving MAEs are faster and last longer than centripetally moving MAEs, while McColgin (1960) reported that velocity thresholds measured with the use of a small (1.75 deg) luminous line were slightly lower for vertical than for horizontal displacement. Data from Richards (1971) are inadmissible: to produce different directions he masked a rotating spiral to leave a bow-tie shaped aperture and varied the orientation of the long axis of the aperture. He thus confounded changes in sensitivity to particular directions with the changes in sensitivity to *any* direction as a function of retinal location which are known to exist (see McColgin 1960).

One possible explanation of the shorter MAEs for horizontal adapting directions could be that DS detectors tuned to such directions are less sensitive than those tuned to other directions, either intrinsically or (more plausibly) because the visual environment holds them in a state of chronic insensitivity. The patterns of visual flow normally experienced as the observer moves through the world (motion parallax, etc) may serve to suppress detectors tuned to horizontal directions more than detectors tuned to, say, vertical directions. Scott et al (1966) favour such an explanation for their obtained difference between centrifugally and centripetally moving MAEs (centrifugal adaptation is less effective than centripetal because it is more frequent in the environment, so producing weaker centripetally moving MAEs). They found that very prolonged adaptation to either direction in the laboratory eliminated the difference. Physiological explanations based upon asymmetries in detector bandwidths or cell numbers are less convincing because they cannot be translated into variations in MAE duration without ad hoc assumptions. [MAE

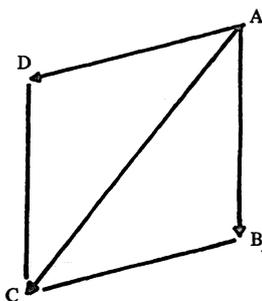
duration is assumed to reflect length of time to recover sensitivity, and therefore depth of desensitisation (see Sekuler and Pantle 1967; Pantle 1974; Keck et al 1976; Sekuler et al 1976).]

However, the question of major interest here is not the precise explanation of the mechanism underlying these data, but rather that of how the visual system integrates across the outputs of its DS detectors to produce motion signals; in operational terms, how it integrates the effects of two simultaneously presented adapting directions to produce a resultant MAE. Let us now consider how the direction of the resultant MAE might vary as one alters the angular difference between the adapting directions; the data from experiment 1 can be used to generate predictions derived from the two models described earlier.

The ratio model predicts two phases in MAE direction: the first phase is confined to differences between the adapting directions small enough to be within one bandwidth of sensitivity—since the adapting directions are detected by a single set of detectors, there should be one MAE direction corresponding to the direction given by their oppositely tuned partners, namely the direction opposite that which bisects the two adapting directions. The second phase covers all differences between adapting directions greater than one bandwidth of sensitivity—there should, in principle, be *two* equally likely MAE directions present, because the adapting directions are disparate enough to stimulate different opponent-process pairs (for example, when they are 90° apart). There are always two possible pairs of detectors suffering an imbalance, and the ratio model makes no provision for integration across directions other than strictly opposite, so the two possible MAE directions should be present independently, perhaps simultaneously or perhaps in alternation. Vertically moving adapting stimuli are stronger, according to experiment 1, so vertically moving MAEs may be more frequent.

These predictions from the ratio model can be contrasted with the predictions from the distribution-of-activity model. It was proposed earlier that perceived direction is extracted by taking the weighted average of all detectors exceeding the critical S/N ratio. So, according to this proposition, the direction of a MAE produced by adapting to one direction is the weighted average of all those detectors which are firing above the S/N threshold. Hence, if a second adapting direction is added, and therefore a second MAE, the direction and duration of the resultant combined MAE can be derived by taking the weighted average of the two individual MAEs (recall the statement earlier that the weighted average should be correlated with the magnitude of the movement signal).

Experiment 1 furnished data on the expected strengths of the two individual MAEs, so with the use of simple trigonometry they can be combined into a resultant combined MAE. Thus, in figure 3, line AB represents the direction and duration of the MAE produced by adaption to a stimulus moving vertically



$$AC^2 = BC^2 + AB^2 - 2BC \times AB \cos \angle ABC; \quad (1)$$

$$\frac{BC}{AC} = \frac{\sin \angle BAC}{\sin \angle ABC}$$

therefore

$$\sin \angle BAC = \frac{BC \times \sin \angle ABC}{AC} \quad (2)$$

Figure 3. Equations used to derive the predictions from the distribution-of-activity model. See text for details.

upwards, while line AD represents the direction and duration of the MAE produced by adaption to a stimulus which may be moving in any direction from upwards through to downwards (the MAE shown here would be produced by a stimulus moving at 75° clockwise). With the use of equation (2) the direction of the combined MAE ( $\angle$  BAC) can be predicted. Applying equation (2) to the data obtained in experiment 1 yields the function shown in figure 4 (in fact the data from only three of the subjects were used, because the fourth subject did not take part in experiment 2). The solid line represents the predicted direction while the broken line follows the angle opposite that which bisects the two adapting directions (it bisects the two individual MAEs). Note that the predicted direction deviates towards a more vertically downwards direction than the direction bisecting the two individual MAE directions, reflecting the prepotency of vertically moving MAEs found in experiment 1.

Thus the ratio and distribution models make different predictions about the direction of the MAEs resulting from adaptation to two directions. The ratio model predicts two phases in MAE direction as a function of the angular separation of the adapting directions, while the distribution model predicts that MAE direction will change continuously, conforming to the directions shown in figure 4.

Experiment 2 was designed to attempt a distinction between these alternative predictions. It involved adapting simultaneously to two directions and then determining the direction of any resultant MAEs.

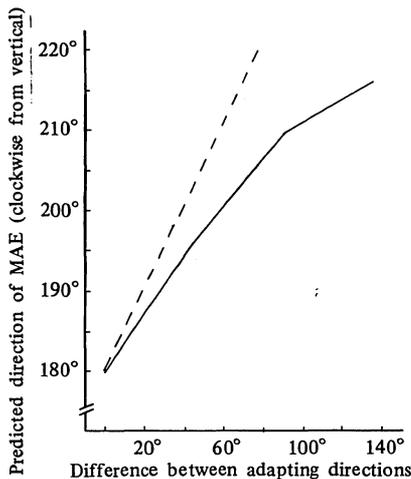


Figure 4. MAE direction as a function of the angular difference between two simultaneously presented adapting directions: predictions from experiment 1 (solid line).

### 3 Experiment 2

#### 3.1 Methods

3.1.1 *Subjects.* Nine subjects took part in this experiment. All were members of Reading University, aged between twenty and thirty-three years. All but one were not aware of the experimental predictions.

3.1.2 *Stimuli and apparatus.* Exactly the same stimuli and apparatus were used as in experiment 1, with two modifications. Firstly, a second adapting field was added (viewed via a beam-splitter) identical to the single field used in experiment 1 except that it only moved upwards. The two fields were viewed simultaneously. Secondly, adjustable luminous bars were presented simultaneously with the test field (superimposed via a half-silvered mirror) thus allowing determination of MAE directions.

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The bars consisted of two small (0.74 deg long) line segments which skirted the perimeter of the test field and fell along a diameter passing through the central fixation spot. They were in fact slots cut in a back-illuminated metal disc which could be edge-rotated by means of a servo-controlled motor (operated by the subject). The bars had a luminance of  $1.8 \text{ cd m}^{-2}$ .

### 3.1.3 *Design and procedure*

The independent variable was the angular difference between the two adapting directions. One adapting direction always moved upwards. The other could be set by the experimenter to move in any one of ten different directions, namely 0, 20, 40, 60, 80, 100, 120, 140, 160, and 180° clockwise from upwards. It should be stressed that these two adapting directions were always clearly distinguishable. [Resolution only deteriorates when the directions differ by less than about 15° (see Mather and Moulden 1980).]

The dependent variable was the direction of any resultant MAEs. In a particular trial, subjects were first exposed to the composite adapting stimulus for 80 s. This adapting stimulus then alternated continuously with the test stimulus (composed of the same two dot fields, but made stationary). The test stimulus was presented for periods of 1.3 s while the adapting stimulus was presented for periods of 4.5 s. In the presence of the test stimulus, the bars skirting the perimeter of the test field were illuminated, and the subject was required to align them with the axis of any illusory movement in the test field. Subjects also gave verbal descriptions of the MAE direction, because the bar settings alone are ambiguous (corresponding to two possible directions, 180° apart) and the experimenter wished to know whether one or two MAE directions were visible. The continuous alternation of adapting and test stimuli proceeded until subjects were satisfied with the position of the bars. There was then a pause of 1–2 s while the computer recorded the voltage through a potentiometer linked to the adjustable bars (and the position of the bars was offset), and then the alternation recommenced. The procedure was repeated until subjects had made three settings in a condition. The ten conditions were performed in a single session, and a break of at least 1 min separated successive conditions. The order of these conditions was pseudo-random; over the nine subjects, each condition occurred at least once in each possible order position (in other words, a  $9 \times 9$  randomised Latin square, with the tenth condition intermingled). An unrecorded practice condition was given at the start of the session.

### 3.2 *Results*

Subjects only ever reported a single MAE direction, which apparently remained the same over the three settings made for each condition. The group means ( $\pm 1 \text{ SE}$ ) in each condition are shown graphically in figure 5 (solid line). The individual points in the 160° and 180° conditions of figure 5 are data points for the individual subjects reporting MAEs in those conditions (five subjects reported MAEs in the 160° condition, and three subjects reported MAEs in the 180° condition).

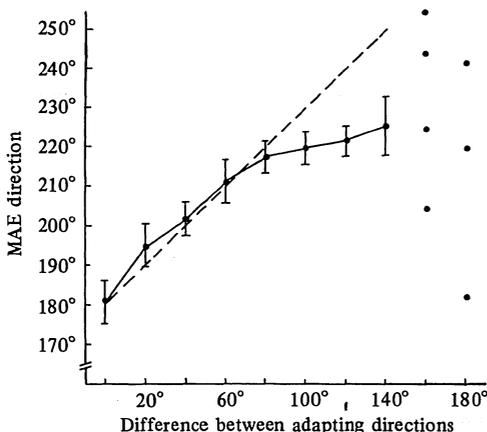
The directions predicted by the distribution-of-activity model derived from experiment 1 are compared with the results of experiment 2 in figure 6 (data from the same three subjects in each experiment). The dashed function represents the predictions and the continuous function represents the obtained data. As can be seen, they are in fairly close agreement.

### 3.3 *Discussion*

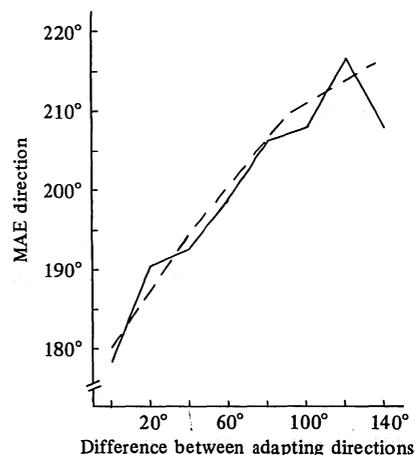
The results give unequivocal support to the predictions of the distribution-of-activity model. There is no support for the opponent-process ratio model; only one after-effect was ever reported, for example when one adapting direction moved vertically

upwards and the other moved rightwards at  $90^\circ$ , the resultant MAE moved downwards to the left, a direction intermediate between the aftereffects that would have been generated by the adapting directions when presented individually (one MAE would move downwards, and the other leftwards). This implies that the visual system *can* compare outputs across detectors other than those tuned to opposite directions, otherwise it would not be able to produce the integrated MAE. Moreover, the integration takes the form of a weighted average or vector addition.

The fact that fewer numbers of subjects reported MAEs as the adapting directions approached  $180^\circ$  opposition draws attention to a second important feature of the adapting configuration—its effects on MAE duration. The distribution-of-activity model makes specific predictions about the nature of the decline in duration as the angular difference between adapting directions increases. Equation (1) in figure 3 combines the durations of the individual aftereffects produced by separate adaptation (lines AB and AD) into the duration of the integrated aftereffect produced by simultaneous adaptation to two directions (line AC). Performing these calculations on the data obtained in experiment 1 yields the upper dashed duration function in figure 7. MAE duration declines monotonically as the difference between the two directions increases, because the length of the vector sum decreases. However, such a simple vector addition of the two MAEs implies that there is always perfect summation between the effects of the two adapting stimuli (i.e. there is always twice as much desensitisation from adapting to two directions as from adapting to one direction). Such an assumption seems plausible as long as the two adapting directions are close enough in direction to fall within one bandwidth of sensitivity. One might expect greater activity, and subsequent desensitisation, in a detector being stimulated by two directions at once than in a detector being stimulated by just one direction. However, as the difference between the two directions increases, such summation becomes unlikely; the two directions are far enough apart to affect different sets of detectors. In this case one adapting direction would not contribute to the desensitisation generated by the other simultaneously present direction, so there would be zero summation between the two directions, depicted by the lower



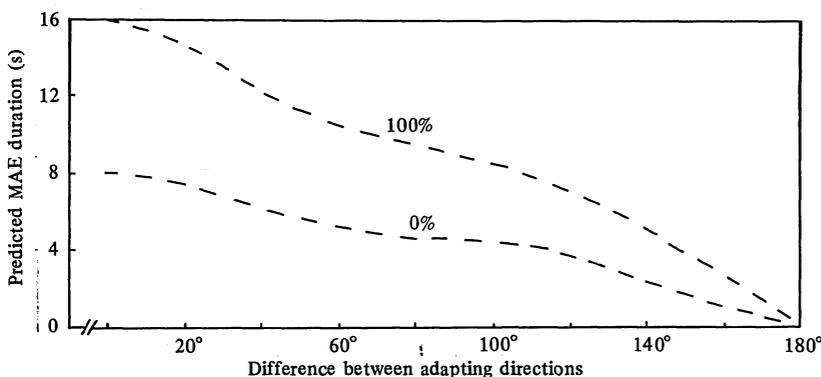
**Figure 5.** Mean MAE direction as a function of the angular difference between two simultaneously presented adapting directions. Vertical bars represent 1 S.E. about each mean. Individual points in the  $160^\circ$  and  $180^\circ$  conditions are data points for the individual subjects reporting MAEs in those conditions.



**Figure 6.** MAE directions: predictions from experiment 1 (dashed line) compared with results from experiment 2 (solid line), three subjects only.

dashed line in figure 7. The nature of the decline under zero summation is the same as that under the assumption of perfect summation, except that for each angular difference between adapting stimuli the predicted duration is halved (mathematically, the zero summation function is the weighted average of the two individual MAEs, rather than the vector sum which is represented by perfect summation). The most likely result is a combination: when the two adapting directions are within a single bandwidth of sensitivity, their adaptive effects may summate in accordance with the vector-addition prediction, while when the two directions are beyond this bandwidth they may act independently (in that one adapting direction does not 'add' any adaptation to the MAE generated by the other adapting direction) in accordance with the zero-summation prediction.

Although the ratio model has already been discredited by the results of experiment 2, its predictions on MAE duration will be described briefly here for comparison with the predictions of the distribution-of-activity model. Consider how the effects of the two adapting directions will be distributed amongst the various oppositional pairs of detectors as their angular difference increases from identity ( $0^\circ$ ) to opposition ( $180^\circ$ ). For angular differences small enough to allow the two directions to stimulate the *same* set of detectors, the adaptive effects will summate to a greater or lesser degree (as suggested earlier); as the angular difference increases, the summation (and therefore MAE duration) will decline. Moving to the other extreme, when the angular difference is great enough for the directions to affect oppositely tuned detectors, their adaptive effects will begin to cancel out; the cancellation will be virtually complete when the directions are exactly opposite each other ( $180^\circ$ ). However, there should be a range of differences between these extremes when the directions are too far apart to stimulate the same DS detectors, but not far enough apart to stimulate oppositely tuned detectors. The two directions cannot interact because they must be affecting different oppositional pairs of detectors, so there will be no change in MAE duration. The breadth of this 'independence' range depends in part upon the tuning bandwidth of the detectors (the adapting directions can only summate when they are within one bandwidth, and cancel out when they are within the bandwidths of oppositely tuned detectors), but also upon: (i) the degree to which the adaptive effects of the two inducing directions summate when they are impinging on the same set of detectors; and (ii) the rate of decline in sensitivity to directions other than optimal. There may be less than perfect summation of adaptive effects, and/or the decline in sensitivity may be negatively accelerating, both of which would widen the 'independence' range (at some angular differences, detectors marginally affected by just one direction rather than weakly affected by



**Figure 7.** MAE duration as a function of the angular difference between two simultaneously presented adapting directions: predictions from experiment 1.

the two directions will produce the longest MAEs). The limiting case in which there is no 'independence' zone but a continuous decline in duration would only occur if the tuning bandwidth was  $180^\circ$  wide, *and* if the detectors retained considerable sensitivity to directions close to the edge of their tuning curve. However, there is no evidence (either psychophysical or physiological) that motion detectors are so widely tuned, and sensitivity functions in the physiological literature are often Gaussian-shaped, so the detectors retain little sensitivity to stimuli near the edge of the tuning curve. The direction-shift results reported earlier are assumed to reflect bandwidths of inhibition (e.g. Marshak and Sekuler 1979), and do not necessarily reflect the bandwidths of the mechanism underlying adaptation in MAEs. A more complete description of the predictions of the ratio model can be found in Mather (1979).

To summarise, then, the ratio model predicts a three-branched duration function: for smaller differences between the adapting directions duration will decline (decreasing summation); for intermediate differences, duration will remain constant (independence); and, for large differences approaching opposition, duration will decline again (increasing cancellation). The distribution-of-activity model predicted a monotonic decline in duration (within precisely defined limits). In experiment 3, MAE *durations* were determined as a function of the angular difference between two adapting directions.

## 4 Experiment 3

### 4.1 Methods

4.1.1 *Subjects*. Four subjects took part in the experiment, two males and two females. All were members of Reading University, aged between twenty-two and thirty-three. All of them were unaware of the experimental predictions.

4.1.2 *Apparatus*. Exactly the same stimuli and apparatus were used as in experiment 2, except that luminous bars were not employed. Instead, a timer-counter started automatically at the end of the adapting period (to be stopped by the subject to indicate the cessation of the MAE).

4.1.3 *Design and procedure*. The independent variable was the difference in direction between the two simultaneously presented adapting fields. One adapting field always moved vertically upwards, while the other adapting field could be set by the experimenter to move in any one of ten different directions, namely 0, 20, 40, 60, 80, 100, 120, 140, 160, and  $180^\circ$  clockwise from vertically upwards.

The dependent variable was the duration of any subsequent MAE. Each trial consisted of two phases; the first consisted of an 80 s exposure to the two adapting directions, and in the second phase the two fields were made stationary and a timer-counter was started automatically. Subjects were instructed to press a button which stopped the clock as soon as any motion in the test field ceased, and to declare immediately if no aftereffect motion was present at all. Three such trials were performed in succession for each condition, separated by a break of 1–2 s (while the experimenter recorded the time elapsed on the counter). There was a total of ten conditions and these were done in two sessions of five each. Assignment of conditions to each session and their order within a session were randomised. A break of at least 80 s separated successive conditions in a session, and an unrecorded practice condition was given at the start of each session.

### 4.2 Results

Each subject provided three estimates of MAE duration in each condition. Figure 8 plots both the mean of these three settings for each subject (in the small graphs) and the overall mean duration in each condition (in the large graph). From inspection

of the overall means, it appears that MAE durations decrease smoothly and monotonically as the difference between the adapting directions increases. There is no hint of any plateau in durations for intermediate direction differences. A trend analysis revealed that only the linear component of the obtained duration function reached significance, as predicted by the distribution model ( $F_{1,27} = 46.022$ ;  $p < 0.001$ ). The cubic trend predicted by the ratio model was nonsignificant ( $F_{1,27} = 0.554$ ; n.s.). 96.6% of the treatment variation was attributable to the linear component while 1.2% was attributable to the cubic component. These statistics are not affected in any important way when subject BM (who shows the clearest linear trend) is omitted from the analysis.

The predictions from the distribution-of-activity model are compared with the obtained durations in figure 9 (the same subjects took part in each experiment). The obtained durations conform well with the upper curve until a direction difference of about  $60^\circ$  is reached, and reaches the lower curve by a direction difference of about  $100^\circ$ . No significant changes in either predictions or data result from expressing durations as proportions of the maximum duration for each subject, rather than as absolute durations.

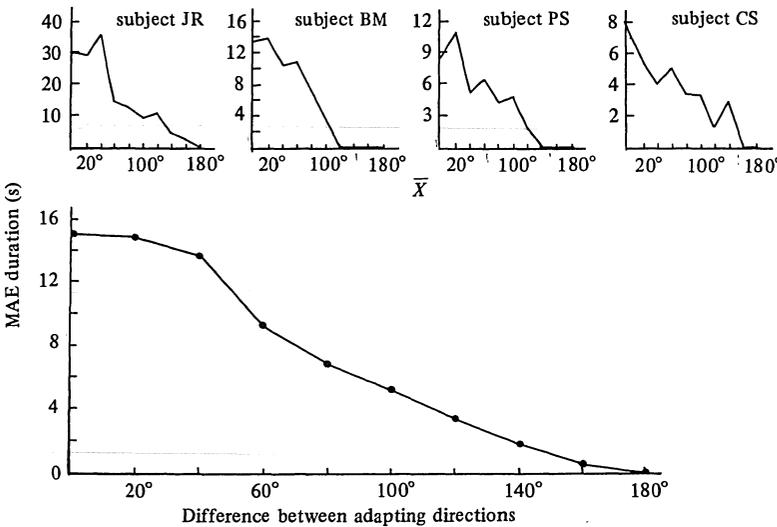


Figure 8. MAE durations as a function of the difference between two simultaneously presented adapting directions. The small graphs show the individual subject results, and the large graph shows the mean results.

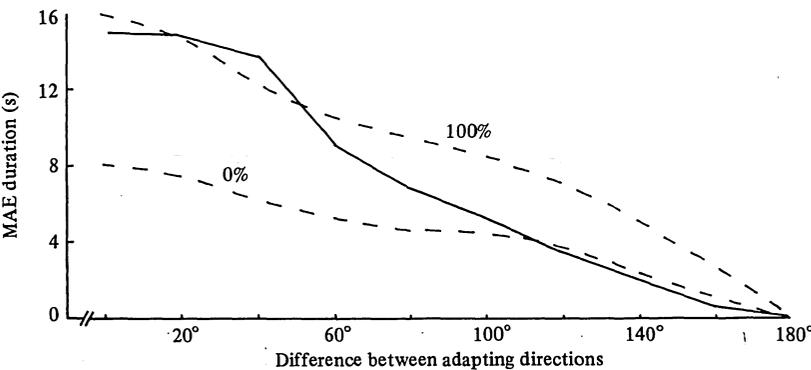


Figure 9. MAE durations: predictions from experiment 1 (dashed lines) compared with results from experiment 3 (solid lines).

### 4.3 Discussion

From the results, two conclusions appear justified:

- (i) data on MAE duration give no support at all to the predictions of the simple ratio model;
- (ii) calculations derived from the propositions of a distribution-of-activity model allow MAE durations obtained from adapting to one direction alone (in experiment 1) to predict aftereffect durations produced from adaptation to two directions simultaneously.

The obtained function moves gradually from perfect summation (upper predicted curve) to zero summation (lower predicted curve) as the angular difference between adapting directions increases. It thus seems that the adapting directions do summate in their effects to a certain extent, although this summation seems to decline rapidly as the difference between the two adapting directions increases. The two directions are less likely effectively to stimulate a *single* common set of detectors, and so each direction is less likely to add any adaptation to the aftereffect generated by the other direction. It may also be that MAE durations flatten off at small angular differences between adapting directions because there is a 'ceiling' effect (the system is already maximally adapted by one direction alone, so adding a second has little effect). But the fact that obtained durations in experiment 3 were generally double those in experiment 1 for the smallest angular differences (compare figures 1 and 8) argues against this effect as a contributing factor. In fact, the doubling implies near perfect summation at small angular differences, as seen in figure 9.

To summarise, the propositions of a distribution-of-activity model (as described here and elsewhere) enable the empirically determined durations of two individual aftereffects to be converted, with some accuracy, into both the *duration* and the *direction* of the combined aftereffect arising from simultaneous adaptation to the two inducing stimuli. The success of these transformations adds weight to the view that the distribution model specifying the rules of the transformations represents a meaningful description for the way the visual system operates in this situation.

Accordingly, it is concluded that the best available account for the MAE is a model which allows integration across a very wide range of DS detectors, rather than integration only across oppositely tuned detectors. Evidence in support of such a model is also available from experiments on shifts in apparent direction (Levinson and Sekuler 1976; Marshak and Sekuler 1979; Mather and Moulden 1980).

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