VARIABLE AND CONSTANT ERRORS OF PERCEIVED ANGLE SIZE

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Abstract

Experiments were carried out to characterise the perception of angles in terms of the acuity and constant error of comparisons of acute angle sizes. Both measures, determined by the forced choice method of constant stimululi, were found to increase linearly with stimulus angle size. Constant errors varied systematically with stimulus orientation, following the oblique-effect (Apelle, 1971), while acuities did not. The differential expansion of acute angles was found to decrease with increased stimulus duration, stabilising after about 0.5 second.

Despite the previous success of the hypothesis that perceptual expansion of acute angles is an orientation contrast effect due to lateral inhibitory interactions between channels selectively responsive to different orientations, the present observations proved inconsistent with predictions derived from this hypothesis concerning both acuities and constant errors, and temporal variation of these measures. Results of adaptation and masking experiments also failed to show meridional anisotropies of the selectivities of orientation channels, which were considered necessary assumptions for the explanation of meridional variation of perceived angular extent by the lateral inhibition hypothesis.

The discrepancy between the present results and previous observations which were consistent with the orientation contrast hypothesis was attributed to the fact that in the majority of previous studies perceived orientation was measured, not perceived angular extent The present data, therefore, do not contradict the orientation contrast model, but suggest that this contrast is not a sufficient explanation of the misperception of angular extent. As an alternative, it was proposed that variation of perceived angular extent results from meridional anaisotropies in the scaling of an orientation metric derived from the integration of outputs from orientation selective channels.

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Contents

Chapter 1. The Perception of Angle Size and Orientation

1.1 Angle Perception and the Illusions of Direction

The processes by which angles are perceived by the human visual system and the means by which they are represented have been of interest to sensory psychologists since the second half of the nineteenth century, initially because of the role which they were believed to play in the induction of the misperceptions which are found in many of the so-called geometric visual illusions. A number of studies since then have been concerned with simple angle figures in the hope of understanding and explaining how more complex angle-based figures such as the Poggendorff and Zöllner illusions give rise to distortions in perceived visual space. As early as 1866 Helmholtz (1962 pt III, p 196) was able to state that "... as a general thing acute angles, composed of smaller angles distinctly marked, seem to be relatively too large compared to obtuse or right angles not thus divided." The picture referred to (Fig. 1.1) may be interpreted in terms of the filled-space category of illusions - although the connection

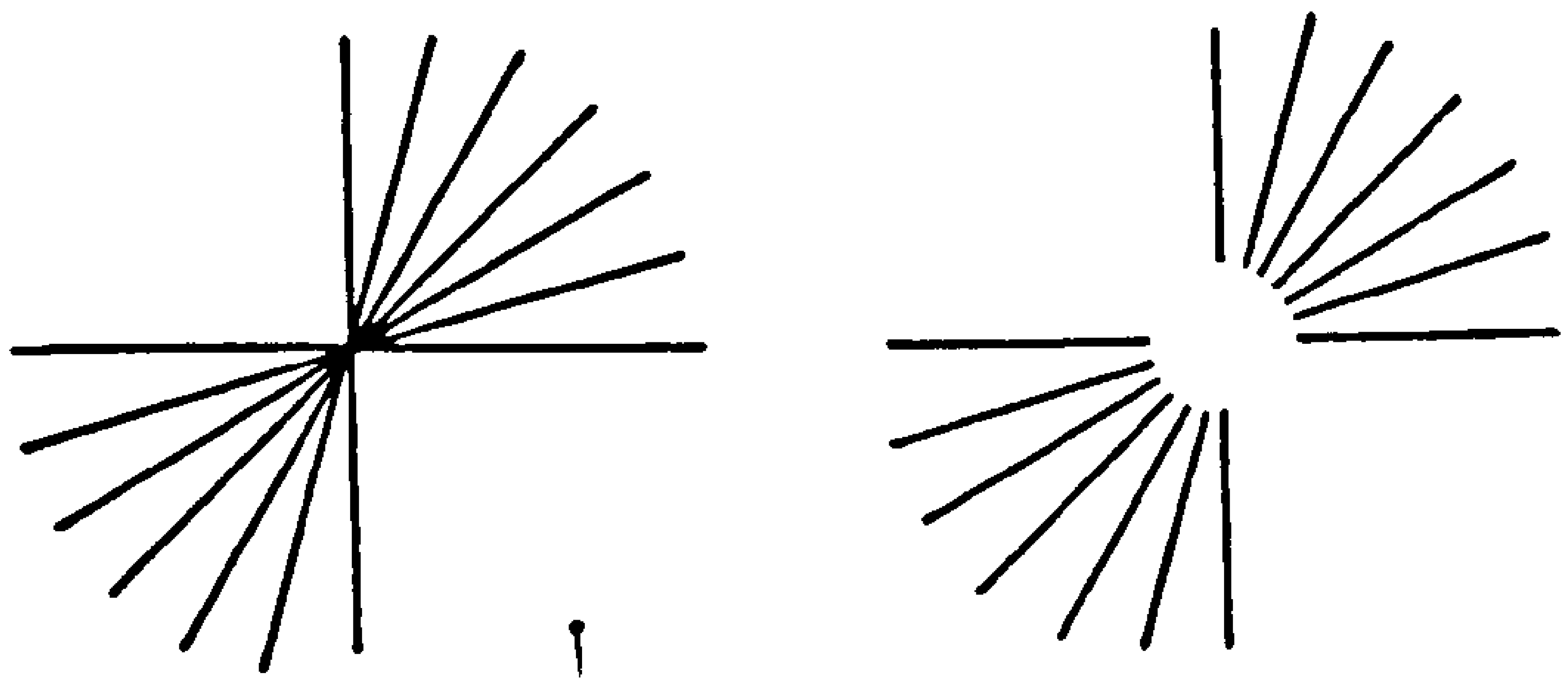


Fig 1.1 (a) Perceptual expansion of acute angles demonstrated by the apparently greater size of the top left and bottom right right angles in comparison with the top right and bottom left right angles.

(b) The angle enlargement effect does not require the physical presence of angle vertices. (Both figures after Helmholtz, 1856).

of this phenomenon with the simple expansion of acute angles is not yet evident. He continues, with reference to an earlier illustration (Fig. 1.2): "...the apparent magnification of an acute angle is such that its two sides are expanded..." This view was reaffirmed by Wundt (1902, p 137) who observed that "...acute angles are overestimated, obtuse angles are underestimated, and that the direction of the lines forming the angle varies accordingly..."

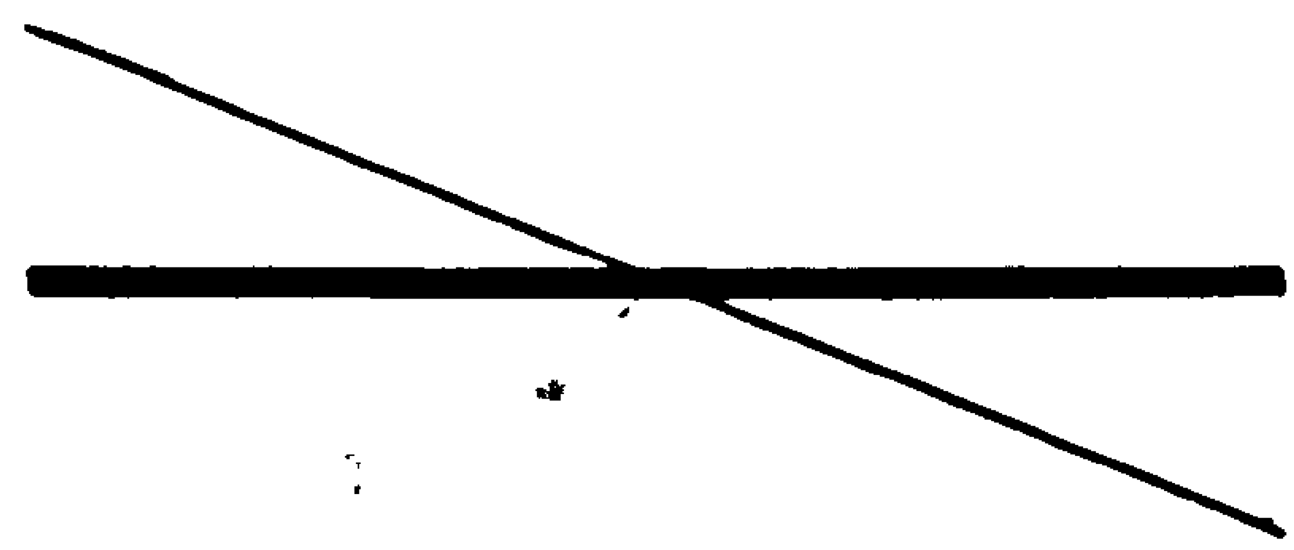


Fig 1.2 Basic example of perceived expansion of acute angles (Helmholtz, 1856).

One of the earliest comprehensive studies of simple angles was performed by Jastrow (1892). His results indicate that angles of 15° were slightly overestimated, but those between 30° and 75° were underestimated. The underestimates fell to zero again at 90° then, between 90° and 120° became overestimates once more. The error fell to zero at 135°, angles between 150° and 165° being again underestimated. This study indicates that over large ranges acute angles are underestimated and obtuse angles overestimated, thus directly contradicting the reports of Helmholtz and Wundt. Jastrow's method, however, is open to severe logical criticism. His subjects viewed a card on which an angle was displayed, which they were then asked to reproduce in a drawing. By this procedure, however much the subjects over- or underestimated the angles perceptually, they should have made accurate reproductions (subject to some random error) because to draw an angle which looked like the original, they would have to draw one the same size. The perceptual error would thus be included in their drawings. If, as a result of overestimation of angle size, his subjects drew bigger angles, then the reproduced angles would also look bigger. Evidently, therefore, the constant errors in Jastrow's study must be attributable to some source other than that which leads to the observations reported by Helmholtz and by Wundt.

Beery (1968) replicated Jastrow's findings, that acute angles are underestimated and obtuse angles overestimated, but made the same mistake as Jastrow, if not even more obviously. His subjects merely reproduced an angle which remained continuously visible. Fisher (1969) pointed out Jastrow's error and repeated the study using a method of absolute judgments. From his findings he was able to support the view that acute angles are overestimated while obtuse angles are underestimated, with the zero error points occurring at between 90° and 110° and also at about 180°. As has been pointed out by Burns and Pritchard (1972) and by Robinson (1972), Fisher's method is just as logically unsound as was that of Jastrow and of Beery. Subjects learn the labels which they attach to angle sizes as a result of experience with angles of a known size. Thus an angle of 45° will be labelled as '45°' however much the internal representation may be distorted. As Robinson writes: "Fisher's results are just as mysterious as Jastrow's, and it is just as much a mystery that they follow the majority opinion as that Jastrow's do not." (Robinson, 1972, p 82). To confound the issue still further, Fisher replicated Jastrow's method in a later experiment and obtained results similar to those of Jastrow and of Beery.

In a further attempt at a comprehensive study of the effect of a number of parameters believed to influence the perceived size of angles, i.e. angle size, bisector orientation and presence or absence of visual cues, Maclean and Stacey (1971) showed that the differences between the results of Fisher and those of Jastrow and of Beery can be reliably obtained, the critical variable being response mode. Verbal identification of angle size, as in Fisher's study, leads to an underestimation while graphic reconstruction leads to an under-estimation of acute angles. However, while this study does confirm the reliability of the results found in earlier experiments, as a study of the perception of angle size it is no more valid than those already mentioned, for the same reasons. The differences between the stimulus angle size and the response angle size cannot be considered as measuring misperceptions of angle size, because to do so would require the assumption that the stimulus is seen veridically while the response suffers the perceptual distortion under investigation.

By using a rather more indirect technique to determine the perceived angle size the difficulties related above (which are to be found in all direct matching techniques) may be overcome. This approach has been applied by Ogasawara (1956, cit. Oyama, 1960) using the figure shown as Fig. 1.3, subjects being asked to adjust the upper line until it appeared to be co-linear with one arm of the angle. His reasoning was that any perceived change in angle size implies

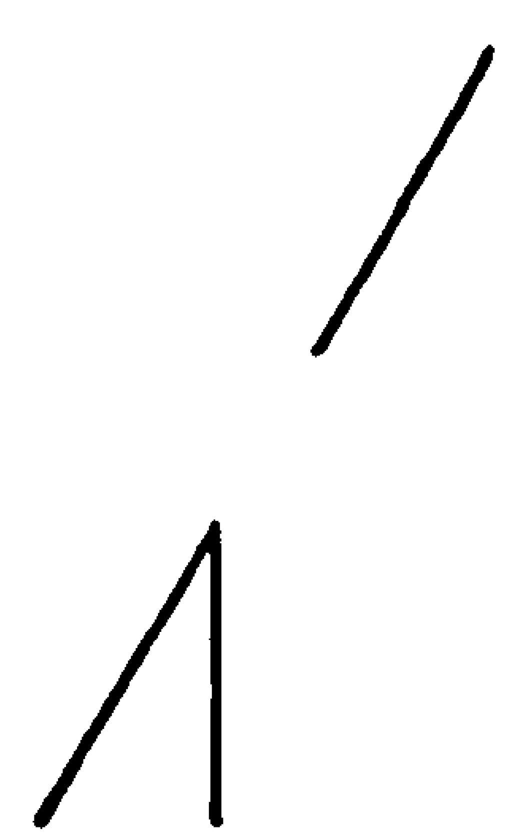


Fig 1.3 Stimulus configuration used by Ogasawara (1956, cit. Oyama, 1960).

a corresponding change in the perceived orientations of the arms of the angle. In order to detect this change in orientation, the line which is not part of the angle, and which is presumably not influenced for this reason, is set at the same apparent orientation as the adjacent arm of the angle. The difference between the orientations of the two lines is then taken as a measure of the extent to which perceived angle size differes from the real angle size. Ogasawara found a maximum for angles of 25^{o} - 30^{o} which fell to zero at 90^{o}, the direction of the error being such as to indicate that acute angles are overestimated. He also showed that when the lower oblique line was crossed by several parallel lines the illusion increased with the number of intersecting lines, although the shape of the function remained the same.

Using the similar Ebbinghaus figure (Fig. 1.4), an earlier study by Morinaga (1932, cit. Oyama, 1960) showed that the angular separation between the two arms

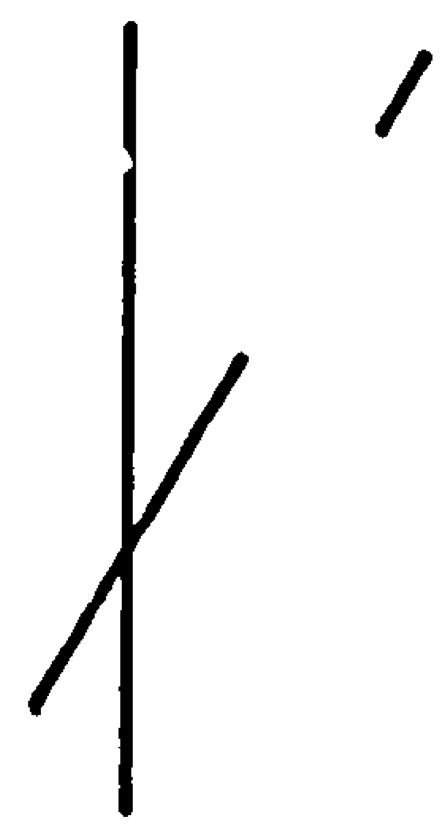


Fig 1.4 Ebbinghaus figure used by Morinaga (1932, cit. Oyama, 1960).

of the angle was not the sole determinant of the perceived angle size, which is also dependent on the orientation of the angle. Morinaga found the error of alignment of the dash with the oblique line to be greatest when both lines lay in the same quadrant, neither being either vertically or horizontally oriented.

Bouma and Andriessen (1970) used a test figure similar to that of Ogasawara, differing in that a dot was set by the subjects to be colinear with the arm of the angle, rather than another line segment. This procedure has the advantage that the dot can undergo no perceptual distortion of direction which may have occurred in the experiments of Morinaga and of Ogasawara. Varying both angle size and orientation, Bouma and Andriessen found the perceived enlargement of angle size to occur maximally with 45^{o} between test and induction line, falling to zero at 90^{o} - a value rather larger than that found by Ogasawara. Their results for the orientation of the induction line for a constant angle size differed also from those of Morinaga in that the greatest effect was found with vertical or horizontal inducing lines, with vertical lines exerting a slightly stronger influence than horizontal lines and oblique inducing lines exerting the smallest effect. Further experiments showed that when the test line was replaced by two dots representing the end-points (separation 28 min. arc) the results were similar although the magnitude of the perceived expansion of the angle was somewhat reduced.

Blakemore, Carpenter and Georgeson's (1970) investigation of the effect of angle size and orientation on perceived angle size used error in setting a comparison line parallel to one arm of an angle in the presence of the other arm at different angular separations, compared to that made in the absence of the third line, as the estimate of the perceptual expansion of acute angles and reduction of oblique angles. They found the maximum error to occur with angle sizes of around 10° falling to zero at 90° with the maximum underestimation of obtuse angles occurring at 165° - 170°. The latter angle size may be interpreted as a virtual acute angle of about 10° - 15°, complementary to the obtuse angle, showing perceptual expansion. Studies of the effect of the orientation of the test figure (Carpenter & Blakemore, 1973) gave results agreeing with those of Bouma and Andriessen (1970), the maximum effect occurring with lines close to the vertical or horizontal.

In another study (Maheux, Townsend & Gresock, 1960) a segment of the Zöllner illusion containing two angles, as shown in Fig. 1.5, was used. The subjects

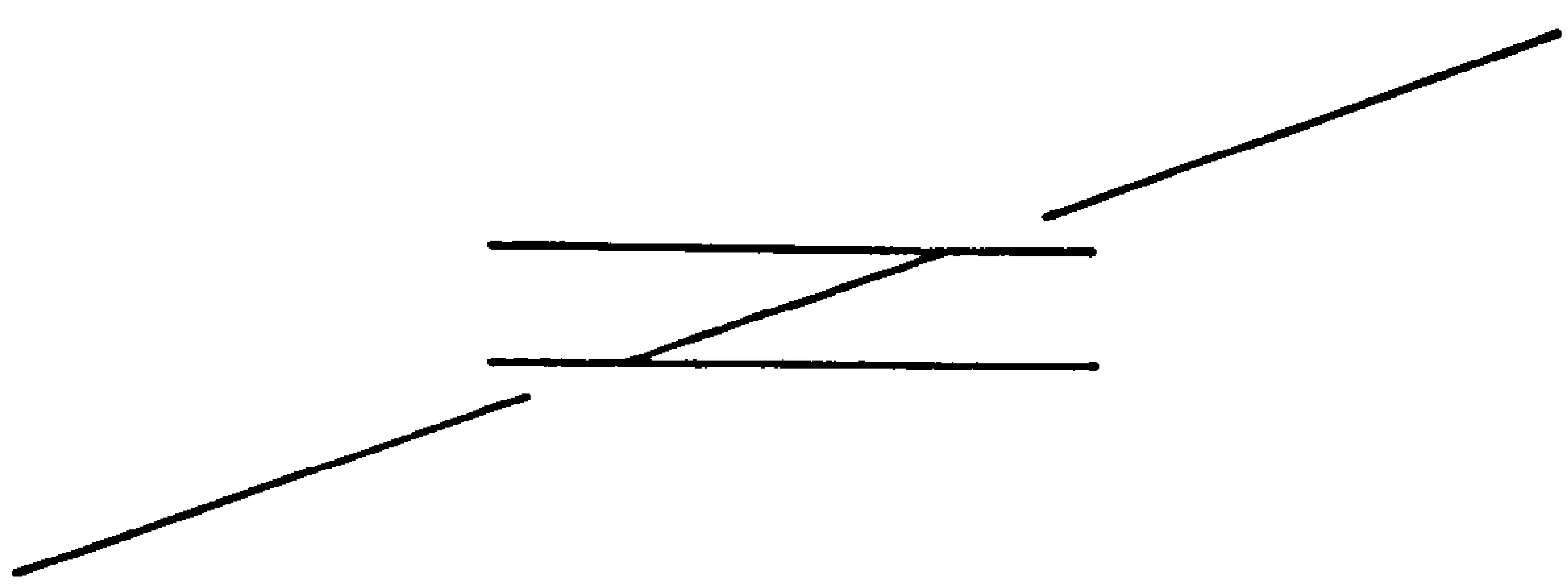


Fig 1.5 Stimulus configuration used by Maheux, Townsend & Gresock (1960).

were asked to set the orientation of the test line so that it had the same orientation as that of the two pointers. The difference between this orientation of the line segment and that obtained in the control when the parallels were not present was taken as the measure of perceptual expansion. This was found to at a maximum for 10° angles, diminishing rectilinearly with increasing angle size. The effect of orientation of the stimulus figure was not studied.

Of those experiments which can be considered as logically sound there is, therefore, an overall agreement concerning the occurrance of the perceptual overestimation of acute angles and underestimation of obtuse angles, although there is some dispute as to which angle sizes result in the greatest error, experimental results ranging from 10° to 45°. With reference to the effect of stimulus orientation, only Morinaga's results are at variance with the others, which show the greatest effect with vertically or horizontally oriented angles and the smallest with obliquely oriented angles. Lennie (1971) has also investigated the effect of the orientation of an angle on its perceived size. He asked subjects to adjust one arm of an angle of variable bisector orientation until the angle was judged to be of the same size as a second angle whose bisector was horizontal. The two angles had a common vertex. He found minimum differences when the test angle was vertical or horizontal, but when it was oblique the settings made showed the test angle to be perceived as appreciably smaller than the horizontal angle, a difference of about 8°- 9° being found for 40° angles. His findings give further support, therefore, to the conclusion that the overestimation of acute angles is greatest when they are bisected by the horizontal and vertical and least when the bisector of the angle lies on a main diagonal.

As Wundt (1898) pointed out, there is a large set within the class of geometric optical illusions in which angles, particularly acute angles, seemed to be the active elements. He suggested that certain figures containing angles may be constructed such that the perceptual enlargement of the component angles introduces distortions into the figure which compound to generate an illusion caused by the misperception the the direction or orientation of the lines of which the figure is composed. The role of the over- and underestimation of acute and obtuse angles in the induction of the distortions seen in these illusions, however, has not been universally accepted, principally because of the disagreements already mentioned concerning the behaviour of angles with sizes between 45° and 90°. There are also some figures which show angular or directional distortion, but which do not contain angles as such. These have been taken by several writers to demonstrate that recourse to the mechanisms involved in the misperception of angle size is not sufficient to explain these illusions.

Perhaps the best known of the illusions of direction is the Zöllner illusion shown in Fig. 1.6. In the first detailed work to be published on this figure Zöllner (1860) reported that the maximum illusion was obtained when the longer lines were oriented at 45° (or 135°), the illusion falling to a minimum as the figure is rotated until these lines are vertical or horizontal. This observation has been confirmed by Judd and Courten (1905) and by Morinaga (1933) as well as by a number of more recent studies.

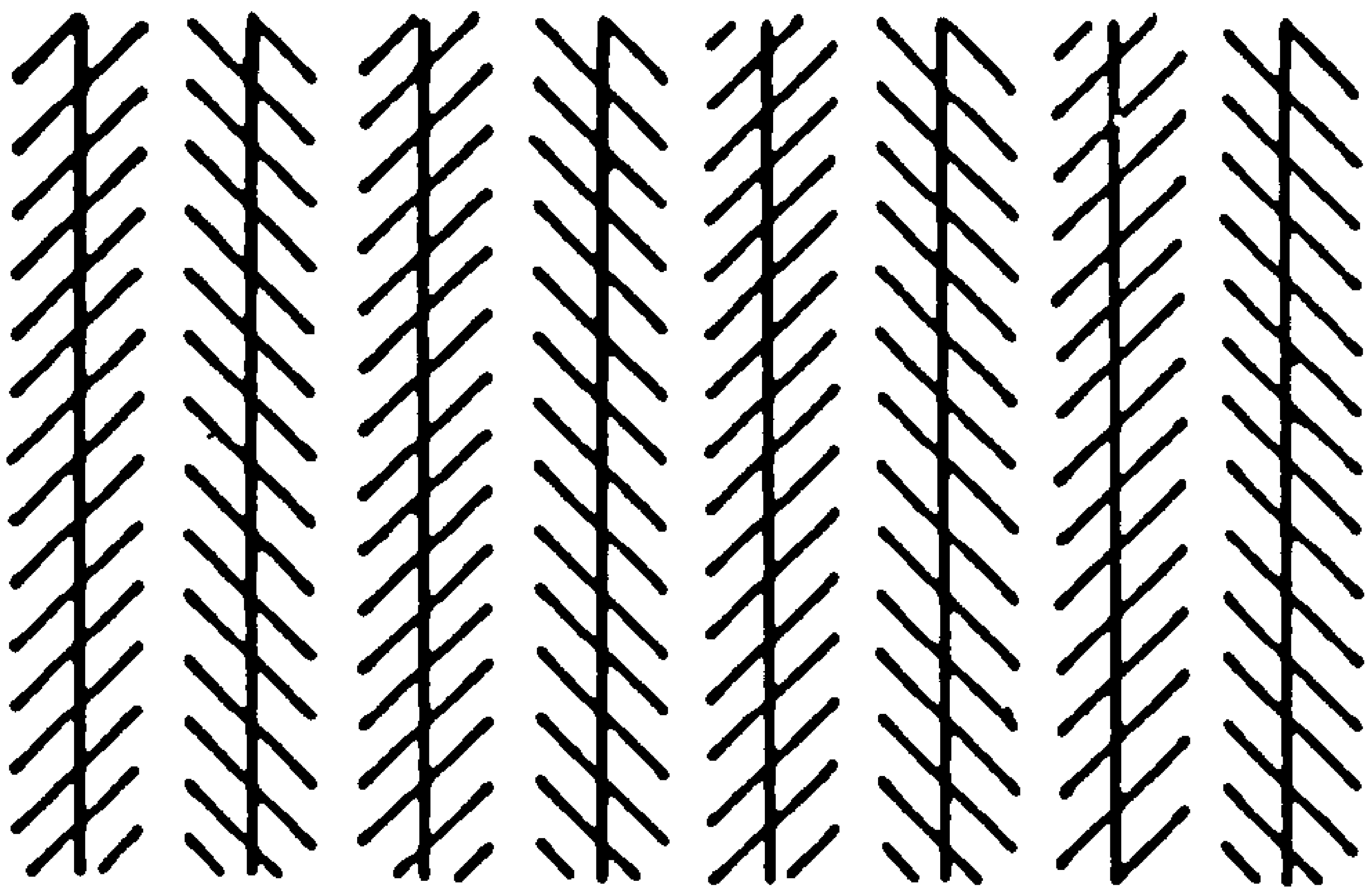


Fig 1.6 Zöllner illusion.

The effect of varying the angle of intersection of the main (test) lines with the background (inducing) lines of the figure, as determined by a number of studies is not so consistent between investigations. A summary of the results obtained is given in Table 1.1. The main differences in the findings shown are between those who report a continuous diminishing of the illusion and those who report that the sign of the illusion changes at about a 45° intersection angle, returning to zero at an angle of 90°. No reason has been suggested for this somewhat glaring discrepancy which divides the studies into two groups. It is worth noting that apart from Day (1965) the other workers who report this finding, Hoffman and Bielchowsky (1909) and Gibson and Radner (1937), used similar displays, although not the most reduced version of the Zöllner figure. Furthermore, the effect claimed by Day (1965), using a full Zöllner figure with intersection angles of 62.5° is barely perceptible, if at all, and is certainly less than half the magnitude obtained with the 22.5° intercept, which is the strength reported.

The second disagreement is in the intersect angle required to give the maximum illusion - found by Maheux, Townsend and Gresock and by Gibson and Radner to

SOURCE	ILLUSION CHARACTERISTIC	FIGURE USED
Morinaga (1933)	Max. at 20°-30°, falling sharply at 20°, slowly at 30°, to zero at 90°.	Zöllner figure
Day (1965)	Max at 15°, zero at 40°, reversal between 45° and 90°	Zöllner figure
Wallace & Crampin (1969)	Max. at 15°-20°, shape of curve as Morinaga, reversals at 2°.	Zöllner figure
White (1971,1975)	Max. at 20°, curve as obtained by Morinaga.	Zöllner figure
Oyama (1975)	Max. at 15°-30° (according to values of other variables) Minimal by 45°, reversals at 10°.	Zöllner figure
Gibson & Radner (1937)	Max. at 10°, zero at 45°, reversals at 45°.	Single T-line with Background of one orientation (half Zöllner)
Hoffman & Biel-chowsky (1909)	Max. at 20°, decreasing to zero at 45°, reversal at 45°-90°.	Single line with oblique intercepts
Maheux, Townsend & Gresock (1960)	Max. at 10°, decreasing to minimum at 60°.	Two parallels with one oblique.

TABLE 1 - Summary of results obtained when size of Zöllner illusion is measured as a function of angle between background and test lines.

be 10^{o}, in comparison with the value of 15^{o} - 20^{o} found by the others. There are two major differences between the experimental stimuli which may contribute to this lack of agreement. One is the number of obliques, or the background density. The implication of this variable was demonstrated by Heymans (1897) and has since been quantified by Wallace and Crampin (1969), White (1971) and Oyama (1975). All these studies show that illusion magnitude increases as a function of background density. Wallace and Crampin report further that after correcting their data for line thickness as well as background density, the intersect angle required for maximum illusion is 10^{o}, thus bringing their findings in line with those of Maheux et al. and of Gibson and Radner. Presumably the application of similar corrections to the other results would bring these too into agreement.

The other difference is in where the measurement was made. In the work of Wallace and Crampin it was made on the horizontally oriented parallels, whereas in that of Maheux et al. it was made on the oblique intersect, the orientation of which varied but did not approach the horizontal or the vertical. As will be discussed later, this question of orientation is a fundamental one and could well explain the results shown to be anomalous, particularly with reference to the change of sign effect at angles greater than 45^{o}.

A number of other features have been abstracted from the Zöllner illusion in order to identify those which make an active contribution to the effect. Wallace (1966) refers to Heyman's (1897) finding that the illusion is stronger with increases in the number of obliques, and asks which features of these repetitive obliques are important. In particular, is it their overall direction in relation to the test lines which is important, or is it their straightness - would a series of zig-zag lines be just as effective? The figures used are shown in Fig. 1.7; for each pattern the illusion was viewed at five distances - 80, 130, 200, 300 and 450 cm. The wavy line was found to reduce the illusion at short distances, but with increasing viewing distance there was a marked increase in the magnitude of the illusion; at 300cm pattern B gives an illusion as large as that given with the control. Wallace concludes that at short distances overall direction alone of the intersects is not sufficient to generate the illusion, the background lines must also be straight. As the viewing distance increases, however, the waviness becomes less important and overall direction becomes the important feature:

"Of the two wave patterns, B produces more distortion than C, which means that it possesses more linearity. This despite the fact that the slope of the waves in B is greater i.e. deviates more from the overall direction than the slope in C. The important difference then is not this, but the fact that

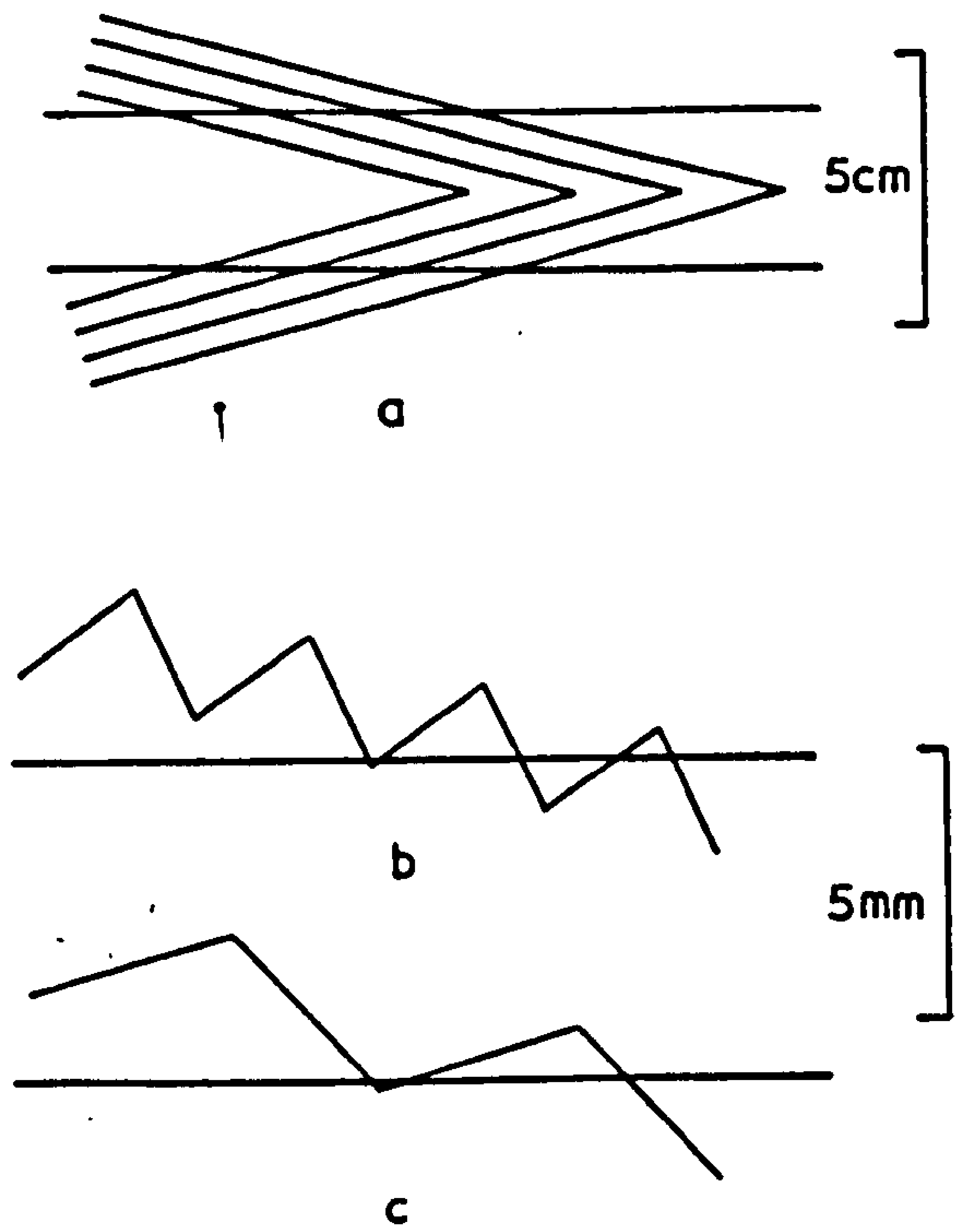


Fig 1.7 Stimuli used by Wallace (1966).

B is twice the frequency of C. Now one can consider these patterns as 'dotted' lines, the dots being the wave peaks. In order for the perceptual system to determine the overall direction of the line a certain minimum number of dots must be sampled. Since, however, there are twice as many per unit length in B than in C a small fixed sample of B gives more overall direction information than the same size sample of C. It would seem that it is the direction of the lines as determined by these samples which distorts the direction of the main test lines." (Wallace, 1969)

These findings suggest that it may not be the intersection of the test lines with the background field of lines as such, but the interaction of the 'directionality' of the test lines with that of the background field, as abstracted by the perceptual system, which gives rise to the illusion effect of the Zöllner figure. In other words the effect is not one of contour interaction, but one of orientation interaction. If this is so, then it need not be a necessary condition for the illusion that the lines intersect, as is indicated by one of Heyman's (1897) figures. This possibility, together with the prediction that "there will be a critical distance (measured as visual angle) separating the background lines from the test lines at which the distorting interaction no longer occurs" was investigated by Wallace (1969). The results of the first experiment are shown in Fig. 1.8(a) from which it is immediately apparent that the presence of the gap does not abolish the illusion, that is, that the intersection is not a necessary condition for the illusion.

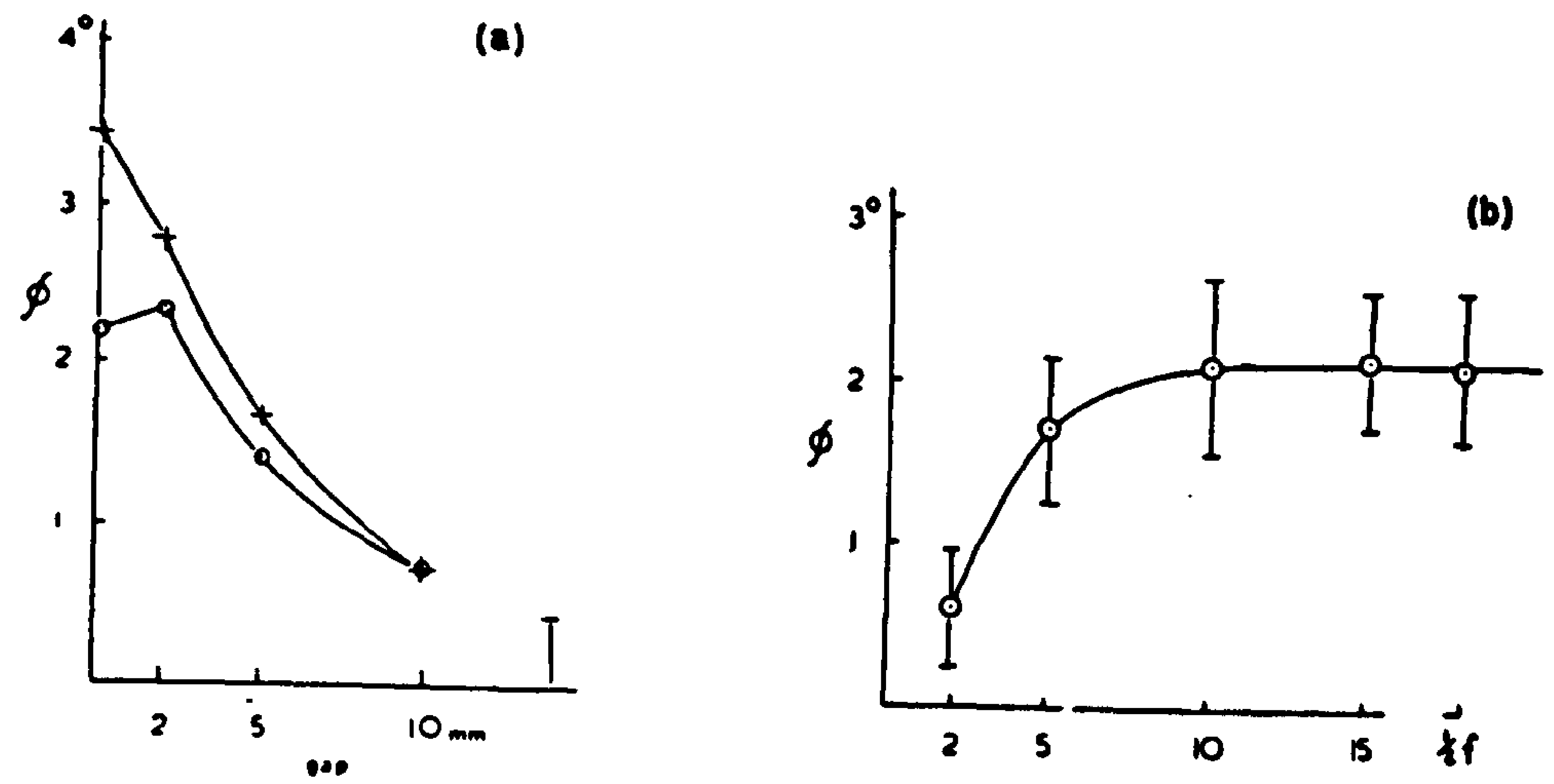


Fig 1.8 (a) Zöllner illusion magnitude as a function of the size of the gap between transversal and background.

(b) Zöllner illusion magnitude as a function of length of background lines. (Both figures from Wallace, 1969)

In a second experiment a converse configuration was used to measure the effect of lengths of background lines on the size of the illusion. If there is a critical distance for interaction between orientations, then with increasing length of background lines the illusion should increase, but should reach an asymptote at some point beyond which further increases of line length have no effect. The lengths of the background lines were such that the perpendicular distances from their ends to the test lines were equivalent to the different gap sizes in the first experiment. In addition a 15mm line was added. The results from this experiment are shown in Fig. 1.8(b). The curve reaches an symptote at 10mm, suggesting that for the intersect angle of 15^{o} used, parts of the background more than 10mm perpendicular distance from the test lines do not contribute to their distortion.

The results of these two experiments appear to be in good agreement. Both indicate a limiting distance of 10mm beyond which the background lines have little effect on the test lines. In the apparatus used, this distance corresponds to a visual angle of 1 deg. arc. Oyama (1975) has also investigated the effect of gap size with more steps than Wallace (1969) as well as at a number of different intersect angles between 10° and 40°. Not only was the finding that the illusion persisted in the absence of physical intersection of the lines repeated, but it was also found that there was a significant interaction between gap size and angle of intersection. As the gap between the background and the test line was increased, the angle at which the maximum illusion was found was seen to decrease. In a subsequent experiment Oyama determined the relation between line length and illusion magnitude (cf. Wallace, 1969), again at a number of different intersection angles. These results compare well with those obtained by Wallace, the magnitude functions reaching an asymptote at lengths of between 45 and 60 min. arc. Here too angle size was found to interact with the primary independent variable. In this instance the peak magnitude was found at smaller angles as the line length increased. The relation between these two sets of interactions is, however, neither obvious nor made explicit although both main effects are quite consistent in their estimates of the limiting distance for interactions between the two orientations present in the stimulus.

White (1972) provides further evidence for the notion that the interacting variables in the Zöllner illusion and therefore, perhaps, in all distortions of perceived orientation which may described as perceptual expansion of acute angles, are orientations of lines rather than the lines themselves as explicit contours. He proposed that a straight line can be considered as a row of dots with zero separation. "The criterion for when a line is not a line is

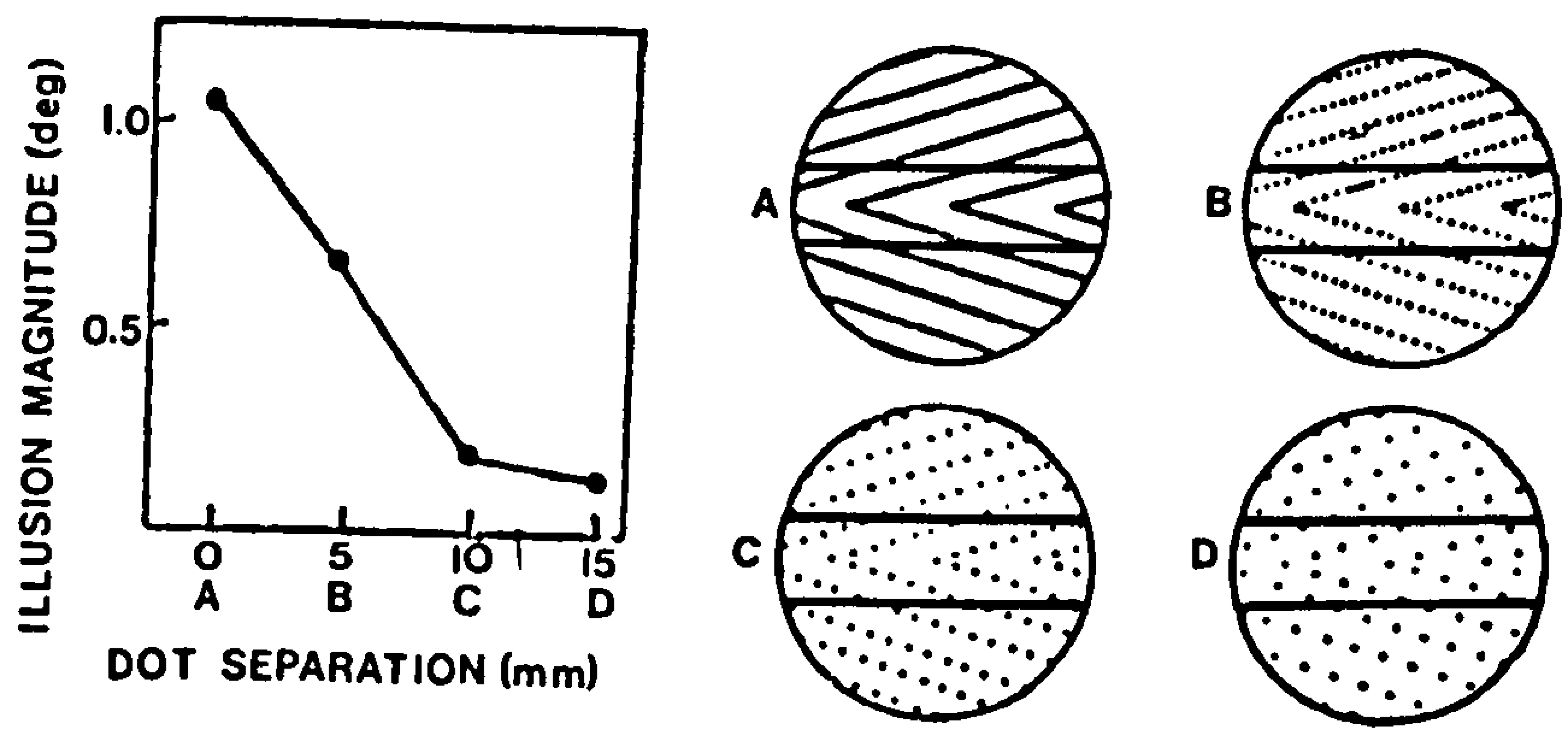


Fig 1.9 Results obtained for increasing dot separations in the backgrounds of the Zöllner illusion figures shown (White, 1972).

given by a certain dot separation depending on the nature of the surrounding implicit contours. In the present instance (Fig. 1.9) the surrounding contours were virturally unrecognisable when the dot separation was 15mm (1.4 deg.arc), i.e. when it was equal to the perpendicular distance between the adjacent contours. Dotting a line thus results in a decreased overall intensity of the corresponding explicit contour." As his results show, this reduction of the 'intensity' of the contour results in a corresponding decrease in the illusion magnitude which fell to zero at a separation of 10-15mm; at which the dot-defined lines were no longer recognisable as lines.

Degradation of a continuous line into fragments which act as sub-optimal stimuli for the perceptual mechanisms which extract orientation information from the pattern under inspection thus results in a decrease in the contrast between these orientations. It might be expected, therefore, that if the 'intensity' or efficacy of the lines were differentially altered in a different way, a similar result would be obtained. To test this hypothesis Wallace (1975) measured the effect of different background line luminance contrasts on the magnitude of the Zöllner illusion. The results were fully in accordance with the expectation, illusion magnitude showing a linear relation to log luminance contrast.

This study compares favourably with a variation of Blakemore, Carpenter and Georgeson's (1970) experiment reported by Parker (1974). Parker used essentially the same stimulus as did Blakemore et al., but differentially varied the luminances of the lines forming the angles. For a constant luminance of line A (the inducing line - see Fig. 1.10), decreasing the luminance of line B gave an increase in the illusion magnitude. When the

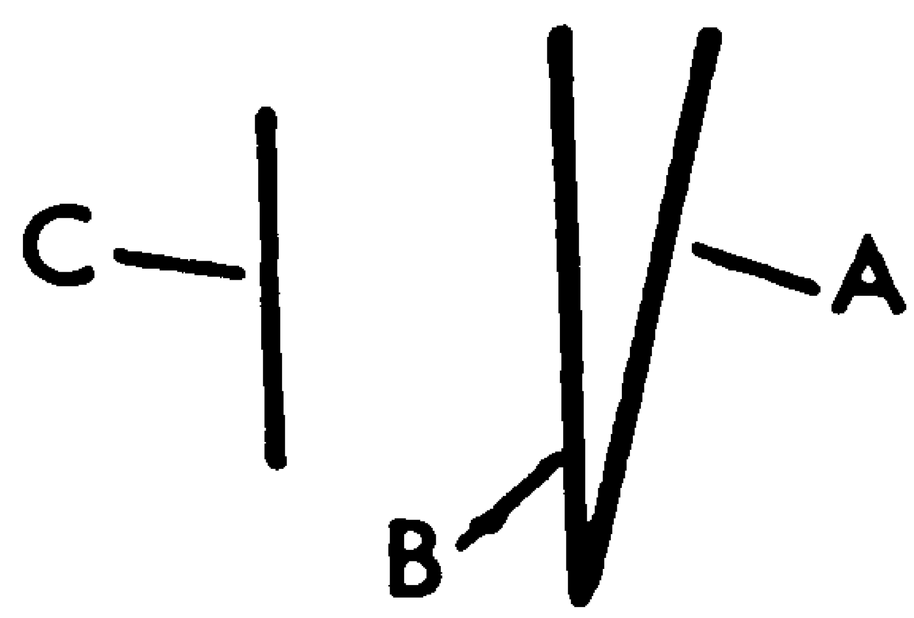
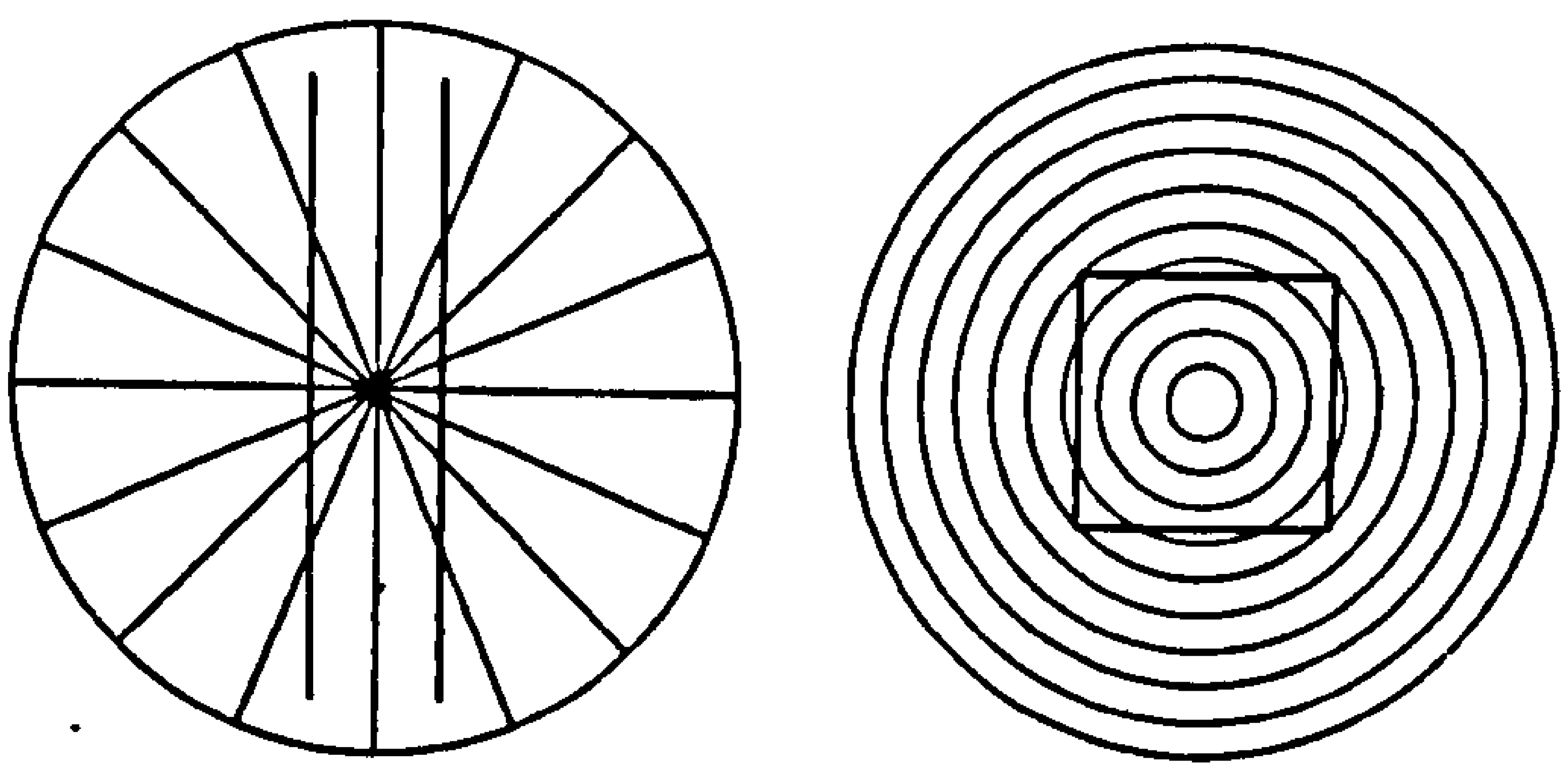


Fig 1.10 Stimulus configuration used by Parker (1974).

luminance of line B was held constant and that of line A reduced the illusion magnitude decreased. Concomitant reduction of the luminances of lines A and B gave no significant change in illusion magnitude. The close similarity of the consequences of these corresponding manipulations performed on the two stimulus patterns, one the simple angle and the other the more complex Zöllner figure, offers further evidence in support of Helmhotz's origianl proposal that the key factor in the illusions of direction is the perceptual expansion of acute angles.

The Zöllner figure may be considered as one of a set of illusions which comprise a small number of lines superimposed on a background field of regularly spaced lines of a different orientation. It was perhaps the use of the term background field which led Orbison (1939) to explore the consequences of superimposing figures such as lines squares, circles etc. onto fields of concentric circles or radii of circles and to account for the induced distortions from a Gestaltist viewpoint. He proposed that 'fields of force' were set up by the background lines, presumably in the visual cortex. Any line crossing this 'force field' would interact with it and be distorted to a predictable degree in a predictable direction. If, for example, the crossing lines were radial to a background of concentric circles, or arcs on a field of radii (with a common centre for both arcs and radii), then the 'forces' would be prefectly balanced and there would be no distortion. If the crossing lines did so at any angle other than 90°, then they would be distorted in the direction of the lines where the forces were balanced. Thus, in Fig. 1.11a, the lines of the square are distorted in



(a) (b)

Fig 1.11 Orbison figures.

the direction of the radial lines and in Fig. 1.11b the two parallel lines are distorted in the direction of the concentric circles.

As it is now evident that the neural mechanisms subserving the perception of orientation do not operate in terms of 'fields of force' Orbison's theory has little explanatory value. As description, the characteristic behaviours of the intersecting lines deduced from his figures are in general agreement with those studies of the Zöllner illusion described above, as exemplified by the findings of Wallace and Crampin (1969), White (1971) and Oyama (1975). Those studies which reported a cross-over (zero illusion) at angles of 45° are therefore in disagreement with Orbison's findings, as well as with the findings of the other Zöllner studies. Berliner and Berliner (1948) cited Hoffmann and Bielchowsky's (1908) study as a refutation of Orbison's proposals and, using this data of Hoffmann and Bielchowsky, advanced a hypothesis of their own to account for this type of distortion. Struck by the resemblance of this data to a sinusoid, they gave a mathematical expression to fit it: which, they claimed, enables the prediction of the amount of distortion which will be produced by an Orbison-type figure:

For d = amount of distortion
a = angle of tilt of the background lines (angle of intersection)
c = constant coefficient
e = error coefficient

$$d = c.\sin 4a + e$$

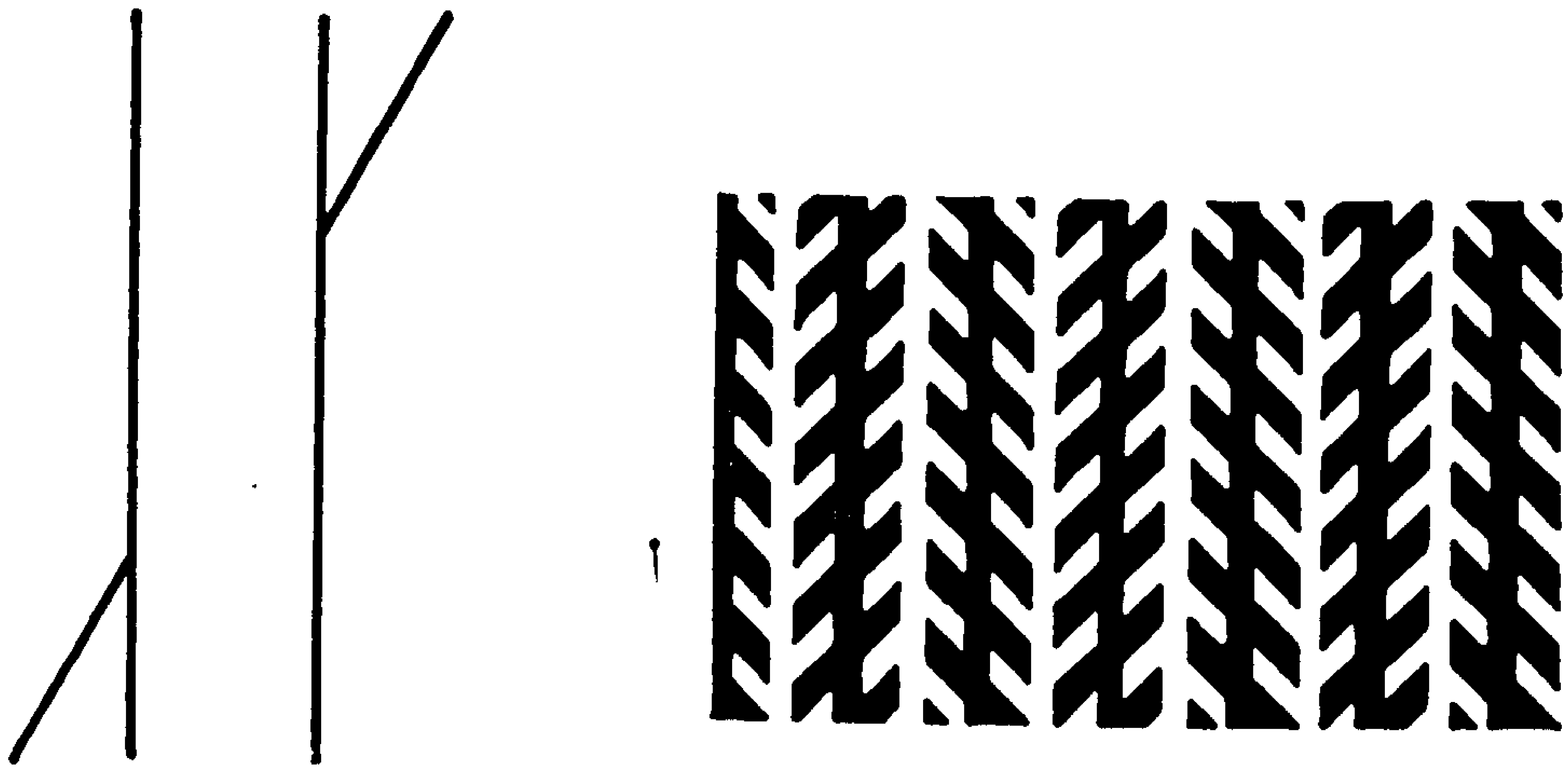
Insofar as this expression predicts the findings of Hoffmann and Bielchowsky, including the reversal of the illusion at angles between 45° and 90°, then the bending of the test line would vary in direction according to whether it intersected the background lines at angles greater or less than 45°. This prediction was experimentally corroborated by Kristof (1960) using one half of the Hering figure. The prediction of zero illusion at 45°, followed by a reversal of illusion at angles between 45° and 90° is, of course, also supported by the results of Day (1965) and Gibson and Radner (1937) on the Zöllner type illusion.

The Berliners go on to point out that when a single line crosses a field of parallel lines at an angle, the observation is not a bending of the line, but a rotation, as can be seen in the stimulus configuration of the Zöllner figure. In the Hering and the Wundt figures and in the Orbison figures the angle of intersection changes systematically and so the line appears curved - an 'integration' (term used by Berliner and Berliner, 1948) of the changes of orientation at each intersection or 'locus of distortion' (Crassini & Over, 1974) or, as it were, as a smoothed polygon.

But, however useful the Berliner and Berliner expression, or its post hoc modifications may be for predicting the distortions to be expected from various figures of this general class, it is descriptive and not explanatory. Nothing whatsoever is said about the mechanisms of the perceptual system whereby inputs give non-veridical outputs.

The outstanding unresolved feature in this discussion so far is the disagreement between those studies which report a biphasic illusion function and those in which the illusion magnitude function is monotonic. Although no systematic study of this discrepancy has been published to date, a possible hint of its resolution may be found in the results of Virsu and Taskinen (1975) who studied the effect on perceived contrast and orientation of the test line brought about by the introduction of a second line at angular separations between 2° and 90°. Error in perceived orientation was plotted as a function of angular separation of the two lines and was shown for each subject. While none of the functions could be properly termed biphasic, two of the three subjects show negative illusions at angles greater than 70° and 80°. That of the third subject has no negative component at large angles and the pooled data shows a typical monophasic function. It must be admitted, however, that these small inter-subject differences do not approach the almost symmetrically biphasic function published by Day (1965), for example.

Another well-known geometric illusion - the Poggendorff illusion (Fig. 1.12a) - has often been cited as a further example of a figure which appears perceptually distorted as a consequence of the apparent expansion of acute angles. Zöllner



(a) (b)

Fig 1.12 (a) Basic Poggendorff figure.

(b) Version of the Zöllner figure from which Poggendorff claimed his figure was derived.

(1860) mentioned this figure, and also referred to a disagreement between Poggendorff and himself as to whether the two illusion were identical. Zöllner denied this, attributing Poggendorff's claim to a particular instance of the Zöllner figure (Fig. 1.12b) in which each intersection could be considered as a Poggendorff figure. He claimed that when the Zöllner figure was drawn with thin lines the putative Poggendorff component was no longer present. Hering (1861), however, first interpreted the Poggendorff illusion as being a result of the perceptual enlargment of acute angles and so identified it with the Zöllner illusion which Helmholtz (1866) had already interpreted in the same way.

In a recent critical study by Day and Dickinson (1975) both the apparent change in orientation and the apparent lateral translation of the transversal of the Poggendorff figure were measured by using stimuli of the type shown in Fig. 1.13b, derived from Tolanski's version of the Poggendorff figure, at a number of intersect angles. While the changes in the perceived orientation

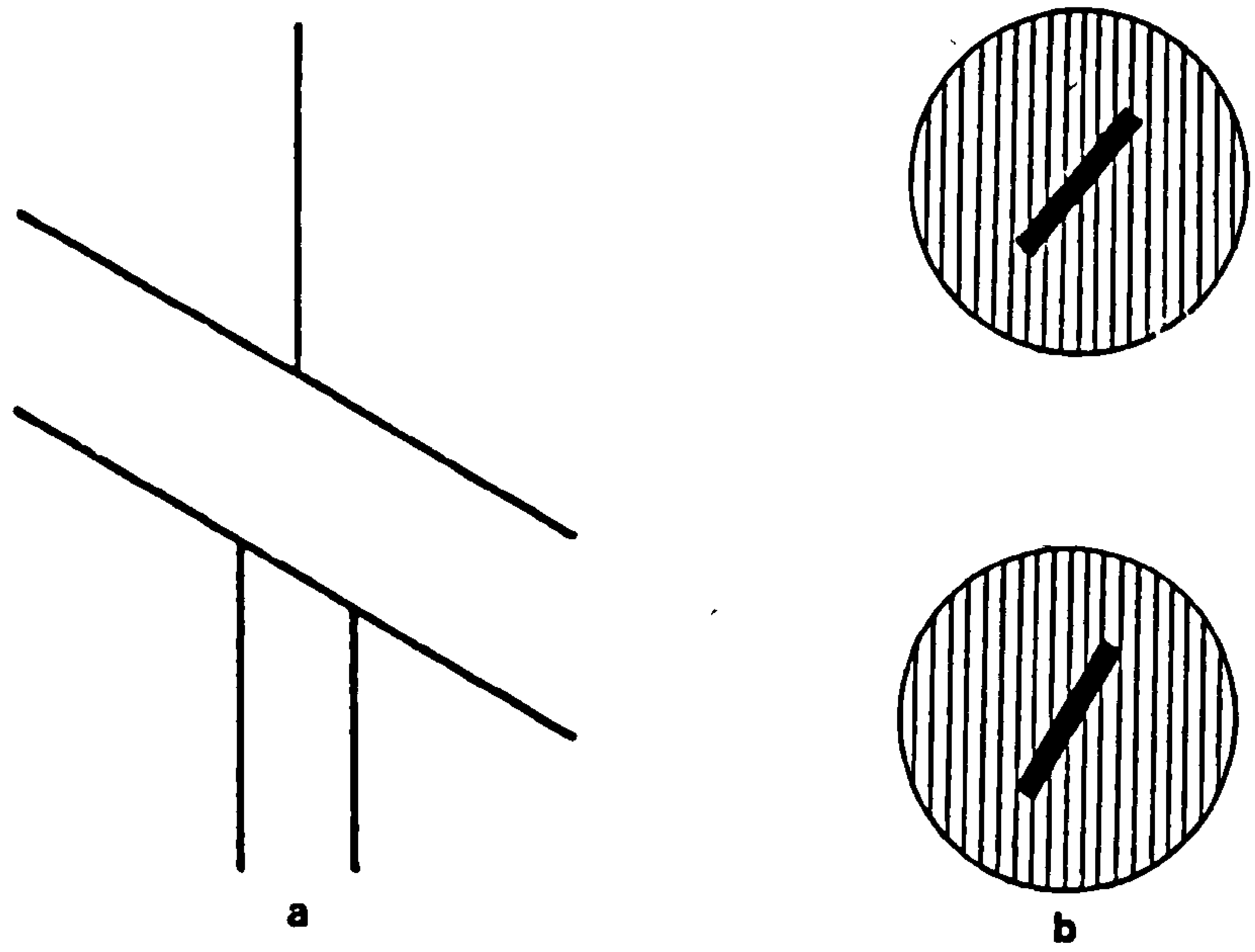


Fig 1.13 (a) Tolanski's (1960) variant of the Poggendorff figure showing illusory loss of colinearity in the absence of any illusory change in perceived orientation.

(b) Stimulus figures used by Day & Dickinson (1975).

of the transversals were small and unsystematic, the translation effect was unequivocal. It may be concluded, therefore, that the Poggendorff illusion is not one of orientation and is unrelated to the Zöllner illusion and its variants. Despite its obvious interest, therefore, it is beyond the scope of this discussion.

It has been shown that perceptual distortion of orientation, whether in simple or in relatively complex figures, varies in degree according to the orientation of the figure based on a given angle of intersection between the background (or inducing) component and the foreground (or test) component. The notion that these perturbations of visual space are due to some sort of interaction between the directionality or orientation of the lines in the figures rather than to the physical presence of angles has also been introduced (Wallace, 1966; White, 1972). The phenomena described above have been termed, therefore, orientation contrast effects (Gibson, 1937 - by analogy to colour and brightness contrast), the magnitude of the apparent contrast being a function of both the relative orientations (angular separations) and the absolute orientations of the pattern elements. Furthermore, these pattern elements need not necessarily be lines, but any 'line-like' luminance contrast configuration to which the concept of orientation may be meaningfully applied.

Unlike the earlier studies, more recent examinations of these orientation contrast effects have often been carried out with explicit reference to various hypothetical mechanisms, the elaboration of which has been made possible through interaction of advances in the understanding of the neurophysiological mechanisms which mediated the processing of visual information as it passes through the various levels of the visual system. Before these notions are discussed in greater detail, however, a further section will be devoted to the review of phenomena which have been reported in the investigation of the perception of orientation of contours. This will deal with the perception of single lines and their orientation, including the so-called 'oblique effect'. Also covered will be those aspects of the adaptation aftereffect phenomena relevant to this study.

1.2 The Perception of Orientation

It has been observed repeatedly that even in the absence of clinical astigmatism visual acuity is highest for vertical and horizontal lines, and lowest for lines of intermediate orientations. This effect was termed 'retinal astigmatism' by Shlaer (1937) in view of his proposal that the effect was of retinal origin. As will be seen, Shlaer's arguments for the retinal origin of the effect were rather tenuous and there are other explanations of his findings. For this reason an alternative term for this phenomenon, meridional anisotropy, will be adopted.

The effect was first reported by Emsley (1925) who noticed it incidentally while studying clinical astigmatism. He wrote, "This marked preference for lines in a certain direction, after the optical defect of the eye has been fully corrected, constitutes a kind of residual astigmatism....the reason for it is to be sought in the lens substance, or the humours, or at the retina or even further back along the optic nerve." Since that time, hypotheses have been proposed locating the mechanisms responsible for meridional anisotropy at all of these locations.

Since this time a large number of studies have been directed toward the characterisation of meridional anisotropy in both humans and animals, as well as toward an explanation of the effect. Many of the earlier studies have been reviewed by a number of authors (Lichtenstein, 1957; Taylor, 1963; Appelle, 1972) so only a summary of the findings will be presented here.

In the last 30 years experimental investigation into the orientation response of the visual system has shown the meridional anisotropic effects to be manifest in all aspects of vision (Timney & Muir (1976) have shown the effect to be present in Chinese subjects, as well as Caucasians, but with about half the magnitude). Acuity, as determined by measurements of the detection threshold for fine lines, has been shown to be higher for horizontal and vertical lines than for oblique lines (Higgins & Stultz, 1948, 1950; Ogilvie & Taylor, 1959). These observations have been repeated when the target to be detected was a bar grating (Hamblin & Winser, 1927; Campbell, Kulikowski & Levinson, 1966).

When the test measures the ability of the subject to assess the orientation of a clearly visible line the results are essentially similar. Jastrow (1892) and Kaufmann, Reese, Volkman and Rogers (1947), among others, have shown the unsigned average deviations of subjects' setting of a stimulus line to the vertical or horizontal to be about 1^{o}. When the line was to be set to the oblique (45^{o}) errors of up to 6^{o} were reported. In a study using the conventional absolute judgment method, Rath, Alluisi, and Learner found a higher amount of stimulus-response equivocation for oblique lines, compared to vertical or horizontal lines. In other words, the representation of the orientation of oblique lines is less precise than is that of verticals and horizontals.

When the experimental task was to set a point to appear colinear with a single test line, Bouma and Andriessen (1968) found accuracy of performance to be poorest for obliquely oriented lines. They also found a systematic tendency for oblique lines of intermediate orientation to appear closer to the horizontal or vertical than they actually were. When the test measure of accuracy of perceived orientation is parallelism rather than co-linearity the oblique effect is still evident. Takala (1951) showed the test and comparison lines successively, but his finding that the accuracy of the parallelism setting is greatest for vertical and horizontal lines and least for 45^{o} obliques was fully consistent with the observations of Sulzer and Zener (1953), Rochlin (1955) and Andrews (1965, 1967a,b) who all showed test and comparison lines simultaneously. Andrews also pre-figured Bouma and Andriessen's (1968) observations concerning the constant errors in perceived orientation by using a comparison stimulus whose orientation error was extremely small compared with that of the test line. When the stimulus duration was brief, however, the direction of the constant error was found to be reversed, so that lines appeared to be closer to the 45^{o} oblique than they actually were.

In his study of the Troxler effect, Goldstein (1967, 1968) found that in the Troxler effect and under conditions of binocular rivalry, obliquely oriented test lines showed higher disappearance frequencies than vertical or horizontal test lines. Ellis (1975) observed line fragmentation under steady fixation, rather than whole disappearances, and corroborated Goldstein's observation showing that fragmentation frequencies were highest for oblique orientations. He also showed that when the subject was rotated to an orientation 45^{o} from the vertical, the effect showed a phase shift of 45^{o}. This observation is in agreement with those of Findley and Parker (1972) and of Lennie (1974) who used measurements of photopic visual sensitivity and of acuity to show meridional anisotropy to be locked onto retinal rather than gravitational orientation.

In a similar study in which stabilised images rather than fixated images were used, MacKinnon, Forde and Piggins (1969) found the same results for the effect of stimulus orientation of fragmentation frequency as did Ellis (1975). Despite the apparently reasonable arguments that afterimages are equivalent to optically stabilised images, neither Evans (1967) nor Wade (1972) have found any effect of line orientation on either the duration of line visibility or on the duration of unitary disappearance. The suggestion that optically stabilised images do differ in some respects from flash-produced retinal afterimages is substantiated further by Schmidt, Cosgrove and Brown (1972) who repeated the measure of fragmentation frequency using an optically stabilised image (Clowes & Ditchburn, 1959) and showed a consistent oblique effect.

Finally, by measuring acuity with gratings produced on the retina itself through interference of two laser beams intersecting on the retina, it has been shown that the oblique effect persists despite this by-passing of the optics of the eye (Campbell & Green, 1965; Mitchell, Freeman & Westheimer, 1967; Watanabe, Nori, Nagota & Hiwatashi, 1968).

Following on from the proposal of MacKay (1957, 1961, 1967) that the visual system contains a population of neural subsystems differentially sensitive to contour direction, Andrews (1965, 1967a) developed a model for the perception of orientation and the meridional anisotropy of the visual system. He proposed the existence of a set of orientation selective 'filter' units in the visual system. The characteristics of these filters sufficient to describe the observed perceptual performance were defined as follows:

(1) Each filter responds to a range of presentation orientations; the response characteristic is bell-shaped and has extensive tails.
(2) Filters vary in selectivity. Those 'tuned' to orientations near the horizontal and vertical are most selective.
(3) Most filters receive inputs from both eyes.
(4) Integration of filter responses is achieved by mutual inhibition, which takes a matter of seconds to reach a steady level.
(5) The inhibition between filters is subject to adaptation.

These filters were uniformly distributed with reference to orientation. Bouma and Andriessen (1968) proposed an alternative model which was similar to that of Andrews except that their filter characteristics were identical at all orientations, but the filters were differentially distributed with reference to orientation. Andrews (1967a) had, in fact, already mentioned a model of this form, but had rejected it on the grounds that it did not predict the changes of perceived stimulus orientation with increased stimulus duration that he had observed (Andrews, 1967a).

A large number of neurophysiological studies of the response characteristics of single units in the visual cortex, initiated by Hubel and Wiesel's discovery that many cells in this region are selectively tuned with reference to the orientation of the stimulus have provided a neural basis for the filter-type hypothesis. At the same time psychophysical studies under a number of experimental methods have confirmed the existence of channels selectively tuned to orientation and attempted to define the characteristics of these channels, and the way in which they interact.

Sekuler (1965) and Parlee (1969) using backward masking, Houlihan and Sekuler (1968) using forward masking and Campbell and Kulikowski (1966) using simultaneous masking have all shown that the extent to which the detectability of the the target is affected by the presence of the masking stimulus is determined largely by the relative orientations of the two stimuli. At angular separations of greater than 45° the magnitude of the masking effect is equivalent to that of a homogeneous field of equivalent luminance. As the angular separation of the two stimuli is decreased the amount of masking increases to a maximum at zero separation.

In all these studies it was found that at angular separations of about 15° the masking effect was reduced by about one half. Phase differences between target and masking gratings did not alter the results (Campbell & Kulikowski, 1966; Sekuler, 1965), nor did the use of different targets. An illuminated stripe (Houlihan & Sekuler, 1968), a grating (Campbell & Kulikowski, 1966) and a dark bar (Sekuler, 1965) all gave essentially the same result. Even Parlee's (1969) use of a bar as both masking and target stimuli did not lead to essentially different observations. Campbell and Kulikowski also compared the masking characteristics of channels tuned to vertical and oblique orientations. As well as repeating the observation that the sensitivity of the oblique channels is lower than that of vertically tuned channels, they observed the half-width of the masking function for vertical stimuli to be 25% narrower than that for obliquely oriented stimuli.

Stimuli presented outside of the 'perceptual moment' can also affect the response to a stimulus, as is known from adaptation phenomena. In this situation, as demonstrated by Barlow and Hill (1963), prolonged stimulation will reduce the responsivity of some feature-analysing mechanisms. A rationale can be given, similar to that on which the masking experiments were based, that the amount by which the perception of a test stimulus is affected by prior viewing of another adaptation stimulus will provide some estimate of the extent to which the two stimuli are processed by the same mechanisms. In fact, a whole range of phenomena result from prolonged inspection of an adapting stimulus, most of which have been used in the study of orientation perception.

According to Blakemore and Sutton (1969) those aftereffects which might be expected to follow stimulus specific adaptation fall into four classes:

(1) The strength of the sensation should decline throughout adaptation.

(2) After adaptation it should be more difficult to detect a stimulus handled by that channel.

(3) Because of imbalance in opponent channels, a sensation of opposite value should arise spontaneously after adaptation.

(4) The appearance of stimuli of different value, but within the same modality should be distorted after adaptation.

In the orientation domain effects in classes (1) and (2) have been demonstrated by Blakemore, Muncey and Ridley (1971, 1973). They found further that the time courses of the induction period and recovery period of perceived contrast were very similar to those of threshold elevation (class 2 aftereffect) found by Blakemore and Campbell (1969) in a similar study. Blakemore et al. (1973) proposed, therefore, that threshold elevation is a special instance of the general effect of reduction of apparent contrast. In their measurement of the effect of relative orientation between the test and adapting gratings they found apparent contrast reduction to decrease exponentially, becoming minimal with separations of 45°. The half-width of the function was found, however, to be about 8° which is substantially less than that of 15° reported in the masking studies.

A larger number of studies have been concerned with threshold elevation following adaptation (Gilinsky, 1967; Gilinsky, Boyko & Baras, 1967; Gilinsky, 1968) have used a number of criteria for detectability in their experiments, which all showed threshold elevation when the adapting and test stimuli were of similar orientation. Mayo, Gilinsky and Jochnowitz (1968) and Gilinsky and Mayo (1971) found no effects with angular separations greater than about 20°, but the half-width of the adaptation function was comparable to that determined by Blakemore, Muncey and Ridley (1973). Using adaptation periods ranging from 50msec to 1000msec, Gilinsky and Cohen (1972) found that the half-width of the adaptation function decreased with increasing adaptation, from about 26° at the shortest duration to about 12° after 1 minute. This study gives further support to Andrews' proposal that the selectivity of orientation filters varies with stimulus duration as lateral inhibitory interactions stabilise. Finally, Maffei and Campbell (1970) have shown the adaptation effect to be reflected in reductions of the cortical evoked potential while no corresponding changes in the electroretinogram were observed.

Class (3) adaptation aftereffects have been reported by MacKay (1957) and threshold reductions for orientations orthogonal to the adapting orientation were observed by Gilinsky (1967).

The class (4) aftereffect in which the appearance of stimuli of a different value but within the same submodality as the adapting stimulus is distorted following adaptation is exemplified in the orientation domain by the tilt aftereffect, described first by Gibson (1933). Since then many studies of this aftereffect have been reported. The change in the perceived orientation of the test stimulus is in such a direction as to enhance the perceived separation of the adapting and test stimuli (Gibson, 1933; Gibson & Radner, 1937; Gilinsky & Mayo, 1971) and the angular separation giving the strongest effect is 7° - 8° (Gilinsky & Cohen, 1972; Campbell & Maffei, 1971).

Stimulus variables have been found to have a significant effect on the size of the tilt aftereffect. The magnitude of the change in perceived orientation is greater in peripheral vision than in central vision (Muir & Over, 1970; Over, 1971; Over, Broerse & Crassini, 1972). This is consistent with the finding of Hubel and Wiesel (1962) that the receptive fields in the periphery are larger than those in the Area Centralis, especially in view of the demonstration by Watkins and Berkely (1974) that the orientation specificity of units in the cat visual cortex is correlated with the size of the receptive fields of the units inversely. Parker (1972) has shown that if the contrast of the adapting grating is lower than that of the test grating the magnitude of the effect is increased; when the relative contrast of the gratings is reversed, then the magnitude of the effect is decreased. The dependence of the tilt aftereffect on the spatial frequencies of the adapting and test gratings is undecided. While Campbell and Maffei (1971), Collins (1970), Maffei and Campbell (1971) and Parker (1972, 1973) have all found the effect to be independent of the spatial frequencies of the two gratings, Blakemore and Campbell (1969) and Ware and Mitchell (1974) have fount the tilt aftereffect to be spatial frequency specific.

Although there are a number of quantitative inconsistencies between the studies described, qualitatively all the expectations outlined by Blakemore and Sutton (1969) concerning the consequences of adapting out one of an array of orientationally selective mechanisms are fulfilled. So far as can be seen, then, the human visual system behaves in a manner which can be described in terms of an array of 'filter' mechanisms which are selectively tuned for different orientations. Furthermore, these filters hsow a decline in response with protracted stimulation - adaptation - so that after such stimulation a state of reduced sensitivity is attained. Although it is postulated that each filter has a preferred orientation - that which on input gives the maximum response from the filter - it will also respond to a range of different orientations, the response decreasing monotonically with increased difference between the input orientation and the preferred orientation. There is evidence that the response decreases exponentially as the angular separation between the stimulus orientation and the preferred orientation of a given filter is increased until a separation is reached at which the filter no longer responds.

These inferred properties of orientation processing mechanisms in the human visual system are consistent with the discoveries of neurones in the visual cortex of the cat and monkey, as discovered in physiological studies. On this evidence it may be assumed that in the human visual cortex, as the the cat and the monkey cortex, the orientation of a contour is represented not in terms of the spatial characteristics of a pattern of excitation on the cortical surface, but in terms of the distribution of responses of the set of orientation selective filters. The perceived orientation of the stimulus corresponds to the location of some characteristic of the response distribution in the 'orientation space' defined by the set of filters.

1.3 Orientation Contrast and Lateral Inhibition

On the basis of the characteristics of the tilt aftereffect, summarised in the preceding section, Coltheart (1971a) proposed an explanation of the tilt aftereffect based upon the earlier proposal of Sutherland (1961) and similar to that described by Day (1962, 1965). When a straight-line contour is being inspected, a range of orientation-sensitive units will be stimulated. Those units whose preferred orientation coincides with the orientation of the stimulus will respond most strongly. Other units will respond less strongly, their response rate depending inversely on the degree of departure of the stimulus orientation from the unit's preferred orientation. It is supposed that the perceived orientation yielded by this pattern of response is given by averaging the preferred orientations of all the units which respond, having weighted each of these preferred orientations by the extent to which the unit is responding above its spontaneous discharge level.

It is assumed for the purpose of exposition that for humans the range of orientations to which a single unit will respond is $\pm 20^{\circ}$ about its preferred orientation (as suggested by Campbell & Kulikowski, 1966 and Mayo et al. 1968). Suppose a subject inspects an I-figure - a line tilted at $+10^{\circ}$ (the plus sign indicating a clockwise departure from the vertical). In this case, units with preferred orientations between -10° and $+30^{\circ}$ will respond to the $+10^{\circ}$ figure. With protracted viewing, these units will adapt. If a vertical line, the T-figure, is now inspected, units from -20° to -10° will respond with normal vigour, since they were not stimulated during the inspection of the I-figure and hence will not have adapted. However, units with preferred orientations from -10° to $+20^{\circ}$ will be in a state of reduced sensitivity because they were stimulated throughout the inspection period. They will respond less strongly therefore to the vertical stimulus than they ought. As a consequence, the weighted average response to the vertical line will be biased in the negative direction, instead of being 0°, as would normally be the case. The vertical line will be perceived, therefore, as having a counterclockwise tilt - that is, there will be a negative aftereffect.

The direct relationship between aftereffect magnitude and duration of inspection of the I-figure, and the inverse relationship between aftereffect magnitude and time since I-figure offset are obviously deducible from this analysis. So is the 'distance paradox': in general the magnitude of the tilt aftereffect is inversely related to the angular separation between the two figures, except when they have almost identical orientations. Here the aftereffect is very small, and an increase in the angular separation of the two figures can produce a larger aftereffect. This is to be expected because when the I-figure and the T-figure almost coincide, the distribution of adapted units is almost symmetrical about the T-figure. Only when the two figures differ appreciably in orientation will a sizeable asymmetry begin to emerge.

Despite the apparently good fit of this model to the data derived from adaptation studies, there appeared to be a major shortcoming of the theory in that whereas the threshold elevation and apparent contrast reduction effects had been shown to be specific to spatial frequency (Blakemore & Campbell, 1969; Blakemore & Nachmias, 1971; Blakemore, Muncey & Ridley, 1973), the tilt aftereffect was reported by Collins (1970), Campbell and Maffei (1971) and Parker (1972, 1973) to be only slightly sensitive to spatial frequency differences between the adapting and the test stimuli. This led to the suggestion (Campbell & Maffei, 1971) that two different neural sub-populations were responsible for the differing spatial frequency characteristics of the adaptation effects. This unsatisfactory position is further complicated by Georgeson's (1973) demonstration that the simultaneous tilt illusion - which apart from the temporal factor is equivalent to the tilt aftereffect - shows similar spatial frequency selectivity to that shown by the spatial frequency shift effect (Blakemore, Nachmias & Sutton, 1970), as well as to that of the orientation-specific effects of adaptation on thresholds and apparent contrast.

In the study of Campbell and Maffei (1971), however, the adapting gratings had rectilinear luminance profiles and therefore adaptation was not limited to any single spatial frequency. Parker (1972) did use sinusoidal gratings, but these were of equal physical contrasts. In this case it is possible that the results were confounded by the fact that stimuli of equal physical contrast might not be equally effective at different spatial frequencies, especially as the relative contrast of adapting and test gratings is an important variable in determining the magnitude of the tilt aftereffect (Parker, 1972), and the visual system is differentially sensitive to different spatial frequencies (Campbell & Green, 1965).

Taking these two factors into consideration, Ware and Mitchell (1974) re-examined the spatial tuning of the tilt aftereffect, departing from Parker's (1972) method mainly in that in order to make stimuli at different spatial frequencies more comparable, the contrast of the gratings was always kept at a fixed increment (0.75 log units) above the subject's contrast threshold for adaptation.

The outcome of this refined procedure was that differences of spatial frequency between adapting and test stimuli resulted in a reduction of the magnitude of the tilt aftereffect, the slope of the reduction curve being quite comparable to those obtained for the other classes of aftereffect, as well as to that shown by the simultaneous orientation contrast effect. Thus, on the basis of this new evidence, there is no need to postulate a different neural mechanism for the tilt aftereffect.

There is, therefore, little argument against the retention of a hypothesis based on the notion of feature analysers in that it allows the rotation of lines and edges as a whole, thus avoiding some of the difficulties raised for the older theories by Sutherland (1961). Such a hypthesis goes further than any earlier attempt toward providing a theoretical model whereby psychophysical phenomena such as the oblique effect and the tilt aftereffect, as well as the effect of adaptation on thresholds for lines of similar and different orientations, may be understood. At the same time this model has been extended to include the perception of simple line figures containing more than one orientation simultaneously.

In their simultaneous masking study Campbell and Kulikowski (1966) showed that the threshold for detection of a grating was elevated in the presence of another suprathreshold grating whose orientation was similar to that of the test grating. Parlee (1969), using single lines as masking and test stimuli, showed that the masking effect is not attributable solely to the fact that the two stimuli overlap, but that an inhibitory effect of orientation detectors on detectors for similar orientations must also be taken into account. These data are in accordance with the postulate of Andrews (1965) that there is mutual inhibition between orientation detectors such that "when a short-line stimulus causes filters to respond, all but a few are inhibited completely when the inhibition has had time to reach a certain level and these respond in a proportion which determines the angle seen." (Andrews, 1965, p1219). Andrews also postulated, in accordance with the findings of Hartline and Ratliff (1957) that the inhibitory output of a detector is proportional to its level of excitation. These postulates account for the high acuities supported by orientation detectors despite their relatively wide tunings.

Blakemore, Carpenter and Georgeson (1970) proposed a model for the perception of simple angle figures in which the neural representation of an angle figure is the summation of the neural representations of each of the lines presented singly More specifically, it was proposed that the orientation selective mechanisms in the human visual system are each excited by a relatively narrow band of orientations and inhibited by a broader band, both the inhibitory and excitatory functions being centred on the optimal orientation of the detector. On presentation of a single line, those detectors with optimal orientations around that of the single line will be excited, while those further away will be inhibited. The overall activity in the orientation domain will then correspond to the response curve of a single detector, which in turn is the sum of the excitatory and inhibitory weighting functions of the detector (Fig. 1.14).

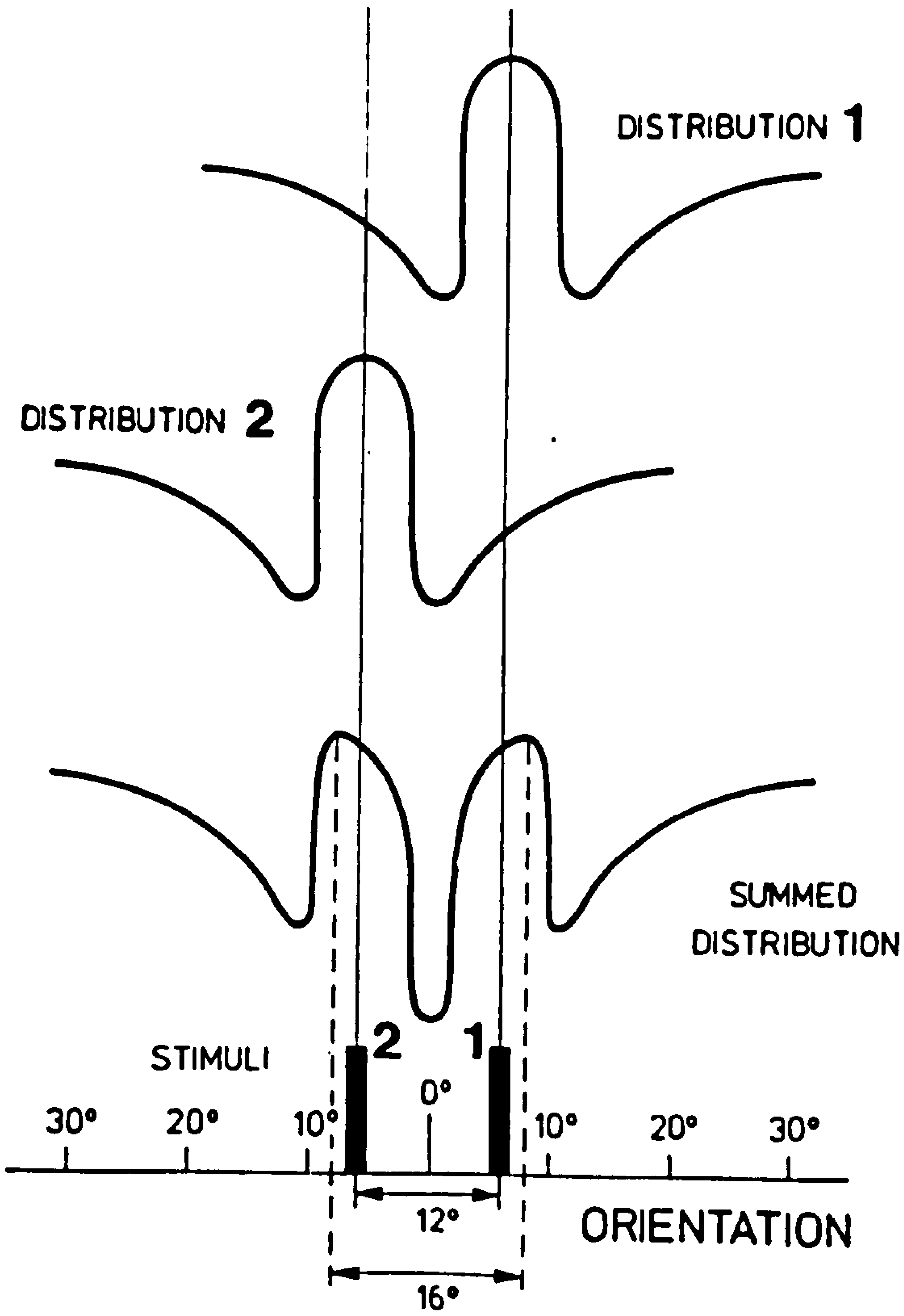


Fig 1.14 Diagram illustrating the perceived expansion of acute angles according to Carpenter & Blakemore's proposed mechanism based on lateral inhibition between orientation-selective channels in the orientation domain (From Carpenter & Blakemore, 1973).

The distribution of activity produced on the perception of an angle figure, assuming linear summation of excitation and inhibition, will be the sum of the two distributions produced by each of the component single lines. If the orientation of a line is assessed by the identification of the most active neurones, that is by identifying the position in the orientation domain of the peak(s) of the distribution, then this model predicts that when the angle size is sufficiently small for the distributions to overlap in part, then the two peaks of the distribution will be shifted apart from one another, and so the angle will appear larger than it actually is (see Fig. 1.14) This fits the known behaviour of perceived angles. It must be stressed, however, that the X-ordinate in this case represents orientation not spatial location, and that changes in the positions of the excitation-inhibition curves represent changes in orientation, not changes in location. This explanation of the expansion of acute angles in terms of lateral inhibition in the orientation domain should not be confused with theories in which inhibition in the position domain is said to cause apparent 'repulsion' of neighbouring contours (von Bekesy, 1967; Ganz, 1966b).

To measure the size of the effect, subjects adjusted the orientation of a comparison line until it appeared parallel to one arm of an angle which was fixed, the orientation of the other arm being systematically varied (Fig. 1.15). The distance between lines B and C had been determined such that there was a minimal influence of line A on settings of C. This procedure is based on the assumption, therefore, that the distorting effect of one line on another is localised, as any non-localised effect would influence line C just as much as line B, so that no effect would be observable. Biases in settings for parallelism were also previously measured, and the final results adjusted accordingly. Errors in the setting of C were determined for values of angle size ranging from 0° to 180° for each of a number of orientations of line B between 0° and 90°. For all values of B's orientation the maximum distortion was found for

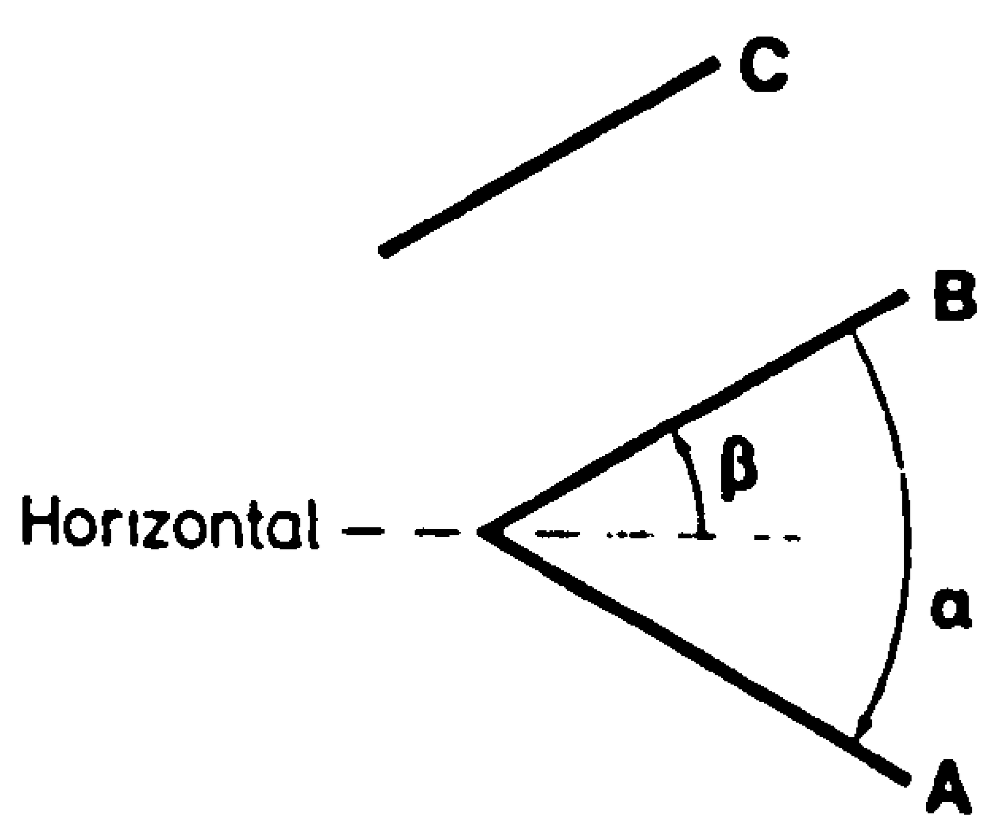


Fig 1.15 Stimulus configuration used by Carpenter & Blakemore (1973).

angles of 15°, but the error decreases more sharply when line B is horizontal or vertical than it does when line B is closer to the main oblique. For all orientations of B the error was zero for angles of 90°, and became negative for larger angles - as would be expected from the earlier findings that obtuse angles appear smaller than they are.

As Carpenter and Blakemore (1973) point out, these results could be explained in two ways. Either the spread of influence from A (in the orientation domain) is greater when A is horizontal or vertical than when it is oblique; or the spread of sensitivity of B to the influence of A is greater when B is oblique than when it is vertical or horizontal. A further experiment was undertaken to distinguish between these two possibilities. If B is set between 0° and 45°, and the shape of the angle expansion curve determined first with A at a greater angle (near the oblique) and then with A at a smaller angle (near the horizontal) then the second hypothesis predicts that the expansion should fall off equally in both directions, while the first suggests that the decline of angular distortion should be steeper on the side where A is nearer the oblique. The results were that the distortion falls off more rapidly when A is near the oblique, suggesting the first hypothesis to be correct, i.e. the changes in distortion are due to changes in the properties of A's 'output field' rather than in B's 'input field'.

From these data Carpenter and Blakemore (1973) conclude that if angle expansion is due to lateral inhibition in the orientation domain, then units optimally sensitive to oblique lines draw their inhibitory input from a broader range of orientations than do units tuned to the horizontal or vertical. This is shown by the slower fall-off of effect when B is oblique than when it is vertical or horizontal. Conversely, the inhibitory outputs of vertically and horizontally tuned units - the 'skirts' shown in Fig. 1.14 - are broader for horizontal and vertical orientations than for obliques.

In a final series of experiments by these authors, a fourth line, line D, was added to the display, having the same origin as lines A and B. A and B were set to such orientations as to give a large perceptual distortion, and the effect of varying the orientation of D was measured. Assuming no interactions between the influences of A and D on B and a simple linear system, it would be expected that the final angular distortion of B would be the sum of the effects due to A and D. The results showed that rather than increasing the displacement of B, the effect of line D was a reduction of distortion; the degree of decrease being greater the closer D approached A. In other words, line

D causes disinhibition - by inhibiting the inhibitory effect of A, indicating the inhibitory interaction put forward as the mechanism of angle expansion must be of the recurrent type.

The theoretical conclusions drawn from these findings are summarised thus:

> "If inhibition and excitation are really both linear, as Fig. 1.14 demands, then our data set rather stringent limits on the shape of the actual distributions of activity. First of all, since we find shifts of orientation of up to some 3°, it must follow that the convex-topped, excitatory portion of the distribution could not be narrower than twice this, i.e. 6°. Similarly, since angular changes are induced by line A forming an angle of only 5° with line B, at only 5° from the centre of the distribution the inhibitory "skirt" (with downward slope) must have already started. Unfortunately, it is extremely difficult to make observations with angles of less than 5° because the thickness of the lines tends to make them amalgamate near the apex. But it is difficult to believe that we should not have found some expansion with an angle of say 3°, if the apparatus had permitted it. As it is, the swift descent between 3° and 5°, which imparts a rather unphysiological appearance to the functions of Fig. 1.14, is necessary to meet these two conditions. Thus the assumption that excitation and inhibition add linearly is almost certainly wrong. On the other hand, if the recurrent inhibition acted presynaptically or in some other way to reduce the gain of the inputs, it would be possible to obtain angle expansion with angles smaller than the maximum angular change observable. We therefore conclude tentatively that the inhibition between human orientation detectors could be presynaptic rather than postsynaptic." (Carpenter & Blakemore, 1973, pp 300-301)

With some quantitative differences, these observations are similar to those of Bouma and Andriessen (1970) who also found maximal distortion of the perceived slant of a test line when the inducing line was either horizontal or vertical. Their results differ mainly in that whereas the angular separation giving maximal effect was 15° in the study of Carpenter and Blakemore (1973), Bouma and Andriessen did not obtain maximum effect until the angle between the two lines was as great as 45°. This difference was remarked upon with reference to the maximum effectiveness of smaller angles from 10° - 20° in the Zöllner illusion, for example, but they had "no evidence pertinant to the explanation of this apparent discrepancy" (Bouma & Andriessen, 1970, p 337).

A possible source of this difference in results may lie, however, in the different procedures used in the studies. Bouma and Andriessen used essentially the same technique as they had employed in their earlier study of the perception of the orientation of line segments (Bouma & Andriessen, 1968). This entailed the adjustment by the subject of a dot along an axis perpendicular to the test line until it lay on the imaginary extension of this line. The dot is assumed to be unaffected by any factors which distort the perceived orientation of the test line, and any misalignment is therefore taken as a measure of the difference between the perceived orientation and the physical orientation.

That the results obtained in both the single line studies and the angle studies are consistently different from corresponding studies in which the perceived orientation was estimated by means of setting a reference line to the same orientation as the test line (Andrews, 1965; Blakemore et al., 1970) suggests that the two tasks - orientation matching and line extrapolation - are mediated by different perceptual processes which differ in their operating characteristics with reference to orientation information. This identification of the method of measurement as the source of the discrepant estimates of induced orientation bias, rather than the differences between the stimulus patterns used, is supported by Wallace and Crampin's (1969) report that the maximum effect in the Zöllner illusion is found when the angle between the parallel transverses and the background is around 15°. In this study, for which the stimulus is necessarily quite different from those used by both Blakemore's group and Bouma and Andriessen, the change in perceived orientation of the transverse was measured as the change in orientation required to give the two transversals the appearance of parallelism - a precedure which is close to that used by Blakemore et al., and which gives comparable results.

A recent study by Emerson, Wenderoth, Curthoys and Edmonds (1975) compared the perceived orientations of a line in a stimulus configuration used by Lennie (1971). Both the parallelism and the colinearity methods were used and it was found that there were consistent differences between the two methods. This support gives further support to the suggestion that the differences between the angle expansion results of Bouma and Andriessen and those of other workers are due to the differences in methods used.

Bouma and Andriessen (1970) also made measurements of the size of effect when two dots (separation 28 min. arc) were substituted for the test line. Little quantitative difference was found between the magnitudes of orientational displacements of full lines and dots, indicating that at this separation the two dots representing the end points of the lines may act as a sufficient stimulus for the appropriate orientation analyser. This finding supports their earlier observation that line end-points are equivalent to line segments under some conditions (Bouma & Andriessen, 1968).

To explain their results Bouma and Andriessen (1970) did not invoke the concept of lateral inhibition, but proposed instead that the presence of the 'induction' line causes a reduction in the sensitivity of detectors tuned to that orientation and at the same time enhances the sensitivity of detectors tuned to the orthogonal orientation. "Because of these changes in the sensitivity envelope of the set of tuned orientation detectors, the test line now brings about different excitations in the sensors, to the effect that an extra bias is formed towards the perpendicular of the induction line" (Bouma & Andriessen, 1970, p 343). This, however, is suggested by Carpenter and Blakemore (1973) as being the result of lateral inhibition. In arriving at this formulation, their basic model proposed for the perception of orientation in the earlier paper (Bouma & Andriessen, 1968) is modified so that the detectors are now equally distributed along the orientation dimension, with different sensitivities - maximum for vertical and horizontal orientations and minimum for 45° obliques. Enhancement of sensitivity for orthogonal contours following adaptation has also been reported by Gilinsky (1967) and Gilinsky, Boyko and Baras (1967).

That the perceptual expansion of acute angles could be explained solely in terms of differential adaptation of orientation detectors was claimed by Coltheart (1971b) in his criticism of the lateral inhibition explanation given by Blakemore, Carpenter and Georgeson (1970). As Blakemore, Carpenter and Georgeson (1971) point out in their reply to Coltheart, the two alternative explanations predict opposite effects in the case where a third line is added to the angle figure, between the two arms of the angle. Adaptation theory predicts an increased distortion of perceived orientation of the test line (A) whereas the lateral inhibition theory predicts the reduction of effect - disinhibition - which was observed experimentally.

Further reasons for deciding upon the lateral inhibition explanation of angle expansion given by Blakemore et al. (1970) were firstly, that the effect remains when the subject makes his settings in 3-4 seconds, with long rest periods between each adjustment, implying a very short build-up time for the supposed adaptation. Secondly, because the observer generally glanced back and forth between lines B and C, recovery from 'adaptation' must have been very fast to prevent the perceived orientations of lines B and C being equally influenced by line A. Adaptation studies (e.g. MacKay, 1957; Blakemore & Campbell, 1969; Gibson, 1933) have shown that the time constants for adaptation are too long to fit these observations. Coltherart (1971b) claimed, however, that very short exposure times do lead to measurable adaptation effects (e.g. the tilt aftereffect) which, furthermore, have very steep decay functions. This claim has been recently substantiated by Sekuler and Littlejohn (1974) who found that the magnitude of the tilt aftereffect following an induction period of 18 msec. was the same as that following an exposure of 10 seconds. Protracted viewing - even for several seconds as mentioned by Coltherart - is not critical for the tilt aftereffect which is therefore tha product of a process with a relatively short time constant. In view of the evidence from disinhibition, this lead Blakemore et al. (1971) to propose that "far from the simultaneous effect being due to some ill-defined 'adaptation' or satiation' of orientation detectors, the Gibson effect itself may be due to the long-lasting consequences of prolonged inhibition. Adaptation may be due to lateral inhibition, but certainly not the reverse" (Blakemore, Carpenter & Georgeson, 1971, p 419). In this case Blakemore, Muncey and Ridley (1973) suggest that adaptation experiments (and those involving masking) may be measuring the broad tuning properties of this inhibition rather than the excitatory tuning characteristics themselves.

Yet another argument against adaptation theories of tilt aftereffects is the finding that the tilt induction can work backwards in time. Matin (1974) showed that under some circumstances and inducing field which followed the test target temporally could produce a tilt aftereffect. If the tilt aftereffect is related to an orientation specific threshold elevation, as has been proposed, it should be expected that this temporal sequence should generate threshold changes as well. The data of Matin (1974) are therefore consistent with the backward masking results of Sekuler (1965).

The notion that the tilt aftereffect is mediated by the same mechanisms as those which give rise to the angle expansion illusion received further support from Parker's (1974) investigation of the effect of different relative luminances of the two lines forming an angle, under conditions similar to those used by Carpenter and Blakemore (1973). He found that there was a progressive increase in the magnitude of the apparent angular separation of the two lines as the test line was made dimmer than the inducing line. When the luminance of the test line was held constant and that of the inducing line decreased, the magnitude of the effect diminished. These findings correspond well with his earlier results for the effect of different relative luminances on the tilt aftereffect (Parker, 1972). When taken together with the similarity between the tilt aftereffect and the simultaneous orientation contrast effect (Georgeson, 1973; Blakemore, 1973) and with Ware and Mitchell's (1974) study of the spatial tuning of the tilt aftereffect, these findings present strong evidence for the hypothesis that all these effects are closely related.

A further observation supporting this hypothesis has been presented by Over, Broerse and Crassini (1972). They showed that the difference between the simultaneous effects measured in central and peripheral vision corresponded well to those found for the tilt aftereffects measured under these two conditions.

These psychophysical studies may be taken, therefore, as providing supportive evidence for the hypothesis that the phenomenon of perceptual expansion of acute angles is a result of a lateral inhibitory process which operates between orientation detectors in the human visual system. Blakemore et al. (1970) and Carpenter and Blakemore (1973) have proposed that the response characteristic of an orientation detector may be considered as a summation of two functions, one excitatory and one inhibitory. Both functions, which may be approximated by the Gaussian function, have their absolute maxima at the same point in the orientation domain, but that of the excitatory function is greater than that of the inhibitory function. On the other hand, the range of the inhibitory function is greater than that of the excitatory function.

Benevento, Creutzfeldt and Kuhnt (1972) have made intra-cellular recordings from the cat visual cortex which suggest that the "retinotopic input to cortical cells is excitatory and that inhibitory intracortical connections between neighbouring cells or columns may account for some of their trigger features". The intracellular records showed that the response of these cells to slits moving across their receptive fields consisted of both excitatory post-synaptic potentials and inhibitory post-synaptic potentials. When the slits were optimally oriented and moving in the preferred direction excitation prevailed and the firing threshold was reached, whereas when the optimally oriented stimulus was moved in the non-preferred direction excitation was not sufficient to reach threshold. Changes of the orientation of the stimulus also resulted in striking changes in the proportion of inhibition to excitation - showing the inhibitory inputs to the cell to be orientationally selective - as are the suprathreshold spike responses of simple and complex cells. This inhibition was produced by changes in orientation as small as 10° and was present over a much wider range than excitation. Benevento et al. suggest further that the excitation which reaches a cortical cell or column is derived from the retino-geniculate projection to the cortex, giving a coarsely tuned excitatory input - the specificity of the cell being shaped by inhibitory inputs from neighbouring columns.

Also recording from the cat visual cortex (areas 17 and 18), Blakemore and Tobin (1972) first used moving bars to determine the preferred direction and orientation tuning of single units. When a tuning curve had been determined the cell was then stimulated with a bar at its preferred orientation, but with all of the stimulus screen around the receptive field filled with a high contrast grating which moved back and forth at random. Responses from the unit were recorded for each of a series of orientations of the surround grating. The effect of the grating was to inhibit the response over a range of orientations which was centred on the same orientation as the peak of the tuning curve. This inhibitory tuning curve showed a wider width than that given initially, which may be considered as the summation of the excitatory and inhibitory units.

The results from these two physiological studies are in very good agreement with the predictions made from the psychophysical studies described above, and with one another. Blakemore and Tobin (1972) re-state the proposal of Benevento et al. (1972) that the direct input to each cortical cell might make it into a crude orientation filter, while inhibition from cells in the same and neighbouring columns could sharpen up the tuning curve.

The discovery that gamma-amino-butyric acid (GABA) acts as an intracortical inhibitory neurotransmitter (Iverson, Mitchell & Srinivasan, 1971) which is reversibly blocked in the presence of bicuculline (Curtis, Duggan, Felix & Johnston, 1970) has given a further possibility of testing the hypothesis that the direct excitatory input from the LGN to visual cortical cells is broadly tuned, the stimulus specificity of these cells being effected by even more broadly tuned intracortical inhibitory connections with neighbouring cells. If the specificity of a visuo-cortical cell along any stimulus dimension is the result of intracortical inhibition mediated by GABA, then the blocking of GABA with bicuculline should result in an increase in the breadth of orientation tuning as wll as, for example, a reduction of the specificity of the cell with reference to directionality of movement etc.

Pettigrew and Daniels (1973) have reported that intravenous administration of bicuculline increased the breadth of orientation tuning, the responsiveness and the spontaneous activity of complex cells. The response characteristics of complex cells were modified also in that 'on' and 'off' areas could be discriminated with flashing spots - behaviour usually taken to be characteristic of simple cells. Hypercomplex cells were found to lose their inhibitory end zones and become responsive to lines which had previously been too long to be effective stimuli. All these changes are as would be expected. Simple cells, however, were found to become less responsive, and sometimes more narrowly tuned. These reported results, therefore, are partially in support of and partially in conflict with the hypothesis.

Rose and Blakmore (1974) carried out studies of the effect of bicuculline on the tuning characteristics of visual cortex cells using both intraveneous and topical application. Following intravenous application no consistent changes in the responses of two simple and three complex cells were recorded. This finding, together with the inconsistency of the results of Pettigrew and Daniels (1973), was attributed to the fact that intraveneously administered bicuculline has unknown potential influences on extracortical neural systems - such as the retina (Strchschill & Penwein, 1969), LGN (Phyllis, 1971) and reticular system (Tebecis, Hösli & Hass, 1971) - all of which are likely to change the activity of cells in the visual cortex in unpredictable ways which may not necessarily be attributable to the blocking of intracortical inhibitory inputs.

In order to limit the spread of effect of bicuculline and so reduce these uncertainties, Rose and Blakemore (1974) studied the effect of topically applied bicuculline on three simple cells and five complex. Under these conditions the orientation tuning of all three simple cells was broadened, and the other predictions described above were fully realised in two of the cells. Two of the cells also showed three- and five-fold increases in the receptive field area. The five complex cells showed more varied responses. Two showed increases in breadth of tuning, one of these also fulfilled all the other predictions of the hypothesis under examination. A third complex cell showed no consistent response to the application of bicuculline. The fourth was unusual in that clear inhibitory side flanks in its orientation tuning curve were observed prior to the application of bicuculline. The drug abolished these side flanks as well as increasing the breadth of tuning and the peak response. The fifth complex cell had a very similar receptive field and tuning curve to the fourth. Immediately following application of bicuculline both the peak response and the breadth of tuning decreased, but after 45 minutes both parameters increased to above the level before the drug was given. However, after more than two hours under the drug the inhibitory side flanks persisted, with strong inhibition even for a stimulus perpendicular to the preferred orientation. Rose and Blakemore have interpreted this as indicating the presence of some non-orientation specific inhibition, possibly not GABA-mediated, which may operate in addition to the orientation-specific inhibition in some or all cells.

Although the theoretical expectations are not unequivocally fulfilled in this study, the results obtained lend some support to the notion that the response specificity of at least some cells in the visual cortex is increased by an intracortical inhibitory mechanism mediated by the neurotransmitter GABA. Although topical application of drugs to the brain may lead to a more localised zone of influence of the drug, a relatively large volume of the brain will still be affected, a volume far greater than that containing, for example, one column.

The difficulty in attributing the cause of the changes, or lack of changes, in the receptive field organisation and response characteristics of a cell to either blockage of specific, stimulus-determined inhibitory inputs, or to more wide-spread or generalised changes in non-specific inhibitory processes following the administration of bicuculline can be greatly reduced by a third method of drug application - that of iontophoresis - employed by Sillito (1975a,b). Using this technique, very small quantities of a substance can be applied to the immediate vicinity of the cell under study, with a high degree of precision, via micropipettes running alongside the recording electrode.

Under these conditions Sillito (1975b) found the behaviour of cells under the influence of bicuculline to be more consistent than that observed in the other two studies. All cells, whether simple or complex showed a reduction in orientation specificity, a reduction or elimination of directional specificity and an increase in the overall size of the receptive field from which a response could be elicited. Two types of change of orientation specificity were seen according to the type of the cell. In simple cells the loss of orientation specificity was restricted such that cells which prior to the iontophoretic application of bicuculline responded to only one of the range of stimulus orientations (spaced at 25° intervals), were effectively stimulated by several orientations under the influence of bicuculline. Only a relatively small number of simple cells showed a response to all orientations after treatment. These observations are consistent, therefore, with the hypothesis that simple cells receive a broadly tuned excitatory input, the response tuning curve being made sharper by intracortical inhibitory inputs in the orientation domain.

For complex cells the picture was rather different. In the majority of cases orientation selectivity was almost completely lost following application of bicuculline, many cells responding as strongly to stimulus orientations at 90°

to the previously preferred orientation, with approximately the same response magnitude to these orientations as to the preferred orientation. In this case the observations suggest that the input to complex cells is not orientation specific, all the specificity normally observed being attributable to intra-cortical inhibition. These and other differences in the responses of simple and complex cells to bicuculline administration contribute further evidence against the simple hierarchical convergence model of Hubel and Wiesel.

While the physiological evidence cited is strongly in favour of the existence of lateral inhibitory processes which operate between neighbouring orientation analysers in the visual cortex, it is not yet sufficient to enable the relation between the neural mechanisms and the perceptual correlates to be made explicit. The results of the bicuculline experiments only demonstrate that intracortical inhibition is largely, but not wholly responsible for the specificity of the response of single units, as was proposed on the basis of psychophysical evidence from, for example, Parlee (1969). However, while data have been presented detailing the tuning curves of units with and without inhibitory inputs (Rose & Blakemore, 1974a; Sillito, 1975b) and also showing the inhibitory tuning curve compared with the response curve of units in the presence of inhibition (Benevento, Creutzfeldt & Kuhnt, 1972; Blakemore & Tobin, 1972), hardly any data are yet available which either directly compare or enable the comparison the the pure inhibitory function and the pure excitatory function with that of the cell under normal experimental conditions, although some idea of their relations may be derived from Rose and Blakemore (1974a, Fig. 1, p 377). Furthermore, neither Blakemore and Tobin (1972) nor Benevento et al. (1972) specify whether their units were simple or complex. This information is of particular importance in the light of the recent demonstrations (Watson & Berkely, 1974; Rose & Blakemore, 1974b; James, 1976) that simple and complex cells have significantly different orientation selectivities, notwithstanding the further possibility that these two classes of cells may be involved in quite different information processing systems (Ikeda & Wright, 1972, 1974; Maffei & Fiorentini, 1973).

1.4 An Appraisal of the Lateral Interaction Hypothesis for Orientation Contrast

In the experimental determination of the existence and characteristics of multiple-channel feature analysing mechanisms in the visual system of humans, whether operating in the domain of orientation, spatial frequency, retinal disparity or any other dimension of visual perception, a great deal of reliance has been placed on the data provided by adaptation experiments for the reasons given by Blakemore and Sutton (1969). So long as the nature of the adaptation process - that is the underlying neural mechanisms whose activity is responsible for the various perceptual consequences of the prolonged viewing of any spatio-temporal luminance distribution - remain unspecified, then the usefulness of this paradigm is limited. As the history of adaptation studies shows, until Ganz (1966a,b), the reduction in sensitivity following adaptation was attributed to some kind of 'fatigue' or 'satiation' of neurones consequent to prolonged excitation. Ganz proposed an alternative explanation: the reduction in activity of a unit (or channel) following adaptation is not due to a passive reduction in the excitability of the unit, but rather is an active elevation of threshold due to the longer time constant of the inhibitory response of the system which outlasts the excitatory response. In this way, he argued, the similarity between simultaneous contrast effects (illusions) and successive contrast effects (aftereffects) could be explained. Although the neural model to which this principle was applied was inappropriate, Blakemore, Muncey and Ridley (1973) have suggested that the principle itself may still hold, the aftereffects of adaptation being due to prolonged inhibition rather than to over-excitation (Blakemore, Carpenter & Georgeson, 1971). In this case adaptation experiments (and those involving masking) may be measuring the properties of inhibitory processes rather than the excitatory characteristics themselves.

The joint hypothesis that adaptation effects are a consequence of inhibitory processes whose activity outlasts the duration of the stimulus and that the sensitivity functions of these inhibitory processes are wider than those of the excitatory processes predicts that it should be possible to adapt a channel using a stimulus to which that channel does not give an excitatory response. While investigating the red-blue specificity of channels selectively tuned to the spatial frequency of vertical gratings (Blakemore & Campbell, 1969), Sharpe (1974) found that adapting to a pattern of one colour (e.g. red) can significantly elevate the contrast threshold for a pattern of the same or similar spatial frequency of the other colour (blue), even when the luminance of the adapting stimulus is too low to excite the colour channel responsible for the detection of the test grating. As it had been shown in the same study that the spatial frequency-specific channels are also colour specific insofar as the superimposition of a uniform background of one colour upon a sinusoidal grating of another colour has no effect on the subject's contrast threshold for that grating, cross-colour adaptation cannot, therefore, be a result of prolonged excitation. It is much more likely, as Sharpe concludes, that it is the result of prolonged inhibition of those spatial detectors responding to the test pattern by other spatial detectors stimulated by the adapting pattern. Sharpe and Mandl (1977) report further that this cross-colour adaptation is orientation-specific: the threshold elevation for gratings of a different colour from that of the adapting grating was only found for gratings whose orientation was the same or similar to that of the adapting grating.

In an analogous way Dealey and Tolhurst (1974) demonstrated that spatial frequency channels could be adapted by gratings sub-threshold to the adapted channel and concluded similarly that the adaptation aftereffects were the result of prolonged inhibition. Within the spatial frequency domain Tolhurst (1972) has found evidence which suggested that lateral inhibitory interactions occurred between detectors selectively tuned to spatial frequency. These inhibitory interactions would explain the simultaneous spatial frequency (or texture density) contrast effects (MacKay, 1973; Klein, Stromeyer & Ganz, 1974) which parallel those found in the orientation domain, while the spatial frequency selective adaptation aftereffects (Blakemore & Campbell, 1969; Blakemore & Sutton, 1970; Blakemore, Nachmias & Sutton, 1970; Blakemore, Ridley & Muncey, 1971), which are similarly analogues of those found in the orientation domain, would be explained by the prolonged inhibition hypothesis.

Although directly comparable studies have not been carried out in the orientation domain, the findings of Sharpe and Mandl (1977) suggest that orientation-specific adaptation is a consequence of the same process. As well as the fact that allsimultaneous and successive contrast effects found in the orientation domain are also spatial frequency specific and may be considered, therefore, as the same phenomena as spatial frequency specific adaptation, certain experimental discrepancies in the measurement of channel bandwidths have been noted in both domains. Spatial frequency channel widths as determined by adaptation techniques (Blakemore & Campbell, 1969; Tolhurst, 1972, 1973) have shown relatively little variation between studies but have been consistently broader than those determined by sub-threshold summation techniques (Sachs, Nachmias & Robson, 1971; Kulikowski & King-Smith, 1973). Similarly, particularly after Movshon and Blakemore's (1973) revision of Campbell and Kulikowski's (1966) data, most estimates of the half-widths of threshold elevation curves following adaptation of orientation selective channels give a value of about 7^{o}. The bandwidth as estimated by Kulikowski, Abadi and King-Smith (1973)employing the sub-threshold summation technique is considerably less - about 3^{o}. Since the sub-threshold summation method measures the extent to which the sensitivity to a line is enhanced in the presence of gratings or lines of various orientations at sub-threshold contrasts, the half-width measured in this way may be interpreted as the excitatory half-width of the channel - subthreshold stimuli causing no threshold elevation (Tolhurst, 1972; Dealy & Tolhurst, 1974). The present evidence suggests, therefore, that sub-threshold summation methods measure the bandwidth of the inhibitory effect exerted on neighbouring channels by the stimulated channel.

Now, the model proposed by Carpenter and Blakemore (1973) is based on an assumption that the excitatory response functions of orientation detectors have equivalent characteristics for all orientations while the inhibitory functions are wider for vertically and horizontally tuned detectors than for intermediate orientations. Despite the number of studies of the tuning of orientation detectors by adaptation, masking or subthreshold summation techniques, only one study of each of these types has included comparisons of tuning characteristics of the pertinent effect at different orientations. Campbell and Kulikowski (1966) found that the masking function was wider for oblique orientations than for vertical adapting stimuli, by about 3^{o}, but they did not examine any intermediate orientations. In a more comprehensive study Hirsch, Schneider and Vitiello (1974) showed that although the expected oblique effect for detection threshold was found - the threshold for oblique gratings being higher than that for verticals and horizontals - no differences were found between the adaptation tuning curves determined after adapting to gratings at 0^{o}, 22^{o}, 45^{o}, 67^{o} and 90^{o}. It has already been argued that masking and adaptation phenomena are supported by the same mechanisms and, as outlined above, there is evidence to show that these phenomena reflect the tuning characteristics of inhibitory processes. However, even if the former argument cannot be sustained, given the latter neither of these findings support the model described by Blakemore et al. (1970) and Carpenter and Blakemore (1973).

Differences in characteristics of the channels tuned to vertical and horizontal orientations and those tuned to oblique orientations cannot be attributed to differences in excitatory response characteristics either. Using the subthreshold summation technique Abadi (1974) has shown that the relations between relative sensitivity and angular difference between test and background gratings at test orientations of 90° and 45° cannot be distinguished. In both cases the half-widths obtained were about 3.7°. Further results obtained by Abadi show that astigmats exhibit no differences between the tuning curves for the subthreshold summation effect at their affected and unaffected orientations. Freeman and Thibos (1973) have shown that subjects who have reduced resolution for patterns of particular orientations due to astigmatism variation also show a decreased visual evoked potential elicited by a target at the deprived orientation. Thus, although the astigmat shows a reduced V.E.R.at the deprived orientation analagous to the reduced V.E.R. found by Maffei and Campbell (1970) for oblique orientations as compared with vertical orientations in normal subjects, in neither instance is there a corresponding alteration of orientation selectivity for the affected channels whether it is the excitatory or inhibitory characteristic which has been measured.

Since the demonstration that cats do not show meridional anisotropies when tested behaviourally (Bisti & Maffei, 1974), cat neurophysiological data cannot be considered to be of direct relevance in determining the source and nature of human meridional anisotropies. Although no work has been published concerning the measurement of contrast sensitivity etc. as a function of orientation in monkeys by behavioural methods, Mansfield (1974) has shown that populations of neurones responding to vertical or horizontal orientations are larger than those responding to intermediate orientations when counted in the striate cortex. That these differences in population size diminish in a markedly similar way to that in which human meridional anisotropies decrease in both animals as a function of retinal eccentricity suggests that the oblique effect should be considered in these terms. In view of the evidence contradicting the assumption made by Blakemore et al. (1970) that the tuning of inhibitory inputs to orientation selective channels varies with preferred orientation, it appears, therefore, that any explanation for the oblique effect, with reference to both lines and angles, must rest on the assumption that the population differences found by Mansfield in the monkey must also exist in the human visual system.

1.5 Preface to the Experiments

At the commencement of this study it was intended to use detailed observations of the constant errors in the perception of angle size and of the response error distributions - the variable error - to elaborate a detailed quantitative model of the interactions between orientation analysers. It was expected that these measures, particularly the error distributions, would give useful information concerning the response profiles of orientation analysers which, as Carpenter and Blakemore (1973) have pointed out, appear markedly non-physiological under their hypothesis.

As work progressed, the data collected became increasingly difficult to account for in terms of the lateral inhibitory interaction explanation of the perceptual expansion of acute angles. The emphasis of this study consequently was changed, with the primary objective now being to gather more detailed observations concerning the perception of angle size, with specific attention being given to the dynamics of the interaction between line stimuli of differing orientations.

While the majority of the experiments described were directly concerned with angle patterns, therefore, two brief experiments were carried out to look further at the orientation specific adaptation and masking effects. These were prompted particularly by the results obtained by Abadi (1974), Bisti and Maffei (1974), Hirsch, Schneider and Vitiello (1974) and Mansfield (1974), the implications of which were discussed in section 1.4. Because these two experiments relate to the assumptions underlying the lateral inhibition hypothesis, rather than to its predictions and performance, they have been presented first, although they were not performed until the end of the study. The masking experiment, particularly, was performed under severe limitations of time and should be taken as suggestive rather than definitive.

Chapter 2: Tuning Characteristics of Orientation Selective Channels

Experiment 1. McCollough Effect in Horizontal and Oblique Channels

The tuning characteristics of the inhibitory and excitatory functions of the orientation selective analysers in the human visual system feature prominently in current theories of orientation processing. The way in which tunings of the inhibitory functions vary with the preferred orientation of the analyser is a critical parameter in the most widely held explanations of the apparent expansion of acute angles and the variation of the magnitude of this apparent expansion with the orientation of the angle. Evidence suggesting that the inhibitory tuning characteristic of orientation specific channels is invarient with reference to the preferred orientation of the channel has already been presented (chapter 1.4). Before considering the detailed studies of angle perception, therefore, it was considered necessary to obtain more data concerning the relative tuning of orientation analyser inhibitory functions using a paradigm not yet reported in the literature - the orientation contingent colour aftereffect. The information so derived will enable a reduction of the number of alternative models to be taken into consideration when the implications of the angle studies are discussed.

Method

a) Stimulus Materials

The two orientations compared were 0° (horizontal) and 135°. Adapting stimuli were projected from prepared 35mm slides shown through a remotely controlled projector with an internal timing mechanism which automatically changed slides at a preset interval. The slides were made up in the following way:

Red - (590nm - 670nm) 1 layer of 'Cinemoid' gelatin filter No. 4.

Green - (480nm - 560nm) 1 layer of 'Cinemoid' gelatin filter No. 24

on either side of a square-wave grating which subtended a frequency of 2 cycles/degree at the viewing distance of 1.4m. These combinations gave approximately equal luminances on projection.

b) Adapting Procedure

All subjects were exposed to two adapting orientations, both the horizontal and the oblique. These sessions were separated by two days from one another.

The subject sat with head maintained in an upright postiion by a bite bar, in front of a projection screen at a viewing distance of 1.4m. The adaptation patterns, projected from slides, were viewed with both eyes. The internal timer of the projector was set to change slides at 5 second intervals and immediately after each change the subject pressed a button which reversed the direction of motion of the slide-carrier so that the same two slides were seen in a repeatedly alternating sequence. To protect against lapses of memory on the part of the subject, the sequence of slides in the carrier was: opaque, red, green grating, red, opaque. Subjects were intstructed to let their eyes roam around the target to minimise the build up of conventional afterimages, and to keep their eyes closed at the end of the 20 minute adaptation period to 'store' the effect until testing (MacKay & MacKay, 1975a).

c) Test Procedure

The two test patterns used in the measurement of the orientation contingent colour aftereffect (OCCA) magnitude are shown in Fig. 2.1 (a,b). Each had a rear-lit window - the C-section in pattern 1 and the central disc in pattern 2 - surrounded by a front-illuminated field. The two orientations in pattern 2 are orthogonal.

The magnitude of the OCCA was measured by having the subject adjust the colour of the light passing through the rear-illuminated window until it matched that of the surround. The apparatus by means of which this measurement was carried out was a slightly modified version of that described by MacKay and MacKay (1975b), as shown in Fig. 2.2. Rear

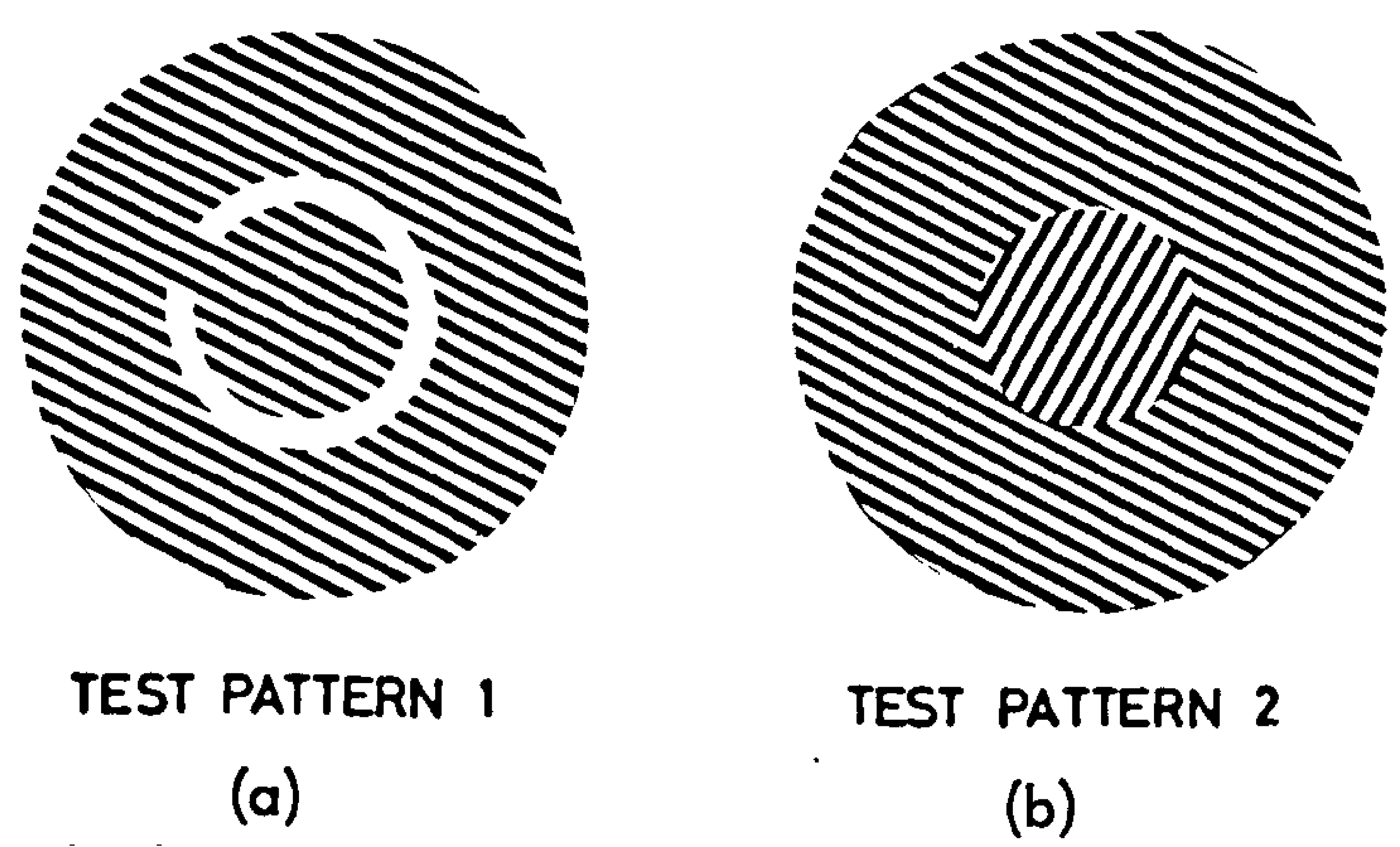


Fig. 2.1 The two test patterns used in the measurement of the strength of the OCCA, for details see text.

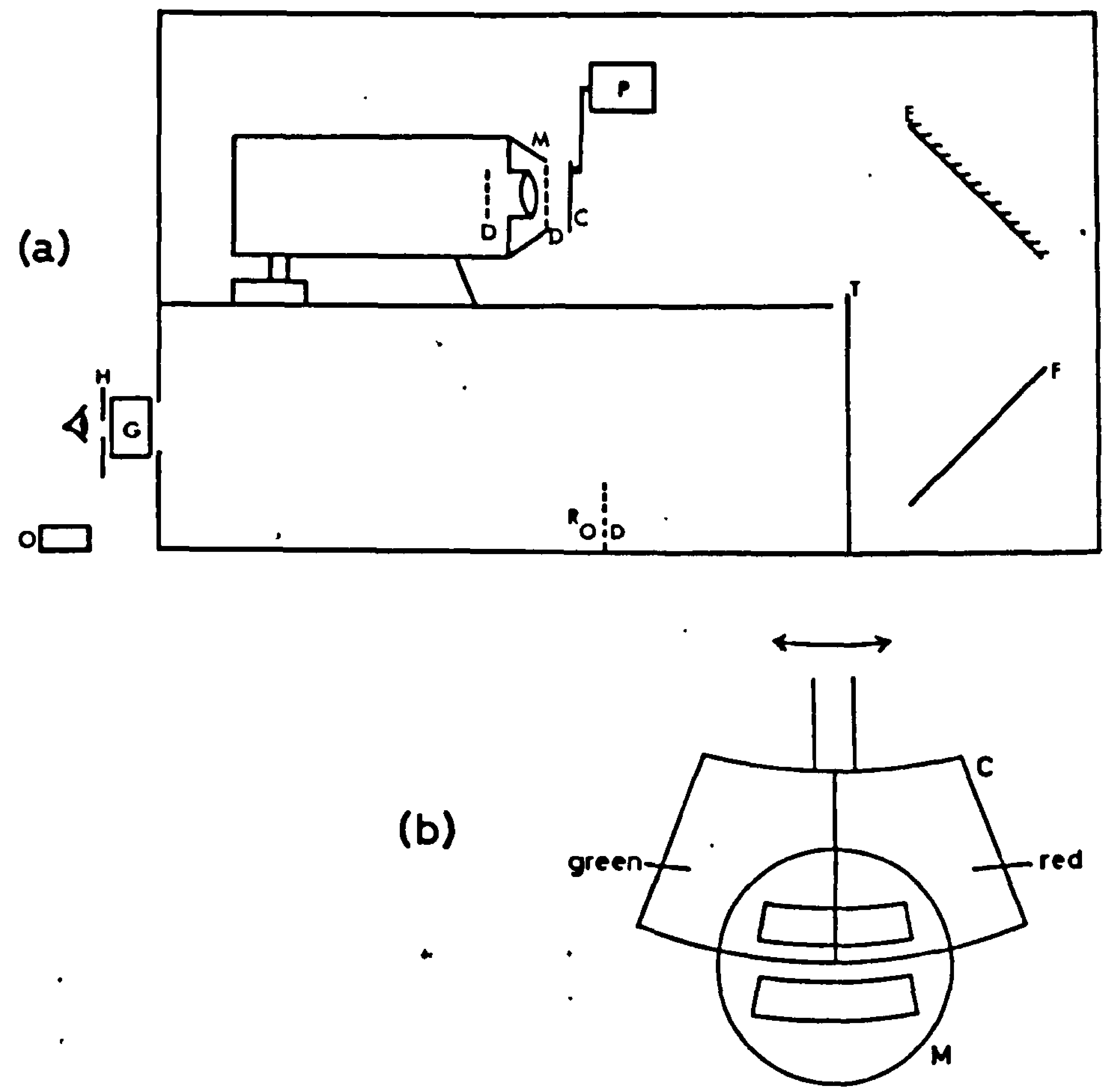


Fig. 2.2 Apparatus for measuring pattern contingent chromatic aftereffects.
(a) Whole apparatus, (b) detail of adjustable colour filter as viewed from T.
C - movable red and green filters; M - mask with slits, over projector lens;
F - diffusing screen (white card); P - pen motor; D - diffusing tissue; C - chin rest;
T - test pattern; R - low-voltage 'pea-bulb; E - mirror; G - dove prism; H - viewing aperture.

illumination was provided by a 100w projector with a diffusing screen (D) in the slide holder and a red/green filter (C), moved by a pen-motor (P), situated in front of a translucent aperture over the lens. The arrangement was such that the displacement of the red-green boundary (i.e. the excess of red over green, or vice versa) was linearly related to the pen motor current. A second aperture in the mask (M) allowed a fixed amount of white light to dilute the saturation of the beam (Fig. 2.2(b)). The reflector screen (F) ensured that there was maximum mixing of the light colours. Front illumination of the test pattern was provided by two low-voltage bulbs whose yellowish light (about 1.45 log ft lamberts) approximately matched the whitest mix seen through the rear-illuminated window.

The test pattern was viewed through a dove prism which was rotated, by the experimenter, in 5° steps from adapting orientation minus 90° up to adapting orientation plus 90°. A measure of the OCCA was made at each orientation.

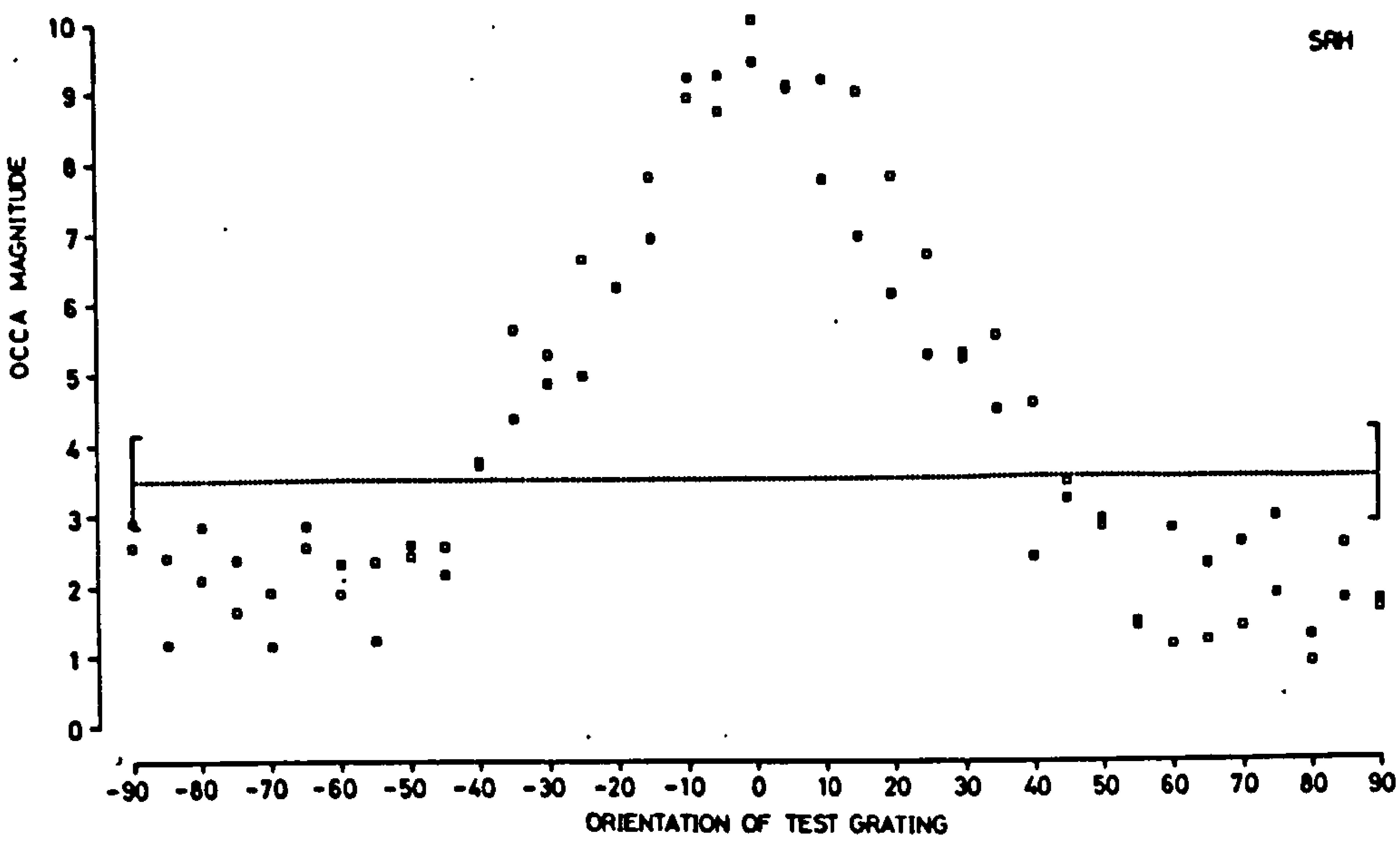
In the test apparatus the subject sat with chin supported and the untested eye overed with an eye-patch. While viewing the test window he adjusted its colour (by rotating a smooth control knob which controlled the pen-motor current) until its perceived hue matched that of the surround. When satisfied, the subject recorded the current in the pen motor by pressing a switch connected to an X-Y recorder. The position of the pen on the X-axis was determined by the orientation of the dove prism while the postion on the Y-axis recorded the pen motor current. A micro-switch in the chin rest, feeding a DC bias into the Y-input enabled a separate plot for each eye. Prior to each adapting session each subject was tested in this manner in order to establish a control baseline. Two observations were recorded for each eye at each orientation, one on the upward sweep and another on return.

The arithmetic mean of the post-adaptation measures minus the pre-adaptation measure was taken for each orientation. For comparison these resulting magnitudes were then normalised against the maximum peak-to-peak value for that trial.

Results

Tuning curves for the OCCAs are shown in Figs 7.3 and 7.4. The dashed horizontal line crossing each curve represents the mean pre-adaptation level with vertical bars at each end showing $\pm$ one standard deviation. Points above the base line represent colour settings redder than those made for the same orientations in the pre-adaptation control run, greener settings are represented by points below the baseline.

Comparison of the two tuning curves obtained for each subject-test pattern revealed no significant difference between the effects of the two adapting orientations (paired comparison t-test). These results agree with those of Hirsch, Schneider and Vitiello (1974), therefore, and disagree with those obtained by Campbell and Kulikowski (1966).



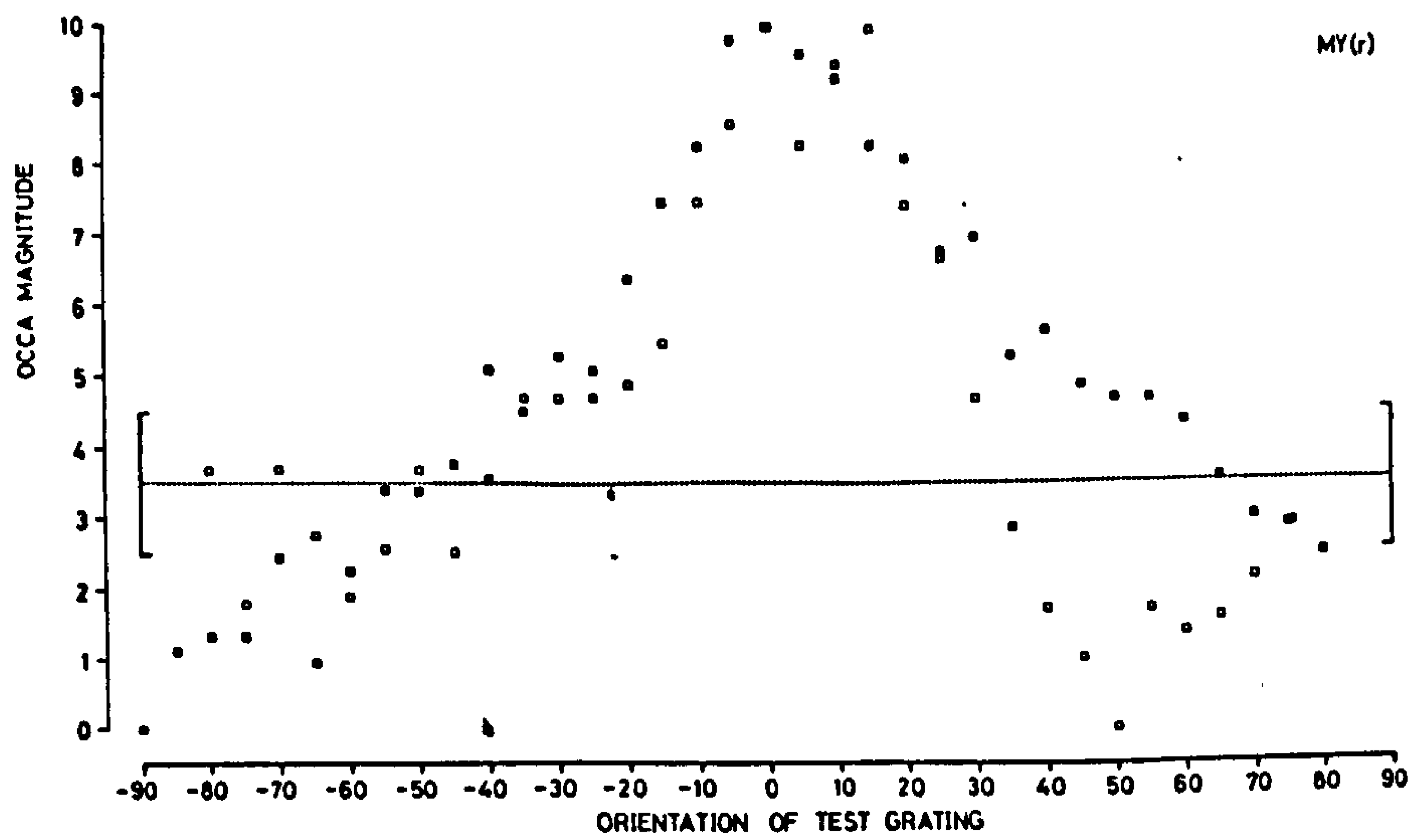


Fig. 7.3 OCCA magnitudes obtained with test pattern 1. Closed squares indicate OCCA magnitudes following adaptation to the horizontal grating; open squares indicate OCCA magnitudes following adaptation to the oblique grating.

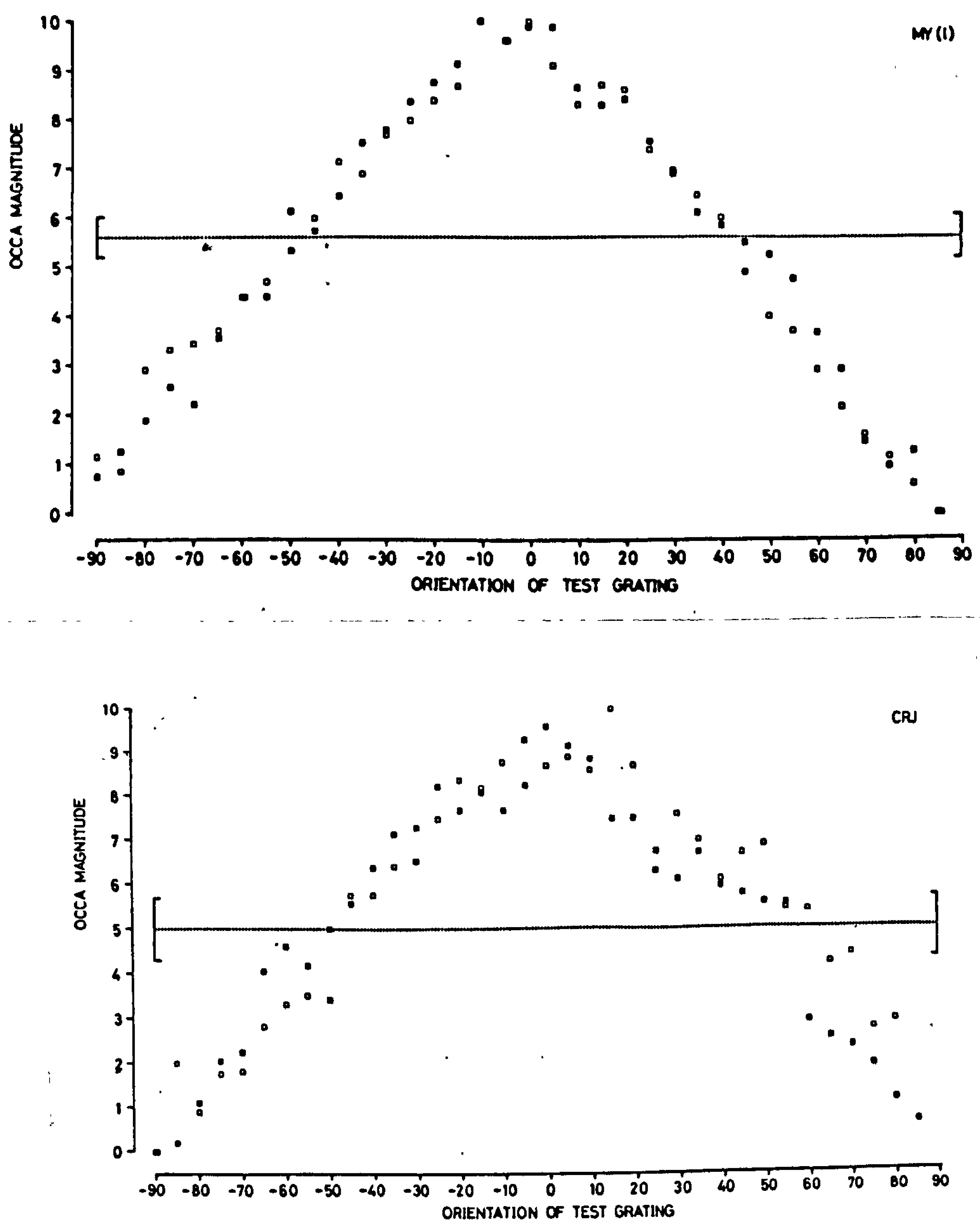


Fig. 7.4 OCCA mgnitudes obtained with test pattern 2. Closed squares indicate OCCA magnitudes following adaptation to the horizontal grating; open squares indicate OCCA magnitudes following adaptation to the oblique grating.

Subject	Estimated $\frac{1}{2}$-width	Test Pattern
SRH	18.25°	1
MY(r)	24.50°	1
MY(l)	23.75°	2
CRJ	28.50°	2

Table 2.1 Estimated half-widths of the OCCA

In Table 2.1 estimated half-widths of the adaptation effects are given for each subject. These are derived from the segments of the tuning curves above the pre-adaptation baseline, to which a straight line was fitted by the method of least squares, and from which the angular separation required to give a halving of the OCCA magnitude was determined. The figures given in the table are the means for the two halves of the tuning curve. Although there are large differences between subjects, intra-subject variation appears to be low, as is illustrated by the two values given for subject MY, which represent results for the two different test patterns used.

Although only one of the colour stimuli (green) was associated with a pattern of stripes, in both test-pattern conditions the results show that some colour has become associated with directions outside the range of the negative aftereffect. The curves show that while this is the case for both test patterns, the magnitude of greenness recorded was relatively smaller for the test figure containing only one orientation of stripes than it was for that containing the two orthogonal orientations. It can also be seen that when the test pattern contained only one direction, the green aftereffect appears as a noisy but relatively uniform level. In the presence of the orthogonal orientations, however, the magnitude of the green aftereffect bears a definite relation to the test pattern orientation.

Discussion

The results obtained in this experiment demonstrate that there is no difference between the tuning characteristics of horizontal and oblique orientation selective channels, as measured by the orientation specific colour aftereffect. Because most other studies of the orientation specificity of adaptation have used sinusoidal gratings (e.g. Blakemore & Nachmias, 1971; Blakemore, Muncey & Ridley, 1973), direct comparisons between previous results and the results presented here is not really practicable. This is especially so in the face of the finding that until an 'equivalent contrast' transformation is applied to the raw data the half-width of the adaptation tuning curve may vary between 10° and 50° according to the spatial frequency of the adapting grating (Blakemore & Nachmias, 1971). Hirsch, Schneider and Vitiello (1974), however, did use square-wave gratings (5.2c/deg.) as adapting and test stimuli, and report tuning curves for two subjects. The half-widths of these two curves are approximately 25° and 35° - values which are of approximately the same magnitude as those obtained in the present study, despite the differences in the spatial frequencies of the gratings used.

That the two different studies, using similar stimuli, should obtain comparable results, despite the difference in the experimental paradigms suggests that the characteristic of the visual system being measured is the same in both experiments. Following the argument that this characteristic is indeed the inhibitory output function of the orientation selective channels, then Creutzfeldt's (1974) proposal that the orientation specificity of the McCollough effect is a consequence of a "temporary alteration of inhibitory connections between colour sensitive cells and orientation sensitive cells in cortical columns" is consitent with the experimental findings.

The results of both the current study and that of Hirsch et al. exclude differences between the ranges of inhibitory output of channels tuned to the vertical/horizontal and those tuned to obliques as a possible explanation for observed meridional variations in the magnitude of simultaneous orientation contrast phenomena. The discrepancy between the adaptation studies and the masking study of Campbell and Kulikowski (1966) which does show a difference between vertical/horizontal and oblique channels, though not in the direction expected under the Carpenter and Blakemore (1973) hypothesis, remains unresolved. In view of this a brief attempted replication of the simultaneous masking experiment was carried out as the second experiment in this series.

Experiment 2. Simultaneous Masking Functions of Vertical and Oblique Channels

Method

Masking and test gratings were generated on the screens of two Hewlett-Packard HP - 1300 display oscilloscopes postioned so as to be superimposed when viewed through a beam-splitting cube. Only a central, circular area of each screen was visible (subtending 8.25 deg. arc to the observer), the remainder being masked off with black card. Under the dim room illumination used during the experiment the surround luminance of this circular field was 0.77 cd./m^2. (All direct luminance measures were made with an SEI photometer)

Both gratings were derived from the same original X-Y-Z signals, giving identical square gratings of 2 cycles per degree, in phase. The field luminance, in the absence of both masking and test grating modulation of the raster was 14.97 cd/m^2. The contrast of the masking grating, with an unmodulated test field was 0.57 (C = lmax - lmin / lmax + lmin). The orientation of the test grating was fixed at 90° relative to the screen so the oblique masking grating had to be obtained by physical rotation of the whole oscilloscope. The signal which generated the test grating was passed through a sine-cosine potentiometer, which enabled continuous variation of the orientation of the test grating, whose contrast was also under the control of the observer.

Contrast thresholds for the test grating were obtained with the mask field unmodulated, at orientations -5°, -10°, -15°, -20°, -25°, -35°, -45° and -90° relative to each of the masking orientations (90° and 45°). The observer used the method of adjustment, four distinct contrast settings being obtained for each of these orientations. The threshold modulation depth of the test grating was directly read from an oscilloscope monitoring the Z-input to the test 'scope. These measures were then repeated in the presence of the masking gratings, eight separate threshold settings were made at each test-grating orientation, one on each of four sweeps away from the masking orientation and one on each of the return sweeps.

The observer, SRH, had normal uncorrected vision, viewing was binocular and no artificial pupils were used.

Results

The contrast thresholds and the relative threshold elevation due to the presence of the masking gratings at the two orientations are given in Table 2.2 and the masking functions are shown in Fig. 2.5. The two masking functions were compared using the paired observation t-test, and were not found to be significantly different ($t = 0.9$, d.f. $= 7$).

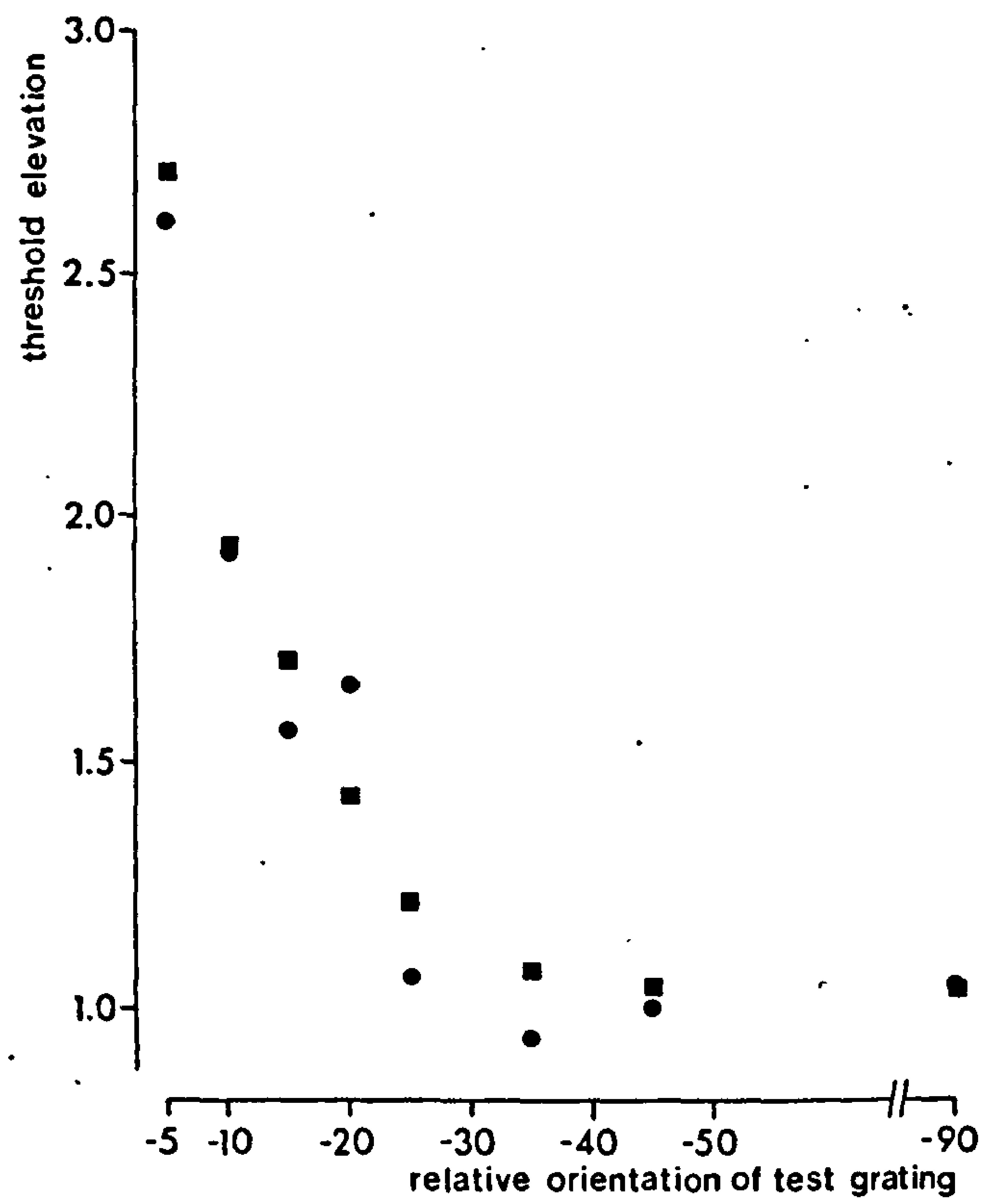


Fig. 2.5 Relative threshold elevations for the two masking orientations; ● - 90° mask, ■ - 45° mask.

Discussion

The results obtained from this brief masking study are in good agreement with those obtained for orientation-specific grating adaptation (Hirsch, Schneider & Vitiello, 1974) and the orientation contingent colour aftereffect (Experiment 1), which give no evidence for differences in the tuning characteristics of the orientation specificity of the effects at vertical/horizontal and oblique orientations. Although the half-

Relative Orientation of Test Grating	Vertical Mask (90°) Unmasked Contrast Threshold	Vertical Mask (90°) Masked Contrast Threshold	Vertical Mask (90°) Relative Threshold Elevation	Oblique Mask (45°) Unmasked Contrast Threshold	Oblique Mask (45°) Masked Contrast Threshold	Oblique Mask (45°) Relative Threshold Elevation	Difference (E90-E45)
-5°	0.057	0.150	2.61	0.072	0.196	2.71	-0.10
-10°	0.064	0.123	1.93	0.070	0.136	1.94	-0.01
-15°	0.066	0.103	1.56	0.070	0.119	1.70	-0.14
-20°	0.051	0.084	1.65	0.066	0.094	1.42	0.23
-25°	0.070	0.074	1.06	0.060	0.072	1.21	-0.15
-35°	0.074	0.070	0.94	0.055	0.060	1.08	-0.14
-45°	0.074	0.074	1.00	0.051	0.053	1.04	-0.04
-90°	0.051	0.053	1.04	0.072	0.074	1.03	0.01

$t = 0.90$, $d.f. = 7$

Table 2.2 Masked and unmasked contrast thresholds for 90° and 45° masking grating orientations.

widths of the functions derived in these studies vary according to the experimental method used, suggesting that there are some differences in the precise details of the underlying mechanisms responsible for these phenomena in terms of their responses to the slight variations in the stimulation techniques, there are good reasons to believe that the adaptation aftereffects and the masking effects do reflect the inhibitory characteristics of the orientation selective channels in the visual system (Parlee, 1969; Dealey & Tolhurst, 1974). The nature of the mechanisms underlying the McCollough effect are still not fully elaborated (Ellis, 1977), but if the observed orientation specificity of this effect does prove to be derived from the adaptation of the orientation selective channels which are responsible for the simpler orientation selective effects, then the observations relating to this phenomenon also show a lack of difference between vertical/horizontal and oblique channels.

Conclusion

Further examination of the relative tuning characteristics of orientation-specific channels tuned to vertical or horizontal orientations and to oblique orientations was provoked by reports that adaptation and sub-threshold summation effects revealed no differences between the tuning characteristics of channels selective for these orientations. These findings are in agreement with neurophysiological studies which have shown similarly that the tuning characteristics of single units in the visual cortex of the cat (Rose & Blakemore, 1974b) and of the primate (Mansfield, 1974) do not differ according to the preferred orientation of the unit. The brief studies reported here provide further corroboration of these findings and, consequently, contribute to the doubt cast on any hypotheses concerned with the perceptual expansion of acute angles which are based on differential inhibition or excitation as a function of orientation.

Chapter 3: Automated Method of Constant Stimuli

All further studies to be described were based on one principal experimental procedure and were carried out using the same techniques for stimulus generation and response recording. These procedures and techniques will be described in detail in this chapter although some particulars may be given, where appropriate, in the description of specific studies in later chapters.

a) Psychophysical Methods

The dependent variables in all the following studies were the means and standard deviations of response error distributions. The procedure adopted for the determination of the values of these quantities under the range of stimulus conditions employed was the method of constant stimuli where the subject has to make a forced choice according to his perception of the relative magnitudes, along the attribute under consideration, of two simultaneously presented stimuli, or between a single stimulus and some internal representation of a quality such as verticality or orthogonality.

Traditionally this procedure is rather lengthy and tedious for the subject insofar as many trial runs may be required in order to determine an approximation to the mean of the response error distribution (equivalent to the PSE) which may differ considerably from the PPE. Even when the PSE is determined, given no prior information concerning the standard deviation of the response error distribution, many stimulus presentations are required to accurately estimate the slope of the psychometric function - which is equivalent to the standard deviation of the error distribution. In the face of these difficulties much of the research concerned with the perception of orientation and angle size has been carried out using alternative procedures such as the staircase method and its derivatives or the method of adjustment.

While these procedures do give reasonable estimates of the constant errors or biases (as determined by taking the difference between the PPE and the PSE), they are not especially suitable as indicators of the standard deviations. As the standard deviation of the response error distribution represents the minimum difference between the stimulus components required for the perception of this difference to a response-correct criterion, i.e. the difference threshold, which was one of the variables under investigation in this series of studies, neither of these two methods was considered appropriate. Fortunately, however, Andrews (Andrews, 1967a; Andrews, Butcher & Buckley, 1973; Andrews, Webb & Miller, 1974) has derived an experimental procedure based on the method of constant stimuli. This version overcomes the practical drawbacks mentioned by selecting for presentation to the subject only those stimulus difference levels within a range about 2.5 times the standard error of the response distribution. This stimulus range, symmetrically disposed about the mean of the response error distribution is that which defines the psychophysical function most accurately. Although this technique would be extremely laborious were the experiment to be run under human control, it is easily implemented when the system is under computer control.

One run of an experimental session comprised approximately 120 stimulus presentations preceded by a set of pre-run trials. Twenty-one levels of difference between stimulus components were available to the controlling computer program, ten on each side of the PPE, as well as the zero difference level itself. The pre-run used a staircase method to obtain an estimate of the PSE and the width of the range of stimuli to be used in the main run. This part of the run was terminated after three reversals of direction of stimulus level change. The mean of the four (out of 21) stimulus levels at which reversals occurred was taken as the initial working PSE, while the difference between the last pair of highest and lowest stimulus levels obtained - the two levels at which the two last reversals occurred - gave the intial estimate of the width of the range of stimuli required for the main run.

According to the values of these two parameters four stimulus levels were selected for presentation. The particular stimulus to be presented on each trial was selected by a random number generator. The selection was constrained, however, to ensure that the same stimulus was never shown more than twice in succession, and did not have the same sign (with reference to the mid-point of the stimulus distribution) more than five times in succession. This saves the subject from the disturbing feeling that he ought to be responding 'the other way'; which may lead to a shift in criterion (an over-readiness to respond in the opposite way to recent responses).

After the first thirty trials in the main run the response error distribution was systemmatically compared with a series of optimal response distributions, each derived from possible stimulus distributions (Andrews, personal communication). According to the goodness of fit between the observed and expected distributions the stimulus distribution was either unchanged, or changed to that from which the expected distribution which best fitted the observed distribution was derived.

In this way the response error distribution was optimised for the subsequent computation of the psychometric function. The criteria by which the goodness of fit was judged were input to the program at the beginning of each run. The values of these criteria were not varied throughout the series of studies carried out using this system. Subsequently this 'TEST' procedure was called by the main 'RUN' program at the end of each group of fifteen trials and the response error distribution represented by the thirty most recent responses used to monitor and change the stimulus set, if necessary, in the same way. Thus responses to 120 stimulus presentations (falling into eight groups of fifteen) were obtained and recorded.

The number of stimulus presentations was not set to 120 in order to allow for the various unpredictable events which tend to occur during experimental sessions. If the subject was not able to fixate correctly for a given presentation, due to coughing or sneezing for example, he was requested not to record a response. Alternatively, should the subject 'realise' that he has pressed the wrong response button, he was able to cancel that response. In these cases the tally of responses was not incremented, the criterion for termination of a run being not 120 presentations but 120 responses.

At the end of each run the response distributions were printed out by teletype in blocks of 15 so that within run variations of the PSE and stimulus range (and thus of the standard deviation of the response distribution) could be detected. An accumulated response distribution was also printed. The computer then carried out a Probit analysis (Finney, 1952) on the results. This analysis gives the median of the response error distribution and a rate of change of the error probability, as a function of the increasing magnitude of the signed difference between the sizes of, for example, the two angles in the stimulus, in the region of the median. If the error distribution is normal, these define repectively the mean and the standard deviation of the distribution. The analysis program 'PROBIT' computed a chi-square for the goodness of fit between the response error distribution and the normal distribution derived from the computed median and slope. On the rare occasions that the chi-square value was so large that the response error distribution could not be considered as a good approximation to a normal distribution the results for that run were discarded and the run repeated as the precision of the resulting estimates of the distribution parameters would be too low. On no occasion did any experimental stimulus condition give response error distributions which were consistently not normally distributed.

Probit analyses were made for each half-run, as well as for the whole run, but differences between half-runs usually proved small. Where there were large differences between half-runs, inspection of the blocked printout of responses almost invariably indicated that the stimulus set designated by the pre-run were inappropriate and that the bulk of the first half of the run had been taken up by adjustments of the stimulus set toward one which was appropriate. If this occurred the run was repeated, by-passing the pre-run and starting the run proper with the stimulus set on which the discarded run had stabilised. When this was done the repeat run was usually satisfactory. On the few occasions when it was not satisfactory it was found that the print-out showed a reversion to the stimulus ensemble selected by the initial pre-run. Under these circumstances the run was again repeated and the first run considered as an inexplicable aberration. This sequence of events occurred only several times out of the hundreds of runs carried out for the whole series.

b) Experimental Apparatus: I Hardware

The basic block diagram of the experimental system hardware is shown in Fig. 3.1.

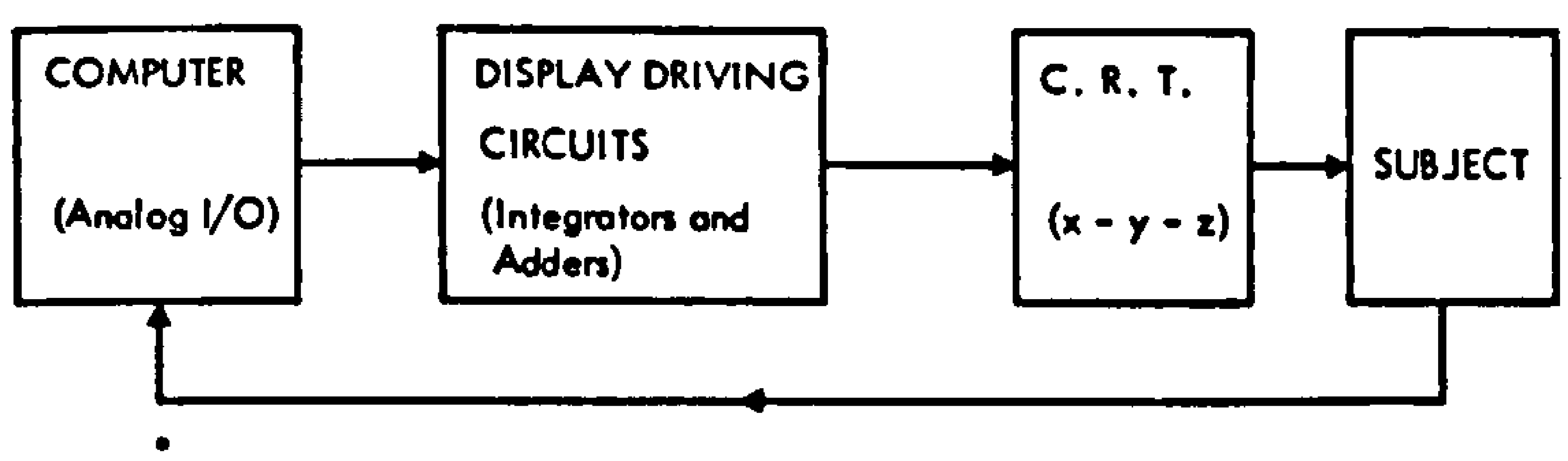


FIG. 3.1 Block diagram showing the basic plan of the computerised experimental system.

On the basis of the stimulus specification input at the beginning of the run the necessary voltages required to define the stimulus pattern for display on the CRT (LAN Electronics Display Unit 419DD), operating in the X-Y mode, were computed by the program 'COMP'. All stimulus patterns comprised no more than 4 lines and a fixation point. Assuming that all four lines and the fixation point were required for a particular stimulus pattern, the voltages required to define the pattern were:

a) X and Y voltage levels to define the origins of the lines and the location of the fixation point;

b) X and Y voltage levels to define the end points of the lines.

A minimum of four analogue outputs were required, therefore, for the minimum specification of the pattern components. Line origin loci and the fixation point coordinates were computed with reference to a screen of dimensions 1052 by 1052 units (in practice 1000 by 1000) corresponding to the resolution of the 10-bit summators of the analogue outputs.

The screen centre corresponded, therefore, to (500,500) which in turn corresponded to (0,0) volts.

In order to make maximum use of the 10-bit resolution provided by the analogue outputs, all voltage levels for line end-point descriptions were computed independently of the physical length of the line to be drawn. Where possible this variable was set by off-line adjustment of the signal amplitude. Exceptions to this rule were made when a comparison line longer than the stimulus lines was required for one of the studies to be described. The positions of the end-points were calculated as $X_e = 5.\cos\theta$, $Y_e = 5.\sin\theta$; where θ is the orientation of the line required, referred to the horizontal (0^o), the range of the analogue outputs being $\pm$ 5 volts.

Stimulus timing was also under direct computer control. The basic unit of stimulus duration timing was set at 1 msec. during which one stimulus component (line or point) was drawn on the CRT. A secondary unit of 5 msec. was the time taken for the most complex stimulus pattern - four lines plus fixation point - to be drawn on the CRT once. The repetition rate for the whole stimulus was, therefore, 200 Hz, well above flicker fusion frequency. One further output, in addition to the stimulus defining voltages, was a timing synchronisation pulse generated by the computer at 1KHz. This pulse was derived from one of the analogue output registers. Although the analogue voltage outputs were 10-bit the output registers were 12-bit, corresponding to the 12-bit word-length of the PDP-8, each bit being independently accesible. This pulse, taken from bit 0 of one of the output registers, which did not contribute to the voltage summator of the analogue voltage output, was used to regulate the timing of the operations carried out by the custom-built integrating circuits between the computer and the CRT amplifiers. A more detailed block diagram of the system is shown in Fig. 3.2.

In this "interface", which was distal to the computer and proximal to the CRT stimulus display, the X and Y voltage levels defining the line end points were integrated to give a ramp-like waveform. After integration these X and Y signals were summed with the voltages defining the line origins and transmitted to the X and Y amplifiers of the CRT. The circuit diagram for the X channel of the interface is shown in Fig. 3.3. With the exception of the operational amplifier providing the switching voltages to the f.e.t.s in the integrator, which served both X and Y channels, the Y channel was identical and, therefore, is not shown.

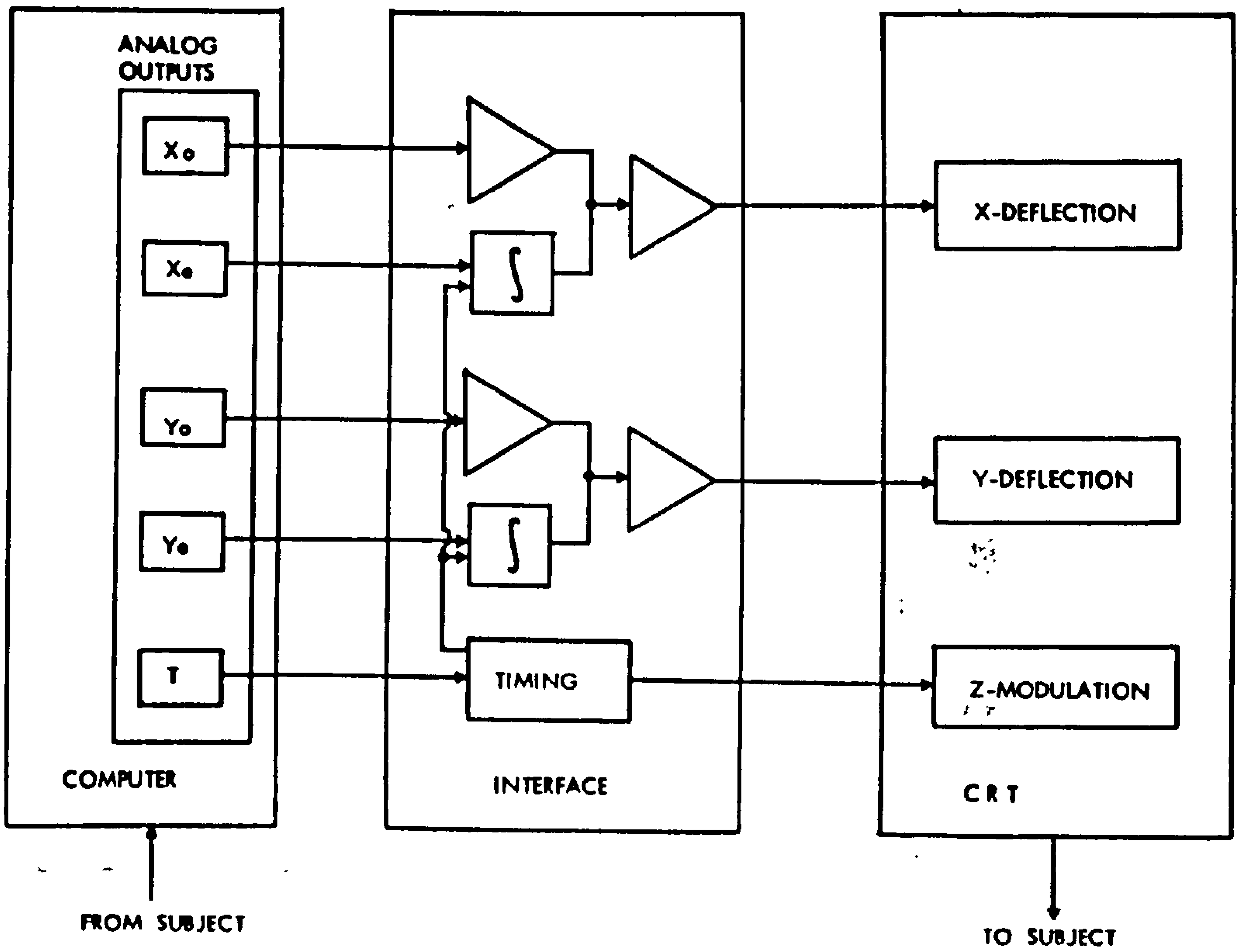


FIG. 3.2 Block diagram illustrating the functional components of the stimulus generating apparatus.

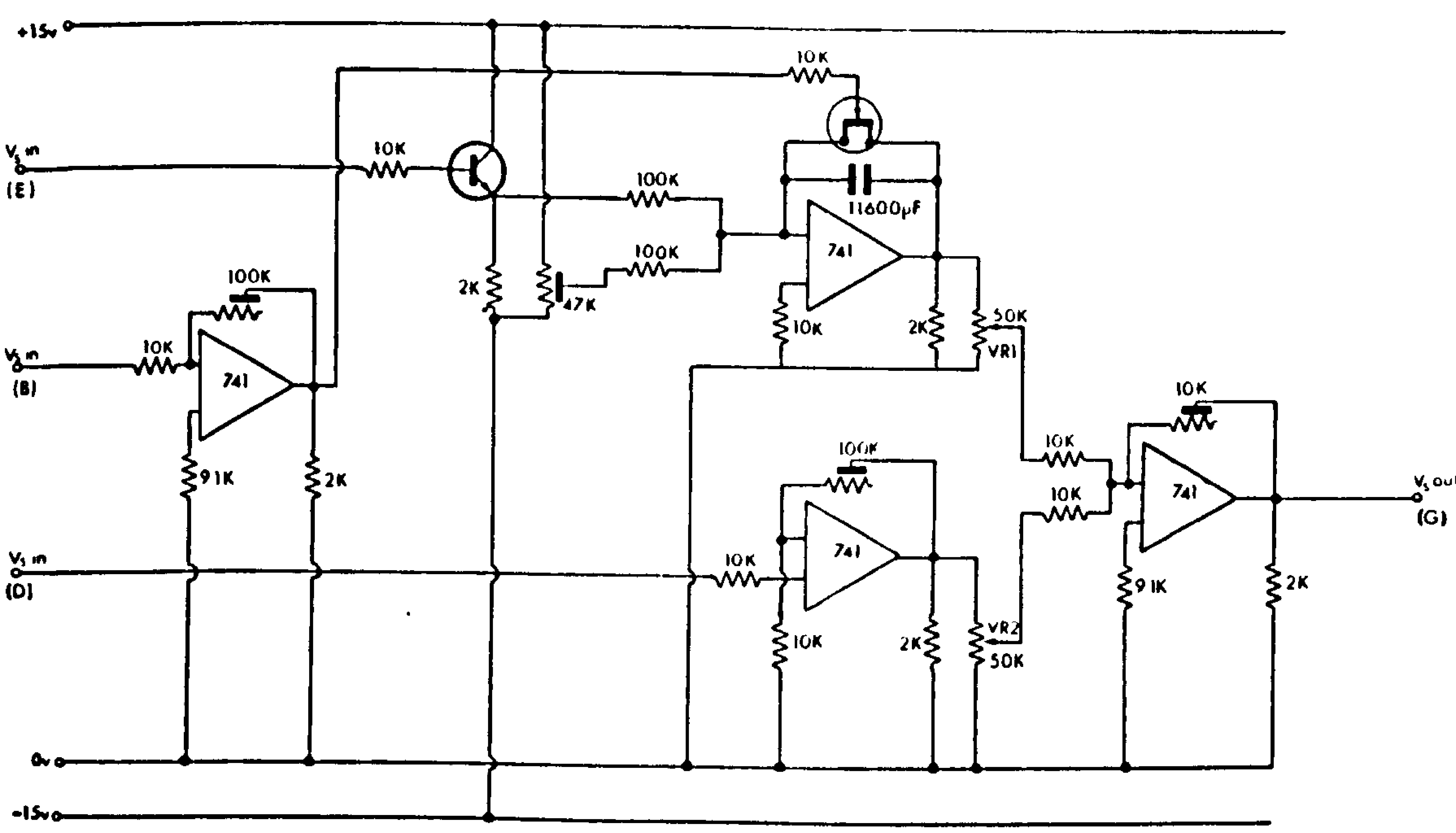


FIG. 3.3 Circuit diagram for the X-channel of the stimulus generating interface. VR1 and VR2 enable independent attenuation of the ramp and offset components of the signal respectively.
(Capital letters at inputs and outputs refer to the waveforms shown in FIG. .6.)

The timing circuitry comprised three stages of signal processing. In the first the brief timing pulse generated by the computer triggered a monostable whose pulse width was set to approximately 950 microseconds. This pulse was passed to the integrator f.e.t.s via the inverting operational amplifier on the X-channel board, putting them into conducting states and thus initiating the integration of the voltages representing the X and Y components of the line end-point. This monostable pulse was also used to trigger a second monostable whose pulse width was variable and from which the Z-modulation signal was derived. This variable pulse-width was, therefore, one of the means by which the line lengths of the pattern were varied. (This method was chosen when other circumstances permitted, as it affected the line length directly, while use of the potentiometers on the integrator outputs required recalibration to ensure that the maxima were the same for each channel. These potentiometers were usually used for such fine adjustment. Variation of the gains of the X and Y amplifiers of the oscilloscope had the same drawback, as well as the further drawback of affecting the line origin voltage magnitudes, and so were not used.)

A variable time constant RC network was added to the input end of the second monostable which enabled the blanking out of undesirable oscillations in the X and Y ramp waveforms, generated at the onset of integration. This blanking out of the initial few microseconds of the ramps required compensation in the computation of the line origin coordinates. The delay also gave the possibility of introducing the absence of angle vertex as a potential experimental factor, the size of the gap being continuously variable. The circuit as described so far is shown in Fig. 3.4.

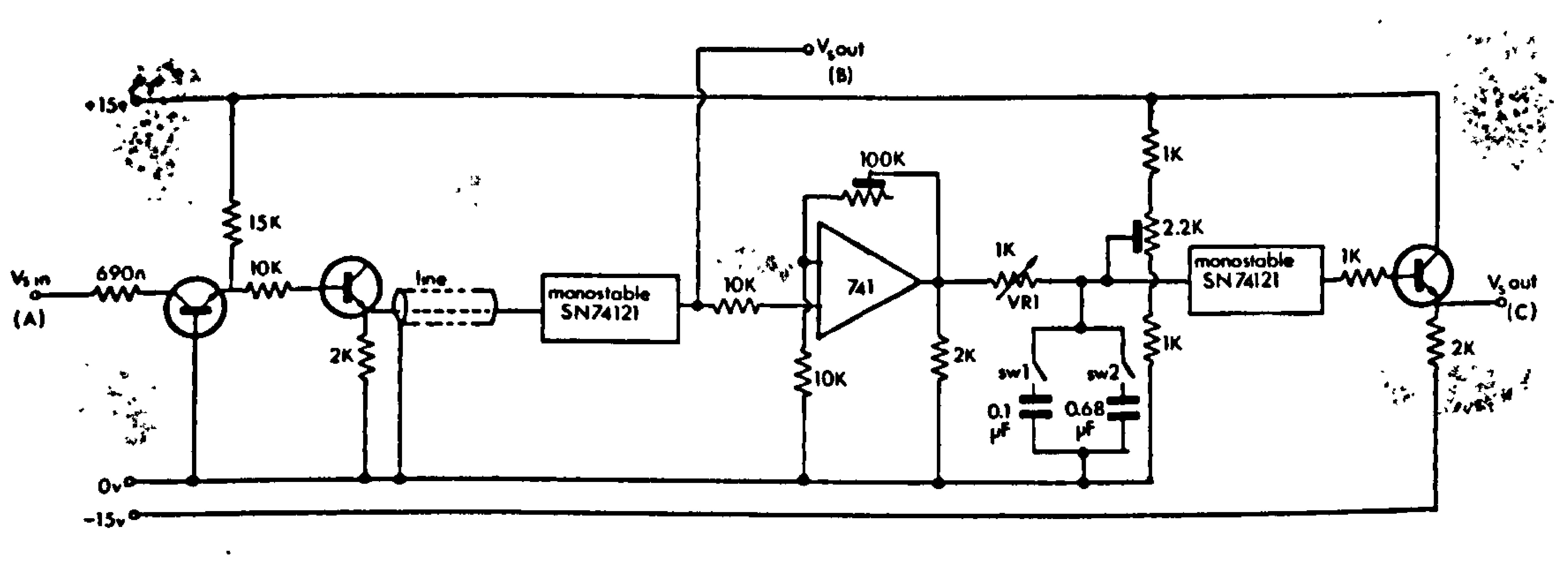


FIG. 3.4. Circuit diagram for the first two stages (see text) of the Z-modulation channel. VR1 enables variation of the delay between the trigger signal and the onset of the output of monostable 2. (Capital letters at inputs and outputs refer to the waveforms shown in Fig. 3.7).

The third stage of the Z-channel was required because of the slow respnse of the Z-channel of the oscilloscope. Although the CRT phosphor was a fast TV phosphor, the relation between Z-input and phosphor output, for a rectangular input is shown in Fig. 3.5. Presumably the slow response was in the amplifier.

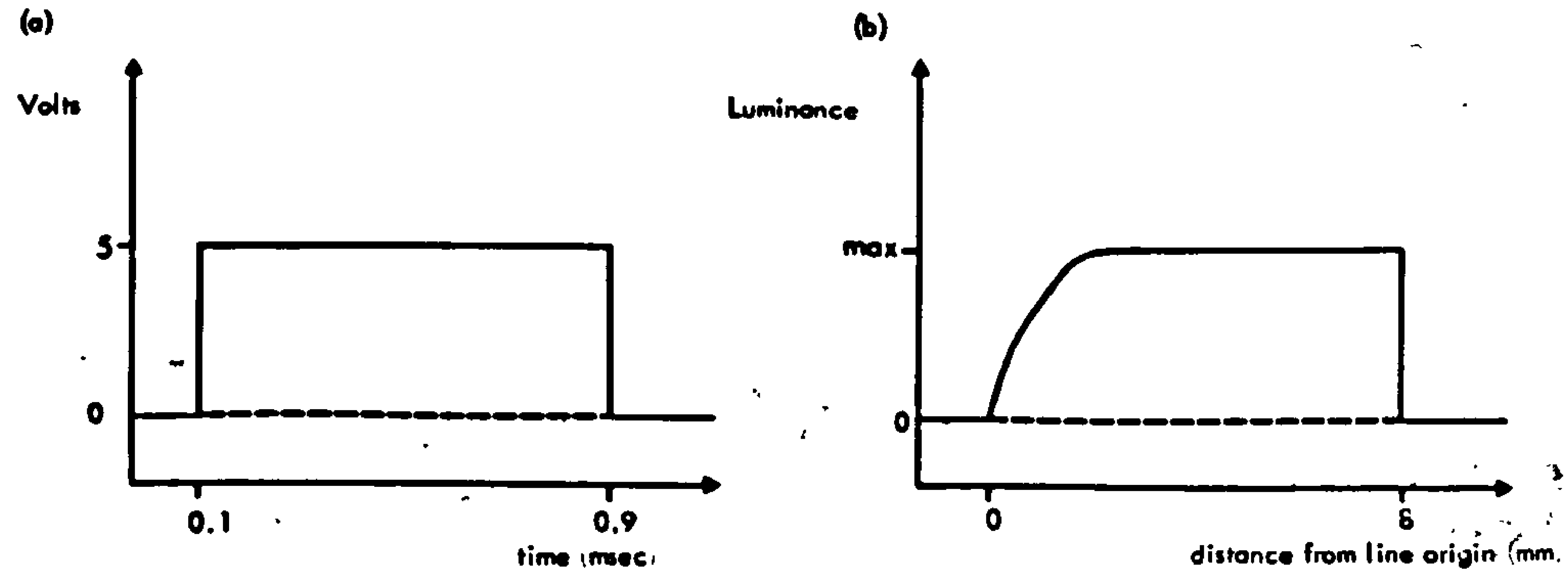


FIG. 3.5 Graph (a) shows the input to the Z-channel of the display oscilloscope, graph (b) illustrates the type of response actually obtained.

The change in luminance along the line on the CRT was immediately obvious and was therefore compensated for by adding to the rectangular Z-modulation signal its positive differential. The accuracy of this derivative was not quantitatively of importance and so a simple transisor differentiator was used. In order to be able to compensate for the changes in the shape of the waveform (b) in Fig. 3.5 with changes in the line-length introduced by altering either the X and Y signal amplitudes or the X and Y amplifier gains a variable time constant was incorporated into the differentiator. The circuit diagram for the compensating stage is shown in Fig 3.6.

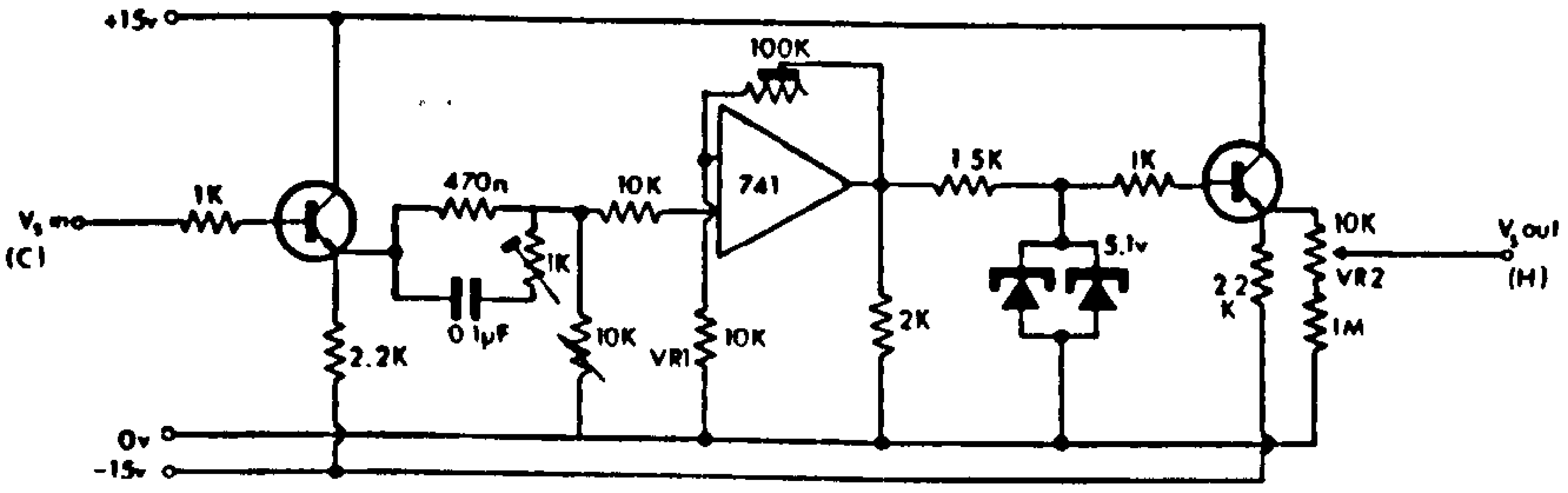


FIG. 3.6 Circuit diagram used to compensate for the defficiency illustrated in Fig. 3.5. By varying VR1 the input to the Z-channel of the display oscilloscope was manipulated until a line of uniform luminance was obtained. VR2 enabled variation of the maximum output voltage. (Capital ltters at input and output refer to the waveforms shown in Fig. 3.7).

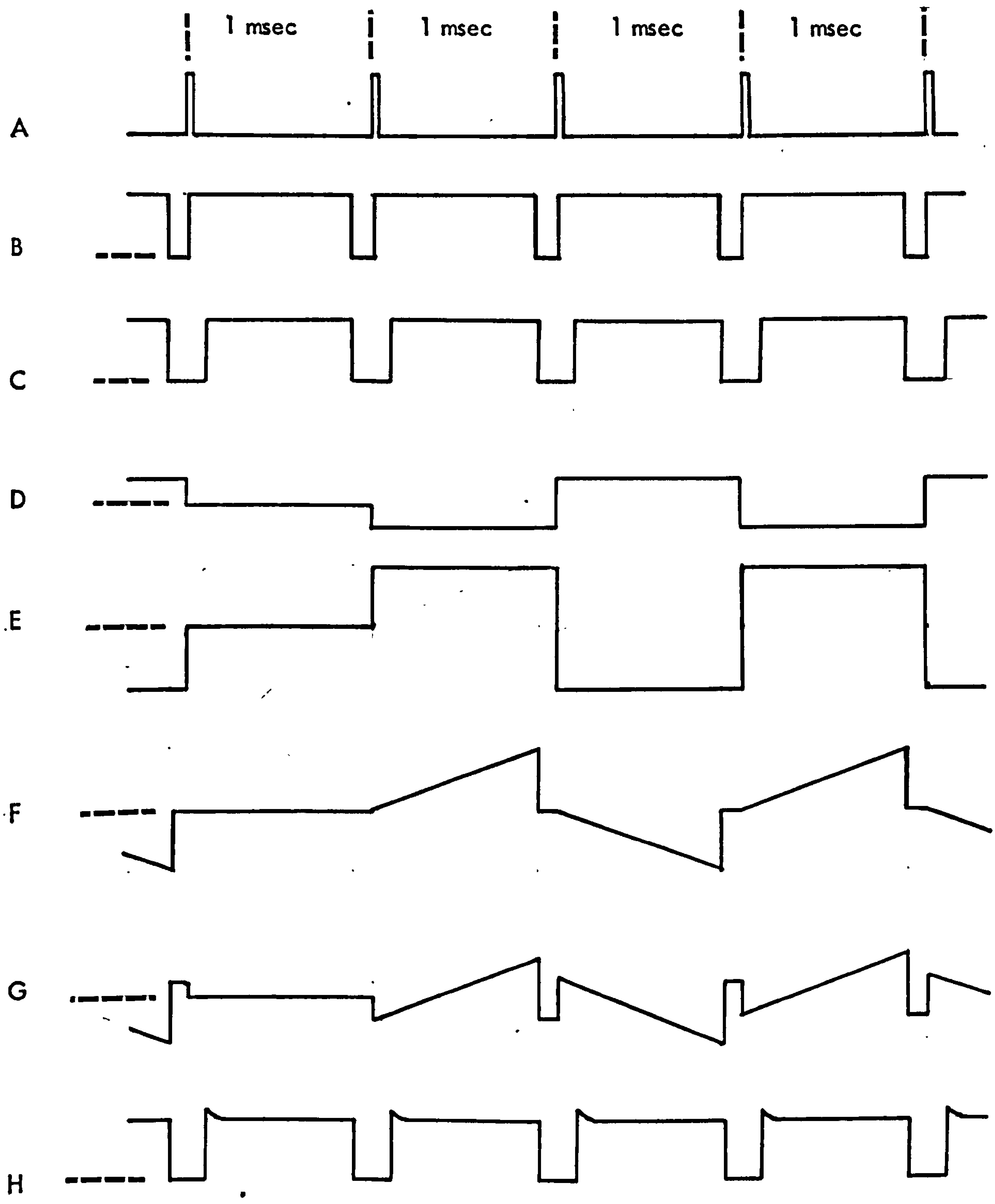


FIG. 3.7 Signal waveforms at various stages of the computer/display interface:
A. Bit zero of analog output register - input to monostable 1.
B. Output of monostable 1.
C. Output of monostable 2.
D. Origin coordinate voltage (X_o).
E. Line endpoint voltage (X_e).
F. Integrator output.
G. Summed integrator output + origin coordinate voltage.
H. Z-modulation input.

Responses were recorded by means of micro-switch push buttons which set general purpose flags in the computer, which were examined by the program at appropriate times. Four flags were available, enabling the running of two subjects simultaneously. At certain stages in the run the push buttons could also be used to select different pathways through the program.

c) Experimental Apparatus: II Software

The basic structure of the program set is shown in Fig. 3.8:

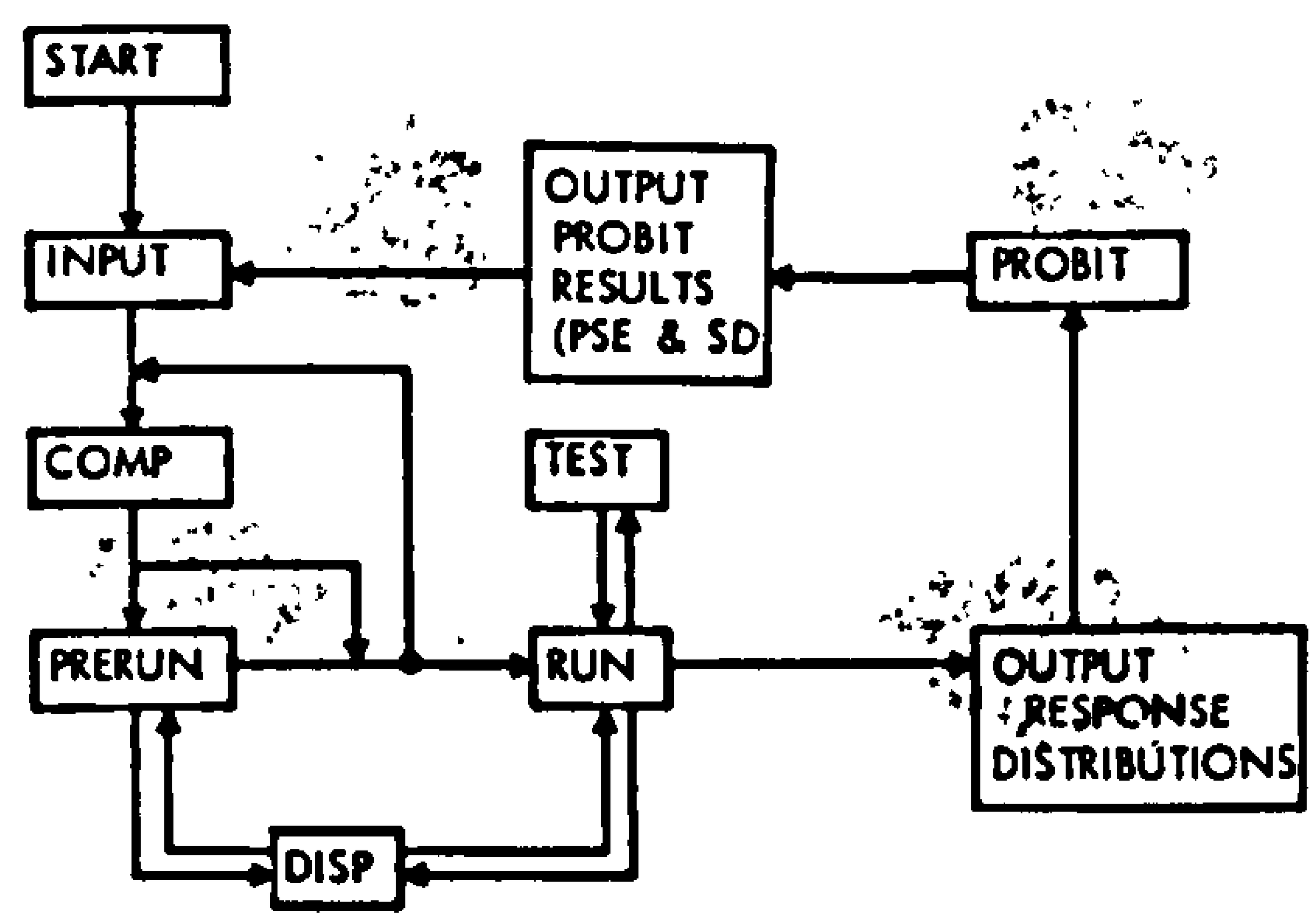


FIG. 3.8 Block diagram showing the flow-paths between the programs and subroutines used for running the experiments, driving the display and analysing responses.

The functions of these programs and subroutines were as follows:

(a) START: To initialise those variables which inform 'INPUT' that it is being called for the first time and that it is not being called from 'PROBIT'.

(b) INPUT: When called from 'PROBIT' this program first performs the output of the probit analysis. This was necessary because the amount of core taken up by 'PROBIT' for the performance of the data analysis did not leave sufficient room for the inclusion of output instructions. When called from 'START' this segment is skipped. Primarily the function of 'INPUT' was to record run and subject identification codes, the parameters defining the stimulus pattern, its timing, and the definition of the set of stimuli, e.g. the distance between each of the 23 stimulus levels. The initial mid-point and range-width for the constant stimulus method are also entered, and the response recording arrays are cleared.

(c) COMP: This program computes the screen origin co-ordinates for all the stimulus components and the voltage levels required to draw each of the twenty-three stimulus patterns.

(d) PRERUN: Before obtaining an initial estimate of the mid-point and range-width of the four stimulus levels required for the main run, this program first generates a sequential display of the 23 stimulus levels commencing with those for which an 'A' response is appropriate and proceeding through to those for which a 'B' response is appropriate. This display familiarises the subject with the stimuli and the way in which he should respond. The display duration parameters are also set up in this program.

(e) DISP: This subroutine, called by both 'PRERUN' and 'RUN' actually draws the stimulus on the CRT face. The numbers representing all the required voltage levels for the stimulus are transferred to unsubscripted variables before commencement of the display so that they may be accessed in the minimum time. Variables determining whether or not any particular stimulus component is to brighted up or not are also set up at this stage. As described in the previous section, the bright-up of any stimulus component is initiated by a pulse delivered when bit zero of one of the output registers is loaded. If the component in question is not to be shown, e.g. if the stimulus pattern being used comprises only three lines, then a zero is loaded into this bit and thus no pulse is generated. A flow chart for this subroutine is shown in Fig. 3.9. Each of the segments responsible for drawing one stimulus component also contains a timing loop with a counter set to an empirically determined value which gives an interval of 1 msec. between brightup initiating pulses. One pass through these segments draws the stimulus once completely, taking 5 msec. and this is repeated until the display has been shown for the required amount of time.

(g) RUN: As the whole sequence of programs was written to run up to two subjects in tandem some apparent peculiarities in the logic of this program may be resolved when this is taken into account. Basically, on entry to the program a stimulus is presented to the first subject, followed by a 2-3 second delay to give time for

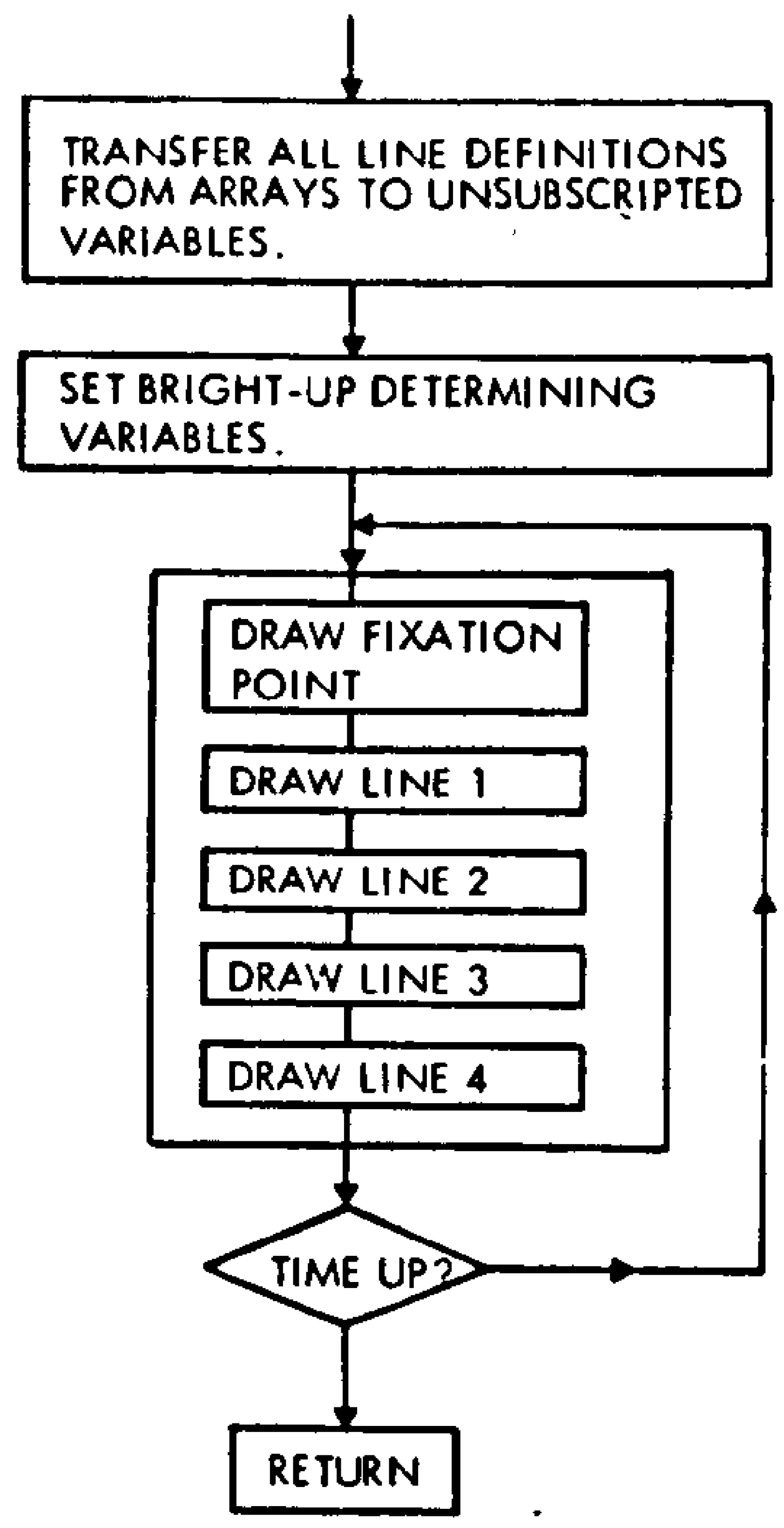


FIG. 3.9 Block diagram showing the sequence of operations performed by the display-driving subroutine 'DISP'.

responding - the interstimulus interval. The program then logs and processes the response to the second subject's previous response; on the first presentation all actions are dummies. Now, the program presents a stimulus to the second subject and processes the previous response of the first subject. The run is terminated when the subjects have made 120 responses. The run may be aborted for a subject if his next stimulus, as dictated by the stimulus selection criteria of random number, stimulus set mid-point and range width, is outside the range of the full stimulus set of 23. In this case, if there are two subjects, the run will continue for the remaining subject.

(h) OUTPUT: Printout of raw data for the subjects is controlled by this program.

(i) PROBIT: The analysis of results is performed by 'PROBIT', using the subroutine 'NDTR'. 'PROBIT' then passes control to 'INPUT' for printing out of the results and initiation of the next run.

Full listings of the subroutines 'DISP' and 'TEST' are given in Appendix I, as these are the two program segments most likely to be of general interest. A sample annotated console listing is shown as Fig. 3.10.

```
NSUB= 1       MY            DATE:23 MAY

VDIST= 150     SCALE: 20    LINE LNTH= 0.8
CRITERIA: 20/20    FIX.PT: 0
INTER-STIM T=2     DISP TIME=2.00

EXP. VARIABLE: 0       INCREMENT: 1.0       AXIS: 000
ANGLE SIZE= 045        ORIENTATION= 000     ANG.SEP= 135
SEPARATION, L1: 000    L2: 000

   K2(1)= 11/1
R/NO.= 46
RUN: 31.1 / M



MY
9     3 0 3   3 0 3                                           1 0 1
10    5 0 5   6 1 7   4 0 4   4 0 4   2 1 3   3 1 4   3 0 3   4 2 6
11                    2 2 4   3 1 4   4 0 4   2 1 3   2 2 4
12    1 1 2                                           1 2 3   1 5 6
13    2 3 5   1 4 5   2 2 4   2 2 4   1 4 5   1 3 4   0 5 5   0 2 2
14                    0 3 3   0 3 3   0 3 3   0 4 4

RUN: MY     23 MAY

  X      (DEG.)      (MIN.ARC)        A     B     N     T
 -2.     -2.00       -0.6400          7     0     0     7
 -1.     -1.00       -0.3200         31     5     0    36
  0.      0.00        0.0000         13     6     0    19
  1.      1.00        0.3200          3     8     0    11
  2.      2.00        0.6400          9    25     0    34
  3.      3.00        0.9599          0    13     0    13


              PSE     S(PSE)     SD       S(SD)     CHI-SQ
 1ST HALF     1.21    -0.312    -1.495    0.314     3.06/4
 2ND HALF     0.26    -0.277    -1.418    0.314     2.04/4
WHOLE RUN     0.70    -0.207    -1.509    0.225     3.25/4

LINE LENGTH=  18.334
```

Fig. 3.10 Consol listing of input to program, response distributions and results of probit analysis

Chapter 4 Acuity and Constant Error in Angle Perception I

Prior to conducting experiments aimed at the elucidation of neural mechanisms underlying the perception of angle size a set of studies of the effects of systematic variation of several spatial parameters of angle stimuli was carried out. Apart from gaining information concerning the effects of the selected parameters on perceived angle size, these studies also served to demonstrate that the apparatus used was sufficiently sensitive to register the known effects of manipulation of the stimulus characteristics. Replication of two standard studies was also used to determine that the subject(s) were 'normal' with reference to the oblique effect and to the illusory expansion of acute angles.

4.1 Effect of spatial parameters on perceived angle size.

Onley and Volkmann (1958) showed that the oblique effect extended to the perception of right angularity or orthogonality. When subjects were required to set a line perpendicular to the remainder of the stimulus (in an 'X', 'L' or 'T' configuration) performance was best for all figures when the arms of the angle were vertical or horizontal and worst when they were oblique. This example of the oblique effect was manifest in both constant error and variance of constant error measures of performance. Similar findings have since been reported by Weene and Held (1966) and Fisher (1969). As Andrews (1967a) showed that difference thresholds for orientation were smallest for vertical and horizontal orientations, an initial study of the perception of right angles, using the apparatus described in the preceding chapter, was considered as appropriate for testing both the oblique effect and the sensitivity of the apparatus.

A further factor, investigated by Andrews (1967a), which might influence the perception of orientation or angle size, is retinal location. It has been shown by a number of studies (Berkely, Kitterle & Watkins, 1975; Mansfield, 1974; Muir & Over, 1970; Over, Broerse & Crassini, 1972; Watkins & Berkely, 1974) that acuity for orientation, constant errors, spread of adaptation effects and the magnitude of the meridional anisotropy vary with increasing retinal eccentricity. These studies treated eccentricity with reference to the whole visual field and so are not precise enough to enable estimation of any effects which may be found within a radius of about 2 deg. arc of the fixation point. As anatomical studies show (Polyak, 1941) the diameter of the elements of the retinal mosaic show a substantial increase in size within this radius. If this increase in the size of the elements of the retina does affect acuity, then obviously such an effect must be taken into consideration when ideal acuities or biases are derived from models. In order to determine whether or not eccentricities of such a relatively small magnitude have any systematic effect on acuity for orientation or angle size or on biases in perceived angle size, retinal location was introduced as one of the independent variables in this study, the other being orientation of the bisector of the angle.

Experiment 3: Perception of Orthogonality

Methods

The experiment was carried out using the computerised method of constant stimuli described in chapter 3 above. The basic stimulus used was a single right angle and a fixation point. The set of 21 possible stimulus levels comprised angles greater and less than 90°. As well as varying the orientation of the bisector of the angle at 22.5° intervals between runs, the location of the angle in the visual field, with reference to the fixation point, was systematically varied. The configurations used are shown in Fig. 4.2 (inset). Two runs were carried out for each orientation and position. Each experimental run consisted of 120 responses to 2 second stimulus presentations, the response being to indicate whether the stimulus angle appeared to be greater or less than 90°. Stimuli were separated by a 2 second response period/interstimulus interval with a further second for acquisition of the fixation point. With the exception of location 6 (fig. 4.2), the fixation point was also shown during the stimulus interval in order to maintain good fixation.

The subject had normal uncorrected vision. Usually an experimental session lasted between 1 and 2 hours; even after the longer sessions the subject experienced no sense of 'visual strain'.

Results

The effects of variation of angle orientation and retinal location of the angle on the threshold for departure from orthogonality are shown in Fig. 4.1. Analysis of variance showed retinal location to have no significant effect on threshold for orthogonality (Table 4.1) whereas the effect of angle orientation was found to be significant ($p < 0.01$, Table 4.1). The geometric mean thresholds at each orientation, pooled across location are shown also in Fig. 4.1. The graph shows the expected oblique effect with minimum thresholds for vertical and horizontal component lines and maximum thresholds for obliquely oriented lines.

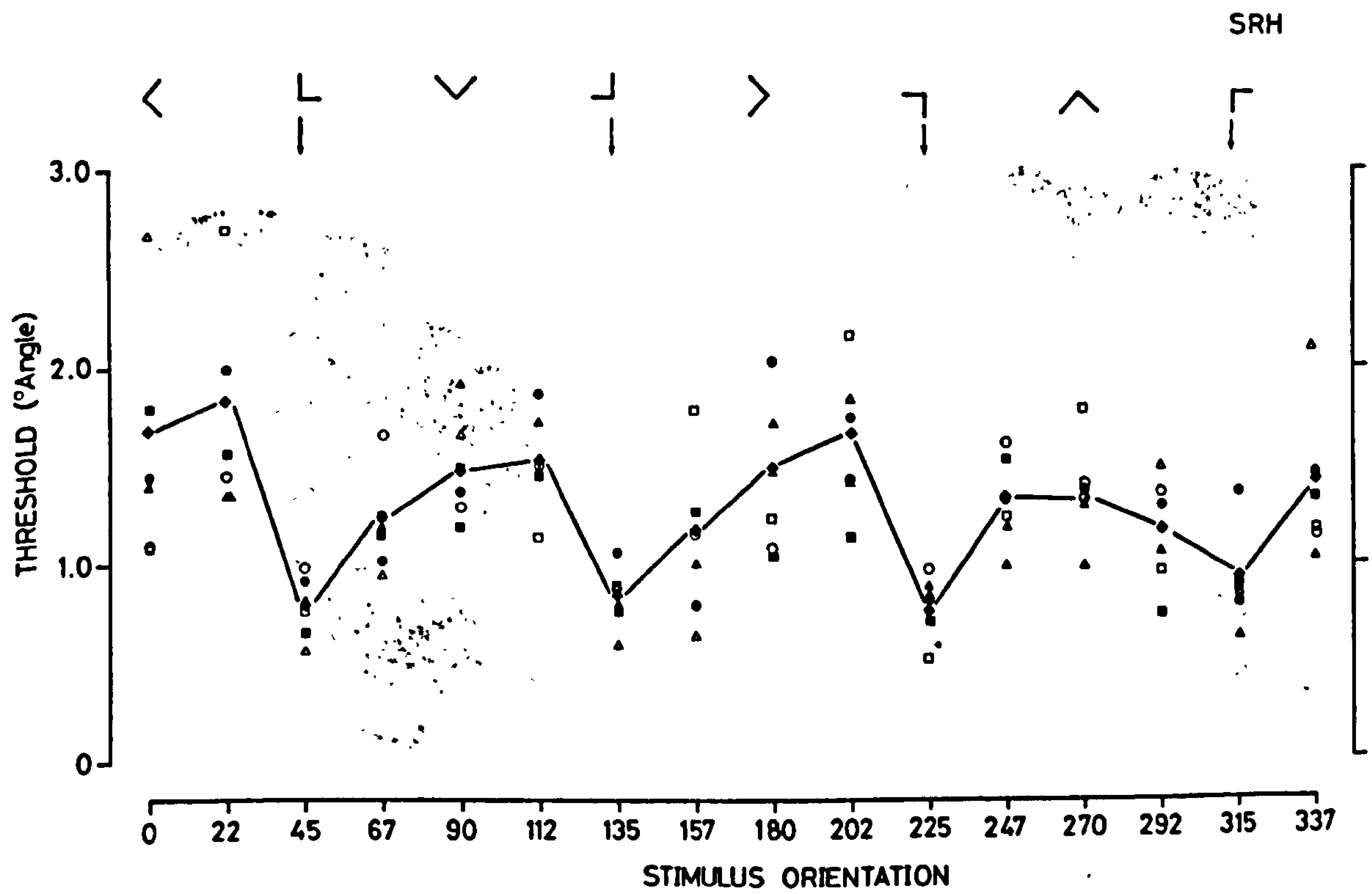


FIG 4.1 Thresholds for orthogonality shown as a function of stimulus orientation and retinal location. With reference to Fig. 4.2 the locations are: ▲ - 1, ■ - 2, ● - 3, ○ - 4, □ - 5, △ - 6; mean - ◆ .

Source of Variance	Sum of Squares	d f	Variance estimate	F-ratio	
Orientation	8.88	15	0.59	5.36	$p < 0.01$
Location	0.49	5	0.10	0.88	n.s.
Residual	8.29	75	0.11		
Total	17.66	95			

Table 4.1 Analysis of variance summary table for thresholds: Experiment 3

Weene and Held (1966), in their study of perceived orthogonality as a function of stimulus orientation, obtained results which suggested that different quadrants show variations in the strength of the effect of orientation. In order to test for this effect on acuity, a further analysis of variance was carried out for which the results obtained in the present study at equivalent orientations in each quadrant were pooled across retinal location. It was found that while the effect of orientation remained significant (Table 4.2, $p < 0.01$), there was no difference between the four quadrants.

Source of Variance	d.f.	Sum of Squares	Variance Estimate	F-ratio	
Orientation	3	1.19	0.40	15.42	$p < 0.01$
Quadrant	3	0.04	0.01	0.54	n.s.
Residual	9	0.23	0.03		
Total	15	1.46			

Table 4.2 Analysis of variance summary table for comparison of difference thresholds obtained at equivalent orientations in the four quadrants (Experiment 3).

The minimum observed thresholds are somewhat larger than those reported by Onley and Volkmann (1958) who used line lengths of 2 deg. 44 min. arc as compared with the 18 min. arc line lengths used here, but Andrews (1967b) has shown that acuity for orientation increases with line length.

The observed biases or constant errors are shown for each retinal location in Fig. 4.2. Both orientation and retinal location were found to influence the contstant error in perceived orthogonality ($p < 0.05$ for both factors, Table 4.3) in contrast to the finding for threshold. As was expected from previous studies cited above, constant errors were minimum for angle orientations where the lines comprising the angle were vertical or horizontal, and maximum where the lines were oblique.

Source of Variance	Sum of Squares	d f	Variance estimate	F-ratio	
Orientation	274.48	15	18.30	2.48	$p < 0.05$
Location	129.81	5	25.96	3.51	$p < 0.05$
Residual	554.29	75	7.39		
Total	958.58	95			

Table 4.3 Analysis of variance summary table for constant errors: Experiment 3.

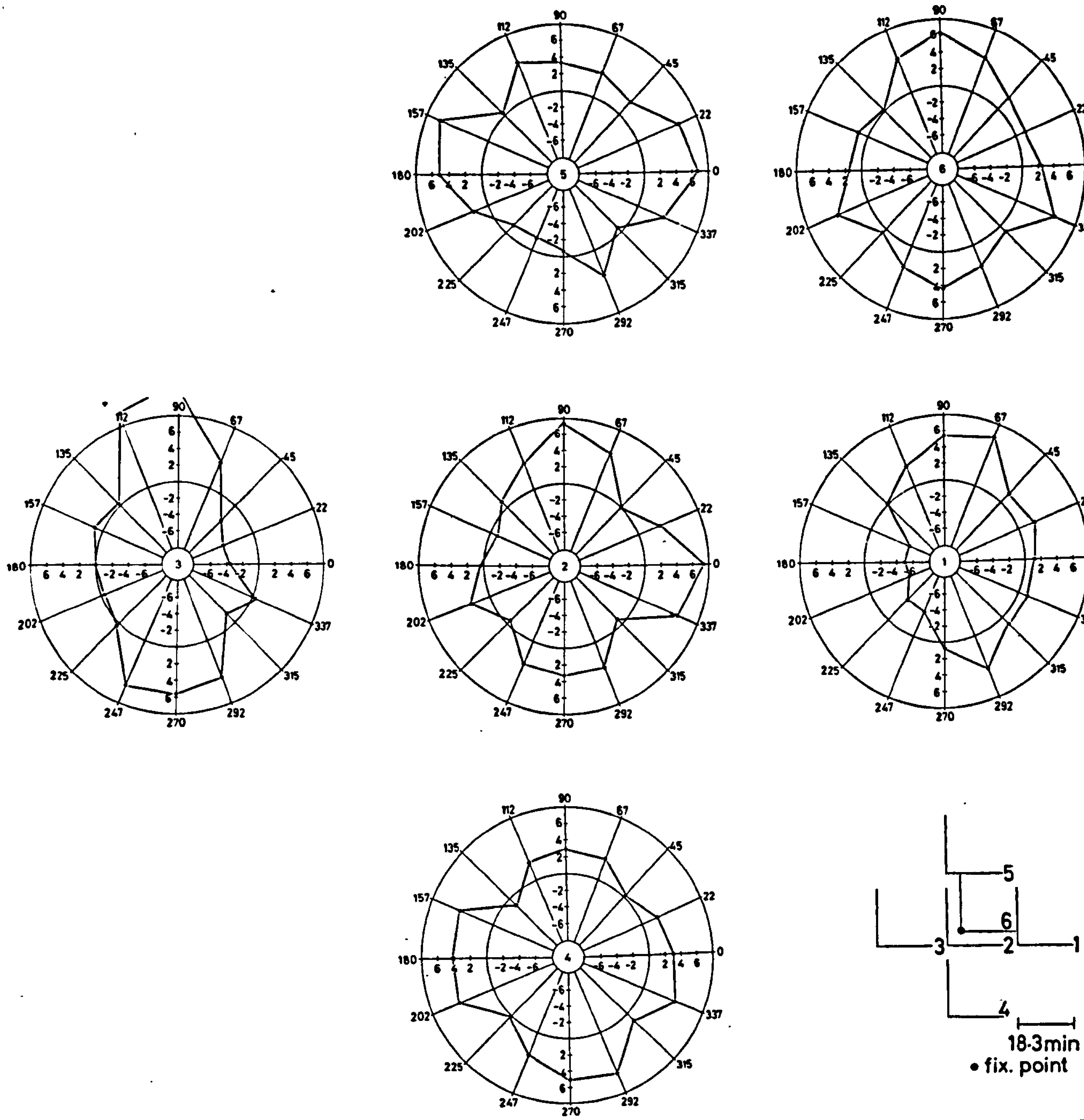


FIG 4.2 Biases in perceived orthogonality as a function of orientation of the angle bisector and the location of the angle with reference to the fixation point. The inset (lower right) shows the locations used, with reference to the fixation point. The numbers at the centres of the graphs correspond to those labelling the angles in the inset. The radial coordinates represent the amount of bias in degrees, the bisector orientation is shown around the circumference.

In most locations the constant errors were positive, indicating that right angles at oblique orientations are perceived as being less than 90° but there are sufficient counter-examples (Fig. 4.2 graphs 1, 3, and 5 especially) to show that this cannot be generalised to a principle.

Discussion

The finding that there were no consistent effects of orientation on the constant errors of perceived orthogonality casts some doubt on the generalisability of Weene and Held's (1966) report of differences between quadrants. They found the constant errors to be greatest for the upper left and upper right quadrants. Although such asymmetries were found in the present study, the orientations at which the greatest constant errors were recorded showed a tendency to change from one retinal location to another. Further, the observed differences in patterns of constant error at different retinal locations cannot be attributed, as was suggested, to the increase in size of the retinal elements with increasing eccentricity. Whatever effect this may have had, the effect would have displayed some radial symmetry in the pattern of the graphs as a whole presented in Fig. 4.2. It is suggested, therefore, that the differences between the perceived angle sizes at the different locations in the foveal visual field exposed in this study reflect local variations in the scaling of the metrics defined by the analyser groups receiving their inputs from the different retinal locations. This being the case, it may be expected that the relationship between constant error and orientation at a given location would show a tendency to fluctuate over relatively long periods of time, of the order of weeks or months. It may be concluded that within the fovea the retina may be considered as homogeneous with reference to acuity and subject to random variations with reference to scaling. The scaling variations are likely to be manifest in the foveal projection areas of the visual cortex, of course, and not in the retina itself.

The occurrance of minimal constant errors at angle orientations giving vertical and horizontal lines (oblique bisector orientations) is consistent with the model presented by Andrews (1967a). According to this model obliquely oriented lines should also show minimal constant error as the arrays of orientation analysers show symmetry about the main obliques, as they do about the horizontal and vertical. This prediction was not supported by the experimental observations which showed constant errors to be maximal for angles with oblique lines. This finding suggests that the perceived characteristics of lines as parts of angles may differ from those of lines seen in isolation from lines of other orientations.

The difference thresholds observed in this study showed no deviation from the expected meridional anisotropy effect, whereas neither the retinal location nor the quadrant in which the angle bisector lay had any significant effects. It is apparent, therefore, that constant errors and difference thesholds are sensitive differentially to aspects of the stimulus. On the basis of the results obtained in this study alone it is not possible to detail which aspects of the stimulus determine the bias and which the difference threshold in terms of any hypothetical mechanism for angle perception. This matter, however, will receive further attention in subsequent chapters of this thesis.

The results obtained during this study show that the experimental apparatus was capable of registering the effects of orientation on perceived angle size and difference thresholds and that the subject SRH showed the expected oblique effect.

Experiment 4: Matching of Right Angles

On the basis of the results obtained in the first part of this chapter, it is possible to make some predictions concerning the performance for the task of matching two right angles of the same orientation, one on either side of the fixation point. For difference threshold, it would be expected that the effect of orientation be the same as that for parallelism or orthogonality, maximum thresholds occurring at oblique line orientations and minimum thresholds at vertical and horizontal orientations. The predicted constant errors are shown in Table 4.4. These were obtained by taking the difference between the constant errors obtained at locations 1 and 3 in Experiment 3, these locations corresponding to the locations of the two angles to be compared in the present experiment.

Methods

The experimental procedure was identical to that employed for the previous experiment with the exception of the stimulus used. Instead of presenting one angle at a time, two angles were presented simultaneously at locations corresponding to locations 1 and 3 in experiment 3. The task of the subject was to determine which of the two angles presented appeared the smaller, and to respond accordingly. Two runs were carried out at each orientation. The subject used was the same person.

Results

Difference thresholds for the comparison of right angles are shown in Fig. 4.3

Bisector Orientation	Bias at Location 1	3	Difference (1 - 3)	Expected Bias	Observed Bias
0	1.59	-3.6	5.19	-5.19	-1.40
22	2.37	-3.91	6.28	-6.28	-1.48
45	1.31	-2.07	3.38	-3.38	-0.17
67	6.19	3.63	2.56	-2.56	-0.66
90	5.35	11.95	-6.60	6.60	0.62
112	2.69	9.87	-7.18	7.18	-0.67
135	0.03	0.40	-0.37	0.37	-0.32
167	-5.32	1.36	-6.68	6.68	1.41
180	-4.99	0.28	-5.27	5.27	-0.43
202	-5.21	-0.19	-5.02	5.02	0.41
225	-3.47	0.41	-3.88	3.88	-0.80
247	-3.33	5.91	-9.24	9.24	-0.47
270	-0.90	5.69	-6.59	6.59	0.87
292	-4.25	4.72	-9.97	9.97	0.19
315	1.23	-1.64	2.67	-2.67	0.09
337	1.65	0.33	1.32	-1.32	-0.70

Table 4.4: Biases from Experiments 3 at locations 1 & 3 are shown in columns 2 and 3. The differences in column 4 are signed such that if the angle at position 1 is greater than that at position 3 the difference is positive; if the converse is true then the difference is negatively signed. In Experiment 4, if angle 1 appears greater than angle 2 at PPE, then the bias will be negative, and vice versa; the expected biases will have the opposite sign to the calculated differences. The observed biases are shown in the final column.

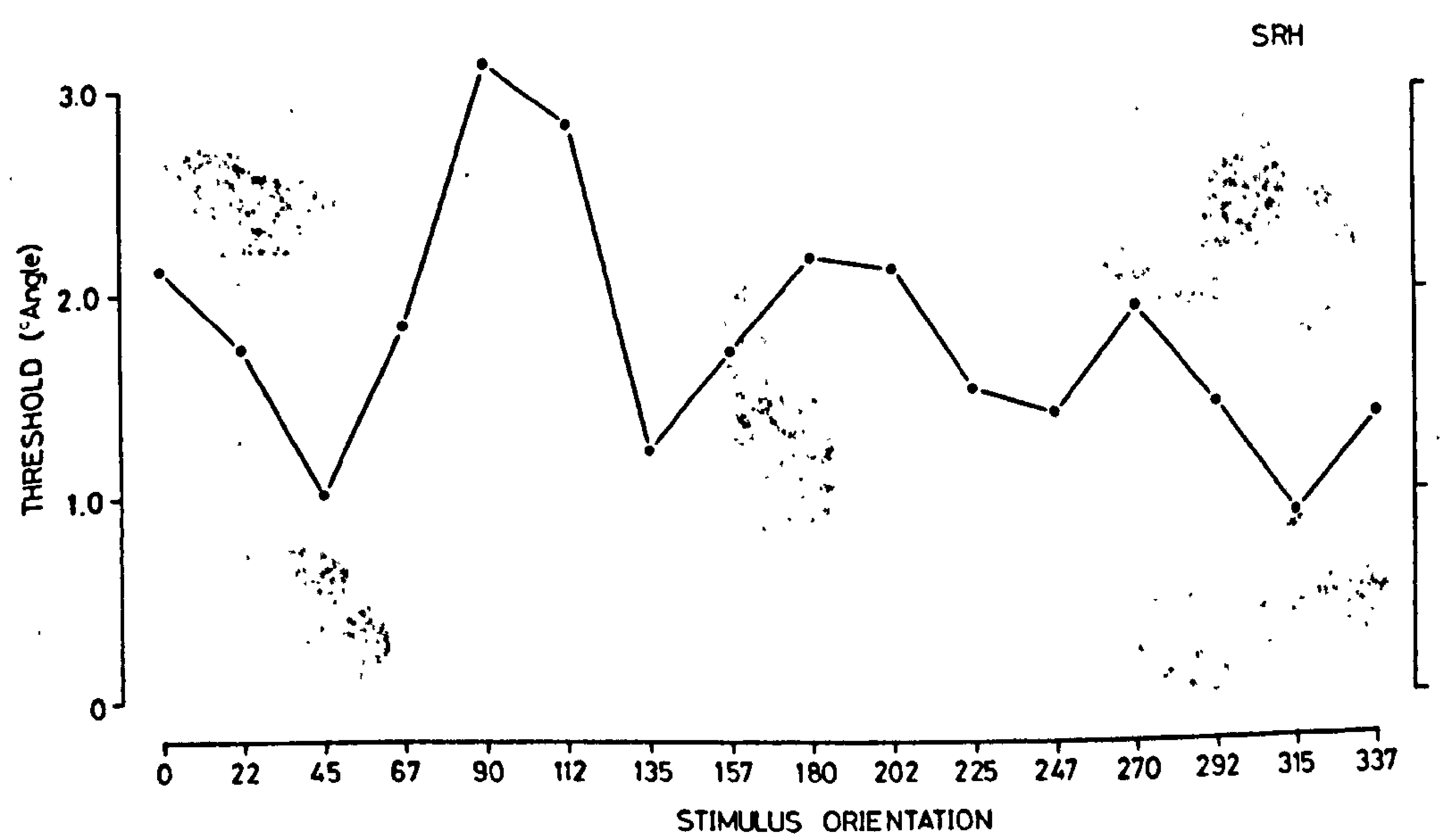


FIG 4.3 Effect of stimulus orientation on threshold for perceived equality of right angles.

as a function of bisector orientation of the angles. As in the previous study, the expected oblique effect is evident. The observed biases are shown in Table 4.4 and in graphic form in Fig. 4. It is evident that there is little agreement between the predicted values for the biases and the observed values.

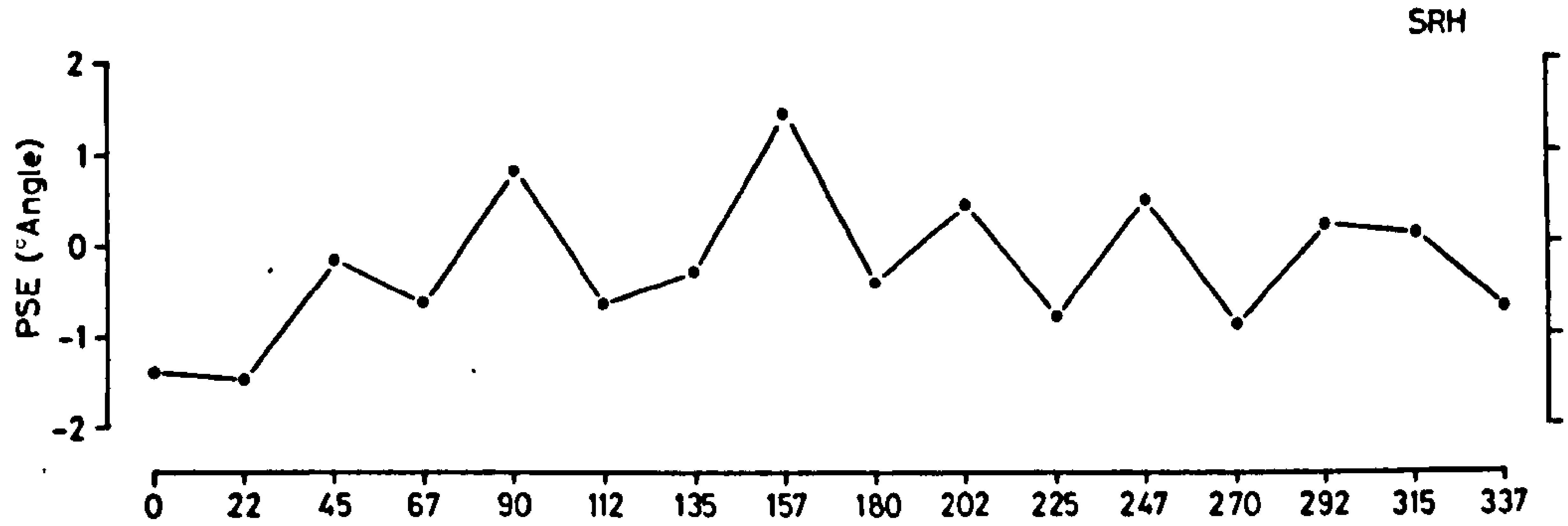


FIG 4.4 Effect of stimulus orientation on constant error in comparison of right angles.

The observed biases are considerably smaller than were expected, and there is no consistent agreement even between the signs of the expected and of the observed values.

Discussion

These results are substantially in agreement with those obtained in the preceding study, so far as the difference thresholds are concerned. Rotation of the stimulus angles gives a regular fluctuation of difference threshold, with minima and maxima occurring when the component lines are vertical and horizontal and oblique respectively. The lack of such systematic variations in observed biases, with the exception of minima (near zero) biases occurring when the component lines coincide with the vertical and horizontal, raises a question concerning the predictability of performance on a relatively complex comparison task on the basis of performances on simpler tasks which may be considered as elements of the more complex task. A similar lack of predictability was found in Experiment 3 where it was found that constant errors in judgements of orthogonality did not fully agree with expectations based on the observed biases from judgements of parallelism. This question will be considered further in following chapters.

4.2 Comparison of Angle Sizes: acuity and constant error as functions of angle size, orientation and line length.

Experiment 5: Comparison of angle sizes - horizontal reference angle.

The perceptual expansion of acute angles has been shown to be influenced by the orientation of the angle (Blakemore, Carpenter & Georgeson, 1970; Carpenter & Blakemore, 1973; Lennie, 1971) and by the size of the angle (Carpenter & Blakemore, 1973). The effect will be examined, with reference to explanatory hypotheses in a later chapter; the studies to be described here represent an exploratory study of the effect of orientation, angle size and line length on the perceived expansion of acute angles. These studies were undertaken for three reasons: (1) to ensure that the effect could be replicated with the apparatus and methods used, (2) to collect data describing the behaviour of the effect under a wider range of conditions than is available in the literature, (3) to relate the acuity for angle size to other acuities by comparing the effects of line lengths on the performances obtained for different stimuli.

Method

Measures of difference threshold and constant error were obtained using the automated method of constant stimuli. The basic stimulus used is shown in Fig. 4.5(a) and the range of the 21 possible stimuli available in any run is indicated in Fig. 4.5(b), together with the sign conventions used in reference to the stimulus and results. This is essentially the same stimulus pattern as was used by Lennie (1971) although in his study the method of adjustment was used. A negative bias indicates that at the PSE angle II (ROS) was set larger than angle I (POQ) and, therefore, that angle II appeared smaller than angle I at the PPE. A positive bias indicates that the reverse was the case.

In all cases the bisector of angle I was oriented at 0° (horizontal), so that the absolute orientation of angle II is equivalent to the relative orientation of the bisectors of the two angles. The full range of possible configurations used, obtained by the systematic variation of angle size and orientation, is shown in Fig. 4.6.

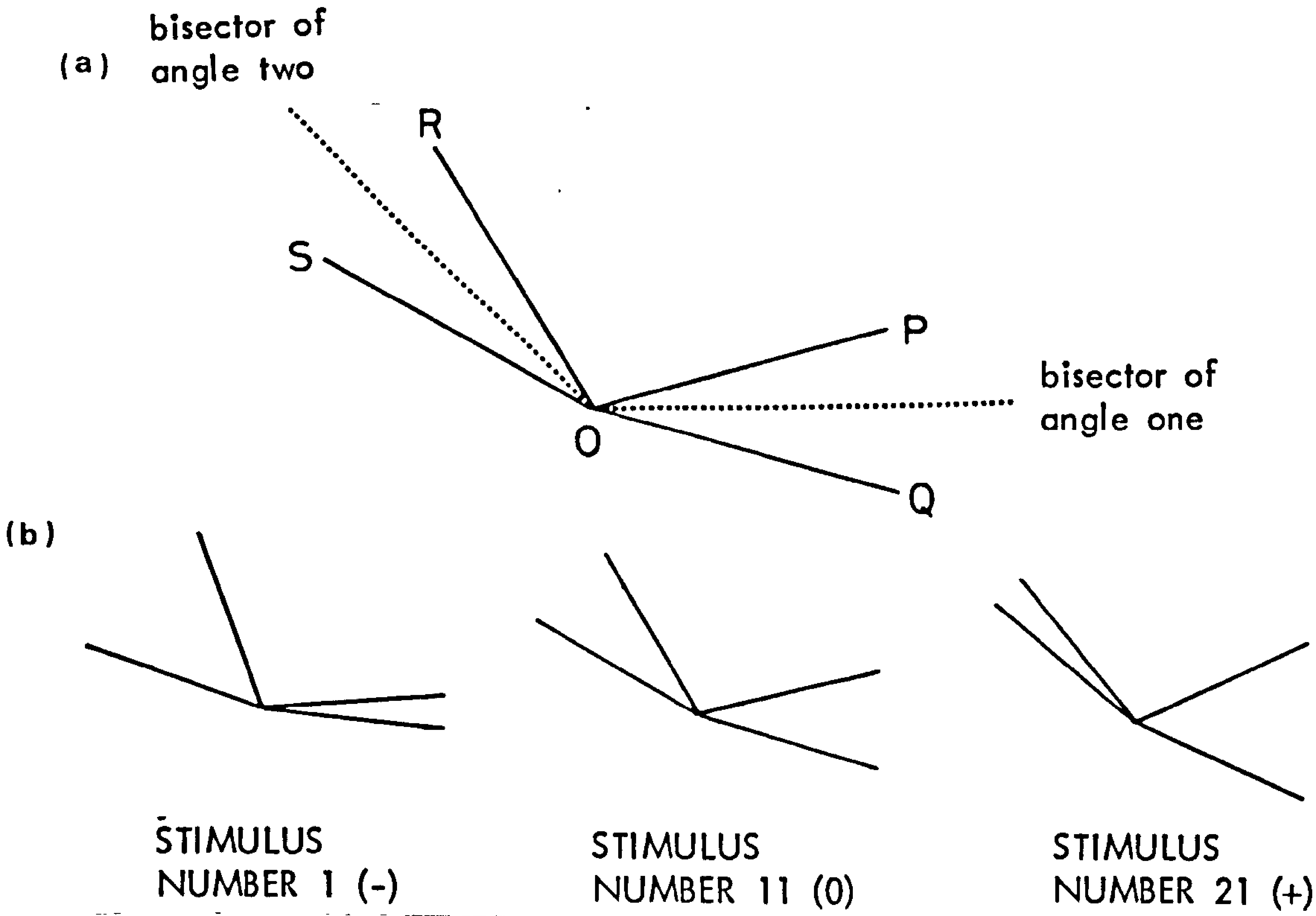


FIG 4.5 (a) Basic stimulus configuration used in Experiment 4.
(b) The three patterns represent the range of possible patterns available to the subject in a given run.

Only one observer was subjected to the full set of stimulus configurations, other observers were used only to confirm the replicability of the results obtained in the later, critical experiments. The subject SRH had normal uncorrected vision and was experienced in this type of spatial acuity experiment. Stimuli were viewed under normal illumination (1 x 40 watt fluorescent tube) in a small room with no other sources of illumination.

For all runs comprising this study, the stimulus duration was 2 seconds preceded by a one second presentation of the fixation point. As the fixation point coincided with the common vertex of the angles it was suppressed during the presentation of the stimulus. Each presentation was followed by a two second interstimulus interval. Viewing distances were 50cm or 150cm according to the angular subtense required.

Results

(a) Constant errors

Lennie's finding that horizontally and vertically oriented acute angles appear larger than obliquly oriented angles is substantiated by the results shown in

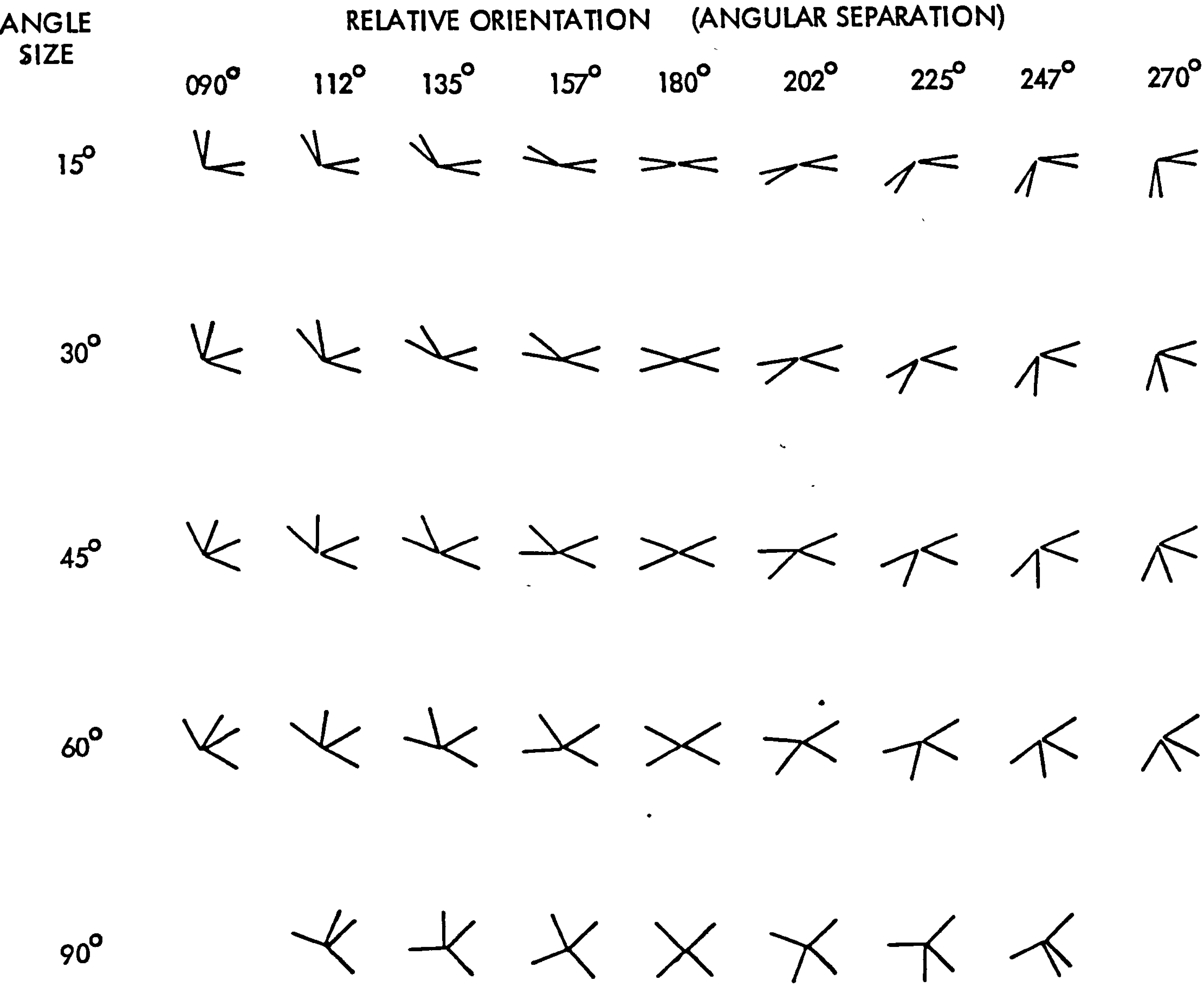


FIG 4.6 The full range of stimuli used in Experiment 4 (with the exception of the 90° angles), obtained by crossing orientation of test angle (angle II) with angle size for each line length. The line lengths in the diagram are 2/3rds the length of the actual stimulus line lengths generated on the CRT for a line subtending 0.3 deg. arc.

Fig. 4.7. The characteristic 'W' pattern is not exhibited for the smallest angles (15°), but the effect is strong for the other angle sizes, though there appears to be an interaction effect with line length. Analysis of variance (Table 4.5) shows that the three factors: orientation, angle size and line length all exert a significant infuence ($p < 0.01$) on the perceived relative angle sizes. All two-factor interactions are also significant ($p < 0.01$), but the three factor interaction is not. Bias as a function of line length is shown in Fig. 4.8. Bearing in mind that there is an interaction effect between line length and orientation, a tendency for bias to increase with increasing line length is apparent, levelling off between 0.6 deg. arc and 1.0 deg. arc, as illustrated

FIG 4.7 Effect of relative orientation on the perceived relative sizes of acute angles: The angle sizes were: ● - 15°, ▲ - 30°, ■ - 45°, ▼ - 60°. The line lengths were (a) 0.3 deg. arc, (b) 0.6 deg. arc, (c) 1.0 deg. arc, (d) 3.0 deg. arc. (Angular separation = relative orientation).

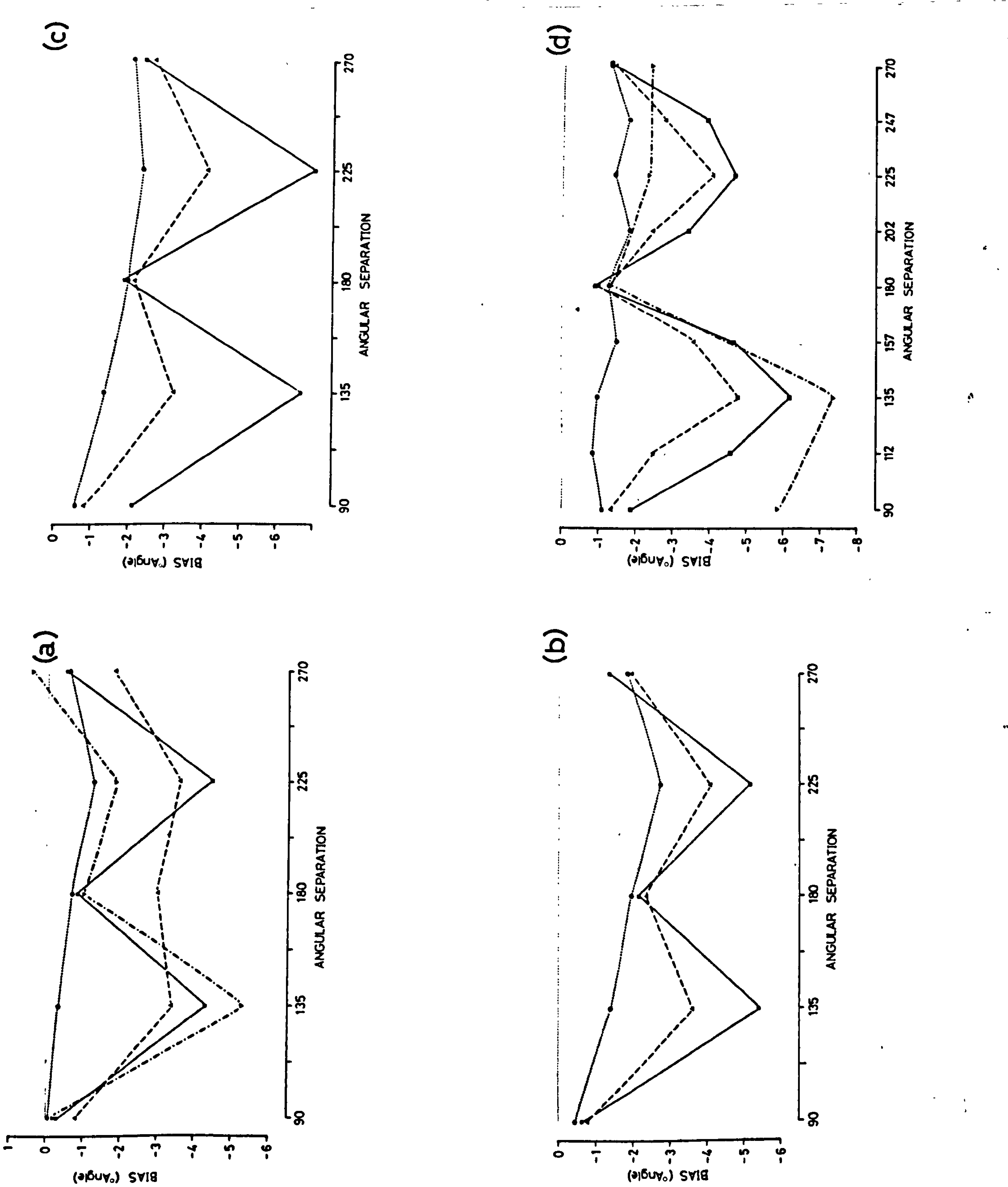


FIG 4.8 Effect of line length and relative orientation on the perceived relative sizes of acute angles. The test angle orientations were: ● - 90°, ◆ - 135°, ▲ - 180°, ■ - 225°, ▼ - 270°. Broken lines indicate obliquely oriented test angles and continuous lines Indicate vertical and horizontal test angles. The angle sizes were: (a) 15°, (b) 30°, (c) 45°, (d) 60°.

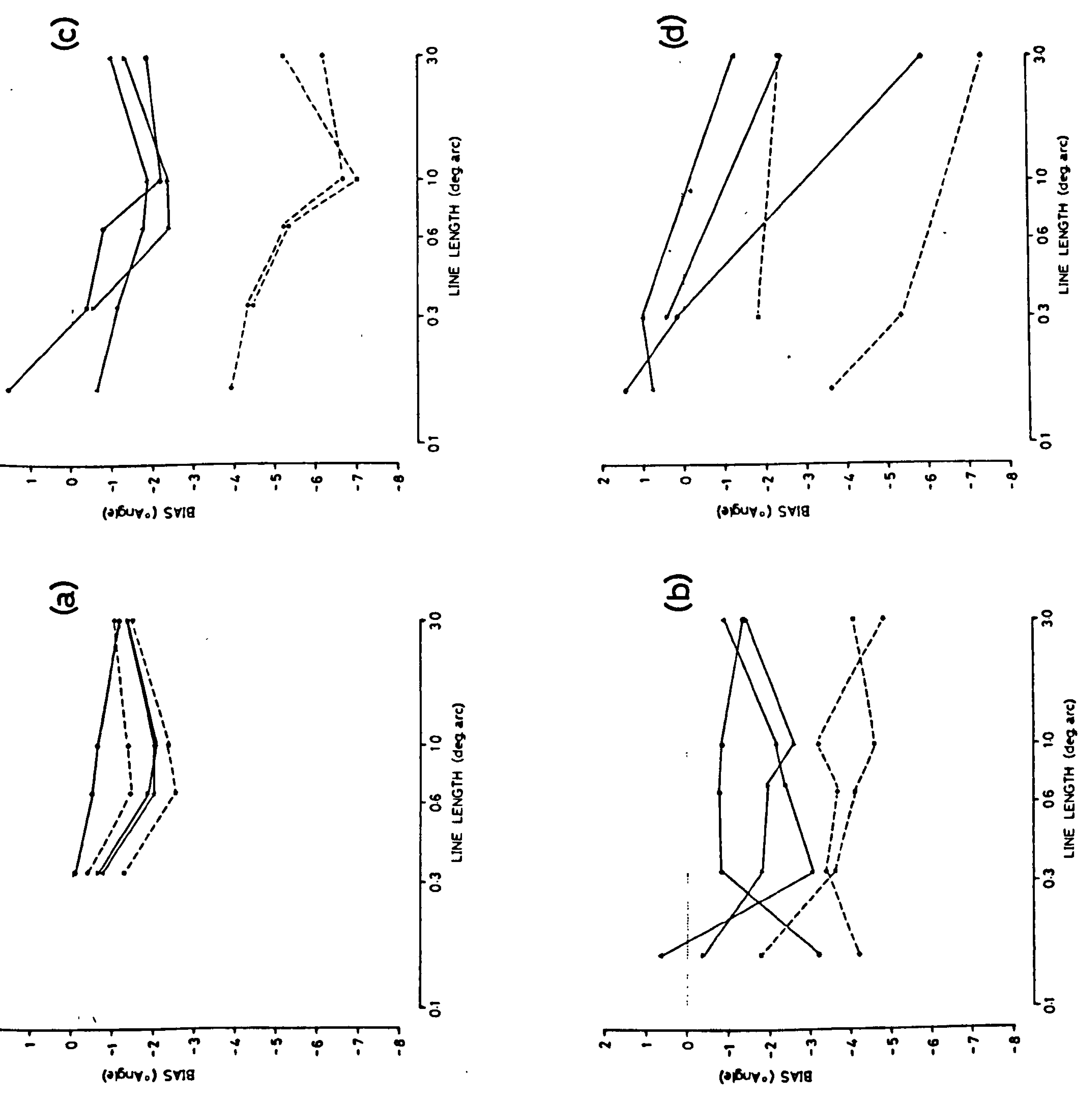
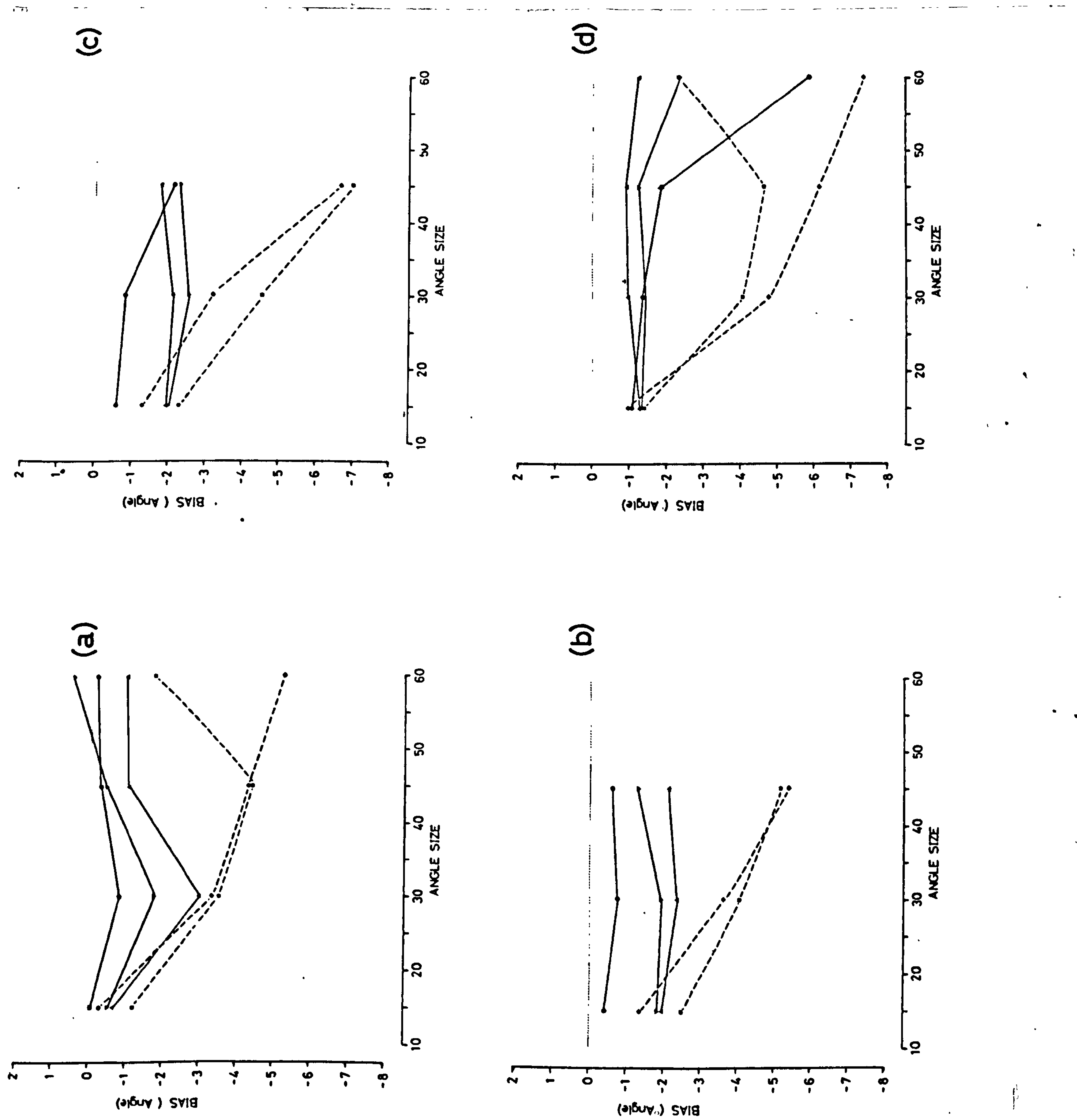


FIG 4.9 Effect of angle size on the perceived relative sizes of acute angles. The orientations were: ● - 90°, ◆ - 135°, ▲ - 180°, ■ - 225°, ▼ - 270°. Broken lines indicate obliquely oriented test angles and continuous lines indicate vertical and horizontal test angles. Line lengths were: (a) 0.3 deg. arc, (b) 0.6 deg. arc, (c) 1.0 deg. arc, (d) 3.0 deg. arc.



most clearly in Fig. 4.8(c). Other graphs in this series show, however, that this tendency is by no means unequivocal.

The effect on bias of the third variable, angle size is shown in Fig. 4.9. The distinction between vertical/horizontal angles and oblique angles is brought out clearly, with the exception of the 225° orientation test angles in graphs (a) and (d). Despite the range of angle sizes used, there is little marked effect of increasing angle size when the angles to be compared are horizontal or vertical, with one exception to be seen in Fig. 4.9(d). When the test angle is oblique, however, the effect of increasing angle size is to increase the bias even up to the maximum angle size of 60°.

Source of Variance	d.f.	Sum of Squares	Variance Estimate	F-ratio	
Line length	3	15.732	5.244	23.69	$p < 0.01$
Angle size	2	63.691	31.845	143.88	$p < 0.01$
Orientation	4	146.217	36.554	165.16	$p < 0.01$
L x A	6	9.048	1.508	6.81	$p < 0.01$
L x O	12	13.099	1.092	4.93	$p < 0.01$
A x O	8	73.219	9.152	41.35	$p < 0.01$
L x A x O	24	8.313	0.346	1.56	n.s.
Residual	60	13.280	0.221		
Total	119	342.599			

Table 4.5 Analysis of variance summary table for comparison of constant errors obtained in Experiment 5.

(b) Difference Thresholds

The effects of the three independent variables line length, angle size and relative orientation are shown in Figs 4.10 to 4.13. Analysis of variance showed all three to have a significant effect of the difference threshold ($p < 0.01$, Table 4.6), and interaction effects between length and angle size

Source of Variance	d.f.	Sum of Squares	Variance Estimate	F-ratio	
Line length	3	0.457	0.152	4.89	$p < 0.01$
Angle size	2	12.497	6.248	201.61	$p < 0.01$
Orientation	4	1.106	0.277	8.90	$p < 0.01$
L x A	6	0.529	0.088	2.84	$p < 0.05$
L x O	12	0.602	0.050	1.61	n.s.
A x O	8	0.885	0.111	3.55	$p < 0.01$
L x A x O	24	1.244	0.052	1.66	n.s.
Residual	60	1.869	0.031		
Total	119	19.189			

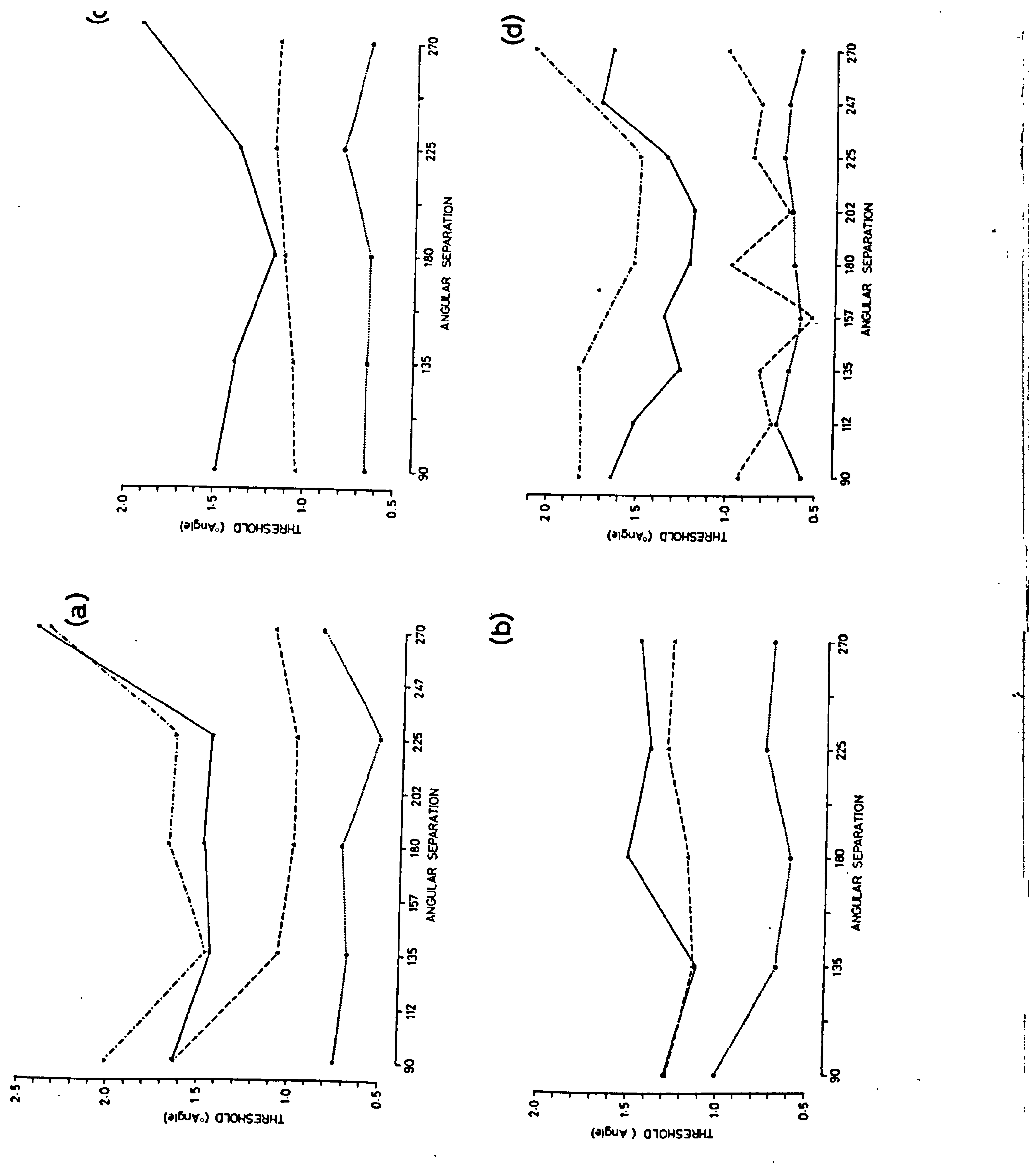
Table 4.6 Analysis of variance summary table for comparison of difference thresholds obtained in Experiment 5

and between relative orientation and angle size were also significant. The remaining two-factor interaction and the three-factor interaction did not show a significant effect.

In Fig. 4.10 each graph shows differing angle sizes at a given line length, while in Fig. 4.11 the graphs show different line lengths at the same angle sizes. In Fig. 4.12 the effect of line length is shown and in Fig. 4.13 the main variable is angle size.

The most clear cut effect is that of angle size. For most relative orientations and all line lengths the threshold for angle size increases with the size of the angles to be compared. Although the effect is not independent of orientation, it can be seen that overall, orientation does not exert a systematic effect, as is indecated by Figs. 4.10 and 4.11. Similarly, differences in line length do not substantially alter the slopes of the graphs. Neither line length nor relative orientation, when considered as the main independent variables, appear to have a simple relationship with the acuity for angle size.

FIG 4.10 Effect of relative orientation on acuity for angle size. The angle sizes were: ● - 15°, ▲ - 30°, ■ - 45°, ▼ - 60°. The line lengths were: (a) 0.3 deg. arc, (b) 0.6 deg. arc, (c) 1.0 deg. arc, (d) 3.0 deg. arc. (Angular separation = relative orientation).



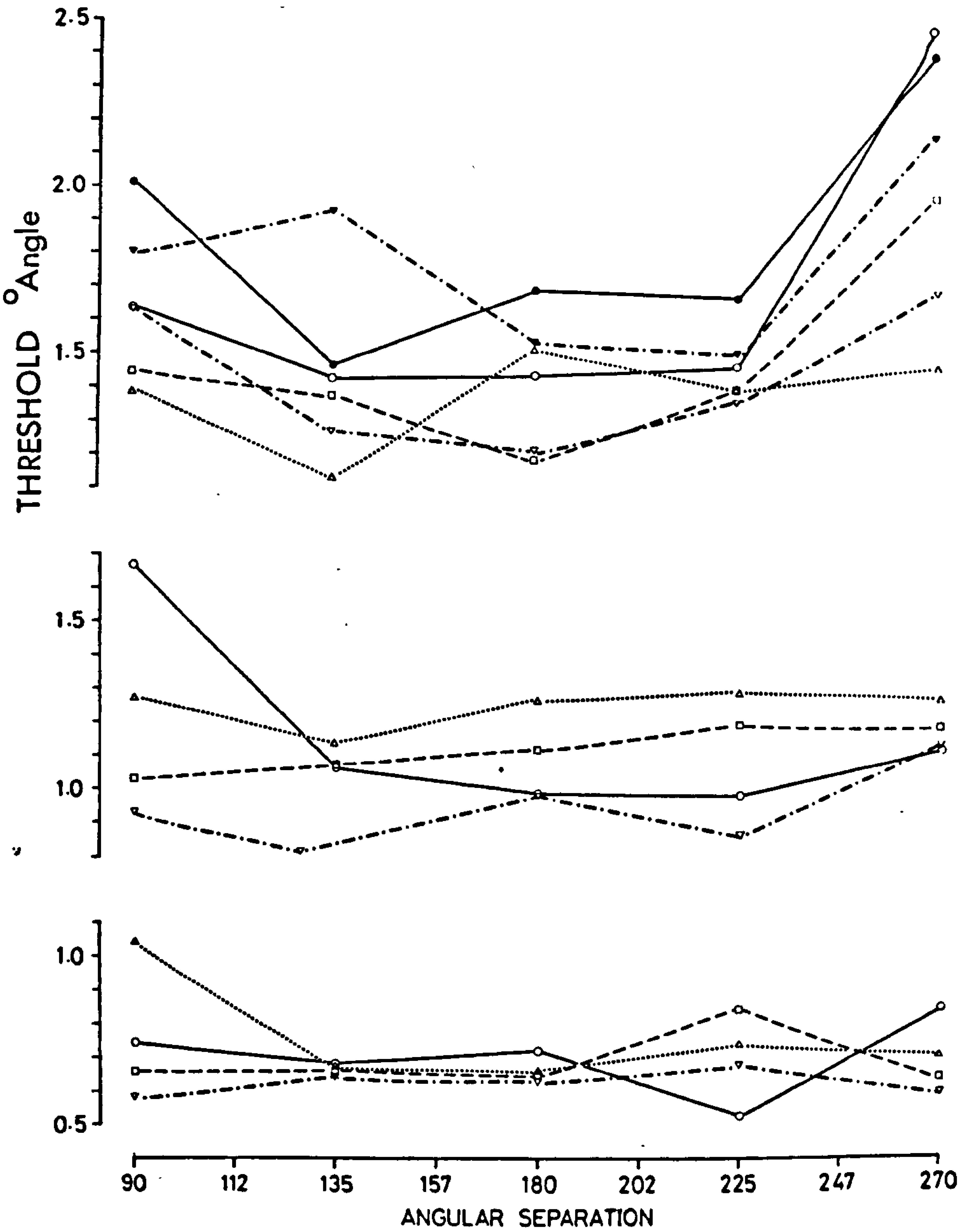


FIG 4.11 Effect of relative orientation on acuity for angle size. The line lengths were: ● - 0.3 deg. arc, ▲ - 0.6 deg. arc, ■ - 1.0 deg. arc, ▼ - 3.0 deg. arc. The angle sizes were: (a) 45° (open symbols) and 60° (closed symbols), (b) 30°, (c) 15°. (Angular separation = relative orientation).

FIG 4.12 Effect of line length on acuity for angle size. The test angle orientations were: ● - 90°, ◆ - 135°, ▲ - 180°, ■ - 225°, ▼ - 270°. Broken lines indicate obliquely oriented test angles and continuous lines indicate vertical and horizontal test angles. Angle sizes were: (a) 15°, (b) 30°, (c) 45°, (d) 60°.

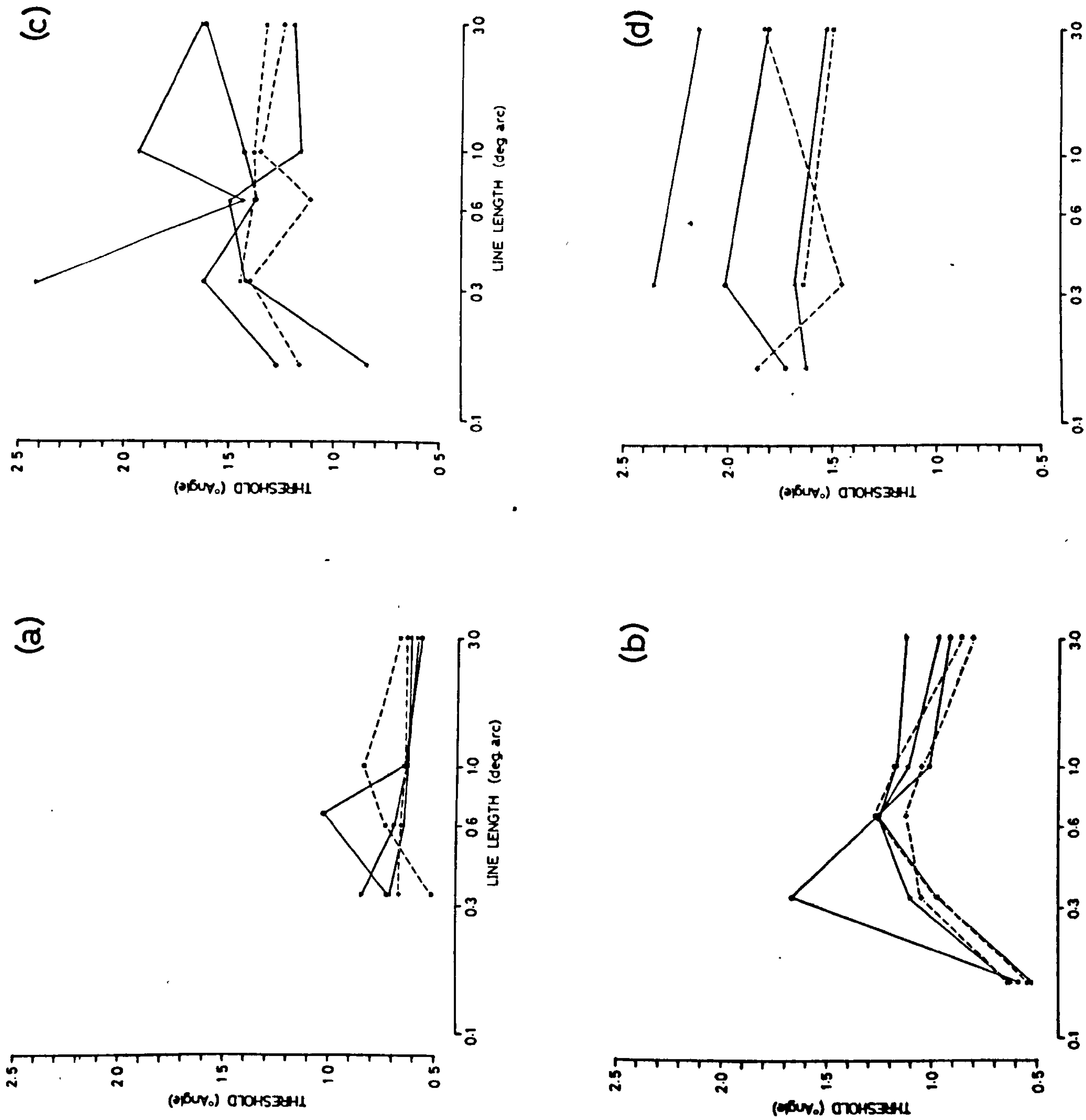
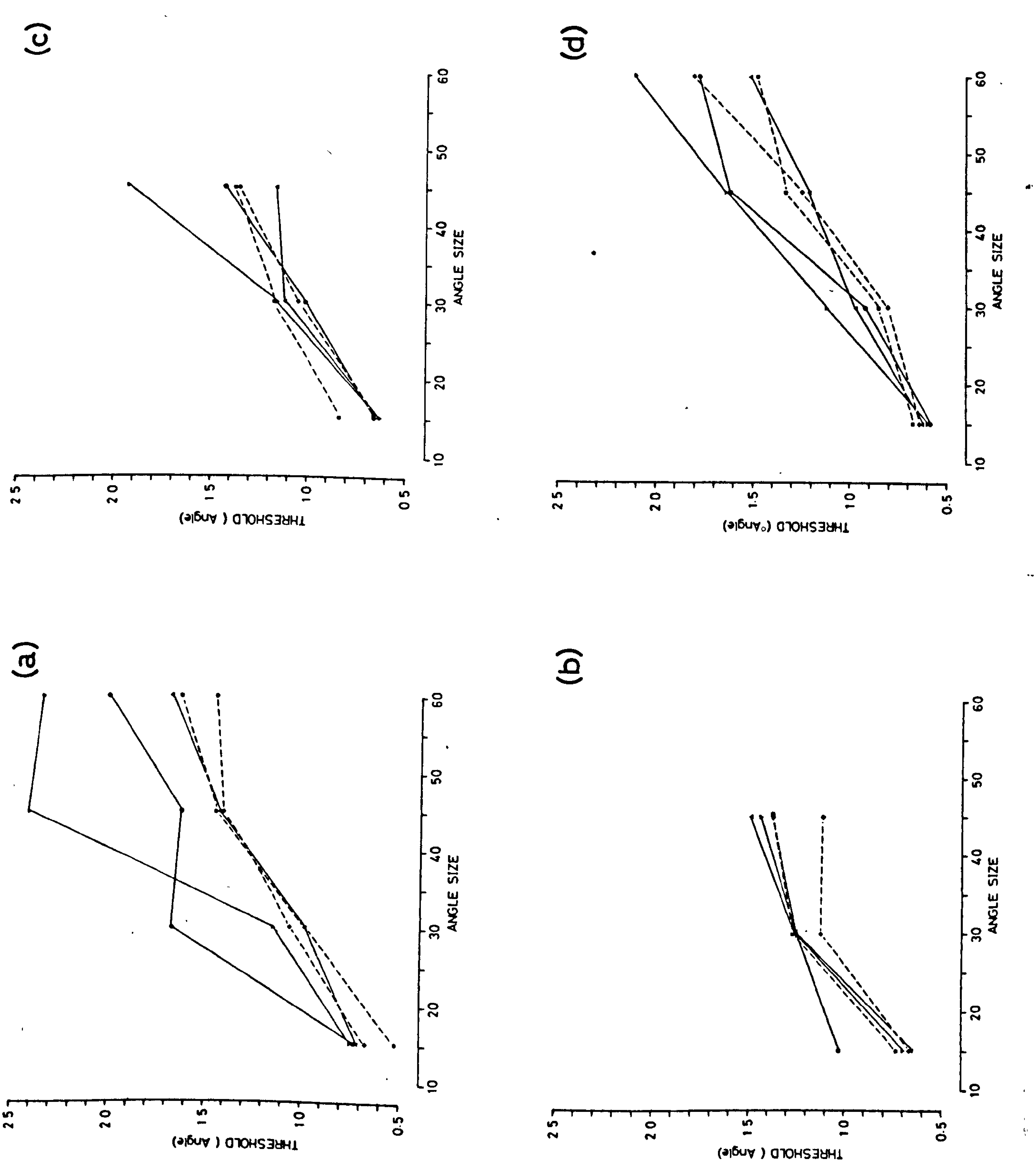


FIG 4.13 Effect of size of angles on acuity for angle size. The relative orientations were: ● - 90°, ◆ - 135°, ▲ - 180°, ■ - 225°, ▼ - 270°. Broken lines indicate obliquely oriented test angles and continuous lines indicate vertical and horizontal test angles. Line lengths were: (a) 0.3 deg. arc, (b) 0.6 deg. arc, (c) 1.0 deg. arc, (d) 3.0 deg. arc.



Discussion

(a) Constant Error

The results obtained for variations of bias with relative orientation are in agreement with Lennie's observations (1971) that the perceived difference between angles is greatest when the test angle (angle II) is oriented obliquely and the comparison angle (angle I) is oriented horizontally. The 'W'-shaped graph is preserved for all the angle sizes used, with the exception of the smallest (15^{o}). This finding is also in agreement with other studies (chapter 1) which have also shown that the perceived expansion of acute angles is greatest when the angles are vertically or horizontally oriented.

The effect of line length on the perceived relative sizes of angles or on the magnitude of the perceived expansion of acute angles has not been reported in the literature, and the findings of the present study do not lend themselves to any simple unequivocal interpretation. The graphs shown in Fig. 4.8, when 'averaged' by eye suggest that the relation between bias and line length has the form of an inverse U with the maximum (negative) bias occurring at line lengths of about 1 deg. arc. Fig. 4.8 (d) is not of great value here, as observations at intermediate line lengths were not made at an angle size of 60^{o}. These observations do not compare well with Andrews' (1967b) observations for the effect of line length on constant errors for parallelism which showed the constant error to decrease with increasing line length. In his study minimum biases were usually attained with line lengths of approximately 23 min. arc.

The relation between bias and angle size presents some difficulty for those theories which explain the perceptual expansion of acute angles simply in terms of orientation contrast mediated by lateral inhibitory interactions between orientation analysers. As the angle size increases, the separation of the active analysers in the orientation domain becomes greater and, therefore, according to lateral inhibition models the strength of the inhibitory interactions will become weaker. As it is the differences between perceived angle sizes which are being measured in this experiment some increase in the bias would be expected up to a maximum angle size, beyond which there should be a decrease. This prediction is based on the already questionable assumption that the width of the inhibitory output range of the vertical and horizontally tuned orientation analysers is greater than that of obliquely tuned analysers. Following this assumption, as the angle size increases the separation of the lines in the oblique angle will become greater than the range of mutual interaction sooner than will the separation of the lines in the horizontally oriented comparison angle. Eventually the separation of the lines in the horizontal angle will also exceed the maximum range for interaction, and in so doing the perceived difference between the sizes of the angles should diminish to zero. This tendency should be accelerated, perhaps even to the extent that the sign of the bias shows reversal, as the component lines in the comparison angle approach the obliques with increasing angle size and so the strength of the mutual inhibitory interaction for a given separation diminishes. At the same time the component lines of the test angle, at an oblique orientation, will be approaching the vertical and horizontal and so the magnitude of interaction for a given separation will accordingly increase, thus reinforcing the tendency for a decrease of the perceived difference between the sizes of the two angles.

It has already been shown by adaptation studies (Hirsch, Schneider & Vitiello, 1974; this thesis, chapter 2) that the assumption of different inhibitory tuning curves for oblique and horizontal or vertical orientation analysers is untenable. Also the estimated widths of these tuning curves is probably barely sufficient to maintain perceptual expansion by inhibitory interaction for angles as great as 60°. These estimated total widths of inhibitory tuning curves have been given values of between 45° and 60° in various studies, the most quoted value being about 50° (Hirsch et al., 1974; Lovegrove, 1976; Movshon & Blakemore, 1973; Sharpe & Mandl, 1977; this thesis, chapter 2). The half width of these tuning curves is considerably less, being of the order of 6°-12° or about 25° according to the study considered, so the strength of the inhibitory effect at the maximum range is relatively small. Even without the assumption of different tuning characteristics, therefore, the mutual inhibition explanation of the perceptual expansion of acute angles would predict a decrease in the perceived difference in angle size, with oblique test angles, as the angle size tends toward the maximum of the range for mutual interaction.

Although the results presented in Fig. 4.9 are not unequivocal on this point, those biases observed at the largest angle sizes are so large as to be beyond doubt. Conversely, for small angles which would be expected to show the greatest apparent expansion, and therefore the greatest differences for different orientations, no systematic variation was observed. The biases for the 15° angle are in fact comparable to biases obtained for comparisons of angles of equivalent orientations, independent of orientation (see chapter 5). These findings indicate, therefore, that the processes underlying the perceptual expansion of acute angles cannot be explained simply in terms of lateral interactions between orientation detectors, despite the close agreement of Blakemore, Carpenter & Georgeson's (1971) and Carpenter and Blakemore's (1973) findings with this model.

(b) Thresholds

The many studies reviewed in chapter 1 demonstrate that acuity for orientation is greatest when the stimulus orientation is vertical or horizontal, and least when the stimulus orientation is oblique. On the basis of these data alone it would be expected that threshold for angles size, if simply determined by the orientation difference thresholds for single lines, would be greatest when the lines comprising the angle stimulus are close to the vertical or horizontal and least when the lines are closer to the main obliques. In this study orientation and angle size as independent variables are confounded, but least so for the smallest angles size of 15^{o}. The orientation effect on acuity for these small angles would be expected to be most obvious, giving the typical sinusoid-like variation of acuity with increasing angular separation of the bisectors of the two angles, as the test angle departs from the vertical toward the oblique, to the horizontal and so on. For the smaller angles (15^{o} and 30^{o}) this expectation is evidently quite erroneous, as the results illustrated in Fig. 4.10 and 4.11 show.

The same reasoning applies to the relation between acuity for angle size and the size of the angle. As the size of the angle changes, then at different bisector orientations the lines comprising the test angle should be perceived better or worse as the angle size changes. For example, at a test angle orientation of 135^{o}, as the size of the angle increases the component lines move further and further away from the bisector of the angle and become nearer and nearer to the horizontal. The converse is true for vertically or horizontally oriented test angles. However, as Fig. 4.12(a) shows, there is a consistent increase in threshold with increasing angle size, for all orientations. At the same time as the lines in the test angle are, for example moving from, e.g. 135^{o} to the vertical and horizontal, the lines of the comparison angle are, by the same amount, approaching the obliques. Consideration of this factor only leads to the expectation that, for a given anglular separation of test and comparison angles, the acuity should remain approximately constant. This prediction too, however, does not reflect the experimental observations which are repeated for all orientations and line lengths employed, that acuity decreases with increasing angle size. Although the relation between acuity for angle size and the size and orientation of the angles will be considered further in the following chapter, the observations derived from this experiment strongly suggest that the acuity for angle size is not determined simply by the combined acuities for the lines comprising the angles.

The effect of the third factor, line length, on the difference threshold for angle size appears to be no more predictable from other measures of acuity than were the effects of orientation and angle size predictable from earlier studies. Andrews (1967b) and Andrews, Butcher and Buckley (1973) have both repeated earlier findings and shown new observations that increasing line length results in a reduction of threshold for a number of spatial acuity tasks. The results from this study can only be compared to the earlier observations for the longer lines, as 18 min. arc was the shortest line length used. Also, the number of subjects is hardly appropriate to detailed generalisation for quantitative rules. However, as the results illustrated in Fig. 4.13 show, there is little obvious systematic relation between threshold and line length, although line length was shown to have a significant effect on the difference threshold (Table 4.6).

Experiment 6: Comparison of angle sizes - Oblique reference angle.

The final experiment to be described in this chapter was a variation of the experiment just discussed, for which the stimulus set employed was rotated through 45° so that the bisector orientation of the comparison angle was 45° and that of the test angles was varied in 22° steps from 135° to 315°. This variant was introduced as a check on the consistency of the method, the subject and the effect to be measured, with reference to the results obtained in the preceding experiment. As Experiment 5 showed that the perceived size of a horizontal angle was greater than that of obliquely oriented angles, it was expected that the 'W'-shaped graphs obtained with a horizontal comparison angle would be inverted to become an 'M'-shape with an oblique comparison angle. As the test angle should appear greater (at PPE) than the comparison angle at relative orientations of 135° and 225°, the maximum biases should have a positive sign.

Method

Apart from the changed orientation of the stimulus all other conditions under experimenter control were identical to those in the previous experiment. The line length was 18 min. arc, and the angle size was 30°.

Results

The outcome of this study was, with the exception of one aberrant point on the graph, fully consistent with expectations. The results are shown in Fig. 4.14, together with the graph for the results of the previous study for the same angle size and line length. Despite the obviously outre point at a relative

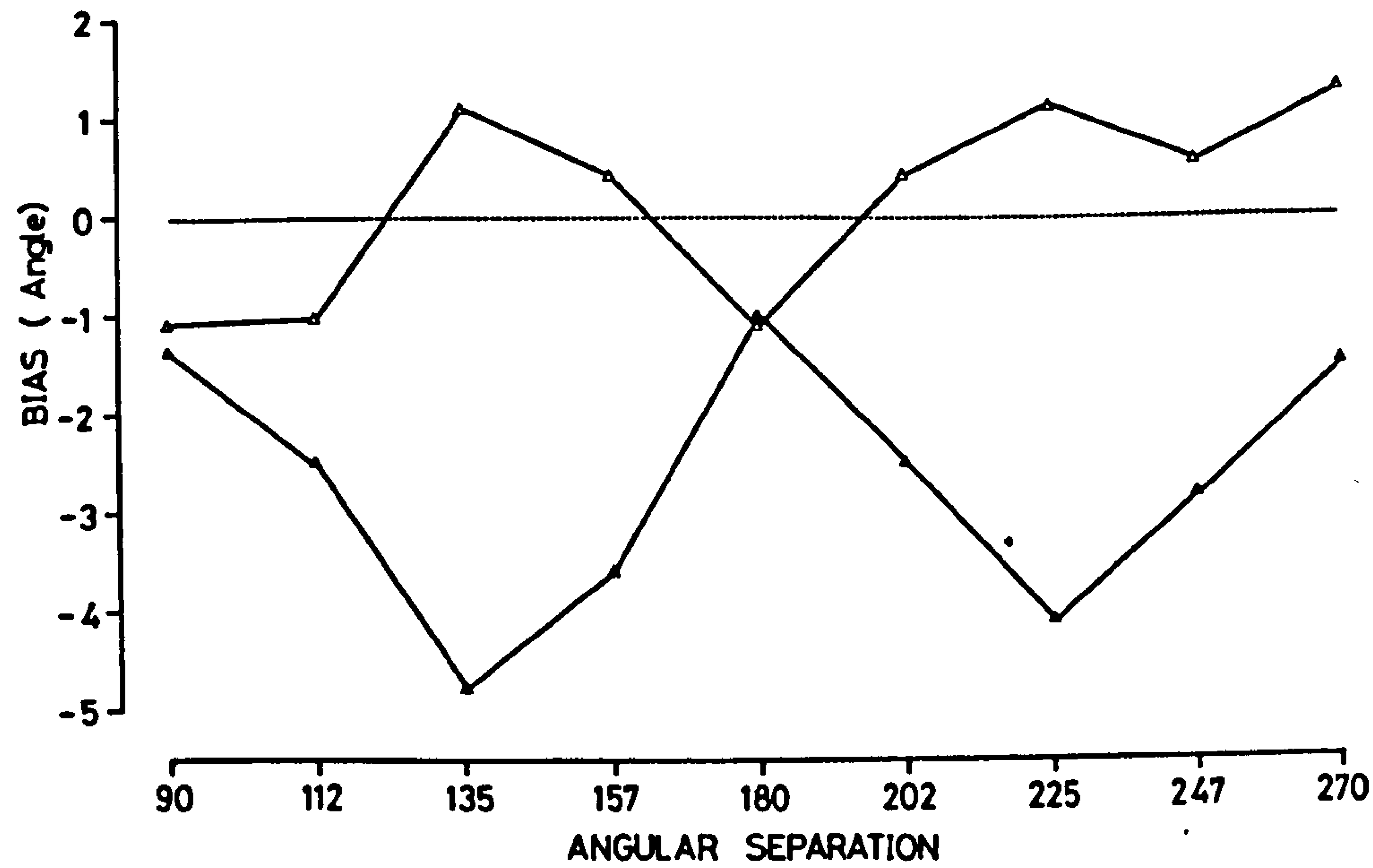


FIG 4.14 Effect of relative orientation on the perceived relative sizes of acute angles. The bisector orientations of the comparison angles were: ▲ - 0°, △ - 45°.

orientation of 270°, the coincidence of the minima for the two conditions is reassuring, although it is not clear why there should be an identical non-zero constant error, with such a high consistency where the test and comparison angle orientations are equivalent.

Conclusions

Two experiments described in this chapter have shown that the apparent size of an acute angle varies with the orientation of the bisector of the angle such that, with reference to a horizontal comparison angle, the size of the test angle is minimum when the bisector lies on one of the major obliques. Conversely, when the comparison angle lies on a main oblique, the test angle is maximally larger than the comparison angle when its bisector is horizontal or vertical. It is confirmed, therefore, that an acute angle appears larger when it is horizontal or vertical than it does when it is oblique. Given that acute angles are perceptually expanded, then this expansion is least for obliquely oriented angles.

The influence of line length on the amount of perceptual expansion of acute angles is to increase the difference between obliquely and horizontally oriented angles. The magnitude of the difference between the comparison angle and oblique test angles is also increased by increases of the size of the two angles. 15° angles did not show any consistent differences between horizontal and oblique orientations. The perceived difference of size of the horizontal and oblique angles appears at about 30° and subsequently increases with increases of angle size.

The acuity or difference threshold for angle size was also found to be influenced by all three experimental variables of which, however, only angle size showed an obvious relation to acuity, difference threshold increasing with increasing angle size. The rate of increase was largely unaffected by the line length or by the relative orientations of the test and comparison angles. No obvious relationship between acuity for angle size and either relative orientation or line length of the two angles to be compared was discernible.

The study described above has the shortcoming that full comparisons between the perception of orientation and the perception of angles are complicated by the fact that the stimulus variables of orientation and angle size were confounded. Further studies will be described in the following chapter which attempt to disentangle these two variables.

General Conclusions

Where the experiments described in this chapter attempted to repeat earlier findings concerning the perception of angles the results were favourable. Some results obtained by extending this study beyond those previously reported showed that despite the successful repetitions, the perception of angles has neither been fully described nor explained. Those hypotheses which have been proposed do not generalise to observations covering a relatively wide range of stimulus values, particularly of angle size. Some of these observations - especially those concerning the biases obtained in experiments 3 and 4, and the effects of angle size and orientation on both bias and threshold in experiment 5 - suggest that the perception of angles cannot be fully understood on the basis of a knowledge of orientation perception alone. Angularity appears to be a property recognised as such by the visual system, rather than as differences between orientations. The studies to be described in the following chapters will examine the perception of angles and angle size more closely in an attempt to reach a better understanding of the mechanism whereby the visual system processes information concerning angular extent.

Chapter 5 - Acuity and Constant Error in Angle Perception: II

Introduction

The results obtained from Experiments 3 and 4 described in the previous chapter showed that acuities for comparisons of angle size followed the pattern expected from the behaviour of single lines, when the angles were right angles. The difference threshold was lowest when the lines comprising the angles lay on the vertical or horizontal and highest when the lines were oblique. In the first part of that experiment (Expt. 3) it was found that a similar pattern was shown for judgments of orthogonality. The difference threshold for departures from a right angle was smallest when the angle was oriented such that the component lines were vertical and horizontal, and greatest when the lines were oblique. The constant errors obtained in these two studies, however, were not so easily explained, appearing to vary arbitrarily, and not conforming to expectations generated by any current hypotheses concerned with the perception of orientation.

When the angles were acute, as in Experiment 5, however, the expectations derived from single line or single orientation studies were not fulfilled. In this study the angle sizes and orientations of the angles interacted in such a way that, except when in the horizontal orientation, the orientation of the lines was not equivalent. Although the results for difference thresholds show little pattern at all, any expected pattern of fluctuations of threshold would be quite complex. For this reason a further study of the effect of orientation and angle size on acuity was carried out in which the angles to be compared were identical in both size and orientation, varying only in retinal location which, as was shown in Experiment 4, has no effect on acuity within the eccentricity used.

Method

As before, the experiment was carried out using the computerised method of constant stimuli. The basic stimulus shown to the subject was made up of two angles and a fixation point, as illustrated in Fig. 5.1 (a). The stimulus set for a given run was composed of 21 pairs of angles varying from angle I greater than angle II to angle I smaller than angle II. As usual, stimulus number 11 represented the PPE with angle I equal to angle II.

The effects of three variables were investigated in the two experiments comprising

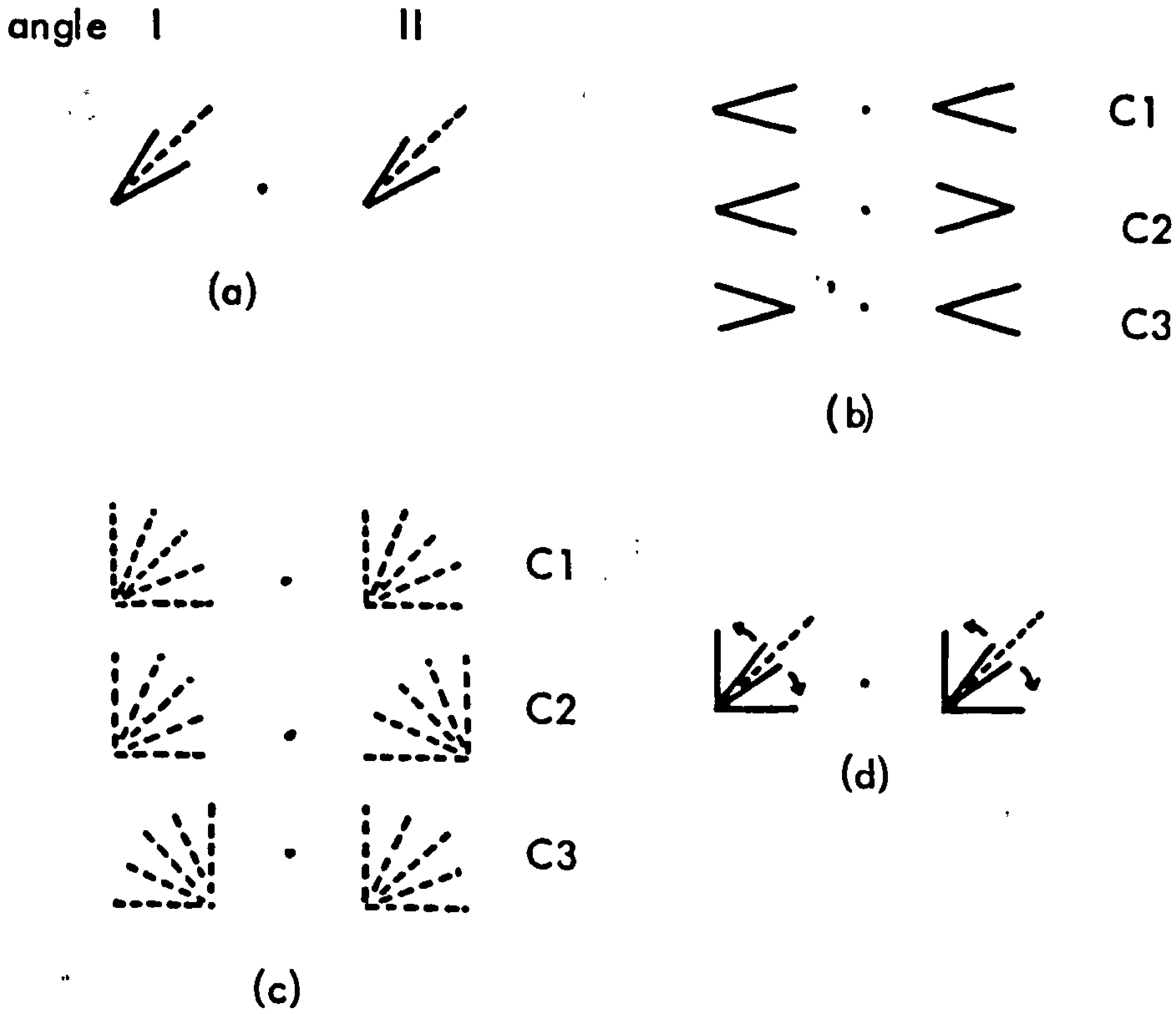


FIG. 5.1 Stimuli used in experiments 7 & 8: (a) basic stimulus pattern, the dotted lines represent the bisector of the angles; (b) the three cofiguration variants C1, C2 and C3; (c) the effect of varying the orientation of the angle bisector on the three variants, the dotted lines represent the angle bisectors; (d) the stimulus as used with angle size as the independent variable for a given angle orientation. The 3 orientations used were 45°, 90° & 0° (The relation between the angles and the fixation points is not representative of the stimulus patterns used in which an adjustment was made so that the distance from the fixation point was set with reference to the 'centre of gravity' of the angle, which was maintained at a constant distance from the fixation point for any orientation or angle size.)

this study: angle size, angle orientation and stimulus configuration - as shown in Fig. 5.1 (b - d). The inclusion of the three configurations C1, C2 and C3 controlled for the possibility that the different proximities of the vertex or end-points of the angles to the fixation points, within the eccentricity used, might lead to ambiguous results for the effect of orientation when the orientations of the angles were identical, as in C1. In the first experiment the main independent variable was angle size and in the second the effect of orientational changes on thresholds for a constant angle size was determined.

For all stimuli the line length was 18.33 min. arc (referred to as 0.3 deg. arc) and the distance between the centres of gravity of the angles was 1.5 deg. arc.

5.1 Experiment 7 - Comparison of angle sizes: Acuity and Constant Error as a Function of Angle Size.

In three sets of runs the size of the angles comprising the stimulus was varied between 15° and 90° at three orientations - horizontal (0°), oblique (45°) and vertical (90°) in configuration C1 (Fig. 5.1b). The angle sizes were 15°, 30°, 45°, 60° and 90°, increasing as shown in Fig. 5.1 (d). The subject, SRH, had normal uncorrected vision.

Four runs were made for each angle size at 0° and 90° angle orientations and six at 45°.

Results

The thresholds obtained at each angle size for the three orientations are shown in Fig. 5.2. For all orientations of the angles, the difference threshold was found to increase with increasing angle size. While this increase is maintained

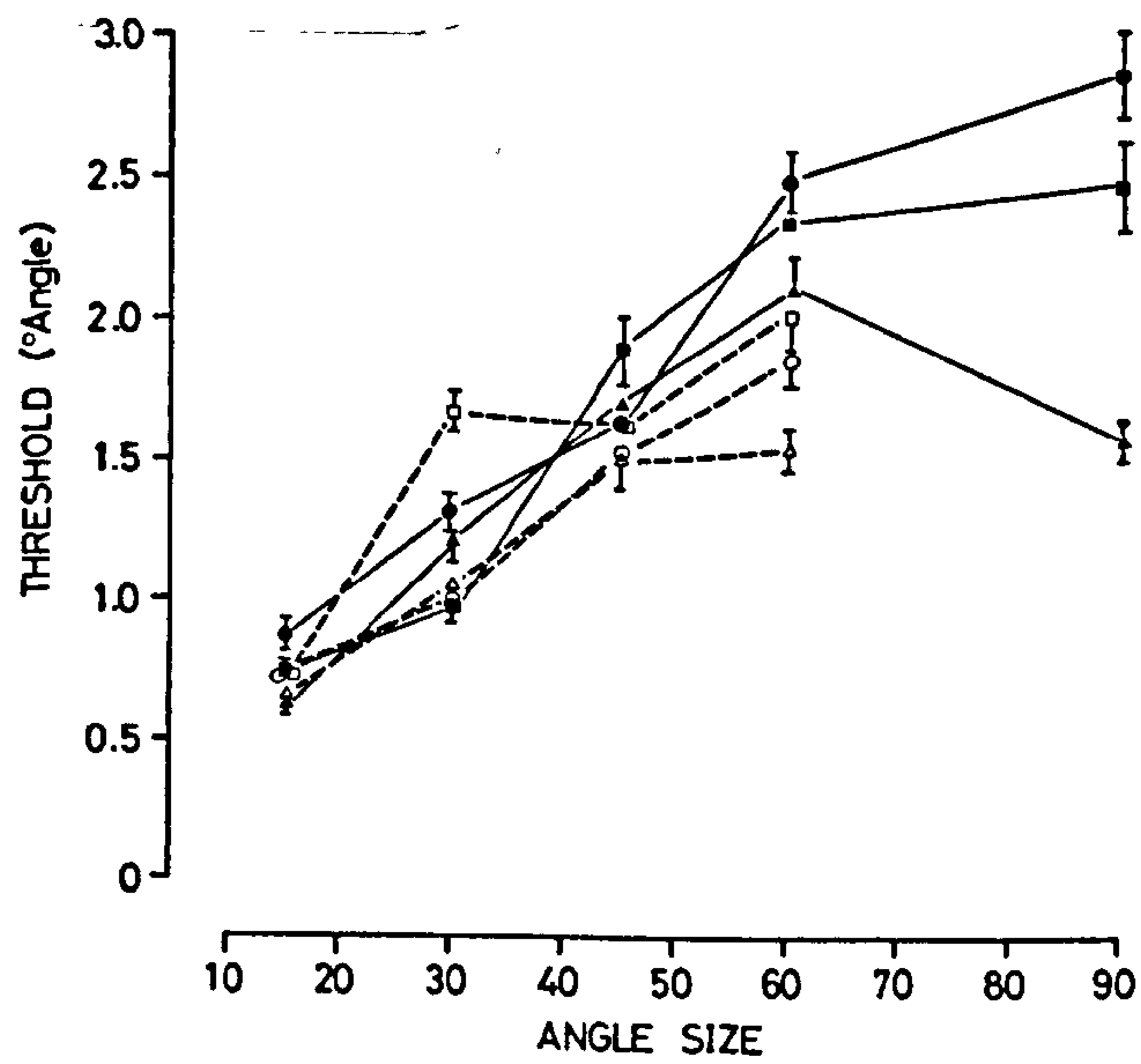


FIG. 5.2 Effect of angle size on the difference threshold for angle size. The solid symbols and lines show the results of the present experiment (7): ● - 0°, ■ - 90°, ▲ - 45°. The open symbols represent the thresholds observed in experiment 5 for the closest corresponding orientations: ○ - 180°, □ - 90°, △ - 135°.

for the vertically and horizontally oriented angles, for the obliquely oriented angle the threshold starts dropping again after an angle size of 60°, and the threshold for the oblique 60° angle is rather lower than that for the vertical or horizontal angles of the same size.

In absolute terms the thresholds at 90°, vertical and horizontal orientations, compare reasonably with the results obtained in Experiment 4 where the stimulus was identical to that for the 90° angles size in this experiment. Comparison of the results obtained in this experiment with those obtained in Experiment 5, for the same line length and the closest equivalent orientations (90°, 135° and 180°, see Fig. 4.13a) reveals that the thresholds obtained for an angle size of 15° are very similar in both experiments for all orientations. The similarity between the observations from the two experiments at 30° is quite good, but at 45° the experiments show some divergence. While the thresholds for the vertical and horizontal angles (in comparison with the horizontal reference angle) continue to increase, with the horizontal and vertical angle thresholds of the present experiment, the threshold for the oblique 60° angle is considerably lower than that for any orienation in this experiment, including the oblique angle whose threshold is already lower than that of the remainder. This observation is opposite to that which may have been expected on the basis of the threshold relation to orientation from single lines. In Experiment 5 the separations of the lines comprising the two angles from the nearest horizontal or vertical are 30° for the lines in angle I (the comparison angle) and 15° for the lines in angle II (the test angle). In the present experiment, because the bisector orientation of both angles is 45°, the distance of all the component lines from the vertical and horizontal is 15°. It might have been expected, therefore, that the performance in the present experiment would have been better than that in the previous one. In fact the reverse was found to be the case.

The biases corresponding to these threshold observations are shown in Fig. 5.3, together with their equivalents from experiments 4 and 5. With the exception of the one aberrant point from experiment 5 (30° angle at 180° relative orientation) the biases for the vertical and horizontal angles in the earlier experiments fall within the same range of values as those found in the present experiment. The biases for the obliquely oriented test angle from experiment 5 increases with increasing angle size, reflecting the different apparent sizes of horizontally and obliquely oriented angles.

The biases obtained in this study and in the earlier experiment 5 for the non-oblique test angles show that even when angle sizes are equal and orientations equal or equivalent, relatively large constant errors occur in an apparently arbitrary fashion. These constant errors appear to have a range of approximately $\pm 2^{\circ}$ and so obviously must be taken into account should any quantitative modelling of the apparent size difference effect be undertaken. Similarly arbitrary constant errors betwen equal stimuli in different retinal locations hve already been reported in this investigation (experiments 3 and 4) and in Andrews' study of perceived orientation (Andrews, 1967a, p 979ff.).

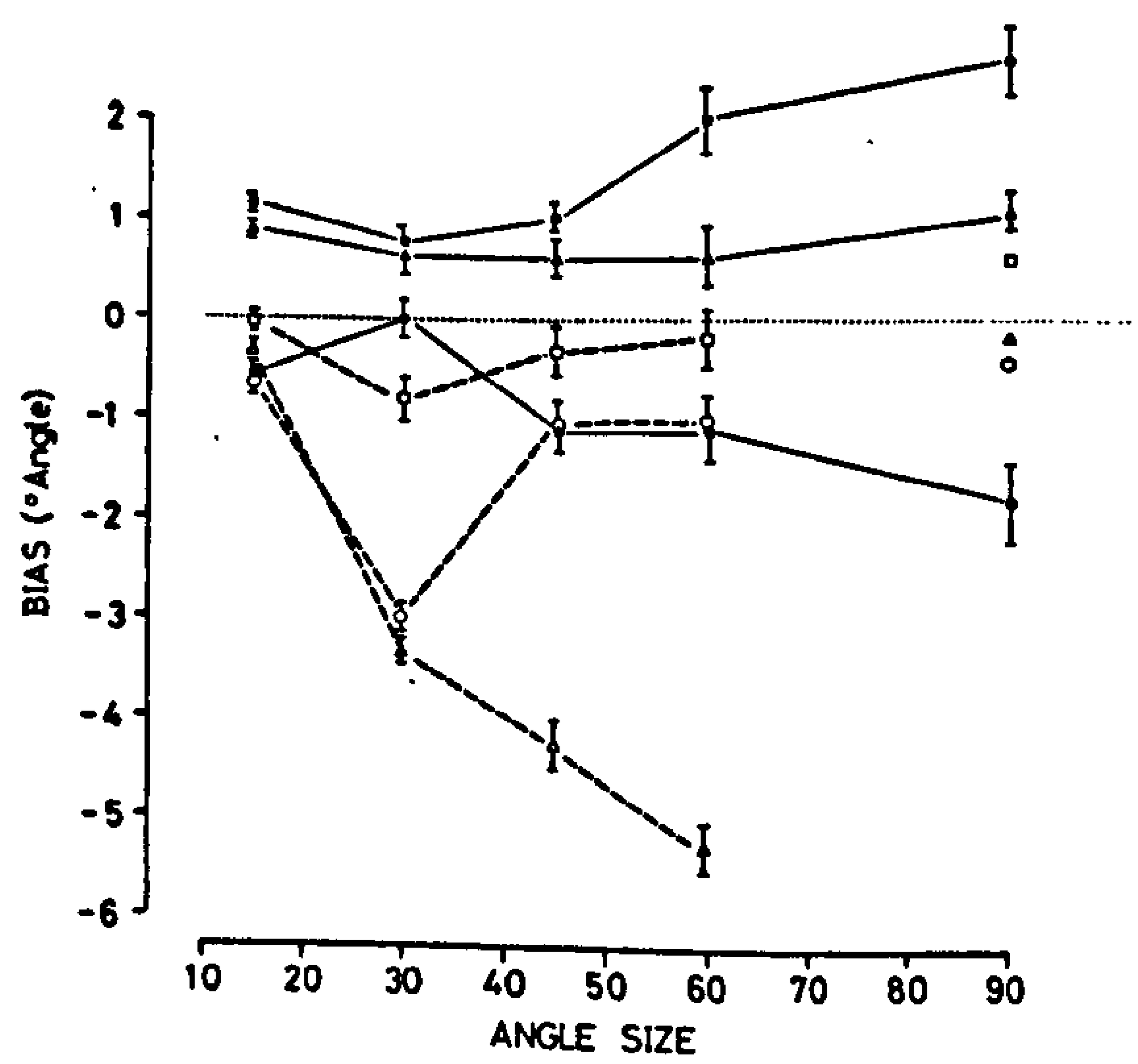


FIG. 5.3 Effect of angle size on constant error. The solid symbols and lines show the results of the present experiment (7): ● - 0°, ■ - 90°, ▲ - 45°. The open symbols for angle sizes 15° to 60° represent the biases observed in experiment 5 for the closest corresponding orientations: ○ - 180°, □ - 90°, △ - 135°. The values represented by the open symbols at an angle size of 90° are taken from Experiment 4, in which the stimuli were identical to those used in this experiment.

The characteristics of this arbitrary constant error are similar to those found by Andrews in his study - it varies with time (experiments 4 and 6 were separated by several months) and it appears to be of random magnitude with reference to retinal location. The occurrance of this component of constant error was attributed by Andrews to 'random scaling errors, which simply reflect random biases in recent visual inputs' which give rise to local differences in adaptation or level of inhibition.

Discussion

The aim of this experiment was to test the predictability of acuity for angle size from the known meridional anisotropy of acuity for single lines. The prediction tested was as follows: For vertical and horizontal angles, increasing angle size would give a monotonic increase in difference threshold up to a maximum at 90°. For oblique angles, because at small angle sizes the component lines are closest to the oblique ($\pm$ 7.5° for 15° angles) the threshold would be expected to be highest for the smallest angles and steadily decrease until the component lines lay on the vertical and horizontal for 90° angles, which would give the lowest thresholds. As the results of the experiment have shown this prediction was largely , but not totally, erroneous.

For small angles, with vertical and horizontal bisectors, the expectation was fulfilled. The major discrepancy is that the threshold for angle sizes between 15° and 45° do not show any substantial orientation effect. This observation had been suggested by the findings in Experiment 5, but the present findings obtained in the absence of difficulties raised by the stimulus configuration used in experiment 5 support this observation. The evidence indicates, therefore, that difference thresholds for angles of less than 45° do not show meridional anisotropy.

At angle sizes greater than 45° the expected separation of threshold magnitudes between horizontal-vertical and oblique angles did appear. While for the vertical-horizontal angles the threshold continued to increase as the angles became larger, and their component lines approached the main obliques, the threshold for the oblique angles began to decrease as the component lines approached the vertical and horizontal, thus repeating the finding of experiments 3 and 4 that acuity measures for right angles do show the expected oblique effect. Small angles, then, appear to behave differently from angles of about 60° or greater. At the larger angle sizes the component lines are subject to the meridional anisotropy of the visual system, indicating that there is a substantial qualitative difference at some stage of visual processing between the representation of angles greater than 60° and angles less than 60° in size. This difference could be attributable either to the existence of some form of interaction between the neural representations of the lines forming small acute angles or to the existence of a mechanism which somehow processes angle size as a quantity independently of the processing of orientation.

There are several hypotheses concerned with the perception of orientation which postulate interactions between orientation analysers, described in chapter 1, section 5, which will be reviewed and examined experimentally in the following chapter. However, as was shown in chapters 2 and 4, observations have already been made which question these hypotheses as they stand.

The results obtained in this experiment, for constant errors in the comparison of angle size, have already been discussed above. When these findings are considered together with those obtained in experiment 5, the observation that constant error increases with angle size, made in that experiment, can be qualified. In the present experiment rather large constant errors were found which although differing with angle size, did not show any consistent tendency to increase systematically with increasing angle size. These findings parallel the earlier observation (see Fig. 4.9) that such systematic increases in bias were only associated with comparisons of angles of different relative orientations. It is confirmed, therefore, that there are two possible sources of constant error in the angle-matching task, one which is arbitrary and which arises from random differences in scaling from one retinal location to another (this is not to imply that the source of the error is necessarily in the retina) and another which is a measure of perceived differences between the sizes of angles at different orientations. Only this second component increases with increased angle size. This is one of the observations referred to above which calls into question the inhibitory interaction explanation for the perceived differences in angle size since it is typical of an interaction of this sort that the strength of the interaction, and consequently of the magnitude of the perceptual manifestation, should diminish with increasing separation of the interacting units of the 'receptor surface' (Mach, 1868b; Cornsweet, 1970; Hartline & Ratliff, 1958).

5.2 Experiment 8 - Comparison of Angle Size: Acuity and Constant Error as a Function of Stimulus Orientation and Configuration.

Because of the controversial nature of the finding that small angles do not show the expected meridional anisotropy of the visual system, which has been established for almost every visual function where stimulus orientation is a variable (Appelle, 1971; chapter 1, section 2) a further experiment was carried out to investigate the influence of orientation on acuity for angle size in more detail.

Methods

The influence of two variables was measured in this experiment, as final tests of the preceding observations - these were stimulus orientation and stimulus configuration. Using the basic stimulus shown in Fig. 5.1(a) the three configurations shown in Fig. 5.1(b) were tested at the orientations shown in Fig. 5.1(c). The orientations were: 0°, 22°, 45°, 67° and 90°. The angle size was 15° and the line length 18.3 min. arc and separation of the angles, 90min arc. Subject SRH had normal uncorrected vision; subjects DTM and KB had vision corrected to normal with spectacles.

Results

The effects of orientation on difference threshold are shown in Fig. 5.4. An initial 3-way analysis of variance showed subjects and orientations to be significant sources of variance ($p < 0.01$) while configurations were not a significant factor (Table 5.1). Subsequent analyses of the data from each

Source of Variation	d.f.	Sums of Squares	Mean Squares	F-ratios	
Subjects	2	0.148	0.074	7.21	$p < 0.01$
Configuration	2	0.010	0.005		
Orientations	3	0.719	0.240	23.55	$p < 0.01$
Subj. x Conf.	4	0.036	0.009		
Subj. x Orient.	6	0.202	0.034	3.27	$p < 0.01$
Conf. x Orient.	6	0.037	0.006		
S. x C. x O.	12	0.104	0.009		
Residual	36	0.371	0.010		
Total	71	1.628			

Table 5.1 Analysis of variance summary table for difference thresholds obtained in experiment 8.

subject (Tables 5.2 - 5.4) show configuration is not significant for any subject, as would be expected from the first analysis, and that orientation is a significant factor only for subjects DTM and SRH. The observations for each of these two subjects were pooled across configurations and submitted to Tukey's test for post hoc comparison of means. The results of the Tukey test showed that for both subjects, only the difference threshold at 0° orientation was significantly different from thresholds obtained at all other orientations ($p < 0.05$). No threshold observation other than at 0° was significantly different from a threshold at any orientation other than the horizontal.

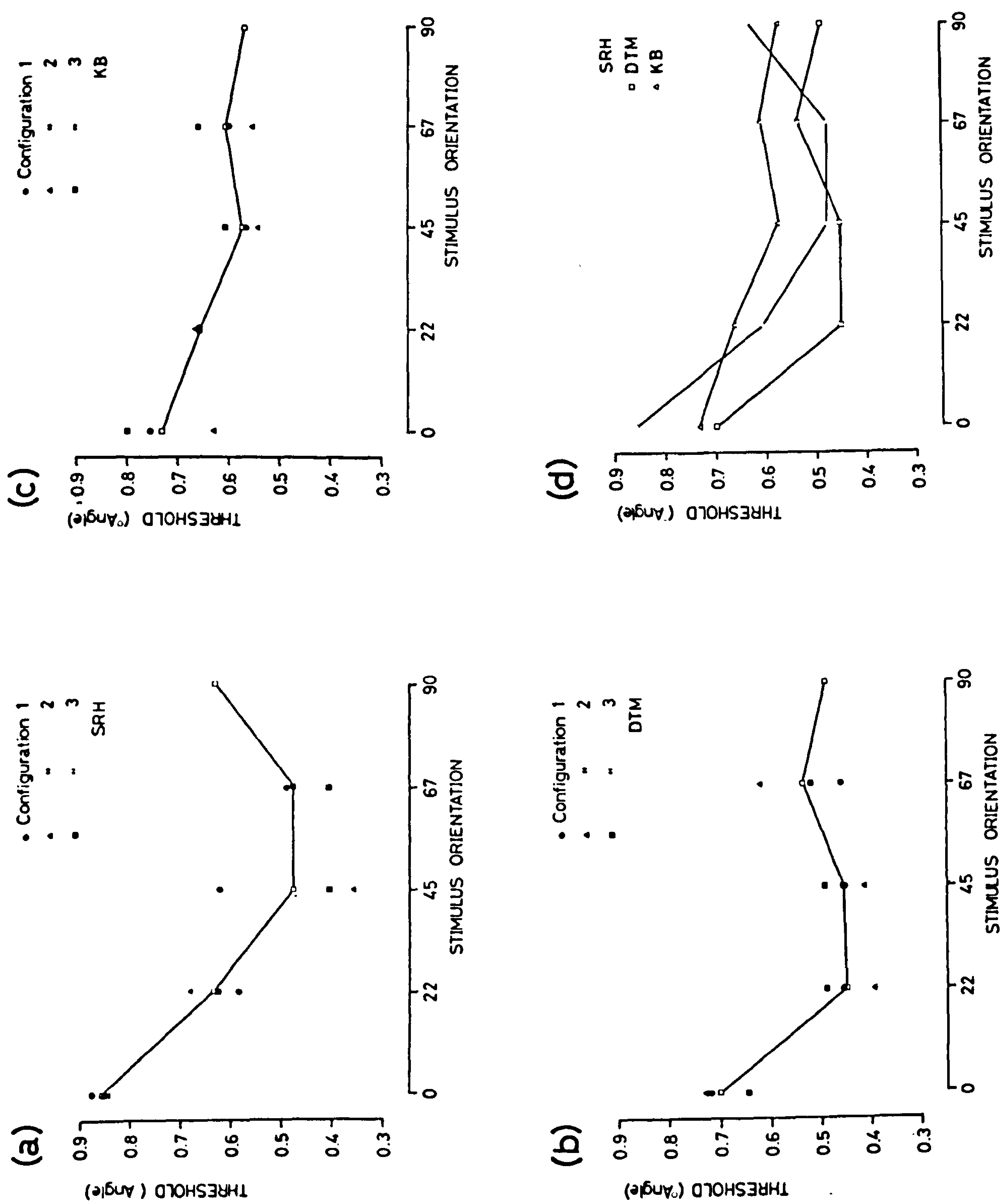


FIG. 5.4 Effect of stimulus orientation on difference threshold for angle size. Graphs (a) - (c) show individual results for each subject for each of the three stimulus configurations; the open symbols represent the mean thresholds (rms) at each orientation. Graph (d) shows the mean thresholds for each subject.

Source of Variation	d.f.	Sums of Squares	Mean Squares	F-ratio	
Configuration	2	0.017	0.008	8.53	n.s.
Orientation	3	0.604	0.201	50.12	p< 0.01
Conf. x Orient.	6	0.075	0.012	3.11	n.s.
Residual	12	0.048	0.004		
Total	23	0.745			

Table 5.2 Analysis of variance summary table for difference thresholds obtained in Experiment 8 for subject SRH.

Source of Variation	d.f.	Sums of Squares	Mean Squares	F-ratio	
Configuration	2	0.003	0.001	0.15	n.s.
Orientation	3	0.236	0.079	9.15	p< 0.01
Conf. x Orient.	12	0.103	0.009	0.91	n.s.
Total	23	0.389			

Table 5.3 Analysis of variance summary table of difference thresholds obtained in Experiment 8 for subject DTM.

Source of Variation	d.f.	Sums of Squares	Mean Squares	F-ratio	
Configuration	2	0.027	0.013	0.73	n.s.
Orientation	3	0.080	0.027	1.47	n s.
Conf. x Orient.	6	0.019	0.003	0.18	n.s.
Residual	12	0.220	0.018		
Total	23	0.346			

Table 5.4 Analysis of variance summary table for difference thresholds obtained in Experiment 8 for subject KB.

The observed constant errors for the comparisons of angle sizes in this experiment are shown in Fig. 5.5. Analysis of variance (Table 5.5) showed a significant effect between subjects ($p < 0.05$) and between orientations ($p < 0.01$) but not between configurations. Further comparison of the mean constant errors at each angle orientation, for each subject pooled over configurations revealed no systematic trends in the variation of constant error with angle orientation.

Source of Variation	d.f.	Sums of Squares	Mean Squares	F-ratio	
Subjects	2	4.743	2.371	3.59	p< 0.05
Configuration	2	0.975	0.487	0.79	n.s.
Orientation	4	17.046	4.262	6.453	p< 0.01
S. x C.	4	1.291	0.323	0.52	n.s.
S. x O.	8	3.258	0.407	0.65	n.s.
C. x O.	8	10.781	1.348	2.14	p <0.05
S. x C. x O.	16	12.140	0.759	1.31	n.s.
Residual	45	26.022	0.578		
Total	89	76.254			

Table 5.5 Analysis of variance summary table for constant errors obtained in Experiment 8.

Significant differences were found only for subjects SRH and KB, DTM's results showed no significant effect of orientation on constant error. For KB only the bias at 67° was significantly different from any other bias ($p < 0.05$) while for SRH 5 out of the 10 possible pairwise comparisons showed a significant difference: $0^{\circ} - 45^{\circ}$, $0^{\circ} - 67^{\circ}$, $0^{\circ} - 90^{\circ}$, $22^{\circ} - 67^{\circ}$, $45^{\circ} - 67^{\circ}$, at $p < 0.05$. The lack of any systematic relationship between stimulus orientation and bias, and the lack of consistency between subjects for those differences which were found repeats the findings of experiments 3,4 and 6 reinforcing the interpretation of such observations that the constant errors obtained for comparisons of angles differing only in retinal location reflect arbitrary variations in angle scaling across the presumably cortical mapping of the retina.

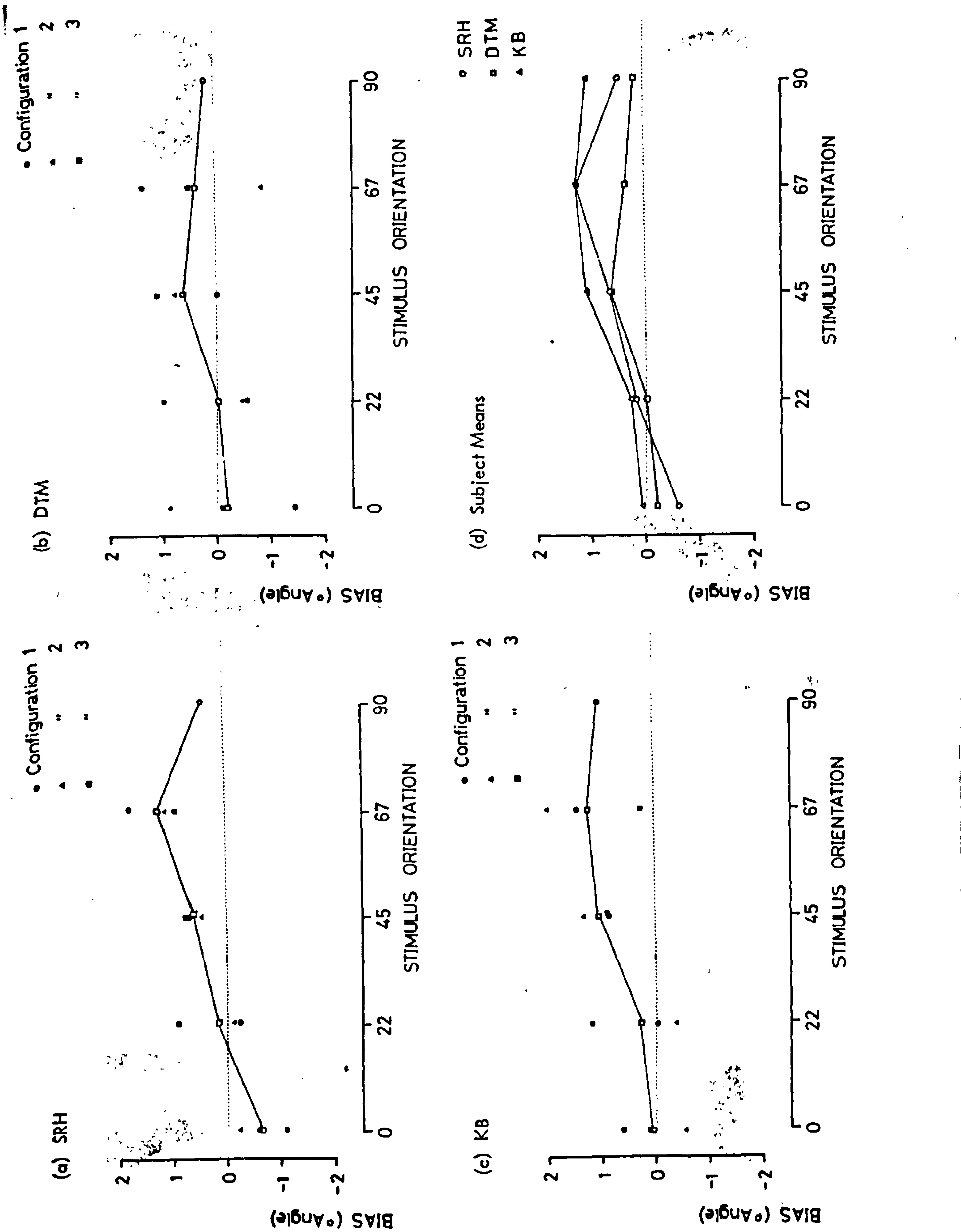


FIG. 5.5 Effect of stimulus orientation on constant error in comparison of angles of equal sizes and equivalent orientations. Graphs (a)–(c) show individual results for each subject for each of the 3 stimulus configurations. Graph (d) shows the mean constant error for the three subjects.

Discussion

The major finding of this experiment is the confirmation of the observation made in experiment 5 that difference threshold or acuity for angle size is not systematically dependent on the orientation of the stimulus angles. In the present experiment the size of the angles was held constant, and the bisectors of the two angles to be compared were at the same orientation. It is not the case, therefore, that differences in acuity have been submerged beneath the confounding of absolute orientation, relative orientation and angle size as was possible with the stimulus set used in experiment 5. These results are also consistent with those obtained in the previous experiment which showed that for angle sizes up to 45° - 60° there was no difference between difference thresholds for vertical, horizontal and oblique angles. The consistency of these findings is marred only by the observation that the threshold at 0° was significantly different from the remainder for subjects SRH and DTM. Significant differences between orientations were found in experiment 5 but, as in this experiment, these differences were not those which would have been predicted from the oblique effect as described.

On the basis of the results obtained from experiments 5, 7 and 8 it is concluded that small angles (45° - 60° or less) are not subject to the oblique effect found for comparable discrimination tasks where the stimulus contains single orientations only. These findings substantiate the doubts raised in the discussion of experiment 5 concerning the role of so-called orientation analysers in the perception of angles.

CHAPTER 6: The Time Course of the Perceived Expansion of Acute Angles.

Results obtained from the Orientation Contingent Colour Aftereffect and the masking studies demonstrate that the differences between the perceived sizes of an acute angle at different orientations cannot be due to differences in the inhibitory tuning characteristics of orientation selective channels. Evidence presented by Abadi (1974) has shown further that this effect cannot be attributable to differences in the excitatory tuning curves of these channels, which again were found to be equivalent for vertical and horizontal and oblique orientations.

Andrews (1965, 1967a) has shown that there are constant errors in the perceived orientations of single lines, such that for flash presentations of stimuli the perceived orientation was biased toward the oblique, while for lines presented for longer durations (greater than 500 msec.) the direction of the bias was reversed. Further characteristics of the empirical response error distributions showed tha bias to be minimal for vertical, horizontal and oblique lines, with maxima occurring between the horizontal or vertical and the obliques. This finding was explained in terms of asymmetries of the response distributions, such that the longer tails are always in the direction toward the oblique. Only response distributions to vertical, horizontal and oblique orientations were proposed to be symmetrical.

The observed biases in percieved orientation were thus explained in terms of differences in the response characteristics of the orientation selective channels. According to this model, although the sign and magnitude of the constant error in the perceived orientations may vary as a function of the amount of lateral inhibition, and therefore of stimulus duration, neither the existence of the constant error nor the differences in the selectivity between the detectors tuned to different orientations is claimed to be a consequence of the mutual inhibition between the detectors.

According to Blakemore's model, and other possible models based on the inhibitory interaction model derived from the brightness contrast paradigm; displacement of perceived orientation leading to the perceived expansion of acute angles is consequent on the presence of two adjacent orientations in the stimulus and a subsequent displacement of the peaks of activity in the orientation domain. As illustrated by Blakemore's representation (see Fig. 6.1) this displacement, due to summation of inhibition in the region where the inhibitory profiles of the two detectors overlap enhances the apparent angular separation of the lines comprising the angle, resulting in the illusion.

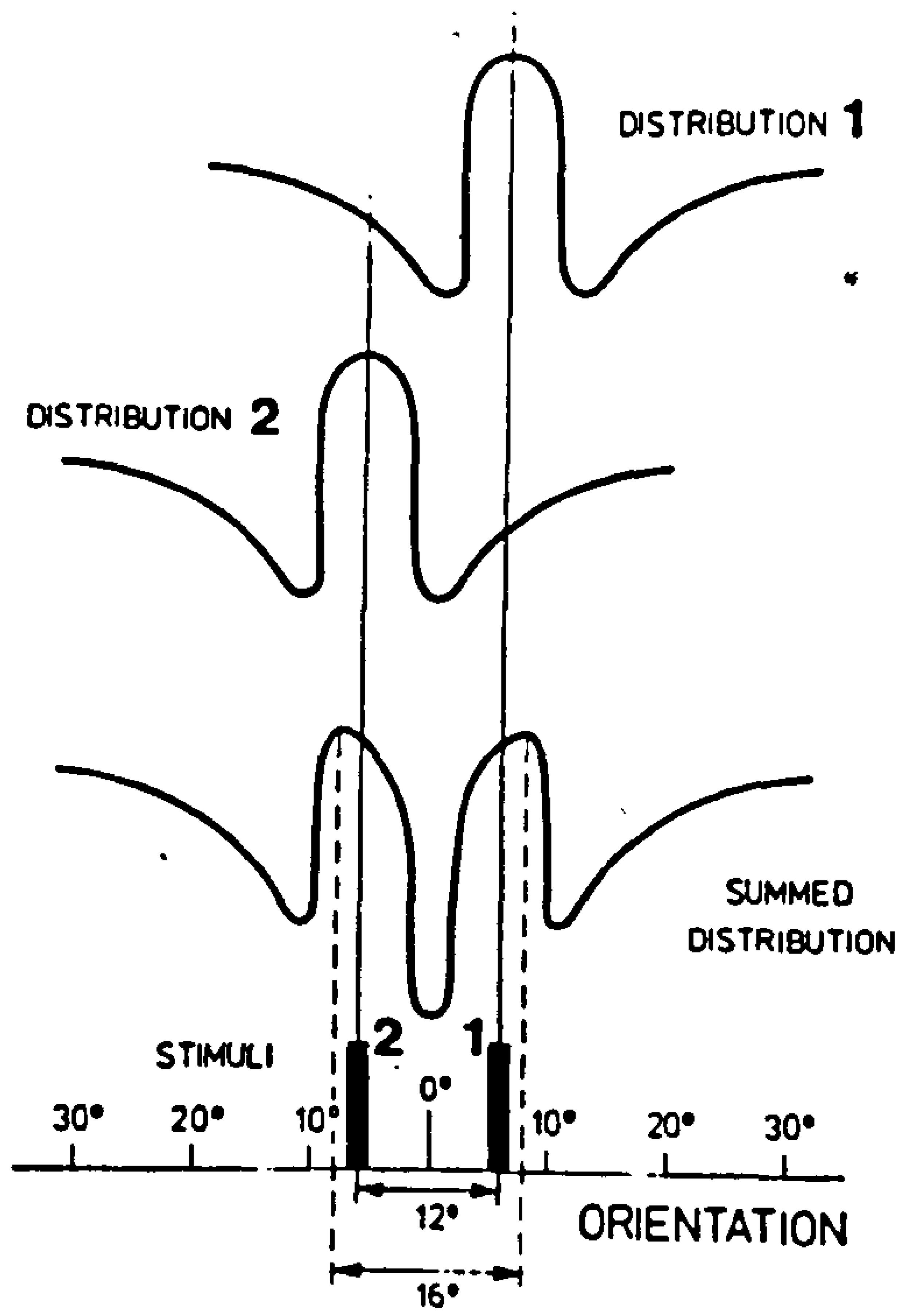


FIG. 6.1 Diagram of the stimuli and response characteristics, within the orientation domain, for a system of neurones that undergo mutual lateral inhibition. Distributions 1 and 2 show responses to each of the lines presented singly, the third distribution shows the sum of 1 and 2. The summation of the inhibitory profiles of 1 and 2 leads to a 'repulsion' of the peaks of acrivity representing the orientations of the lines and thus to an apparent expansion of the angle. (After Carpenter & Blakemore, 1973, p289)

Although the hypotheses of Andrews and of Blakemore appear superficially to be similar, there are certain fundamental differences. Andrews proposes that while there is mutual inhibition between orientation detectors, which builds up with time, there are already biases in perceived orientation which, being present and large for even the briefest stimulus durations (c. 10 msec.) cannot be attributable to the presence or build-up of lateral inhibition. Furthermore, the directions of these biases, and their changes in magnitude and sign with time, consequent on increases in inhibitory interactions are such that the largest difference between the perceived sizes of horizontally and obliquely oriented angles will be observed for brief stimulus durations. As stimulus duration increases the differences in perceived angle size will diminish, and with longer durations may even show reversal.

Carpenter and Blakemore (1973), on the other hand, suggest on the basis of some rather cursory experiments that "the process producing this phenomenon has a characteristic growth time-constant of less than a second or two" (op. cit. p 298). Insofar as the expansion of perceived angle size is in their view fully contingent on lateral inhibition, it would be expected, therefore, that the size of the illusion be an increasing function of time for stimulus durations up to at least 0.5 seconds.

This being the case, a testable distinction can be drawn between the two models described. That of Carpenter and Blakemore predicts that the magnitude of the effect will increase with time, while Andrews' model suggests that the effect will be present even at the shortest durations and will diminish or even reverse with longer stimulus durations. An experimental test between these two predictions was therefore carried out.

Experiment 9

Methods

The experiment was carried out using the computerised method of constant stimuli described in chapter 3 above. The basic stimulus pattern used is shown in Fig. 6.2 (a) and the set of 21 possible patterns is indicated by the examples in Fig 6.2 (b). An obtained negative bias indicates that at the

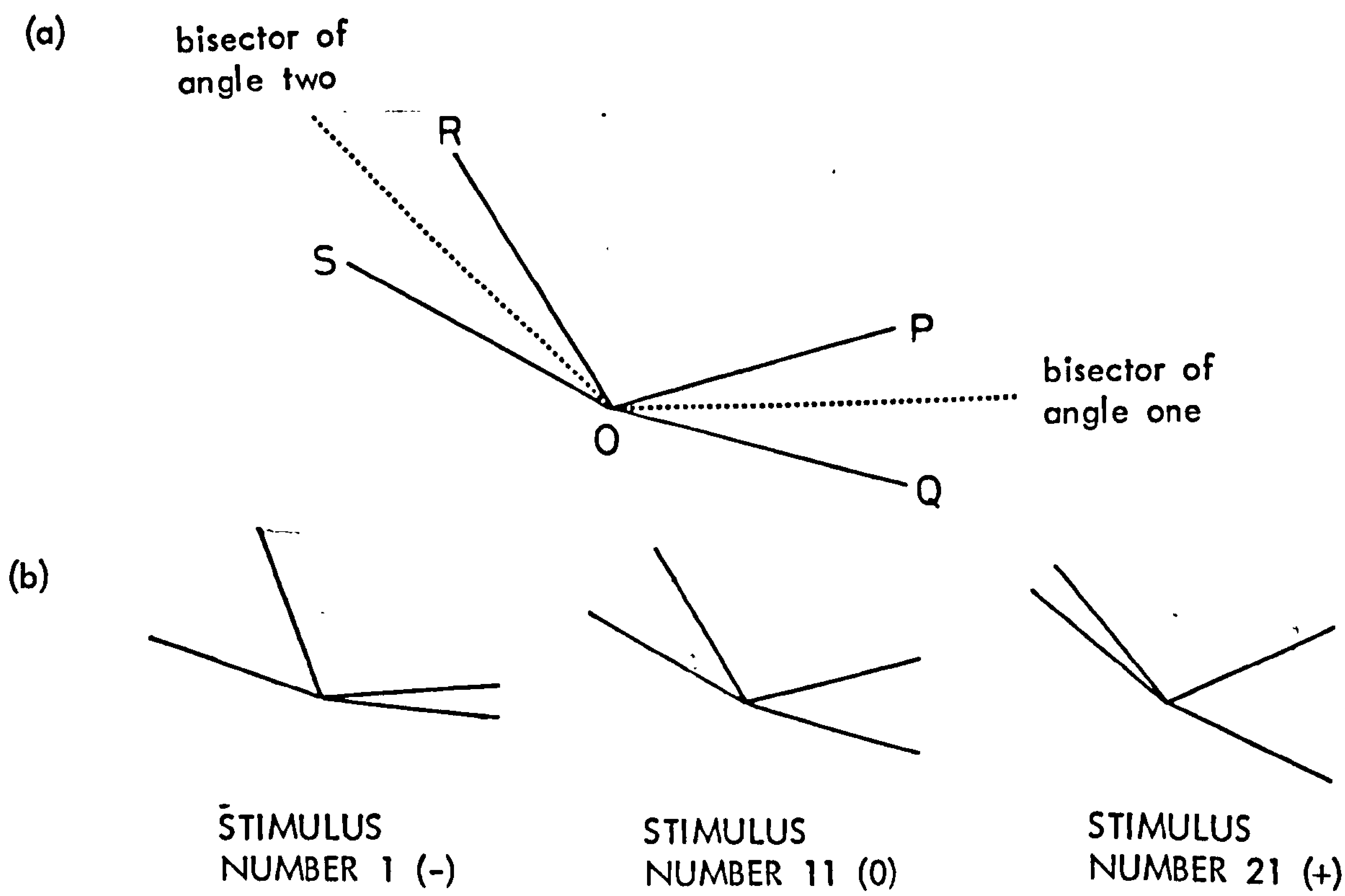


FIG. 6.2. (a) The basic stimulus configuration used in Experiment 1. (b) Range of stimulus configurations available during any one run. The signs in parentheses indicate the position of the stimulus in the stimulus range.

PSE angle II (ROS) was set larger than angle I (POQ) and, therefore, angle II appeared smaller than angle I at the PPE. An obtained positive bias indicates that the reverse was the case. The lines comprising the stimuli were 0.3 deg. arc in length with a thickness of c1 min. arc. The presentation sequence was: 1 second fixation point; stimulus duration as experimental variable; 2-3 second interstimulus interval, according to the preference of the subject. All sessions took place under normal level artificial light (fluorescent tube).

Subject SRH had normal uncorrected vision, subject DTM had normal vision after correction with spectacles.

Results

For this experiment and those following in this chapter, the results concerning difference thresholds will be dealt with together, after the consideration of the results concerning bias effects.

Fig. 6.3 shows the results obtained at different line lengths with an angle size of 30°, the bisectors of the two angles being separated by 135°, as shown in Fig. 6.2. At this orientation the apparent difference in size between the two angles, when objectively equal, is at a maximum (Lennie, 1971; chapter 4 above).

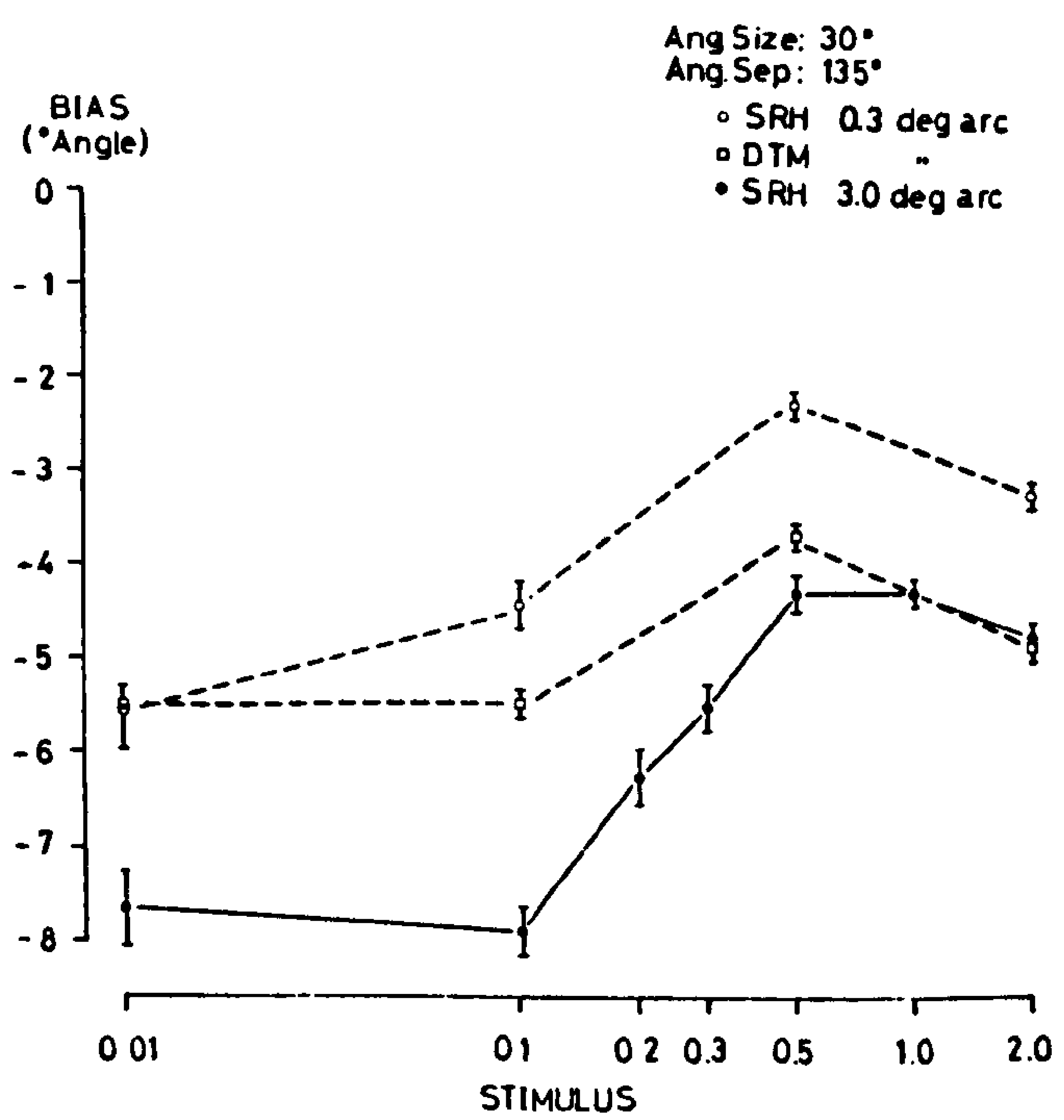


FIG. 6.3 : The effect of stimulus duration on perceived relative angle size.

In all cases there was an overall decrease in the magnitude of the illusion with increasing stimulus duration. The graphs also illustrate the inter-subject variation in the absolute magnitudes of the effect. Despite these differences between subjects, however, the time-course of the effect remained similar for the two subjects at both line lengths.

The observed changes in the perceived difference in the sizes of the two angles shows the effect to diminish with time, as is predicted by Andrews' model. Had the alternative hypothesis been true, that as a result of the build-up of inhibitory influences with increasing time the error in perceived angle size should grow, the perceived difference between the sizes of the two angles would be expected to increase - horizontally oriented angles being subject to a greater degree of perceptual enlargement than obliquely oriented angles. The agreement with Andrews' hypothesis is, however, marred by the inflexion in the curves occurring at a duration of 0.5 seconds, where the trend is reversed and assumes a direction consonent with the hypothesis proposed by Carpenter and Blakemore (1973) in that the apparent difference in angle sizes tends to increase with further increases in stimulus duration up to the longest duration used, 2 seconds.

Further investigations showed, however, that this inflexion is not a distinctive characteristic of the process underlying the errors in perceived angle size. Fig. 6.4 shows the time course of the apparent difference in angle size effect as the relative orientation of the angles is varied. As can be seen, although there are marked differences in the amount by which the relation between stimulus duration and bias is non-monotonic at the different relative orientations this degree does not appear to be systemmatically linked with any of the parameters manipulated. The presence of this inflexion cannot be taken, therefore, to indicate an 'Andrews-stage' followed by a 'Blakemore-stage' in the dynamic attributes of the effect.

Despite these favourable results, a problem remains in that the data shown in Fig. 6.5, derived from studies already described, are in close agreement with results obtained by Lennie (1971). These results, he claimed, are inconsistent with Andrews' model in that the errors in the perceived orientations of the component lines, as derived from these measurements is always in the direction toward the obliques. Andrews' model predicts that for longer stimulus durations biases in perceived orientation should tend toward the nearest horizontal or vertical. Lennies' proposed explanation of his findings is based, however, on the premise 'differential inhibition' between orientations

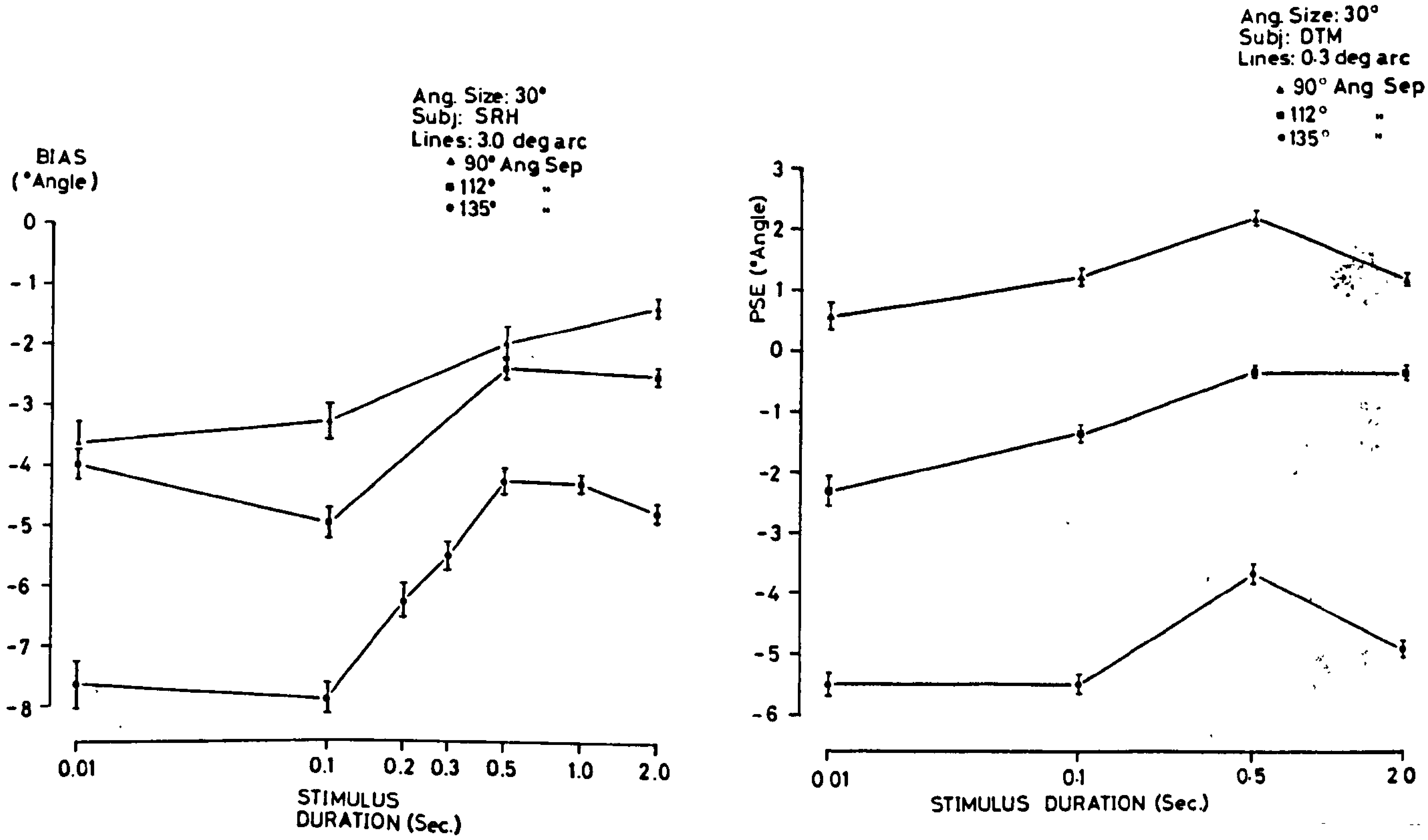


FIG. 6.4 Effect of stimulus duration on perceived relative angle size for three angular separations between the bisectors of the test and the comparison angles.

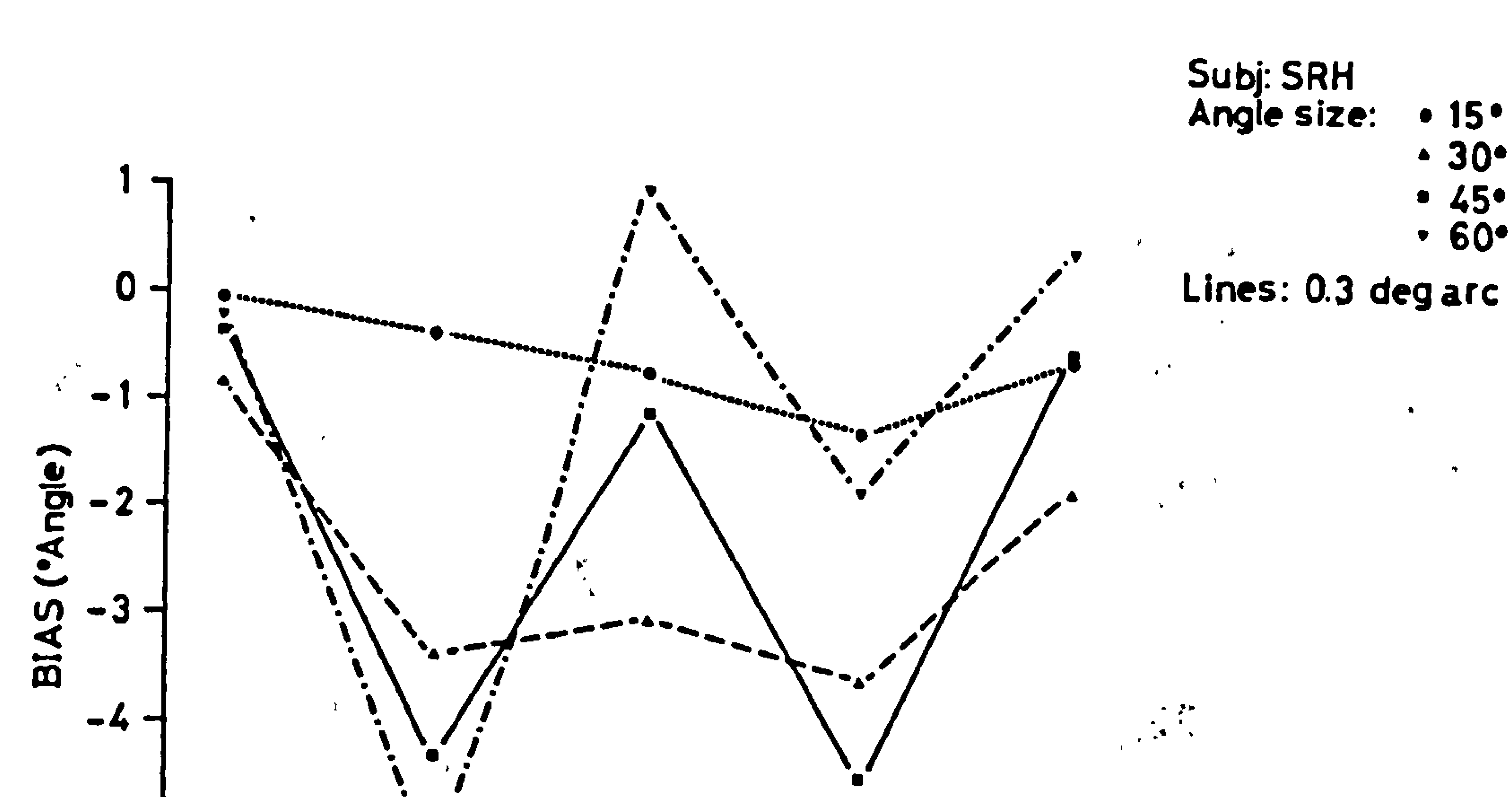


FIG. 6.5 Variation of perceived relative angle size as a function of relative orientation (angular separation) of the comparison and test angles. The angle size was 3° and the line length 0.3 deg arc at a stimulus duration of 2 seconds.

such that "this inhibition is greater between detectors tuned to vertical and horizontal than it is between those tuned to other orientations." The results already presented, obtained from adaptation and masking experiments (chapter 2) have already shown there to be no observable differences in the inhibitory characteristics of orientation analysers (also Hirsch et al., 1974; Abadi, 1974). However, although Lennie's hypothesis for the explanation of his results cannot be accepted, his observations that the error in the perception of angle size implies an error in the perception of orientation in a direction opposite to that predicted by Andrews' hypothetical orientation analysers are substantiated. While the dynamics of the effect are, therefore, in agreement with Andrews' model, its behaviour with variations of perceptual error according to stimulus orientation is not.

Experiment 10

In order to try and resolve this contradiction a further series of runs was conducted in which the changes of the perceptual bias to a stimulus containing only one orientation were measured as a function of stimulus duration. The aim of this part of the study was to determine whether the perceived size of an angle could be predicted from some simple combination of perceived orientations. The orientations studied were those corresponding to the orientations of the lines making up the angles used in the previous experiment, where the orientation of the bisector of the test angle was 135°.

Methods

The perceived orientations of the four lines comprising the stimulus figure in the previous experiment were estimated by measuring the constant error for parallelism (Andrews, 1965) at each of the four orientations. The computerised method of constant stimuli was employed. For these studies the stimulus comprised two lines, one either side of the fixation point at equal distances, as shown in Fig. 6.6.

On the basis of Andrews' (1967b) finding that bias is least and acuity greatest with long lines - compared to 10 min arc - the comparison line was set at a length of 4 deg. arc, and was visible to the subject throughout each run. The test line was of the same length as the arms of the angles in the previous study - 0.3 deg. arc. Although it cannot be assumed that the perceived orientation of the comparison line was unbiased, what bias there was could be considered to be very small compared to that of the perceived bias in the orientation of the test line. Presentation durations for the test lines were 0.01 sec., 0.5 sec. and 2 seconds. The two subjects used were SRH and DTM, as in Experiment 9

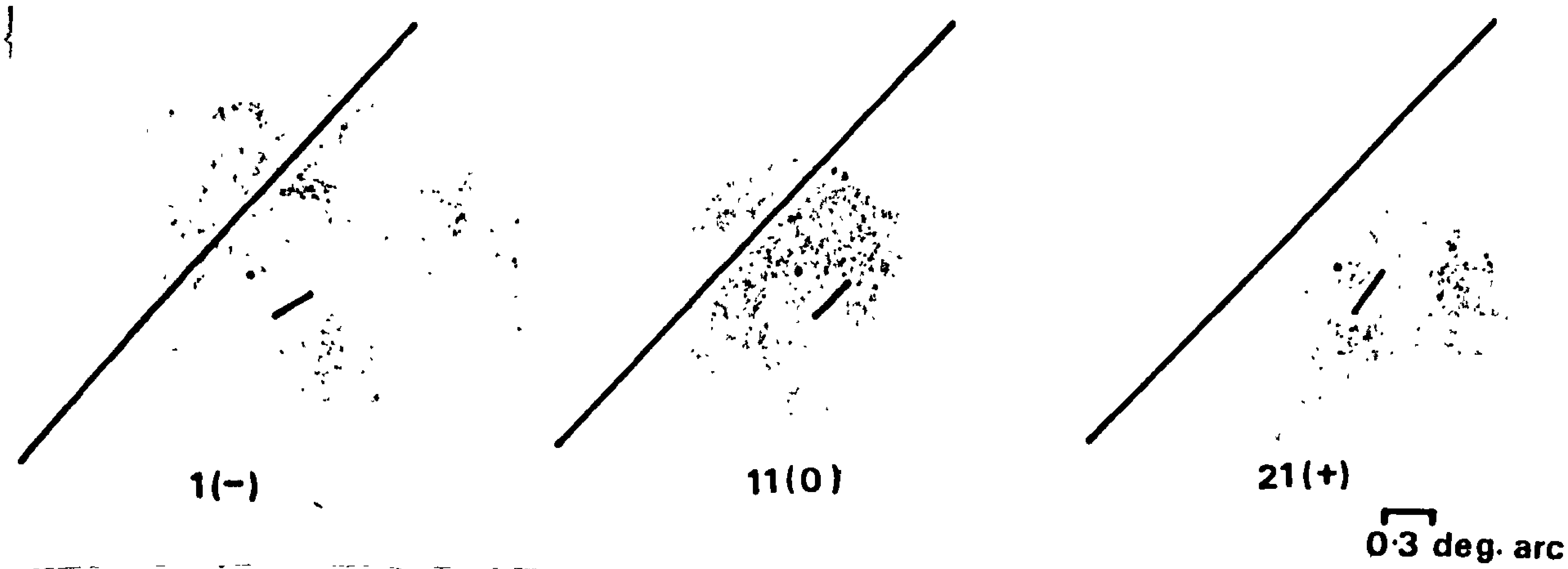


FIG. 6.6 Range of stimulus configurations for the parallelism study. The signs in parentheses indicate the position of the stimulus in the stimulus range, and are opposite to the sign of the bias. If the PSE is represented by a stimulus with a positive sign it is inferred that at PPE the test line was seen at an orientation less than that of the comparison line, by the same magnitude as the bias.

Results

As can be seen in Fig. 6.7 no greatly non-monotonic change in the perceived orientation of single lines was observed for any of the orientations which comprised the stimulus configuration of the angle experiment. The changes of perceived orientation of the line segments with time have been re-plotted in Fig. 6.8 so that the biases and the directions of change of bias at each orientation of the stimulus may be more clearly seen. The information presented in this figure is summarised in Table 6.1.

Taking the signs of the biases and the directions in which these biases change with increasing stimulus duration there are no inconsistencies between the two subjects. However, little unequivocal support is offered to either of the two hypotheses under examination. At 150° and 15° the lines appeared closer to the horizontal than did the comparison line, while at 120° and 345° the biases were toward the obliques. For the shorter durations only half of these results are in agreement with the findings of Andrews (1967a) - the observations at 120° and 345°. None of the results support the differential inhibition

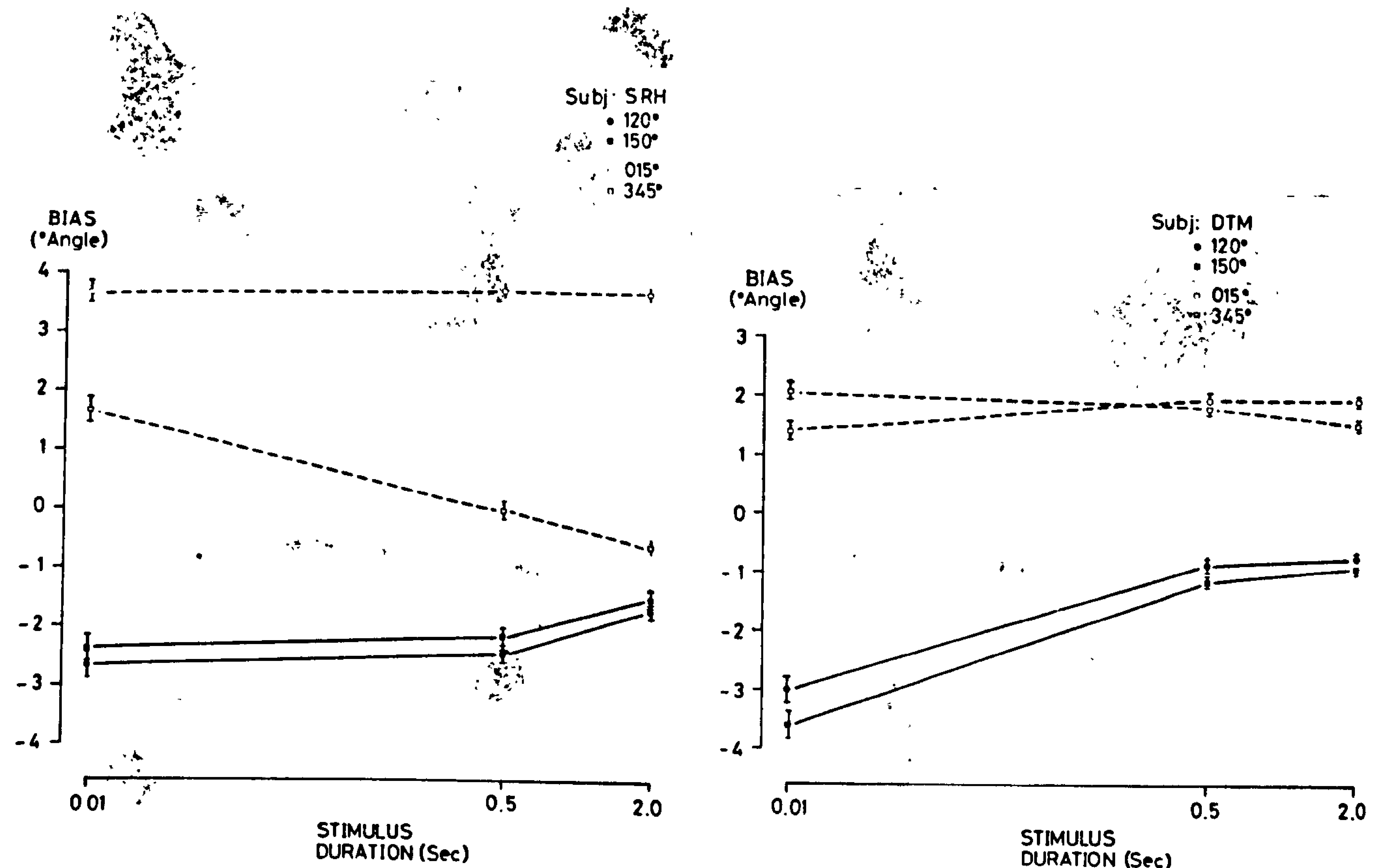


FIG. 6.7 Effect of stimulus duration on perceived relative orientation of the test line with reference to the comparison line using the stimulus shown in Fig. 6.6.

hypothesis since it is assumed that at these short durations the inhibition which is responsible for the biases does not contribute much to the response characteristics of the detectors. For all but the 15° line which showed little or no change of bias with increasing stimulus duration, the changes of bias show more agreement with Andrews' observations in that the magnitudes of the biases decreased. With the exception of the 150° line, this entails a change in perceived orientation away from the oblique and toward the nearest horizontal or vertical. The perceived orientation of the 150° line, however, which for the shorter durations was biased toward the horizontal rather than toward the oblique, moved closer to the oblique - at both durations showing behaviour inconsistent with that predicted by Andrews' hypothesis. In the light of such apparently conflicting results, it does not seem reasonable to conclude in favour of either hypothesis on the basis of these two studies.

By finding the angular separations of the two pairs of lines at each stimulus duration, a prediction of the perceived relative sizes of the two angles can be made. In this way it is possible to test the unlikely assumption that the perceived angle sizes are determined solely by the perceived orientations of the component lines as seen in isolation. The expected biases derived following this procedure are shown in Fig. 6.9. It is immediately obvious that there is

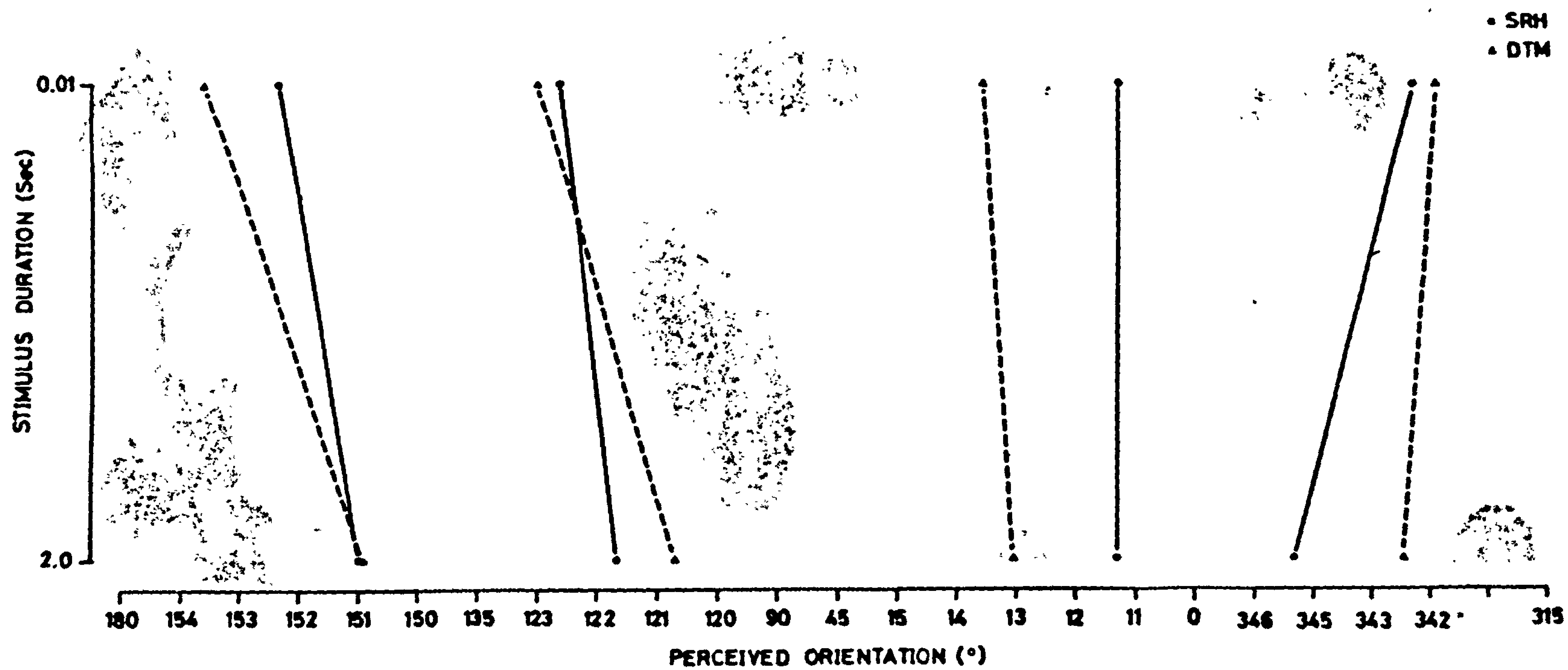


FIG. 6.8 The data presented in Fig. 6.7 are re-plotted here to emphasize the biases and directions of change of bias with time for the shortest and longest stimulus durations.

● Subject: SRH

Orientation	Stimulus duration 10 msec.	2 sec.	Effect of increased stimulus duration.	Direction of change of bias with increased dur.
345°	343.33 Bias to Obl.	345.33 Bias to H	Change from bias to Obl. to bias to H.	Oblique to Horizontal
015°	11.31 Bias to H.	11.31 Bias to H		No change
120°	122.63 Bias to Obl.	121.70 Bias to O.	Reduced bias to Oblique.	Oblique to Vertical
150°	152.35 Bias to H	150.99 Bias to H	Reduced bias to Horizontal	Horizontal to Oblique.
●Subject: DTM				
345°	342.93 Bias to Obl.	343.45 Bias to O.	Reduced bias to Oblique.	Oblique to Horizontal
015°	13.58 Bias to H.	13.05 Bias to H.	Increased bias to Horizontal	Oblique to Horizontal
120°	123.00 Bias to Obl.	120.70 Bias to O.	Reduced bias to Oblique	Oblique to Vertical
150°	153.61 Bias to H.	150.92 Bias to H.	Reduced bias to Horizontal.	Horizontal to Oblique

Table 6.1 The influence of stimulus duration on the perceived orientation of the test test line in the parallelism study, presented graphically in Figs 6.7 and 6.8 are summarised here together with the directions of changes of perceived orientations observed between the longest and shortest stimulus durations.

little similarity between these graphs and those which were obtained experimentally. The main difference is in the sign of the bias, which indicates that horizontally oriented angles should appear smaller than the obliquely oriented angles. This prediction is in direct opposition to the findings of these and other studies (Lennie, 1971; Carpenter & Blakemore, 1973) that an angle oriented horizontally appears larger than an obliquly oriented angle. Furthermore, half the perceived angle sizes predicted from the single line data are smaller than the actual angles (see Table 6.2) - a prediction wholly inconsistent with the finding that acute angles are perceptually expanded.

Subject	Orientation of Angle (30°)	Perceived Angle 10 msec.	Size 2 sec.
SRH	0°	27.98	25.98
	135°	29.72	29.29
DTM	0°	30.65	27.60
	135°	30.61	30.22

Table 6.2 The entrants for perceived angle size are calculated from the perceived orientations of single lines, at the two stimulus durations shown in Table 6.1. These figures result in the predicted time course of the perceived differences in angle size shown in Fig 6.9.

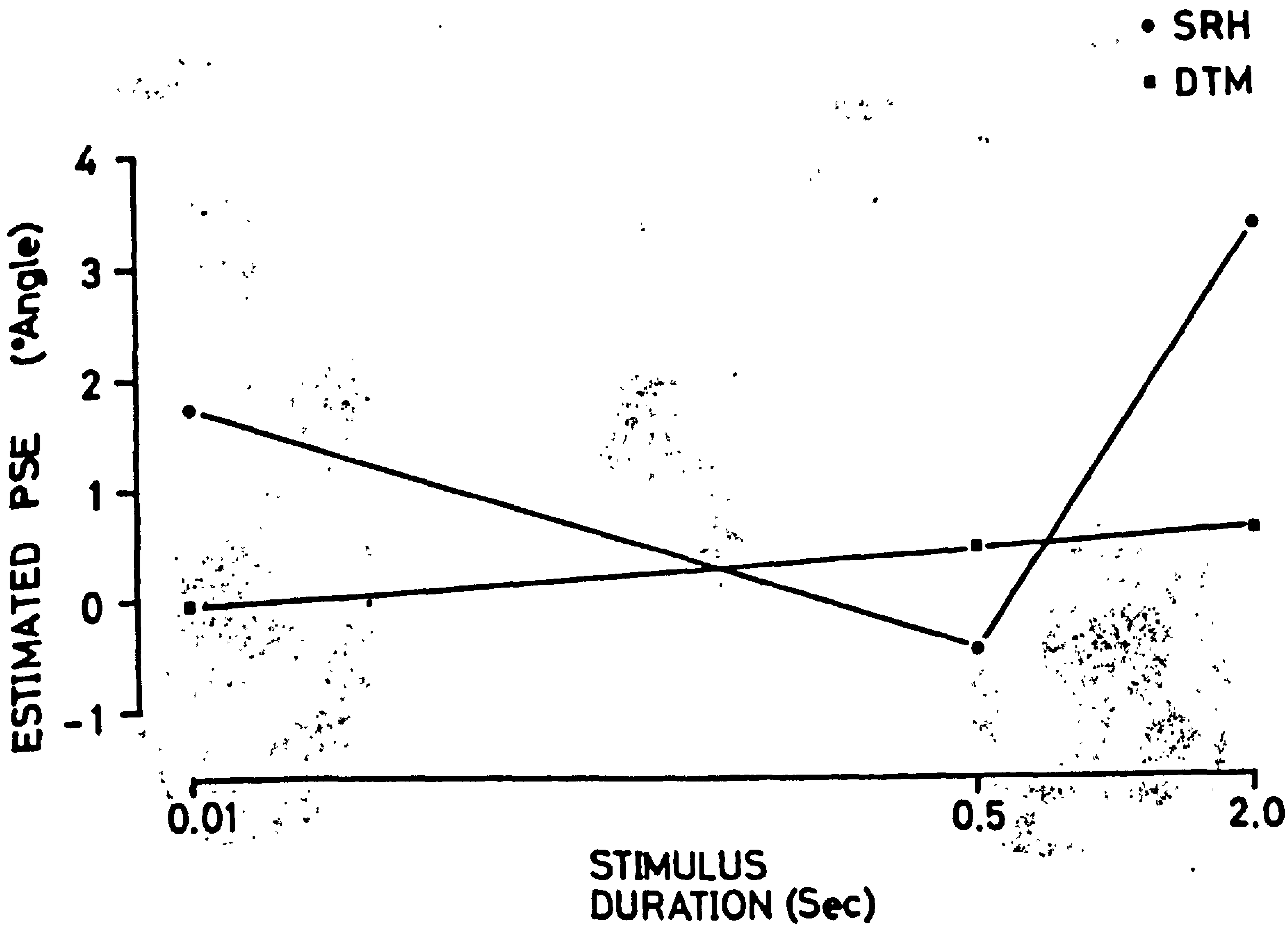


FIG.. 6.9 Predicted time course for the perceived relative sizes of angles in the configuration used in Experiment 1. The predictions are derived from the parallelism study as summarised in Table 6.2.

Subject: SRH

Orientation	10 msec.	2 sec.	Effect of i

It may be concluded, therefore, that neither the perceived size of an angle nor the perceived relative sizes of two angles of different orientations can be predicted from a knowledge of the perceived orientation of the component single lines in the absence of further information concerning the perceptual mechanisms involved with the simultaneous perception of lines of differing orientations. The results obtained also cast some doubt on the generality of the two hypotheses which have been considered as possible explanations of the process underlying the perception of angles.

Experiment 11

Both these hypotheses postulate that the changes in the perceived orientation of lines taken either singly or in angle patterns is a consequence of inhibitory interactions operating between orientation selective feature analysers. A further experiment in this series was carried out in order to determine whether the influence of lateral inhibition on perceived angle size could be isolated, and if so, what form this influence would take.

Following the suggestion (Blakemore, Muncey & Ridley, 1973) that the 'tuning curves of feature detectors as measured in masking and adaptation experiments may describe the inhibitory characteristics of these detectors which decay slowly with time, rather than their excitatory characteristics', experiments by Sharpe (1974) in the colour domain and by Dealy and Tolhurst (1974) in the spatial frequency domain have provided evidence in support of this hypothesis. The experiments of Kulikowski, Abadi and King-Smith (1974) which showed that the tuning curves for orientation analysers, as revealed by the method of subthreshold summation, which presumably depends on excitatory summation, are considerably narrower than those derived by other methods, give further indirect support.

This being the case, adaptation to a grating should establish a high level of inhibitory activity in the orientation domain, roughly comparable to that which follows prolonged viewing of a line stimulus. Thus, if the perceived orientation of a contour is a function of the amount of inhibitory input to the pertinant orientation detectors, it would be expected that a period of adaptation to a grating would 'prime' the system with reference to the perceived orientation of a subsequently presented line of the same actual orientation as the grating. That is to say, the build-up of inhibition during adaptation should result in the perceived orientation of a briefly presented line approximating that of a line presented for a more extended duration.

Methods

The experimental procedure followed in this experiment was precisely the same as that followed in the preceding experiment with the exception that prior to the commencement of a run the subject had 5 minutes to freely gaze at a photograph of a bar grating at the same orientation as the comparison line in the stimulus and with approximately the same line width. Between each 10 msec. stimulus presentation the subject viewed the grating for a further 3 seconds during the interstimulus interval. The orientations used the Experiment 10 were used again in this experiment. The subjects taking part were SRH and DTM.

Results

The results of this experiment are shown together with those of the previous experiment in Fig. 6.10. In view of the rather uncontrolled nature of the experiment, due to the inability to guarantee a constant level of adaptation throughout the duration of each run, a quantitative comparison the the two sets

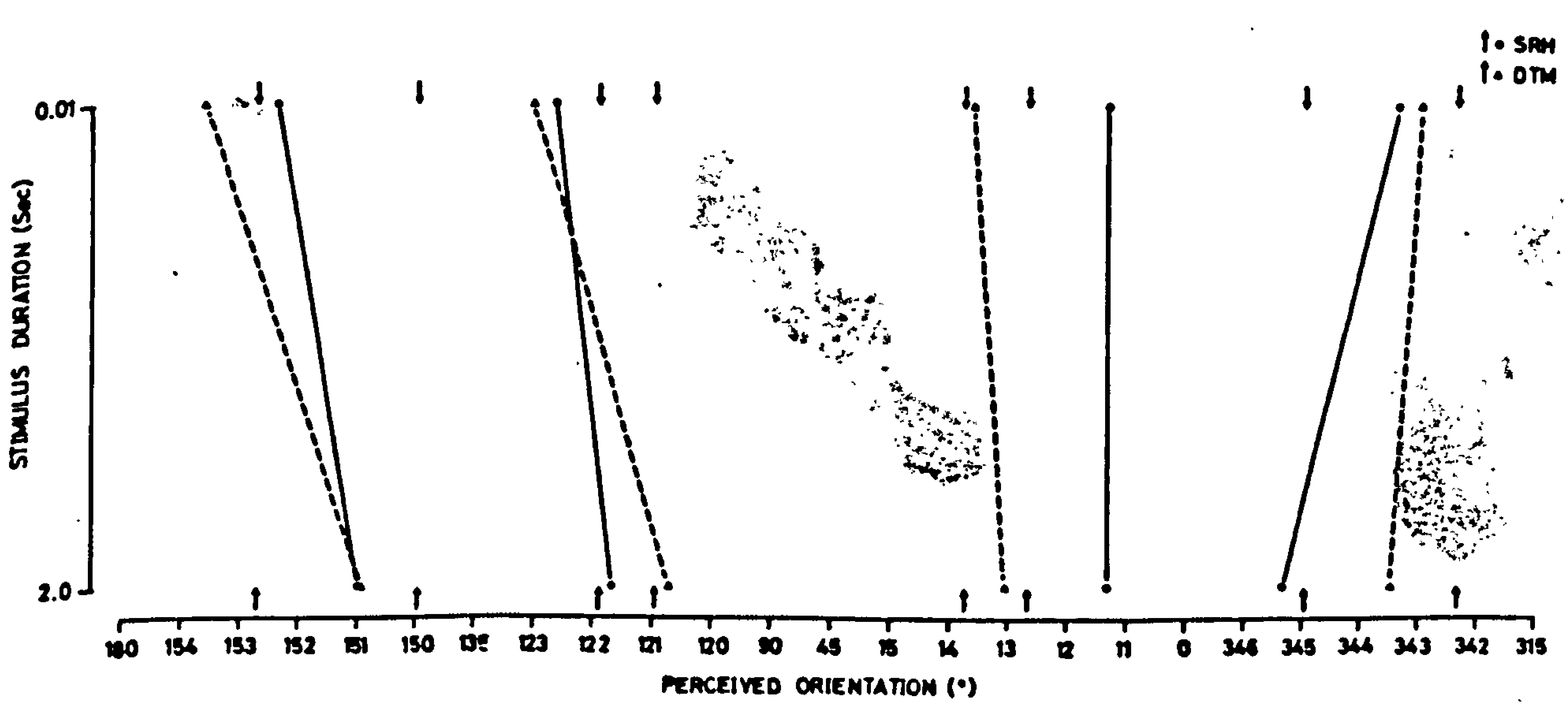


FIG. 6.10 Effect of prior adaptation on the bias for parallelism, superimposed on the results of the previous study. The arrows indicate the bias for a 10 msec stimulus duration, and are shown at the top and bottom to facilitate comparison of the post-adaptation bias with both the long and short stimulus presentations in the absence of adaptation.

of results is not justified. Qualitatively, the expectation that the effect of a longer stimulus duration on the perceived orientation can be simulated for short duration presentations by prior adaptation is fairly well upheld. Of the points of discrepancy, both subjects showed the expected change for the 15° line, which had not been found at all in Experiment 10, leaving only the contrary result for DTM at 345° unexplained. Here the shift was in the direction opposite to that which was expected.

Discussion

The results of Experiments 9 and 10 show that as the time for which the stimulus is presented to the visual system is increased the constant error in the perception of the orientation of the line or lines comprising the stimulus becomes smaller. In several instances a reversal of the sign of the bias was found for single lines, the constant error for the two second presentation thus being in the opposite direction to that found for the shortest durations. The demonstration that similar changes in perceived orientation can be induced by adaptation to a grating of the same orientation as the test line indicates that the mechanism responsible for the reduction in constant error involves lateral inhibitory processes, operating in the orientation domain, as was originally proposed by Andrews (1965). The finding that neither the perceived size of the angle, nor the apparent relative sizes of angles of different orientations can be simply predicted by combining the apparent orientations of single lines offers further evidence for the existence of interactions between the channels responsible for the detection of lines, and the analysis of their orientations, where more than one line is presented simultaneously. This is especially evident in the prediction, based on the perceived orientations of single lines, that acute angles should appear smaller than they actually are (see Table 6.2). Insofar as the constant error in the comparison of angle sizes does not show a change of sign, or a levelling off around zero, this interaction appears to show at least one characteristic of the system proposed by Blakemore et al. (1970) even though the time course of the constant error magnitude is in a direction opposite to that which would have been expected of such a system.

An attempt to modify either of the two models to accommodate these observations, however, would be ill-advised, as the observed biases of perceived orientation found in Experiment 10 show when referred to the horizontal and vertical rather than to the stimulus orientation. Both hypotheses give clear predictions for the direction in which the biases should lie, but the data are not consistent with either. Some orientations were found to be biased to the obliques at longer durations, as predicted by the Blakemore et al. (1970) inhibition model; other orientations appeared biased toward the vertical and horizontal, as found by Andrews (1967a).

A further difficulty for the models of both Andrews and Blakemore et al. has been pointed out by Lennie (1971). When 40° angles are used in the 135° configuration (see Fig. 6.2) there should be no apparent difference in their magnitudes since all four arms are at the same orientation with respect to the vertical and horizontal, and the interactive effects should therefore cancel. It has been shown, both by Lennie and in this study (chapter 4) that it is at this relative orientation that the effect is greatest.

Difference Thresholds - Experiments 9, 10 & 11

Although these experiments were primarily concerned with the effects of stimulus duration on perceived angle sizes and line orientations, i.e. the biases, the difference threshold measures obtained as a matter of course during the experiments are not without interest. According to the model developed by Andrews (1965, 1967a) the function of lateral inhibitory interactions between orientation analysers is to integrate the responses of these analysers over time, the perceived orientation corresponding to maxima in the resulting pattern of inhibition.

"For very brief stimuli, mutual inhibition does not stabilise. Response frequencies following stimulation are small and subject to large sampling variation. The maximum in the pattern of inhibition may occur at an inappropriate orientation....For longer exposures, mutual inhibition stabilises. Infrequent responses are reduced or shut off, and the variation of the point at which the maximum occurs becomes smaller;....The distribution of apparent slope will be narrower and more symmetrical than with flashed presentations." (Andrews, 1967a, p 994)

The thresholds obtained for the discrimination of angle size as a function of stimulus duration are shown in Fig. 6.11 (a)- (c). In all cases there is a decrease in threshold with time of presentation. These findings are, therefore, consistent with the notion that some integrating process does operate to reduce the weight of small, inappropriate responses to the response distribution representing the perceived orientation. Further, the graphs show a marked tendency to flatten beyond the 0.5 second point, in agreement with Andrews'

FIG. 6.11 Figs (a) - (c) show difference thresholds for angle size as a function of stimulus duration. Figs (d) - (f) show the biases corresponding to the threshold curves shown in the first three graphs.

suggestion that the time constant for the integrating inhibitory process is about half a second (Andrews, 1967a). Although changes in threshold do occur between 0.5 second and 2 second presentations these changes are small in comparison with the changes which were found for increases in stimulus duration from 10 msec. to 0.5 sec.

When the time courses for the changes in threshold and for the changes in bias are taken together, however, some difficulty arises. If, as Andrews proposed, both changes in threshold and changes in bias are consequences of the same process, the growth of mutual inhibitory interactions between orientation analysers, it would be expected that their time courses would have similar characteristics. Comparison of the data presented in Figs. 6.11 (a) - (c) and (d) - (f) show that this is not the case; none of the reversals of the bias are reflected in the thresholds obtained for the longer stimulus durations.

These data suggest, therefore, that the positions of the inhibitory maxima in the pattern of activity of orientation analysers are not necessarily invariant for given stimulus conditions. In other words, although there is a consistent reduction in the width of the response distribution with increasing time for integration, the process may not 'home' consistently to one perceived orientation on an absolute scale. Rather, the final perceived orientation may be determined not only by the characteristics of the stimulus, but also by the state of the analysers. This state could be determined, perhaps, by adaptive effects with much longer time constants than those of the stimulus-induced inhibitory interactions. Long-term shifts of perceived orientation have already been found, independent of the short term effects of stimulus presentation (Andrews, 1967a).

It is possible, then, that the short-term narrowing of the response distribution of an analyser is generated and maintained by the activity following the presentation of a stimulus, while the perceived orientation or angle size is a resultant of the superimposition of this activity onto an 'uneven', changing, representation space. The metric characteristics of this space would be due to the sensitivity characteristics of the neural analysers at the time of stimulation. These characteristics would be themselves determined by the long term 'perceptual diet' to which these analysers had been exposed.

This interpretation of the data assumes that Andrews' postulates concerning the mechanism of orientation analysers applies equally to the perception of angular extent. If this were the case, analysis of angular extent would entail the neural representation of angular extent as the distance between the peaks of activity representing the orientations of the lines comprising the angle. Changes in perceived angle size would entail, therefore, changes in the separation of the distributions of activity representing the lines. The shortcomings of any simple 'orientation-contrast' model which is based on lateral inhibitory interactions have already been described. This means, therefore, that although the reduction with time of the variance of the response distributions of the oriéntation analysers may be attributable to a lateral inhibition process, the change in perceived angle size, and necessarily of perceived orientation of the components of angles, cannot be attributed to this process alone.

If lateral inhibitory interactions between channels cannot be responsible for the changes of perceived angular extent with time, then these effects may be caused by differences in the 'receptor surface' in the orientation domain. The finding that the sensitivity to lines, gratings etc. varies with stimulus orientation so that sensitivity is highest for vertical and horizontal orientations and lowest for oblique orientations has already been extensively covered in chapter 1. Neurophysiological studies (Mansfield, 1974) have shown that the thresholds of individual neurones in the primate striate cortex do not vary with orientation. The same study did show, however, that in the foveal projection area of the monkey cortex cells tuned to vertical and horizontal orientations were markedly more numerous than cells tuned to other orientations.

It is suggested that the properties of orientation analysers are the characteristics of populations of cells each of which has, on average, the same threshold (the actual threshold of any given cell at a given time may be found to vary). All units in a particular analyser need not have the same preferred orientation. Instead, analyser membership depends on the population to which the individual neurone is most closely connected. In neural terms this population could be represented by the columns first reported in the visual cortex of the cat by Hubel and Wiesel (1959). Subsequent studies have shown that there is a distribution of preferred orientations of the neurones comprising one columnar unit.

The composition of these analyser-populations is constrained by the finding that analysers tuned to different orientations (horizontal, vertical and oblique) do not differ in their bandwidths. As the overall sensitivity of an analyser is being considered to be dependent on the number of sensitive units, the slope of the analyser response distributions must be sharper. This is in agreement with the findings of Rochlin (1955), Andrews (1967a), and Bouma and Andriessen (1968) who showed that estimates of perceived orientation were more precise for vertical and horizontal stimuli than for oblique stimuli. Thus, Andrews illustration (Andrews, 1967a, Fig. 12; reproduced here as Fig. 6.12) of the 'response frequency to flash stimulation of hypothetical direction-sensitive neural units' would describe the response frequency distributions

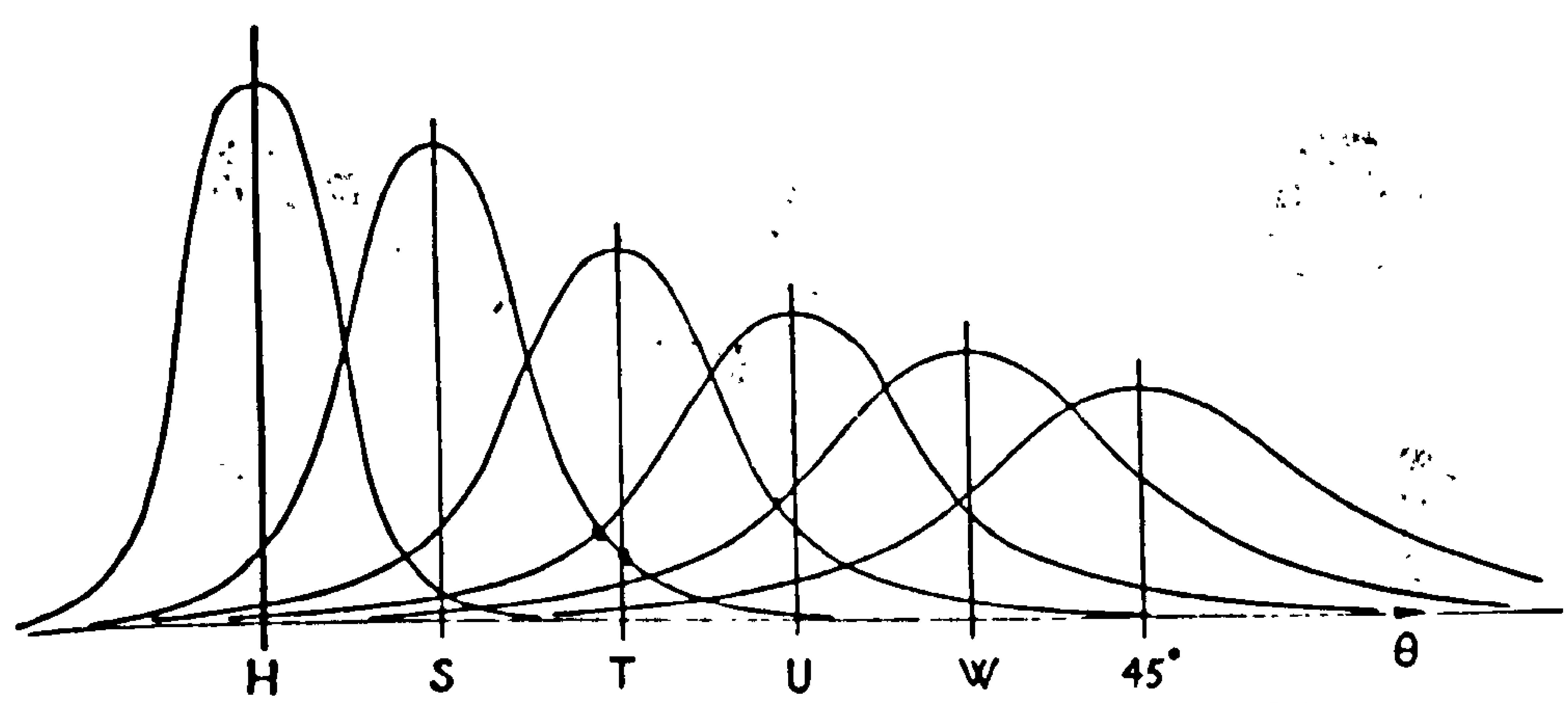


FIG. 6.12 Response frequency to flash stimulation of hypothetical direction sensitive neural units as represented by Andrews (1967a).

of the orientation analysers described here as columns, but not the response characteristics of the units of which the analysers are composed. Insofar as the sensitivity characteristics of the analyser reflect the characteristics of the population of neurones belonging to the analyser, these curves would also be expected to reflect the frequencies of occurance of cells tuned to an orientation as the preferred orientation of the analyser (the mean preferred orientation of the cells within the column) varies.

In order that this model does not assume the characteristics of that of Blakemore et al. (1971) a further proposal must be made: inhibitory interactions should be predominantly within analysers, serving to reduce the widths of their response distributions, and so not to give a contrast effect due to between-analyser inhibitory interactions.

As neurophysiological studies have shown (Sillito, 1975b; Creutzfeldt, Kuhnt & Benevento, 1974; Creutzfeldt, Innocenti & Brooks, 1974), however, excitatory input to orientation selective cells in the cat visual cortex is rather broadly tuned, the high selectivity being a function of inhibitory inputs. The cortical distance over which such inhibition is effective has been estimated as about 800 micrometers (Hess, Negishi & Creutzfeldt, 1975) while all orientations are represented within an area of a hypercolumn- 300 - 500 micrometers in diameter. As the neural unit of function corresponding to the orientation selective channel is the column, the existence of intercolumnar inhibitory connections implies that inhibitory interaction occurs both within analysers and between analysers. The assumption required for the interpretation above is, therefore, untenable.

Those characteristics of orientation analysers which would be necessary for the explanation of perceived angle sizes in terms of combinations of perceived orientations cannot, therefore, be substantiated.

Further evidence opposing the notion that angles are perceived in terms of combined outputs of orientation analysers is provided by the comparison of difference thresholds for angle size with those obtained for orientation. These data are presented in Table 6.3. Here the difference thresholds for angle

Subject	Stimulus orientation	Stimulus durations 10 msec		500 msec		2 sec	
SRH	015°	1.348	1.817	0.793	0.629	0.701	0.491
	345°	1.623	2.634	0.977	0.955	0.715	0.511
	120°	1.397	1.952	1.041	1.084	0.710	0.504
	150°	1.733	2.999	1.165	1.357	0.955	0.912
	Angle	2.157	4.6526	0.972	0.945	0.991	0.982
DTM	015°	0.917	0.841	0.742	0.551	0.497	0.244
	345°	1.125	1.266	0.817	0.666	0.691	0.478
	120°	1.496	2.238	0.626	0.392	0.508	0.258
	150°	1.729	2.989	0.671	0.450	0.705	0.497
	Angle	1.341	1.798	0.897	0.805	0.988	0.976
		s	s^2	s	s^2	s	s^2

TABLE 6.3 Difference thresholds (standard deviations and variances) for orientations and for equivalent angles made up of the four orientations. (For explanation see text).

size and perceived orientation are shown for the two subjects at three stimulus durations.

The difference threshold, as the standard deviation of the normal distribution most closely resembling the response error distribution, is a measure of the variability of perceived orientation or angle size. If it were the case that the perception of angle size is mediated wholly by combinations of outputs from orientation analysers, then it would be expected that the variability of perceived angle size would equal the total variance of all the estimated orientations comprising the angles under comparison. As the figures in Table 6.3 show, this is not the case. In fact, the variability of perceived angle size is closer to that for one line (and occasionally two) than to four lines. This surprisingly low variance of perceived angle size estimation indicates that the orientation estimates in angle perception are more accurate than are those in the perception of the orientation of single lines in the parallelism task. As this leads to an implausibly high orientation acuity for each component line a more likely interpretation of these observations is that acuity for angle size is not directly derived from the orientation acuity for single lines. This interpretation is consistant with that of the observed constant errors. The conclusion derived from consideration of the biases obtained in these experiments comparing the perception of angle size with the perception of orientation, that the processes by which angle size is perceived bear no simple relation to those processes by which orientation alone is perceived, is supported further by these findings concerning the difference thresholds for the two tasks, and reinforces the findings presented in chapters 4 and 5.

Finally, in the third experiment of this set, during which subjects adapted to a grating prior to estimating the orientation of the test line, the relation between perceived orientation, difference threshold and adaptation was examined. If the perceptual consequences of adaptation, the aftereffects, were the result of a reduction in sensitivity due to slowly decaying inhibition of analysers sensitive to the adapting stimulus then, if the increase of acuity with increased stimulus duration is also a consequence of inhibitory activity, pre-adapation to an orientation would be expected to reduce the difference threshold for short duration stimuli at the same orientation in the following way. During the adapting period, as the subject viewed a grating at a given orientation, the analyser corresponding to that orientation would be the most excited and consequently liable to the greatest inhibitory influence. The test stimulus will be presented, therefore, to an analyser which is already, presumably, in a state corresponding to that following prolonged viewing of the stimulus. As the test stimulus was well supra-threshold, the expected result of this procedure would be that the 'outlying' responses found for short duration presentations of the stimulus under non-adapted conditions would be inhibited thus giving a difference threshold corresponding to longer duration stimuli.

As the results given in Table 6.4 show, this expectation was not fulfilled.

Subject	Stimulus Duration	Stimulus Orientation 120°	150°	015°	345°
SRH	10 msec	1.397	1.732	1.348	1.632
	500 msec	1.041	1.165	0.793	0.977
	2 sec	0.710	0.955	0.701	0.715
	10 msec (adapted)	1.082	1.950	1.538	1.455
DTM	10 msec	1.496	1.729	0.917	1.125
	500 msec	0.626	0.671	0.742	0.817
	2 sec	0.508	0.705	0.497	0.691
	10 msec (adapted)	1.125	1.187	0.836	0.642

TABLE 6.4 Difference thresholds for parallelism (single orientation) obtained for various stimulus durations and after adaptation to a grating of the same orientation.

In all but one case (Subject DTM at 345°) the thresholds obtained following prior adaptation to the grating were found to be closer to the values obtained for the short duration presentations (without prior adaptation) than to the long (2 sec.) stimulus presentations.

In retrospect, however, this experiment was somewhat misconceived. Tolhurst (1975a,b) has shown that there is strong evidence supporting the existence of two parallel visual information processing systems in humans, comparable to the X- (sustained) and Y- (transient) systems demonstrated in the cat retinal ganglion cells by Enroth-Cugell and Robson (1966) and in the cat visual cortex by Ikeda and Wright (1974,1975). It may be supposed that in this adaptation experiment the short duration stimulus was processed largely by the transient system whereas the adaptation primarily influenced the sustained system as the grating was stationary. From this point of view it would not be expected that the difference threshold for short duration presentations would be influenced by prior adaptation, there being no evidence to date for inhibition of the transient system by the sustained system, although inhibition operating from transient to sustained has been proposed on the basis of neurophysiological evddence (Singer & Bedworth, 1973) and psychophysical evidence (Breitmeyer & Ganz, 1976). If this interpretation of the data is correct then it is likely that the improvement of acuity resulting from increases of stimulus duration is to some extent reliant on the increased involvement of the sustained system in the processing of the stimulus orientation, and not simply to the build-up of inhibition. Improvements of acuity from medium duration to long duration stimuli, e.g. from 50 - 100 msec upward, will still be a consequence of integration of responses through inhibition, as this improvement at these durations cannot be attributed to the increasing involvement of the sustained system.

The finding that there was some effect of adaptation to the grating suggests that for both short and long duration presentations perceived orientation may be referred to a common underlying metric which is influenced by prior inputs to orientation analysers. These inputs may arise from either the sustained or the transient systems.

Conclusions

Despite the attractive simplicity of the model proposed by Cappenter and Blakemore (1973) as an explanation for the perceived expansion of acute angles, results of the three experiments described in this chapter show it to be untenable in its current form. The notion that orientaion analysers exert mutual inhibitory interactions was not refuted as such, but it was shown that if anything this process operates to reduce the effect, or at least the differences between the strengths of the effect at different orientations insofar as the magnitude of this difference was found to decrease with increasing stimulus duration. This finding was consistent with the model elaborated by Andrews (1967a,b).

The results obtained from the second experiment described in this chapter were not, however, fully consistent with those obtained under similar conditions by Andrews. Furthermore, comparison of the biases and thresholds obtained in this experiment with those obtained in the first experiment indicate that the relation between perceived orientation and perceived angle size is not a simple one. Modification of Andrews' hypothesis in such a way as to embrace the current findings generated a prediction which was not consistent with available neurophysiological evidence, and which, therefore, was abandoned.

Although the third experiment to be described was considered to have been inappropriate to the question for which it was designed, the results obtained were consistent with the currently held hypothesis that there are two parallel information processing systems within the visual pathway, the 'sustained' system and the 'transient' system. The results also corroborated the hypothesis that although the transient system exerts an inhibitory effect on the sustained system, this inhibitory interaction is not reciprocated. This experiment did not, however, shed any new light on the relation between perception of orientation and the perception of angle size.

Chapter 7: A Metric for Perceived Angular Extent?

All the experiments described so far have been designed with reference to the hypothesis that the visual system decomposes the visual scene, at least partially, into edges and contours. In terms of these elements, as abstracted by the cortical striate feature-analysers, the visual input is transmitted to post-striate regions of the brain. Because, however, the cortical analysers are non-independent and interact mutually through lateral inhibitory connections, contrast effects were supposed to lead to enhancement of separations between orientations represented by feature analysers sufficiently close together to mutually distort their response distributions.

Although the observations made in a number of varied studies, described in chapter 1, have been in agreement with hypotheses framed in these terms, the results of the experiments described in preceding chapters have not been consistent with this hypothesis. Any further description of the mechanism underlying the perception of angle size must, therefore, not only encompass the data obtained in the present study, but also those obtained in the previous studies, including the neurophysiological evidence for the existence of orientation selective channels with mutual inhibitory interactions, which is quite independent of the psychophysical evidence from which these systems may be deduced. The data obtained in the preceding studies, however, while clearly inconsistent with the type of hypothesis outlined above do not appear to fall into any self-consistent patterns from which an alternative explanation may be derived.

For these reasons it was decided to carry out a further series of experiments which made no reference to hypotheses concerning the neural processes underlying the perception of angles, but which were intended to characterise the perceptual attributes of angles in such a way as to determine whether or not a metric space for angle size as a perceptual quantity is reflected in the activity of the visual system.

7.1 Experiment 12: Additivity of Perceived Angular Extent

The first experiment was intended to determine whether or not additivity was a property of such a metric, if it exists - for example, is the perceived size of a 30° angle equal to the sum of the perceived sizes of the two adjacent 15° angles included in the 30° angle? If this were the case, then a magnification factor, the ratio of percieved angle size to actual angle size would be constant for all angle sizes, fluctuating only with any meridional anisotropy of the metric for angular extent, to the degree that such anisotropy is present.

In fact perceived angle size cannot be related to actual angle size for, in order to make such a comparison the perceived angle must somehow be compared to the real angle. In order for such a comparison to be made the observer must view both and measure the difference between the two, an operation which is manifestly impossible. It is, however, unnecessary to use actual angle size in the comparison. The perceived size of any angle will do, so long as it remains a reference angle and is not included into the metric. The assumption was made, therefore, that a horizontal angle (0° bisector orientation) would be taken as a reference and, for no other purpose than numerical convenience, the perceived size of this angle was said to be equal to its physical size. Because, as is demonstrated in experiments 5 and 6, angles of this orientation show the largest perceptual enlargement, it would be expected that the magnification factor (M) would be less than unity for all other test orientations and minimum when the test angle is oriented about the main obliques.

<u>Methods</u>

	Stimulus Angle Size 15°	30°	45°	60°
Angle Orientation (1st quadrant)	97			
	112	105	112	
	127			120
	142	135		
	157		157	
	172	165		
	187			180
Angle Orientation (2nd quadrant)	202	195	202	
	217			
	232	225		
	247		247	240
	262	255		

Table 7.1 Bisector orientations of test angles in Experiment 12

The method and stimulus configurations used in this experiment were identical to those used in Experiment 5. In order to investigate the additivity of angular extent the bisector orientations of the test angles were as listed in Table 7.1.

The stimulus duration was set at 2.00 seconds with a two or three second inter-stimulus interval, according to the preference of the subject. The stimulus line length was 18 minutes of arc.

Subjects SRH and SG had uncorrected normal vision, subject DTM had corrected normal vision. Trials in the first quadrant were run on all three subjects and SRH did runs covering both the first and the second quadrant.

Results

In order to calculate the magnification factor (M) the units of the metric were normalised to a circle of 360° by first re-scaling the raw perceived angle sizes (a) so that a quadrant or semicircle of perceived angular extents summed to 90° (or 180°), for each stimulus angle size (A). For each angle size, therefore, a normalising constant (K) was derived - $K=90/\Sigma a$ - and normalised perceived angular extents (a') calculated: $a' = K.a$. The magnification factor was then calculated as the ratio (a'/360)/(A/360), which reduces to $M = a'/A$.

As the untransformed values for perceived angular extent were found to be significantly different for the three subjects ($p < 0.01$ at all angle sizes, see Table 7.8, 7.9, 7.10), magnification factors were derived separately for each subject. The results are shown in Fig. 7.1 and in Tables 7.2 to 7.4. The vertical bars in the graphs represent the estimated standard error of the magnification factor (M), and were derived from the expression:

$$s_{(M)} = \frac{K.s_{(a)}}{A}$$

where $s_{(a)}$ is the rms of the standard errors of the constant errors of perceived angle size.

On the basis of the normalised perceived angular extents (a') for a stimulus angle size (A) of 15° expected magnification factors for larger angles were calculated (EM). Each of pairs of a' subsumed by 30° stimulus angles were added (see Table 7.1) and divided by 30 to give the estimated magnification factors, which are shown in columns 5 and upward in Tables 7.4 to 7.9. EM values for 45° stimulus angle sizes were similarly derived by summing the appropriate triplets of a' (Table 7.1). For subject SRH EM values were also calculated for stimulus angles of 60°, both from adjacent tetrads of a' derived from 15° stimulus angle sizes and from adjacent pairs of a' derived from 30° stimuli. Tables 7.4 to 7.9 show, therefore, for each subject the untransformed perceived angle size (a) - the PSE, the normalised perceived angle size (a'), the magnification factor (M) and the expected magnification factors (EM) for the larger stimulus angle sizes based on the perceived angle sizes with 15° and 30° stimulus angles, at each test angle orientation.

For each subject and at each stimulus angle size the observed magnification (M) was compared with the estimated magnification (EM) using the t-test statistic for matched pairs (2-tail). No significant differences between M and EM were found for any of the tests carried out. These results show clearly that the perceived angular extent of, for example, a 30° stimulus angle can be predicted simply by adding together the perceived angle sizes of the two adjacent 15° angles subsumed by the 30° angle. This property of additivity has been found to extend over the whole range of angle sizes tested in this study.

It is demonstrated therefore, that at some level of the visual system a metric for angular extent is encoded. This metric surface is not topographically identical to the physical dimension of angle size, under an orientation-independent transformation, as the metric for perceived angular extent shows a regular meridional anisotropy. As a consequence of this anisotropy it is not possible to reverse the direction of prediction of perceived angular extents from greater to smaller angles by simple division: $a'_{15} \neq a'_{30}/2$. However, given a'_{30} and one a'_{15}, the other a'_{15} may be found.

The apparent similarity of the curves for M as a function of angle orientation across subjects was tested using analysis of variance, the summary tables for which are presented as Tables 7.11 to 7.13 for the three angle sizes. No significant differences were found between subjects although the differences between orientations were preserved ($p < 0.01$).

These observations corroborate those reported in chapter 4, experiment 5, in showing the W-shaped curve of perceived angular extent as a function of test angle orientation. In both this study and the forementioned previous study- the PSEs do not show the difference between vertical and horizontal orientations of the test angle which are shown when magnification factor is considered as a function of orientation. The present observations indicate then, that the vertical and horizontal orientations are not precisely equivalent with reference to perceived angular extents at these orientations, although both orientations are different from obliques. Similar findings were reported in chapter 5.

One observation which is not consistent with earlier findings is the meridional anisotropy shown with the 15^{o} test angles for all subjects. In the previous studies (Expt. 5), in which only SRH took part, the characteristic W-shaped curve for constant error was not found with stimulus angles of this size. Again this is only manifest for the variation of M with rotation of the test angle, and is not clearly evident in the untransformed data.

Angle Size = 15°

Orient.	a	a'	M	EM30	EM45	EM60(15)
97	15.43	16.32	1.088			
112	16.08	17.01	1.134	1.109	1.059	
127	13.62	14.40	0.960			1.023
142	12.97	13.72	0.915	0.936		
157	13.82	14.62	0.975		0.958	
172	13.99	14.80	0.987	0.979		
187	13.51	14.29	0.953			0.973
202	13.96	14.77	0.985	0.966	0.962	
217	13.13	13.89	0.926			
232	13.87	14.67	0.978	0.949		
247	14.47	15.31	1.021		1.023	0.998
262	15.26	16.15	1.077	1.046		
	170.11	180.26				

K = 1.058 s(M) = 0.007

Table 7.2 PSE (a), a', Magnification Factor (M) and Expected Magnification Factor (EM) for subject SRH at 2.00 second stimulus duration (see text)

Angle Size = 30°

Orient.	a	a'	M	EM30	M-EM30	EM60 (30)
105	30.75	31.73	1.058	1.109	-0.051	
135	26.69	27.54	0.918	0.936	-0.018	0.987
165	28.44	29.35	0.978	0.979	-0.001	
195	29.06	29.99	1.000	0.966	0.034	0.988
225	27.63	28.51	0.950	0.949	0.001	
255	31.78	32.79	1.093	1.046	0.047	1.020
	174.35	179.91				

K = 1.032 s(M) = 0.005

Angle Size = 45°

Orient.	a	a'	M	EM45	M-EM45
112	44.97	46.36	1.030	1.059	-0.029
157	40.74	42.00	0.933	0.958	-0.025
202	42.51	43.83	0.974	0.962	0.012
247	46.30	47.74	1.061	1.203	0.038
	174.52	179.93			

K = 1.031 s(M) = 0.004

Table 7.2 continued

Angle Size = 60°

Orient.	a	a'	M	EM60(15)	M-EM60(15)	EM60(30)	M-EM60(30)
120	62.05	60.19	1.003	1.203	-0.020	0.987	0.016
180	60.91	59.09	0.985	0.973	0.012	0.988	-0.003
240	62.58	60.71	1.012	0.998	0.014	1.020	-0.008
	185.54	179.99					

K = 0.9701   s(m) = 0.004

Table 7.2 continued.

Angle Size = 15^{o}

Orient.	a	a'	M	EM30	EM45
97	13.35	14.94	0.996		
112	14.06	15.73	1.049	1.020	0.993
127	12.60	14.09	0.939		
142	12.93	14.46	0.964	0.949	
157	13.22	14.79	0.986		1.002
172	14.28	15.97	1.065	1.022	
	80.44	89.98			
K = 1.119	s(M) = 0.007				

Angle Size = 30^{o}

Orient.	a	a'	M	EM30	M-EM30
105	31.01	31.93	1.064	1.020	0.044
135	27.98	28.81	0.960	0.949	0.011
165	28.40	29.24	0.975	1.022	-0.047
	87.39	89.98			
K = 1.0298	s(M) = 0.005				

Table 7.3 PSE (a), a', Magnification Factor (M) and Expected Magnification Factor (EM) for subject LTM at 2.00 second stimulus duration (see text).

Angle Size = 45^o

Orient.	a	a'	M	EM45	M-EM45
112	46.32	47.15	1.047	0.993	0.054
157	42.11	42.87	0.953	1.002	-0.049
	88.43	90.02			
K = 1.018	s(M) = 0.003				

Table 7.3 continued.

Angle Size = 15^o

Orient.	a	a'	M	EM30	EM45
97	13.16	14.74	0.983		
112	14.54	16.28	1.085	1.033	1.006
127	12.75	14.28	0.952		
142	13.36	14.96	0.997	0.974	
157	12.96	14.51	0.967		0.994
172	13.60	15.23	1.015	0.991	
	80.37	90.00			
K = 1.120	s(M) = 0.008				

Angle Size = 30^o

Orient.	a	a'	M	EM30	M-EM30
105	29.33	31.15	1.038	1.033	0.003
135	27.16	28.84	0.963	0.974	-0.011
165	28.27	30.02	1.001	0.991	0.010
	84.76	90.02			
K = 1.062	s(M) = 0.004				

Table 7.4 PSE (a), a', Magnification Factor (M) and expected Magnification Factor (EM) for subject SG at 2.00 second stimulus duration (see text).

Angle Size = 45°

Orient.	a	a'	M	EM45	M-EM45
112	42.18	45.89	1.020	1.006	0.014
157	40.57	44.14	0.981	0.994	0.013
	82.75	90.03			

K = 1.088 s(M) = 0.004

Table 7.4 continued.

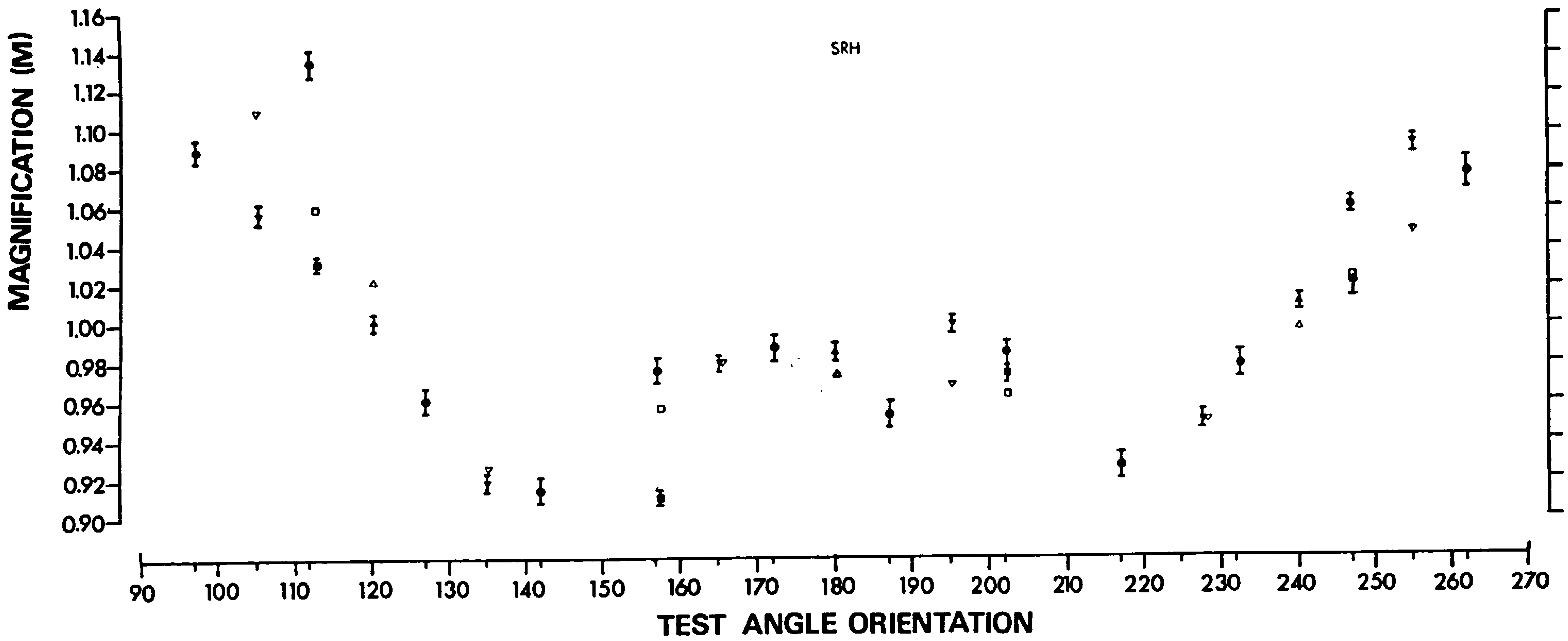


FIG. 7.1 Magnification factor (M) shown as a function of test angle orientation for subject SRH. Angle sizes are represented as: ● - 15°, ▼ - 30°, ■ - 45°, ▲ - 60°. The bars represent s_M. Open symbols show respective estimated M as derived by adding the perceived angular extents of the smaller component angles. The colours show the corresponding data for subjects DTM and SG.

In view of the positive outcome of this experiment a further series of runs was carried out to examine the orientation related characteristics of the magnification factor under conditions of brief stimulus presentation.

Method

With the exception of the stimulus duration which was set at 0.01 seconds, runs in this series were in all respects as similar as possible to the previous series. Only stimuli in the first quadrant were employed, however, for all subjects.

Results

The raw data were treated in the same way as were those for the previous runs with the 2 second stimulus duration. The values for a, a', and M, together with K, $s_{(M)}$ and EM are shown in Tables 7.5 to 7.7. Values of M as a function of orientation are shown in Fig. 7.2. At each angle size and for each subject the observed and expected values of the magnification factor were compared using the matched pair t-test. Once again no significant differences were found.

For the analysis of the effects of orientation and subject on the size of M, data from the previous experiment were included so as to evaluate the influence of the two stimulus durations. Summary tables are given in Tables 7.11 to 7.13. The differences attributable to changes in test stimulus orientation were found to be significant ($p < 0.01$) but neither differences between subjects nor differences between the stimulus durations contributed to the observed differences between individual observations. A corresponding analysis of variance of the untransformed PSE data showed the effects of all three factors - stimulus duration, orientation and subjects - to be significant ($p < 0.01$, see Tables 7.8 to 7.10).

In all respects, therefore, the characteristics of the relation between magnification factor and the orientation of the test angle with reference to the horizontal comparison angle are comparable across subjects and are invarient with respect to stimulus duration - for those durations used. These two factors both have significant effects on the constant errors of perceived angular extent showing, therefore, that although the absolute values of relative magnitudes of test and comparison stimuli vary between subjects and with changes of stimulus duration, the relative proportions of the quadrant or semicircle taken up by the component angles remain constant.

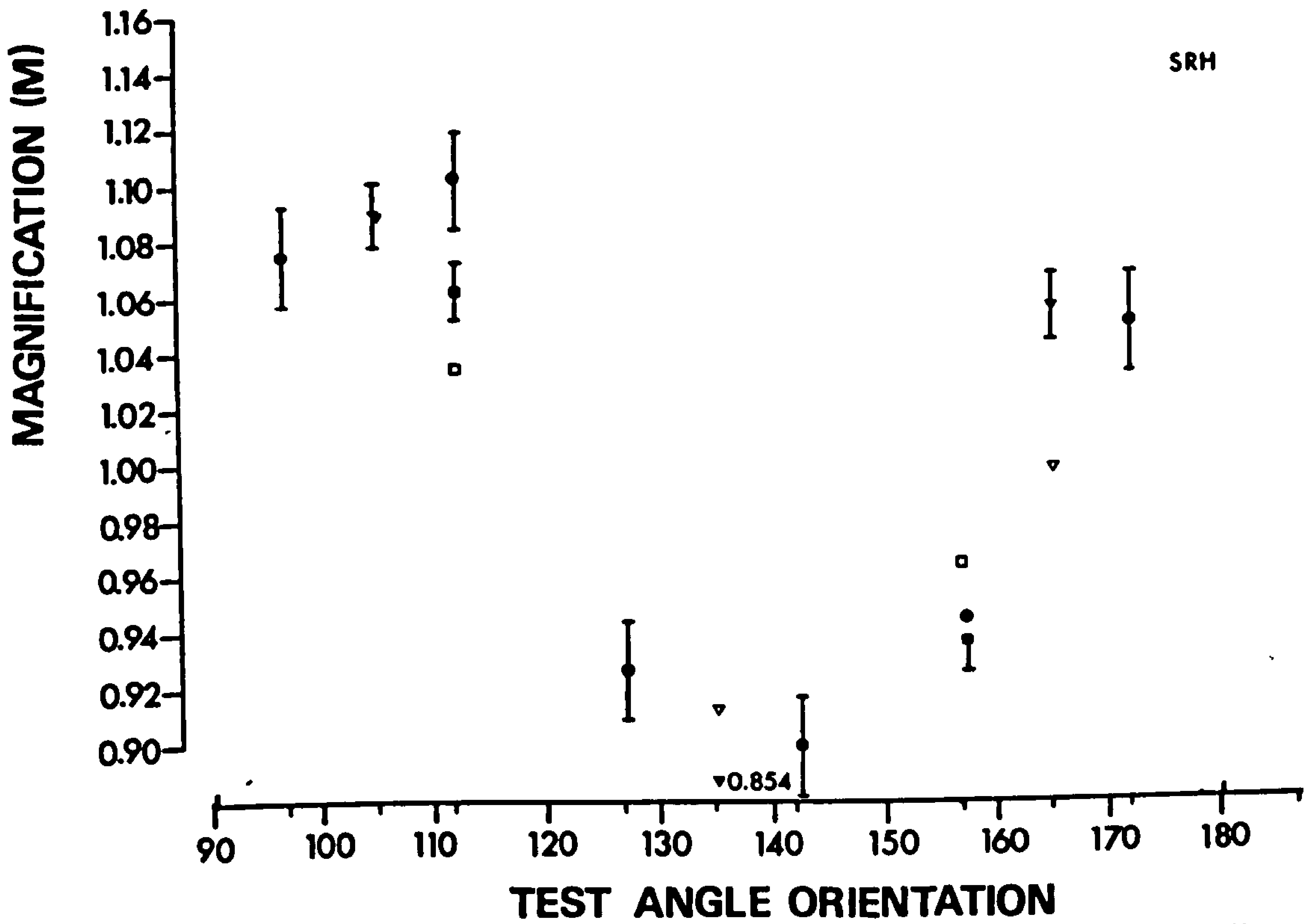


FIG. 7.2 Magnification factor (M) shown as a function of test angle orientation at a stimulus duration of 0.01 seconds, for subject SRH. Angle sizes are represented as: ● - 15°, ▼ - 30°, ■ - 45°, ▲ - 60°. The bars represent s_M. Open symbols show the respective estimated M as derived by adding the perceived angular extents of the smaller component angles. Colours, show the corresponding data for subjects DTM and SG.

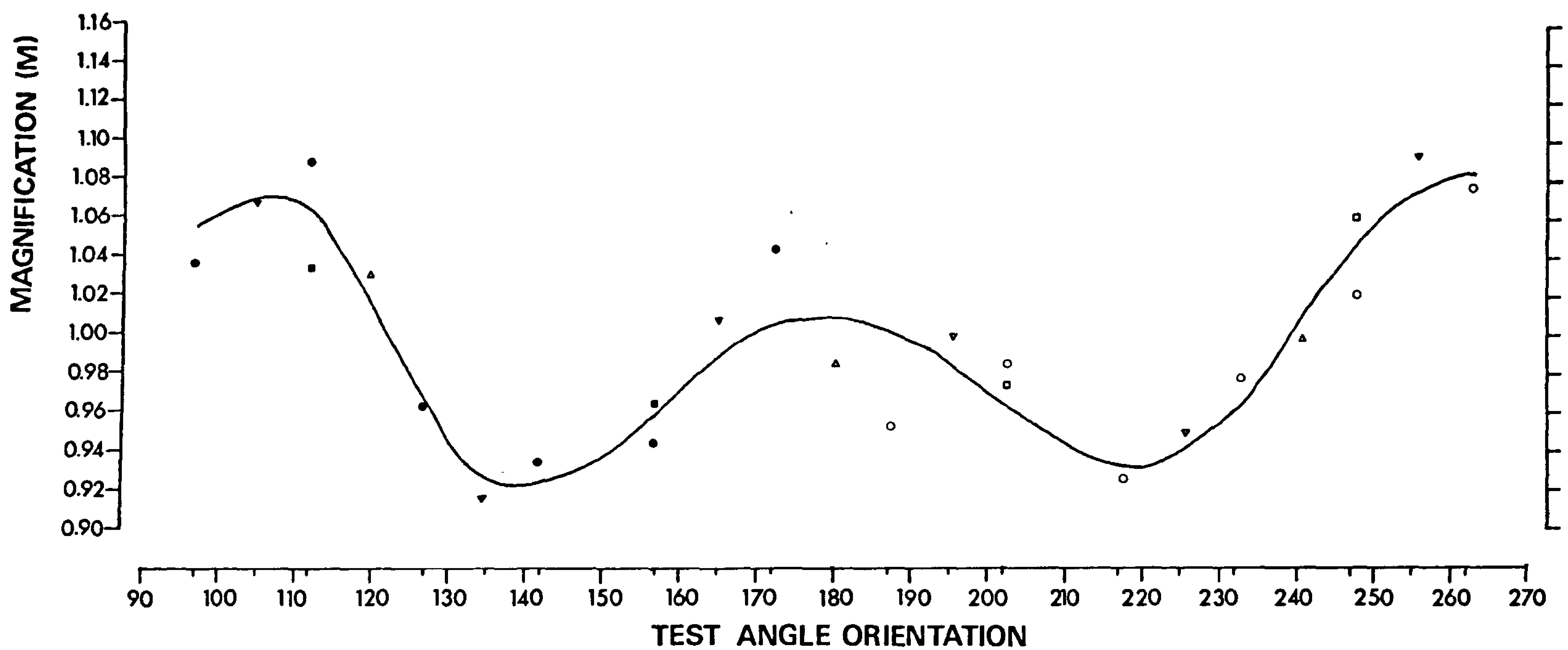


FIG. 7.3 Magnification factor (M) as a function of orientation - the observations have been averaged across subjects and stimulus durations. The angle sizes are: - 15°, - 30°, - 45°, - 60°. Solid symbols represent pooled data, open symbols represent points for which observations were made with SRH alone. The curve was fitted by eye.

Angle Size = 15°

Orient.	a	a'	M	EM30	EM45
97	13.65	16.13	1.075		
112	14.00	16.55	1.103	1.089	1.035
127	11.76	13.90	0.927		
142	11.42	13.50	0.900	0.913	
157	11.99	14.17	0.945		0.965
172	13.34	15.77	1.051	0.998	
	76.16	90.02			
K = 1.182	s(M) = 0.018				

Angle Size = 30°

Orient.	a	a'	M	EM30	M-EM30
105	29.57	32.70	1.090	1.089	0.001
135	23.16	25.61	0.854	0.913	-0.059
165	28.68	31.72	1.057	0.998	0.059
	81.41	90.03			
K = 1.106	s(M) = 0.012				

Table 7.5 PSE (a), a', Magnification Factor (M) and Expected Magnification Factor (EM) for subject SRH at 0.01 second stimulus duration (see text).

Angle Size = 45°

Orient.	a	a'	M	EM45	M-EM45
112	42.11	47.84	1.063	1.035	0.028
157	37.13	42.18	0.937	0.965	-0.028
	79.24	90.02			
K = 1.136	s(M) = 0.011				

Table 7.5 continued.

Angle Size = 15°

Orient.	a	a'	M	EM30	EM45
97	13.32	16.37	1.091		
112	13.17	16.19	1.079	1.085	1.062
127	12.40	15.24	1.016		
142	11.06	13.59	0.906	0.961	
157	10.07	12.38	0.825		0.938
172	13.23	16.26	1.084	0.955	
	73.25	90.03			

K = 1.229 s(M) = 0.012

Angle Size = 30°

Orient.	a	a'	M	EM30	M-EM30
105	26.22	32.46	1.082	1.085	-0.003
135	21.06	26.07	0.869	0.061	-0.092
165	25.43	31.48	1.049	0.955	0.094
	72.71	90.01			

K = 1.238 s(M) = 0.011

Table 7.6 PSE (a), a', Magnification Factor (M) and Expected Magnification Factor (EM) for subject LTM at 0.01 second stimulus duration (see text).

Angle Size = 45°

Orient.	a	a'	M	EM45	M-EM45
112	44.13	45.10	1.002	1.062	-0.060
157	43.94	44.90	0.998	0.938	0.050
	88.07	90.00			

K = 1.022   s(M) = 0.006

Table 7.6 continued.

Angle Size = 15^{o}

Orient.	a	a'	M	EM30	EM45
97	14.20	14.90	0.993		
112	15.34	16.10	1.073	1.033	1.016
127	14.02	14.72	0.981		
142	13.14	13.79	0.919	0.950	
157	13.81	14.49	0.966		0.984
172	15.23	15.99	1.066	1.016	
	85.74	89.99			
K = 1.050	s(M) = 0.013				

Angle Size = 30^{o}

Orient.	a	a'	M	EM30	M-EM30
105	31.67	32.34	1.077	1.033	0.044
135	27.78	28.36	0.945	0.950	-0.005
165	28.72	29.32	0.977	1.016	-0.039
	88.17	90.02			
K = 1.021	s(M) = 0.009				

Table 7.7 PSE (a), a', Magnification Factor (M) and Expected Magnification Factor (EM) for subject SG at 0.01 second stimulus duration (see text).

Angle Size = 45^{o}

Orient.	a	a'	M	EM45	M-EM45
112	43.72	46.98	1.044	1.016	0.028
157	40.20	43.20	0.960	0.984	-0.024
	83.94	90.18			
K = 1.075	s(M) = 0.010				

Table 7.7 continued.

Source of Variation	d.f.	Sums of Squares	Mean Squares	F-ratio	
Duration	1	8.178	8.178	21.594	$p < 0.01$
Subject	2	29.829	14.915	39.380	$p < 0.01$
Ang.Orient	1	67.302	67.302	177.700	$p < 0.01$
D x S	2	14.857	7.428	19.614	$p < 0.01$
D x O	1	0.4E-5	0.000	0.000	n.s.
S x O	2	4.832	2.416	6.379	$p < 0.05$
D x S x O	2	5.634	2.817	7.437	$p < 0.01$
Residual	12	4.545	0.379		
Total	23	135.18	5.877		

Table 7.10 Analysis of variance summary table for PSEs obtained with 45^{o} angle stimuli (Expt. 12).

Source of Variation	d.f.	Sums of Squares	Mean Squares	F-ratio	
Duration	1	0.2E-4	0.000	0.011	n.s.
Subject	2	0.4E-3	0.000	0.099	n.s.
Ang. Orient	5	0.118	0.024	13.098	$p < 0.01$
D x S	2	0.4E-3	0.000	0.096	n.s.
D x O	5	0.016	0.003	1.815	n.s.
S x O	10	0.023	0.002	1.279	n.s.
D x S x O	10	0.018	0.002		
Total	35	0.176	0.005		

Table 7.11 Analysis of variance summary table for magnification factors (M) obtained with 15^{o} stimulus angles (Expt. 12).

Source of Variation	d.f.	Sums of Squares	Mean Squares	F-ratio	
Duration	1	8.378	8.378	47.78	$p < 0.01$
Subject	2	10.295	5.148	29.36	$p < 0.01$
Ang. Orient	5	38.251	7.650	43.631	$p < 0.01$
D x S	2	17.903	8.952	51.06	$p < 0.01$
D x O	5	2.986	0.597	3.407	$p < 0.05$
S x O	10	7.923	0.793	4.518	$p < 0.01$
D x S x O	10	4.770	0.470	2.720	$p < 0.01$
Residual	36	6.312	0.175		
Total	71	96.818	1.364		

Table 7.8 Analysis of variance summary table for PSEs obtained with 15° angle stimuli (Expt. 12).

Source of Variation	d.f.	Sums of Squares	Mean Squares	F-ratio	
Duration	1	25.857	25.857	123.089	$p < 0.01$
Subject	2	29.371	14.687	69.913	$p < 0.01$
Ang. Orient	2	102.58	51.254	243.986	$p < 0.01$
D x S	2	57.611	28.805	137.123	$p < 0.01$
D x O	2	11.836	5.918	28.170	$p < 0.01$
S x O	4	7.024	1.756	8.359	$p < 0.01$
D x S x O	4	4.846	1.212	5.768	$p < 0.01$
Residual	18	3.781	0.210		
Total	35	242.84	6.938		

Table 7.9 Analysis of variance summary table for PSEs obtained with 30° angle stimuli (Expt. 12).

Source of Variation	d.f.	Sums of Squares	Mean Squares	F-ratio	
Duration	1	0.4E-4	0.00004	0.045	n.s.
Subject	2	0.2E-3	0.00008	0.086	n.s.
Ang. Orient	2	0.071	0.035	36.547	$p < 0.01$
D x S	2	0.4E-3	0.0002	0.202	n.s.
D x O	2	0.010	0.005	5.198	n.s.
S x O	4	0.005	0.001	1.194	n.s.
D x S x O	4	0.004	0.001		-
Total	17	0.090	0.005		

Table 7.12 Analysis of variance summary table for magnification factors obtained with 30^{o} stimulus angles (Expt. 12).

Source of Variation	d.f.	Sums of Squares	Mean Squares	F-ratio	
Duration	1	0.1E-3	0.00013	0.098	n.s.
Subject	2	0.3E-3	0.00013	0.097	n.s.
Ang. Orient	1	0.016	0.016	12.079	$p < 0.05$
D x S	2	0.2E-3	0.00011	0.078	n.s.
D x O	1	0.2E-4	0.00002	0.016	n.s.
S x O	2	0.002	0.001	0.804	n.s.
D x S x O	2	0.003	0.001		-
Total	11	0.022	0.002		

Table 7.13 Analysis of Variance summary table for magnification factors (M) obtained with 45^{o} angle stimuli (Expt. 12).

7.2 Experiment 13: Magnification Factor (M) as a Function of Angle Size

The observations described above are consistent with the notion that angular extents are coded as such by the visual system, and that adjacent perceived angular extents of small angles (15° - 30°) may be added to give the perceived angular extents of the larger angle subsuming the smaller ones. The hypothesis presented in the introduction to this chapter included, however, the proposal that the magnification factor at a given orientation should be constant. The test angle orientations required in the previous experiment (Expt. 12) to test the notion of additivity were such that very few angle sizes utilised test angles at the same orientations, and so the proposed consancy of the magnification factor at a specific orientation could not be well tested. This shortcoming was remedied by carrying out one further experiment in which data were collected to determine whether M is, in fact, constant for all angle sizes at a given orientation.

Method

The experiment was corried out using the method of constant stimuli under the same conditions as described for the previous experiment. The test angle was set at a bisector orientation of 135° and two runs were made by each of the subjects at angle sizes from 15° to 45° in 5° steps at each stimulus duration - 0.01 seconds and 2.00 seconds. The order of presentation of angle sizes was randomised.

Results

The PSEs for each subject were converted to perceived angular extents (a') subject by subject using K, averaged across angle sizes for each subject for each duration. These data are presented in Table 7.14. The results are shown graphically in Fig. 7.4. As the previous experiment has shown a lack of significant effect on M by subject differences and stimulus duration differences all the observations were pooled for the calculation of regression and correlation coefficients.

The regression coefficient $b_{a'.A}$ was found to be 0.958 with the correlation between a' and A being 0.981. The value of the slope of the line is equivalent to M and is not greatly divergent from the values obtained for M at 135° in the previous experiment (mean M, averaged across subjects and durations was

Subj.	Dur.	Stimulus Angle Size 15°	20°	25°	30°	35°	40°	45°
SRH	0.01	15.59	18.90	23.08	26.43	33.33	37.41	41.25
	2.00	16.19	18.60	23.38	28.36	34.35	36.77	41.90
SG	0.01	16.00	19.93	25.41	29.14	35.87	36.52	41.77
	2.00	16.63	20.10	25.69	29.54	38.37	41.46	46.25
DTM	0.01	14.42	20.03	26.39	24.06	36.90	42.02	46.79
	2.00	15.57	18.78	24.84	29.54	36.02	37.79	45.53

Table 7.14 Values for a' obtained during Expt. 13.

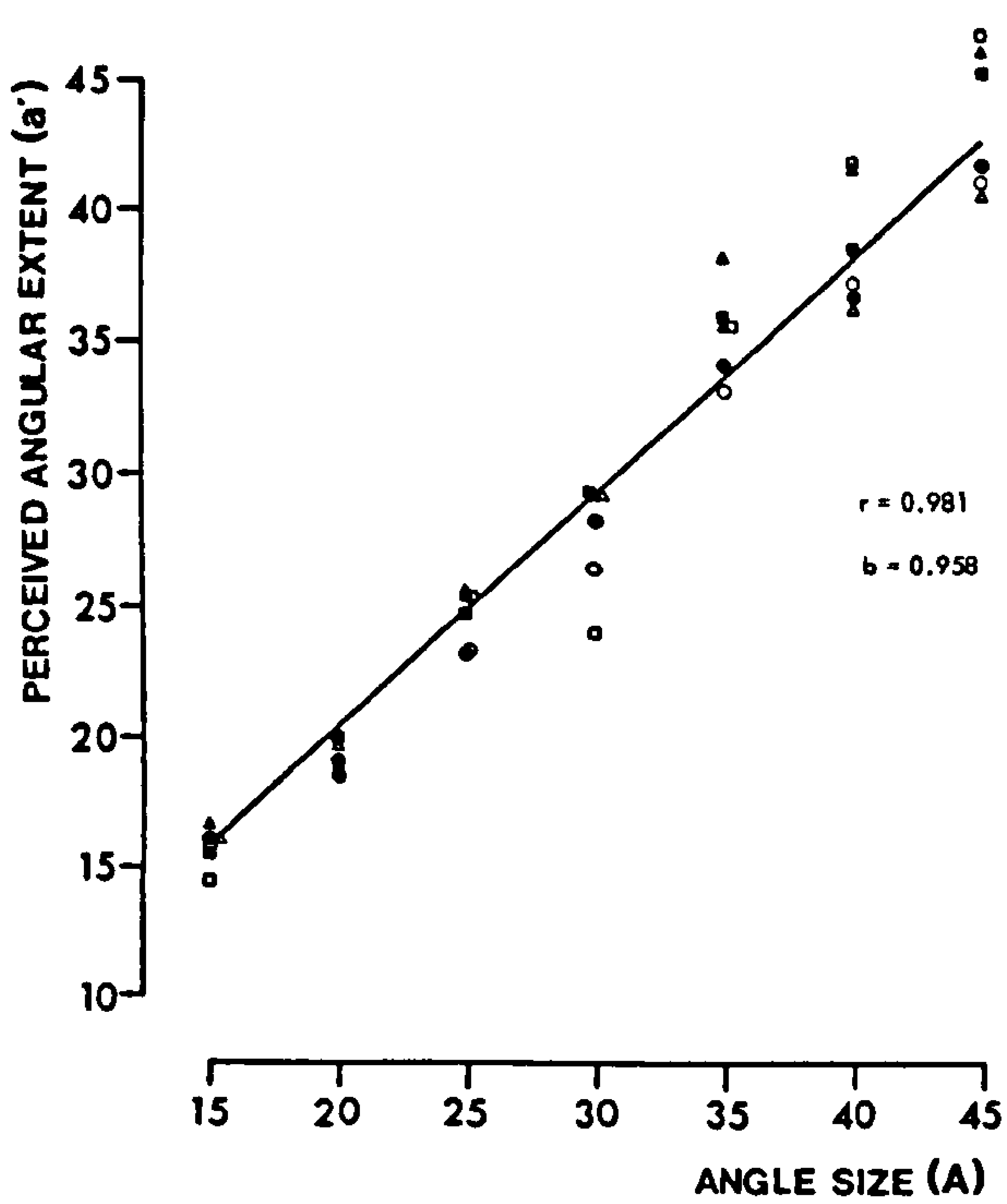


FIG. 7.4 Perceived angular extent as a function of angle size with a horizontal comparison angle and a test angle at 135°. Closed symbols represent observations for 2.00 second stimulus durations and open symbols those for 0.01 second stimulus durations. The subjects were: ● - SRH, ■ - DTM, ▲ - SG.

0.915 at 135°). The linearity of the relation between stimulus angle size and perceived angular extent is consistent with the hypothesis that at a given test angle orientation the magnification factor is a constant.

7.3 Difference Threshold for Perceived Angular Extent as a Function of Stimulus Angle Size

It was suggested in the results of Experiment 5 and has been confirmed in the results of Experiments 12 and 13 above that the constant error in perceived angular extent is a constant proportion of the size of the stimulus angle, which varies with the orientation of this angle. This suggests in turn that at some stage of visual processing the magnitude of the perceived angular extent is registered as the linear combination of some perceptual units of angular extent, the size of which varies according to the location of this 'unit' in the orientation domain. Alternatively, the magnitude of the perceived angle could be represented in terms of an 'intensity' code whereby the spike frequency represents the magnitude of the angle.

If it is supposed that there is a certain precision associated with each 'unit' or 'interval' of perceived angular extent then, accordingly, as the intervals are integrated there would be some proportionate loss in the precision of the estimate of the final perceived angular extent. Observations made in preceding experiments have shown that the difference threshold for angle size does indeed increase with increasing stimulus angle size (Expts 5, 7 and 9) although in these experiments observations were made only with three or four angle sizes. To investigate the relation between these two variables more closely the threshold measures obtained in Experiment 13 were examined. These data are shown in Fig. 7.5.

An analysis of variance showed all three factors - subject, stimulus duration and angle size to be significant influences on difference threshold, together with all interaction terms ($p < 0.01$, Table 7.15). Comparison of the graphs in Fig. 7.5 suggested, however, that these differences may be the consequence of including the observations from DTM at the 10 msec. stimulus duration in the analysis as these are obiously different from the corresponding observations for the other two subjects. Further analysis, eliminating these observations, showed the three factors to retain their level of significance (Table 7.16). It may be concluded therefore that the between subject differences are valid and not simply attributable to 'deviant' observations from DTM.

FIG. 7.5 Difference threshold for angle size as a function of stimulus angle size for the three subjects. The closed symbols show observations for the 2.00 second stimulus duration and the open symbols show observations made at stimulus durations of 0.01 seconds.

Source of Variation	d.f.	Sums of Squares	Mean Squares	F-ratio	
Subject	2	3.439	1.719	85.055	$p < 0.01$
Duration	1	27.801	27.801	1375.22	$p < 0.01$
Ang. Size	6	10.950	1.825	90.277	$p < 0.01$
S x D	2	1.537	0.769	38.018	$p < 0.01$
S x AS	12	1.729	0.144	7.129	$p < 0.01$
D x AS	6	2.831	0.472	23.342	$p < 0.01$
S x D x AS	12	1.120	0.093	4.617	$p < 0.01$
Residual	42	0.849	0.020		
Total	83	50.258	0.606		

Table 7.15 Analysis of variance summary table for difference thresholds obtained in Expt. 13.

Source of Variation	d.f.	Sums of Squares	Mean Squares	F-ratio	
Subject	1	1.008	1.008	41.754	$p < 0.01$
Duration	1	24.955	24.955	1033.76	$p < 0.01$
Ang. Size	6	10.673	1.779	73.684	$p < 0.01$
S x D	1	0.107	0.107	4.440	$p < 0.05$
S x AS	6	0.473	0.079	3.266	$p < 0.05$
D x AS	6	3.076	0.513	21.239	$p < 0.01$
S x D x AS	6	0.182	0.030	1.254	n.s.
Residual	28	0.676	0.024		
Total	55	41.150	0.748		

Table 7.16 Analysis of variance summary table for thresholds obtained in Expt. 13, omitting the observations from DTM.

Regression analysis showed high correlations between angle size and difference thresholds and, with the exception of subject DTM, a difference in regression coefficients between the two stimulus durations, the slope for the shorted duration stimulus being greater than that for the longer durations. The results of this study demonstrate, therefore, that the difference threshold for perceived angular extent is a linear function of the stimulus angle size, and that the slope of this function may be substantially smaller for long stimulus durations than for brief stimulus durations.

The difference between the graphs for SG and SRH and that for DTM indicates that the differences between slopes are not a necessary consequence of differing stimulus durations, suggesting that the visual system has a choice of strategies which may be adopted for discrimination between angular extents, one of which is more effecient than the other, but perhaps more difficult to employ under conditions of brief stimulus presentation.

7.4 Discussion

The rationale behind the experiments described in this chapter was to try to identify a regular pattern in the responses of the visual system to angle stimuli, outside of the frame of reference provided by the lateral inhibition model for interaction between orientation analysers. A working hypothesis that there may be a perceptual metric for angular extent was adopted, and the stimuli used were selected in order that this hypothesis could be tested and, if supported by the observations, elaborated.

The data obtained from the first experiment (Expt. 12) provided intial support for the hypothesis that a regular perceptual scale of angular extent can be derived, which is related to physical angle size by a 'magnification factor', M, which was found to vary as a function of test stimulus orientation (Fig. 7.3). This finding was supported by the data obtained in the second experiment (Expt. 13) in which the relation between stimulus angle size and perceived angular extent was examined in more detail at a fixed orientation. Perceived angular extent was shown to be linearly related to stimulus angle size with a proportionality constant $M = 0.958$ at a test angle orientation of 135°.
The value of the magnification factor is only relative, however, depending on an assumed perceived angular extent for the comparison angle. As the absolute value for this measure cannot be determined, the perceived angular extent of the comparison angle was arbitrarily set equal to the physical angle size. Any

change in this assumed magnitude would shift the curve depicted in Fig. 7.3 about the horizontal axis, but would not change the shape of the curve. As the apparent expansion of acute angles is known to be greatest at the horizontal and vertical the values of M derived in this study are overestimates - the assumed reference perceived angular extent being rather smaller than its probable value.

The fluctuations in perceived angular extent thus characterised simply redescribe the well-known fact that obliquely oriented acute angles are seen as being smaller than vertically or horizontally oriented angles of the same size. The stimulus orientations used, however, enabled the determination of a further attribute of the metric for perceived angular extent, namely that of additivity. Thus, within the range of angle sizes tested, it was shown that the perceived angular extent of a large angle could be predicted as the sum of the perceived angular extents of the smaller angles contained within the larger angle.

As the untransformed values for perceived angular extent were shown to be significantly different at the two stimulus durations, and for the three subjects, the magnitudes of the units of the notional perceived angular extent metric are evidently both duration dependent and subject specific. After the transformation of the perceived angular extents the effects of both stimulus duration and subject differences were lost, indicating that given perceived angular extents maintain constant relative magnitudes according to their meridional locations, and consequently represent constant proportions of the perceptual scale, whatever the stimulus duration.

The scaling factor which relates the physical circle of 360^{o} to the perceptual scale of perceived angular extent varies not only between subjects, therefore, but also with stimulus duration. The values of the normalising constants shown in Table 7.17 indicate that, on the whole, the absolute values of the notional perceptual units of perceived angular extent increase with increased stimulus duration, although subject SG does not follow this trend.

It would appear, on the basis of these observations, that at some level in the visual system, angles are represented in terms of the angular extent embraced by the lines delineating the angle and that the size of the angle is represented by the summing of the outputs of orientationally adjacent neural systems. This simplistic conceptualisation is not intended to stand as an explanation

Subject	Angle Size	$K_{0.01}$	$K_{2.00}$
SRH	15°	1.182	1.058
	30°	1.106	1.032
	45°	1.136	1.031
DTM	15°	1.229	1.119
	30°	1.238	1.030
	45°	1.022	1.018
SG	15°	1.050	1.120
	30°	1.021	1.062
	45°	1.075	1.088

Table 7.17 Values of the normalising constant K derived in Experiment 12 (see text).

of the process of angle perception, but only to act as a point of departure for subsequent discussion. In terms of a model of this type, angular extent can be supposed to be represented as an amount of neural activity which bears a positive, monotonic and apparently linear relation to the size of the stimulus angle - at least over some part of the range of activity. The amount of activity is determined by the number of subordinate units activated.

This notion receives support from the results of experiment 15 which show the difference threshold for angle size to be a linear function of the magnitude of the test angles. In other words, over the range of angle sizes tested, the difference threshold follows Weber's Law - $\Delta I/I = K$ - in which I is the intensity or magnitude of the stimulus and ΔI is the difference threshold. Although most stimulus variables to which Weber's Law has been applied can be considered as intensity variables, e.g. light intensity, pain, sound intensity, pressure, etc., some stimulus variables which have been related to perceptual continua by Steven's Power Law, considered to give a better fit to psychophysical scaling data (Stevens, 1970), are more comparable to perceived angular extent, e.g. visual length and visual area. These are both abstracted perceptual magnitudes whose quantity representation is dependent on prior processing of the input, in contrast to other intensity variables for which it can be shown that the strength of neural response is proportional to the intensity of the stimulus at the receptor surface - e.g. in rods or cones of the retina.

The fact that a visual-perceptual variable can be described in terms of an intensity continuum by no means implies that the variable must be coded in the pre-striate or striate levels of the visual system in terms of simple increasing spike frequency of some population of neurones as are, for example, brightness and loudness. In view of what is known of the receptive field characteristics at these levels of the visual system, such an encoding mechanism cannot be postulated, there being no reported physiological findings that describe angle-shaped receptive fields.

White and Riggs (1974) have claimed evidence supporting the existence of 'angle detectors' in the human visual system derived from a contingent colour aftereffect study. This study, however, is liable to the criticism made by MacKay and MacKay (1974) of similar claims for the existence of curvature analysers. They suggested that in these studies the so-called angle or curvature contingent colour aftereffect can be easily explained in terms of the simple orientation contingent colour aftereffect in that there is a simple association of colour and tilt in the left and right halves of the retina during adaptation. When the adapting pattern is swept across the retina so that all parts of the retina are exposed to all parts of the adapting pattern, the colour aftereffect is not found.

To date, therefore, there is neither neurophysiological nor psychophysical evidence to support the hypothesis that the perception of angles is mediated by channels in the visual system that are selectively tuned for angle size, comparable to the channels postulated for orientation and spatial frequency. This being the case, any orientation information utilised in the perception of angle size must be derived in some way from the output of those orientation selective channels that are known to exist in the human visual system.

Chapter 8: The Perception of Angular Extent

In this chapter an attempt will be made to integrate the observations made in the preceding experiments, and to examine the implications of these observations for current models of the processing of orientation information in the visual cortex. In the first section, the observations will be summarised from the point of view of performance; the theoretical implications will be dealt with in the second part. Most of the arguments, concepts and hypotheses pertinant to this discussion have been described in detail either in chapter 1 or in association with the experiments to which they were appropriate. In the discussion to follow, therefore, concepts which have been elaborated in previous chapters will be referred to only as is appropriate to the requirements of the discussion.

8.1 Factors Influencing Variable and Constant Errors of the Perception Of Angles.

The results obtained in the preceding experiments have shown both the acuities and the constant errors for comparisons of angular extents to be influenced by a number of stimulus variables. The variables investigated, together with summaries of their effects of perceptual performance with angle stimuli, are described in this section. The effects of these variables on acuities for angle size will be considered first.

8.1.1 Effects on Acuity for Perceived Angular Extent.

(a) Retinal Location

Ultimately, the accuracy with which aspects of visual stimuli may be specified in the visual system is limited by the size of the elements of the retinal mosaic. According to the anatomical studies of Polyack (1941) the size of retianl cones increases from about 20 sec. arc at the centre of the fovea to about 40 sec. arc at an eccentricity of 2 deg. arc. If the accuracy with which angular extents may be specified and compared is, in fact, limited only by the functional grain of the retina within the foveal and parafoveal regions, it would be expected that performance decrements would be observed according to the eccentricity of the stimuli. Furthermore, the involvement of any local features of the stimulus in the evaluation of perceived angular extent might also be revealed by observed differences of performance when stimuli are disposed on the retina such that different parts of the angles - the vertices and bases, for example - were more or less distant from the centre of fixation.

According to the results obtained in experiment 3, concerning acuities for orthogonality (Fig. 4.1) and from experiment 8, concerned with acuities for comparisons of angular extents, the location of the stimulus on the retina and its configuration within an eccentricity of $\pm$ 2 deg. arc has no significant effect on the accuracy with which estimates of angular extents can be made by the observer. It may be concluded that the limitations on accuracy are imposed at some level of the visual system subsequent to the retinal receptor surface.

(b) Line Length

The effect of line length on acuity for angle size was investigated briefly in experiment 5. Although the influence of this stimulus variable on performance was found to be significant, the relationship between the line length and acuity was by no means unequivocal. Most of the 'noisiness' of these observations occurred with line lengths of less than 0.6 deg. arc, beyond which increases of length tend to result in a slight gain in acuity. For shorter lines the acuity tends to increase from line lengths of 0.16 deg. arc up to lengths of 0.6 deg. arc. Even over this range, however, the changes of acuity were not great, the largest improvement in acuity (excluding the most extreme data points) was only 1°.

In Andrews' (1967b) study of the influence of line length on acuity for orientation the greatest improvements of performance occurred as the length of the test line was increased up to about 0.15 deg. arc after which there was a smaller but continuous improvement of acuity with further increases of line length. The difference between the acuity functions of orientation with line length, and angular extent with line lenght, if valid, contributes to the evidence in support of the hypothesis developed in this thesis, that the mechanism by which information contributing to the perception of angular extent is processed is not identifiable with the operation of orientation-selective channels and their interactions alone.

(c) Stimulus Duration

The influence of increasing stimulus duration on acuity for angle size, as observed in experiment 9, was at least qualitatively consistent with the results obtained by Andres (1967a) for orientation acuity. A continuous improvement of the accuracy of the comparisons of angle sizes was observed as stimulus duration was increase from 10msec. to about 500msec (Fig. 6.11). Little observable improvement of performance was observed with longer stimulus durations than 1 second. These findings suggest that, whatever the mechanism underlying the perception of angular extent, some temporal integration of neural responses occurs, resulting in a narrowing of the response error distribution. A possible relation between the variance of the response error distribution for perceived orientation and the perception of angular extent is developed in the next section of this chapter (8.2).

(d) Stimulus Orientation

Both the absolute orientation of angle bisectors and the relative orientations of the two angles comprising the stimulus were tested for effects on acuity for angular extent. In experiment 8 acuities were obtained over a range of orientations, with the configuration of the angles such that the absolute orientations of the bisectors of the angles was either identical, or symmetrical about the vertical axis. As described in 8.1.1(a), differences of stimulus configuration had no effect on acuity. Significantly different effects of orientation on acuity were observed for the three observers, one of whom (KB, Fig 5.4) showed no effect at all of orientation on acuity. The remaining observers showed significantly different acuities only between the horizontal angles and angles of all other orientations, performance being worst with the horizontal angles.

When the influence of relative orientation - the angular separation between the bisectors of the two stimulus angles - was investigated in experiment 5 it was found, once again, that at least some different orientations of test angle gave performances statistically different from those given at other orientations. As with the results of experiment 8, however, the relation between test angle orientation and acuity bore little resemblance to the meridional anisotropy of the acuity for orientation. The worst performances occurred at test angle orientations of 90° and 270° (with a horizontal reference angle (Figs 4.10 and 4.11), and even this observation was not consistent for all line lengths and angle sizes.

(e) Stimulus Angle Size

The relation between acuity for angle size and the stimulus angle size was the one relationship including acuity which was both consistent and systematic in all experiments which supplied relevent data (experiments 5, 7 and 13). The presentation of the results from experiment 5 in figure 4.13 clearly shows acuity to decrease with increasing stimulus angle size - and at the same time demonstrates the absence of a systematic orientation effect. Although the shapes of the graphs drawn for each line length differ (the line length by angle size interaction was found to be significant), the overall trend for acuity to decrease as a monotonic function of angle size is evident. This finding was repeated in the results of experiment 7 where the orientations of the bisectors of the two stimulus angles were identical or equivalent.

In experiment 13 acuities for angle size were obtained at smaller intervals of stimulus angle size than in the previous experiments, using a stimulus configuration identical to that used in experiment 5. For all observers and for both 10msec. and 2 second stimulus durations the difference threshold was found to increase monotonically with stimulus angle sizes from 15° to 60°. Linear regressions were fitted to each set of data (Fig. 7.5), which accounted for between 0.61 and 0.96 of the variance of the observations. Differences between subjects were found to be significant, as were differences between acuities obtained at the two stimulus durations..The slope of the regression line was relatively shallow for the longer stimulus durations (b = 0.018 approx.). For the shorter stimulus durations the curves were vertically displaced, showing an overall decrement of performance, and for two of the subjects the slope increased by a f ctor of about 3. The third subject showed only a slight increase in slope, from 0.018 to 0.026.

8.1.2 Effects on Constant Errors of Perceived Angular Extent

The constant errors of perceived angular extent measured in the preceding experiments refer only to the differences between the perceived angular extents of the two stimulus angles. The constant error gives the magnitude of the difference, and its sign indicates which of the angles appeared larger than the other when both were of equal size. The data obtained do not, therefore, show what was the perceived size of the angle, compared to an absolute physical magnitude. The assumption was made on the basis of previous studies that acute angles appear perceptually expanded; the constant error, therefore, reflects differences in the misperception of angular extents.

(a) Retinal Location

Some measurable constant error was observed in all the experimental conditions investigated in this study. Results obtained in experiment 8 showed that when the angles to be compared differed only in their location and arrangement on the retina the constant error was within the range $\pm 1^{\circ}$. There were no significant differences between the constant errors observed at any of the three configurations of angles included in this experiment, but the variation between subjects was found to be significant.

In experiments 5 and 7 larger constant errors were observed, in the range $\pm 2^{\circ}$, which again were not associated with any differences between the two stimulus angles other than in their dispositions on the retina. These results demonstrate, therefore, that while variation of the position of an angle on the retina can lead to quite substantial variation of perceived angular extent, such variations are non-systematic within an eccentricity of 2 deg. arc. It is suggested that this component of the observed constant error is representative of local variation of the scaling of a perceptual metric for angular extent. Similar random variation of constant error has been reported by Andrews (1967a) for the perceived orientation of line segments.

(b) Line Length

The influence of varying stimulus line length on constant error was similar to its influence on acuity in that little consistent systematic effect could be discerned in the one experiment where line length was manipulated as an independent variable (experiment 5). A greater emphasis was given to other independent variables - stimulus duration, orientation and angle size - through the course of this study, and investigation of the effects of line length was not pursued in greater detail.

The results that were obtained showed line length to contribute significantly to the observed variance of constant error, both as a main effect, and in interaction with stimulus angle size and stimulus orientation. The graphs presented in figure 8.4 show the relation between line length and constant error to be non-monotonic, and for some angle sizes to be either U-shaped or inverse U-shaped according to the angle size and the orientation of the test angle. The clearest results were obtained with an angle size of 45°; here the constant error was found to increase as the length of the line was increased from 0.16 deg. arc to a maximum at lengths of 1.0 deg. arc. Further increases of line length lead to a slight decrease in the magnitude of the constant error. In view of the paucity of the data obtained, however, no interpretation of these observations was made.

(c) Stimulus Duration

The relation between constant error and stimulus duration was investigated in experiment 9, the results of which showed the perceived difference between the sizes of the two angles comprising the stimulus to show an overall decrease as the time for which the stimulus was visible was increased. Examination of the data presented in figures 6.3 and 6.4 reveals relatively little change in constant error to occur as the stimulus duration was increased from 10msec to 100msec. The majority of the observed decrease occurred at stimulus durations between 100msec. and 500msec; as the stimulus duration was increased to 2 seconds further, smaller and less consistent changes in the magnitude of the constant error were observed.

Significant change of constant error magnitude was seen with a vertical test angle and horizontal reference angle, where orientation-dependent constant error is minimal. This finding suggest that while the observed constant error, in principle, may be partitioned into an orientation-dependent component and an orientation-independent component, both components are subject to reduction of magnitude as the stimulus is visible for longer periods of time. The time course of the change of constant error of perceived angular extent is comparable to that observed by Andrews (1967a) for changes of perceived orientation.

(d) Stimulus Orientation

The relation between the magnitude of perceived differences between the sizes of angles at different orientation has been investigated extensively, using a number of different configurations (chapter 1.1). The results obtained in the present sudy were consitent with those obtained in previous experiments insofar as the maximum difference of perceived angular extent was observed when an oblique angle was compared with a vertical or horizontal reference angle, oblique angles being perceived as smaller than vertical or horizontal angles. With the exception of the small angles used in experiment 5 (15^{o}), this relation was observed consitently in the results from experiments 5,6,9 and 12.

In experiment 12 it was shown that, after normalisation, the relation between the perceived sizes of the test and reference angles of the stimulus could be expressed as $a' = M.A$; where a' is the normalised perceived angular extent, A is the stimulus angle size and M is a magnification (scaling) factor whose value varies as a function of the orientation of the test angle relative to the horizontal reference angle. In this experiment it was also found that while stimulus duration had the expected effect on the untransformed constant errors, no effect of stimulus duration on the value of the scaling factor (m) was found for a given stimulus orientation.

(e) Stimulus Angle Size

Stimulus angle size as a determinant of the magnitude of the constant error of perceived angular extent was investigated in experiments 5,7,12 and 13. In the first of these data were obtained which suggested that the constant error increases with the size of the stimulus angles, where the test angle was oblique and the reference angle horizontal. When the test angle was horizontal or vertical the magnitude of the constant error was unaffected by the stimulus angle size. The absence of any effect of angle size on constant error under similar conditions was confirmed in experiment 7 where no substantial change of constant error was observed for any stimulus orientation when the orientations of the two stimulus angles were identical, or equivalent with reference to the vertical or horizontal axis. There are, therefore, as suggested earlier, two components to the constant error; one independent of stimulus angle size and orientation, the other dependent on the value of these stimulus variables.

In experiment 12 it was found that the constant errors of perceived angular extent were additive: The constant error for a large stimulus angle was found to be equal to the sum of the constant errors of perceived angular extent for the smaller adjacent angles subsumed by the larger angle, after normalisation. In other words, the value of the scaling factor (M) is constant for a given test angle orientation. This observation was confirmed in experiment 13, the results of which showed 0.96 of the variance of the observed constant errors to be accounted for by a linear regression of normalised perceived angular extent onto stimulus angle size. In this experiment no significant variation between observers was found for the normalised constant errors. At the test angle orientation used in this experiment (135°), the relation between the normalised perceived angular extent and stimulus angle size was found to be expressable as $a' = 0.958.A$. This value of M was in fairly good agreement with that obtained for this orientation in experiment 12.

8.2 Mechanisms Underlying the Perception of Angular Extent

Current hypotheses concerned with the perception of forms defined by contours of a number of orientations all make the fundamental assumption that the perception of angles - the areas enclosed by intersections of contours - is essentially an extension of the process by which the orientations of these contours are perceived when presented singly. The various models developed for the explanation of orientation perception have been reviewed in chapter 1. Thus, whatever the supposed characteristics of orientation analysers and of interactions between them, it is apparent that many workers have assumed that angles are represented in the visual system not as angular extents, but as co-occurrences of the representations of lines of differing orientations. The differences between the perceived sizes of angles and the actual sizes of the angle stimulus, together with the effects of illusions of orientation or direction, have been attributed to the occurrance of lateral inhibitory interactions between the orientation analysers which respond selectively to the orientations of the lines comprising the stimulus.

The observations which provided the evidence that lateral inhibitory interactions do occur between orientation analysers have also been reviewed in detail in chapter 1. These observations were derived primarily from adaptation and masking studies, especially, for example, those of Dealy and Tolhurst (1974) and Sharpe and Mandl (1977) which have demonstrated that the adaptation aftereffect can be induced by stimuli that are sub-threshold to the analysers which subsequently show threshold elevation effects. The response of the adapted channels to stimuli to which these channels are not excitatively sensitive, necessarily, must be generated by inputs from channels which are sensitive to the adapting stimuli. The source of these inputs has been identified as the lateral inhibitory connections between the orientation-selective analysers, which have been observed in neurophysiological studies of single unit activity in the visual cortex (e.g. Benevento, Creutzfeldt & Kuhnt, 1972; Blakemore & Tobin, 1972; Fries, Albus & Creutzfeldt, 1977).

Initial arguments against the direct, causal implication of orientation contrast due to lateral inhibitory interactions between orientation analysers in the misperception of angular extent (presented in chapter 1.4) rely primarily on the observation by Hirsch, Schneider and Vitiello (1974) that there are no differences between the adaptation tuning curves, and hence inhibitory tuning characteristics, measured after prolonged viewing of stimuli of a number of different orientations. The differences between the inhibitory tuning characteristics at different orientations which Hirsch et al. failed to find were originally postulated so that observed meridional variation of the perceptual expansion of acute angles could be accounted for by the hypothesis that misperception of angular extent was a manifestation of orientation contrast. Further evidence for the absence of any meridional variation in the orientation specificity of adaptation and masking effects has been presented in the results of experiments 1 and 2 of the present study. Meridional variation of perceived angular extent cannot be explained as a consequence of differential inhibition between orientation analysers, therefore, when evidence for the required meridional variation of the inhibitory characteristics of orientation analysers cannot be found.

An alternative explanation for the observed meridional variation of percieved angular extent could have been based on the premise of differential selectivity of the excitatory responses of orientation analysers, but for Abadi's (1974) demonstration that this characteristic too is meridionally isotropic. A further alternative hypothesis, based on Mansfield's (1974) report that there are more neurones in the primate visual cortex tuned to vertical and horizontal orientations than to oblique orientations was attempted in chapter 6. Consequences of the assumptions made in this model, however, proved to be inconsistent with other known characteristics of inhibitory interactions between orientation-selective neurones in the visual cortex, thus rendering the hypothesis untenable. Furthermore, subsequent neurophysiological studies of the primate visual cortex have failed to repeat Mansfield's observations, finding the numbers of neurones tuned to different orientations to be statistically equivalent (Schiller, Finlay & Volman, 1976; Poggio, Doty & Talbot, 1977).

Even in the absence of these problems, Carpenter and Blakemore (1973) have raised further difficulties with their description of the shapes of the tuning characteristics which would be required in order to give the observed magnitudes of the perceptual phenomena associated with acute angles. The available data concerning the tuning characteristics of cortical orientation-selective neurones do not exhibit the extremely narrow response profiles depicted by Carpenter and Blakemore, and thus detract further from the likelihood that the misperception of angular extents can be explained either directly or solely in terms of orientation contrast induced by inhibitory interactions between orientation-selective cortical analysers. While orientation contrast may contribute to these effects, it is insufficient to explain them.

Further evidence that the apparent enlargement of angular extents is a consequence of some perceptual process other than contrast enhancement between the perceived orientations of the line components of an angle, caused by lateral inhibition, is provided by the results of the experiments described in the preceding chapters of this thesis. The observations which constitute this evidence were made in studies of the time course of the development of meridional differences of perceived angular extent, and of the relation between constant errors of comparisons of angular extents and the sizes of the stimulus angles. Detailed elaborations of the implications of these observations for current hypotheses have been presented in chapters 6 and 5 respectively. For the benefit of further discussion these findings will be summarised.

Firstly, inhibitory activity has been shown to develope more slowly than excitatory activity by Ratliff, Hartline and Miller (1963) in Limulus while corroborative observations for human orientation analysers have been presented by Andrews (1965). As demonstrated by the time-course of adaptation aftereffects, this inhibition also outlasts excitatory activity. Any perceptual phenomenon dependent on inhibitory interaction should be expected, therefore, to show an increase in magnitude from stimulus onset until a stable equilibrium between excitatory and inhibitory activities is attained. As the data obtained in experiment 9 demonstrate, the perceived differences between the sizes of horizontally oriented and obliquely oriented acute angles diminishes with increasing stimulus duration up to 0.5 - 1.0 seconds. This period is comparable to the time constant for the stabilisation of inhibitory interactions described by Andrews. If the change of perceived angular extent with increasing stimulus duration is a consequence of temporal integration of responses, mediated by lateral inhibition, then the inhibitory interactions appear to effect a reduction of meridional differences of perceived angular extent, rather than the induction of this effect.

The evidence presented by the observed relation between constant errors of perceived angular extent and the stimulus angle size is rather more indirect. Briefly, as the separation between the mutually inhibiting orientation channels increases, the strength of their mutual influence diminishes, as has been demonstrated by conventional studies of orientation-specific masking and adaptation, as well as by physiological observations of lateral inhibitory activity. Thus, as the stimulus angle size, and hence the separation of the constituent orientations, is increased, the magnitude of any perceptual expansion of angular extent should diminish as the strength of the inhibitory interactions between the constituent orientations diminishes. When separation is large enough, there should be no perceptual expansion of angular extent, and consequently no difference between perceived angular extents other than the residual constant error found for comparisons of identically oriented angles in experiments 7 and 8. The only interactions which might occur at the larger stimulus angle sizes would be those between the adjacent arms of the two different angles. This interaction, however, would act in such a direction as to reduce perceived differences of angular extent or, conceivably, to a reversal of the sign of the difference.

The results obtained in experiment 5 do not fit this expectation at all, increasing the size of the stimulus angles resulted in a monotonic increase of the constant error, representing the perceived difference between the angular extents of the two stimulus angles, with stimulus angle sizes of up to 60°. Meridional differences of constant errors were conserved across the range of stimulus angle sizes with the exception only of the smallest angle sizes used (15°).

These observations, which were repeated in greater detail in experiments 12 and 13, were particularly puzzling as they disagree not only with the predictions of the lateral inhibition hypothesis for the perceptual expansion of acute angles, but also with previously published results obtained with other simple angle-based stimulus configurations and Zöllner-type stimuli, as well as with those obtained from masking and adaptation experiments. Out of all the available data concerning the perception of orientation and angular extent, those obtained in the present study appear unique in their lack of consistency with both currently held hypotheses and other empirical data.

There is, however, one substantial difference between the experiments described in the preceding chapters and the majority of other studies concerned with the perception of angles. This difference lies in the actual perceptual comparison made by the observers, from which estimates of the misperception of angular extent are derived. An analysis of this difference, one of methodology, may lead to an understanding of, if not an explanation of, the apparent conflict between the observations described herein, and those described elsewhere.

In the majority of previous studies the perceptual task performed by the observer has been referred to the orientation of one of the lines comprising the stimulus pattern. Usually, the observer has either adjusted the orientation of a line until it appeared parallel to a comparison line or, in other experiments, the position of a dot (or line segment) has been adjusted until the dot (or line) appeared to be co-linear with the test line. It is assumed by both these techniques that the adjustable reference line or dot is beyond the range of influence of any parts of the stimulus which may influence the apparent orientation of the test line. Both these methods give an estimate of the perceived orientation of the test line. The difference between estimates made with the test line alone and estimates made in the presence of a second line forming an angle, or in the presence of an inducing field is a measure of the change in perceived orientation of the test line, caused by the presence of adjacent orientations and explained by means of lateral inhibitory interactions which lead to perceived orientation contrast enhancement. These procedures are directly comparable to those used to measure conventional tilt aftereffects and the equivalent simultaneous orientation contrast phenomena observed when adjacent gratings of appropriate angular separations are used as stimuli.

The perceptual contrast thus observed is, of course, in the same direction as that implied by the perceptual expansion of acute angles. The proposal that lateral inhibitory interactions are the cause of the perceptual expansion of acute angles entails, however, the assumption that perceived angular extent is equivalent to the difference of the perceived orientations of the lines comprising the angle. Consequently, the perceptual expansion of acute angles is assumed to be equivalent to the change of the perceived orientation of a line induced by the presence of another line or pattern of lines with a similar orientation.

The stimulus configuration used in the majority of the experiments of the present study, derived from Lennie's (1971) technique, requires a different task of the observer. The experimental procedure using this stimulus does not derive an estimate of perceived angular extent from measures of perceived orientation but, instead, the observer is required to compare angular extents directly, and to make judgments on the basis of these comparisons. Furthermore, except in the conditions either where the angular separations of the bisectors of the angle is 180°, or where one of the lines of each angle is separated from the other by 180°, line orientations cannot be used by the observer as cues for the equality of the angles[1].

The conflicting observations obtained under these two techniques indicate that the two tasks, as analysed above, cannot be considered as equivalent and that the perceptual demands that they impose upon the observer must, therefore, be different. This being the case, the results obtained in the present study constitute evidence against the above argument relating the perceptual expansion of acute angles to orientation contrast through the falsification of the definition of perceived angular extent as the difference of the perceived orientations of the lines comprising the angle pattern. On the basis of this finding, a new hypothesis will be considered which, expressed in its simplest form, proposes that mechanisms other than those described by mutually inhibiting orientation analysers are involved in the perception of angular extent, some characteristics of which will be described later in this chapter.

1. Emerson, Wenderoth, Curthoys and Edmunds (1975) have already shown that radically different results are obtained when angle-matching and end-point matching techniques are used in conjunction with the Lennie stimulus configuration. They also demonstrated that the difference between the two sets of results obtained was attributable to the nature of the task, rather than to the different loci of attention which may be employed in the performance of the two tasks.

The working hypothesis thus proposed, that orientation processing and the processing of angular extent utilise different perceptual mechanisms, is supported by further observations made in the present series of experiments. These observations are concerned with the threshold for detection of differences of angle size. If the perceived size of each angle was derived from the difference between the perceived orientations of the two lines describing each angle then, in order to compare the sizes of two angles the orientations of each of the four lines comprising the two lines would have to be assessed. The accuracy with which the two angle sizes could be compared, therefore, would be expected to reflect the accuracies with which the orientations of the four component lines can be established. Consequently, the meridional variation of acuity for angle size would be expected to appear in the difference thresholds for angle size comparisons. Neither of these expectations was fulfilled.

Previous measures of acuity for orientation of straight line segments, of lengths comparable to those used in the majority of the experiments under discussion have been: Andrews (1967b), 0.2° - 0.5°; Bouma and Andriessen (1968), 0.5° - 1.0°; Westheimer, Shimamura and McKee (1976), 0.3°. Even the best of these acuities is within the range of difference thresholds for angular extent, found with an angle size of 15°. This would imply, under the orientation difference hypothesis for angle perception, that the accuracy with which perceived angular extents can be derived from the perceived orientations of four stimulus lines is the same as that with which the orientation of a single line can be compared to that of, for example, a long, continuously visible line. The variance of the perceived orientations of the component lines in the two-angle stimulus would be no more than half that of the perceived orientations of single lines.

Although some sharpening of the response tuning curves of individual orientation anlysers would be expected as a consequence of lateral inhibitory interactions at small stimulus angle sizes, the consequent improvement of the accuracy of the estimation of the orientations of the component lines due to this process would be expected to decrease with increasing angle size. After a certain angle size the separations of the orientations would be greater than the range of lateral interactions and no further decrement of performance accuracy would be expected. On the basis of masking studies, the range of inhibitory interactions is estimated to be about 45°; at larger angular separations the interactions are minimal. Also, the strength of interaction decreases in an exponential-like manner, the half-width of which is about 12°. From this data, therefore, the loss of improvement of acuity due to increasing angular separation of the stimulus line components would be expected to be a negatively accelerated monotonic function, flattening out at stimulus angle sizes of about 45°.

The observed function did not have this form, but showed the difference threshold to increase linearly with increasing stimulus angle size up to the largest angle sizes used - 60°. Thus, although inhibitory interaction between orientation analysers could lead to an enhancement of the average acuity for orientation of the lines comprising the angles, it could not account for the observed relation between acuity and stimulus angle size. It is also unlikely that the increase in average accuracy of orientation estimation due to the influence of lateral inhibitory interactions on the response characteristics of the active analysers would be sufficient to account for the observed acuities for the comparison of small acute angles.

In a similar way it can be argued that if perceived angular extent was derived from the combined outputs of orientation analysers, without the involvement of any other perceptual mechanism, it would be expected that the poorest acuity for angle size would not be much worse than the combined acuities for the orientations of the line components, under similar conditions. That the error increases linearly as a function of increasing stimulus angle size indicates that the performance decrement is not the result of information loss at the time when the responses of individual analysers are combined. Were this the case, any error introduced by combination of outputs should be independent of the separation of the analysers in the orientation domain. As has been shown by the data obtained, this too is not the case.

The second finding relating to the difference threshold for perceived angle size, which also supports the hypothesis that angular extent is a perceptual quantity other than orientation difference, is the absence of meridional anisotropy of angle acuity. Although the data obtained in experiments 5, 7 and 8 show that stimulus orientation does influence the accuracy with which angular extents can be compared, there is no evidence at all for a systematic relation between the orientation of the angles and the difference threshold. This observation, particularly, in view of the apparent ubiquity of the systematic influence of stimulus orientation on sensitivity and selectivity when perceived orientation has been investigated. The absence of meridional variation of the acuity for angle size cannot be attributed to the characteristic of a process which integrates orientation information with an inefficiency large enough to mask meridional variation of the accuracy of orientation information, for this would lead to lower acuities than those which were observed.

Acuities of the observed magnitudes could be achieved, perhaps, if the information upon which the angle comparisons were based was the relative separation of the arms of the angles. The task carried out by the observer would be then reduced to the comparison of two linear distances. This hypothesis can be rejected, however, by consideration of the constant errors which would arise, were this the adopted procedure. The constant error in comparisons of linear distance is itself influenced by the relative orientations of the distances to be compared - the well known vertical-horizontal illusion (Robinson, 1972 p96f). Applying this effect to the comparison of angle sizes by means of the comparison of arm separations, the constant error would be maximum when one angle was vertical and the other horizontal, the horizontal angle appearing greater than the vertical angle. As the angular separation of the bisectors of the angles was increased, with the reference angle remaining horizontal, the constant error would decrease continuously until a minimum was reached when both angles were horizontal. As shown by Lennie's (1971) data and by those obtained in experiments 5, 6 and 12 of this study this pattern of fluctuation of bias does not appear in the observed constant errors of comparisons of angle sizes. The possibility that arm separation constitutes the basis for comparisons of angular extent is thus rejected, as is any other explanation which relies on a comparison of simple, linear separations of components of the two stimulus angles.

Neither the observed characteristics of the constant errors in the comparison of angular extents nor the accuracy with which these comparisons are performed, therefore, are adequately explained by the hypothesis that angular extents are perceived as differences between component orientations of the angles, and misperceived as a consequence of apparent contrast enhancement between those orientations. The consistency of this hypothesis with results obtained in previous studies can be accounted for by the observation that, while these studies have been concerned, ostensibly, with the perception of angular extent, the techniques used have actually measured perceived orientations. The observations made in these studies can be explained, therefore, by a hypothesis framed in terms of orientation analysers which was initially proposed to explain interactions between perceived orientations observed under different experimental paradigms. The proposal of the hypothesis that direct comparisons of angle sizes are made in terms of perceived angular extents, and not with explicit reference to the perceived characteristics of the orientations of the lines which define the angles, gives a satisfactory account of the contradiction between many of the observations made in previous studies and those described in the preceding chapters.

The aim to the last two experiments to be described, experiments 12 and 13, was the systematic investigation of the characteristics of perceived angular extent, considered as an integral perceptual quantity. These investigations postulated the existence of a perceptual metric for angular extent as an initial working assumption, and were designed to explore some of the properties of this metric. The information thus gained, it was intended, would give some indication of the way in which angular extent is encoded by the visual system.

Assuming perceived angular extent to be an integral quantity, by which is meant one which cannot be analytically reduced to some other perceptual dimensions - such as orientation in the present instance - the first question of interest concerns the relation between the stimulus angle size and the corresponding perceived angular extent. If such a relation between angle size and perceived angular extent can be determined, and is found to be a continuous function, then the objective scale of angle size and the corresponding subjective scale of angular extent are topologically equivalent.

As was expected, the relation obtaining between stimulus angle size and perceived angle size was found to be continuous and meridionally anisotropic, reflecting the established characteristics of perceived angular extent. It was also found that the same scaling factor (M) was applicable to all sizes of angle included in the experiments, at a given orientation, suggesting that magnitudes of perceived angular extent are combined by some process of linear summation. This observation was verified by comparison of the perceived angular extents of the larger angle stimuli with predictions derived by summing the perceived angular extents of smaller adjacent angles subsumed by the larger angle. The differences between the observed and expected magnitudes of perceived angualr extent were found to be non-significant.

The constancy of M at a particualr orientation (θ) was further corroborated by the results of experiment 13 which showed that about 0.96 of the variance of perceived angular extent can be accounted for by the linear regression of perceived angular extent onto stimulus angle size. The data from these two experiments show, therefore, that the perceived angular extent of a stimulus angle is determined by a scaling factor whose magnitude varies according to the orientation of the bisector of the angle. The meridional anisotropy of M, as depicted in figure 7.3, can be approximated by a function of the form $M = f(\cos 4\theta)$ although a further factor varying as a function of $\sin 2\theta$ should be included in order to account for the difference between the magnitudes of M at horizontal and vertical orientations.

The perceptual metric for angular extent can be considered, therefore, as a regular elastic deformation of the objective metric for angle size, such that the unit interval of the subjective metric is related to that of the objective metric by a transfer function of the form:

$$\Psi(A) = A.[(k.\cos 4\theta + a) + (l.\sin 2\theta + b)]$$

Equations of this form have already been proposed by Berliner and Berliner (1948) to describe the distortions induced by Orbison figures and by Lichtenstein (1963) to describe the visibility characteristic of fine lines, both as functions of stimulus orientation. Consequently, the perceived angular extent of any stimulus angle, compared to that of a reference angle of a specified orientation, can be considered as the linear sum of the unit intervals subsumed by the projection of the angle figure onto this metric. Such a process would account for the data pertaining to the constant errors of perceived angular extent obtained in experiments 12 and 13.

Given the properties of the metric for perceived angular extent, as determined by the scaling factor M and its meridional variation, a further postulate is required to account for the observed difference thresholds for the comparison of angular extents. The difference threshold, at a given orientation of the test angle relative to the reference angle, was found to increase linearly with stimulus angle size and, consequently, with perceived angular extent. It is proposed, then, that there are errors associated with the magnitude of each unit interval which summate linearly as the intervals are combined. This would be expected since, of course, these errors would be included in the magnitudes of the unit intervals which contribute to any perceived angular extent. This proposal extends the scope of the hypothesis so that it can now account for both the constant errors of comparisons of perceived angular extents and the accuracies with which the comparisons are made. In order that the observed absence of meridional variation of acuity be conserved, these errors cannot be associated with the actual magnitudes of the unit intervals.

According to the transfer function described above, the unit interval of perceived angular extent is greater at vertical and horizontal loci in the orientation domain than at oblique loci. Considered in this way, the postulated perceptual metric for angular extent does exhibit one characteristic of the orientation domain which has been explained in terms of the orientation-selective channel hypothesis. Using the method of absolute judgments, Rath, Alluisi and Learner (1961) found there to be greater response equivocation at oblique orientations than around the horizontal or vertical. This means that if the metric were to be divided into equal intervals according to the objective scale, more orientations would be found in the intervals in oblique regions than in those around the horizontal and vertical. It follows from this that the separations between orientations about the obliques tend to be smaller than those around the horizontal and vertical. This is implied, of course, by the lower acuities for orientation observed at oblique orientations revealed by difference threshold methods.

The perceptual metric for angular extent can be seen, therefore, to reflect that attribute of the perceptual orientation domain manifest in the meridional variation of acuity for orientation, rather than that attribute which is manifest in constant errors of perceived orientation. Consequently, the meridional characteristics of perceived angular extent could be derived from the variances of the response distributions of orientation analysers rather than from the central tendencies of these distributions. In this way the unparsimonious requirement for a separate mechanism for the perception of angular extent is obviated.

Andrews (1964) has proposed that the metric of the two-dimensional visual space is determined by the statistics of visual input in such a way that the average contour separation over a period of integration is seen as uniform. The characteristics of percieved orientation determined in later experiments by Andrews (1967a) are consistent with the application of this principle to an orientation metric - the response distributions of orientation analysers being such that, averaged over time, the distribution of activity of orientation analysers will be uniform across all analysers. The characteristic of the orientation anlysers by which this uniformity is achieved is manifest in the meridional variation of the empirical response distributions of the analysers which, in turn, is responsible for the meridional anisotropy of the orientation metric, as manifest in the observed magnitudes of difference thresholds for orientation. It is proposed, then, that the meridional variation of perceived angular extent is attributable to the same source as is the meridional variation of acuity for orientation.

Despite the apparent incompatibility between the orientation analyser model for the perception of orientation and orientation differences and the observed characteristics of perceived angular extent, it now appears that these observations can be accommodated by the hypothesis, provided that the distinction between perceived orientation and perceived angular extent is maintained. As has been shown, these two perceptual variables can be distinguished operationally by means of different experimental procedures, according to whether measurement is made of the variable and constant errors of perceived orientation, or of variable and constant errors of perceived angular extent.

According to the scheme so far developed, therefore, the perception of both orientation and angular extent is mediated by the same set of cortical neural mechanism, after all, but by different attributes of the response characteristics of these mechanisms. When, as defined by the experimental task, the emphasis is on contour orientation the data obtained reflect the central tendencies of the distribution of activity amongst orientation selective analysers. When the emphasis is on angular extent, the data obtained in the experiment reflect the second moment of the empirical response distributions - the variance.

The phenomenon of perceived orientation contrast, and its changes with time, have been accounted for by reference to the effect of lateral inhibitory interactions between orientation analysers on the location of the central tendency of the response distributions of the analysers in the orientation domain. The failure of the attempt to relate the temporal changes of perceived angular extent to the changes of perceived orientation, even when the observers were the same for the two sets of measurements made in experiments 9 and 10, is now comprehensible. In order to account for the effect of increased stimulus duration on constant errors of comparisons of angular extent, the influence of the operation of lateral inhibitory interactions on the variability of the responses of orientation analysers and, consequently, on the perceptual metric for orientation and angular extent, must be examined.

As lateral inhibition between orientation-selective analysers builds up, the variability of the possible response of each analyser to a stimulus is reduced by the suppression of extreme responses. The effect of lateral inhibition on perceived orientation results from the influence of the change of higher moments of the response distribution on the central tendency of the distribution. When two orientations are presented simultaneously the result of this process is the 'repulsion' of the peaks representative of the two perceived orientations, and the occurrence of the phenomenal orientation contrast enhancement.

The reduction of the variability of the response distributions, considered in terms of the perceptual metric for angular extent, will result in a reduction of the magnitude of the unit interval of the metric in the region of excitation. Consequently, the distance between the two orientations, specified with reference to the sum of the unit intervals of the metric, <u>not</u> by the difference between the two perceived orientations, will decrease and, thus, the magnitude of the perceived angular extent will decrease. The results of experiment 9 are in agreement with this hypothesis, therefore, so long as meridional anisotropy of the metric is conserved over increased stimulus duration, as was shown to be the case in experiment 12.

The conservation of meridional anisotropy and the invariance of the scaling factor (M) over increasing stimulus duration, with the consequent reduction of unit interval magnitude brought about by lateral inhibition, while maintaining the constancy of relative perceived angular extents, implies variation in the system which is, so far, unaccounted for. This variation occurs in the raw, un-normalised constant error data which were found to vary across both stimulus durations and observers, and which is summarised by the factor used to normalise the summed relative perceived angular extents contained within a quadrant or semi-circle of 90° or 180° in the treatment of the raw data obtained in experiments 12 and 13. This factor adds further complexity to the relation between the objective and subjective metrics for angular extent which is not covered by the transfer function relating unit intervals of the objective and subjective metrics. Further investigation would be required for the determination of the nature and identity of this additional factor.

The re-analysis of the perception of angular extent described in this section, based on the data obtained in experiments 12 and 13 led to the elaboration of a new hypothesis which accounts for the majority of the observations made in those experiments. Subsequent examination of the relation between the operation of orientation-selective analysers, as described by Andrews, and the observed characteristics of perceived angular extent as interpreted by this new hypothesis has shown that the distinction between the mechanisms for the perception of orientation and for the perception of angular extent is not so great as had been concluded on the basis of the inconsistency between the observations made in this study and those expected under the prior orientation-analyser hypothesis. Both the present observations and those which led to the development of the orientation analyser model can be explained in terms of this model if the variable errors of perceived orientation are considered as contibuting to the function of orientation-selective analysers in the visual process, as well as the constant errors.
Under this reformulation of the description of the operation of cortical, orientation-selective, mutually inhibiting channels the static and dynamic attributes of the perception of both orientation and angular extent are explained and the apparent contradictions discovered initially are resolved.

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Appendix I: Tables of Constant Errors (biases) and Variable Errors (standard deviations) obtained in experiments 3 - 13. Following each table of biases and standard deviations is a second table for the same experiment showing the standard errors of the biases and standard deviations of the response distributions.

The first value given in each cell of the tables is the bias, or the standard error of the bias; this is followed by the standard deviation, or the standard error of the standard deviation. In the majority of the tables, two sets of values are given for each cell, with a third set of values, the mean and the root mean square of the bias and the standard deviation respectively.

Experiment 3: Biases and Standard Deviations.

Orientation	Stimulus Location 1		2		3		4		5		6	
0	1.59	1.450	6.76	1.794	-3.60	1.397	3.43	1.103	7.03	1.088	2.68	2.667
22	2.37	1.999	2.84	1.561	-3.91	1.344	2.37	1.458	5.72	2.708	1.29	1.344
45	1.31	0.908	0.19	0.655	-2.07	0.816	0.09	0.970	2.02	0.766	1.99	0.550
67	6.19	1.022	4.84	1.156	3.63	1.192	2.63	1.660	3.27	1.340	4.26	0.945
90	5.35	1.369	6.44	1.184	11.95	1.905	2.94	1.288	3.36	1.484	6.16	1.654
112	2.69	1.869	3.49	1.451	9.87	1.720	2.34	1.501	4.61	1.146	4.27	1.469
135	0.03	1.060	1.17	0.758	0.40	0.793	-1.09	0.881	0.35	0.888	0.32	0.595
157	-5.32	0.787	-0.82	1.267	1.36	0.993	4.58	1.158	6.61	1.783	1.35	0.629
180	-4.99	2.038	1.60	1.042	0.28	1.705	4.45	1.180	5.29	1.231	1.68	1.464
202	-5.21	1.756	2.80	1.144	-0.19	1.411	4.79	1.534	2.20	2.176	4.16	1.839
225	-3.47	0.810	-0.11	0.712	0.41	0.872	1.69	0.794	-1.19	0.506	0.94	0.845
247	-3.33	1.325	3.02	1.571	5.91	1.194	3.19	1.621	-1.45	1.256	2.60	0.992
270	-0.90	1.386	3.65	1.343	5.69	1.302	5.69	1.223	-0.46	1.799	4.38	0.982
292	4.25	1.310	3.67	0.753	4.72	1.067	5.84	1.379	3.22	0.974	2.88	1.507
315	1.23	1.376	-0.59	0.800	-1.44	0.638	1.12	0.906	-0.55	0.873	2.01	0.856
337	1.65	1.459	5.64	1.348	0.33	1.053	4.33	1.154	3.92	1.180	5.64	2.096

Experiment 3: Standard errors of Biases and Standard Deviations.

Orientation	Stimulus Location 1		2		3		4		5		6	
0	0.215	0.230	0.258	0.302	0.197	0.213	0.165	0.168	0.167	0.160	0.354	0.536
22	0.274	0.341	0.240	0.286	0.197	0.209	0.210	0.219	0.369	0.495	0.197	0.227
45	0.144	0.135	0.126	0.099	0.132	0.126	0.152	0.154	0.131	0.121	0.111	0.094
67	0.153	0.161	0.173	0.168	0.178	0.180	0.369	0.374	0.189	0.225	0.165	0.144
90	0.198	0.217	0.184	0.176	0.199	0.175	0.193	0.203	0.215	0.263	0.235	0.263
112	0.217	0.304	0.212	0.235	0.183	0.185	0.218	0.242	0.169	0.178	0.210	0.240
135	0.161	0.174	0.127	0.114	0.132	0.119	0.139	0.150	0.145	0.138	0.115	0.109
157	0.135	0.123	0.178	0.203	0.143	0.146	0.214	0.256	0.246	0.290	0.118	0.112
180	0.271	0.378	0.158	0.163	0.237	0.269	0.168	0.182	0.187	0.205	0.206	0.246
202	0.250	0.278	0.187	0.195	0.199	0.234	0.213	0.261	0.308	0.353	0.263	0.290
225	0.127	0.136	0.122	0.104	0.136	0.131	0.137	0.128	0.102	0.086	0.135	0.123
247	0.236	0.299	0.212	0.265	0.180	0.194	0.214	0.295	0.185	0.205	0.159	0.162
270	0.203	0.218	0.198	0.213	0.181	0.206	0.181	0.184	0.249	0.294	0.147	0.148
292	0.190	0.198	0.130	0.115	0.162	0.163	0.184	0.224	0.152	0.145	0.220	0.244
315	0.203	0.209	0.128	0.136	0.113	0.107	0.142	0.133	0.142	0.138	0.136	0.126
337	0.201	0.238	0.197	0.219	0.159	0.151	0.176	0.181	0.178	0.192	0.299	0.398

Experiment 4

Orientation	PSE	SD	s(PSE)	s(SD)
0	-1.40	2.115	0.290	0.362
22	-1.48	1.705	0.254	0.266
45	-0.17	1.178	0.202	0.225
67	-0.66	1.841	0.266	0.278
90	0.62	3.226	0.442	0.706
112	-0.67	2.832	0.371	0.523
135	-0.32	1.233	0.180	0.196
157	1.41	1.703	0.236	0.279
180	-0.43	2.170	0.304	0.407
202	0.41	2.124	0.287	0.354
225	-0.80	1.530	0.220	0.248
247	0.47	1.412	0.202	0.227
270	-0.87	1.935	0.254	0.350
292	0.19	1.451	0.215	0.228
315	0.09	0.903	0.141	0.141
337	-0.70	1.398	0.195	0.225

Experiment 6: Standard Errors of bias and standard deviation

Angle Size	Test Angle Orientation 135°		157°		180°		202°		225°	
30°	0.138	0.148	0.118	0.115	0.183	0.187	0.154	0.148	0.124	0.126
	0.119	0.112	0.125	0.125	0.159	0.151	0.135	0.130	0.116	0.098
	0.129	0.131	0.122	0.120	0.171	0.170	0.145	0.139	0.120	0.113

Angle Size	Test Angle Orientation 247°		270°		292°		315°	
30°	0.145	0.152	0.171	0.164	0.153	0.162	0.123	0.110
	0.124	0.118	0.189	0.177	0.158	0.151	0.132	0.126
	0.135	0.136	0.180	0.171	0.156	0.157	0.128	0.118

Line length = 3.0 deg. arc (178.6 min. arc)

Stimulus duration = 2.00 seconds.

Experiment 6: Biases and Standard Deviations

Angle Size	Test Angle Orientation 135°		157°		180°		202°		225°	
30°	-1.09	0.893	-0.82	0.710	1.10	1.257	0.62	1.008	-1.20	0.784
	-1.14	0.706	-1.23	0.767	0.92	1.045	0.22	0.807	-0.97	0.606
	-1.11	0.805	-1.02	0.739	1.01	1.156	0.42	0.913	-1.11	0.701

Angle Size	Test Angle Orientation 247°		270°		292°		315°	
30°	0.43	0.900	1.15	1.106	0.84	1.043	1.96	0.681
	0.39	0.713	1.06	1.273	0.24	0.988	1.56	0.770
	0.41	0.812	1.11	1.192	0.58	1.016	1.81	0.727

Line length = 3.0 deg. arc (178.6 min. arc)

Stimulus duration = 2.00 seconds.

Experiment 5: Standard Errors of bias and standard deviation

Angle Size	202°		225°		247°		270°	
15°	0.119	0.110	0.127	0.127	0.109	0.113	0.106	0.110
	0.117	0.105	0.107	0.098	0.133	0.110	0.108	0.100
	0.118	0.108	0.117	0.113	0.122	0.112	0.107	0.105
30°	0.121	0.105	0.129	0.121	0.142	0.143	0.168	0.167
	0.109	0.118	0.142	0.147	0.123	0.108	0.164	0.167
	0.115	0.112	0.136	0.135	0.133	0.127	0.166	0.168
45°	0.261	0.238	0.174	0.186	0.242	0.276	0.242	0.273
	0.182	0.170	0.248	0.250	0.264	0.244	0.226	0.257
	0.226	0.207	0.214	0.220	0.253	0.260	0.234	0.265
60°			0.222	0.242			0.304	0.328
			0.272	0.244			0.314	0.368
			0.248	0.244			0.309	0.349

Test Angle Orientation

Line length = 3.0 deg. arc (178.6 min. arc)

Stimulus duration = 2.00 seconds.

Experiment 5: Standard Errors of bias and standard deviation

Angle Size	90°		112°		135°		157°		180°	
15°	0.107	0.096	0.132	0.121	0.124	0.113	0.117	0.108	0.119	0.113
	0.105	0.114	0.113	0.113	0.100	0.102	0.103	0.095	0.113	0.101
	0.106	0.105	0.123	0.117	0.113	0.108	0.110	0.102	0.116	0.107
30°	0.157	0.148	0.127	0.113	0.128	0.129	0.105	0.100	0.162	0.163
	0.142	0.131	0.130	0.121	0.133	0.137	0.092	0.092	0.146	0.149
	0.150	0.140	0.128	0.117	0.131	0.133	0.099	0.096	0.154	0.156
45°	0.222	0.232	0.244	0.242	0.179	0.207	0.236	0.190	0.199	0.216
	0.247	0.283	0.254	0.242	0.236	0.198	0.260	0.244	0.157	0.161
	0.235	0.259	0.249	0.242	0.209	0.203	0.248	0.219	0.179	0.190
60°	0.260	0.272			0.250	0.298			0.250	0.256
	0.302	0.300			0.276	0.288			0.254	0.236
	0.282	0.286			0.266	0.293			0.252	0.246

Test Angle Orientation spans the 90°–180° columns.

Line length = 3.0 deg. arc (178.6 min. arc)

Stimulus duration = 2.00 seconds.

Experiment 5: Biases and Standard Deviations

Angle Size	202°		225°		247°		270°	
15°	-1.83	0.674	-1.51	0.811	-1.93	0.641	-1.10	0.615
	-1.79	0.615	-1.35	0.547	-1.65	0.695	-1.45	0.577
	-1.81	0.645	-1.43	0.692	-1.79	0.669	-1.27	0.596
30°	-1.82	0.679	-3.38	0.779	-2.46	0.939	-0.95	1.123
	-3.04	0.647	-4.73	0.950	-2.94	0.700	-1.85	1.141
	-2.43	0.663	-4.05	0.869	-2.75	0.828	-1.40	1.132
45°	-3.28	1.468	-4.13	1.203	-3.56	1.786	-1.14	1.730
	-3.54	0.850	-4.00	1.494	-4.24	1.672	-1.39	1.589
	-3.41	1.199	-4.65	1.356	-3.90	1.721	-1.26	1.661
60°			-2.48	1.306			-1.18	2.108
			-2.16	1.680			-3.58	2.144
			-2.32	1.505			-2.38	2.126

Line length = 3.0 deg. arc (178.6 min. arc)

Stimulus duration = 2.00 seconds.

Experiment 5: Biases and Standard Deviations

Angle Size	Test Angle Orientation									
	90°		112°		135°		157°		180°	
15°	-1.19	0.570	-0.67	0.790	-1.14	0.755	-1.40	0.693	-1.29	0.638
	-1.02	0.590	-1.02	0.641	-0.77	0.537	-1.59	0.478	-1.26	0.629
	-1.10	0.580	-0.84	0.719	-0.97	0.655	-1.49	0.595	-1.27	0.634
30°	-1.48	0.980	-1.71	0.741	-4.61	0.782	-3.90	0.561	-1.12	1.036
	-1.21	0.877	-3.26	0.763	-4.96	0.844	-3.22	0.498	-0.77	0.927
	-1.34	0.930	-2.48	0.752	-4.78	0.814	-3.56	0.530	-0.98	0.983
45°	-2.29	1.486	-4.20	1.448	-5.58	1.279	-4.52	1.168	-1.26	1.377
	-1.48	1.779	-4.94	1.586	-6.72	1.240	-4.74	1.514	-0.58	1.046
	-1.88	1.639	-4.57	1.519	-6.15	1.260	-4.63	1.352	-0.92	1.223
60°	-6.28	1.622			-6.86	1.884			-1.00	1.538
	-5.42	1.976			-7.82	1.762			-1.52	1.518
	-5.85	1.808			-7.34	1.824			-1.26	1.528

Line length = 3.0 deg. arc (178.6 min. arc)

Stimulus duration = 2.00 seconds.

Experiment 5: Standard Errors of bias and standard deviation

Angle Size	90°		135°		180°		225°		270°	
15°	0.110	0.102	0.118	0.118	0.124	0.129	0.140	0.151	0.101	0.092
	0.117	0.114	0.122	0.104	0.106	0.102	0.114	0.103	0.128	0.131
	0.114	0.108	0.120	0.111	0.115	0.116	0.128	0.129	0.115	0.113
30°	0.222	0.194	0.218	0.202	0.208	0.186	0.236	0.198	0.210	0.204
	0.194	0.166	0.198	0.188	0.222	0.182	0.240	0.188	0.222	0.186
	0.208	0.181	0.208	0.195	0.215	0.184	0.238	0.193	0.216	0.195
45°	0.272	0.266	0.258	0.270	0.224	0.222	0.230	0.232	0.270	0.276
	0.218	0.184	0.214	0.184	0.204	0.198	0.244	0.218	0.328	0.308
	0.246	0.229	0.237	0.231	0.214	0.210	0.237	0.225	0.300	0.292

(Columns grouped under "Test Angle Orientation".)

Line length = 1.0 deg. arc (59.5 min. arc)

Stimulus duration = 2.00 seconds.

Experiment 5: Biases and Standard Deviations

Angle Size	Test Angle Orientation 90°		135°		180°		225°		270°	
15°	-0.39	0.637	-1.27	0.708	-1.78	0.688	-2.27	0.934	-1.90	0.470
	-0.81	0.670	-1.41	0.599	-2.13	0.600	-2.36	0.658	-2.15	0.805
	-0.60	0.657	-1.32	0.656	-1.95	0.646	-2.31	0.808	-2.02	0.659
30°	-0.56	1.190	-3.02	1.136	-2.00	1.092	-4.70	1.192	-2.60	1.202
	-1.10	0.860	-3.38	0.990	-2.24	1.162	-4.40	1.188	-2.54	1.156
	-0.83	1.038	-3.20	1.066	-2.12	1.128	-4.55	1.190	-2.57	1.179
45°	-2.11	1.796	-6.88	1.618	-3.02	1.288	-7.82	1.380	-2.20	1.712
	-2.16	1.092	-6.40	1.122	-0.56	1.068	-6.14	1.412	-2.44	2.180
	-2.13	1.486	-6.64	1.392	-1.79	1.183	-6.98	1.396	-2.32	1.960

Line length = 1.0 deg. arc (59.5 min. arc)

Stimulus duration = 2.00 seconds.

Experiment 5: Standard Errors of bias and standard deviation

Angle Size	Test Angle Orientation 90°		135°		180°		225°		270°	
15°	0.165	0.152	0.119	0.119	0.119	0.117	0.126	0.136	0.122	0.126
	0.160	0.152	0.114	0.107	0.109	0.086	0.123	0.111	0.119	0.107
	0.163	0.152	0.117	0.113	0.114	0.103	0.125	0.124	0.121	0.117
30°	0.206	0.226	0.182	0.174	0.154	0.164	0.189	0.216	0.173	0.183
	0.159	0.166	0.159	0.178	0.186	0.202	0.175	0.191	0.192	0.219
	0.184	0.198	0.171	0.176	0.171	0.184	0.182	0.204	0.183	0.202
45°	0.232	0.198	0.206	0.206	0.272	0.234	0.254	0.240	0.262	0.260
	0.252	0.246	0.214	0.196	0.258	0.224	0.242	0.240	0.228	0.220
	0.242	0.233	0.210	0.201	0.265	0.229	0.248	0.240	0.246	0.241

Line length = 0.6 deg.arc (41.25 min.arc)

Stimulus duration = 2.00 seconds

Experiment 5: Biases and Standard Deviations

	Test Angle Orientation									
Angle Size	90°		135°		180°		225°		270°	
15°	-0.67	1.019	-1.45	0.694	-2.06	0.722	-2.71	0.741	-1.64	0.739
	-0.19	1.048	-1.30	0.648	-1.84	0.442	-2.26	0.738	-2.01	0.665
	-0.43	1.034	-1.38	0.671	-1.95	0.599	-2.49	0.740	-1.83	0.703
30°	-0.68	1.482	-3.23	1.161	-2.21	1.028	-3.76	1.378	-1.86	1.171
	-0.87	1.049	-4.05	1.104	-2.51	1.287	-4.38	1.185	-2.01	1.353
	-0.77	1.284	-3.64	1.132	-2.36	1.165	-4.07	1.285	-1.93	1.265
45°	-0.50	1.284	-5.74	1.136	-2.58	1.534	-5.02	1.394	-0.32	1.318
	-0.76	1.478	-5.04	1.114	-1.70	1.478	-5.32	1.384	-2.36	1.574
	-0.63	1.384	-5.39	1.125	-2.14	1.506	-5.17	1.389	-1.34	1.452

Line length = 0.6 deg.arc (41.25 min.arc)

Stimulus duration = 2.00 seconds

Experiment 5: Standard Errors of bias and standard deviation

	Test Angle Orientation									
Angle Size	90°		135°		180°		225°		270°	
15°	0.121	0.099	0.107	0.111	0.119	0.116	0.113	0.100	0.140	0.123
	0.139	0.121	0.134	0.131	0.126	0.124	0.098	0.085	0.145	0.145
	0.130	0.111	0.121	0.121	0.123	0.120	0.106	0.093	0.143	0.134
30°	0.241	0.268	0.155	0.174	0.159	0.155	0.148	0.139	0.162	0.190
	0.229	0.247	0.166	0.157	0.147	0.158	0.163	0.171	0.162	0.176
	0.235	0.258	0.161	0.166	0.153	0.157	0.156	0.156	0.162	0.183
45°	0.244	0.256	0.208	0.198	0.202	0.206	0.238	0.248	0.316	0.304
	0.270	0.256	0.272	0.264	0.284	0.284	0.246	0.224	0.384	0.412
	0.257	0.256	0.242	0.233	0.246	0.249	0.242	0.236	0.352	0.362
60°	0.326	0.344	0.262	0.240	0.284	0.256	0.248	0.316	0.394	0.390
	0.286	0.262	0.226	0.212	0.250	0.262	0.290	0.286	0.308	0.278
	0.307	0.306	0.245	0.226	0.268	0.259	0.270	0.253	0.354	0.339

Line length = 0.3 deg. arc (18.3 min. arc)

Stimulus duration = 2.00 seconds

Experiment 5:: Biases and Standard Deviations

Angle Size	Test Angle Orientation 90°		135°		180°		225°		270°	
15°	-0.13	0.642	-0.17	0.585	-0.58	0.702	-1.37	0.598	-0.26	0.833
	0.02	0.830	-0.50	0.766	-0.79	0.741	-1.12	0.446	-0.87	0.867
	-0.06	0.742	-0.34	0.682	-0.69	0.722	-1.25	0.528	-0.57	0.850
30°	-0.32	1.639	-3.36	1.058	-3.00	1.013	-3.48	0.887	-1.78	1.119
	-1.33	1.611	-3.38	1.070	-3.03	0.966	-3.68	1.083	-1.82	1.111
	-0.83	1.625	-3.37	1.064	-3.02	0.990	-3.58	0.985	-1.80	1.115
45°	-0.56	1.552	-4.04	1.120	-1.36	1.040	-4.74	1.428	-0.32	2.132
	-0.12	1.704	-4.56	1.700	-0.78	1.820	-4.14	1.480	-0.68	2.706
	-0.34	1.628	-4.30	1.440	-1.07	1.482	-4.44	1.454	-0.50	2.436
60°	0.00	2.308	-6.04	1.632	0.22	1.760	-2.18	1.384	0.00	2.692
	0.41	1.714	-4.54	1.278	1.81	1.602	-1.42	1.886	0.84	1.992
	0.20	2.033	-5.29	1.466	1.02	1.683	-1.80	1.654	0.42	2.368

Line lenth = 0.3 deg. arc (18.3 min.arc)

Stimulus duration = 2.00 seconds

Experiment 7: Biases and Standard Deviations

Stimulus Orientation	Stimulus Angle Size 15°		30°		45°		60°		90°	
0°	-0.69	0.928	0.53	1.110	-2.08	1.236	-1.33	1.795	-2.04	2.399
	-0.45	0.823	-0.28	1.227	-0.52	1.318	-0.44	1.830	-1.00	2.516
			-0.28	1.172	-1.02	1.866	-0.99	2.846	-1.22	3.536
			-0.08	1.706	-1.03	2.044	-1.91	3.260	-3.17	2.938
	-0.57	0.877	0.00	1.325	-1.16	1.653	-1.16	2.515	-1.86	1.882
45°	0.73	0.653	0.03	1.266	0.57	1.257	0.64	1.794	0.08	1.523
	0.65	0.593	0.96	0.965	.0.20	1.054	-0.33	1.538	0.46	1.123
			0.13	1.346	-0.22	1.692	0.88	3.234	0.41	1.435
			0.54	1.599	-0.59	1.681	-0.03	1.763	0.64	1.594
	0.90	0.595	0.79	1.014	1.10	1.848	1.34	2.011	0.77	1.756
	1.15	0.589	0.68	1.114	1.32	1.943	-0.04	2.049	2.42	1.683
	0.86	0.608	0.60	1.189	0.58	1.672	0.59	2.109	1.06	1.575
90°	1.32	0.746	0.78	0.971	1.59	1.924	1.46	2.556	2.45	2.234
	0.90	0.781	0.65	1.036	0.36	1.910	2.51	2.129	2.64	2.718
	1.11	0.764	0.72	1.004	0.97	1.917	1.98	2.352	2.59	2.488

Experiment 7: Standard Errors of bias and standard deviation

Stimulus Orientation	Stimulus Angle Size: 15°		30°		45°		60°		90°	
15°	0.147	0.156	0.158	0.172	0.185	0.198	0.248	0.278	0.321	0.404
	0.141	0.130	0.201	0.196	0.186	0.217	0.259	0.284	0.355	0.399
			0.176	0.183	0.295	0.329	0.388	0.385	0.547	
			0.230	0.275	0.252	0.311	0.412	0.631	0.385	0.547
	0.144	0.144	0.193	0.210	0.234	0.270	0.335	0.449	0.388	0.487
45°	0.115	0.109	0.178	0.197	0.176	0.200	0.239	0.301	0.207	0.240
	0.116	0.101	0.151	0.137	0.157	0.180	0.209	0.258	0.175	0.183
			0.202	0.201	0.248	0.271	0.476	0.600	0.200	0.224
			0.219	0.255	0.232	0.257	0.247	0.284	0.232	0.239
	0.116	0.096	0.161	0.141	0.249	0.293	0.308	0.301	0.243	0.295
	0.113	0.095			0.258	0.331	0.279	0.338	0.236	0.260
	0.116	0.105	0.189	0.202	0.206	0.230	0.311	0.386	0.204	0.223
90°	0.134	0.116	0.147	0.146			0.352	0.411	0.310	0.350
	0.130	0.119	0.170	0.154	0.267	0.301	0.301	0.339	0.373	0.456
	0.132	0.118	0.159	0.150			0.327	0.377	0.343	0.406

Experiment 8: Standard Errors of bias and standard deviation

	Subject					
Configuration	SRH		DTM		KB	
All	0.121	0.100	0.107	0.092	0.123	0.105
	0.117	0.098	0.097	0.083	0.114	0.094
	0.119	0.099	0.102	0.088	0.119	0.100

Stimulus orientation = 90°

At this stimulus orientation all configurations are equivalent

Experiment 8: Standard Errors of bias and standard deviation

Configuration	Stimulus Orientation 0°		22°		45°		67°	
1	0.144	0.151	0.115	0.112	0.104	0.091	0.113	0.101
	0.112	0.110	0.122	0.128	0.111	0.106	0.115	0.102
	0.129	0.132	0.119	0.120	0.108	0.099	0.114	0.102
2	0.113	0.112	0.111	0.093	0.102	0.088	0.122	0.111
	0.126	0.118	0.130	0.143	0.121	0.104	0.101	0.086
	0.120	0.115	0.121	0.121	0.112	0.096	0.112	0.099
3	0.125	0.123	0.127	0.121	0.100	0.085	0.108	0.108
	0.148	0.137	0.098	0.101	0.135	0.113	0.123	0.116
	0.137	0.130	0.113	0.111	0.119	0.100	0.111	0.112

Subject KB

Experiment 8: Standard Errors of bias and standard deviation

Configuration	Stimulus Orientation							
	0°		22°		45°		67°	
1	0.116	0.087	0.108	0.089	0.111	0.089	0.099	0.094
	0.144	0.147	0.061	0.027	0.106	0.083	0.100	0.080
	0.131	0.121	0.088	0.066	0.109	0.086	0.100	0.087
2	0.126	0.116	0.086	0.064	0.099	0.088	0.124	0.109
	0.133	0.112	0.098	0.082	0.094	0.066	0.110	0.094
	0.130	0.114	0.092	0.074	0.097	0.078	0.117	0.102
3	0.108	0.109	0.106	0.089	0.103	0.086	0.106	0.106
	0.121	0.116	0.093	0.097	0.108	0.088	0.102	0.091
	0.115	0.113	0.100	0.093	0.106	0.087	0.104	0.099

Subject DTM

Experiment 8: Standard Errors of bias and standard deviation

Configuration	Stimulus Orientation 0°		22°		45°		67°	
1	0.147	0.156	0.107	0.096	0.115	0.109	0.102	0.086
	0.141	0.130	0.116	0.100	0.116	0.101	0.102	0.094
	0.144	0.144	0.112	0.098	0.116	0.105	0.102	0.090
2	0.126	0.115	0.120	0.113	0.089	0.072	0.102	0.091
	0.148	0.147	0.117	0.112	0.091	0.062	0.103	0.089
	0.137	0.132	0.119	0.113	0.090	0.067	0.103	0.090
3	0.139	0.146	0.114	0.091	0.088	0.061	0.103	0.089
	0.127	0.141	0.125	0.106	0.103	0.083	0.100	0.088
	0.133	0.144	0.120	0.099	0.096	0.073	0.102	0.089

Subject SRH

Experiment 8: Biases and Standard Deviations

Configuration	Subject: SRH		Subject: DTM		Subject: KB	
All	-0.07	0.634	-1.17	0.529	1.28	0.641
	0.93	0.629	1.49	0.443	0.75	0.494
	0.43	0.632	0.16	0.488	1.02	0.572

Stimulus Orientation = 90°

At this orientation all configurations are equivalent

Experiment 8: Biases and Standard Deviations

Configuration	Stimulus Orientation 0°		22°		45°		67°	
1	0.10	0.888	0.34	0.598	0.92	0.533	1.65	0.616
	0.15	0.595	-0.40	0.715	0.80	0.599	1.22	0.590
	0.13	0.756	-0.03	0.659	0.86	0.567	1.44	0.603
2	-0.71	0.599	0.06	0.540	1.83	0.440	1.60	0.651
	-0.43	0.658	-0.84	0.777	0.80	0.633	2.36	0.445
	-0.57	0.629	-0.39	0.669	1.32	0.545	1.98	0.558
3	0.91	0.713	1.20	0.785	0.96	0.465	1.44	0.600
	0.30	0.877	1.17	0.497	0.82	0.729	-0.89	0.726
	0.61	0.799	1.18	0.657	0.89	0.611	0.26	0.666

Subject KB

Experiment 8: Biases and Standard Deviations

Configuration	Stimulus Orientation 0°		22°		45°		67°	
1	-1.86	0.524	-0.89	0.524	-0.12	0.458	2.29	0.494
	-1.08	0.870	-0.31	0.375	0.08	0.448	0.36	0.418
	-1.47	0.718	-0.60	0.456	-0.02	0.453	1.33	0.458
2	0.11	0.738	-1.36	0.347	0.93	0.463	-1.54	0.671
	1.65	0.720	0.36	0.437	0.55	0.357	-0.20	0.563
	0.88	0.729	-0.50	0.395	0.74	0.413	-0.87	0.619
3	0.33	0.587	-0.16	0.516	1.03	0.464	0.06	0.562
	-0.58	0.699	1.78	0.456	1.13	0.517	0.94	0.471
	-0.13	0.643	0.97	0.487	1.08	0.491	0.50	0.519

Subject DTM

Experiment 8: Biases and Standard Deviations

Configuration	Stimulus Orientation 0°		22°		45°		67°	
1	-0.69	0.928	-0.18	0.578	0.73	0.653	1.96	0.463
	-0.45	0.823	-0.29	0.590	0.65	0.593	1.47	0.519
	-0.57	0.877	-0.24	0.584	0.69	0.584	1.72	0.492
2	0.02	0.778	-0.50	0.692	0.38	0.367	1.31	0.500
	-0.51	0.907	0.18	0.670	0.54	0.350	0.86	0.453
	-0.25	0.845	-0.16	0.681	0.46	0.359	1.09	0.477
3	-0.86	0.907	1.05	0.543	0.63	0.333	0.86	0.453
	-1.28	0.791	0.64	0.704	0.77	0.471	0.97	0.467
	-1.07	0.851	0.85	0.629	0.70	0.408	0.92	0.460

Subject SRH

Experiment 9: Biases and Standard Deviations

Stimulus Duration	Relative Orientation 90°		112°		135°	
0.01	-3.20	223344	-3.86	1.784	-7.64	2.880
	-4.04	2.496	-4.08	1.652	-7.62	2.640
	-3.62	2.421	-3.97	1.719	-7.63	2.763
0.10	-3.26	2.046	-4.50	1.624	-7.96	1.596
	-3.26	1.628	-5.36	0.968	-7.80	1.352
	-3.26	1.849	-4.93	1.337	-7.88	1.479
0.20					-6.50	1.650
					-5.98	2.146
					-6.24	1.914
0.30					-5.40	1.452
					-5.58	1.764
					-5.49	1.616
0.50	-1.96	1.222	-2.25	1.012	-4.18	1.072
	-1.92	0.926	-2.42	1.378	-4.36	0.860
	-1.94	1.084	-2.34	1.209	-4.27	0.972
1.00					-4.78	1.067
					-3.80	1.088
					-4.29	1.078
2.00	-1.48	0.980	-1.71	0.741	-4.61	0.782
	-1.21	0.877	-3.26	0.763	-4.96	0.844
	-1.34	0.930	-2.48	0.752	-4.96	0.844

Subject: SRH

Angle size: 30°

Line length: 3.0 deg. arc

Experiment 9: Standard Errors of bias and standard deviation

Stimulus Duration	Relative Orientation 90°		112°		135°	
0.01	0.334	0.364	0.280	0.264	0.394	0.460
	0.362	0.386	0.260	0.266	0.395	0.388
	0.348	0.375	0.270	0.265	0.395	0.426
0.10	0.324	0.328	0.264	0.242	0.250	0.266
	0.268	0.262	0.198	0.184	0.234	0.214
	0.297	0.297	0.233	0.215	0.242	0.241
0.20					0.258	0.272
					0.324	0.298
					0.293	0.285
0.30					0.256	0.250
					0.274	0.284
					0.265	0.268
0.50	0.132	0.200	0.224	0.172	0.224	0.188
	0.204	0.172	0.252	0.206	0.196	0.170
	0.172	0.187	0.238	0.190	0.210	0.179
1.00					0.161	0.178
					0.163	0.169
					0.162	0.174
2.00	0.157	0.150	0.127	0.113	0.128	0.129
	0.142	0.131	0.129	0.121	0.133	0.137
	0.150	0.140	0.128	0.117	0.131	0.133

Subject: SRH

Angle size: 30°

Line length: 3.0 deg. arc

Experiment 9: Biases and Standard Deviations

Stimulus Duration	Relative Orientation					
	90°		112°		135°	
0.01	0.48	1.507	-3.78	1.687	-5.89	1.330
	0.69	1.366	-1.99	1.539	-5.05	1.351
	0.59	1.438	-2.29	1.615	-5.47	1.341
0.10	1.41	1.098	-1.79	0.864	-6.50	0.853
	1.14	0.821	-0.74	1.059	-4.41	0.993
	1.28	0.969	[illegible]	[illegible]	-5.45	0.925
0.50	1.74	0.824	-1.35	0.703	-3.48	0.931
	2.72	0.607	0.79	0.604	-3.80	0.851
	2.23	0.724	-0.28	0.655	-3.64	0.897
2.00	0.63	0.750	-1.28	0.692	-5.11	0.961
	1.82	0.616	0.71	0.513	-4.65	1.015
	1.23	0.686	-0.28	0.609	-4.88	0.988

Subject: DTM

Angle size: 30°

Line length: 0.3 deg. arc

Experiment 9: Standard Errors of bias and standard deviation

Stimulus Duration	Relative Orientation 90°		112°		135°	
0.01	0.230	0.234	0.233	0.273	0.188	0.207
	0.201	0.209	0.232	0.236	0.192	0.214
	0.216	0.222	0.233	0.255	0.190	0.211
0.10	0.161	0.162	0.133	0.143	0.142	0.138
	0.132	0.123	0.157	0.170	0.154	0.177
	0.147	0.144	0.145	0.157	0.148	0.159
0.5	0.136	0.130	0.115	0.117	0.145	0.157
	0.110	0.100	0.121	0.095	0.134	0.141
	0.124	0.116	0.118	0.107	0.140	0.149
2.00	0.125	0.115	0.115	0.122	0.151	0.155
	0.113	0.095	0.111	0.092	0.152	0.164
	0.119	0.105	0.113	0.108	0.152	0.160

Subject: DTM

Angle size: 30°

Line length: 0.3 deg. arc

Experiment 9: Biases and Standard Deviations (with standard errors)

Stimulus Duration	PSE	SD	s(PSE)	s(SD)
0.01	-4.95	2.349	0.309	0.415
	-6.12	1.952	0.300	0.330
	-5.54	2.157	0.305	0.375
0.10	-4.74	2.080	0.324	0.312
	-4.01	1.329	0.183	0.199
	-4.38	1.745	0.263	0.262
0.50	-2.27	0.827	0.132	0.123
	-2.25	1.098	0.169	0.158
	-2.26	0.972	0.152	0.142
2.00	-3.00	1.003	0.151	0.157
	-3.52	0.980	0.166	0.157
	-3.26	0.991	0.159	0.157

Subject: SRH

Angle size: 30°

Line length: 0.3 deg.arc

Relative orientation: 135°

Experiments 10 & 11: Biases and Standard Deviations

Stimulus Duration	Without adaptation: Orientation 120°		Without adaptation: Orientation 150°		With adaptation: Orientation 120°		With adaptation: Orientation 150°	
0.01	-2.34	1.427	-2.18	1.883	-0.97	1.195	-0.43	1.904
	-2.84	1.366	-2.43	1.625	-0.89	0.956	0.48	1.995
	-2.63	1.397	-2.35	1.732	-0.93	1.082	0.02	1.950
0.50	-2.61	1.203	-2.05	1.087				
	-2.28	0.849	-2.22	1.238				
	-2.44	1.041	-2.13	1.165				
2.00	-1.32	0.534	-0.57	1.058				
	-2.08	0.851	-1.41	0.840				
	-1.70	0.710	-0.99	0.955				

Subject: SRH

Experiments 10 & 11: Standard Errors of bias and standard deviation

Stimulus Duration	Without adaptation, Orientation 120°		Without adaptation, Orientation 150°		With adaptation, Orientation 120°		With adaptation, Orientation 150°	
0.01	0.243	0.236	0.242	0.312	0.169	0.180	0.261	0.306
	0.207	0.224	0.238	0.257	0.153	0.135	0.277	0.305
	0.226	0.230	0.240	0.286	0.161	0.159	0.269	0.306
0.50	0.172	0.200	0.159	0.169				
	0.132	0.124	0.170	0.195				
	0.153	0.166	0.165	0.182				
2.00	0.110	0.091	0.156	0.170				
	0.139	0.139	0.135	0.136				
	0.125	0.117	0.146	0.154				

Subject: SRH

Experiments 10 & 11: Biases and Standard Deviations

Stimulus Duration	Without adaptation: Orientation 120°		Without adaptation: Orientation 150°		With adaptation: Orientation 120°		With adaptation: Orientation 150°	
0.01	-2.43	1.619	-3.52	1.916	-1.71	0.851	-2.11	1.022
	-3.58	1.362	-3.70	1.519	-2.11	1.344	-3.32	1.332
	-3.00	1.496	-3.61	1.729	-1.91	1.125	-2.71	1.187
0.50	-1.13	0.682	-0.98	0.632				
	-0.57	0.564	-1.30	0.708				
	-0.85	01626	-1.14	0.671				
2.00	-0.18	0.603	-0.03	0.789				
	-1.22	0.391	-1.82	0.609				
	-0.70	0.508	-0.92	0.705				

Subject DTM

Experiments 10 & 11: Biases and Standard Deviations

Stimulus Duration	Without adaptation: Orientation 15°		Without adaptation: Orientation 345°		With adaptation: Orientation 15°		With adaptation: Orientation 345°	
0.01	3.74	1.242	1.94	1.226	2.63	1.468	0.69	1.590
	3.62	1.446	1.41	1.941	2.05	1.604	-0.12	1.306
	3.69	1.348	1.67	1.623	2.34	1.538	0.28	1.455
0.50	3.86	0.858	-0.90	0.783				
	3.68	0.722	0.89	1.138				
	3.77	0.793	0.00	0.977				
2.00	3.94	0.632	-0.23	0.643				
	3.45	0.764	-1.01	0.780				
	3.69	0.701	-0.62	0.715				

Subject: SRH

Experiments 10 & 11: Standard Errors of bias and standard deviation

Stimulus Duration	Without adaptation				With adaptation			
	Orientation				Orientation			
	15°		345°		15°		345°	
0.01	0.183	0.187	0.182	0.199	0.224	0.249	0.215	0.254
	0.219	0.221	0.259	0.316	0.228	0.240	0.191	0.188
	0.202	0.205	0.224	0.264	0.226	0.230	0.203	0.223
0.50	0.134	0.126	0.126	0.130				
	0.129	0.111	0.186	0.182				
	0.132	0.119	0.159	0.158				
2.00	0.115	0.099	0.120	0.110				
	0.132	0.113	0.126	0.127				
	0.124	0.106	0.123	0.119				

Subject: SRH

Experiments 10 & 11: Biases and Standard Deviations

Stimulus Duration	Without adaptation, Orientation 15°		Without adaptation, Orientation 345°		With adaptation, Orientation 15°		With adaptation, Orientation 345°	
0.01	1.51	0.999	2.66	1.020	1.26	0.889	2.29	0.647
	1.33	0.827	1.48	1.221	1.35	0.780	3.10	0.636
	1.42	0.917	2.07	1.125	1.30	0.836	2.69	0.642
0.50	1.95	0.838	2.09	0.993				
	1.95	0.632	1.45	0.590				
	1.95	0.742	1.77	0.817				
2.00	1.96	0.446	1.40	0.555				
	1.95	0.543	1.71	0.805				
	1.95	0.497	1.55	0.691				

Subject: DTM

Experiments 10 & 11: Standard Errors of bias and standard deviation

Stimulus Duration	Without adaptation				With adaptation			
	Orientation				Orientation			
	15°		345°		15°		345°	
0.01	0.156	0.153	0.154	0.146	0.142	0.132	0.119	0.112
	0.132	0.144	0.179	0.203	0.137	0.122	0.120	0.100
	0.144	0.149	0.167	0.177	0.140	0.127	0.120	0.106
0.50	0.132	0.134	0.148	0.160				
	0.114	0.108	0.113	0.104				
	0.123	0.122	0.132	0.135				
2.00	0.112	0.087	0.104	0.100				
	0.113	0.090	0.127	0.121				
	0.113	0.089	0.116	0.111				

Subject: DTM

Experiment 12: Standard Errors of bias and standard deviation

Angle Size	Stimulus Orientation											
	187°		202°		217°		232°		247°		262°	
15°	0.085	0.079	0.113	0.084	0.090	0.098	0.101	0.092	0.093	0.089	0.113	0.105
	0.068	0.079	0.096	0.096	0.090	0.086	0.093	0.090	0.085	0.077	0.098	0.092
	0.077	0.079	0.105	0.090	0.090	0.092	0.097	0.091	0.089	0.083	0.106	0.099
	195°		225°		255°							
30°	0.129	0.143	0.141	0.130	0.140	0.133						
	0.116	0.114	0.124	0.118	0.146	0.141						
	0.123	0.129	0.133	0.124	0.143	0.137						
	202°		247°									
45°	0.170	0.191	0.159	0.166								
	0.257	0.265	0.198	0.235								
	0.218	0.231	0.179	0.203								
	120°		180°		240°							
60°	0.341	0.473	0.237	0.259	0.202	0.238						
	0.196	0.211	0.196	0.226	0.230	0.307						
	0.279	0.366	0.217	0.243	0.221	0.273						

Subject: SRH

Stimulus Duration 2.00 seconds

Experiment 12: Biases and Standard Deviations

Angle Size	Stimulus Orientation											
	187°		202°		217°		232°		247°		262°	
15°	-1.34	0.439	-1.06	0.462	-2.00	0.488	-1.20	0.442	-0.81	0.459	0.24	0.597
	-1.64	0.439	-1.02	0.484	-1.74	0.423	-1.07	0.465	-0.25	0.399	0.29	0.492
	-1.49	0.439	-1.04	0.473	-1.87	0.457	-1.13	0.454	-0.53	0.430	0.26	0.547
	195°		225°		255°							
30°	-0.88	0.795	-2.47	0.856	2.07	0.879						
	-0.99	0.684	-2.27	0.746	1.48	0.918						
	-0.94	0.742	-2.37	0.803	1.78	0.899						
	202°		247°									
45°	-2.20	1.190	1.31	1.065								
	-2.78	1.663	1.29	1.410								
	-2.49	1.446	1.30	1.249								
	120°		180°		240°							
60°	2.01	2.665	0.97	1.643	2.34	1.469						
	2.08	1.388	0.85	1.453	2.83	1.775						
	2.05	2.125	0.91	1.551	2.58	1.629						

Subject: SRH

Stimulus Duration = 2.00 seconds.

Experiment 12: Standard Errors of bias and standard deviation

Subject	Stimulus Orientation 105°		135°		165°	
SRH	0.329	0.345	0.332	0.344	0.319	0.319
	0.335	0.351	0.317	0.405	0.319	0.341
	0.332	0.348	0.325	0.376	0.319	0.330
DTM	0.261	0.236	0.280	0.273	0.277	0.253
	0.275	0.243	0.281	0.282	0.208	0.204
	0.268	0.240	0.281	0.278	0.245	0.230
SG	0.229	0.212	0.235	0.202	0.282	0.310
	0.245	0.226	0.253	0.234	0.315	0.352
	0.237	0.219	0.244	0.219	0.299	0.321

Angle Size = 30°

Stimulus Duration = 0.01 seconds

Subject	Stimulus Orientation 112°		157°	
SRH	0.402	0.474	0.502	0.609
	0.410	0.405	0.453	0.484
	0.406	0.441	0.478	0.550
DTM	0.260	0.238	0.248	0.255
	0.247	0.242	0.291	0.256
	0.254	0.240	0.270	0.256
SG	0.335	0.331	0.366	0.371
	0.413	0.465	0.388	0.376
	0.376	0.404	0.377	0.373

Angle Size = 45°

Stimulus Duration = 0.01 seconds

Experiment 12: Standard Errors of bias and standard deviation

Subject	97°		112°		127°		142°		157°		172°	
SRH	0.192	0.217	0.245	0.258	0.227	0.238	0.250	0.314	0.226	0.275	0.264	0.288
	0.202	0.233	0.211	0.246	0.223	0.239	0.233	0.268	0.256	0.350	0.251	0.292
	0.197	0.225	0.229	0.252	0.225	0.239	0.242	0.292	0.241	0.315	0.258	0.290
DTM	0.133	0.126	0.151	0.157	0.135	0.142	0.162	0.172	0.143	0.142	0.148	0.142
	0.136	0.121	0.168	0.182	0.156	0.160	0.143	0.158	0.123	0.121	0.126	0.124
	0.135	0.121	0.162	0.170	0.146	0.151	0.153	0.165	0.133	0.132	0.137	0.133
SG	0.195	0.220	0.172	0.188	0.182	0.178	0.199	0.237	0.189	0.201	0.168	0.168
	0.197	0.197	0.184	0.190	0.191	0.239	0.196	0.217	0.190	0.191	0.178	0.199
	0.196	0.209	0.178	0.189	0.187	0.211	0.197	0.227	0.190	0.196	0.173	0.184

(Column group header: Stimulus Orientation)

Angle Size = 15°

Stimulus Duration = 0.01 seconds.

Experiment 12: Biases and Standard Deviations

Subject	Stimulus Orientation 105°		135°		165°	
SRH	-0.69	2.228	-7.44	2.363	-1.65	2.182
	-0.17	2.331	-6.23	2.312	-0.98	2.246
	-0.43	2.280	-6.84	2.337	-1.32	2.214
DTM	-3.29	1.451	-9.30	1.792	-3.81	1.580
	-4.27	1.671	-8.58	1.671	-5.32	1.037
	-3.78	1.565	-8.94	1.733	-4.57	1.336
SG	1.70	1.329	-2.22	1.279	-1.04	1.972
	1.55	1.473	-2.22	1.546	-0.52	2.155
	1.67	1.403	-2.22	1.419	-1.28	2.066

Angle Size = 30°

Stimulus Duration = 0.01 seconds.

	Stimulus Orientation 112°		157°	
SRH	-2.97	2.961	-7.21	3.685
	-2.81	2.649	-8.53	3.146
	-2.89	2.809	-7.87	3.426
DTM	-0.57	1.559	-2.95	1.530
	-1.17	1.438	-1.89	1.659
	-0.87	1.450	-1.06	1.596
SG	-1.83	2.241	-5.10	2.424
	-0.74	2.897	-4.50	2.533
	-1.28	2.590	-4.80	2.479

Angle Size = 45°

Stimulus Duration = 0.01 seconds.

Experiment 12: Biases and Standard Deviations

Subject	Stimulus Orientation 97°		112°		127°		142°		157°		172°	
SRH	-1.68	1.323	-0.59	1.642	-3.12	1.480	-3.58	1.876	-2.81	1.672	-0.70	1.863
	-1.02	1.469	-1.41	1.518	-3.35	1.575	-3.57	1.715	-3.21	2.003	-2.62	1.801
	-1.35	1.398	-1.00	1.581	-3.24	1.528	-3.58	1.797	-3.01	1.845	-1.66	1.832
DTM	-2.19	0.798	-2.21	0.983	-2.86	0.844	-4.41	1.091	-4.72	0.917	-1.59	0.850
	-1.16	0.842	-1.45	1.145	-2.34	1.038	-3.46	0.960	-4.21	0.733	-1.95	0.747
	-1.68	0.820	-1.83	1.067	-2.60	0.946	-3.94	1.028	-4.93	0.830	-1.77	0.801
SG	-0.92	1.351	0.65	1.188	-0.71	1.185	-1.99	1.392	-1.16	1.331	-0.72	1.060
	-0.68	1.278	0.02	1.259	-1.26	1.448	-1.73	1.347	-1.22	1.232	1.18	1.266
	-0.80	1.315	0.34	1.224	-0.98	1.323	-1.86	1.370	-1.19	1.282	0.23	1.168

Angle Size = 15°

Stimulus Duration = 0.01 seconds.

Experiment 12: Standard Errors of bias and standard deviation

Subject	Stimulus Orientation 105°		135°		165°	
SRH	0.152	0.136	0.134	0.117	0.143	0.155
	0.131	0.126	0.134	0.125	0.146	0.146
	0.142	0.131	0.134	0.121	0.145	0.151
DTM	0.116	0.117	0.121	0.101	0.112	0.108
	0.139	0.123	0.117	0.098	0.160	0.153
	0.128	0.120	0.119	0.099	0.138	0.132
SG	0.092	0.092	0.087	0.081	0.123	0.116
	0.107	0.094	0.109	0.090	0.116	0.099
	0.100	0.093	0.099	0.086	0.120	0.108

Angle Size = 30°

Stimulus Duration = 2.00 seconds

Subject	Stimulus Orientation 112°		165°	
SRH	0.148	0.145	0.197	0.224
	0.184	0.216	0.165	0.180
	0.167	0.184	0.182	0.203
DTM	0.158	0.158	0.144	0.167
	0.163	0.144	0.154	0.143
	0.161	0.151	0.149	0.156
SG	0.135	0.131	0.131	0.114
	0.131	0.110	0.163	0.162
	0.133	0.121	0.148	0.140

Angle Size = 45°

Stimulus Duration = 2.00 seconds.

Experiment 12: Standard Errors of bias and standard deviation

Subject	Stimulus Orientation 97°		112°		127°		142°		157°		172°	
SRH	0.090	0.068	0.111	0.110	0.098	0.077	0.107	0.086	0.097	0.092	0.101	0.106
	0.099	0.077	0.125	0.113	0.084	0.051	0.091	0.098	0.106	0.085	0.098	0.100
	0.095	0.073	0.118	0.112	0.091	0.065	0.099	0.092	0.102	0.089	0.100	0.103
DTM	0.111	0.116	0.091	0.075	0.097	0.078	0.085	0.071	0.098	0.091	0.094	0.074
	0.088	0.079	0.089	0.056	0.089	0.055	0.089	0.067	0.094	0.081	0.093	0.097
	0.100	0.099	0.090	0.066	0.093	0.067	0.087	0.069	0.096	0.086	0.093	0.086
SG	0.101	0.092	0.113	0.107	0.098	0.079	0.084	0.055	0.093	0.077	0.111	0.092
	0.094	0.071	0.095	0.074	0.099	0.094	0.102	0.087	0.101	0.099	0.094	0.061
	0.098	0.082	0.104	0.092	0.099	0.087	0.093	0.073	0.097	0.089	0.103	0.078

Angle Size = 30°

Stimulus Duration = 2.00 seconds.

Experiment 12: Biases and Standard Deviations

Subject	Stimulus Orientation 105°		135°		165°	
SRH	0.94	0.970	-3.25	0.803	-1.78	0.920
	0.55	0.805	-3.37	0.792	-1.34	0.874
	0.75	0.891	-3.31	0.798	-1.56	0.897
DTM	0.82	0.651	-2.15	0.634	-1.58	0.639
	1.20	0.840	-1.88	0.633	-1.62	1.004
	1.01	0.751	-2.02	0.633	-1.60	0.841
SG	-0.69	0.427	-3.22	0.413	-1.52	0.719
	-0.66	0.505	-2.47	0.436	-1.95	0.604
	-0.67	0.518	-2.84	0.425	-1.73	0.664

Angle Size = 30°

Stimulus Duration = 2.00 seconds

Subject	Stimulus Orientation 112°		157°	
SRH	0.57	0.970	-3.48	1.362
	-0.64	1.332	-5.05	1.121
	-0.03	1.165	-4.26	1.247
DTM	1.37	1.000	-2.90	0.972
	1.27	1.008	-2.88	0.953
	1.32	1.004	-2.89	0.962
SG	-2.80	0.760	-4.14	0.769
	-2.85	0.730	-4.73	0.976
	-2.82	0.746	-4.43	0.878

Angle Size = 45°

Stimulus Duration = 2.00

Experiment 12: Biases and Standard Deviations

Subject	Stimulus Orientation 97°		112°		127°		142°		157°		172°	
SRH	0.36	0.357	1.05	0.644	-1.35	0.413	-2.13	0.448	-1.17	0.450	-1.14	0.560
	0.50	0.397	1.11	0.716	-1.41	0.302	-1.94	0.486	-1.19	0.504	-0.88	0.480
	0.43	0.378	1.08	0.681	-1.38	0.362	-2.03	0.467	-1.18	0.478	-1.01	0.522
DTM	-1.59	0.678	-1.36	0.376	-2.28	0.390	-2.53	0.422	-1.36	0.517	-0.38	0.405
	-1.71	0.397	-0.53	0.311	-2.51	0.308	-1.60	0.352	-2.19	0.418	-1.06	0.487
	-1.65	0.556	-0.94	0.345	-2.40	0.351	-2.07	0.389	-1.78	0.470	-0.72	0.448
SG	-2.00	0.476	-0.57	0.594	-2.39	0.440	-1.47	0.333	-2.21	0.401	-1.40	0.502
	-1.68	0.366	-0.36	0.405	-2.11	0.480	-1.82	0.441	-1.87	0.564	-1.40	0.322
	-1.84	0.424	-0.46	0.508	-2.25	0.460	-1.64	0.391	-2.04	0.489	-1.40	0.422

Angle Size = 15°

Stimulus Duration = 2.00 seconds.

Experiment 13: Standard Errors of bias and standard deviation

Angle Size	SRH		DTM		SG	
15°	0.203	0.219	0.147	0.143	0.150	0.146
	0.202	0.217	0.185	0.203	0.164	0.161
	0.203	0.218	0.166	0.176	0.157	0.154
20°	0.200	0.240	0.191	0.217	0.176	0.161
	0.243	0.284	0.164	0.167	0.235	0.247
	0.222	0.263	0.178	0.194	0.206	0.208
25°	0.249	0.306	0.156	0.165	0.189	0.197
	0.249	0.271	0.232	0.208	0.227	0.253
	0.249	0.289	0.194	0.188	0.208	0.227
30°	0.332	0.344	0.280	0.273	0.235	0.202
	0.317	0.405	0.281	0.282	0.253	0.234
	0.435	0.376	0.281	0.278	0.244	0.220
35°	0.428	0.414	0.263	0.275	0.356	0.309
	0.364	0.394	0.267	0.243	0.371	0.399
	0.396	0.404	0.265	0.259	0.364	0.357
40°	0.468	0.477	0.324	0.325	0.363	0.389
	0.419	0.449	0.287	0.285	0.387	0.496
	0.444	0.463	0.306	0.306	0.374	0.446
45°	0.451	0.504	0.227	0.212	0.474	0.458
	0.451	0.450	0.283	0.265	0.507	0.517
	0.451	0.478	0.280	0.240	0.491	0.488

Stimulus duration = 0.01 seconds.

Experiment 13: Biases and Standard Deviations

Angle Size	SRH		DTM		SG	
15^{o}	-1.19	1.475	-2.86	0.844	0.20	0.949
	-1.49	1.413	-2.34	1.038	0.48	1.073
	-1.34	1.444	-2.60	0.946	0.34	1.013
20^{o}	-3.77	1.448	-2.83	1.290	-0.24	1.089
	-3.10	1.716	-2.73	1.086	-1.76	1.646
	-3.44	1.588	-2.78	1.192	-1.00	1.396
25^{o}	-4.70	1.857	-2.14	1.058	0.09	1.317
	-4.86	1.739	-2.47	1.335	-1.65	1.635
	-4.78	1.799	-2.31	1.204	-0.78	1.485
30^{o}	-6.23	2.312	-9.30	1.792	-2.22	1.279
	-7.44	2.362	-8.58	1.671	-2.22	1.546
	-6.84	2.337	-8.94	1.733	-2.22	1.419
35^{o}	-6.02	2.704	-3.76	1.609	-0.51	2.099
	-5.58	2.507	-2.79	1.567	-1.11	2.576
	-5.80	2.607	-3.27	1.588	-0.81	2.350
40^{o}	-7.21	3.137	-3.43	2.112	-6.10	2.443
	-7.23	2.973	-4.32	1.913	-4.29	2.767
	-7.22	3.056	-3.87	2.015	-5.19	2.610
45^{o}	-8.24	3.088	-4.80	1.332	-5.72	2.995
	-9.48	2.990	-4.84	1.656	-4.63	3.325
	-8.86	3.039	-4.82	1.503	-5.18	3.164

Stimulus duration = 0.01 seconds

Experiment 13: Standard Errors of bias and standard deviation

Angle Size	Subject SRH		DTM		SG	
15°	0.110	0.100	0.097	0.088	0.088	0.081
	0.111	0.109	0.086	0.072	0.103	0.106
	0.111	0.105	0.092	0.080	0.096	0.094
20°	0.121	0.105	0.096	0.093	0.124	0.094
	0.116	0.125	0.095	0.080	0.105	0.091
	0.119	0.115	0.096	0.087	0.162	0.093
25°	0.116	0.112	0.114	0.109	0.114	0.118
	0.113	0.100	0.122	0.130	0.096	0.086
	0.114	0.106	0.206	0.120	0.105	0.103
30°	0.127	0.130	0.121	0.101	0.087	0.081
	0.131	0.111	0.117	0.098	0.109	0.090
	0.129	0.121	0.119	0.099	0.098	0.085
35°	0.153	0.163	0.124	0.112	0.120	0.117
	0.170	0.163	0.116	0.108	0.153	0.144
	0.161	0.163	0.120	0.110	0.127	0.131
40°	0.149	0.145	0.115	0.118	0.130	0.125
	0.138	0.143	0.120	0.113	0.131	0.117
	0.144	0.144	0.118	0.115	0.131	0.121
45°	0.191	0.190	0.169	0.180	0.164	0.179
	0.160	0.188	0.170	0.168	0.177	0.200
	0.176	0.189	0.170	0.174	0.171	0.190

Stimulus duration = 2.00 seconds.

Experiment 13: Biases and Standard Deviations

Angle Size	Subject SRH		DTM		SG	
15°	0.62	0.598	-0.84	0.449	0.32	0.448
	0.27	0.605	-0.67	0.376	0.20	0.503
	0.44	0.601	-0.75	0.414	0.26	0.476
20°	-2.13	0.707	-2.09	0.468	-1.66	0.483
	-2.40	0.675	-2.32	0.389	-1.48	0.480
	-2.26	0.691	-2.21	0.430	-1.56	0.482
25°	-3.00	0.678	-1.18	0.609	-1.74	0.657
	-2.40	0.629	-1.76	0.743	-1.11	0.448
	-2.70	0.654	-1.47	0.679	-1.43	0.562
30°	-2.83	0.793	-2.15	0.634	-3.22	0.413
	-3.06	0.730	-1.88	0.633	-2.47	0.436
	-2.95	0.762	-2.02	0.633	-2.90	0.425
35°	-2.23	0.992	-0.98	0.745	0.41	0.674
	-2.24	1.147	-0.78	0.665	-0.01	0.956
	-2.24	1.072	-0.88	0.706	0.20	0.827
40°	-4.61	0.951	-3.89	0.688	-2.12	0.789
	-5.25	0.884	-4.51	0.704	-1.77	0.650
	-4.93	0.918	-4.20	0.696	-1.95	0.723
45°	-4.98	1.316	-2.13	1.134	-2.19	1.105
	-5.15	1.099	-1.61	1.043	-2.94	1.231
	-5.06	1.212	-1.87	1.089	-2.57	1.167

Stimulus duration = 2.00 seconds

Appendix II: Computer Subroutines - used for on-line control of stimulus presentation and monitoring of response distributions.

The programs written to run the computer-controlled system have been described in chapter 2. Of these, two subroutines are of potential interest, those used to present the stimuli and to monitor and optimise the response distributions of the observers - 'DISP' and 'TEST'. Full listings of these two subroutines are provided in this appendix.

II-1 DISP

X and Y screen coordinates for the line end-points and line origins of each of the 4 lines of the 21 constant stimuli were stored in arrays in the main program and transmitted to unsubscripted variables in the subroutine for speed of access.

IPX1 - IPX4	- X coordinates for endpoints
IPY1 - IPY4	- Y coordinates for endpoints
KOX1 - KOX4	- X coordinates for origins
KOY1 - KOY4	- Y coordinates for origins
KFX,KFY	- X,Y coordinates for fixation point.

After setting the various timing counters, the program enters a loop of five sections, one for the drawing of each of the four lines, and one for the fixation point. One pass through this loop takes 5msec., the number of iterations required was, therefore, t/5 where T is the stimulus duration in milliseconds.

Instructions 6351 and 6352 loaded the X and Y line end-point DAC registers; instructions 6125 and 6315 loaded the X and Y origin DAC registers. Variables G1 - G4, and GF were set to 1 or 0 in bit 0 of the Y origin register to activate the integrators if that line was to be shown.

```
C
C
C      S U B R O U T I N E   S D I S P (KDISP1)
C
C
       SUBROUTINE SDISP(ITF)
       COMMON AN, EA, SB, SSB, ANS, IDF, NR, NR2, NR3, NR4, NR5, JR, KR, LR, DATE,
     2SUBJ, STL1, STL2, STL3, STL4, STL5, STL6, NSUB, ISRUN, SCALE, SLA, KQ,
     3MRUN, ISCON, JSX, L, IO, IDEL, ITD, ITD2, DUR, ITT, IT9, ITS,
     4G1, G2, G3, G4, GF, FV1, FV2, FV3, IV1, IV2, IV3
       COMMON ISDIST, ISCR1, ISCRW, ISEV, SI, SAS, SAO, SEP1, SEP2, ISK2, ISNW,
     2ISKB20, SIL, SIR, SL, SLV, ISNV, N, M, ISN, ISNS, ISNS2, ISNG, ISMIN, ISMAX,
     3ICF, SDX, SPX, ISMA, ISMB, ISMT, IFA, IFX, IFY, IE, IOX1, IOX2, IOX3, IOX4,
     4IOY1, IOY2, IOY3, IOY4, ISX1, ISX2, ISX3, ISX4, ISY1, ISY2, ISY3, ISY4
       DIMENSION AN(3), EA(3), SB(3), SSB(3), ANS(3), IDF(3),
     2SDX(21), SPX(21), ICF(6), IE(5, 11), SUBJ(2), N(2), ISN(2), ISNS(2),
     3ISKB20(2), ISNG(2), M(2), NR(2), NR2(2), NR3(2), NR4(2), NR5(2),
     4ISNW(2), ISK2(2), ISMA(8, 21), ISMB(8, 21), ISMT(8, 21)
       DIMENSION IFX(2), IFY(2), IOX1(2), IOX2(2), IOX3(2),
     2IOX4(2), IOY1(2), IOY2(2), IOY3(2), IOY4(2),
     3ISX1(21), ISX2(21), ISX3(21),
     4ISX4(21), ISY1(21), ISY2(21), ISY3(21), ISY4(21), ISMIN(2), ISMAX(2),
     5KQ(2, 4)
       DIMENSION OX1(2), OX2(2)
C
C
       IPX1=ISX1(ISNS2)
       IPY1=ISY1(ISNS2)
       IPX2=ISX2(ISNS2)
       IPY2=ISY2(ISNS2)
       IPX3=ISX3(ISNS2)
       IPY3=ISY3(ISNS2)
       IPX4=ISX4(ISNS2)
       IPY4=ISY4(ISNS2)
       KOX1=IOX1(L)
       KOX2=IOX2(L)
       KOX3=IOX3(L)
       KOX4=IOX4(L)
       KOY1=IOY1(L)
       KOY2=IOY2(L)
       KOY3=IOY3(L)
       KOY4=IOY4(L)
       KFX=IFX(L)
       KFY=IFY(L)
C
S      JMP BG; G1, 4000; G2, 4000; G3, 4000; G4, 4000; BG, NOP;
       IF (ISEV-1)108, 107, 107
  107  CONTINUE
S      CLA; DCA G3;
  108  CONTINUE
       IDD=4+IFA+1000/ITT
       IF (ISKB20(L))110, 110, 106
C
  106  IF (ITF)103, 103, 101
  101  CONTINUE
```

```
      ITF1=ITF*1000/5
      IT8=0875
      DO 102 I=1,ITF1
S     CLA;TAD \IT9;CIA;DCA TF
S     TAD (764;6351;CLA;TAD (764;6352;CLA/SET DACX1,Y1 TO 0
S     TAD \KFX;6125;CLA;TAD \KFY;TAD (4000;6315;CLA/SET FIX PT.
S     CPAGE 4
S     SKP;TF,0;FT,ISZ TF;JMP FT/TIMING LOOP FOR FIX PT.
S     CLA;TAD \IT8;CIA;DCA TF;
S     CPAGE 2
S     FS,ISZ TF;JMP FS;CLA;
  102 CONTINUE
  103 CONTINUE
      DO 104 J=1,ITT
S     CLA;TAD \IT9;CIA;DCA TT1
S     TAD \IPX1;6351;CLA;TAD \IPY1;6352;CLA
S     TAD \KOX1;6125;CLA;TAD \KOY1;TAD G1;6315;CLA
S     CPAGE 4
S     SKP;TT1,0;ST1,ISZ TT1;JMP ST1/TIMING FOR LINE 1
C
S     CLA;TAD \IT9;CIA;DCA TT2
S     TAD \IPX2;6351;CLA;TAD \IPY2;6352;CLA
S     TAD \KOX2;6125;CLA;TAD \KOY2;TAD G2;6315;CLA
S     CPAGE 4
S     SKP;TT2,0;ST2,ISZ TT2;JMP ST2/TIMING LINE 2
C
S     CLA;TAD \IT9;CIA;DCA TT3
S     TAD \IPX3;6351;CLA;TAD \IPY3;6352;CLA
S     TAD \KOX3;6125;CLA;TAD \KOY3;TAD G3;6315;CLA
S     CPAGE 4
S     SKP;TT3,0;ST3,ISZ TT3;JMP ST3/TIMING LINE 3
C
S     CLA;TAD \IT9;CIA;DCA TT4
S     TAD \IPX4;6351;CLA;TAD \IPY4;6352;CLA
S     TAD \KOX4;6125;CLA;TAD \KOY4;TAD G4;6315;CLA
S     CPAGE 4
S     SKP;TT4,0;ST4,ISZ TT4;JMP ST4/TIMING LINE 4
C
S     CLA;TAD \IFA;SNA;JMP NF
S     CLA;TAD \IT9;CIA;DCA TF1
S     TAD (764;6351;CLA;TAD (764;6352;CLA
S     TAD \KFX;6125;CLA;TAD \KFY;TAD (4000;6315;CLA
S     CPAGE 4
S     SKP;TF1,0;FT1,ISZ TF1;JMP FT1
S     NF,CLA
C
  104 CONTINUE
      GOTO 120
  110 DO 111 I=1,IDD
      DO 111 J=1,ITT
S      CLA;TAD \IT9;CIA;DCA TTD
S     CPAGE 4
S     SKP;TTD,0000;DT,ISZ TTD;JMP DT
  111 CONTINUE
  120 CONTINUE

      RETURN

      END
```

II-2 'TEST'

The variables input to this subroutine were:

ISK2 - the mid-point of the current range of 4 stimuli

ISNW - the stimulus range-width descriptor - i.e. how far from ISK2 the largest and greatest stimuli were.

ISMA
ISMB - the frequencies of A and B responses

NNG - the identity of the current group of 8 responses most recently acquired.

ISCR1
ISCRW - empirically determined criteria which determine the resistance to change of the stimulus set mid-point and range width. A value of 20 was used for each of these in all runs.

IC - array containing the criterion values of response frequencies against which empirical response frequencies are compared (see Appendix III for values)

```
C
C
C     S U B R O U T I N E   T E S T  (KTEST)
C
C
      SUBROUTINE TEST(NNG)
      COMMON AN, EA, SB, SSB, ANS, IDF, NR, NR2, NR3, NR4, NR5, JR, KR, LR, DATE,
     2SUBJ, STL1, STL2, STL3, STL4, STL5, STL6, NSUB, ISRUN, SCALE, SLA, KQ,
     3MRUN, ISCON, JSX, L, IO, IDEL, ITD, ITD2, DUR, ITT, IT9, ITS,
     4G1, G2, G3, G4, GF, FV1, FV2, FV3, IV1, IV2, IV3
      COMMON ISDIST, ISCR1, ISCRW, ISEV, SI, SAS, SAO, SEP1, SEP2, ISK2, ISNW,
     2ISKB20, SIL, SIR, SL, SLV, ISNV, N, M, ISN, ISNS, ISNS2, ISNG, ISMIN, ISMAX,
     3ICF, SDX, SPX, ISMA, ISMB, ISMT, IFA, IFX, IFY, IE, IOX1, IOX2, IOX3, IOX4,
     4IOY1, IOY2, IOY3, IOY4, ISX1, ISX2, ISX3, ISX4, ISY1, ISY2, ISY3, ISY4
      DIMENSION AN(3), EA(3), SB(3), SSB(3), ANS(3), IDF(3),
     2SDX(21), SPX(21), ICF(6), IE(5, 11), SUBJ(2), N(2), ISN(2), ISNS(2),
     3ISKB20(2), ISNG(2), M(2), NR(2), NR2(2), NR3(2), NR4(2), NR5(2),
     4ISNW(2), ISK2(2), ISMA(8, 21), ISMB(8, 21), ISMT(8, 21)
      DIMENSION IFX(2), IFY(2), IOX1(2), IOX2(2), IOX3(2),
     2IOX4(2), IOY1(2), IOY2(2), IOY3(2), IOY4(2),
     3ISX1(21), ISX2(21), ISX3(21),
     4ISX4(21), ISY1(21), ISY2(21), ISY3(21), ISY4(21), ISMIN(2), ISMAX(2),
     5KQ(2, 4)
      DIMENSION OX1(2), OX2(2)
      DIMENSION K(8), JA(8), JB(8), JT(8)
C
C
C     MODIFIED CONST METHOD (MODE 4/5)
C     TEST FOR POSN & WIDTH OF RANGE
C
   10 IZ=ISNW(L)
      IZ1=1/(IZ+1)
      K5=ISK2(L)+3*IZ1
      N0=(IZ+1)/2
      N1=N0*(3-IREM(IZ/2))
      KMIN=K5-N1-2*IZ1
      KMAX=K5+N1+IZ1
      K(1)=KMIN
      K(2)=K5-N0-IZ1
      K(3)=K5+N0
      K(4)=KMAX
S     JMP FD; DIV, 0; CLA; TAD \L; TAD (-1; SZA CLA; JMP F2; TAD \IV;
S     JMP DD; F2, TAD \IV; CLL RTR; RTR; DD, AND (17; DCA \J; JMP I DIV;
S     FD, NOP;
      IF (NNG-1)956, 956, 12
   12 DO 651 MM=1, 4
      IK=K(MM)
      IV=ISMA(NNG, IK)
S     JMS DIV
      JA(MM)=J
      IV=ISMB(NNG, IK)
S     JMS DIV
  651 JB(MM)=J
C
C
```

```
  970 IH=4
      NW1=IZ+IZ1
      NW2=IZ+2-IZ/4
      IF(NNG-1)956,956,950
  950 DO 306 JK=1,4
      N2=KQ(L,JK)
      IV=ISMA(NNG-1,N2)
S     JMS DIV
      J1=J
      IV=ISMB(NNG-1,N2)
S     JMS DIV
      J2=J
      DO 305 JL=1,4
      IF(N2-K(JL))305,307,305
  307 JA(JL)=JA(JL)+J1
      JB(JL)=JB(JL)+J2
      GO TO 306
  305 CONTINUE
      IH=IH+1
      JA(IH)=J1
      JB(IH)=J2
      K(IH)=N2
      IF(N2-KMIN)120,130,130
  120 KMIN=N2
  130 IF(N2-KMAX)306,306,140
  140 KMAX=N2
  306 CONTINUE
C
C     IE(5,N) REFERS TO NW=0
C
      JZ=0
      DO 100 IL=1,IH
      JT(IL)=JA(IL)+JB(IL)
      IF(JA(IL)*JB(IL))100,100,101
  101 JZ=JZ+1
  100 CONTINUE
S     TAD \JZ; TAD (-2; SPA CLA; JMP \104; TAD \JZ; TAD (-4; SPA CLA
S     JMP \103; JMP \106
  104 IZ=IZ-1+IZ1
      NW2=IZ+1
      GO TO 103
  106 IZ=IZ+1-IZ/4
      NW1=IZ+1
  103 IM1=0
      IW=IZ+1+IZ/4+3*(1/(IZ+1))
      IF(K5+IW-21)40,40,41
   41 K5=21-IW
   40 IF(K5-IW)42,42,43
   42 K5=IW+1
   43 IF(K5-KMIN-10)44,44,45
   45 K5=KMIN+10
   44 IF(KMAX-K5-10)46,46,47
   47 K5=KMAX-10
   46 DO 573 I9=1,IH
      ND=K(I9)-K5
```

```
S       JMS NDS
        IEX=JT(I9)*(50*(NDS+1)-NDS*IE(IZ+1,11-ND*NDS))
    573 IM1=IM1+IABS(JA(I9)*100-IEX)
        IM=IM1
S       JMP \576;NDS,0;TAD \ND;AND (4000;CLL;RTL;CIA;SMA
S       TAD (1;DCA \NDS;JMP I NDS
    576 KK=KMAX-KMIN-10
        KK1=KMIN
        KK2=KMAX
        IF(KK)563,563,564
    564 KK1=KMIN+KK
        KK2=KMAX-KK
    563 IF(KK2+IW-21)48,48,49
     49 KK2=21-IW
     48 IF(KK1-IW)50,50,51
     50 KK1=IW+1
     51 DO 520 I1=KK1,KK2
        IM1=0
        DO 503 I4=1,IH
        ND=K(I4)-I1
S       JMS NDS
        IEX=JT(I4)*(50*(NDS+1)-NDS*IE(IZ+1,11-ND*NDS))
    503 IM1=IM1+IABS(JA(I4)*100-IEX)
        IF(IM-IM1-ISCR1)520,520,521
    521 IM=IM1
        K5=I1
    520 CONTINUE
    522 DO 500 I3=NW1,NW2
        IW=I3+I3/5+3*(1/I3)
        IF(IABS(K5-11)+IW-10)700,700,500
    700 IM1=0
        DO 506 I6=1,IH
        ND=K(I6)-K5
S       JMS NDS
        IEX=JT(I6)*(50*(NDS+1)-NDS*IE(I3,11-ND*NDS))
    506 IM1=IM1+IABS(JA(I6)*100-IEX)
        IF(IM-IM1-ISCRW)500,500,569
    569 IM=IM1
        IZ=I3-1
    500 CONTINUE
C
    959 ISNW(L)=IZ
    956 ISK2(L)=K5-3*(1/(1+IZ))
     13 DO 800 M5=1,4
    800 KQ(L,M5)=K(M5)
        RETURN
        END
```

Appendix III: Criterion frequencies for subroutine 'TEST'

The values listed below were stored in the array IE(I,J), where I = NW+1 and J=ISNS. NW describes the current width of the range of stimuli (ISNW) and ISNS the identity of the stimulus out of the set of 21 possible stimuli.

IE(1,1)=100	IE(2,1)=100	IE(3,1)=100	IE(4,1)=100	IE(5,1)= 99
IE(1,2)=100	IE(2,2)=100	IE(3,2)=100	IE(4,2)=100	IE(5,2)= 98
IE(1,3)=100	IE(2,3)=100	IE(3,3)=100	IE(4,3)= 99	IE(5,3)= 96
IE(1,4)=100	IE(2,4)=100	IE(3,4)=100	IE(4,4)= 98	IE(5,4)= 94
IE(1,5)=100	IE(2,5)=100	IE(3,5)=100	IE(4,5)= 96	IE(5,5)= 91
IE(1,6)=100	IE(2,6)=100	IE(3,6)= 99	IE(4,6)= 93	IE(5,6)= 87
IE(1,7)=100	IE(2,7)= 99	IE(3,7)= 96	IE(4,7)= 89	IE(5,7)= 82
IE(1,8)=100	IE(2,8)= 96	IE(3,8)= 91	IE(4,8)= 82	IE(5,8)= 75
IE(1,9)= 96	IE(2,9)= 89	IE(3,9)= 82	IE(4,9)= 73	IE(5,9)= 67
IE(1,10)=82	IE(2,10)=73	IE(3,10)=67	IE(4,10)=62	IE(5,10)=59
IE(1,11)=50	IE(2,11)=50	IE(3,11)=50	IE(4,11)=50	IE(5,11)=50