

ARLIR Article Request Tue Apr 15 13:37:01 PDT 2008

REQUESTING LIBRARY RECEIVING METHODS:

>>Ariel IP Address: 205.227.91.137<<

Odyssey IP Address:

MAIL: Knight Library, ILL Unit, 1299 University of Oregon, Eugene, OR 97403

FAX: 541-346-3094

EMAIL: libill@uoregon.edu

REQUEST ID: 65164

Mail      Electronic      Fax      Local      Pass: \_\_\_\_\_

Patron #: ~~p112308009ore0~~

*Arllir, delivery*

PATRON DELIVERY PREFERENCE: Not Specified

Patron Note:

JOURNAL: Experimental brain research

ARTICLE: Interactions between orientations in human vision.

AUTHOR: Carpenter, R H

YEAR: 1973

MONTH: 10

DAY:

QUARTER:

SEASON:

VOLUME: 18

ISSUE: 3

NUMBER:

PAGES: 287-303

PAGED LOCATIONS: >>9wsu0<<, 6wash, za006, 9unl0, 9cubp

Staff Note:

LOCATION: WSU Owen

CALL NUMBER: QP376 .E9 *v. 18*

HOLDINGS: Locations vary. See individual volume record. v.1-v.153. (1966-2003).

LOCATION: WSU Health Sciences Downstairs

CALL NUMBER: QP376.E9

HOLDINGS: Shelved downstairs alphabetically by title. 1-77(1966-1989).

# Interactions Between Orientations in Human Vision

R. H. S. CARPENTER and COLIN BLAKEMORE

The Physiological Laboratory, University of Cambridge, Cambridge (England)

Received November 22, 1972

**Summary.** Single lines cause changes in the apparent orientation of nearby lines of somewhat different orientation: acute angles are perceptually expanded while obtuse angles apparently contract. This phenomenon is measured by a matching technique and evidence is presented that it is due to recurrent, inhibitory interactions among orientation selective neural channels. In particular, a third line added to an angle figure can have a *disinhibiting* effect on the orientational distortion. Orientation selective channels maximally sensitive to different orientations may have different distributions of inhibitory input in the orientation domain. The results are interpreted in terms of the organization of neurons in the visual cortex. Each cell may receive a crude orientation selectivity from its direct input, and be inhibited, over an even broader range of orientation, by neurons in the same column and adjacent ones.

**Key words:** Lateral inhibition — Orientation detectors — Visual illusions — Visual cortex

## Introduction

Cats, monkeys, rabbits, pigeons, ground squirrels, goldfish and men all have orientation-selective neurons in their visual systems (Hubel and Wiesel, 1962, 1968; Levick, 1967; Maturana and Frenk, 1963; Michael, 1972; Cronly-Dillon, 1964; Marg *et al.*, 1968). Without doubt an analysis of the orientations of contours in the retinal image is a fundamental part of vertebrate vision. Presumably it provides a basis for the visual recognition of objects.

If these orientation detectors do indeed help to encode information about shape, then the narrower the band of orientations to which each detector will respond, the more discriminative the system will be; and this in turn would be expected to enhance shape discrimination and pattern recognition.

Hubel and Wiesel (1962) have put forward an attractively simple neural model for orientation selectivity in the cat's cortex. They propose that a few neurons in the lateral geniculate nucleus, with their concentric receptive fields overlapping in a row on the retina, send fibres to a particular cortical cell. The latter thus spatially summates light within a cigar-shaped receptive field; and any bar-shaped image falling the central region must elicit a large response. As the bar is rotated it falls less and less on the central zone and more and more on the inhibitory surrounds of the contributory geniculate receptive fields. This model is elegant because it is economical, but it cannot be the whole truth. The receptive fields even

F. Schwarz and J. M. Fredrickson

Evoked potential and electrical stimulation  
Posey (Ed.). Cerebral localization and organi-  
Wiscasin Press (1964).

visual cortical areas of the mouse. Johns Hopk.

of the guinea pig ("Cavia porcellus"). Arch.

Dr. L. M. Ödkvist

Department of Otolaryngology

Regional and University Hospital

Linköping

Sweden

Exp. Brain Res. 18, 287-303 (1973)  
© by Springer-Verlag 1973

of simple cortical cells are often quite different: some respond best to abrupt edges, not bars; others are direction selective in their responses to any kind of moving target. Perhaps the greatest difficulty is that a receptive field, typically only two or three times longer than it is broad, could not, in itself, have such a narrow band of preferred orientations as is often found ( $\pm 10-15^\circ$ ). Surely some other mechanism must improve the orientation selectivity of cortical cells.

In 1965, Andrews put forward the idea that inhibition between crude, broadly-tuned orientation detectors whose optimal orientations were similar would lead to a sharpening of their tuning curves and would increase the specificity of the system for signalling the orientation of a single line. His principal evidence was that a short line, flashed so briefly that the hypothetical inhibition could not build up, was often wrongly perceived in orientation by as much as  $30^\circ$ .

Recently we found more evidence for this idea from psychophysical measurements of interactions between line segments in human vision. We have already published a short report (Blakemore *et al.*, 1970) and here we present our findings in full.

#### A Preliminary Model

Figure 1 provides the theoretical justification for our experimental approach. It is a diagram of the stimuli and response characteristics, within the orientation domain, for a system of neurones that undergo mutual lateral inhibition of the type described above. It is assumed that each orientation detector receives a broad excitatory orientational input and is inhibited over an even broader range by detectors with identical and similar preferred orientations. The abscissa represents orientation, so the two delta functions (pulses) marked *stimuli* signify the presence in the visual field of two straight lines of slightly different orientation, forming an angle of  $12^\circ$  with each other. Above the stimulus representation are curves that show the distributions of activity amongst the population of orientation detectors whose optimal orientations cover the range shown on the abscissa. *Distribution 1* is the activity profile set up by stimulus line 1 alone. The detector whose optimal orientation coincides exactly with the angle of the line is, of course, very active, and so are detectors with similar optimal orientations. But the detectors with preferred orientations  $6^\circ$  or so from the angle of the stimulus are more or less strongly inhibited by their active neighbours. Thus the response to a single line is limited to a small band of detector neurones. *Distribution 2* is an identical pattern of activity, shifted along the abscissa, which is set up by stimulus 2. (If these orientation detectors all have identical sensitivity profiles, as a function of orientation, and their optima are evenly spaced along the orientation domain, then the sensitivity profile, or *tuning curve*, for any neurone has exactly the same shape as this activity distribution resulting from a single line shown to the whole population.)

Now imagine that both lines, 1 and 2, are present simultaneously: assuming linear summation of excitation and inhibition, the *summed distribution* represents the pattern of activity that would result. Because of the relation of the peak activity caused by one line to the inhibition set up by the other, the *most active* neurones for the two lines presented together are not the same as when they were presented singly: the peaks are shifted apart.

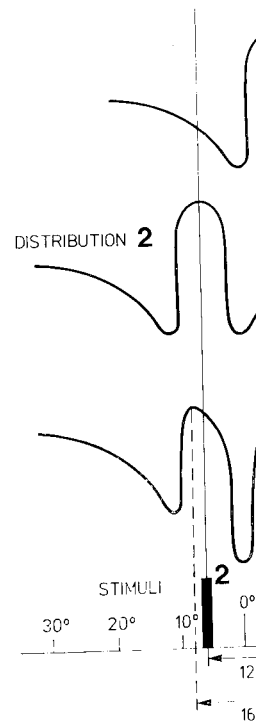


Fig. 1. Illustrating an explanation for angular misperception.

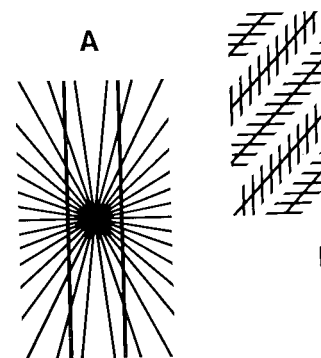


Fig. 2. Three geometric illusions that probably result from lateral inhibition. On the right they are: A. Hering's illusion, B. Müller-Lyer illusion, C. another Müller-Lyer illusion.

If we suppose that the brain identifies the orientation of a line, then the peaks should cause the absolute judgement. The acute angle formed by the lines is, in this case  $16^\circ$  rather than the

erent: some respond best to abrupt edges, in their responses to any kind of moving that a receptive field, typically only two did not, in itself, have such a narrow band ( $\pm 10-15^\circ$ ). Surely some other mechanism that inhibition between crude, broadly- and would increase the specificity of the a single line. His principal evidence was that the hypothetical inhibition could not orientation by as much as  $30^\circ$ . This idea from psychophysical measurements in human vision. We have already (1970) and here we present our findings

ery Model

igation for our experimental approach. e characteristics, within the orientation undergo mutual lateral inhibition of the t each orientation detector receives a s inhibited over an even broader range preferred orientations. The abscissa tions (pulses) marked *stimuli* signify the lines of slightly different orientation, Above the stimulus representation are ity amongst the population of orientation range shown on the abscissa. over the range of the stimulus alone. The detector by stimulus line 1 alone. But the with the angle of the line is, of course, similar optimal orientations. But the so from the angle of the stimulus are ve neighbours. Thus the response to a detector neurons. *Distribution 2* is an e abscissa, which is set up by stimulus tical sensitivity profiles, as a function spaced along the orientation domain, for any neuron has exactly the same, from a single line shown to the whole re present simultaneously: assuming n, the *summed distribution* represents Because of the relation of the peak set up by the other, the *most active* are not the same as when they were

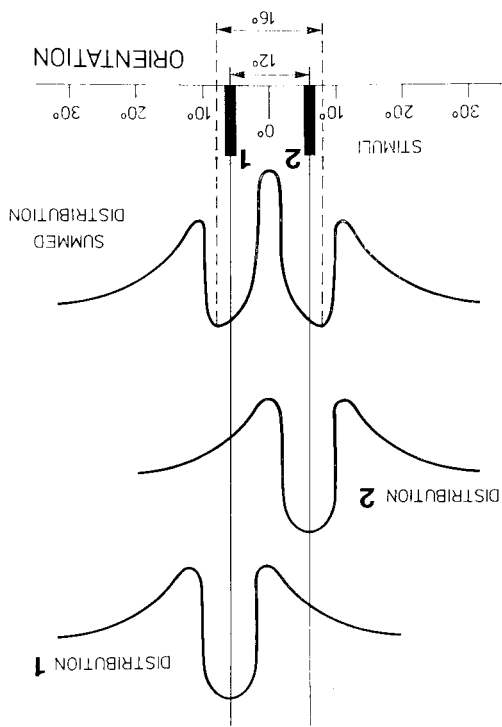


Fig. 1. Illustrating an explanation for angle-expansion. For full description, see text

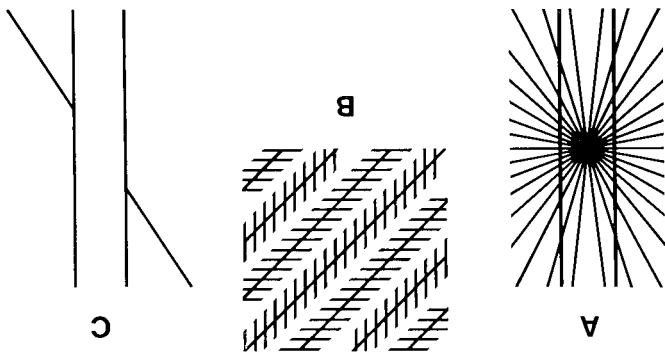


Fig. 2. Three geometric illusions that probably involve the misperception of angles. From left to right they are: A. Hering's illusion, B. Zollner's illusion, C. Poggendorff's illusion

If we suppose that the brain identifies the most active neuron in order to determine the orientation of a line, then when two lines are present this shift in the peaks should cause the absolute orientations of both lines to be wrongly judged. The acute angle formed by the two lines should appear larger than it really is, in this case  $16^\circ$  rather than the true  $12^\circ$ .

Only our theoretical interpretation of this *angle expansion* is novel: the phenomenon itself has been described for more than a century. Wundt, Hering and von Helmholtz all suspected that perceptual distortion of angles underlay many geometric illusions, such as those in Fig. 2 (see Luckiesh, 1922). However, we knew of no detailed and complete measurements of the phenomenon, except those of Bouma and Andriessen (1970) and Weintraub and Virsu (1972) who employed judgements of the extrapolation of line segments, and Fisher (1969) who used subjective naming. In this paper we show that angle expansion can readily be measured directly, by a simple matching technique, and that its properties conform to the notion that it results from inhibitory interactions between orientation detectors. Our hypothesis is fundamentally very similar to that of Nelson (1971) to whom we are grateful for discussion and correspondence, and also to that of Wallace (1969).

### Methods

An observer sat in a darkened room, 80 cm from the screen of a Tektronix 502A oscilloscope (P7 phosphor). The stimuli on the screen were generated by a Digital Corporation PDP-8 computer and generally had the appearance shown by the inset in Fig. 3. The display usually consisted of three bright lines, *A* (the angle line), *B* (the base line), and *C* (the comparison line). *A* always met *B* in the centre of the display, to form an angle, while *C* was at some distance on the opposite side of *B*. The angles, positions and lengths of these lines were under program control. In addition, the orientation of the comparison line, *C*, was under the subject's control: by adjusting a potentiometer he altered the value of an analogue input voltage to the computer, which determined the angle of *C*, relative to *B*. The subject was always required to set the angle of *C* so that it appeared to be parallel to *B*. When satisfied that this was so, the subject, or the experimenter, pressed a button that caused the orientation of *C* to be printed out, and also to be stored for subsequent statistics. During the judgements the observer was permitted to move his eyes and look anywhere within the display. The results were very similar, but the variance of the settings greater, in control experiments in which the subject fixated various points in the display continuously.

Whenever the subject turned the knob it led to momentary blanking of the display, while the calculations for the new orientation of *C* were carried out. However, control experiments, in which the display was continually interrupted at various low frequencies, showed that blanking of this type had no significant effect on the observations.

The luminance of the dim background was about  $0.1 \text{ cd.m}^{-2}$  and that of the bright lines about  $10 \text{ cd.m}^{-2}$ , while their width was approximately 2 min arc. This rather low working luminance reduced distortion and blur of the lines on the oscilloscope screen. In fact the results were much the same in control experiments where we increased the luminance of the lines and the background by about 1.5 log units.

### Results

#### *The Initial Experiment*

Our basic experiment consisted in keeping *B* fixed at a particular orientation and using the settings of *C* to assess the systematic distortions of the apparent orientation of *B* induced by a randomly-ordered series of orientations of *A*. In each series the observer usually made 4 settings of *C* for each orientation of *A*; two such runs constituted a complete experimental session.

#### *Sign Convention for Absolute and Relative Orientation*

Horizontal is  $0^\circ$

Orientations anticlockwise from horizontal are positive, those clockwise from horizontal are negative.

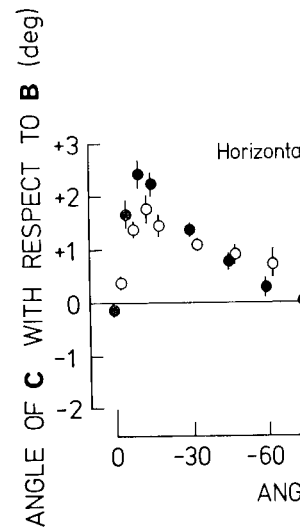


Fig. 3. *The stimulus configuration used in the experiment. A and B were fixed for any one observation. A was rotated until it appeared parallel to B. The graph shows the angle of C relative to B, with B held at  $3^\circ$  clockwise from horizontal in each case shows the angle at which C appeared parallel to B. Thus for values of  $a$  larger than it really is. ● = subject CB, ○ = subject CB (N = 8); the bars show one standard error. The points are relatively laterally displaced to avoid overlapping. The errors were of the same order of magnitude.*

Differences in orientation are expressed in degrees. A clockwise angle in a clockwise direction is negative.

#### *Some Definitions*

- a* Angle between *B* and *A*, measured from *B*
- $\beta$*  Orientation of *B*
- $\gamma$*  Angle between *B* and *D* (a third line, not shown in the figure), measured from *B*
- d* Distance between *B* and *C*
- e* Length of *C*

Figure 3 shows the principal findings of the experiment. The various angles clockwise to *B* ( $a = 0^\circ$  to  $-180^\circ$ ) and the length that they subtended 1 deg at the distance between the centres of *B* and *C*.

With the stimuli arranged in this way, the angle of *C* in the appearance of *B*, judged by the subject, was a function of the angle of *A* was superimposed on *B* ( $a = 0^\circ$ , or continuous with *B* ( $a = -180^\circ$ ), or parallel to *B* ( $0^\circ$  on the ordinate). I

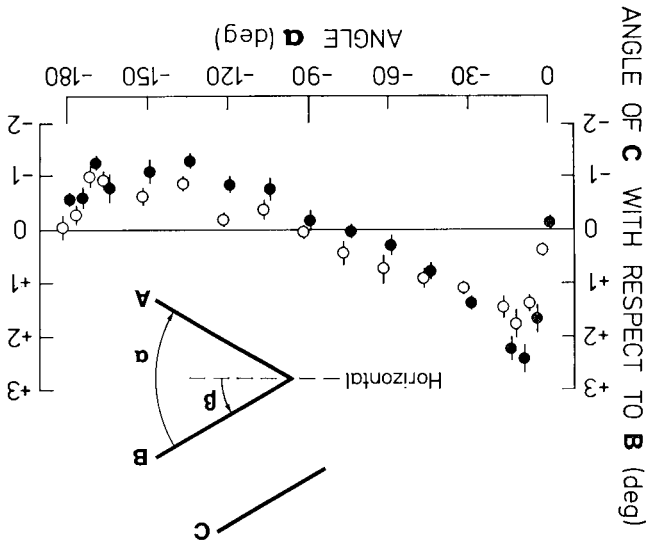


Fig. 3. The stimulus configuration used in most of the experiments is shown in the inset. The lines A and B were fixed for any one observation. The line C could be rotated by the subject to make it appear parallel to B. The graph shows the misperception of orientation as a function of the angle  $\alpha$  between A and B, with B held at  $30^\circ$  to the horizontal (i.e.  $\beta = +30^\circ$ ). The ordinate in each case shows the angle at which the subject sets C, relative to B, when trying to set them parallel. Thus for values of  $\alpha$  between  $0^\circ$  and  $-90^\circ$ , the angle  $\alpha$  appears larger than it really is. ● = subject CB, ○ = subject RHSC; eight observations per point (N = 8); the bars show one standard error on each side of the mean. The two subjects' results are relatively laterally displaced to avoid overlap. In all subsequent experiments the standard errors were of the same order of magnitude, and are not shown in the figures, for clarity.

Differences in orientation are expressed by the same convention: a change of angle in a clockwise direction is negative.

Some Definitions

- a Angle between B and A, measured from B
- $\beta$  Orientation of B
- $\gamma$  Angle between B and D (a third line that can be added to the stimulus figure), measured from B
- d Distance between B and C
- e Length of C

Figure 3 shows the principal finding with B at angle ( $\beta$ ) of  $+30^\circ$  and A at various angles clockwise to B ( $\alpha = 0$  to  $-180^\circ$ ). A and B were both of such a length that they subtended 1 deg at the subject's eyes: C was 0.8 deg in length (e) and the distance between the centres of B and C ( $d$ ) was 0.6 deg. With the stimuli arranged in this fashion there were obviously large changes in the appearance of B, judged by the settings of C, for certain values of  $\alpha$ . When A was superimposed on B ( $\alpha = 0^\circ$ , on the abscissa), perpendicular to B ( $\alpha = -90^\circ$ ) or continuous with B ( $\alpha = -180^\circ$ ), the two observers set C almost exactly truly parallel to B ( $0^\circ$  on the ordinate). But for acute angles, especially about  $-15^\circ$ ,

This angle expansion is novel: the phenomenon of angles underlay many more than a century. Wundt, Hering and (see Lankesh, 1922). However, we knew of the phenomenon, except those of Cornubius and Virsu (1972) who employed segments, and Fisher (1969) who used a technique, and that its properties contribute to that of Nelson (1971) and correspondence, and also to that of

on the screen of a Tektronix 502A oscilloscope generated by a Digital Corporation PDP-8 by the inset in Fig. 3. The display usually B (the base line), and C (the comparison line) with an angle, while C was at some distance on lengths of these lines were under program of an analogue input voltage to the control. The subject was always required to set B. When satisfied that this was so, the subject used the orientation of C to be printed out, during the judgment the observer was within the display. The results were very control experiments in which the subject

momentary blanking of the display, while carried out. However, control experiments, at various low frequencies, showed that the observations. out 0.1 cd.m<sup>-2</sup> and that of the bright lines nearly 2 min arc. This rather low working rate increased the luminance of the lines and

are positive, those clockwise from

$B$  appeared to be rotated away from  $A$ , since both subjects set  $C$  at about  $2^\circ$  anticlockwise to  $B$ . Similarly, obtuse angles between  $A$  and  $B$  led to a small change in the apparent orientation of  $B$  but in the opposite direction.

Obtuse angle contraction and acute angle expansion presumably result from the same influence of one orientation on another. In the experiment of Fig. 3 when  $A$  is at  $-170^\circ$  with respect to  $B$ , forming a large obtuse angle, it has exactly the same orientation as when it lies in the upper right quadrant, at an angle of  $+10^\circ$  to  $B$ . The latter acute angle certainly causes an apparent clockwise rotation of  $B$ . By the same argument, so should the large obtuse angle.

#### Some Control Experiments

Our choice of stimulus conditions, exemplified in Fig. 3, was not arbitrary: we performed a number of preliminary experiments to optimize the dimensions and position of line  $C$ .

The distance between  $B$  and  $C$  ( $d$ ) must certainly influence the measured angular changes in  $B$ . At one extreme, when  $C$  is as close as possible to  $B$ , any effect of  $A$  would be exerted equally on  $B$  and  $C$  and so no error in setting the two parallel would be expected. If the influence of line  $A$  on its neighbours is at all localized, than as  $d$  is increased, one would expect to find the error in setting  $C$  to increase, as it moves out of the field of influence of  $A$ . It is worth noting that if the distorting effect of one line on another were not at all localized, on the retina, then it would be impossible to measure the distortion phenomenon by our technique. It may indeed be true that there is some non-localized influence of  $A$  on  $B$  (which we could therefore not have detected) as well as the localized effects, which we have detected.

The results of changing the distance between  $B$  and  $C$  are shown in Fig. 4A.  $B$  was horizontal ( $\beta = 0^\circ$ ) and  $a$  was  $-10^\circ$ , which produces a large distortion. We gradually increased the separation of  $C$  and  $B$  and found that the measured error increased up to a maximum of about  $+2^\circ$  when the distance was about 40 min arc. Further separation of  $C$  and  $B$  caused no significant increase in the measured distortion but merely made the observer's task more difficult and consequently introduced greater variance in the settings. For this reason, in all our experiments we always fixed  $d$  at 0.6 deg and thus we are confident that we have measured virtually the total localized influence of  $A$  on  $B$ .

The length of  $C$  ( $e$ ) did not influence the magnitude of the distortion but did have a marked effect on the standard deviation of the settings (Fig. 4B), which increased substantially as  $C$  was reduced in length. We decided therefore to make  $C$  long enough to minimize this variance. But we avoided setting  $C$  identical in length to  $B$  since we suspected that such an arrangement (in which  $B$  and  $C$  form two sides of a rectangle) might help the observer to use additional cues (such as the distances between the two ends of  $B$  and  $C$ ) to make settings of parallelism. We therefore chose a length of 0.8 deg for  $C$  throughout the experiments.

#### Constant Errors in Parallel Settings

Much to our surprise we discovered, in another control experiment, that subjects make systematic errors in setting  $C$  parallel to  $B$ , even in the absence of  $A$ . Figure 5 shows these constant errors in parallel settings, both in the total absence of  $A$  (open and filled circles) and for  $A$  continuous with  $B$  (open and filled triangles),

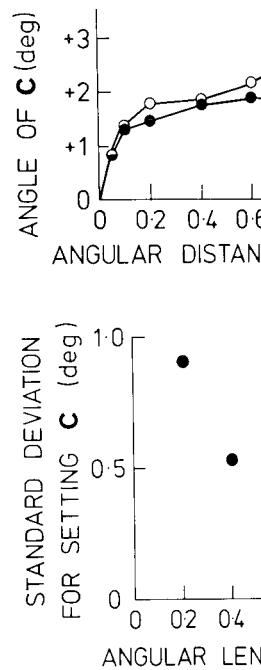


Fig. 4. A) Showing the effect of changing the distance between  $B$  and  $C$  on the angle of  $C$  (ordinate) when  $a = -10^\circ$ . Ordinate sign convention as in Fig. 3. B) Showing the effect of changing the length ( $e$ ) of line  $C$  on the standard deviation of a single setting of  $C$  (ordinate).

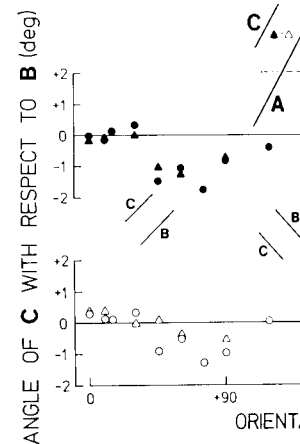


Fig. 5. Showing the error in setting  $C$  as a function of orientation, both in the absence of  $A$  (circles) or with  $A$  forming an angle with  $B$  (triangles) with  $A$  extended from  $B$  ( $a = -10^\circ$ ).

Interactions Between Orientations in Human Vision

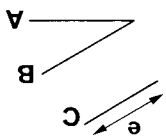
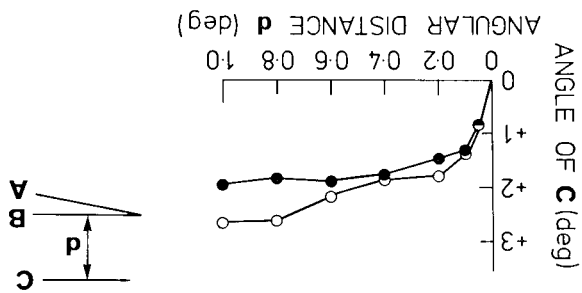


Fig. 4. A) Showing the effect of changing the length  $e$  of line  $C$  (with  $\beta = +30^\circ$  and  $a = -30^\circ$ ) on the standard deviation of a single setting of  $C$  (ordinate) estimated from eight observations. Subject CB

Fig. 4. B) Showing the effect of changing the distance  $d$  between  $B$  and  $C$  with  $\beta = 0^\circ$ ,  $a = -10^\circ$ . Ordinate sign convention as in Fig. 3.  $N = 8$ .  $\bullet = CB$ ,  $\circ = RHSC$ . C) Showing the effect of changing the length  $e$  of line  $C$  (with  $\beta = +30^\circ$  and  $a = -30^\circ$ ) on the standard deviation of a single setting of  $C$  (ordinate) estimated from eight observations. Subject CB

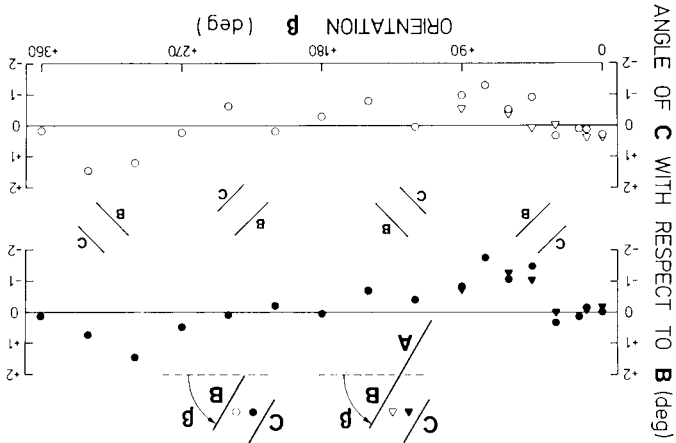


Fig. 5. Showing the error in setting  $C$  as a function of the inclination ( $\beta$ ) of  $B$ , in the complete absence of  $A$  (circles) or with  $A$  forming an extension of  $B$  (triangles).  $\bullet = B$  alone,  $\circ = A$  alone,  $\triangle = A$  and  $B$ ,  $\blacktriangle = A$  extended from  $B$  ( $a = -180^\circ$ );  $\blacktriangleright = CB$ ,  $\circ = RHSC$ ;  $N = 8$

and C. Blakemore  
 since both subjects set  $C$  at about  $2^\circ$   
 s between  $A$  and  $B$  led to a small change  
 e opposite direction.  
 angle expansion presumably result from  
 other. In the experiment of Fig. 3 when  
 a large obtuse angle, it has exactly the  
 er right quadrant, at an angle of  $+10^\circ$   
 s an apparent clockwise rotation of  $B$ .  
 obtuse angle.  
 experiments

certainly influence the measured angular  
 close as possible to  $B$ , any effect of  $A$   
 on its neighbours is at all localized,  
 and the error in setting  $C$  to increase,  
 it is worth noting that if the distorting  
 localized, on the retina, then it would  
 phenomenon by our technique. It may  
 sized influence of  $A$  on  $B$  (which we have  
 the localized effects, which we have

een  $B$  and  $C$  are shown in Fig. 4A.  
 which produces a large distortion. We  
 and found that the measured error  
 n the distance was about  $40$  min arc.  
 significant increase in the measured  
 ask more difficult and consequently  
 this reason, in all our experiments  
 confident that we have measured

agnitude of the distortion but did  
 n of the settings (Fig. 4B), which  
 We decided therefore to make  
 we avoided setting  $C$  identical in  
 arrangement (in which  $B$  and  $C$  form  
 er to use additional cues (such as  
 ) to make settings of parallelism.  
 throughout the experiments.

ner control experiment, that sub-  
 l to  $B$ , even in the absence of  $A$ .  
 settings, both in the total absence  
 with  $B$  (open and filled triangles),

