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~~ Arlir, 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).

by evoked potential and electrical stimulation
olsey (Ed.). Cerebral localization and organi-
Visconsin Press (1964).
isual cortical areas of the mouse. Johns Hopk.

s 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)

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 neurones 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 neurones 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 neurones 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 neurones 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 filling 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 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 (±10—15°). 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°.

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° 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° 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.

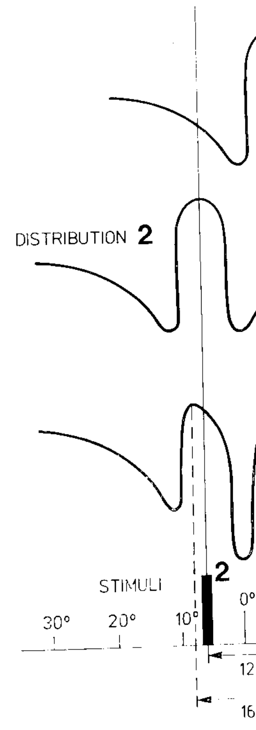


Fig. 1. *Illustrating an explanation for ang*

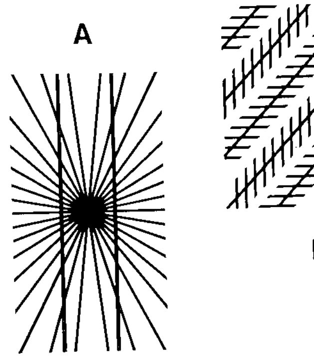


Fig. 2. *Three geometric illusions that probably*
right they are: A. Hering's illusion, B.

If we suppose that the brain iden
determine the orientation of a line, th
the peaks should cause the absolute
judged. The acute angle formed by t
really is, in this case 16° rather than t

erent: some respond best to abrupt edges,
in their responses to any kind of moving
that a receptive field, typically only two
ld not, in itself, have such a narrow band
d (±10—15°). Surely some other mecha-
tivity of cortical cells.

a that inhibition between crude, broadly-
al orientations were similar would lead
nd would increase the specificity of the
single line. His principal evidence was
t the hypothetical inhibition could not
orientation by as much as 30°.

this idea from psychophysical measure-
nts in human vision. We have already
, 1970) and here we present our findings

ry Model

fication for our experimental approach.
e characteristics, within the orientation
dergo mutual lateral inhibition of the
t each orientation detector receives a
s inhibited over an even broader range
preferred orientations. The abscissa
nctions (pulses) marked *stimuli* signify
ht lines of slightly different orientation,
Above the stimulus representation are
ity amongst the population of orienta-
over the range shown on the abscissa.
by stimulus line 1 alone. The detector
with the angle of the line is, of course,
imilar optimal orientations. But the
so from the angle of the stimulus are
ve neighbours. Thus the response to a
tector neurones. *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 neurone 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
.

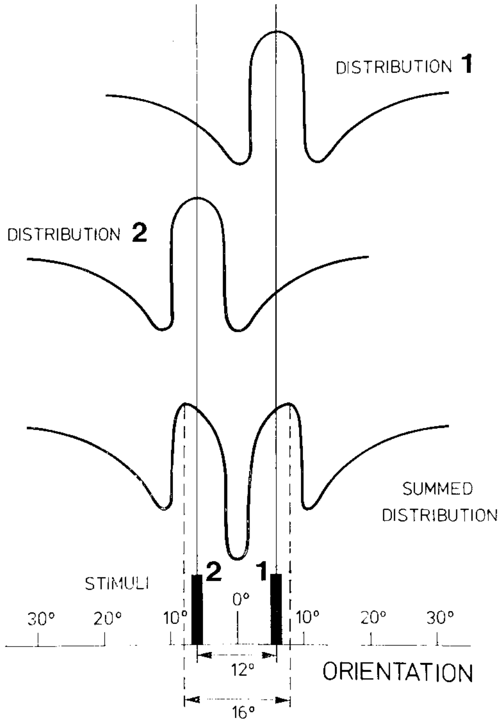


Fig. 1. *Illustrating an explanation for angle-expansion.* For full description, see text

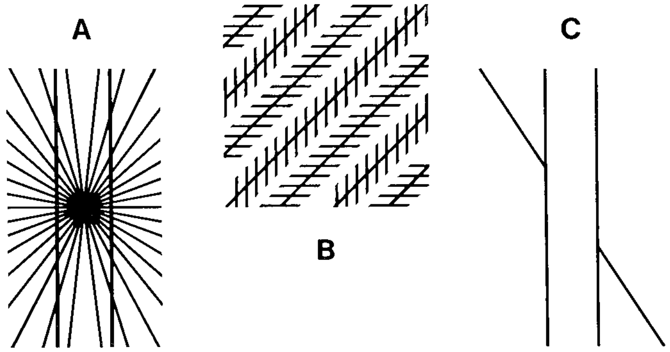


Fig. 2. *Three geometric illusions that probably involve the misperception of angles.* From left to right they are: A. Hering's illusion, B. Zöllner's illusion, C. Poggendorff's illusion

If we suppose that the brain identifies the most active neurone 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° rather than the true 12°.

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 cd.m^{-2} and that of the bright lines about 10 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°

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

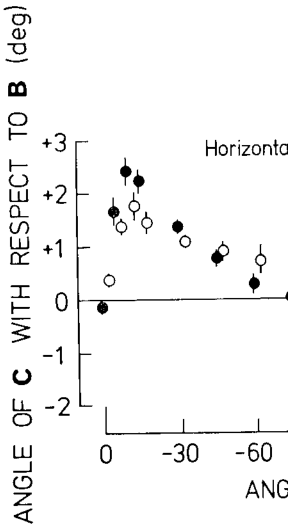


Fig. 3. *The stimulus configuration used in m*
A and *B* were fixed for any one observation.
it appear parallel to *B*. The graph shows th
angle *a* between *A* and *B*, with *B* held at 3
in each case shows the angle at which
to set them parallel. Thus for values of
larger than it really is. ● = subject CB,
(N = 8); the bars show one standard error
are relatively laterally displaced to avoid o
errors were of the same order of magnitu

Differences in orientation are exp
angle in a clockwise direction is nega

Some Definitions

a Angle between *B* and *A*, measu
β Orientation of *B*
γ Angle between *B* and *D* (a th
figure), measured from *B*
d Distance between *B* and *C*
e Length of *C*

Figure 3 shows the principal fin
various angles clockwise to *B* (a =
length that they subtended 1 deg at
and the distance between the centre

With the stimuli arranged in thi
in the appearance of *B*, judged by th
A was superimposed on *B* ($a = 0°$, on
or continuous with *B* ($a = -180°$),
parallel to *B* (0° on the ordinate).

f this *angle expansion* is novel: the pheno-
ore than a century. Wundt, Hering and
ptual distortion of angles underlay many
2 (see Luckiesh, 1922). However, we knew
nts of the phenomenon, except those of
ntraub and Virsu (1972) who employed
segments, and Fisher (1969) who used
ow that angle expansion can readily be
technique, and that its properties con-
ibitory interactions between orientation
ly very similar to that of Nelson (1971)
nd correspondence, and also to that of

ods

om the screen of a Tektronix 502A oscilloscope
generated by a Digital Corporation PDP-8
vn by the inset in Fig. 3. The display usually
B (the base line), and *C* (the comparison line).
rm an angle, while *C* was at some distance on
l lengths of these lines were under program
rison line, *C*, was under the subject's control:
e of an analogue input voltage to the com-
o *B*. The subject was always required to set
B. When satisfied that this was so, the sub-
used the orientation of *C* to be printed out,
During the judgements the observer was
within the display. The results were very
n control experiments in which the subject

o momentary blanking of the display, while
carried out. However, control experiments,
at various low frequencies, showed that
he observations.
out 0.1 cd.m^{-2} and that of the bright lines
ately 2 min arc. This rather low working
n the oscilloscope screen. In fact the results
ve increased the luminance of the lines and

eriment

g *B* fixed at a particular orientation
tematic distortions of the apparent
ered series of orientations of *A*. In
ngs of *C* for each orientation of *A*;
nental session.

ntation

l are positive, those clockwise from

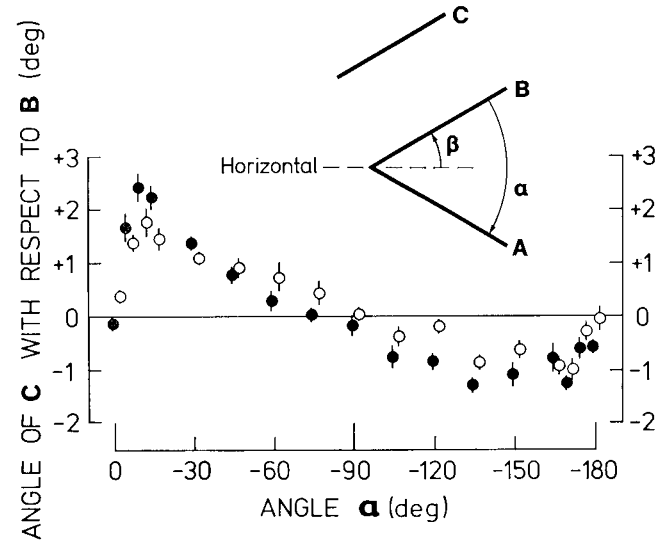


Fig. 3. *The stimulus configuration used in most of the experiments is shown in the inset.* The lines *A* and *B* were fixed for any one observation. The line *C* could be rotated by the subject to make it appear parallel to *B*. The graph shows the misperception of orientation as a function of the angle *a* between *A* and *B*, with *B* held at 30° to the horizontal (i.e. $\beta = +30°$). 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 *a* between 0° and —90°, the angle *a* 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*
- *β* Orientation of *B*
- *γ* 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 (*β*) of +30° and *A* at various angles clockwise to *B* ($a = 0$ to $-180°$). *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 *a*. When *A* was superimposed on *B* ($a = 0°$, on the abscissa), perpendicular to *B* ($a = -90°$) or continuous with *B* ($a = -180°$), the two observers set *C* almost exactly truly parallel to *B* (0° on the ordinate). But for acute angles, especially about —15°, *B* appeared to be rotated away from *A*, since both subjects set *C* at about 2° 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° 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° 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 ($\beta = 0°$) and a was —10°, 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° 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),

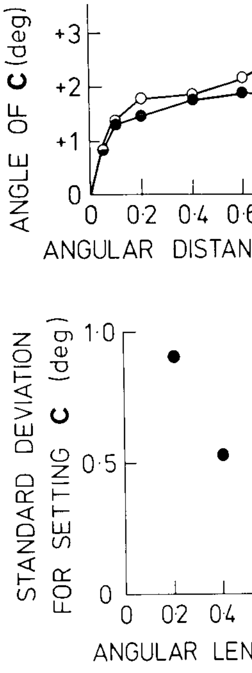


Fig. 4. A) *Showing the effect of changing t*
—10°. Ordinate sign convention as in Fig.
effect of changing the length (*e*) of line *C*
deviation of a single setting of *C* (ordinat

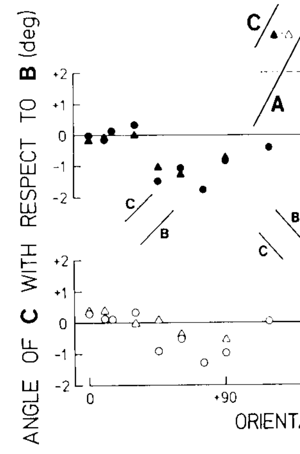


Fig. 5. *Showing the error in setting C as*
absence of *A* (circles) or with *A* forming a
with *A* extended from *B* (a = —

since both subjects set C at about 2°
s between A and B led to a small change
e opposite direction.
ngle 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°
es an apparent clockwise rotation of B.
obtuse angle.

xperiments

nplified in Fig. 3, was not arbitrary:
periments to optimize the dimensions

tainly influence the measured angular
close as possible to B, any effect of A
o no error in setting the two parallel
l on its neighbours is at all localized,
ind the error in setting C to increase,
t is worth noting that if the distorting
ocalized, on the retina, then it would
nomenon by our technique. It may
ized influence of A on B (which we
the localized effects, which we have

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

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

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

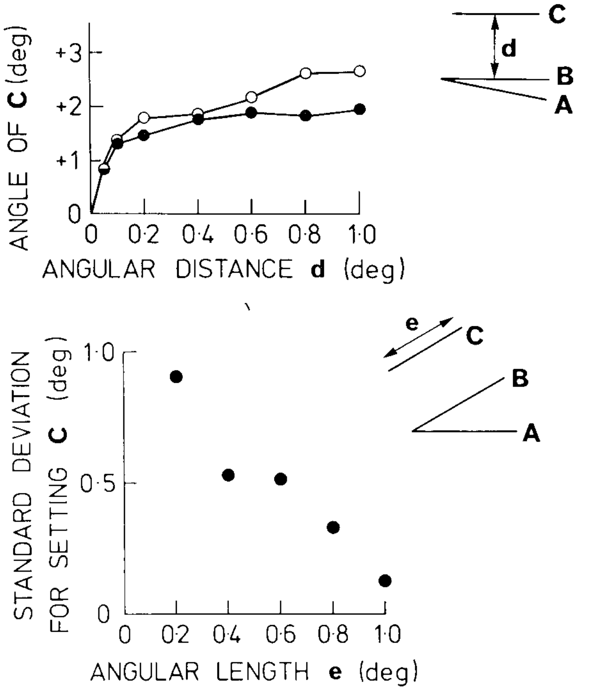


Fig. 4. A) *Showing the effect of changing the distance d between B and C* with $\beta = 0°$, $a = -10°$. Ordinate sign convention as in Fig. 3. N = 8. ● = CB, ○ = RHSC. B) Showing the effect of changing the length (e) of line C (with $\beta = +30°$ and $a = -30°$) on the standard deviation of a single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

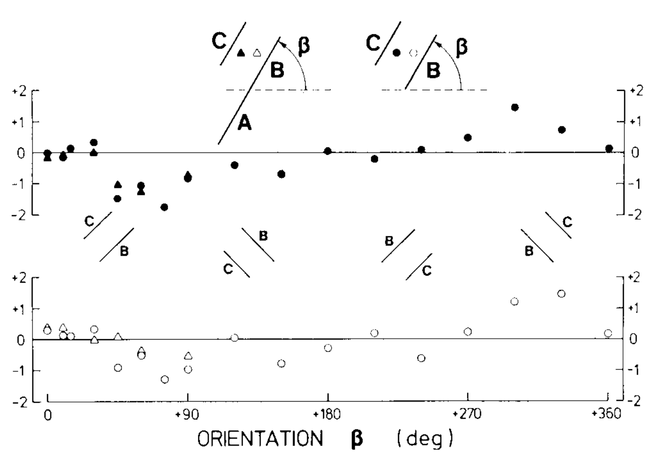


Fig. 5. *Showing the error in setting C as a function of the inclination* (β) of B, in the complete absence of A (circles) or with A forming an extension of B (triangles). ● ○ = B alone, ▲ △ = with A extended from B ($a = -180°$); ● ▲ = CB, ○ △ = RHSC; N = 8

as a function of the orientation of B. Although it is evident that these constant errors varied somewhat between the two observers (and indeed amongst several other subjects that we tested), there are some consistencies in the data. In brief, two close, parallel short lines at any orientation other than very close to horizontal usually *appear* to be diverging towards their top ends. Therefore they are set to converge slightly in order to make them seem parallel. This strange phenomenon was certainly not an artifact of the computer display, nor of some distortion in the oscilloscope, because it peristed if the oscilloscope was tilted through 90° or if the x and y axes of the display were reversed.

Others have discovered standing errors in setting a briefly-exposed short line parallel to a steady long one (Andrews, 1965, 1967) or setting a dot as the apparent extension of a line (Bouma and Andriessen, 1968). However, it is much more difficult to rationalize the occurrence of such errors in a simple comparison of two lines differing only slightly in length. Andrews (1967) has suggested that human orientation detectors may differ slightly in their "calibration" in different parts of the retinal representation. If our subjects tended to fixate consistently at some particular point, say midway between the two lines, then such mis-calibrations might explain our data, but it is still difficult to account for the degree of consistency between observers.

Whatever their cause, these constant errors in setting C parallel to B, even in the absence of a line of some other angle, complicated our task of measuring the influence of A on B for different orientations of the latter. We therefore adopted the following simple procedure to remove these constant errors from our data. For the results of each experimental session, like those illustrated in Fig. 3, the constant error had the effect of shifting the whole curve up or down by an amount equal to the error. We could simply compensate for this by shifting the curve in the opposite direction by an angle equal to the mean parallel-setting error for angles of 0° and 180° between A and B.

Results for Different Orientations of B

Figure 6 is a set of curves, like that in Fig. 3, for B at a number of different orientations, after the above correction for parallel-setting errors. It is clear that this procedure produces good agreement between the two subjects, and this has been verified informally with several other observers.

One noticeable feature of Fig. 6 is that although the maximum size of the perceptual distortion is much the same for each curve, at $\beta = +90°$ and $\beta = 0°$ the error falls off more rapidly (as α increased from —10° to —90°) than it does when β is closer to +45°. The same spread of the distortion is observable for the apparent contraction of obtuse angles (when α is between —90° and —180°).

There are two ways in which this change in shape might be explained. It could be that the spread of influence from A (in the orientation domain) is greater when A is horizontal or vertical than when it is oblique; alternatively, the spread of sensitivity or susceptibility of B to the influence of A is greater when B is oblique than when it is vertical or horizontal. It is not difficult to design an experiment that distinguishes between the two possibilities. If we set B to some orientation between 0° and +45° and observe the shape of the angle-expansion curve first with A at a greater angle (near the oblique) and secondly with A at a smaller angle

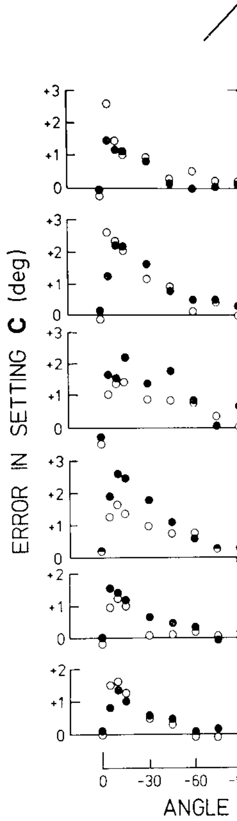


Fig. 6. *A set of curves relating angular mis*
tion of B to the horizontal. In each case t
mean of the constant errors for $\alpha = 0°$ and
in Fig. 5. ○ =

(near the horizontal) then the seco
should fall off equally in both directi
of angular distortion should be steep

Figure 7 shows the results of t
+22.5°: the distortion in fact falls o
oblique, suggesting that the changes
variations in the properties of A's "

If angle-expansion is due to later
this implies that the inhibitory "skir
near the principal meridians than ne
inhibitory flanks of the sensitivity pr
optimally sensitive to vertical or h
tuned to oblique orientations (ass

1ough it is evident that these constant
observers (and indeed amongst several
ome consistencies in the data. In brief,
tion other than very close to horizontal
eir top ends. Therefore they are set to
em parallel. This strange phenomenon
r display, nor of some distortion in the
oscope was tilted through 90° or if the

in setting a briefly-exposed short line
, 1967) or setting a dot as the apparent
n, 1968). However, it is much more
1 errors in a simple comparison of two
ews (1967) has suggested that human
their "calibration" in different parts
tended to fixate consistently at some
wo lines, then such mis-calibrations
lt to account for the degree of con-

rs in setting C parallel to B, even in
mplicated our task of measuring the
of the latter. We therefore adopted
e constant errors from our data. For
those illustrated in Fig. 3, the con-
le curve up or down by an amount
ate for this by shifting the curve in
the mean parallel-setting error for

entations of B

. 3, for B at a number of different
rallel-setting errors. It is clear that
een the two subjects, and this has
ervers.
lthough the maximum size of the
h curve, at $\beta = +90°$ and $\beta = 0°$
from $-10°$ to $-90°$) than it does
he distortion is observable for the
is between $-90°$ and $-180°$).
hape might be explained. It could
ientation domain) is greater when
ique; alternatively, the spread of
of A is greater when B is oblique
difficult to design an experiment
. If we set B to some orientation
f the angle-expansion curve first
econdly with A at a smaller angle

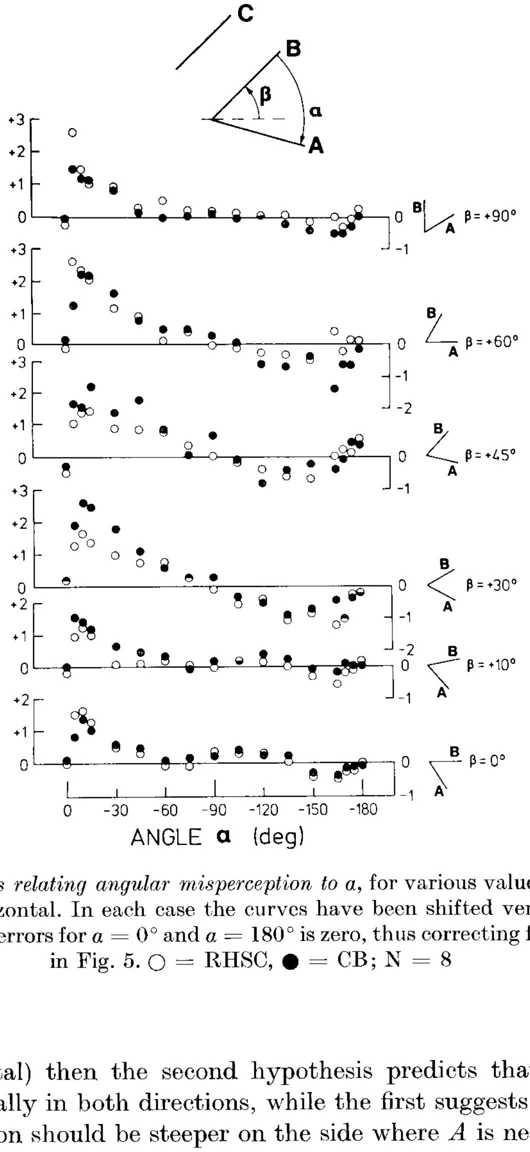


Fig. 6. *A set of curves relating angular misperception to a*, for various values of β, the inclination of B to the horizontal. In each case the curves have been shifted vertically so that the mean of the constant errors for $a = 0°$ and $a = 180°$ is zero, thus correcting for the effect shown in Fig. 5. ○ = RHSC, ● = CB; N = 8

(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.

Figure 7 shows the results of two such experiments, with β at $+30°$ and $+22.5°$: the distortion in fact falls off slightly more rapidly when A is nearer the oblique, suggesting that the changes in shape of the curves in Fig. 6 are due to variations in the properties of A's "output-field" rather than B's "input-field".

If angle-expansion is due to lateral inhibition in the orientation domain, then this implies that the inhibitory "skirts" shown in Fig. 1 are *wider* for orientations near the principal meridians than near the obliques. This in turn means that the inhibitory flanks of the sensitivity profile, or tuning curve, for individual neurones optimally sensitive to vertical or horizontal are *narrower* than those for cells tuned to oblique orientations (assuming even spacing along the orientation

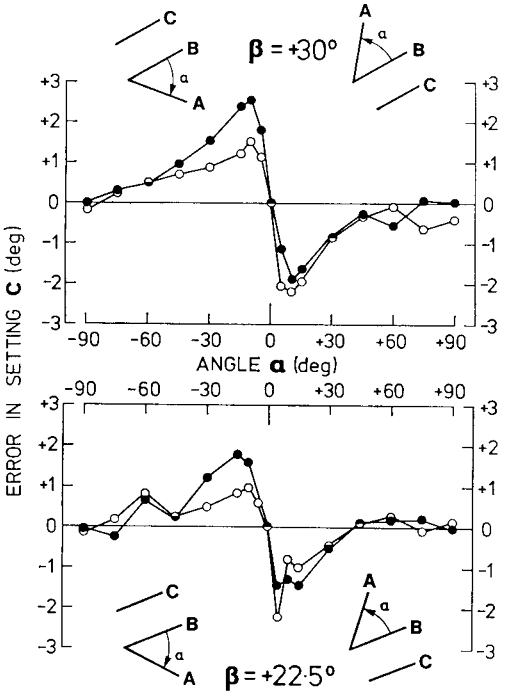


Fig. 7. *Showing the asymmetry in the angle-expansion curve*, with $\beta = +30°$ (upper graph) and $\beta = +22.5°$ (lower graph), between effects when A is rotated clockwise and anti-clockwise from B. The curves have again been shifted so that the error at $a = 0°$ is zero. ● = RHSC, ○ = CB, N = 8

domain). The data of Fig. 6 also imply that the form of the excitatory portions of the tuning curves or activity profiles are not markedly dissimilar at different orientations — a conclusion reached in quite another way by Bouma and Andriessen (1968).

Inhibition or Adaptation?

There is an obvious analogy between this phenomenon of simultaneous interaction between orientations and the successive *tilt after-effect* described by Gibson (1937). If a tilted line is viewed for half a minute or so, a vertical line subsequently exposed to the same retinal region seems temporarily tilted in the opposite direction. This after-effect has been interpreted in terms of a process of "adaptation", "satiation" or "fatigue" of orientation detectors (Sutherland, 1961; Coltheart, 1971). Neurones in the visual cortex are supposed gradually to decrease in sensitivity during prolonged strong stimulation. Such a process might not only account for the successive after-effect but also explain our simultaneous angle-expansion, if one assumes that line A in our stimulus caused such adaptation of detectors tuned to its orientation and similar angles.

Intuitively this seems unlikely because adaptation is usually found to have a long time-course for induction and decay (e.g. Blakemore and Campbell, 1969).

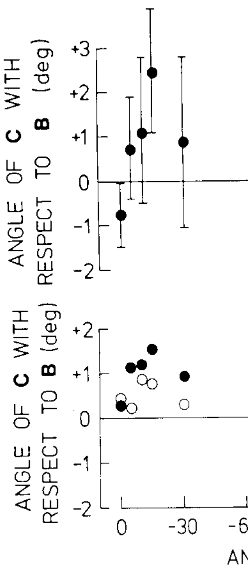
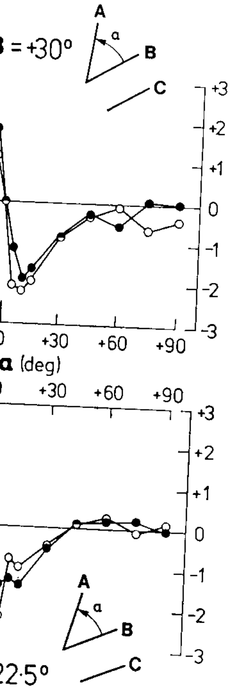


Fig. 8. *A) Showing results for* $\beta = +30°$,
2 msec every 5 sec). The bars show two s
observations. There is no correction for cc
$\beta = +30°$ when the subject was asked to
● = CB, ○ = RHSC; N

However, whatever process induces t
it must have quite a short time-scale.
to move his eyes at will and in fact
B and C during his settings. If the in
very slowly, it is hard to understan
adequately exposed to A to generat
decline of this adaptation would mea
should be equally subject to the infl
sequently no distortion should have
were due to slow-acting adaptation.
fast-acting and can take the form ei
inhibition) or of an added negative
simultaneous angle expansion has a
shorter than most visual after-effects

The Time-Cou

We did two types of experiment
effect. In the first the stimulus disp
mately 2 msec every 5 sec, instead o
while increasing the variance of the s
on the magnitude of the distortions (F
for the production of angle expansion



sion curve, with $\beta = +30°$ (upper graph)
en A is rotated clockwise and anti-clockwise
at the error at $a = 0°$ is zero. ● = RHSC,
= 8

the form of the excitatory portions of
not markedly dissimilar at different
another way by Bouma and Andries-

ptation?

phenomenon of simultaneous inter-
e *tilt after-effect* described by Gibson
te or so, a vertical line subsequently
porarily tilted in the opposite direc-
terms of a process of "adaptation",
ctors (Sutherland, 1961; Coltheart,
sed gradually to decrease in sensiti-
h a process might not only account
our simultaneous angle-expansion,
used such adaptation of detectors

ptation is usually found to have a
. Blakemore and Campbell, 1969).

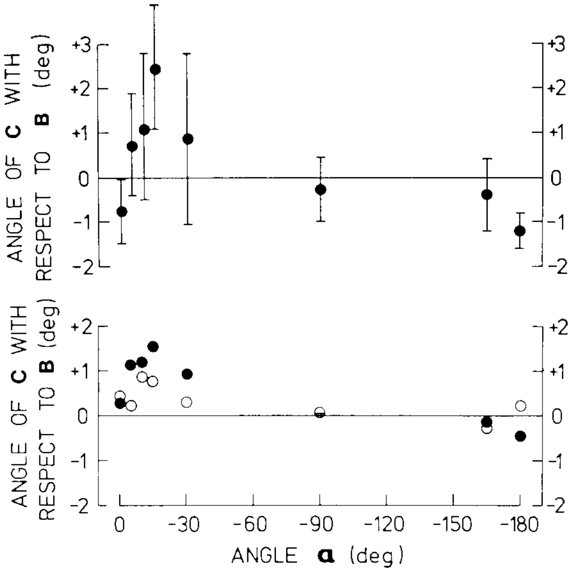


Fig. 8. *A) Showing results for $\beta = +30°$*, obtained using only very brief exposures (about 2 msec every 5 sec). The bars show two standard errors on each side of the mean of eight observations. There is no correction for constant error. Subject CB. B) Showing results for $\beta = +30°$ when the subject was asked to make settings as rapidly as possible (2—4 sec). ● = CB, ○ = RHSC; N = 8; no constant-error correction

However, whatever process induces the angular changes that we have observed, it must have quite a short time-scale. Remember that the observer was permitted to move his eyes at will and in fact he usually looked back and forth between *B* and *C* during his settings. If the influence of *A* were to build up and die away very slowly, it is hard to understand how any one part of the retina could be adequately exposed to *A* to generate adaptation: even if it did, then the slow decline of this adaptation would mean that during eye movements both *B* and *C* should be equally subject to the influence of the adaptation caused by *A*. Consequently no distortion should have been measurable by our method if the effect were due to slow-acting adaptation. Inhibition, on the other hand, is essentially fast-acting and can take the form either of a change in gain (as in pre-synaptic inhibition) or of an added negative signal. The results that follow show that simultaneous angle expansion has a time-course at least an order of magnitude shorter than most visual after-effects.

The Time-Course of the Phenomenon

We did two types of experiment to demonstrate the short time-scale of the effect. In the first the stimulus display was presented in exposures of approximately 2 msec every 5 sec, instead of being shown continuously. This procedure, while increasing the variance of the settings enormously, had no systematic effect on the magnitude of the distortions (Fig. 8A). Thus long exposures are not essential for the production of angle expansion. On the other hand, it might be argued that

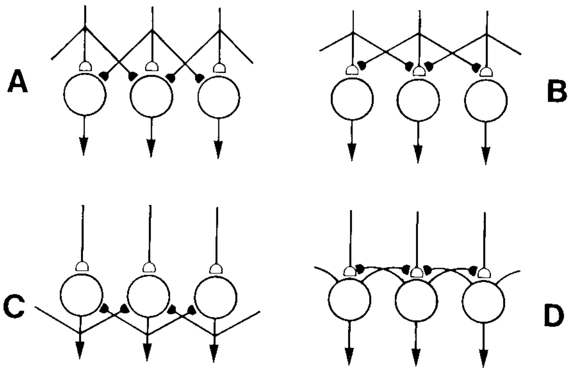


Fig. 9. *Showing four possible configurations of lateral inhibition.* ○— = excitatory ending, ●— = inhibitory ending: the path of transmission of information is downwards. *A* and *B* are non-recurrent, *C* and *D* recurrent: *A* and *C* are post-synaptic, *B* and *D* pre-synaptic. *D* is the only one of these simple arrangements that could easily account for the observed properties of angle expansion

although the exposures were short, the system could perhaps have a long decay time-constant, being "recharged" by the successive short exposures so that the effect builds up over the half minute or so that is required to make each setting.

For this reason we repeated the original procedure with the display left on continuously, but with the subject making each setting as quickly as possible, in 2 to 4 sec, and then looking away for at least 15 sec before repeating the procedure. The results of this experiment are shown in Fig. 8B; again there is merely a slight reduction in the size of the effect.

Thus we conclude that the process producing this phenomenon has a characteristic growth time-constant of less than a second or two.

Disinhibition

Inhibition between neurones may be either *recurrent* (when the inhibition to a cell or its input is delivered at some point proximal to the inhibitory output) or *non-recurrent* (when each is inhibited at a point distal to the inhibitory output). Various alternative forms of inhibitory interconnection are illustrated in Fig. 9 and they are considered in more detail in the *Discussion.*

Our final series of experiments show that these perceptual distortions of angle suffer *disinhibition* if another line is added to the angular display: therefore if an inhibitory mechanism underlies angle expansion, it must be of the recurrent type (Fig. 9C or D).

For these experiments the display was a little different from that in Fig. 3. A fourth line, *D*, also 1 deg long, was added, joining the apex of *A* and *B*. The orientation of *D* could be independently changed, relative to *A* and *B*. Our procedure was to set *A* and *B* at such an angle that *B* suffered a large apparent distortion in orientation and then to vary the orientation of *D* systematically, while continuing to measure the apparent angle of *B*. If there was no interaction between the influences of *A* and *D* on *B*, and the system was a simple linear one, then one

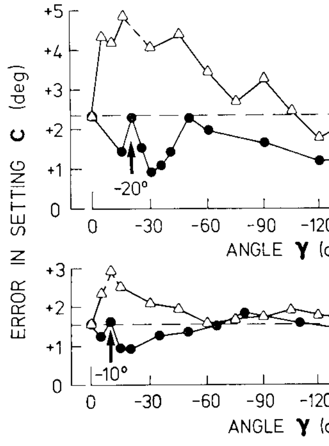


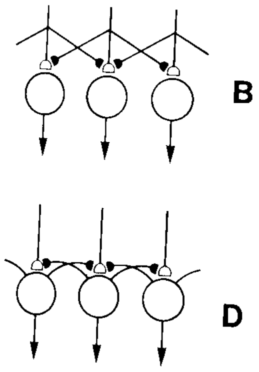
Fig. 10. *Showing disinhibition.* A fourth line
with *B* (see inset). Above: β was fixed at +45
of γ. Below: The same measurements with β
line shows the error due to *A* alone; the ope
simple linear addition of the effects of *A* ar
circles show the actually observed values: it
D when close to *A*, in fact *reduces* the degr
cons

might expect that the final angular dis
due to *A* and that due to *D* (except wh
and thus was not visible: $\alpha = \gamma$).

Figure 10 (open triangles) shows th
simple addition of this sort for two d
for $\beta = +45°$, $\alpha = -20°$: the open tr
priate curve in Fig. 6 ($B = +45°$) displ
equal to the distortion caused by line
parallel-setting errors of Fig. 5. The ope
distortion of *B*, in the presence of bot
of the latter, assuming simple summat
graph is similar but is for $\beta = 0°$ and

The actual data obtained are plott
seen that, far from increasing the dis
line, *D*, is everywhere to *decrease* the
greater, the nearer *D* is to *A*.

D must be considered, therefore,
other words, causing *disinhibition.* W
theoretical interpretation that we dec
angles of *A* and *B* and also using tw
shows that disinhibition is clearly ope
cularly marked when line *B* is at +45°
close in orientation to A (5° or 10° a



teral inhibition. ○— = excitatory ending,
n of information is downwards. *A* and *B* are
st-synaptic, *B* and *D* pre-synaptic. *D* is the
easily account for the observed properties
nsion

em could perhaps have a long decay
ccessive short exposures so that the
hat is required to make each setting.
l procedure with the display left on
ach setting as quickly as possible, in
15 sec before repeating the procedure.
ig. 8B; again there is merely a slight

ng this phenomenon has a character-
nd or two.

n

r *recurrent* (when the inhibition to a
oximal to the inhibitory output) or
nt distal to the inhibitory output).
connection are illustrated in Fig. 9
Discussion.

hese perceptual distortions of angle
the angular display: therefore if an
n, it must be of the recurrent type

tle different from that in Fig. 3. A
ining the apex of *A* and *B*. The
d, relative to *A* and *B*. Our proce-
suffered a large apparent distortion
n of *D* systematically, while con-
there was no interaction between
was a simple linear one, then one

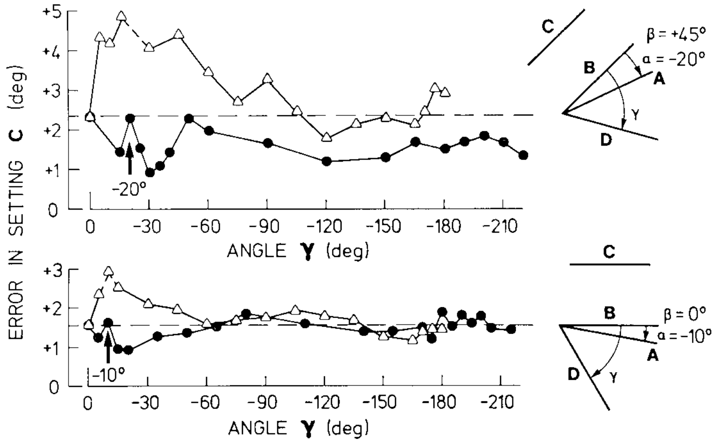


Fig. 10. *Showing disinhibition.* A fourth line *D* was added to the stimulus, forming an angle γ with *B* (see inset). Above: β was fixed at $+45°$, α at $-20°$, and the error measured as a function of γ. Below: The same measurements with $\beta = 0°$ and $\alpha = -10°$. The interrupted horizontal line shows the error due to *A* alone; the open triangles show the calculated angle expansion if simple linear addition of the effects of *A* and *D* is assumed, with no disinhibition. The solid circles show the actually observed values: it is clear that far from linear addition taking place, *D* when close to *A*, in fact *reduces* the degree of angle expansion, Subject CB; corrected for constant error

might expect that the final angular distortion of *B* would be the sum of the effect due to *A* and that due to *D* (except when *D* had exactly the same orientation as *A* and thus was not visible: $\alpha = \gamma$).

Figure 10 (open triangles) shows the expected angle-expansion curves assuming simple addition of this sort for two different configurations. The upper graph is for $\beta = +45°$, $\alpha = -20°$: the open triangles reproduce the data from the appropriate curve in Fig. 6 ($B = +45°$) displaced upwards on the ordinate by an amount equal to the distortion caused by line *A* alone. The ordinate is corrected for the parallel-setting errors of Fig. 5. The open triangles therefore represent the expected distortion of *B*, in the presence of both *A* and *D*, as a function of the orientation of the latter, assuming simple summation of the influences of *A* and *D*. The lower graph is similar but is for $\beta = 0°$ and $\alpha = -10°$.

The actual data obtained are plotted as solid circles in Fig. 10. Here it can be seen that, far from increasing the distortion of *B*, the effect of the disinhibiting line, *D*, is everywhere to *decrease* the distortion: and the degree of decrease is greater, the nearer *D* is to *A*.

D must be considered, therefore, as *inhibiting the inhibitory effect o fA* — in other words, causing *disinhibition.* We considered this result so crucial for our theoretical interpretation that we decided to repeat the observation with other angles of *A* and *B* and also using two untrained and naive subjects. Figure 11 shows that disinhibition is clearly operating in each example, and it seems particularly marked when line *B* is at $+45°$. In every single case in Fig. 11, when *D* was close in orientation to A (5° or 10° away), there was a significant reduction (p

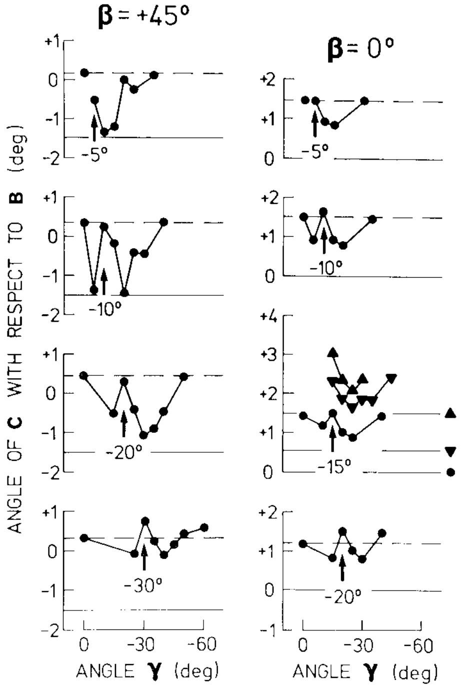


Fig. 11. *Details of the region in which D is near A for a number of runs of the same type as in Fig. 10*, for the various parameters shown. On the left, $\beta = +45°$; $\alpha = -5°, -10°, -20°, -30°$; On the right, $\beta = 0°$; $\alpha = -5°, -10°, -15°, -20°$; ● = CB, ▲ = MR, ▼ = BH; N = 8. Note the great variation in constant parallel setting error at $\beta = 0°$, $\alpha = -15°$ for the three subjects. There is no correction for constant errors, but the setting of C in the absence of A and D is shown as a solid horizontal line: the interrupted lines, as in Fig. 10, show the errors due to A alone

<0.05) in the distortion of B. (Incidentally, Fig. 11 shows especially well that the constant errors in parallel setting can vary considerably from one subject to another.)

Discussion

We argued initially that lateral inhibition within a network of orientation detectors, perhaps identifiable with visual cortical neurones, ought to result in the apparent expansion of acute angles and (by the same argument) contraction of obtuse angles.

The results have shown that such distortions of orientation do occur and that they might be due to recurrent inhibition between orientation detectors. Moreover, neurones optimally sensitive to diagonal lines might draw their inhibitory input from a broader range of orientations than cells tuned to horizontal or vertical. Can one deduce anything about the actual excitation spread in the orientation domain, illustrated schematically in Fig. 1?

If inhibition and excitation are really both linear, as Fig. 1 demands, then our data (Fig. 6) set rather stringent limits on the shape of the actual distributions of

---

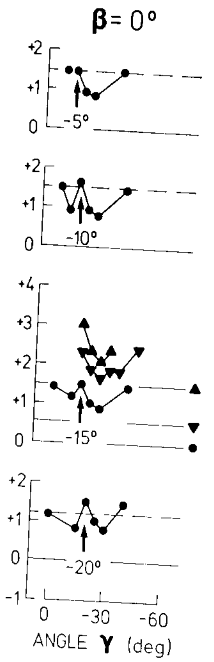
activity. First of all, since we find shif
follow that the convex-topped, excitat
narrower than twice this, i.e., 6°. Simi
line A forming an angle of only 5° wit
centre of the distribution the inhibitor
started. Unfortunately, it is extremely
of less than 5° because the thickness o
near the apex. But it is difficult to be
expansion with an angle of, say, 3°, if t
swift descent between 3° and 5°, whic
ance to the functions of Fig. 1, is neces
assumption that excitation and inhibit
On the other hand, if the recurrent i
in some other way to reduce the *gain*
angle expansion with angles smaller t
able. We therefore conclude tentati
orientation detectors could be presyna

Other theorists have used neuronal
effects and visual illusions. For insta
considered the possibility that simpl
analysers, in the *position domain* wou
(depending on the separation) of nei
account for the contour displacement
Köhler and Wallach (1944) and in ce
figure (see Luckiesh, 1922, Fig. 18). A
involving angles would lead one to e
the angles. Such inhibitory interaction
quate to account entirely for angle ex
the distortion should be limited to th
line appears rotated as a whole.

Our explanation, in terms of late
account for both the magnitude of the
for the position of the lines, at least u

Chiang (1968) has speculated tha
expansion might offer a satisfactory e
complex, illusions (Fig. 2), although
at the vertices) has not been generally
illusions considered by Chiang still o
from the illusion figures (Cumming, 1
of course, be substantially affected by
The application of our model to co
problem. In certain cases it may be po
perceptual distortion in terms of ap
Ollerearnshaw, 1972).

The fact that many illusions pers
dots placed at the vertices and the en
no special problem if we allow orienta



A for a number of runs of the same type as in he left, $\beta = +45°$; $\alpha = -5°, -10°, -20°,$ $-15°, -20°$; ● = CB, ▲ = MR, ▼ = BH; llel setting error at $\beta = 0°$, $\alpha = -15°$ for the errors, but the setting of C in the absence of terrupted lines, as in Fig. 10, show the errors lone

Fig. 11 shows especially well that the ry considerably from one subject to

on

ion within a network of orientation rtical neurones, ought to result in the the same argument) contraction of

ions of orientation do occur and that etween orientation detectors. More- al lines might draw their inhibitory an cells tuned to horizontal or verti- l excitation spread in the orientation

h linear, as Fig. 1 demands, then our 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, then already at only 5° from the centre of the distribution the inhibitory "skirt" (with downward slope) must have 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, 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 (Fig. 9D) 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.

Other theorists have used neuronal inhibition in their models of figural after-effects and visual illusions. For instance, Ganz (1966) and von Békésy (1967) considered the possibility that simple lateral inhibition between point or line analysers, in the *position domain* would cause apparent attraction or repulsion (depending on the separation) of neighbouring contours. Such a process might account for the contour displacement that occurs in the figural after-effects of Köhler and Wallach (1944) and in certain visual illusions, such as the Delboeuf figure (see Luckiesh, 1922, Fig. 18). An extension of the same argument to figures involving angles would lead one to expect small distortions near the vertices of the angles. Such inhibitory interaction in the position domain is, however, inadequate to account entirely for angle expansion. As Sutherland (1961) pointed out, the distortion should be limited to the vertex of the figure, whereas in fact each line appears rotated as a whole.

Our explanation, in terms of lateral inhibition in the *orientation domain* can account for both the magnitude of the distortions and the fact that they generalize for the position of the lines, at least up to about 40 min (Fig. 4A).

Chiang (1968) has speculated that the simple phenomenon of acute angle expansion might offer a satisfactory explanation of many well-known, but more complex, illusions (Fig. 2), although the mechanism he proposed ("diffraction" at the vertices) has not been generally accepted, on the grounds that many of the illusions considered by Chiang still occur when the vertices have been removed from the illusion figures (Cumming, 1968). A mechanism such as ours would not, of course, be substantially affected by the presence or absence of vertices *per se*. The application of our model to complex visual illusions is, however, a tricky problem. In certain cases it may be possible to account for some, but not all, of the perceptual distortion in terms of apparent changes of orientation (Hotopf and Ollerearnshaw, 1972).

The fact that many illusions persist when the figure is represented only by dots placed at the vertices and the ends of the imaginary lines (Coren, 1970) poses no special problem if we allow orientation detectors to be adequately stimulated by pairs of dots at the appropriate orientations. Finally, there is a whole class of illusions, such as the Müller-Lyer figure, where there are apparent changes in the *size* of elements of the stimulus: we can see no way to account for such illusions in terms of angular distortion, although an explanation has been offered on the basis of inappropriate constancy scaling within such figures (Gregory, 1966).

Perhaps the strongest circumstantial evidence for our theory is the fact that it is a physiological reality in the cat's visual cortex. Certainly the orientation selective cells are arranged in a manner that would facilitate inhibition in the orientation domain. Within a single block or *column* of cortical tissue all the neurones respond to the same orientation and there is usually rather a small change in preferred orientation between one column and its neighbours (Hubel and Wiesel, 1962, 1963, 1968). Thus any cortical cell is surrounded immediately by neurones with identical orientational preference and, in the nearby columns, by neurones with slightly different preferences. Thus a simple process of inhibition between cells in each column and the immediately neighbouring columns would result in the mechanism that we propose. Creutzfeldt's group (for example Benevento *et al.*, 1972) have provided direct evidence from quasi-intracellular recordings that intra-cortical inhibition does occur. Blakemore and Tobin (1972 and in preparation) have shown that cat cortical cells are subject to inhibition from a broad range of orientations centred on the optimum angle.

So it appears that orientation detectors receive two orientationally-tuned inputs, a broad *excitatory orientational weighting function*, and an even broader *inhibitory orientational weighting function* contributed by nearby detectors. Both weighting functions peak at the same angle and the interaction between the two produces the typical narrow tuning of cortical cells. It is this sharpening of the response characteristics that provides the advantage of lateral inhibition in the orientation domain. Angle expansion is perhaps a merely unfortunate side-effect.

Acknowledgements: We are grateful to M. A. Georgeson for taking part in some of the early experiments. This research was supported by a grant (No. G970/807/B) to C.B. from the Medical Research Council, London.

References

Andrews, D. P.: Perception of contours in the central fovea. Nature (Lond.) **205**, 1218—1220 (1965).

— Perception of contour orientation in the central fovea. Vision Res. **7**, 975—1013 (1967).

von Békésy, G.: Sensory Inhibition. Princeton: University Press 1967.

Benevento, L. A., Creutzfeldt, O. D., Kuhnt, U.: Significance of intracortical inhibition in the visual cortex. Nature New Biology **238**, 124—126 (1972).

Blakemore, C., Campbell, F. W.: On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. J. Physiol. (Lond.) **203**, 237—260 (1969).

— Carpenter, R. H. S., Georgeson, M. A.: Lateral inhibition between orientation detectors in the human visual system. Nature (Lond.) **228**, 37—39 (1970).

— Tobin, E. A.: Lateral inhibition between orientation detectors in the cat's visual cortex. Exp. Brain Res. **15**, 439—440 (1972).

Bouma, H., Andriessen, J. J.: Perceived orientation of isolated line segments. Vision Res. **8**, 493—507 (1968).

— — Induced changes in the perceived orientation of line segments. Vision Res. **10**, 333—349 (1970).

Chiang, C.: A new theory to explain geometr
tion and Psychophysics **4**, 174—176 (196

Coltheart, M.: Visual feature-analyzers and
78, 114—121 (1971).

Coren, S.: Lateral inhibition and geometric
(1970).

Cronly-Dillon, J. R.: Units sensitive to directi
(Lond.) **203**, 214—215 (1964).

Cumming, G. D.: A criticism of the diffractio
and Psychophysics **4**, 375—376 (1968).

Fisher, G. H.: An experimental study of a
356—366 (1969).

Ganz, L.: Mechanism of the figural after-effe

Gibson, J. J.: Adaptation, after-effect and co
taneous contrast and the areal restriction
(1937).

Gregory, R. L.: Eye and Brain: the Psycholo
Weidenfield and Nicolson 1966.

Hotopf, W. H. N., Ollerearnshaw, C.: The reg
dorff illusion. Brit. J. Psychol. **63**, 359—

Hubel, D. H., Wiesel, T. N.: Receptive fields,
in the cat's visual cortex. J. Physiol. (Lo

— — Shape and arrangement of columns
559—568 (1963).

— — Receptive fields and functional archite
195, 215—243 (1968).

Köhler, W., Wallach, H.: Figural after-eff
Amer. Philos. Soc. **88**, 269—357 (1944).

Levick, W. R.: Receptive fields and trigger f
rabbit's retina. J. Physiol. (Lond.) **188**,

Luckiesh, M.: Visual illusions: Their Cause
Van Nostrand 1922.

Marg, E., Adams, J. E., Rutkin, B.: Rece
Experientia (Basel) **24**, 348—350 (1968).

Maturana, H. R., Frenk, S.: Directional mov
retina. Science **142**, 977—979 (1963).

Michael, C. R.: Visual receptive fields of
ground squirrel. J. Neurophysiol, **35**, 81

Nelson, J.: Illusions as the Mach bands of c
on Contour interaction in the visual syst

Sutherland, N. S.: Figural after-effects and a
(1961).

Wallace, G. K.: The critical distance of in
Psychophysics **5**, 261—264 (1969).

Weintraub, D. J., Virsu, V.: Estimating the
Perception and Psychophysics **11**, 277—

itations. Finally, there is a whole class of
where there are apparent changes in the
see no way to account for such illusions in
explanation has been offered on the basis
n such figures (Gregory, 1966).

evidence for our theory is the fact that
visual cortex. Certainly the orientation
that would facilitate inhibition in the
ock or *column* of cortical tissue all the
on and there is usually rather a small
one column and its neighbours (Hubel
cortical cell is surrounded immediately
reference and, in the nearby columns, by
es. Thus a simple process of inhibition
mediately neighbouring columns would
ose. Creutzfeldt's group (for example
irect evidence from quasi-intracellular
oes occur. Blakemore and Tobin (1972
cortical cells are subject to inhibition
l on the optimum angle.

tors receive two orientationally-tuned
ighting function, and an even broader
contributed by nearby detectors. Both
e and the interaction between the two
tical cells. It is this sharpening of the
advantage of lateral inhibition in the
haps a merely unfortunate side-effect.

eorgeson for taking part in some of the early
grant (No. G970/807/B) to C.B. from the

ces

tral fovea. Nature (Lond.) **205**, 1218—1220

al fovea. Vision Res. **7**, 975—1013 (1967).
niversity Press 1967.
ignificance of intracortical inhibition in the
26 (1972).
of neurones in the human visual system
of retinal images. J. Physiol. (Lond.) **203**,

nhibition between orientation detectors in
37—39 (1970).
ation detectors in the cat's visual cortex.

n of isolated line segments. Vision Res. **8**,

of line segments. Vision Res. **10**, 333—349

Chiang, C.: A new theory to explain geometrical illusions produced by crossing lines. Perception and Psychophysics **4**, 174—176 (1968).

Coltheart, M.: Visual feature-analyzers and after-effects of tilt and curvature. Psychol. Rev. **78**, 114—121 (1971).

Coren, S.: Lateral inhibition and geometric illusions. Quart. J. exp. Psychol. **22**, 274—278 (1970).

Cronly-Dillon, J.R.: Units sensitive to direction of movement in goldfish optic tectum. Nature (Lond.) **203**, 214—215 (1964).

Cumming, G.D.: A criticism of the diffraction theory of some geometric illusions. Perception and Psychophysics **4**, 375—376 (1968).

Fisher, G.H.: An experimental study of angular subtension. Quart. J. exp. Psychol. **21**, 356—366 (1969).

Ganz, L.: Mechanism of the figural after-effect. Psychol. Rev. **73**, 128—150 (1966).

Gibson, J.J.: Adaptation, after-effect and contrast in the perception of tilted lines: II. Simultaneous contrast and the areal restriction of the after-effect. J. exp. Psychol. **20**, 553—569 (1937).

Gregory, R.L.: Eye and Brain: the Psychology of Seeing. World University Library. London: Weidenfield and Nicolson 1966.

Hotopf, W.H.N., Ollerearnshaw, C.: The regression to right angles tendency and the Poggendorff illusion. Brit. J. Psychol. **63**, 359—367 (1972).

Hubel, D.H., Wiesel, T.N.: Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. J. Physiol. (Lond.) **160**, 106—154 (1962).

— — Shape and arrangement of columns in cat's striate cortex. J. Physiol. (Lond.) **165**, 559—568 (1963).

— — Receptive fields and functional architecture of monkey striate cortex. J. Physiol. (Lond.) **195**, 215—243 (1968).

Köhler, W., Wallach, H.: Figural after-effects: an investigation of visual processes. Proc. Amer. Philos. Soc. **88**, 269—357 (1944).

Levick, W.R.: Receptive fields and trigger features of ganglion cells in the visual streak of the rabbit's retina. J. Physiol. (Lond.) **188**, 285—307 (1967).

Luckiesh, M.: Visual illusions: Their Causes, Characteristics and Applications. New York: Van Nostrand 1922.

Marg, E., Adams, J.E., Rutkin, B.: Receptive fields of cells in the human visual cortex. Experientia (Basel) **24**, 348—350 (1968).

Maturana, H.R., Frenk, S.: Directional movement and horizontal edge detectors in the pigeon retina. Science **142**, 977—979 (1963).

Michael, C.R.: Visual receptive fields of single neurones in the superior colliculus of the ground squirrel. J. Neurophysiol, **35**, 815—832 (1972).

Nelson, J.: Illusions as the Mach bands of contour detectors. Paper presented at a conference on Contour interaction in the visual system: Cambridge: 1971.

Sutherland, N.S.: Figural after-effects and apparent size. Quart. J. exp. Psychol. **13**, 222—228 (1961).

Wallace, G.K.: The critical distance of interaction in the Zöllner illusion. Perception and Psychophysics **5**, 261—264 (1969).

Weintraub, D.J., Virsu, V.: Estimating the vertex of converging lines: Angle misperception? Perception and Psychophysics **11**, 277—283 (1972).

Dr. R.H.S. Carpenter
The Physiological Laboratory
Cambridge CB2 3EG
England