Article:

Tolhurst, David and Thompson, Peter Gage (1975) Orientation illusions and after-effects:inhibition between channels. Vision Research. pp. 967-972. ISSN: 0042-6989

Vision Res. Vol. 15. pp. 967-972. Pergamon Press 1975. Printed in Great Britain.

ORIENTATION ILLUSIONS AND AFTER-EFFECTS: INHIBITION BETWEEN CHANNELS

D. J. TOLHURST and P. G. THOMPSON
The Physiological Laboratory, Cambridge CB2 3EG, and
The Psychological Laboratory, Cambridge CB2 3EB, England

(*Received* 9 *December* 1974)

Abstract—The apparent tilt from vertical has been examined for vertical sinusoidal gratings in the presence of an inducing grating which was tilted 12° from vertical. The amount of apparent tilt depended on the contrast of the test grating. At high test contrasts, the grating appeared to be tilted about 2° clockwise; at low contrasts, near threshold, there was little or no apparent tilt. If the inducing grating and test grating were not contiguous but were separated by about 0·4°, there was no apparent tilt at any test contrast. The detection threshold for the test grating was elevated by the inducing grating only when the whole of the test grating was close to the inducing grating. It is argued that these results can be explained if there is an inhibitory interaction between detectors responding to similar orientations and subserving similar parts of the visual field.

INTRODUCTION

Viewing a grating for a few seconds may cause a subsequently-viewed grating in the same region of the visual field to appear distorted in several ways. First, its apparent orientation may be changed, the tilt after-effect (Vernon, 1934; Gibson and Radner, 1937). Second, its apparent spatial-frequency may be changed, the spatial-frequency after-effect (Blakemore and Sutton, 1969). Third, its detection threshold may be elevated (Sekuler and Ganz, 1963; Gilinsky, 1968; Blakemore and Campbell, 1969).

As well as these "after-effects", a grating may be responsible for simultaneous effects: a second grating presented simultaneously, either surrounded by or superimposed on the first grating, may have its appearance changed. Simultaneous orientation effects are well known in the form of several illusions (e.g. Hering, Zöllner and Pogendorff); and more recently, Mackay (1973) has demonstrated a simultaneous spatial-frequency illusion.

There are several similarities between the successive and simultaneous effects. First, in both the orientation and spatial-frequency domains, the after-effect and simultaneous illusion are of comparable magnitude. Second, the simultaneous orientation illusion and the threshold-elevation after-effect show similar spatial-frequency specificity (Georgeson, 1973; Pantle and Sekuler, 1968; Blakemore and Campbell, 1969): as the spatial-frequency of the inducing or adapting grating is made more similar to that of the test grating, so the illusion or after-effect becomes stronger. Third, a similar dependence on the difference between the test and inducing orientations has been found for the threshold-elevation after-effect and for the spatial-frequency after-effect (Blakemore and Nachmias, 1971) and for the simultaneous spatial-frequency illusion (Klein, Stromeyer and Ganz, 1974).

Such quantitative similarities between the successive and simultaneous effects strongly suggest that both types of phenomenon have one underlying cause. There is, however, a problem to be overcome before it can be accepted that the simultaneous and successive illusions arise from a single mechanism. Adaptation causes an elevation of the detection threshold for the test stimulus; while the inducing grating causes no change in threshold for the test grating in the simultaneous illusion (Klein *et al.*, 1974). These authors argue that this observation rules out the suggestion that the successive and simultaneous illusions arise from one cause. Instead, they propose a two-stage model of detection.

The purpose of our paper is to show that a two-stage model is unneccessary. In fact, it is not unexpected that the inducing grating causes little or no change in the detection threshold for the test stimulus even though it may change the appearance of the test grating. The observation can be reconciled qualitatively with the hypothesis that the after-effects of adaptation and the simultaneous illusions arise from the same cause.

Rationale for experiments

Wallace (1969), Wallace and Crampin (1969), and Blakemore, Carpenter and Georgeson (1970) have suggested that inhibition between populations of orientation-specific detectors is responsible for the apparent tilt in simultaneous illusions. A stimulus at one orientation will excite a population of detectors: the most excited detectors will be those optimally sensitive to that orientation, but detectors optimally sensitive to other orientations will also be excited, though less strongly. If a second stimulus is added at a nearby orientation, the detectors responding to this stimulus will inhibit those responding to the first. The amount of inhibition will fall off as the optimal orientations of the interacting detectors are made more different. Thus, the population of detectors responding to the first stimulus will not be uniformly inhibited, and it is this non-uniformity which is thought to give rise to the illusion of apparent tilt (Carpenter and Blakemore, 1973). If some of the detectors are inhibited by the second stimulus, it might be expected that the detection threshold for the first stimulus would be elevated.

Klein *et al.* (1974) found that the appearance of a test grating could be changed by surrounding it with an annulus of another grating. However, there was no change in the threshold for the test grating. At first sight, this might suggest that the model of inhibitory interaction is inadequate, and Klein *et al.* have proposed a two-stage model. At the first stage, there are detectors which do not inhibit each other; they determine the detection threshold for the stimulus. These detectors feed into a second stage (of "integrators") which do inhibit each other. Activity in the "integrators" determines the percept evoked by a stimulus. Thus, in simultaneous illusions, there is no change in threshold because the detectors in the first stage do not inhibit each other; the integrators do inhibit each other and thus cause an illusion of apparent tilt.

Klein *et al.* further proposed that the first stage of detectors could become desensitized by adaptation, resulting in threshold elevation. The input to the second stage of "integrators" will be distorted by the desensitisation of some of the detectors, resulting in an illusion of apparent tilt.

Erection of such a two-stage model is unneccessary. Wallace (1969) found that, not surprisingly, the simultaneous tilt illusion became weaker if the inducing and test figures were separated in space. There was *no* apparent tilt if the figures were separated by a degree of visual angle. Presumably, the inhibitory interactions are localized to an area close to the stimulus. This finding must be recognized when considering the results of experiments similar to those of Klein *et al.*, where the inducing grating *surrounds* the test stimulus and is not superimposed on it. The periphery of the test grating lies close to the inducing grating, whereas the centre of the test stimulus is distant from the inducing grating. One might, therefore, expect the periphery of the test grating to appear very distorted, while the centre of the test grating may appear less distorted or may not be distorted at all. Perhaps, we can explain how a test grating can appear distorted although its detection threshold is unchanged. The grating may be detected by detectors responding to the centre of the test grating, these detectors lying so far from the inducing grating that they are not inhibited. But, a higher contrast test grating may appear distorted because of the contribution of detectors responding to the periphery of the test grating.

This paper tests some predictions of this hypothesis and shows that the centre and periphery of the test grating are affected to different degrees by the *surrounding* inducing grating.

METHODS

The apparent orientation of a vertical sinusoidal grating was determined by adjusting the orientation of a thin, bright line until it appeared to be parallel to the test grating. The apparent orientation of the test grating was changed by (a) surrounding the test grating with an annulus of tilted grating or (b) adapting to a tilted grating.

Stimulus configuration

(*a*) *Simultaneous illusion.* The vertical sinusoidal test grating of spatial-frequency 9 c/deg was displayed on the face of a cathode ray tube (P31 phosphor) by modulating a raster. The screen was viewed from a distance of 114 in. It was circular and subtended 1·5°, and had a mean luminance of 100 cd/m^2. The inducing grating was concentric with the test grating, but its centre was masked out: it covered an annular area with an inner diameter of 1·5° and an outer diameter of 3·5°. The spatial-frequency of the inducing grating was 9 c/deg and its mean luminance was also 100 cd/m^2. This grating had a square-wave luminance profile. It was tilted 12° anti-clockwise from the vertical.

The contrast of the gratings was defined as

$$\frac{L_{max} - L_{min}}{L_{max} + L_{min}}$$

where L is the luminance. The contrast of the test grating was a variable in the experiments. The contrast of the inducing grating was kept constant and was at least 0·7.

The comparison line, whose orientation was variable, was visible in the same plane as the test and inducing gratings. It was 1·5° in length and could be rotated about its centre which was 4° to the right of the centre of the test grating. The line was generated on an oscilloscope by feeding a triangular-wave of 100 Hz into the y-axis and a similar triangular-wave into the x-axis. The amplitude of the signal to the y-axis was fixed while the amplitude and sign of the signal to the x-axis were varied to change the line's orientation. The stimulus configuration for this part of the experiment is illustrated in Fig. 1.

(*b*) *Adaptation.* The test stimulus was identical to that used in the experiments on the simultaneous illusion, and the comparison line was again 4° to the right of the centre of the test grating. The adapting grating was similar to the inducing grating (above) except that it was a disc with diameter of 3·5° and was centred at least 10° from the centre of the test grating.

Control of the orientation of the comparison line

The orientation of the line was controlled by a PDP-11/20 Digital computer which varied the amplitude of the triangular-wave fed to the x-axis of the oscilloscope. At the beginning of a trial, the line was presented at an orientation chosen randomly by the computer, but within 5° of the previous setting for that particular stimulus. The orientation of the line was then under the control of the observer who was in charge of two buttons. One button caused the computer to tilt the line 0·25° clockwise; the other button caused a 0·25° anti-clockwise shift.

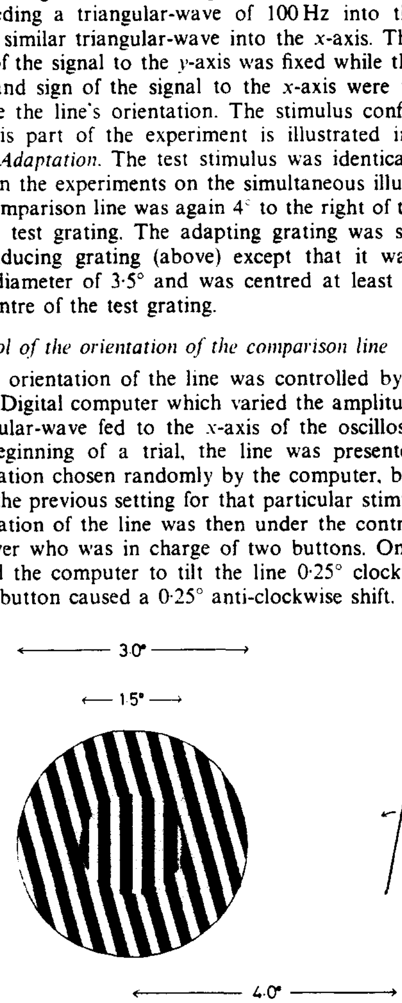

Fig. 1. Stimulus configuration for investigating the simultaneous tilt illusion, used for the experiments in Figs. 2 and 3. The test stimulus was a sinusoidal grating of 9 c/deg covering an area with diameter of 1·5°. The test grating was vertically oriented. The test grating could be surrounded by an annular inducing grating, internal diameter of 1·5° and external diameter of 3·5°. Its spatial frequency was also 9 c/deg, but it was tilted 12° anti-clockwise from the vertical. A comparison line, whose orientation was variable under the observer's control, was centred 4° to the right of the centre of the test grating. The line was 1·5° long and rotated about its centre.

The observer repeatedly pushed the buttons as he thought appropriate, and the computer recorded the orientations at which the observer changed from tilting the line clockwise to tilting it anticlockwise, or vice versa. When the direction of orientation change had reversed 4 times, the trial ended. The apparent orientation was taken as the mean of the four orientations at which a reversal occurred. A trial lasted less than 10 sec.

Procedure

Initially, the contrast threshold for the test grating was determined by the method of adjustment. Ten test contrasts were then chosen for the main part of the experiment. The lowest contrast was about 0·05 log units above threshold and the interval between successive contrasts was 0·15 log units.

The apparent orientations of the test gratings were first determined before adaptation and in the absence of the annular inducing grating. The test grating was presented at the ten contrasts and the observer, *while viewing the centre of the test grating*, adjusted the orientation of the line. The ten contrasts were presented once each in a random order chosen by the computer. This process was repeated 5 times so that the value taken for the apparent orientation at each contrast was the mean of five independent settings, with a standard error of about 0·25°.

(*a*) *Simultaneous illusion.* The contrast threshold for the test grating was determined in the presence of the inducing grating. The 10 test contrasts were the same as for the controls. The apparent orientation of each was determined 5 times, as above. The observer was instructed to view the centre of the test stimulus and to avoid looking directly at the annular grating. Between trials, he was instructed to look away from the display for about 10 sec. It was hoped that this procedure would reduce the chance of adaptation to the inducing grating.

(*b*) *Adaptation.* The observer viewed the adapting grating for 3 min, moving his gaze across it to prevent the generation of after-images. The contrast threshold for the test grating was then determined. The apparent orientation of the ten test contrasts was redetermined with 20 sec further adaptation between each trial. After adaptation, the two lowest test contrasts were no longer visible; these stimuli were ignored.

The two authors acted as observers. No artificial pupils or artificial refraction were used as the observers were emmetropic.

RESULTS

To explain how a surrounding inducing grating will cause a change in the apparent orientation of a test grating without elevating its detection threshold, we are proposing that the inhibitory influence of the inducing grating does not extend as far as the centre of the test grating. The appearance of and the threshold for the centre of the test grating should not be changed; the periphery of the test grating, lying close to the inducing grating, will have its appearance distorted and detection threshold elevated.

Informal observation of the simultaneous tilt-illusion provides support for the hypothesis. A vertical test grating was surrounded by an annulus of a grating tilted 12° anti-clockwise from the vertical. When the test grating was of moderate or high contrast, we noticed that the grating did not appear to be tilted uniformly. Rather, the centre of the test grating appeared to be nearly vertical, while 0·25–0·5° of the periphery of the test grating appeared to be tilted slightly clockwise (that part of the test grating lying nearest to the inducing grating). When the contrast of the test grating was reduced towards threshold, it was noticed that the periphery of the test grating became invisible at a higher contrast than the centre. The following experiments attempt to quantify these observations.

At low contrasts, it is proposed that detectors sensitive to the centre of the test grating are active alone, because detectors responding to the periphery of the test grating are so inhibited by the inducing grating that they are not active enough for threshold to be exceeded. The low contrast test grating should not appear to be tilted. As the contrast is increased, so more of the detectors responding to the periphery of the test grating will exceed threshold and will contribute to the percept of the stimulus; these detectors are suffering inhibition from the inducing grating and, as more become active, so the test grating should appear more tilted. Figures 2 and 3 show how the apparent tilt of a 9 c/deg sinusoidal grating changes with its contrast. In the absence of an inducing grating and before adaptation, the apparent orientation of the test grating is, not surprisingly, independent of test contrast. But, when the high contrast inducing grating is added to the stimulus, the test grating appears little tilted at near-threshold contrasts; as the contrast is increased, so the test grating appears to be more tilted, reaching a maximum clockwise tilt of about 2°.

For comparison, the Figures include data on how the size of the tilt after-effect depends on the contrast of the test grating. Confirming Parker (1972), we find that the illusion is strongest at low test contrasts and falls as the test contrast is raised, the opposite of the simultaneous illusion.

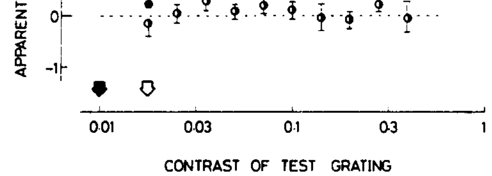

Fig. 2. The apparent tilt from vertical of the sinusoidal vertical test grating as a function of it contrast. The half-filled circles show the apparent tilt when there was no inducing grating present and before adaptation. The filled arrow shows the contrast threshold for the test grating under these conditions. Zero on the ordinate may not be true vertical; it is the mean of half-filled circles. The filled circles show the apparent tilt when the inducing grating was added to the stimulus display; the inducer was tilted 12° anti-clockwise from the vertical and caused an apparent clockwise tilt of the test grating. The open circles show the apparent tilt of the test grating after adapting to a grating tilted 12° anti-clockwise from vertical. The open arrow shows the threshold contrast after adaptation. Standard errors of the mean of five orientation judgements are shown.

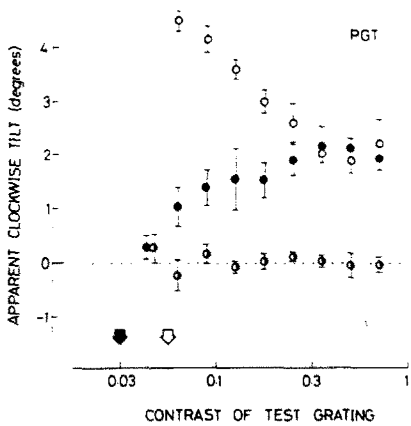

Fig. 3. As for Fig. 2, but data for a second observer.

These data support the hypothesis that the centre and periphery of the test grating are behaving differently because they are at different distances from the inducing grating. Confirmation might be obtained by examining the two regions of the test grating separately by masking out parts of the test grating. The centre could be masked to allow examination of the periphery, while the periphery could be masked to allow examination of the centre. These experiments were attempted, but it was found difficult to make consistent judgements of orientation even in the absence of the inducing grating. First, the bars of the grating were now very short; second, the sharp curvature of the small masks themselves caused an apparent distortion of the test grating.

At second best, we carried out the experiment illustrated in Fig. 4, where the test grating remained as a disc with a diameter of 1·5° while the annulus dimensions were changed (2·25° i.d. and 4·25° o.d.). The test grating and inducing grating were separated by 0·375°. The upper part of Fig. 4 shows the stimulus configuration. The results show that, at all test contrasts, there was little apparent tilt, confirming Wallace's (1969) suggestion that inhibition between detectors falls off rapidly as the stimuli are spatially separated.

We were unable to make consistent orientation judgements when the test grating was masked to a small disc or a small annulus, but we were able to determine the detection thresholds for these stimuli. The thresholds were determined by the method of adjustment using the technique of Dealy and Tolhurst (1974). The results are presented in Table 1. Each threshold is the mean of five settings with an average standard error of about 0·015 log units. The elevations of threshold with stars attached are significant at the 95 per cent level.

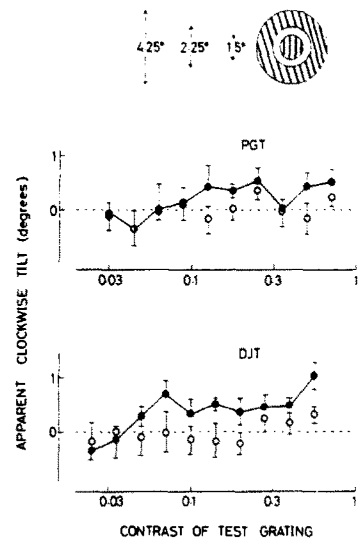

Fig. 4. A similar experiment to those of Figs. 2 and 3, except that the dimensions of the inducing stimulus have been changed. Its internal diameter is increased to 2·25°, the outer diameter to 4·25°. The configuration is shown in the upper part of the figure. The open circles show the apparent tilt in the absence of an inducing grating. Again, zero on the ordinate is the mean of the open circles. The filled circles show the apparent tilt when the inducing grating is added. Data for two observers are shown.

Table 1. Contrast thresholds for vertical sinusoidal gratings of 9 c/deg

Dimensions of grating: Test	Dimensions of grating: Inducing	Threshold contrast: Control	Threshold contrast: +Inducer	Threshold elevation (log units)
Subject DJT				
Disc (1·5)	Annulus (i.d. 1·5)	0·018	0·019	0·013
Disc (0·75)	Annulus (i.d. 1·5)	0·026	0·027	0·02
Disc (0·75)	Annulus (i.d. 0·75)	0·025	0·030	0·069*
Annulus (i.d. 0·75, o.d. 1·5)	Annulus (i.d. 1·5)	0·041	0·053	0·012*
Subject PGT				
Disc (1·5)	Annulus (i.d. 1·5)	0·021	0·023	0·043*
Disc (0·75)	Annulus (i.d. 1·5)	0·025	0·025	0·0
Disc (0·75)	Annulus (i.d. 0·75)	0·025	0·03	0·09*
Annulus (i.d. 0·75, o.d. 1·5)	Annulus (i.d. 1·5)	0·032	0·043	0·13*

The dimensions of the test grating were variable, either a disc or an annulus whose dimensions (in degrees of visual angle) are shown in the left-most column. Thresholds were determined in the absence of an inducing grating and in the presence of an inducing grating, a 9 c/deg square-wave grating tilted 12° anti-clockwise from the vertical. The dimensions of the inducing grating were also variable. It was always annular, with outer diameter of 3·5°; the internal diameter is indicated in the second column of the Table. The right-most column shows the elevation of threshold caused by the addition of the inducing grating.

* Significant at the 95 per cent level.

With the stimulus configuration used in the first experiment (Figs. 2 and 3), there was little change in threshold caused by the inducing grating. We propose that the centre of the test grating is too far from the inducing grating to be affected by it and that it is this part of the grating which is detected at threshold. Only the periphery of the test grating is affected. This was confirmed by the threshold measurements. When the periphery of the test grating was masked out, leaving the inducing grating unchanged, there was again no change in the threshold for the small test grating when the inducing grating was added. But, when the centre of the test grating was masked out, the threshold for the grating in the periphery of the test stimulus was elevated by the presence of the inducing grating.

Last, the threshold was determined for the centre of the test grating in the presence of an inducing grating whose inner diameter was reduced; the inducing grating and small test grating were now contiguous. The inducing grating caused an elevation of threshold.

These findings provide support for Wallace's (1969) proposal that the supposed inhibition between orientation-specific detectors is restricted to detectors subserving much the same part of the visual field. In experiments where a test stimulus is *surrounded* by an inducing stimulus, it is important to recognise that not all parts of the test stimulus are going to be affected to the same extent. In some circumstances, one part of the test stimulus may be used by the observer; in other circumstances, another part of the test stimulus may be used. Klein *et al.* (1974) have suggested that, because adaptation causes threshold elevation whereas a simultaneous inducing grating does not, the mechanisms underlying the after-effects of adaptation and the effects of a simultaneous inducing grating must be different. However, this finding can be reconciled with the notion that the two kinds of illusion arise from one cause. After adaptation, the whole of the test stimulus will be affected (the adapting stimulus is usually at least as big as the test stimulus); but, a surrounding inducing grating will have a non-uniform effect on the test grating.

DISCUSSION

Many experimental observations make it attractive to believe that the after-effects of adaptation and the simultaneous illusions have a common cause. The magnitude of the apparent shift in orientation or spatial-frequency is similar in the two kinds of illusion. The adapting orientation giving the most pronounced tilt after-effect is similar to the orientation of inducing grating giving the most pronounced simultaneous illusion. The spatial-frequency after-effect and simultaneous spatial-frequency illusion have a similar dependence on the orientation of the adapting or inducing gratings.

The most widely accepted model of after-effects is that first proposed by Sutherland (1961): after-effects of adaptation can be explained if there are detectors in the visual system which respond to limited ranges of some stimulus variable (e.g. orientation and spatial-frequency) and if these detectors become fatigued by prolonged viewing of a stimulus which excites them. Hubel and Wiesel (1959, 1962, 1968) have shown the existence of orientation-specific neurones in the cat and monkey visual cortex. Barlow and Hill (1963) and Maffei, Fiorentini and Bisti (1973) have shown that neurones in the retina of the rabbit and the visual cortex of the cat become less sensitive after an excitatory stimulus has been presented for a few seconds.

A mechanism such as that described above supposes that adaptation is an after-effect of excitation, and the question arises whether or not the same mechanism can satisfactorily account for the simultaneous illusions. Coltheart (1971) has argued that simultaneous illusions arise from rapid adaptation to the inducing figure. But this is an unsatisfactory explanation since the effects of adaptation (after-effects) take about 1 min to build up to a maximum (Gibson and Radner, 1937; Hammer, 1949) while the simultaneous illusions are just as strong when the stimuli are presented for only a fraction of a second (Carpenter and Blakemore, 1973). Further, the strength of the simultaneous illusions can be decreased by addition of a third element to the figure ("disinhibition"), a phenomenon not easily explained on the rapid adaptation hypothesis (Blakemore *et al.*, 1970; Carpenter and Blakemore, 1973).

A more satisfactory model of simultaneous illusions is in terms of inhibition between detectors: detectors excited by the inducing stimulus would inhibit those excited by the test stimulus. Deutsch (1964) and Ganz (1966) suggested that some figural after-effects could be explained in terms of lateral inhibition in the domain of space: a stimulus in one part of the visual field would interact with a stimulus in another part so that the stimuli appeared to be further apart than in reality. Of more relevance to the specific illusion considered in this paper is the model proposed by Wallace (1969) and Wallace and Crampin (1969) who suggested that the lateral inhibition was in the domain of orientation as well as in the domain of space. Detectors optimally sensitive to one orientation would inhibit detectors optimally sensitive to other (similar) orientations. Inhibitory interactions of this kind have been shown between orientation-specific neurones in the cat visual cortex (Creutzfeldt, Kuhnt and Benevento, 1974; Blakemore and Tobin, 1972). Inhibition between detectors optimally sensitive to different spatial-frequencies could explain the frequency illusion described by Mackay (1973) and Klein *et al.* (1974), and Tolhurst (1972) and Barfield and Tolhurst (1975) have provided evidence for such interactions in the frequency domain.

If simultaneous illusions arise from inhibitory interactions, perhaps the after-effects of adaptation should be seen as arising from prolonged inhibition rather than from prolonged excitation as Sutherland had originally proposed (Blakemore, Carpenter and Georgeson, 1971; Tolhurst, 1972). Maffei *et al.* (1973) found that neurones in the cat visual cortex could be desensitised by prolonged presentation of stimuli which did not excite the neurones. Adaptation is not due solely (if at all) to fatigue caused by prolonged excitation. Psychophysical experiments lead to the same conclusion (Sharpe, 1974; Dealy and Tolhurst, 1974). Adaptation may result from prolonged inhibition of the test detectors by detectors excited by the adapting stimulus.

Before it can be accepted that after-effects and simultaneous illusions have one underlying mechanism (inhibition), two out-standing problems must be resolved.

First, Georgeson (1973) found that the amount of apparent tilt in the simultaneous illusion depends on the difference between the spatial-frequencies of the test and inducing gratings. However, Parker (1972) found that the tilt after-effect was not spatial-frequency specific: Ware and Mitchell (1974) have recently failed to replicate the latter result, finding that the tilt after-effect is spatial-frequency specific.

Second, adaptation causes a sizeable elevation of the threshold for a test stimulus, while the inducing grating apparently causes no or little change in the threshold in the simultaneous illusion (Klein *et al.*, 1974). The results of our paper provide support for a hypothesis for explaining this apparent embarrassment for the idea that after-effects and simultaneous illusions have one underlying cause. Results obtained with the stimulus configuration used by Klein *et al.* (and by ourselves) should be interpreted with the recognition that not all parts of the test stimulus will be affected to the same extent by the presence of the inducing grating: the inducing grating surrounds the test stimulus and is not superimposed on it.

Acknowledgements—We would like to thank Drs. O. Braddick and J. A. Movshon for helpful criticism. PGT received a scholarship from the Social Sciences Research Council. The computer was provided by the Medical Research Council.

REFERENCES

Barfield L. and Tolhurst D. J. (1975) Detection of complex gratings by the human visual system (in preparation).

Barlow H. B. and Hill R. M. (1963) Evidence for a physiological explanation of the waterfall phenomenon and figural aftereffects. *Nature, Lond.* **200**, 1345–1347.

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

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

Blakemore C., Carpenter R. H. S. and Georgeson M. A. (1971) Lateral thinking about lateral inhibition. *Nature, Lond.* **234**, 418–419.

Blakemore C. and Nachmias J. (1971) The orientation specificty of two visual aftereffects. *J. Physiol., Lond.* **213**, 157–174.

Blakemore C. and Sutton. P. (1969) Size adaptation: a new aftereffect. *Science, N.Y.* **166**, 245–247.

Blakemore C. and Tobin E. A. (1972) Lateral inhibition between orientation detectors in the cat's visual cortex. *Expl Brain Res.* **15**, 439–440.

Carpenter R. H. S. and Blakemore C. (1973) Interactions between orientations in human vision. *Expl Brain Res.* **18**, 287–303.

Coltheart M. (1971) Is there lateral inhibition in the visual cortex? *Nature, New Biol.* **231**, 256.

Creutzfeldt O. D., Kuhnt U. and Benevento L. A. (1974) An intra-cellular analysis of visual cortical neurones to moving stimuli: responses in a cooperative neuronal network. *Expl Brain Res.* **21**, 251–274.

Dealy R. S. and Tolhurst D. J. (1974) Is spatial adaptation an aftereffect of prolonged inhibition? *J. Physiol., Lond.* **241**, 261–270.

Deutsch J. A. (1964) Neurophysiological contrast phenomena and figural aftereffects. *Psychol. Rev.* **71**, 19–26.

Ganz L. (1966) Mechanisms of figural aftereffects. *Psychol. Rev.* **73**, 128–150.

Georgeson M. A. (1973) Spatial frequency selectivity of a visual tilt illusion. *Nature, Lond.* **245**, 43–45.

Gibson J. J. and Radner M. (1937) Adaptation and contrast in perception of tilted lines. *J. exp. Psychol.* **20**, 453–469.

Gilinsky A. S. (1968) Orientation specific effects of the pattern of adapting light on visual acuity. *J. opt. Soc. Am.* **58**, 13–18.

Hammer E. R. (1949) Temporal factors in figural aftereffects. *Am. J. Psychol.* **62**, 337–354.

Hubel D. H. and Wiesel T. N. (1959) Receptive fields of single neurones in the cat's striate cortex. *J. Physiol., Lond.* **148**, 574–591.

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

Hubel D. H. and Wiesel T. N. (1968) Receptive fields and functional architecture of the monkey striate cortex. *J. Physiol., Lond.* **195**, 215–243.

Klein S., Stromeyer C. F. and Ganz L. (1974). The simultaneous spatial frequency shift: a dissociation between the detection and perception of gratings. *Vision Res.* **14**, 1421–1432.

MacKay D. M. (1973) Lateral interaction between neural channels sensitive to texture density. *Nature, Lond.* **245**, 159–161.

Maffei L., Fiorentini A. and Bisti S. (1973) Neural correlate of perceptual adaptation to gratings. *Science, N.Y.* **182**, 1036–1038.

Pantle A. J. and Sekuler R. W. (1968) Size detecting mechanisms in human vision. *Science, N.Y.* **162**, 1146–1148.

Parker D. M. (1972) Contrast and size variables in the tilt aftereffect. *Q. Jl exp. Psychol.* **24**, 1–7.

Sekuler R. W. and Ganz L. (1963) Aftereffect of seen motion with a stabilized retinal image. *Science, N.Y.* **139**, 419–420.

Sharpe C. R. (1974) The colour specificity of spatial adaptation: red–blue interactions. *Vision Res.* **14**, 41–51.

Sutherland N. S. (1961) Figural aftereffects and apparent size. *Q. Jl exp. Psychol.* **13**, 222–228.

Tolhurst D. J. (1972) Adaptation to square wave gratings: inhibition between spatial frequency channels in the human visual system. *J. Physiol., Lond.* **226**, 231–248.

Vernon M. D. (1934) The perception of inclined lines. *Br. J. Psychol.* **25**, 186–196.

Wallace G. K. (1969) The critical distance of interaction in the Zöllner illusion. *Percept. Psychophys.* **5**, 261–264.

Wallace G. K. and Crampin D. J. (1969) The effect of background density on the Zöllner illusion. *Vision Res.* **9**, 167–177.

Ware C. and Mitchell D. E. (1974) The spatial selectivity of the tilt aftereffect. *Vision Res.* **14**, 735–737.