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# Two-dimensional tilt illusions induced by orthogonal plaid patterns: effects of plaid motion, orientation, spatial separation, and spatial frequency

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**Abstract.** Tilt illusions occur when a drifting vertical test grating is surrounded by a drifting plaid pattern composed of orthogonal moving gratings. The angular function of this illusion was measured as the plaid orientation (and therefore its drift direction) varied over a 180° range. This was done when the test and inducing stimuli abutted and had the same spatial frequency, and when the test and inducing stimuli either differed in frequency by an octave, or were spatially separated by a 2 deg blank annulus, or both differed in frequency and were also separated by the annulus (experiments 1-4). The obtained angular function was virtually identical to that obtained previously with the rod and frame effect and other cases involving orthogonal inducing components, with evidence for illusions induced both by real-line components and by virtual axes of symmetry. Although the magnitude of the illusion was very similar in all four experiments, there was evidence to suggest that largest real-line effects occurred in the abutting same-frequency condition, with a pattern of results similar to that obtained previously with the simple one-dimensional tilt illusion. On the other hand, virtual-axis effects were more prominent with gaps between test and inducing stimuli. A fifth, repeated-measures, experiment confirmed this pattern of results. It is suggested that this pattern-induced tilt effect reflects both striate and extrastriate mechanisms and that the apparent influence of spatially distal virtual axes of symmetry upon perceived orientation implies the existence of AND-gate mechanisms, or conjunction detectors, in the orientation domain.

## 1 Introduction

Recent research into the determinants of the orientation illusions has produced psychophysical data which appear related to neurophysiological evidence for more global mechanisms in cortical areas beyond V1 (eg Wenderoth and Johnstone 1987). In particular, it has been found that large gaps between inducing and test stimuli, or remote surrounding contours, respectively, may not affect or may modulate orientation illusions. Such findings suggest that even simple tilt illusions have determinants more complex than lateral inhibition between orientation-selective neurons in striate cortex as suggested, for example, by Carpenter and Blakemore (1973). Additional psychophysical investigations may thus draw attention to novel stimuli which might be used as probes in the neurophysiological investigation of single neurons.

This research is concerned with an analogue of the rod and frame illusion (RFI), an orientation illusion which can be considered a variant of the tilt illusion (TI). However, prior to our conducting the experiments reported below, we were unaware of the relationship between the effects we were to measure and the RFI, so the stimulus parameters we selected for the initial experiments were chosen for quite different but specific reasons. These are briefly explained because they are relevant to the experiments.

In several recent investigations of both the psychophysical and the neurophysiological properties of visual mechanisms, crossed drifting sine-wave gratings have been counterclockwise), and drifting in the directions 135° and 225°, respectively, observers report the percept of a single coherent plaid drifting towards the left, ie in the direction 180° (Adelson and Movshon 1982; Movshon et al 1985). Neurophysiological studies have shown that, whereas neurons in monkey striate cortex (V1) respond only to the components of such a display, as do some cells in extrastriate middle temporal area (MT), at least some cells in MT respond to the pattern. That is to say, V1 cells and some MT cells respond twice as the whole pattern rotates through 180°, once when one grating is aligned with the preferred orientation of the cell and again when the other grating is so aligned. In contrast, at least a proportion of MT neurons respond only when it is the perceived plaid orientation that is aligned with the cell's preferred direction (as previously determined with a single grating) and do not respond to the components (Movshon et al 1985).

Based upon these observations, Wenderoth et al (1988) measured motion aftereffects (MAEs) induced on a single vertical grating by a drifting plaid pattern, but the components of the plaid were presented either simultaneously or in alternation. In addition, the relative orientations of the plaid components were varied symmetrically around horizontal so that the composite plaid always appeared to drift horizontally. Whereas the MAE magnitude decreased linearly as the *alternating* components deviated more from the vertical test grating, this was not the case in the simultaneous condition. Wenderoth et al (1988) suggested that the simultaneous plaid MAE, being in part pattern-selective rather than component-selective, reflects an extrastriate (perhaps MT) contribution to the MAE.

Given the fact that extrastriate receptive fields frequently are much larger and less specifically tuned to spatial position than are V1 receptive fields (eg Allman et al 1985; Maunsell and Newsome 1987), we began to examine displays in which central test gratings were surrounded by drifting plaid stimuli spatially removed from the test. We observed a robust illusion not of motion but of tilt. Experiments were then conducted using a single plaid orientation with the component gratings oriented 60° and 150° (30° clockwise, CW, and 60° counterclockwise, CCW, of vertical). Various combinations of component drift directions gave plaids drifting in different directions, despite the fixed orientations. Not only were tilt illusions obtained when there was a gap of 2 deg between the test grating and the inducing annulus; but no reliable illusions were obtained when the plaid abutted the test grating (Johnstone and Wenderoth 1989). At that stage, we had observed an apparently pattern-specific tilt illusion which may or may not have been dependent upon the pattern motion, the component orientations, or both.

Since the illusions we obtained were small, albeit robust, it seemed logical to measure the complete angular function of the illusion. This would provide information on the size of the effect at different component orientations in the illusion. Experiments 1 to 4, described below, were designed to provide such data. In the event, the angular functions obtained were those characteristic of the RFI. Prior to describing the experiments, then, we first describe the RFI and its relationship to the simple TI.

The tilt illusion refers to the misperception of the orientation of a test line or grating when it is superimposed on, or intersected by, an inducing line or grating in a different orientation. Angular separations between test and inducing stimuli of up to about 50° typically result in repulsion (also called *direct*) effects, so that the test orientation appears pushed away from the inducing orientation. Larger angular separations often



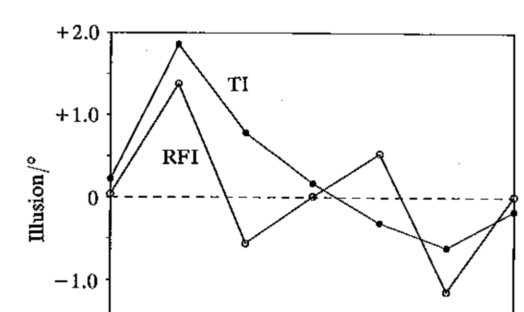
effects are called positive, and indirect or attraction effects are called negative, as shown by the filled symbols in figure 1.

The rod and frame illusion occurs when a vertical line is surrounded by a square but tilted inducing frame. Beh et al (1971) first showed that, as the surrounding frame was tilted from vertical through 90° to horizontal, the angular function of the illusion was that shown by the open circles in figure 1. In an attempt to explain this function, Beh et al proposed a 'major axes hypothesis' (MAH). They asserted that the test line appears tilted away from whichever of the frame's four axes of mirror symmetry is nearest vertical. As the square is tilted, say, clockwise (CW) through 90°, the axis nearest vertical is tilted CW for tilts of 0–22.5°; between 22.5° and 45°, it is tilted counterclockwise (CCW); then, between 45° and 67.5°, tilted CW; and, finally, between 67.5° and 90°, tilted CCW. Note that the same descriptive hypothesis applies to the TI: when the inducing line or grating is tilted CW near vertical, the axis nearest vertical is that corresponding to the grating's main lines and is CW; nearer horizontal, the virtual axis orthogonal to the main lines is nearest vertical and CCW. Thus, the TI angular function can also be described in terms of repulsion from the inducing axis of symmetry nearest vertical [although the magnitude difference between these effects remains unexplained, as Wenderoth (1977) has discussed].

In addition, of the four axes of symmetry of a square, two (vertical and horizontal) coincide with real lines of the frame, so-called *main-line axes* (Howard 1982) whereas the other two (the diagonals) are purely *virtual axes*. For descriptive purposes, let us equate *direct* effects (in both the TI and the RFI) with *main-line* effects; and *indirect* effects with *virtual-axis* effects. In these terms, indirect (virtual-axis) effects are those shown by the two central rod and frame peaks and by the negative TI peak in figure 1; direct (main-line) effects are those shown by the outer rod and frame peaks and the positive TI peak.

Using this descriptive system, then, we shall refer to tilt illusions induced by crossed gratings in the same way. Crossed orthogonal gratings also have two main-line and two virtual axes of symmetry: direct effects will refer to illusions which can be described as repulsion from a main-line (ie component grating) axis nearest vertical; indirect effects can be described as repulsion from a virtual axis (ie crossed-grating angle bisector) nearest vertical. The simple TI induced by a single grating will be termed the one-dimensional effect or 1-D TI; crossed-grating or square-frame effects will be termed 2-D TIs.

The aims of the experiments to be reported can now be restated in terms of the above definitions. Johnstone and Wenderoth (1989) observed that drifting crossed



gratings oriented 60° (ie 30° right of vertical) and 150° (ie 60° left of vertical) induced an apparent CW tilt in a vertical grating which thus was set CCW to appear vertical. This is an indirect effect: it reflects repulsion from the virtual axis of the plaid which is oriented 105° (15° left of vertical). In these terms, the fact that the effect was small is not surprising: indirect effects typically are of the order of 0.5 - 1.0° (ie figure 1; Wenderoth and Johnstone 1988a, 1988b). Experiments 1 to 4 thus were designed to measure the complete angular function of the 2-D TI.

General methods used in all the experiments are described first, followed by the individual experiments.

## 2 General methods

Stimulus displays were presented on the flat screen of a Tektronix 608 display monitor (P31 phosphor), interfaced with an Innisfree ('Picasso') image generator and a PDP 11/23 minicomputer. Subjects used the outer pair of three microswitches to rotate a circular 0.6 deg visual angle sine-wave test grating to the perceived vertical. A press on the central switch signalled completion of the adjustment, caused the setting to be recorded by the computer, and removed the current display.

Experimenter and subject were located in adjacent laboratories. Intrasession communication was possible via an intercom system, and a slave monitor in the experimenter's cubicle enabled monitoring of the subject's settings. Subjects viewed the display in a dark windowless cubicle. All external cues to vertical were removed by attaching to the screen a flat black aluminium mask in which a 6.75 deg diameter hole had been cut, and by draping black cloth over the area between the screen and the padded forehead-, temple-, and chin-rest which held the subject's head. The head rest was positioned 57 cm from the screen, so that 1 cm on the screen subtended 1 deg visual angle.

The image generator was modified to run automatically via the minicomputer and a custom-designed D/A interface. This allowed up to three different screens to be interleaved at a rate of 188 Hz and software enabled these screens to be constructed using an on-screen menu. So, for example, the inducing annulus containing drifting crossed gratings was constructed by interleaving two of the three screens, one containing one grating drifting within an annulus, the other containing the other grating drifting within an identically positioned annulus. The rate of interleaving ensured that the display was not seen to flicker.

The central test grating always had a spatial frequency of 5 cycles $deg^{-1}$ and, when the subject adjusted it, it rotated at a speed of 5.9° $s^{-1}$ in $\frac{1}{3}$° steps, giving the appearance of continuous motion. The maximum luminance of the light bars was 10.4 cd $m^{-2}$ and the minimum luminance of the dark bars was 2.1 cd $m^{-2}$, measured on a low-frequency grating with a Tektronix J16 (1 deg) digital luminance probe. Thus, the Michelson contrast of the test grating, defined as $(L_{max} - L_{min})/(L_{max} - L_{min})$ was 0.67. The crossed inducing gratings each had the same luminance values as the test, but because of luminance summation at their intersects plaid contrast was slightly higher (0.75). All unfilled portions of the screen had a luminance of 2.8 cd $m^{-2}$ and during intertrial intervals (5 s) the screen was blanked at 6.8 cd $m^{-2}$, sufficient to eradicate afterimages between conditions.

## 3 Experiment 1

Experiment 1 was designed to measure the angular function of the 2-D TI when the test



drifted in the 180° direction, the component gratings were oriented 45° and 135°, and they drifted, respectively, in the directions 135° and 225°. In condition 2, the gratings were oriented 35° and 125° and drift directions were 125° and 215° respectively. These 10° steps in orientation and direction continued to condition 19, where the grating orientations were 225° and 135°, and drift directions were 315 and 45 deg.

In this experiment, the spatial frequency of the gratings composing the plaid was the same as that of the test grating, ie 5 cycles $deg^{-1}$. All gratings drifted with a temporal frequency of 2 cycles $s^{-1}$. Thus the velocity of the test grating, given by temporal frequency over spatial frequency, was 0.4 deg $s^{-1}$. Plaid velocity is given by $V_p = V_c(\cos\theta)^{-1}$, where $V_c$ is component velocity and $\theta$ is half the angle between the gratings. Plaid velocity therefore was 0.57 deg $s^{-1}$. The thickness of the inducing plaid annulus was 2 deg (inside diameter 4.6 deg, outside diameter 6.6 deg).

### 3.1 *Method*

3.1.1 *Subjects.* There were six subjects, members of an optional advanced undergraduate course in Perceptual Systems, who were providing data for their own class exercise but who, at the time of the experiment, were entirely naive about every aspect of the experiment.

3.1.2 *Procedure.* Apart from one subject who was myopic in the right eye and used her left eye, all subjects viewed monocularly with an eyepatch over the left eye. The instruction was always to fixate the centre of the test grating when it was present. Discussion after the experiment suggested that all subjects were able to maintain fixation as required. Within each of the nineteen plaid orientation conditions, subjects made two consecutive pretest settings to vertical (surround absent), followed by four test settings (inducing surround present). For these six trials, starting position of the test grating was random within ±10° of vertical. A break of 15 s occurred between each such set of six trials, although the subject was required to maintain head position during that time. The complete set of one hundred and fourteen settings (nineteen orientations × six settings) required a testing period of about 90 min, including a long halfway break, during which the subject strolled the corridor. Five practice settings were given prior to the experiment, with randomly selected conditions. Careful bracketing in adjustment prior to making a final setting was encouraged.

The illusion was defined as the algebraic difference between the mean of the four consecutive tests and the mean of the preceding two pretests, in any set of six trials. This convention meant that test settings more CW than pretests were scored as positive (+) illusions; test settings more CCW were scored as negative (−) illusions. The order in which the nineteen orientation conditions were completed was completely randomized.

### 3.2 *Results*

The mean illusions obtained in experiment 1 are shown in figure 2a. The variable on the abscissa is the direction of plaid drift, which is perfectly correlated with the orientations of the component inducing gratings, as shown by the arrow (direction) and cross (component orientations) insets on the lower and upper abscissae of figure 2a. However, note that although drift direction varied through a full 180°, the component grating orientations began at the obliques (180° direction), cycled through 90° to become oblique again (90° direction) and then repeated the identical cycle of orientations (90° to 0° directions). Thus, the similarity of the left and right halves of the

### 3.3 *Discussion*

The angular function in figure 2a clearly is of the class of function previously obtained with a stationary test stimulus and an inducing stimulus comprised of an outline square frame. Thus, each half of the figure 2a function, contained within drift directions 180° to 90° and 90° to 0°, is similar to the frame inducing stimulus function in figure 1. The apparent difference in phase exists only because, in terms of the figure 1 abscissa, these two half functions in figure 2a cover the inducing orientation range 135° to 45° and not 90° to 0°. That is, a component orientation is aligned with vertical at 90° on the figure 1 abscissa but halfway between the directions 140° and 130° and also 50° and 40° in figure 2a.

Before discussing these results in more detail, it will be useful to deal with experiments 2 to 4, which were similar to experiment 1 except that the effects of abutting inducing stimuli and different inducing spatial frequencies were examined.

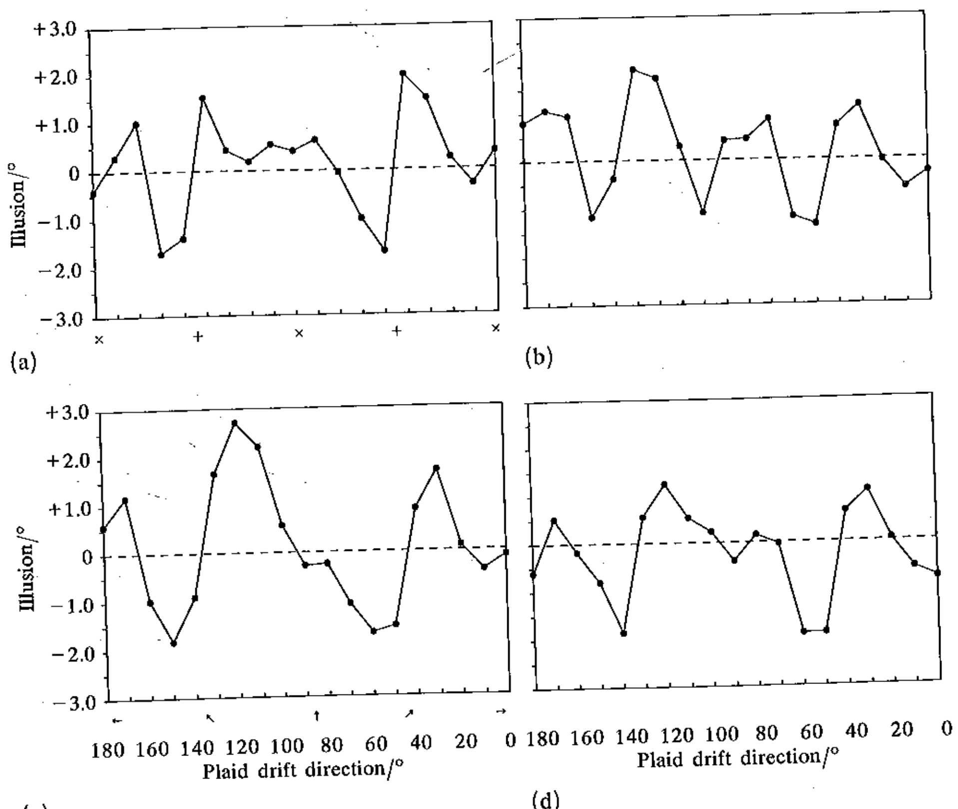



**Figure 2.** Angular functions of the two-dimensional tilt illusion (2-D TI).
(a) Experiment 1: component inducing frequencies 5 cycles $deg^{-1}$; annulus gap 2 deg; $N = 6$.
(b) Experiment 2: component inducing frequencies 2.5 cycles $deg^{-1}$; annulus gap 2 deg; $N = 6$.
(c) Experiment 3: component inducing frequencies 5 cycles $deg^{-1}$; annulus gap zero; $N = 8$;
(d) Experiment 4: component inducing frequencies 2.5 cycles $deg^{-1}$; annulus gap zero; $N = 8$.
Arrows along lower abscissa show plaid drift directions at (from left to right) 180°, 135°, 90°,
[illegible] component orientations corresponding



## 4 Experiments 2 to 4

Unless otherwise specified, the methods and stimuli in these three experiments were as in experiment 1.

### 4.1 *Method*

4.1.1 *Subjects.* There were six subjects in experiment 2, and eight in each of experiments 3 and 4. These were drawn from the same population as those in experiment 1. The differences in sample size were unavoidable because, given the relatively long test session, some subjects were unable to complete all four experiments.

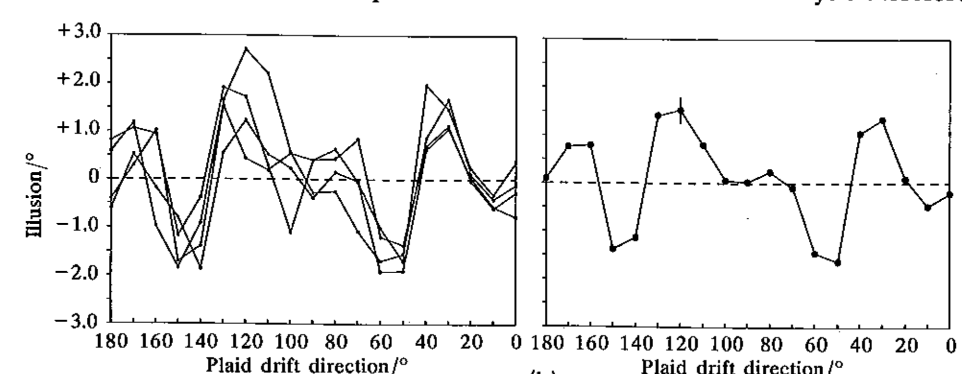
4.1.2 *Stimuli.* In experiment 2, all conditions were as in experiment 1 except that each of the component inducing gratings had a spatial frequency of 2.5 cycles $deg^{-1}$. With temporal frequency maintained at 2 cycles $s^{-1}$, each component then had a velocity of 0.8 deg $s^{-1}$ and the composite plaid velocity was 1.13 deg $s^{-1}$.

In experiments 3 and 4, stimuli were identical, respectively, to those in experiments 1 and 2 except that the 2 deg annulus gap between test and inducing stimuli was removed, so that the 2 deg thick inducing annulus directly abutted the test grating.

### 4.2 *Results*

Angular functions obtained in experiments 2 to 4 are shown in figures 2b–2d, respectively, and they very closely resemble the function obtained in experiment 1 (figure 2a). In each case, the main effect of drift direction was significant (experiment 2, $F_{18,90} = 5.67$, $p < 0.0005$; experiment 3, $F_{18,126} = 7.83$, $p < 0.005$; and experiment 4, $F_{18,126} = 4.89$, $p < 0.0005$). It can be noted that the data of the individual subjects were very similar, so that the standard errors in all four experiments were quite small (0.42, 0.42, 0.64, and 0.43 in experiments 1 to 4, respectively).

To illustrate the similarity between the four angular functions in figures 2a–2d, the means for each of the functions were entered in a simple subjects by treatments analysis *as if* these four sets of means were the data of four single subjects. Figure 3a shows the results of experiments 1 to 4 superimposed; and figure 3b shows the overall average of the four functions. The error bar indicates ±1 standard error obtained from the mean square error of the analysis. The between-subjects effect was not significant ($F_{3,54} = 2.03$, $p > 0.05$), indicating no significant difference between the main effects in figures 2a–2d. This test, however, indicates only that the *means* of the functions are similar and when, as in this case, illusions are both positive and negative, the means are not a good measure of the depth of modulation. An additional analysis therefore was



carried out on the absolute (nonsigned) illusions. The mean unsigned illusions corresponding to the groups in figures 2a–2d were 0.82°, 0.86°, 1.08°, and 0.74° and analysis of variance showed that these means were not significantly different ($F_{3,54} = 1.89$, $p > 0.05$). However, it is noticeable from both the graph and this analysis that illusions appear to be generally larger in the same-frequency abutting condition (figure 2c).

More detailed examination of the data of experiments 1 to 4 provided the impetus for experiment 5. First, when Johnstone and Wenderoth (1989) obtained their small indirect effects, these were induced with drift directions halfway between abscissa values of 100° and 110° and also 10° and 20° in figures 2–3. Under the conditions common to their experiments (figures 2a and 2b), three out of four of these effects are small and negative, consistent with their result. Second, we have shown previously (Wenderoth and Johnstone 1988a) that in the case of the 1-D TI, introducing gaps or spatial-frequency differences between test and inducing stimuli reduces direct but not indirect TIs. To obtain some indication of whether the same is true of the 2-D TI, obtained direct and indirect effects were averaged for each of the functions in figures 2a–2d. Direct effects, which occurred when a component grating was oriented 15° from vertical, occurred at drift directions 150°, 120°, 60°, and 30°; indirect effects were estimated by averaging the effects which spanned the orientation in which a virtual axis would be 15° from vertical, ie the effects at drift directions of 160° and 170°; 100° and 110°; 70° and 80°; and 10° and 20°. Because direct (and indirect) effects were either positive or negative depending upon whether the axis nearest vertical was oriented CW or CCW, for *this analysis only*, effects in the *expected direction* were called positive, ie effects were called positive if they exhibited repulsion from the relevant axis of symmetry.

The results of the analysis are shown in table 1 and two aspects of these data are of interest. First, as we reported earlier in the case of the 1-D TI (Wenderoth and Johnstone 1988a), direct effects are largest under abutting same-spatial-frequency conditions. The introduction of a gap or a different inducing frequency reduces direct effects. Second, but unlike the situation for the 1-D TI, indirect effects do not occur reliably under the abutting conditions. This result, however, is precisely that reported by Johnstone and Wenderoth (1989). In the light of these tendencies, experiment 5 was designed to test directly for this pattern of results.

**Table 1.** Summary of average direct and indirect two-dimensional tilt illusions (in °) in experiments 1 to 4.

| | Spatial position/frequency | | | |
|---|---|---|---|---|
| Effect | abut/same | abut/different | gap/same | gap/different |
| Direct | +1.98 | +1.25 | +1.15 | +1.30 |
| Indirect | −0.45 | +0.03 | +0.16 | +0.58 |

Because direct (and indirect) effects were either positive or negative depending on whether the axis nearest vertical was CW or CCW, for *this analysis only*, effects in the *expected direction* were called positive, ie effects were called positive if they exhibited repulsion from the relevant axis of symmetry.



therefore, the axis of symmetry nearest vertical was 15° CW of vertical. Thus, unlike experiments 1 to 4, in which direct and indirect effects occurred in both CW and CCW directions, both effects in this experiment were predicted to occur in the CW (+) direction. In this case, then, illusion was defined as the mean of test settings minus the mean of the pretests, so that direct and indirect effects were both positive, if in the expected direction.

The results of experiments 1 to 4 suggested that inducing motion may have little effect on the 2-D TI because the average function (figure 3b) was remarkably symmetrical to the left and right of the 90° drift direction. This is not surprising if the 2-D TI is an analogue of the RFI, which occurs with stationary stimuli. Accordingly, all inducing and test components were stationary in experiment 5. Pilot observations indicated that effects were similar whether viewing was monocular or binocular and whether the inducing annulus was 2 deg or 1 deg thick. We used both latter options in this experiment.

There were eight conditions in the experiment: two inducing–test stimulus gap conditions (no gap, 2 deg gap) by two spatial-frequency conditions (same—test 5 cycles $deg^{-1}$, inducing components each 5 cycles $deg^{-1}$; different—test 5 cycles $deg^{-1}$, inducing components 2.5 cycles $deg^{-1}$) by two plaid orientation conditions (direct, indirect).

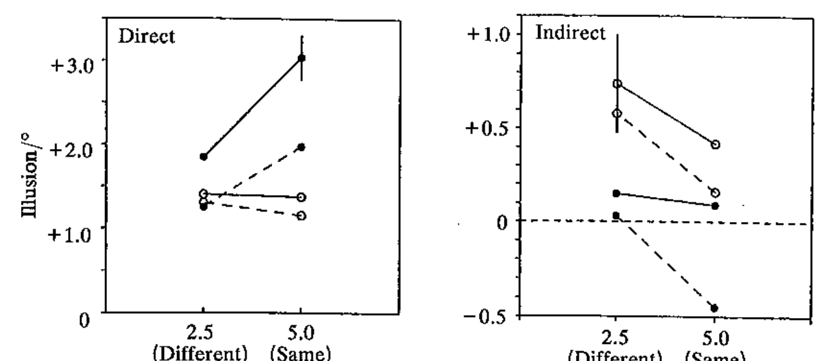
### 5.1 *Method*

5.1.1 *Subjects.* There were twenty-four subjects, drawn as volunteers from an introductory Psychology course in return for nominal course credit. All had emmetropic or corrected vision.

5.1.2 *Procedure.* All other procedures were as in previous experiments, with all subjects tested under every condition.

### 5.2 *Results*

The mean obtained illusions are shown by the solid lines in figures 4a (direct effects) and 4b (indirect effects). All of the obtained means were in the expected direction, ie positive. A simple subjects by treatments analysis of variance with seven planned orthogonal contrasts indicated the following. First, for direct effects, in the abutting condition, the mean illusion was larger for the same-spatial-frequency condition (+3.04°) than for the different-frequency condition (+1.85°) ($F_{1,161} = 10.44$, $p < 0.005$). In the gap conditions, the means were similar for the respective frequency conditions (+1.37° and +1.40°) and the difference was not significant ($F_{1,161} = 0.006$, $p > 0.05$).



Averaging over frequency, the abutting conditions produced a larger TI (+2.45°) than the gap conditions (+1.39°) ($F_{1,161} = 16.59, p < 0.0005$).

While none of the same comparisons for indirect effects was significant, there may have been a type II error because the overall mean gap illusion (+0.58°) was apparently larger than the abut effect (+0.12°) ($F_{1,161} = 3.11, p < 0.10$). Independent tests of single means showed that one indirect effect, the +0.74° mean obtained in the gap, 2.5 cycles deg$^{-1}$ condition, was different from zero ($t_{23} = 2.85, p < 0.01$).

For purposes of comparison, the data from experiments 1 to 4 (ie from table 1) are plotted as dashed lines in figures 4a and 4b and are remarkably similar, considering the small sample sizes in experiments 1 to 4.

### 5.3 *Discussion*

The data shown in figure 4a very closely resemble those obtained by Wenderoth and Johnstone (1988a) for the 1-D direct effect. In the case of the 1-D indirect effect, Wenderoth and Johnstone's data showed no overall effect of gaps or spatial frequency on the indirect effect. However, the results reported here are entirely consistent with those of Johnstone and Wenderoth (1989), who found that indirect 2-D TIs occurred only in gap conditions.

The general similarity of the results of this experiment and the data extracted from experiments 1 to 4 (table 1; figures 4a and 4b) are consistent with the view that motion is a parameter not relevant to the 2-D TI), as the earlier symmetry of the functions in experiments 1 to 4 had suggested.

## 6 General discussion

These experiments have demonstrated that the tilt illusion induced on a central vertical test grating by a surrounding orthogonal plaid pattern follows the angular function previously reported for the RFI (experiments 1 to 4); that this 2-D TI, discovered in the context of moving stimuli, is not dependent on motion (experiments 1 to 5); and that the 2-D direct effect, like its 1-D counterpart, is tuned for similar test and inducing spatial frequency and position, whereas the indirect 2-D TI, like its 1-D counterpart, is not. However, the 2-D indirect effect, unlike the 1-D TI, appears only to occur when the inducing stimulus is remote from the test stimulus. Both table 1 and experiment 5 suggest that the indirect 2-D TI is larger not only when a gap exists but also when test and inducing spatial frequencies differ, a tendency in these results which requires further investigation.

Earlier, a purely descriptive account of the RFI was outlined, the 'major axes hypothesis' (MAH). Although this hypothesis is purely descriptive, it has received some empirical support in the context of both the rod and frame illusion and its variants (Wenderoth 1977) and in other contexts. For example, Wenderoth and Curthoys (1974) showed that 1-D TIs induced by single lines were nonadditive: whereas single inducing lines oriented 30° CCW *or* 60° CW induced negative illusions (direct and indirect, respectively), an inducing cross formed by the conjunction of the two inducing lines induced a positive illusion, as if the virtual axis of symmetry induced the 2-D TI. Wenderoth (1977) also reported that the angular function of TIs induced by stationary crossed orthogonal square-wave gratings was identical to the RFI angular function and, in preliminary experiments, that TIs induced by *nonorthogonal* gratings were also accounted for by the MAH. Although the test stimulus in these experiments was a



Finally, Hartley (1982) demonstrated a series of orientation illusions in which test and inducing components were widely separated in space (1–6 deg) with no diminution in the illusion as separation increased and which were predictable in terms of the orientation of the virtual axis of bilateral symmetry of the inducing display. Because the 1-D TI is reduced markedly by test–inducing stimulus separation, Hartley proposed that processes more global than lateral inhibition between VI orientation-selective channels (eg Carpenter and Blakemore 1973) are involved in the rod and frame illusion and the effects he reported. He concluded (page 375):

> "A plausible interpretation is that axes of symmetry, extracted by interactions in the orientation domain that operate over broad areas of the retinal field, have perceptual consequences much like physically present facets of the retinal image ... . Symmetry discrimination would be a part of a global texture perception system in contrast to form recognition, which is a local scrutiny system relying on all stages of feature extraction ... . Replacing a figure by its axes of symmetry could be used to separate figure and ground, to determine orientation, and to classify input loosely."

In similar vein, Wenderoth and Beh (1977, page 67) suggested that when the square frame in the rod and frame illusion is tilted around 45° "it may be the tilt of the whole 'global diamond' ... which determines the illusory effect on the rod".

There is precedence in the literature on visual pattern recognition for the idea that discrimination of global features of a stimulus, such as an axis of symmetry, a texture difference or pattern motion, is achieved by some kind of neural comparator analogous in function to a logical AND-gate; indeed, Shepherd and Brayton (1987) have suggested that dendritic spines may provide the basis for such logical operations. Thus, to explain the 'emergence' of pattern-selective neurons in MT which respond to the motion of a crossed-grating plaid, Movshon et al (1985) proposed that these MT cells ('second-stage 2-D analyzers') might require simultaneous activation of V1 cells tuned to the component orientations and directions ('first-stage 1-D analyzers') before they will respond. Julesz et al (1973) put forward a model of texture discrimination in which

> "the stimulus is first analyzed by local feature extractors that can detect only simple features ... of given sizes and orientations. Then the outputs of these ... are evaluated by a global processor that can ... compare at most two such outputs" (page 391)."

Another example is Marr's (1982, page 66) theory of zero-crossing detectors which is dependent upon logical AND-devices.

We have suggested elsewhere (Wenderoth and Johnstone 1987) that just as there might be cells in MT and other extrastriate areas which respond to pattern rather than component motion, so there might be other cells along the extrastriate pathways which respond, via logical AND-wiring, to pattern rather than component *orientation*. This would help to account for all of the psychophysical data which demonstrate the salience of axes of symmetry (Wenderoth 1977) and for the evidence, as in the rod and frame and related effects, that axes of symmetry are treated by the visual system as weak but real lines, as if they are coded as contours. There is a growing body of evidence for total receptive fields (TRFs), stimulus interactions over distances much larger than the classic receptive field (CRF), which may result from feedback to V1 from extrastriate areas or may arise within extrastriate areas (Allman et al 1985; Maunsell and Newsome 1987). An extrastriate locus of our putative orientation conjunction detectors would account for the fact that illusory effects induced by axes of symmetry are relatively the fact that V1 neurons are tuned tightly to spatial frequency and position and would be unlikely to mediate illusions induced remotely. It has been proposed that the direct-1D TI has both striate and extrastriate components because gaps attenuate but do not eradicate the effect (Johnstone and Wenderoth 1989). This is also true of spatial-frequency differences. Wenderoth and Johnstone (1988a) observed a 75% reduction in the direct 1-D TI with a 2 octave difference, as did Georgeson (1973), who also obtained a 30 - 50% reduction when the difference was 1 octave. In the analysis of 2-D direct effects from experiments 1 to 4 (table 1) we obtained a 37% reduction in the 2-D TI when the frequency of the inducing plaid was 1 octave lower than the test frequency; and the corresponding reduction in experiment 5 was 39%. These considerations suggest some common mechanisms for the 1-D and 2-D TI, although we have obtained no consistent evidence for direction selectivity in the 2-D TI, whereas the 1-D TI is larger when test and inducing gratings drift in the same direction (Carney 1982; Johnstone and Wenderoth 1989).

Others have suggested alternate mechanisms for the RFI but these are not necessarily incompatible with our suggestions. Ebenholtz has shown that the rod and frame illusion increases with frame size and is independent of manipulations which affect other perceptual phenomena which have to do with the perception of form, depth, and size (eg Ebenholtz 1985a, 1985b). He has claimed, as a result, that the illusion

> "can be regarded as the static analogue of vection, contributing to the control of body posture and egocentric orientation via the angular orientation of images represented in peripheral vision" (page 109)."

Ebenholtz has suggested that the site of the effect is to be found in the ambient rather than the focal visual system, where low-level visuovestibular interactions occur. It has been reported in addition, that small frame effects (under 10°) *are* affected by the variables relevant to focal vision, so that the small and large frames may be processed by the focal and ambient systems, respectively (Ebenholtz 1985b), a suggestion consistent with that of DiLorenzo and Rock (1982), who proposed that similar mechanisms explain the 1-D TI and the small, but not large, frame effect. One result which does not comfortably fit this hypothesis is Ebenholtz's (1985a) report that the large frame effect is blur specific, and thus by inference, spatial-frequency specific, a characteristic less likely to be a property of a visuovestibular interactive system which, as Ebenholtz notes, is independent of manipulations concerned with the perception of spatial variables such as form, depth, and size.

Recently, Maunsell (1987) reviewed evidence for the two kinds of visual system (which he terms 'spatial' and 'object') and related these two systems to be extrastriate magnocellular (M) and parvocellular (P) pathways, respectively. He noted that interactions between cortex and superior colliculus occur entirely along the M stream and that little is yet known about the overlap between the two systems, which might arise either by physically mixed inputs or by each system's "possessing rudimentary capabilities for the function of the other" (page 85). It might be that the rod and frame illusion does depend upon both V1 and extrastriate mechanisms, as we have suggested, and that some feedback to lower centres is involved. Overlap between the focal and ambient systems could account for the frequency specificity of the rod and frame illusion and ...ount for differences between small and large frame effects.



Peterhans and von der Heydt 1987), is at least suggestive of extrastriate involvement. Of primary importance, however, is that the rod and frame analogue we have devised is a stimulus far more amenable to manipulation of neurophysiologically relevant parameters than a square outline frame. We have presented some evidence that the abutting but not the distal plaid illusion is spatial-frequency specific, by varying frequency directly. All of our stimuli were 6.6 deg in size, or less. It would be of interest, and relevant to theories of the rod and frame effect, to examine the 2-D TI with very large peripheral plaids. Such large field plaid illusions may differ in many ways from small field effects. For example, we have suggested that the small field effect may not be dependent upon plaid motion or motion direction: this may not be the case with large peripheral stimuli.

There is another important reason to distinguish between large and small frame effects. Ebenholtz (1985c) argued that large frame effects could not be accounted for in terms of 'relational determination' because the illusion was independent of the relative sizes of rod and frame; ie contour proximity, which increases the direct TI, the Zöllner illusion, and related effects (see Wenderoth and Johnstone 1988a), does not modulate large frame effects. Coren and Hoy (1986), on the other hand, showed that small frame illusions drawn on paper and presented on a flat table in full-cue conditions *were* dependent on relative frame/rod sizes. They concluded (page 162) that their small frame effects

> "... seem to be more analogous to a traditional visual-geometric illusion of orientation, and seem to be strongly affected by relational factors rather than visual-vestibular interactions ... . Furthermore, these effects are measurable in simple printed rod-and-frame arrays which seem to be independent of a gravitational component.""

If Coren and Hoy are correct, then small frame effects may also occur at orientations other than vertical when measurement requires parallel matching, as in the case of the simple TI (O'Toole and Wenderoth 1977). To date, such measurements have proved difficult because a matching line would need to be placed far enough from a tilted frame not to be affected by the frame's contours, requiring rather peripheral matching stimuli. One advantage of our analogue RFI display may be that such measurements can be more easily made. In any case, it is to be hoped that further investigation using the 2-D TI paradigm may help to relate the rod and frame effect more closely to the extant body of evidence on interactions between orientations in human vision.

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# Depth interpolation with sparse disparity cues

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**Abstract.** The interpolation of stereoscopic depth given only sparse disparity information was investigated. The basic stimulus was a rectangle with zero disparity at one edge, and 20 or 30 min visual angle disparity at the other. The depth assigned to the ambiguous intervening locations was measured by means of a small briefly-flashed binocular comparison spot. For a stimulus consisting of a uniform rectangle presented on a background of random dots with zero disparity, interpolated depth was greater for a high mean contrast between rectangle and background than for a low mean contrast. Relative to a linear interpolation between the edges, a larger difference in edge disparity resulted in poorer depth interpolation. Depth interpolation based on rivalrous information was examined by filling the stimulus rectangle with narrow-band filtered noise which was uncorrelated between the two eyes. Four different passbands which were matched in apparent contrast were investigated. The results demonstrate that the rivalrous low-spatial-frequency content was resistant to interpolation; rivalrous high spatial frequencies did not interfere with depth interpolation. High-spatial-frequency stimuli yielded a percept similar to the uniform-field condition, whereas low-spatial-frequency stimuli lay in a depth plane near or even behind the background. In the latter case a transparent plane was perceived which was linearly interpolated between the two edges, and which floated above the rivalrous noise.

## 1 Introduction

When uniform rectangles of slightly different widths are presented to each of the two eyes, the subject usually perceives a rectangle tilted in depth (Ogle 1950; Blakemore 1970; Wilson 1976; Tyler and Sutter 1979; Halpern et al 1987). This observation is interesting because the only cue to depth is the disparity of the edges. Areas in the center of the rectangle are perceived as having intermediate depth values, although no point-by-point matching is possible. It is this process of inferring intermediate depth values between sparse disparate elements that we term 'depth interpolation'. The depth values assigned to these intermediate locations we call 'interpolated depth' since the observers are asked to judge the depth of these locations relative to a comparison stimulus with a well-defined disparity value. By using the term interpolated depth, we do not mean to imply a particular mechanism used to infer these depth values (such as spline interpolation, etc), but simply that a depth has been assigned to locations where disparity is ambiguous, and that this perceived depth is based, in part, on the depth values at locations where disparity is well-defined. In this paper, the term 'depth' is always used as a psychological magnitude, and 'disparity' as a stimulus variable.

Consider the stereogram illustrated in figure 1. In this stereogram only the edges carry disparity information. The disparities of the six edges in the stimulus are, from left to right, 0, 2, 4, 4, 2, and 0 min visual angle (from a viewing distance of 50 cm). These well-defined disparity values are illustrated as filled squares in figures 2a and 2b. We have shown this stereogram to a large number of observers, and two percepts predominate. Some subjects perceive the grey stripes as flat (as in[...]