ArticleReach Paging Slip / Cover Sheet

Ariel EKW
7/5

07/03/2008

Citation Information

Journal: Perception

Article: Possible neural substrates for orientation analysis and perception.

Author: Wenderoth, P

Local CN: BF 311 .P348

Volume: 16 Issue: 6

Quarter: Season:

Number: Month:

Day: Year: 1987

Pages: 693 - 709

Patron Note:

Staff Note:

Paged Locations: >>9ore0<<, za014, 9wsu0, za006, 9cubp, ... (1 of 7 sites paged)

ISSN: **0301-0066** EISSN:

Request **80543**

Ariel patron: arlir,delivery

Note (Journal Title)

Ariel IP: 205.227.91.137

Patron's Library Information

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

Email: borroill@uoregon.edu
Fax: 541-346-3094

Patron Information

Patron Number: p1123080@9ore0
Patron Type: ARLIR faculty
Patron Email: prd@uoregon.edu
Preference: Not Specified

Holdings Information

Location: KNIGHT HOLDINGS: v.1 1972-v.36 2007
Call Number: BF 311 .P348

Perception, 1987, volume 16, pages 693-709

Possible neural substrates for orientation analysis and perception

Peter Wenderoth, Syren Johnstone
Department of Psychology, University of Sydney, Sydney, NSW 2006, Australia
Received 11 December 1987

Abstract. Recent research into the response properties of extrastriate visual cortical mechanisms has revealed single-cell functional organisation which closely parallels certain global and apparently emergent properties of psychophysical observation. An attempt is made to relate previous data on orientation illusions and aftereffects to these extrastriate mechanisms and new data which cannot be explained adequately by V1 (striate) orientation channels are discussed. Conversely, properties of cells in areas such as V3, V4, MT, and others seem to provide an obvious neural substrate for global interactions. It is suggested that psychological 'explanations' couched in terms of 'hypotheses' or 'cognitive problem solving' lack heuristic value, and that, in contrast, the properties of extrastriate cells can suggest novel experimental psychophysical paradigms which are designed to probe these higher-order global mechanisms more or less selectively.

1 Introduction

Perceptual illusions occur when there are discrepancies between physical events and the perceptual representation of those events. It can be argued that such illusions are byproducts of otherwise normal perceptual processes which occasionally result in illusory percepts under particular, perhaps unusual, conditions. The study of illusions aims to discover the nature of mechanisms normally involved in perceptual processing by considering the conditions under which these processes can lead to misperceptions. This discussion is principally concerned with two particular illusions of orientation, the rod-and-frame illusion (RFI) and the tilt illusion (TI), which usually are regarded as separate effects. As in Wenderoth (1977), they are treated here as members of a single class of orientation effects, which also includes other cases.

The RFI occurs when a vertical test rod is surrounded by a tilted square frame; the tilt illusion occurs when a vertical line or grating is superimposed upon or surrounded by a tilted line or grating. In both cases the rod or line appears nonvertical. In the light of recent neurophysical and psychophysical evidence, we propose to argue that the RFI and the TI can be regarded as sharing common neural mechanisms.

The generic stimulus display from which all exemplars of this orientation illusion class can be derived consists of a vertical test line or grating superimposed on or surrounded by n gratings intersecting at angles of $180°/n$ (Wenderoth and Beh 1977). For the RFI the inducing stimulus consists of all or part of two intersecting orthogonal gratings. Wenderoth (1977) found that the angular function of illusions induced by orthogonal gratings was identical to that induced by a square outline frame. The TI occurs when the inducing stimulus consists of a single grating. The various other RFI variants studied by Wenderoth (1973, 1977), including rectangular, triangular, octagonal, etc frames (ie, figures with 3, 4, ..., n sides), can be produced by varying either the relative spatial frequencies of the gratings, their number, or their relative orientation.

The RFI has been studied mainly by measuring judgements of vertical both when a test line (rod) is presented alone (pretest control measure) and when it is surrounded by a tilted square frame (test measure), the difference between these two measures being taken as the illusion induced by the frame on the perceived rod tilt. When the frame tilt is systematically varied from upright through 90° (ie, from 90° to 0°), the rod at first appears tilted opposite to the frame (roughly in the range 90° to 60°) and then tilted towards it (60° to 45°); at 45° there is no illusion; the rod then appears tilted away from the frame again (45° to 30°) and, finally, tilted towards it once again (30° to 0°). In an attempt to explain this angular function, Beh et al (1971) proposed a 'major axes hypothesis' (MAH). They asserted that the square frame has four axes of symmetry and when the frame is upright these are aligned with vertical, horizontal, and the two oblique diagonals. According to Beh et al (1971), the rod always appeared tilted away from whichever axis of symmetry is closest to vertical, with no illusion when one of the axes is vertical and the other axes are symmetrically disposed about it. Thus, as the frame tilts between 90° and 45°, first the nearest axis is the initially upright one, but it then becomes the diagonal axis on the other side of vertical, accounting for the change in illusion direction between 90° and 45°. No illusion occurs at 45° because the diagonal axis is vertical. A similar analysis applies to frame tilts between 45° and 0°. Note that the square frame (or orthogonal gratings) and also a single grating have two kinds of axes of symmetry: those which are parallel with the real lines of the figure (main line axes) and those which are not (virtual axes). In the case of the RFI, the main line axes are parallel to the sides of the frame (or grating lines) and the virtual axes are the diagonals of the frame (or the bisectors of the angles at the grating intersects). A single grating or line used to induce the TI has a main line axis parallel to the inducing figure and a virtual axis orthogonal to it.

Although the MAH was found to require some additional postulates to account for asymmetries in the data (Wenderoth 1977), it has received empirical support (eg, Hartley 1982). All of the data on the RFI and its variants seemed to suggest that axes of symmetry are treated by the visual system as weak but real lines, as if they are coded as contours (Wenderoth 1977; Wenderoth and Beh 1977; Hartley 1982). Because they found that the full RFI could not be predicted by summing illusions produced by components of the complete display, Wenderoth and Beh (1977) concluded that the illusion reflected more global than local processes, especially since the frame is distal from the rod. Noting that the RFI is zero for 45° frame tilts, Wenderoth and Beh (1977, page 67) suggested that

> "... although the component lines (local features) of the frame are tilted +45° and −45°, it may be the tilt of the whole 'global diamond' (ie, 0°) which determines the illusory effect on the test rod: the vertical test rod and the vertical diamond may excite the same visual-orientation-selective 'channels'".

Moreover, Hartley (1982, page 375) concluded his discussion this way:

> "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. It may be that symmetry plays an important role in pattern recognition ... . 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."

The TI differs in one important respect from the RFI: typically, the inducing line or grating is superimposed upon, or at least abuts, the test line, so that relatively localised processes, such as lateral inhibition in the orientation domain acting upon classic receptive fields (see below), provide possible mechanisms. Wallace (1969), Tolhurst and Thompson (1975), and Virsu and Taskinen (1975) found that the TI was largely abolished when there were gaps of the order of 1 deg between test and inducing stimuli, whereas the RFI typically occurs with larger gaps.

Figure 1 shows examples of the angular functions of the TI and the RFI; the positive illusions are those in which the test line is *set* in the same direction as inducing tilt (as defined by the experimenter). Negative effects are in the opposite direction. These data show that settings tend always to be in the direction of the axis of symmetry nearest vertical and that large effects occur when this axis coincides with a main line axis (ie, positive TI; first positive and last negative peak of the RFI), with smaller effects when the nearest axis is virtual.

Let us refer to the main line axis effects as *direct* effects and the virtual axis effects as *indirect* effects. Although these data can be *described* by saying that settings err towards the axis of symmetry nearest vertical, in order to *explain* them we seek to understand the neural mechanisms underlying the phenomena. It is towards a consideration of such mechanisms that we now turn.

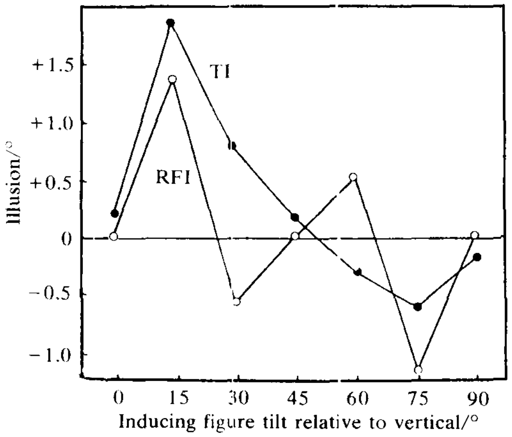

Figure 1. The angular functions of the tilt illusion (TI, solid circles) and the rod-and-frame illusion (RFI, open circles). Data from Over et al (1972) and Beh et al (1971), respectively.

2 Neurophysiological evidence

Evidence has been accumulating rapidly since the discovery of the 'periphery effect' by McIlwain (McIlwain 1964) that studies of classic receptive field (CRF) properties of single neurons in retina, lateral geniculate nucleus (LGN), and striate and extrastriate visual cortex provide only a limited understanding of visual processing mechanisms. Recently, Allman et al (1985a) summarised the body of evidence for stimulus-specific responses beyond the CRF: the data show that in most visual areas the response of a cell to its optimal CRF stimulus can be modified substantially by stimuli presented simultaneously to retinal areas well removed from the CRF. By definition, these modulating stimuli have no effect on the response of the cell in the absence of any CRF stimulus. Allman et al refer to this broader area of influence as the total receptive field (TRF). In addition, Zeki (1975, 1978) suggested that extrastriate cortical areas operate in parallel, with each area dealing primarily with one stimulus property (eg, motion, colour). Extensive investigation of extrastriate cortex, especially in macaque monkey, has revealed cells that have response properties both similar to and qualitatively different from those in V1 (striate cortex) and that have quite complex TRFs. Much of the latter evidence, relating to the motion pathway and the colour and form pathway, has been summarised recently by Maunsell and Newsome (1987).

It is important to stress that, in the process of developing our arguments, we frequently use the properties of neurons in the middle temporal area (MT) as exemplars of extrastriate processing characteristics. On the one hand, this should not be taken to imply that MT is the suggested site for the orientation-selective mechanisms which we propose. On the other hand, although we cannot with certainty exclude subcortical areas in the generation of the illusions with which we are concerned, their orientation tuning does suggest a cortical locus.

Albright (1984) and Albright and Desimone (1987) have compared the properties of receptive fields in MT with those in V1. Although the responses to stationary flashed slits were similar in magnitude in the two areas, orientation and direction tuning were narrower in V1. MT responses to moving stimuli were much stronger and a higher proportion of MT cells were direction specific (Albright 1984). Just as an orientation hypercolumn occupies a horizontal distance of 0.4-0.5 mm in V1, so 'axis-of-motion' modules occupy the same cortical area in MT, and it has been suggested that the trade-off between the much larger receptive fields in MT with its smaller magnification factor means that a visual stimulus will activate roughly an equal number of modules in V1 and MT (Albright and Desimone 1987).

Let us consider properties of TRFs in MT. Many MT cells have properties which are considerably more complex than those reported in V1. Allman et al (1985a, 1985b) reported TRFs in MT which were fifty to one hundred times the CRF area. When the CRF was stimulated with an optimally oriented moving bar the response to the bar could be extensively modulated by random dots drifting in the TRF surround. The nature of the modulation was diverse. Some cells (30%) were inhibited by all drift directions, some (44%) were inhibited by dots drifting in the preferred direction and 8% of the cells were facilitated by dots drifting at 90° to the preferred orientation. Moreover, of the forty-eight cells that were inhibited by TRF drift in the preferred direction, 56% were also inhibited by drift in the nonpreferred direction, and 44% showed facilitation. Considering these MT responses and field sizes, and also TRFs in the colour and form pathways, Allman et al (1985a, 1985b) speculated that such TRFs may be involved in

> "mechanisms for local-global comparisons embedded in visuotopic matrices that may serve as the basis for many functions in vision, such as the perceptual constancies, figure-ground discrimination, and depth perception through motion" (1985a, page 426).

That is, CRFs alone seem unable to account for context-dependent percepts which occur, for example, in the colour constancies, induced motion, and subjective contours, because these frequently occur across large retinal distances. On the other hand, TRFs seem ideally suited to such long-range comparisons.

Next, consider an example of differences in response properties in different areas. Of particular interest here are experiments which employ pairs of orthogonal sine-wave gratings which drift in one direction, orthogonal to their orientations. Depending upon the relative constrasts, frequencies, and speeds of the component gratings, human observers perceive such complex displays either as separate gratings, one drifting over the other ('transparent motion', Adelson 1987), or as a coherent plaid pattern. Movshon et al (1985) have shown how a pattern of constraints uniquely determines the perceived direction of drift in the latter case. Thus, the composite motion direction and velocity is determined by the intersection of lines orthogonal to the motion vectors of the component contours and this is not always equivalent, but sometimes is so, to a simple vector sum. For example, and here the two are equivalent, if the gratings are oriented 135° and 45° (horizontal at 0°) and are drifting in the directions 45° and 135°, respectively, then the composite plaid appears to drift horizontally to the right.

Single neurons in different areas of macaque monkey cortex respond in different ways to such composite stimuli. In V1, all cells studied respond only to the component gratings: as the plaid pattern is rotated through 180°, V1 cells tuned to orientation x and direction y respond first when one of the component gratings has those properties and again when the other grating has them (Movshon et al 1985). Thus, on a polar plot in which radius direction represents orientation and radius length represents response magnitude, V1 cells exhibit a two-lobed response function, and, in addition, there is some cross-orientation inhibition: V1 cells respond less to each plaid component when they are presented jointly than when each is presented alone. Morrone et al (1982; see also Burr and Morrone 1987) have shown that cat V1 simple cells exhibit cross-orientation inhibition: when stimulated with orthogonal gratings or two-dimensional noise, these cells are inhibited such that the slope of their contrast response function is lessened considerably. Complex cells do not exhibit such behaviour and respond well to textured stimuli, as found earlier by Hammond and MacKay (1975).

In contrast, about 25% of cells in MT, an area known to be concerned with the analysis of motion, respond in single-lobe fashion to the composite plaid. Thus, such a cell which responds best to a *single* vertical grating drifting to the right will also respond best to a plaid pattern drifting right with component gratings oriented 135 and 45°, a response which clearly parallels the human observer's perception. Movshon et al (1985) reported that, in a sample of one hundred and eight MT neurons, 40% were component selective whereas 25% were pattern selective, and Albright (1984) found that, of sixty-one MT cells, 29% had a preferred orientation of a moving slit parallel to the preferred direction of motion of a moving spot, a requirement, Albright argued, for pattern-selective neurons of the kind described by Movshon et al (1985).

The idea that TRFs may be the substrate of more global perceptual processes has been put forward by others. Desimone et al (1985) suggested that cells in macaque V4 and inferior temporal cortex (IT) (see Iwai 1985) might be concerned with global processing and constancy, and they pointed out (page 449) that "the sensitivity of most IT neurones to shape appears to be based on a global property of the shape rather than on the size or location of local contours". A similar point was made by Nelson and Frost (1978).

There is precedence in the pattern-cognition literature for the idea that discrimination of global features of a stimulus, such as pattern motion, a texture difference, or an axis of symmetry, is achieved by some kind of neural comparator analogous in function to a logical AND gate, and it has been suggested that dendritic spines may perform such gating functions (eg, Shepherd and Brayton 1987). Thus, to account for the 'emergence' of pattern-selective neurons in MT, Movshon et al (1985) proposed that these 'second-stage 2-D analyzers' might require simultaneous activation of V1 cells tuned to the component orientations and directions ('first-stage 1-D analyzers') in order for them to respond. Similarly, Julesz et al (1973) outlined 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)

Marr's (1982, page 66) model of zero-crossing detectors also is dependent upon logical AND devices.

Just as there exist in MT and other extrastriate cortical areas neurons which respond to global pattern motion and not to the motion of the component contours, so it seems plausible to postulate the existence of neurons which respond to pattern *orientation* and not merely the directions of the component line contours. It is our thesis that component orientations are extracted by V1 as well as by extrastriate neurons, but that global pattern orientations are coded (AND-gated) by cells in higher extrastriate areas, and it is these neurons which account for the apparent psychophysical salience of axes of symmetry. We propose that several orientation illusions include components that derive from lateral inhibitory processes which arise early in visual processing (eg, V1) and other components which arise later, in more global processing areas (eg, V3, MT, VP, V4, and, possibly, V2).

In some respects, these proposals are similar to those suggested by Vogels and Orban (1987) in relation to the oblique effect. They found that practice with both real and illusory contours reduced the oblique effect, but that transfer of training occurred from illusory to real contours, not from real to illusory contours. Because von der Heydt et al (1984) found that some cells in V2, but never those in V1, responded to illusory contours, Vogels and Orban proposed that there are two pathways for contour processing. The first of these includes V1 simple cells and is concerned only with real contours; the second involves extrastriate cortex, possibly V2, and it processes both real and illusory contours. However, we are suggesting the more general hypothesis that the neural substrates of perceptual events which generally are referred to as global are to be found in the extrastriate motion (magnocellular) and colour-form (parvocellular) pathways. Maunsell and Newsome (1987) note that the distance over which spatial interactions occur in extrastriate pathways increases along the pathway from V1 to MT (see Gattass and Gross 1981; Mikami et al 1986b; Albright and Desimone 1987), and they point to the fact that directional interactions occur over distances of 10-20 deg in area 7a, suggesting that the extent of remote interaction may increase further along the pathway.

Finally, Peterhans and von der Heydt (1987) recently reported cells in monkey V2 which responded to spatially separated but synchronously moving dots, and which responded better to a row of dots than to a solid bar. In contrast, V1 cells responded weakly or not at all to such stimuli, and their response fell by one half when a single gap of 2 min visual angle was inserted in the centre of a solid bar. Peterhans and von der Heydt (1987, page P4) concluded that "activity in V2 is more related to object concepts and less to local stimulus features such as luminance or connectedness".

We now consider some psychophysical evidence which relates to these ideas on the role of extrastriate cortex. Our general approach is to probe the visual system with stimulus displays which are less likely to be adequate for V1 neurons but which are known, or seem likely, to stimulate cells in higher areas, a kind of 'psychoanatomy' which Julesz (1971) carried out with random-dot stereograms.

3 Psychophysical evidence

3.1 *The tilt illusion: direct and indirect effects*

It is generally believed that the TI and the tilt aftereffect (TAE) have common mechanisms, the most widely accepted candidate being lateral inhibition between orientation-selective channels in visual cortex, V1 (eg, Blakemore et al 1970; Blakemore and Tobin 1972; Carpenter and Blakemore 1973; O'Toole and Wenderoth 1977; Magnussen and Kurtenbach 1980; Nelson 1969, 1985; Wenderoth et al 1986). One phenomenon associated with the TI and the TAE which was not addressed by the original lateral inhibition theory was the indirect effect. The most frequently studied TI and TAE is the direct effect, the contrast effect which occurs between inducing and test stimuli separated in orientation by 10°-20°, so that the test stimulus appears rotated in the direction away from the inducing stimulus. The indirect effect is a much smaller, assimilation effect which is not always observed and it occurs between inducing and test stimuli separated in orientation by large angles, of the order of 70°-85° (figure 1). However, because the TI and TAE angular functions are virtually identical when indirect effects are obtained (figure 1), and because of various other similarities between the two effects (see Magnussen and Johnsen 1986), a common mechanism seems likely. Thus, reference to the TI in the following discussion implicitly refers also to the TAE.

Although O'Toole and Wenderoth (1977) showed how the inhibition theory could explain indirect effects in terms of *dis*inhibition, predictions from this model were only partially confirmed (Wenderoth et al 1986). A survey of the literature indicates that indirect effects tend not to occur when the illusion display consists of a simple small acute angle (Carpenter and Blakemore 1973; Virsu and Taskinen 1975; Wenderoth and

Johnson 1985; Wenderoth et al 1986), but that they do occur, quite robustly, when the display includes relatively large inducing gratings (Gibson and Radner 1937; Logan 1962; Over et al 1972; Mitchell and Muir 1976; O'Toole and Wenderoth 1977) or relatively long centrally intersecting inducing and test lines (eg, Morant and Harris 1965; Muir and Over 1970). Thus, the indirect effect might be display-dependent and may occur only when the stimulus display is one which is adequate to involve higher-level, more global visual processes.

Bearing in mind the above psychophysical and neurophysiological data, it is possible to formulate a theory of mechanisms underlying major axis effects to supplement the earlier more descriptive version. Wenderoth (1977) proposed that direct effects are relatively large because the test orientation is repelled by a nearest axis of symmetry defined by real contours as well as by the virtual axis. In the case of the TI this is a single line or grating and the axis parallel with it; in the case of the RFI it is the real frame sides and the parallel axis. Indirect effects are smaller because virtual axes, which have less powerful effects, are involved. In the case of the TI, this is the virtual axis orthogonal to the tilted inducing orientation; in the case of the RFI it is the diagonal of the frame. These axes are purely virtual since they coincide with no real contour.

Of course, this hypothesis is little more than another description of the data. In an attempt to devise a possible mechanism for virtual axis effects, Wenderoth (1977) proposed that orientation domain inhibition or disinhibition generated by orthogonal contours might summate along the bisector of the orthogonal contours, thus defining a virtual line, a suggestion later used by Georgeson (1980, 1985) to account for the 'graph paper effect'. However, aspects of Wenderoth's (1977) data were not consistent with this hypothesis. It can now be proposed that direct effects are larger because they arise from features of the stimulus which are processed both by low levels of the visual system (eg, V1) which respond to real contours, and by higher levels which respond to global features (eg, symmetry). Indirect effects, on the other hand, involve only the higher global mechanisms. It is such global mechanisms which might encode a right-tilted square frame as a left-tilted diamond, or a single line tilted 80° right of vertical as a left-tilted object; in both cases the near-vertical virtual axes of symmetry are used.

There is evidence consistent with this proposal. It is well established that the direct TI is large when a vertical test grating is surrounded by an abutting tilted inducing grating but that the effect is markedly reduced when there is a blank annulus gap between the two gratings (eg, Tolhurst and Thompson 1975). The TI is also reduced if the spatial frequency of the abutting inducing grating differs by about two octaves or more from that of the test grating (Georgeson 1973). The latter is true of the TAE as well (Ware and Mitchell 1974). The generally accepted explanation for the decreased effects is that V1 cells are specifically tuned for both spatial position and spatial frequency so that lateral inhibition occurs only between populations of neurons with similar tuning for position and frequency.

We have recently confirmed these findings (Wenderoth and Johnstone 1988a), but have also demonstrated that the same stimulus manipulations have no influence on the indirect TI. Moreover, as the size of the surrounding and abutting inducing annulus was decreased until only 0.25 deg thick, the direct effect was reduced considerably but the indirect effect was changed little in magnitude. In all cases, the direct effect was reduced but not eradicated; it remained at about the size of the indirect effect. We interpreted these data to indicate that the indirect effect arises where receptive fields are larger, at a higher global processing level, and so is unaffected by the size or position of the inducing grating. Because the direct effect was never eliminated, we proposed that it consists of two components, a smaller one arising from higher levels and a larger component resulting from V1 which is position and frequency specific. In MT, one class of cell responds in single-lobe fashion to a drifting plaid but another, larger, class responds, as do all V1 cells, in double-lobe fashion to the component gratings. If the same is true of our hypothetical orientation-selective mechanisms, so that only a proportion of cells are AND gates, either the nongating cells might participate in the extrastriate component of the direct effect, or they may be inhibited by the AND-gating cells. Movshon et al (1985) proposed the latter mechanism in the case of MT, to account for the fact that the plaid component drifts cannot be perceived when coherent motion is seen. Similar inhibition between pattern- and component-orientation-selective mechanisms could account for the fact that a diamond is not simultaneously perceived as a tilted square.

As a final test of our hypothesis of the differential mechanisms of direct and indirect TIs, we surrounded the whole test and inducing complex with a vertical or slightly tilted luminance square frame. Kohler and Wallach (1944) had claimed that they could obtain indirect effects only if other vertical edges were not visible. We speculated that if the indirect effect arose from global processing, the surrounding square might abolish it but this would not be true of the direct effect. That is, based on the Allman et al (1985a, 1985b) proposal that combinations of facilitation and inhibition from the TRF might be involved in the perceptual constancies, we wondered whether the indirect TI could be regarded as arising from such global mechanisms concerned with orientation constancy. Thus, under normal circumstances a rich collection of cues to vertical and horizontal is available in the visual world so that errors in orientation analysis are minimised. Under impoverished laboratory conditions, errors may occur when the inducing grating is the sole reference orientation. Providing global orientation processing mechanisms with the additional datum of the surrounding square might therefore eradicate these errors. This is precisely the result we obtained: indirect effects occurred only in the absence of a surrounding frame, whereas direct effects persisted in its presence. This persistence of direct effects suggested that the direct effect reflects, at least in part, the corruption of orientation processing at a level or stage of visual processing prior to the level(s) at which global information is extracted.

More recently (Wenderoth and Johnstone 1988b), we have shown that direct and indirect TIs both increased in magnitude as stimulus duration decreased and that, even at the shortest duration (25 ms), a surrounding frame reduced indirect effects by two thirds but had no effect on direct TIs. The data also suggested that whereas peak direct effects occurred at the shortest duration, indirect effects peaked later, and that direct effects became relatively independent of stimulus duration earlier (100 ms) than did indirect effects (400 ms). The effect of the frame on indirect TIs when all components were briefly flashed seemed to rule out more cognitive explanations of the frame's influence, and the relative phase lag of indirect and direct TIs is consistent either with later cortical processing of the indirect TI, or with the processing of indirect TIs within more purely sustained parvocellular pathways, or with both.

In relation to these experiments, it is of interest that Ebenholtz and Utrie (1983) found that if the RFI display was surrounded by a *circle* the illusion was reduced by about 75%. No reduction occurred if the circle was present but lay between the tilted frame and the test rod. These findings might be interpreted in terms of the surround circle providing a nontilted global reference orientation, although the authors admitted that it was puzzling that a stimulus devoid of any orientation information should have such an effect. Ebenholtz and Utrie put forward an explanation based on stimulation of the midbrain visuovestibular system by the circle. Given our hypothesis, we wondered whether a surrounding circle might reduce the indirect TI but not, or at least much less, the direct TI. We ran thirty subjects under the relevant conditions. When the luminance circle was absent, the direct and indirect TIs were +1.71° and −0.59°, respectively. When the circle was present, the corresponding effects were +1.87° and −0.27°, respectively. Although the differences are less than dramatic, with a standard error of

0.16, the last of these means (−0.27) was not significantly different from zero but the other three were.

It is interesting to note that in all of Wenderoth's (1977) RFI studies small frame sizes were used and that it is now common procedure to draw a distinction between illusions induced by small (10 deg or less) frames and the larger ones (28 deg) used in more traditional studies such as those of Witkin and Asch (1948). DiLorenzo and Rock (1982) have argued that the relatively small illusions obtained in the former studies (of the order of 1°–3°; see figure 1) are probably explicable in terms of processes similar to those which explain the TI, but that the much larger effects in the latter experiments are not. If this is so, then in terms of our hypothesis, the effects with large frames are entirely due to higher-order global mechanisms. This is so because DiLorenzo and Rock (1982) found that when a 24.75 deg frame, tilted 20°, was surrounded by an upright 40 deg frame, the RFI was abolished. On the other hand, when the inner frame was vertical but the outer frame was tilted the full effect was obtained. If small frame RFIs are due to mechanisms similar to the TI, we would have to predict that similar experiments with small frames would selectively eliminate the smaller indirect frame effects induced by virtual axes but not the larger direct effects induced by main line axes (figure 1).

Further work is needed on the effects of surrounding frames. Although it has long been asserted that the enclosing (surrounding) stimuli affect the appearance of enclosed (surrounded) stimuli more than the latter affect the former (Duncker 1929; Day et al 1979), this does little more than describe the phenomenon. On the other hand, large-area TRF mechanisms in areas such as MT and V4 seem well suited to the analysis of motion, orientation, etc, induced by surrounding or enclosing fields.

3.2 *The two-dimensional tilt illusion*

From figure 1 it can be seen that the TI which occurs with an inducing tilt of 30° is positive whereas that with an inducing tilt of 60° is negative. So, for example, an inducing tilt 30° right of vertical makes a vertical line appear tilted left; an inducing tilt 60° right of vertical makes a vertical line appear tilted right. An inducing tilt 60° *left* of vertical would make a vertical line appear tilted left. What, then, would happen if an observer inspected a crossing inducing display, composed of two centrally intersecting lines tilted 60° left and 30° right of vertical? If the two component TIs merely added in linear fashion, the superposition of the two effects would produce an appearance of left tilt in the test line. However, Wenderoth and Curthoys (1974) showed that in this case the test line appears tilted to the *right*. This nonadditivity of component tilt illusions was consistent with the MAH because the (virtual) axis of symmetry nearest vertical was that oriented 15° left of vertical.

A more complex version of the crossed-line stimulus is the orthogonal drifting grating display used by Movshon et al (1985), which we discussed earlier, and such a stimulus provides a versatile extension of the Wenderoth and Curthoys (1974) paradigm. Consider such a pattern with component gratings oriented 30° right of vertical (ie, 60°; 0° being horizontal) and 60° left of vertical (ie, 150°). As figure 2 shows, depending upon the drift directions of the component gratings, the composite plaid can be seen as a virtual orientation of 105° drifting right or left (figures 2a and 2b, respectively), or as a virtual orientation of 15° drifting up or down (figures 2c and 2d, respectively). We have found (Johnstone and Wenderoth 1988), first, that *stationary* crossed gratings such as this induce small nonadditive TIs, virtually identical to those reported by Wenderoth and Curthoys (1974), even when test and inducing stimuli are separated by a 2 deg blank annulus. This result indicates that plaid motion is not necessary to induce the remote two-dimensional (2-D) TI, and that the virtual-axis effect is not attributable to real Fourier components aligned with the apparent drift direction of a moving plaid.

We also observed that crossed drifting gratings induced larger nonadditive TIs and also that these indirect effects were larger when there was a blank annulus gap between an annulus area containing the drifting plaid and the central drifting vertical test grating. When the plaid and test gratings abutted, the indirect TIs were close to zero.

In more recent experiments (Wenderoth and Johnstone 1988c) we used larger samples of subjects and measured the 2-D TI at other inducing angles. This time, indirect TIs were not zero for an abutting pattern and there was a suggestion that direct effects, induced by real components of the plaid, were larger when the inducing plaid components both abutted the test figure and when they had the same spatial frequency as the test. It seemed that the failure to replicate the earlier findings of Johnstone and Wenderoth (1988) may have been due to the fact that they chose a single nonoptimum plaid orientation where only small effects occurred, ie, indirect effects induced by a virtual plaid axis. Further experiments are required to measure precisely how plaid-induced direct and indirect effects are affected by spatial properties of the display and by plaid motion, but the above results do suggest some common mechanisms for one-dimensional and two-dimensional TIs.

The 2-D TI results have a number of characteristics which seem consistent with the hypothesis that indirect effects (effects induced by virtual axes) arise in extrastriate cortical areas concerned with more global analysis. First, putative V1 simple cell interactions (eg, the direct TI), decrease as gaps or frequency differences are introduced between inducing and test stimuli. Johnstone and Wenderoth (1988) obtained an increase in the indirect 2-D effect with separation and Wenderoth and Johnstone (1988c) observed no obvious decrease. Second, cells in V1 do not respond to the coherent motion direction (and hence, perhaps, a virtual orthogonal axis) of a plaid pattern, whereas a class of cells in MT do. Third, simple cells in cat V1 are inhibited to some extent by simultaneous presentation of one grating at their optimal orientation and another orthogonal grating (Movshon et al 1985). In the presence of 2-D noise, such cells selectively do not respond, or multiplicatively reduce their firing, to two-dimensional stimuli (Morrone et al 1982), but such inhibition is not seen in

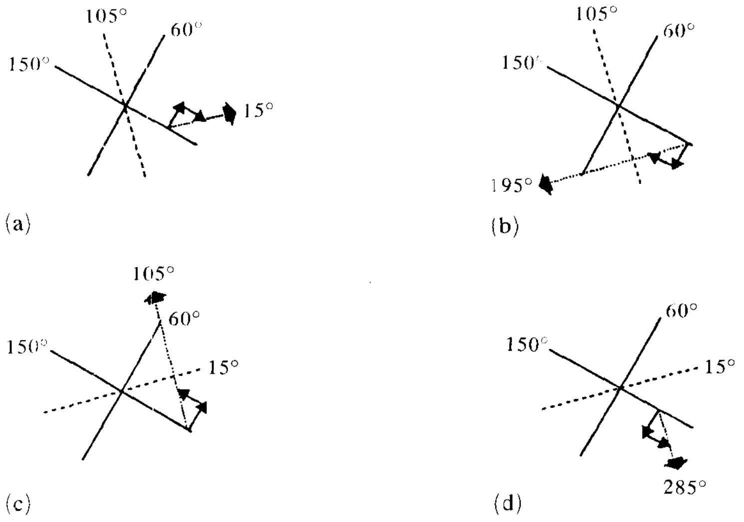

Figure 2. Perceived drift directions of composite plaid patterns. Two superimposed orthogonal gratings, oriented 60° and 150° (solid lines), can be drifted in four combinations of motion orthogonal to their orientations. Thus, in (a) the 60° and 150° gratings drift in the directions 330° and 60°, respectively (solid vectors), and the composite plaid is seen to drift in the 15° direction (dotted line). The three other possible combinations of component direction and the resulting pattern drift directions are shown in (b)–(d).

complex cells. Similar multiplicative reductions in the slope of the contrast response function occur when measures of visual evoked potentials are taken from human observers and when an orthogonal grating is superimposed on a test grating (Burr and Morrone 1987). In addition, application of the GABA blocker bicuculline (i) abolishes orientation selectivity in V1 but not in V2, and (ii) abolishes cross-orientation inhibition in V1 (Burr and Morrone 1987). Thus, a good deal of evidence points to cells other than V1 simple cells being involved in the analysis of two-dimensional stimuli and in the analysis of virtual lines or axes.

It is of interest to note that although cross-orientation inhibition affected the slope of the contrast response function, the intercept (ie, contrast threshold) was unchanged. Morrone et al (1982, page 351) therefore speculated that psychophysical correlates of cross-orientation inhibition must be sought in suprathreshold phenomena, and one which they suggested (although without logical reasoning) was the indirect tilt aftereffect.

3.3 *Pattern-specific motion aftereffect*

Although the motion aftereffect (MAE) is not strictly an orientation illusion, it may involve orientation analysis. The 'aperture problem' (Movshon et al 1985; Maunsell and Newsome 1987) illustrates this point: a moving grating seen through a circular aperture can only be seen as moving orthogonal to its orientation, regardless of its objective motion direction. Hence, any illusory or adaptation effect induced by a moving grating could arise either from its motion direction or from its orientation [and, in relation to this point, we intend to investigate the possibility that the 2-D TI (see section 3.2) can be measured either as an orientation illusion or as a direction-of-motion illusion]. Thus, when Sekuler et al (1968) found that downward-drifting gratings facilitated the threshold for upward-drifting gratings, they suggested that this was due to the common orientation, not the opposite motions. They noted (page 1150) that "Some technique is needed for separating orientation of contour from direction of movement so that the contribution of each may be unambiguously analyzed". One useful way to achieve this end is to use the drifting plaid patterns formed by, say, orthogonal gratings, in which perceived motion direction can be held constant while component orientations may vary, and vice versa.

Movshon et al (1985) reported the results of threshold elevation experiments which were consistent with the hypothesis that 1-D and 2-D motion patterns are encoded at different levels of the visual system. They adapted with either 1-D or 2-D stimulus, that is, either with a single vertical grating drifting left or right, or with a plaid pattern which appeared to drift left or right but which was composed of component gratings oriented 30° and 150°, drifting, respectively, in the directions 300° and 60°. Testing was carried out with both kinds of stimuli so that all four combinations of adapting/test displays were examined. It was found that threshold elevation was much greater when adapting and test patterns were the same than when they were different. This suggested that the different patterns were selectively adapting different visual mechanisms since it was not the case that common motion adapted common mechanisms. Interestingly, inspection of the data (Movshon et al 1985, figure 7) suggests that to the extent that some cross-pattern adaptation did occur, adapting to plaids affected gratings more than adapting to gratings affected plaids. This could be interpreted as consistent with moving plaids being encoded at a higher level (possibly MT), as Movshon et al suggested, which feeds back on to the lower level in inhibitory fashion.

Other evidence for the encoding of gratings and plaids at different sites is provided by Riggs and Day (1980). They were attempting to produce a direction-of-motion contingent aftereffect by adapting *alternately* to orthogonal drifting gratings. Instead of a contingent effect, they found that a variety of test patterns exhibited MAEs in the direction which was the resultant vector of the adapting stimuli. They also found that dichoptic presentation of the adapting gratings (one to each eye) resulted in a monocular test stimulus appearing to move in the direction opposite to the motion seen by that eye; but a binocular test produced the resultant vector MAE. These MAEs in the pattern-of-constraints direction were equally robust when the test stimulus was a field of dots. These perceptual responses are congruent with the response properties of macaque MT neurons which respond to pattern or to component motion and for which moving dot or stroboscopic flashed fields provide a powerful stimulus (Albright 1984; Allman et al 1985a, 1985b; Mikami et al 1986a, 1986b).

We have conducted some preliminary experiments on MAEs induced by drifting plaid annuli on central vertical grating test stimuli (Wenderoth et al 1988). The inducing gratings making up the plaid were presented either alternately or simultaneously so that the perceived motion during adaptation was either alternately up to the right or down to the right, or, in the simultaneous condition, coherent motion was horizontally to the right. We varied the orientations of the component adapting gratings so that the angle between them was 30°, 90°, or 150°, with the components oriented 75° and 105°, 45° and 135°, and 15° and 165°, respectively. The alternating grating conditions showed a linear decrease in MAE magnitude as the component gratings deviated more and more from the orientation of the vertical test grating. In contrast, the simultaneous presentation of the gratings (drifting plaid) resulted in a relative orientation tuning function which exhibited quadratic trend, with a suggestion that the MAE was largest when the component gratings were separated by 90° (ie, components ±45° from vertical). These results seem consistent with the hypothesis that the alternating gratings are encoded at a level of the visual system where the MAE is specific to the component grating orientations, but the plaids are additionally encoded at a higher level tuned to other aspects of the stimulus. One relevant parameter could be the speed of the plaid: as the angle between the component gratings increased, plaid speed increased (ie, temporal frequency was constant but the plaid elements—diamond shapes formed by the crossing of the gratings—increased in size) and there are neurons in MT and V3 which are tuned to speed as well as to other properties (eg, Felleman and van Essen 1987, Maunsell and Newsome 1987), whereas V1 and V4 cells are tuned essentially only to spatial and temporal frequency (Desimone et al 1985; Desimone and Schein 1987; Maunsell and Newsome 1987).

4 Discussion and conclusion

In this paper we have aimed to demonstrate how relatively recent neurophysiological evidence on the properties of extrastriate cortical areas may provide new insights into the mechanisms which underlie some of the more global illusory effects that involve orientation-selective mechanisms. Thus, the properties of cells in areas such as V2, V3, VP, V4, MT, MST, and other areas have suggested new experimental paradigms to probe mechanisms involved in the analysis of orientation by the visual system; they have led to the discovery of new pattern-specific tilt effects; they have pointed to novel stimuli (eg, 2-D drifting plaids) which can be used to separate motion and orientation effects and preferentially to stimulate cortical areas other than V1; and perhaps most important, they have suggested a possible neural basis for the apparent salient effects of virtual axes of symmetry in some orientation illusions (Johnstone and Wenderoth 1988; Wenderoth and Johnstone 1988a).

The preceding discussions of possible neural substrates of more global phenomena have not made reference to long-range intrinsic connections which have been reported in cat and monkey V1 (Rockland and Lund 1983; Livingstone and Hubel 1984). However, there is some controversy about the functional role of these connections.

Thus, it has been claimed that although these may play an important role in TRF mechanisms (Ts'o et al 1986 page 1170), they are exclusively excitatory and link columns of neurons with common orientation preference (Ts'o et al 1986). However, it has also been suggested that, in cat area 18, they link *orthogonally*-tuned neurons (Matsubara et al 1987) and that the cross-correlational technique used by Ts'o et al (1986) cannot detect such connections.

It seems to us important to draw attention to all of these recent neural findings for two reasons. First, now that von der Heydt et al (1984) and Peterhans and von der Heydt (1987) have found cells beyond V1 which respond to subjective contours and to incomplete contours, whereas V1 cells do not, it seems unlikely that theorists would seek to maintain a view that perceptual responses to these contours are in any sense based upon 'hypotheses' or some similar cognitive construct. Presumably numerous other phenomena, once considered to reflect the effects of some sort of process qualitatively different from that provided by basic neural machinery, will be found to have their basis in extrastriate areas. Only ten or so years ago, Rock (1975) argued that basic neural mechanisms seemed able to account for only a limited selection of perceptual phenomena and could not account for percepts which more closely resembled cognitive problem solving. Interestingly, he gave cognitive (subjective) contours as an example. We would claim that psychological 'explanations' based upon such terms as 'hypotheses' or 'cognitive problem solving' are empty of empirical content and obscurantist in that they disguise the need to search for mechanisms which must exist. In this context, it is useful to note that theorists (eg, the Gestaltists) have been criticised for postulating apparently logically-odd 'emergent properties' (eg, a whole is greater than the sum of its parts). However, emergent properties are so described only when there is a failure to include consideration of not simply the parts but their interconnection or relations (see Oatley 1978; Wenderoth and Latimer 1978). Similarly, when neurophysiologists eventually discover the nature of the neural circuitry that allows pattern-selective neurons to be constructed from lower-level direction-selective cells, the 'emergence' of pattern-selectivity in MT will not seem emergent at all.

Second, psychophysical experiments suggest a variety of stimuli which could profitably be employed in searching for extrastriate probe stimuli. For example, we have postulated that virtual axes of symmetry might adequately stimulate some cortical neurons, and perhaps such cells exist beyond V1 in the parvocellular V2-V4 (and beyond) form-colour pathway (Felleman and van Essen 1987). Perhaps 'moving phantoms' (eg, Tynan and Sekuler 1975) provide an adequate stimulus for cells which respond to subjective contours. Cells in MT respond to moving dots, are tuned for velocity, and can show facilitation when the surround of the TRF is stimulated with dots moving in the nonpreferred direction (Allman et al 1985b). It is entirely conceivable that these cells also respond selectively to stationary and *flickering* dots. If so, Allman et al's speculation that relative motion responses in these cells accounts for depth perception through motion may be extended to encompass depth perception through flicker, reported by Wong and Weisstein (1984), and figure-ground segregation through flicker (Wong and Weisstein 1987). It would be of interest to test the response properties of cells at various levels to a virtual oriented edge produced by the boundary between flickering and nonflickering dot regions. At the same time, it might also be prudent to probe V1 and the various subcortical regions with stimuli thought to possess global properties, since the response properties of neurons which are reported reflect not only their intrinsic tuning but also the sample of stimuli selected as probes. It would be unfortunate if the current Zeitgeist which tends to attribute 'global processes' to 'higher neural structures' obscured the quite possible potential of lower structures to perform such global analyses.

Finally, in the light of the proposals we have discussed here, it is interesting to recall a two-factor theory proposed by Morant and Harris (1965) to explain the angular function of the TAE. Gibson and Radner (1937) had suggested that the inducing lines adapt (normalise) towards whichever is the closest spatial axis, vertical or horizontal. This shift in the apparent orientation of the adapting stimulus results in a directionally similar shift in the vertical test stimulus. Hence, inducing lines tilted between vertical (90°) and the right oblique (45°) will result in a counterclockwise apparent shift in the test line, and inducing tilts between 45° and 0° will produce the reverse shift. Kohler and Wallach (1944), on the other hand, suggested a satiation mechanism which always produces direct (repulsion) effects. Morant and Harris noted that a linear superposition of both predicted functions could explain the data: Gibson and Radner's idea predicts equal-magnitude direct and indirect effects with a 45° zero-crossing; Kohler and Wallach's idea predicts only direct effects; but the sum of the two predicts the direct-indirect effect asymmetry which is obtained (figure 1).

Our experiments have shown (Johnstone and Wenderoth 1988, Wenderoth and Johnstone 1988a) that manipulations designed to reduce low-level, putatively V1, contributions to the direct TI reduce that effect roughly to the magnitude of the indirect effect but do not eliminate it altogether. As a consequence, we have proposed that direct effects arise partly from lateral inhibition in V1, but that direct and indirect effects share a common extrastriate component of roughly equal magnitude. It seems not unreasonable to propose that the neural counterparts of Kohler and Wallach's 'satiation' and of Gibson and Radner's 'normalisation' are to be found, respectively, in V1 lateral inhibition and in global extrastriate processes, and that the combination of the two accounts for the angular function of TI and TAE, precisely as Morant and Harris (1965) proposed.

Acknowledgements. This research was supported by a grant (A78515620) from the Australian Research Grants Scheme to the first author. We are grateful to a reviewer who cautioned against assuming that global phenomena are ipso facto extrastriate, and who pointed out that drifting plaids have power in the perceived drift direction.

References

Adelson E H, 1987 "Transparency in motion perception" *Investigative Ophthalmology and Visual Science* **28** (supplement) 232

Albright T D, 1984 "Direction and orientation selectivity of neurons in visual area MT of the macaque" *Journal of Neurophysiology* **52** 1106-1130

Albright T D, Desimone R, 1987 "Local precision of visuotopic organization in the middle temporal area (MT) of the macaque" *Experimental Brain Research* **65** 582-592

Allman J M, Miezin F, McGuinness E, 1985a "Stimulus specific responses from beyond the classical receptive field: Neurophysiological mechanisms for local-global comparisons in visual neurons" *Annual Review of Neuroscience* **8** 407-430

Allman J, Miezin F, McGuinness E, 1985b "Direction- and velocity-specific responses from beyond the classical receptive field in the middle temporal visual area (MT)" *Perception* **14** 105-126

Beh H, Wenderoth P, Purcell A T, 1971 "The angular function of a rod-and-frame illusion" *Perception & Psychophysics* **9** 353-355

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

Blakemore C, Tobin E, 1972 "Lateral inhibition between orientation detectors in the cat's visual cortex" *Experimental Brain Research* **15** 439-440

Burr D, Morrone M C, 1987 "Inhibitory interactions in the human visual system revealed in pattern-evoked potentials" *Journal of Physiology (London)* **389** 1-22

Carpenter R H S, Blakemore C, 1973 "Interactions between orientations in human vision" *Experimental Brain Research* **18** 287-303

Day R H, Millar J, Dickinson R G, 1979 "Induced movement as nonveridical resolution of displacement ambiguity: Effects of enclosure and number of field elements" *Perception & Psychophysics* **25** 23-28

Desimone R, Schein S J, 1987 "Visual properties of neurons in area V4 of the macaque: Sensitivity to stimulus form" *Journal of Neurophysiology* **57** 835 - 868

Desimone R, Schein S J, Moran J, Ungerleider L G, 1985 "Contour, color and shape analysis beyond the striate cortex" *Vision Research* **25** 441 - 452

DiLorenzo J R, Rock I, 1982 "The rod-and-frame effect as a function of the righting of the frame" *Journal of Experimental Psychology: Human Perception and Performance* **8** 536 - 546

Duncker K, 1929 "Über induzierte Bewegung (Ein Beitrag zur Theorie optisch wahrgenommener Bewegung) *Psychologische Forschung* **12** 180 - 259

Ebenholtz S, Utrie J W, 1983 "Peripheral circular contours inhibit the visual orientation control system" *Aviation, Space & Environmental Medicine* **54** 343 - 346

Felleman D J, Essen D C van, 1987 "Receptive field properties of neurons in area V3 of macaque monkey extrastriate cortex" *Journal of Neurophysiology* **57** 889 - 920

Gattass R, Gross C G, 1981 "Visual topography of striate projection zone (MT) in posterior superior temporal sulcus of the macaque" *Journal of Neurophysiology* **46** 621 - 638

Georgeson M A, 1973 "Spatial frequency selectivity of a visual tilt illusion" *Nature (London)* **245** 43 - 45

Georgeson M A, 1980 "The graph-paper effect: subjective stereoscopic patterns induced by moving gratings" *Perception* **9** 503 - 522

Georgeson M A, 1985 "Inferring cortical organisation from subjective visual patterns" in *Models of the Visual Cortex* eds D Rose, V Dobson (New York: John Wiley) pp 223 - 232

Gibson J J, Radner M, 1937 "Adaptation, aftereffect and contrast in the perception of tilted lines: I. Quantitative Studies" *Journal of Experimental Psychology* **20** 453 - 467

Hammond P, MacKay D M, 1975 "Differential responses of cat visual cortical cells to textured stimuli" *Experimental Brain Research* **22** 427 - 430

Hartley A A, 1982 "The roles of axes of symmetry in orientation illusions" *Perception & Psychophysics* **31** 367 - 375

Heydt R von der, Peterhans E, Baumgartner G, 1984 "Illusory contours and cortical neuron responses" *Science* **224** 1260 - 1262

Iwai E, 1985 "Neurophysiological basis of pattern vision in macaque monkeys" *Vision Research* **25** 425 - 439

Johnstone S, Wenderoth P, 1988 "Evidence for extrastriate contribution to basic processes in the analysis of orientation in human vision: The pattern-selective tilt illusion" submitted

Julesz B, 1971 *Foundations of Cyclopean Perception* (Chicago, IL: University of Chicago Press)

Julesz B, Gilbert E N, Shepp L A, Frisch H L, 1973 "Inability of humans to discriminate between visual textures that agree in second-order statistics—revisited" *Perception* **2** 391 - 405

Kohler W, Wallach H, 1944 "Figural-aftereffects: An investigation of visual processes" *Proceedings of the American Philosophical Society* **88** 269 - 357

Livingstone M S, Hubel D H, 1984 "Anatomy and physiology of a colour system in the primate visual cortex" *Journal of Neuroscience* **4** 309 - 356

Logan J A, 1962 "An examination of the relationship between visual illusions and figural aftereffects" PhD thesis, University of Sydney, Sydney, Australia

Magnussen S, Johnsen T, 1986 "Temporal aspects of spatial adaptation. A study of the tilt aftereffect" *Vision Research* **26** 661 - 671

Magnussen S, Kurtenbach W, 1980 "Linear summation of tilt illusion and tilt aftereffect" *Vision Research* **20** 39 - 42

Marr D, 1982 *Vision* (San Francisco, CA: W H Freeman)

Matsubara J A, Cynader M S, Swindale N V, 1987 "Anatomical properties and physiological correlates of the intrinsic connections in cat area 18" *Journal of Neuroscience* **7** 1428 - 1446

Maunsell J H R, Newsome W T, 1987 "Visual processing in monkey extrastriate cortex" *Annual Review of Neuroscience* **10** 363 - 402

McIlwain J T, 1964 "Receptive fields of optic tract axones and lateral geniculate cells: Peripheral extent and barbiturate sensitivity" *Journal of Neurophysiology* **27** 1154 - 1173

Mikami A, Newsome W T, Wurtz R H, 1986a "Motion selectivity in macaque visual cortex. I. Mechanisms of direction and speed selectivity in extrastriate area MT" *Journal of Neurophysiology* **55** 1308 - 1327

Mikami A, Newsome W T, Wurtz R H, 1986b "Motion selectivity in macaque visual cortex. II. Spatiotemporal range of directional interactions in MT and V1" *Journal of Neurophysiology* **55** 1328 - 1339

Mitchell D E, Muir D W, 1976 "Does the tilt aftereffect occur in the oblique meridian?" *Vision Research* **16** 609 - 613

Morant R B, Harris J R, 1965 "Two different aftereffects of exposure to visual tilts" *American Journal of Psychology* **78** 218 - 226

Morrone M C, Burr D C, Maffei L, 1982 "Functional implications of cross-orientation inhibition of cortical visual cells. I. Neurophysiological evidence" *Proceedings of the Royal Society of London, Series B* **216** 335 - 354

Movshon J A, Adelson E H, Gizzi M S, Newsome W T, 1985 "The analysis of moving visual patterns" in *Pattern Recognition Mechanisms* eds C Chagas, R Gattass, C Gross (Rome: Vatican Press) pp 117 - 151

Muir D, Over R, 1970 "Tilt aftereffects in central and peripheral vision" *Journal of Experimental Psychology* **85** 165 - 170

Nelson J, 1969 "The misperception of contour" unpublished manuscript, State University of New York, Stony Brook, New York

Nelson J I, 1985 "The cellular basis of perception" in *Models of Visual Cortex* eds D Rose, V Dobson (New York: John Wiley) pp 108 - 122

Nelson J I, Frost B J, 1978 "Orientation-selective inhibition from beyond the classic visual receptive field" *Brain Research* **139** 359 - 365

Oatley K, 1978 *Perceptions and Representations* (Andover, Hants: Methuen)

O'Toole B I, Wenderoth P, 1977 "The tilt illusion: Repulsion and attraction effects in the oblique meridian" *Vision Research* **17** 367 - 374

Over R, Broerse J, Crassini B, 1972 "Orientation illusion and masking in central and peripheral vision" *Journal of Experimental Psychology* **96** 25 - 31

Peterhans E, Heydt R von der, 1987 "The whole and the pieces—cortical neuron responses to bars and rows of moving dots" in *Seeing Contour and Colour* Proceedings of Satellite Symposium of 2nd World Congress of Neuroscience, Manchester, UK, August 1987

Riggs L A, Day R H, 1980 "Visual aftereffects derived from inspection of orthogonally moving patterns" *Science* **208** 416 - 418

Rock I, 1975 *Introduction to Perception* (New York: MacMillan)

Rockland K S, Lund J S, 1983 "Intrinsic laminar lattice connections in primate visual cortex" *Journal of Comparative Neurology* **216** 303 - 318

Sekuler R W, Rubin E L, Cushman W H, 1968 "Selectivities of human visual mechanisms for direction of movement and contour orientation" *Journal of the Optical Society of America* **58** 1146 - 1150

Shepherd G M, Brayton R K, 1987 "Logic operations are properties of computer-simulated interactions betwen excitable dendritic spines" *Neuroscience* **21** 151 - 165

Tolhurst D J, Thompson P G, 1975 "Orientation illusions and aftereffects: inhibition between channels" *Vision Research* **15** 967 - 972

Ts'o D Y, Gilbert C D, Wiesel T N, 1986 "Relationships between horizontal interactions and functional architecture in cat striate cortex as revealed by cross-correlational analysis" *Journal of Neuroscience* **6** 1160 - 1170

Tynan P, Sekuler R, 1975 "Moving visual phantoms: A new contour completion effect" *Science* **188** 951 - 952

Virsu V, Taskinen H, 1975 "Central inhibitory interactions in human vision" *Experimental Brain Research* **23** 65 - 74

Vogels R, Orban G A, 1987 "Illusory contour orientation discrimination" *Vision Research* **27** 453 - 467

Wallace G K, 1969 "The critical distance of interaction in the Zollner illusion" *Perception & Psychophysics* **5** 261 - 264

Ware C, Mitchell D E, 1974 "The spatial selectivity of the tilt aftereffect" *Vision Research* **14** 735 - 737

Wenderoth P, 1973 "The effects of tilted outline frames and intersecting line patterns on judgments of vertical" *Perception & Psychophysics* **14** 242 - 248

Wenderoth P, 1977 "An analysis of the rod-and-frame illusion and its variants" in *Studies in Perception* eds R H Day, G S Stanley (Nedlands, Western Australia: University of Western Australia Press) pp 95 - 141

Wenderoth P, Beh H, 1977 "Component analysis of orientation illusions" *Perception* **6** 57 - 75

Wenderoth P, Bray R, Johnstone S, 1988 "Motion aftereffect induced by successive and simultaneous adaptation to orthogonal crossed drifting gratings" *Perception* in press

Wenderoth P, Curthoys I S, 1974 "On the non-additivity of visual tilt illusions" *Quarterly Journal of Experimental Psychology* **26** 549 - 555

Wenderoth P, Johnson M, 1985 "What is the appropriate control for the tilt illusion?" *Perception* **14** 275 - 283

Wenderoth P, Johnstone S, 1988a "The different mechanisms of the direct and indirect tilt illusions" *Vision Research* **28** 301 - 312

Wenderoth P, Johnstone S, 1988b 'The differential effects of brief exposures and surrounding contours on direct and indirect tilt illusions" *Perception* in press

Wenderoth P, Johnstone S, 1988c "Two dimensional tilt illusions induced by drifting plaid patterns: Effects of plaid orientation, spatial separation and spatial frequency" submitted

Wenderoth P, Latimer C, 1978 "On the relationship between the psychology of visual perception and the neurophysiology of vision" in *Conceptual Analysis and Method in Psychology* ed J P Sutcliffe (Sydney: Sydney University Press) pp 106 - 117

Wenderoth P, O'Connor T, Johnson M, 1986 "The tilt illusion as a function of the relative and absolute lengths of test and inducing lines" *Perception & Psychophysics* **39** 339 - 345

Witkin H A, Asch S E, 1948 "Studies in space orientation: IV—Further experiments on perception of the upright with displaced visual field" *Journal of Experimental Psychology* **38** 762 - 782

Wong E, Weisstein N, 1984 "Flicker induces depth: Spatial and temporal factors in the perceptual segregation of flickering and nonflickering regions in depth" *Perception & Psychophysics* **35** 229 - 236

Wong E, Weisstein N, 1987 "The effects of flicker on the perception of figure and ground" *Perception & Psychophysics* **41** 440 - 448

Zeki S M, 1975 "The functional organisation of projections from striate to prestriate visual cortex in the rhesus monkey" *Cold Spring Harbour Symposium on Quantitative Biology* **40** 591 - 600

Zeki S M, 1978 "Uniformity and diversity of structure and function in rhesus monkey prestriate visual cortex" *Journal of Physiology (London)* **277** 273 - 290