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## Possible neural substrates for orientation analysis and perception

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**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 by-products 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  $180^\circ/n$  (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  $90^\circ$  (ie, from  $90^\circ$  to  $0^\circ$ ), the rod at first appears tilted opposite to the frame (roughly in the range  $90^\circ$  to  $60^\circ$ ) and then tilted towards it ( $60^\circ$  to  $45^\circ$ ); at  $45^\circ$  there is no illusion; the rod then appears tilted away from the frame again ( $45^\circ$  to  $30^\circ$ ) and, finally, tilted towards it once again ( $30^\circ$  to  $0^\circ$ ). 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  $90^\circ$  and  $45^\circ$ , 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  $90^\circ$  and  $45^\circ$ . No illusion occurs at  $45^\circ$  because the diagonal axis is vertical. A similar analysis applies to frame tilts between  $45^\circ$  and  $0^\circ$ . 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  $45^\circ$  frame tilts, Wenderoth and Beh (1977, page 67) suggested that

"... although the component lines (local features) of the frame are tilted  $+45^\circ$  and  $-45^\circ$ , it may be the tilt of the whole 'global diamond' (ie,  $0^\circ$ ) 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."

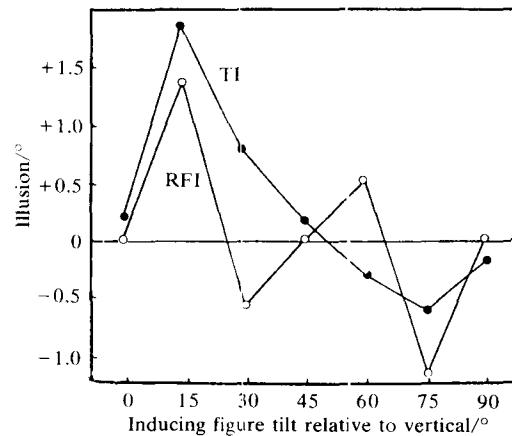
The TI differs in one important respect from the RFI: typically, the inducing line or grating is superimposed upon, or at least abuts, the test line, so that relatively localised processes, such as lateral inhibition in the orientation domain acting upon classic receptive fields (see below), provide possible mechanisms. Wallace (1969), Tolhurst and Thompson (1975), and Virsu and Taskiran (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

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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 Mellwain (Mellwain 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 contrasts, 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 *disinhibition*, 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

