Title

Simulating Tilt Illusions with Lateral Inhibition and a Virtual Axis

Permalink

https://escholarship.org/uc/item/9v519363

Journal

Proceedings of the Annual Meeting of the Cognitive Science Society, 15(0)

Author

Spivey-Knowlton, Michael J.

Publication Date

1993

Simulating Tilt Illusions with Lateral Inhibition and a Virtual Axis

Michael J. Spivey-Knowlton
Center for Visual Science, Meliora Hall
University of Rochester, Rochester, NY 14627
spivey@cvs.rochester.edu

Abstract[1]

When a vertical test stimulus is presented simultaneously within a surrounding stimulus of orientation 10-30° clockwise from vertical, the test stimulus appears slightly counter-clockwise from vertical. In contrast, when the surrounding stimulus is 60-80° clockwise from vertical, the test stimulus appears slightly *clockwise* from vertical. Lateral inhibition between orientation-selective neurons can account for the former effect (repulsion), but not for the latter effect (attraction). However, if an orthogonal "virtual axis" is also present and exerts its own lateral inhibition, both effects can be accounted for. A mathematical model demonstrates quantitatively how this may occur in the visual system. One simulation with narrowly tuned orientation-selectivity functions produced tilt illusions of similar magnitude to that observed with humans at normal presentation durations. A simulation with more broadly tuned functions produced tilt illusions of much greater magnitude, as are found with humans at very short presentation durations. Based on the model's performance, human performance and neurophysiological data, it is suggested that: 1) lateral inhibition may be the immediate cause of both direct and indirect tilt illusions, and 2) the "virtual axis" may be a real neural mechanism and may be found in greater proportion in extrastriate cortex than in striate cortex.

Interactions between orientation-selective cells seem to be a fundamental aspect of the visual system. Despite decades of research, however, it is still unclear what role they play in orientation illusions. The present model provides a successful analog to how certain aspects of orientation perception may be responsible for tilt illusions.

The tilt illusion (TI), also known as simultaneous orientation contrast, occurs when a test stimulus of one orientation is viewed within the surrounding context of an inducing stimulus of a different orientation. Small angular separations between test and inducing stimuli produce a repulsion of orientations, so that if the test stimulus is at true vertical (by convention, 90°) and the inducing stimulus is 10-30° clockwise from that, the test stimulus will appear slightly (1-2°) counter-clockwise from vertical. Conversely, large angular separations (60-80°) produce a weak *attraction* of orientations, causing the vertical test stimulus to appear .5-1° clockwise from vertical. This phenomenon was first discovered with the stimuli presented asynchronously, and was called "the tilt aftereffect" (Gibson & Radner, 1937). Of the theories that have been proposed to account for this effect, such as "normalization" (Gibson & Radner, 1937), "satiation" (Köhler & Wallach, 1944), and "adaptation" (Coltheart, 1971), "lateral inhibition" (Blakemore, Carpenter & Georgeson, 1970) may be the most consistent with recent neurophysiological evidence (e.g., DeValois, Yund & Hepler, 1982; Gilbert & Weisel, 1983). Figure 1 shows how units responding to a 110° stimulus will exert inhibition (dashed line) upon units responding to a 90° stimulus (solid line), thus skewing the peak of their activation clockwise from 90° (dotted line).

Lateral inhibition alone, however, is unable to account for the attraction effect seen at large angular separations. First, the typical formulation of lateral inhibition in which the most immediate neighbor exerts the most inhibition accounts only for repulsion effects. Second, when the inducing stimulus is at 160°, the inhibitory flank from its responsive units is too far away to influence the activation function of the 90° stimulus.

One theory that has been proposed to account for this attraction effect is based on "virtual axes of symmetry" (e.g. Beh, Wenderoth & Purcell, 1971; Wenderoth, van der Zwan, & Johnstone, 1989). It is suggested that the axes of symmetry of an inducing stimulus, though not a visible part of the stimulus, can exert a repulsion effect on stimuli of nearby orientation. Thus, when the inducing stimulus is a grating set at 160°, its orthogonal virtual axis [at 70° (20° clockwise from vertical)] repels the vertical test grating counter-clockwise, thus *toward* the orientation of the inducing stimulus, as shown in Figure 2. Dissociations between direct (repulsion) TIs and
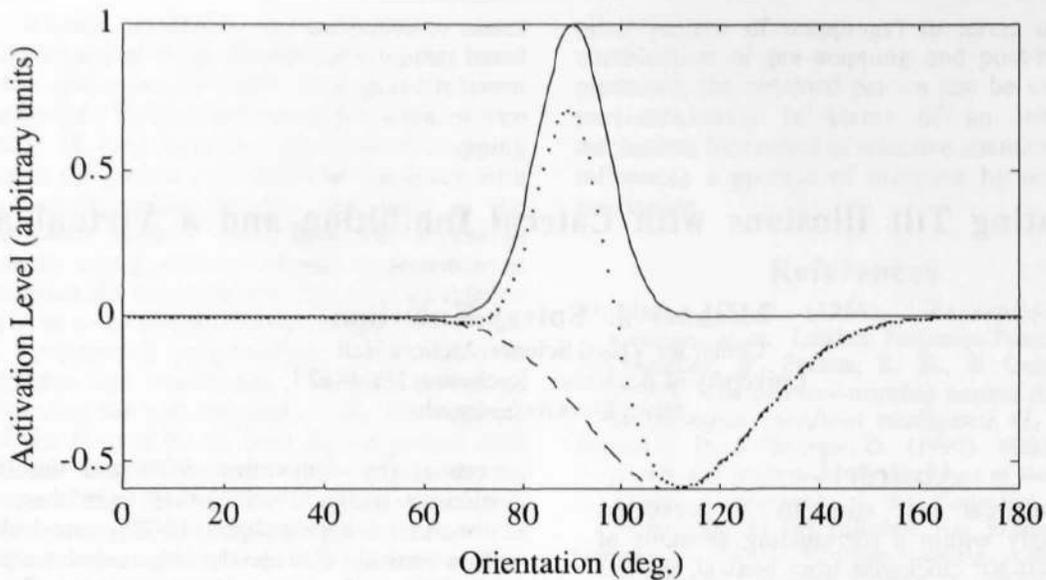
Figure 1. Lateral inhibition from nearby orientation-selective units shifts peak clockwise.
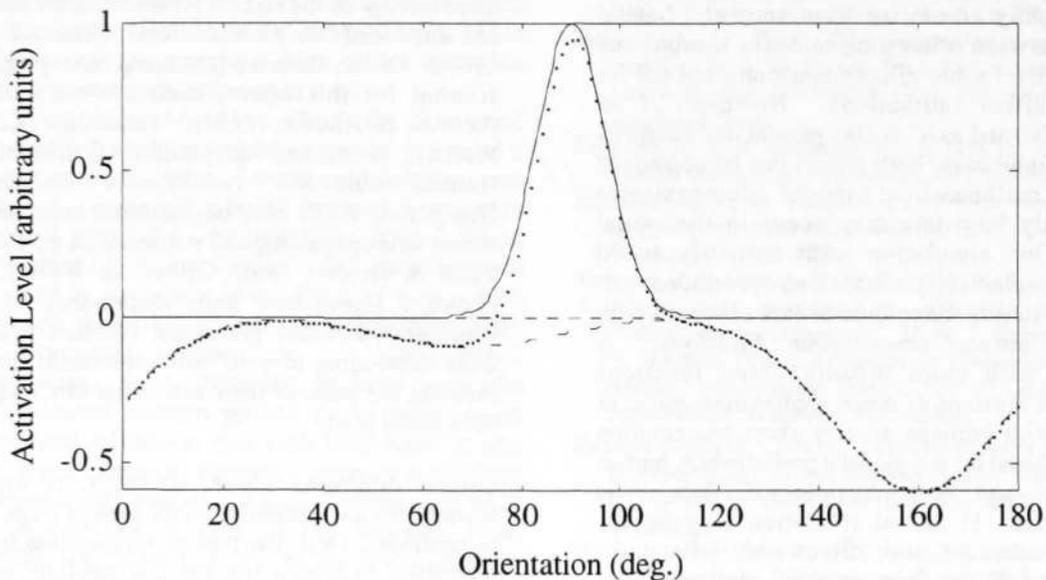
Figure 2. Lateral inhibition from the 160° stimulus (dashed line) has negligible effect on the test stimulus (solid line); but when combined with lateral inhibition from its virtual axis (dot-dash line with shallow trough at 70°) shifts peak of test stimulus counter-clockwise (dotted line).

indirect (attraction) TIs have led Wenderoth and colleagues to hypothesize that direct TIs are due to lateral inhibition from the inducing orientation in striate cortex, but indirect TIs are due to lateral inhibition from the inducing stimulus's virtual axis in extrastriate cortex (cf. Wenderoth et al., 1989).

There is further independent support for a neural substrate to the "virtual axis". Bowker and Sharpe (1979) observed that same/different judgments for two square-wave gratings were much faster when their orientations were 90° apart than when they were 20-60° apart. From this, they suggested that orthogonally tuned orientation channels may interact in a facilitatory manner. Moreover, in striate cortex of the macaque monkey, DeValois et al. (1982) found a small percentage of narrowly-tuned orientation selective cells which had secondary sensitivity peaks at 90° from their primary peaks. The latter finding places some part of the virtual axis in striate cortex,

thus conflicting, at least somewhat, with Wenderoth et al. (1989).

The model presented here involves a simple difference of Gaussians [generally known as a DOG (Marr, 1982)] for test, inducing and virtual axis activation/ inhibition functions. The model, called Difference Of Gaussians ON Illusions of Tilt (DOGONIT), simulates the magnitude of direct and indirect TIs and, somewhat less successfully, the time course of these effects. It is offered as 1) a preliminary quantitative demonstration of how lateral inhibition and an orthogonal virtual axis can accurately account for this orientation illusion, and 2) a source of novel psychophysical and neurophysiological predictions.

Simulations

The first simulation was not designed to capture aspects of the time course of TIs. It simply subtracted two Gaussians, 90° apart, from a positive central Gaussian representing the vertical test stimulus, as in Figure 2. The Gaussian representing the activation function for the test stimulus is defined by function A, that representing the inhibition function for the inducing stimulus is defined by function I, and that representing the inhibition function for the inducing stimulus's virtual axis is defined by function V:

(1) $A(x)=e^{-.01(T-x)^2}$

$I(x)=.6e^{-.0017(T+\theta-x)^2}$

$V(x)=.17I(x-90)$

where x is the point along the orientation dimension, T is the orientation of the target stimulus, and θ is the angular separation between target and inducer. This gave the activation function of the test stimulus, minus inhibition from neighboring units that would also respond to that orientation, a resulting half-amplitude bandwidth of approximately 12°. While this is considerably narrower than the mean bandwidth for orientation-selective cells in striate cortex (~40°), recall that the orthogonal secondary peaks, which may act as a virtual axis mechanism, appear to be associated with more narrowly tuned cells (DeValois et al, 1982). The resultant activation function across orientation is defined by equation (2):

(2) R=A-I-V

The model then averaged the activations across all orientations to produce an *averaged orientation percept*. The activation function R was weighted by the orientation of each unit (any negative values were set to zero), summed, and then divided by the sum unweighted activation. This was accomplished by simple matrix multiplication, equation (3):

(3) p=(R*O)/(R*N),

where O is the range of orientations (1-180), and N is a vector of ones. Subtracting this result from 90 (true vertical) gave the direction and magnitude of the illusion, with direct TIs as positive numbers and indirect TIs as negative. Figure 3 compares the
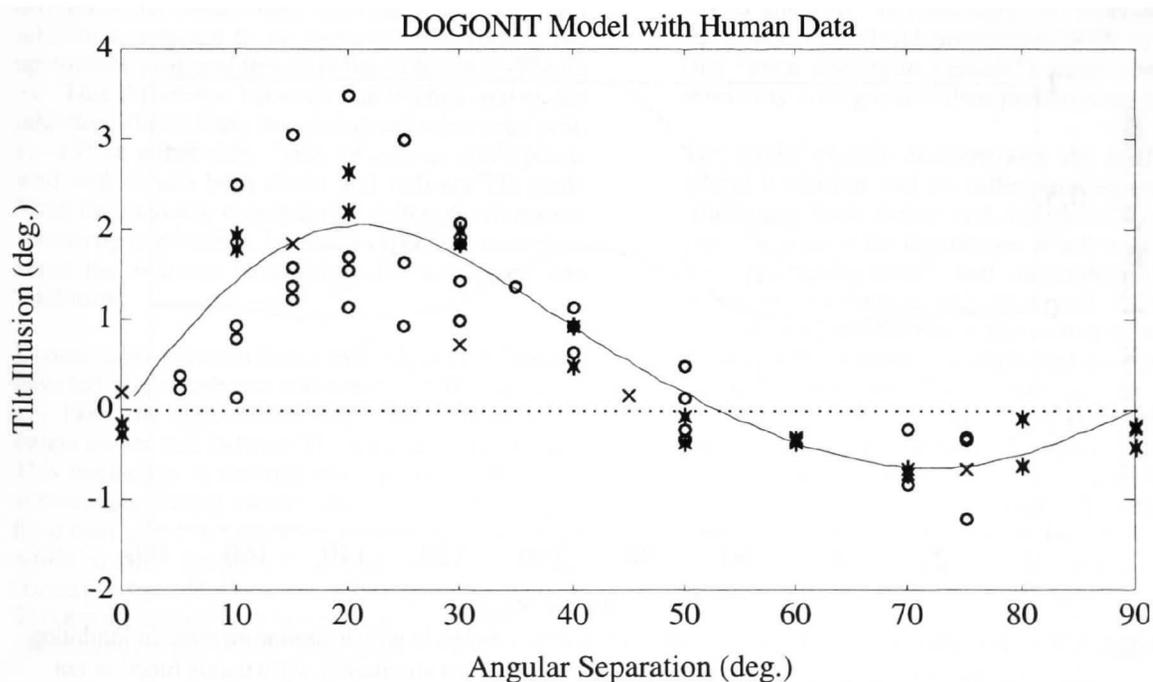
Figure 3. The first simulation compared with psychophysical data for both direct and indirect TIs.

model's performance to human data from O'Toole and Wenderoth (1977) (*'s), Over, Broerse and Crassini (1972) (x's), and Westheimer (1990) (o's). A Pearson-r correlation between the model's output and combined means of the human data revealed a robust correlation: $r^2=.97$.

The close correspondence between the model's performance and human performance allows some hypotheses concerning correspondences between features of the model and features of the visual system. The model used lateral inhibition between neighboring orientation-selective units to produce direct tilt illusions, therefore it predicts that the visual system may do likewise. Moreover, the inhibition function in the model (dashed line of Figure 1) has a bandwidth approximately 20° wider than the activation function (solid line), and 30° wider than the orientation sensitivity function (dotted line). Many different relative bandwidths were tested, but these produced the best fit to psychophysical data. Although inhibitory connections in visual cortex have not been studied in such detail, the model predicts that future research may concur with these relative dimensions. Perhaps most interesting is the necessity of the virtual axis inhibition function in order to simulate *indirect* tilt illusions. Without the virtual axis implemented (V=0), only the direct TI is produced.

A second simulation used larger bandwidths and produced large TI magnitudes similar to that found with very short presentation durations (Calvert & Harris, 1988; Wenderoth et al., 1989; Wolfe, 1984).

In this simulation, the Gaussians were wider than in the previous simulation:

$$(4) \qquad A(x)=e^{-.001(T-x)^2}$$
$$I(x)=.73e^{-.0007(T+\theta-x)^2}$$
$$V(x)=.55I(x-90)$$

This produced an orientation sensitivity function with a bandwidth of 36°. Moreover, the inhibition function is, as before, about 20° wider than the activation function and 30° wider than the orientation sensitivity function. See Figure 4.

When direction and magnitude of the illusion was computed in the same manner as in the first simulation, an angular separation of 15° produced a direct TI of 8.76°, and an angular separation of 75° produced an indirect TI of -2.13°. However, to make this computation sensitive to time course, the model's output had to be decremented by a decay function, $d=.99^t$, where t is the presentation duration in milliseconds and d is not allowed to go below .25. Thus, the averaged orientation percept is defined by: $p=d((R*O)/(R*N))$. With a normal presentation duration (1000ms) this simulation produced a TI function almost identical to that in Figure 3. As before, absence of the virtual axis (V=0) eliminated the indirect TI. Figure 5 compares simulation (lines) with psychophysical data (symbols, from Wenderoth et al., 1989) as a function of presentation duration. The model's output correlated with human data for the direct TI ($r^2=.89$) and for the indirect TI ($r^2=.54$).
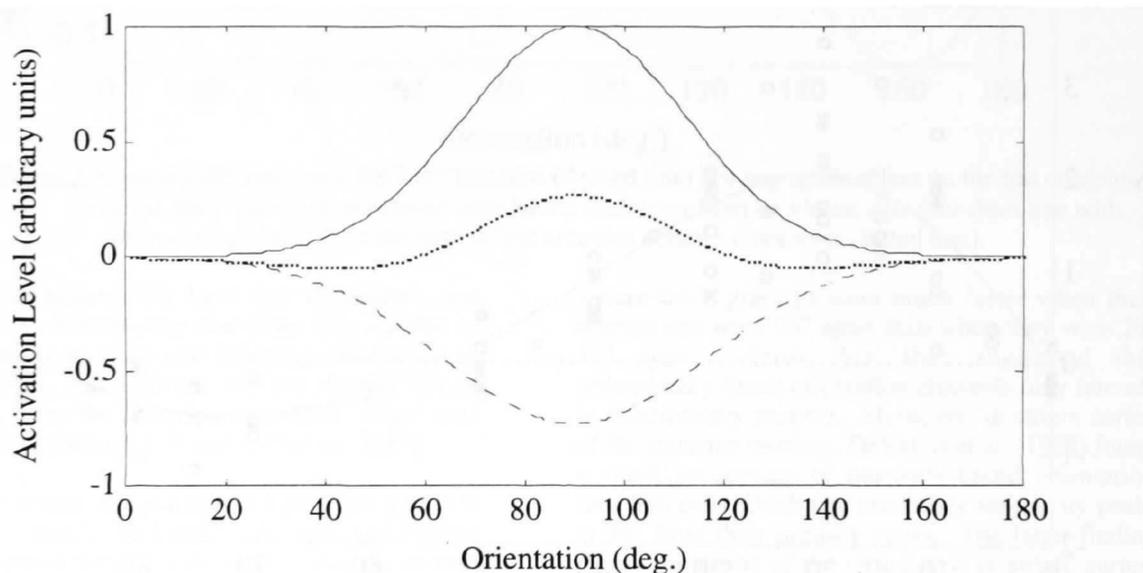
Figure 4. The larger bandwidth orientation sensitivity function was made with a similar increase in inhibition bandwidth (compared to activation bandwidth) as in the first simulation; virtual axis function not shown here.

DOGONIT Model Predictions with Human Data
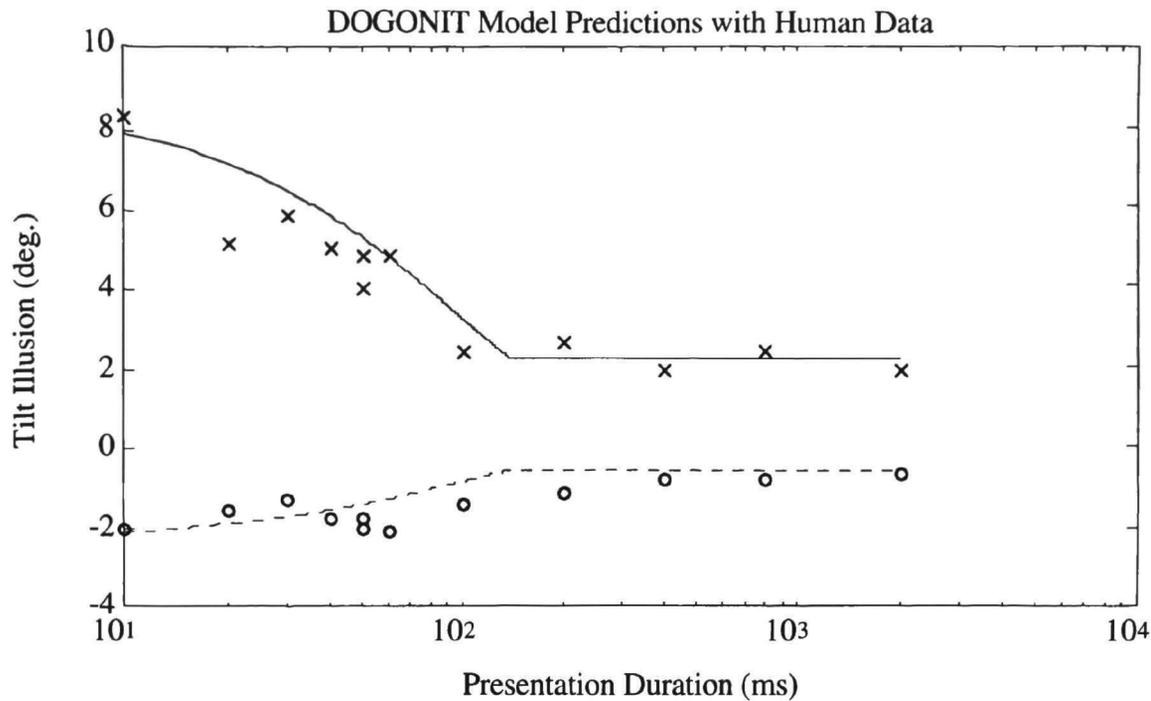
Figure 5. The second simulation modeled the time course of the tilt illusion. Solid line and x's are direct TIs at 15° angular separation, dashed line and o's are indirect TIs at 75° angular separation. See text for discussion.

Discussion

An interesting commonality between these two simulations is that, despite their use of different absolute bandwidths in orientation sensitivity, they each use an inhibition function of approximately 30° greater bandwidth than that of their orientation sensitivity functions. This relatively constant difference in bandwidth, between sensitivity and inhibition, appears to be necessary to produce the appropriate peak and trough in the TI function (Figure 3). This difference between bandwidths makes the inhibitory flanks from orientation-selective cells peak at ~15° on either side. This, of course, corresponds well with where both direct and indirect TIs peak. Thus, the model is robust across different orientation sensitivity bandwidths, but makes specific predictions about the *relative* bandwidths for sensitivity and inhibition.

Dissociations between direct and indirect tilt illusions have led Wenderoth and colleagues (cf. Wenderoth et al., 1989) to hypothesize that direct TIs occur in striate cortex and indirect TIs in extrastriate regions. This distinction is derived from the assumption that surrounding frames (which affect only *indirect* TIs) have their effect in higher levels of visual processing, while spatial frequency differences and similar context-independent features (which affect only *direct* TIs) are associated with lower-level visual processing (Wenderoth et al., 1989). This model is not currently

designed to simulate such dissociations. However, in correspondence with Wenderoth et al.'s (1989) hypothesis that the virtual axis mechanism is predominantly in extrastriate regions, both simulations used a virtual axis inhibition function of greater proportion (.17I and .55I, respectively) than the findings of DeValois et al. (1982) in *striate* cortex would suggest. Interestingly, in Watson's (1990) filter model of visual processing, 50% of the units (his "even chexagon kernels") have considerable sensitivity orthogonal to their preferred orientations.

The model clearly demonstrates the usefulness of lateral inhibition and an orthogonal virtual axis in simulating both direct and indirect TIs. It also provides a basis for hypotheses which may be tested both psychophysically and neurophysiologically. However, the actual existence and locus of the "virtual axis" mechanism in the human visual system remains a hypothesis. An important question, at this point, is: Why would the visual system evolve to develop a virtual axis mechanism? Certainly, it's not there just to create illusions. It is quite possible that the virtual axis is purely an accidental consequence of how the inputs to an orientation-selective cell are organized. For example, in Watson's (1990) even chexagon kernels, three of the seven units in the kernel's hexagonal input lattice are excitatory and align themselves in a particular orientation. The remaining units are inhibitory, but they allow an

957

exactly perpendicular contour to pass between them undetected and thus the kernel exhibits an overall positive activation in response to a contour orthogonal to the its "preferred orientation".

Alternatively, the virtual axis may play a functional role in the generation of reference frames at higher levels of visual processing (cf. Spivey-Knowlton & Bridgeman, in press; Wenderoth et al., 1989), and may even have feedback projections to lower levels. To better understand the function of orientation perception at this level, where visual perception interfaces with visual cognition, further work is needed to demonstrate how explicitly represented coordinate axes could be used in constructing object-centered reference frames (cf. Carlton & Shepard, 1990; Tipper, Driver & Weaver, 1991) or even environment-centered reference frames (cf. Hayhoe, Lachter & Feldman, 1991; Nemire & Cohen, 1993; Rock, Wheeler & Tudor, 1989).

Acknowledgments

References

Beh H C, Wenderoth P M & 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*, 228, 37-39.

Bowker D O & Sharpe L T (1979). Spatial frequency comparisons of rotated gratings. *Perception & Psychophysics*, 26, 108-112.

Calvanio R, Petrone P N & Levine D N (1987). Left visual spatial neglect is both environment-centered and body-centered. *Neurology*, 37, 1179-1183.

Calvert J E & Harris J P (1988). Spatial frequency and duration effects on the tilt illusion and orientation acuity. *Vision Research*, 28, 1051-1059.

Carlton E H & Shepard R N (1990). Psychologically simple motions as geodesic paths: II. Symmetric objects. *Journal of Mathematical Psychology*, 34, 189-228.

Coltheart M (1971). Visual feature-analyzers and after-effect of tilt and curvature. *Psychological Review*, 78, 114-121.

DeValois R L, Yund E W & Hepler N (1982). The orientation and direction selectivity of cells in macaque visual cortex. *Vision Research*, 22, 531-544.

Gibson J J & Radner M (1937). Adaptation, aftereffect and contrast in the perception of tilted lines. I. Quantitative studies. *Journal of Experimental Psychology*, 20, 453-469.

Gilbert C D & Weisel T N (1983). Clustered intrinsic connections in cat visual cortex. *Journal of Neuroscience*, 3, 1116-1133.

Hayhoe M, Lachter, J & Feldman, J (1991). Integration of form across saccadic eye movements. *Perception*, 20, 393-402.

Köhler W & Wallach H (1944). Figural aftereffects: An investigation of visual processes. *Proceedings of the American Philosophical Society*, 88, 269-357.

Marr D (1982). *Vision.* New York: Freeman.

Nemire K & Cohen M M (1993). Visual and somesthetic influences on postural orientation in the median plane. *Perception & Psychophysics*, 53, 106-116.

O'Toole B I & Wenderoth P M (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.

Rock I, Wheeler & Tudor L (1989). Can we imagine how objects look from other viewpoints? *Cognitive Psychology*, 21, 185-210.

Spivey-Knowlton M & Bridgeman B (in press). Spatial context affects the Poggendorff illusion. *Perception & Psychophysics*.

Tipper S P, Driver, J & Weaver, B (1991). Object-centered inhibition of return of visual attention. *Quarterly Journal of Experimental Psychology*, 43A, 289-298.

Watson A B (1990). Algotecture of visual cortex. In C Blakemore (ed.), *Vision coding efficiency.* Cambridge: Cambridge University Press.

Wenderoth P, van der Zwan R & Johnstone S (1989). Mechanisms of orientation illusions. In D Vickers and P Smith (eds.), *Human information processing: Measures, mechanisms and models.* Elsevier: North-Holland.

Westheimer G (1990). Simultaneous orientation contrast for lines in the human fovea. *Vision Research*, 30, 1913-1921.

Wolfe, J M (1984). Short test flashes produce large tilt aftereffects. *Vision Research*, 24, 1959-1964.