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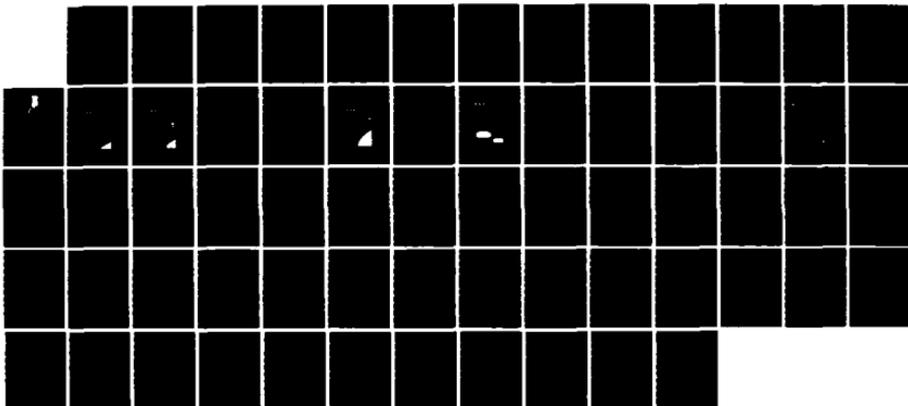
SPATIAL AND TEMPORAL VISUAL MASKING AND VISIBILITY(U)
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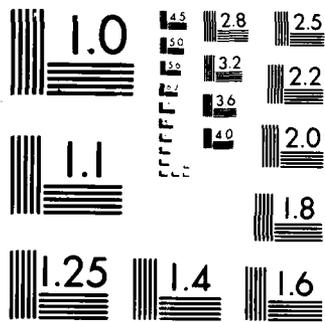
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Spatial and Temporal Visual
Masking and Visibility

ANNUAL REPORT
March 31, 1986

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**Spatial and Temporal Visual
Masking and Visibility**

**ANNUAL REPORT
March 31, 1986**

Grant No: AFOSR-84-0348

Submitted by: Robert A. Smith, PhD
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June 5, 1986

Annual Report for year ending March 31, 1986

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Prepared for: Life Sciences Directorate
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Bolling AFB, DC 20332

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BRIEF SUMMARY

We have continued our studies of spatio-temporal interactions between briefly-flashed lines. The delayed facilitation we have previously reported in these experiments suggested to us that we were tapping a motion-detector system. However extensive experiments which failed to correlate our line interactions with the motion aftereffect and other well-known manifestations of motion detection have convinced us that we are measuring something different. We currently believe that we may be tapping the moving-object detectors described by Burr. We have demonstrated that transient stimulation produces a substantial change in the configuration of inhibition and excitation, as revealed by summation between briefly-flashed lines. We have extended our studies of summation between lines to parafoveal vision, with two interesting results. 1) Unlike most visual functions, spatial summation in the periphery does not increase in direct proportion to cortical magnification. 2) Based on our studies of summation, we predicted and observed that aliasing, though absent in the fovea, should be present in the parafovea. Finally exhaustive studies of velocity discrimination suggest that there do not exist a small number of discrete velocity detectors, but rather a near-continuum of these.

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Brief Summary

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I. GENERAL INTRODUCTION

This introduction is intended to give a reasonably detailed overview, as well as covering some pilot studies which are not discussed in the chapters which follow.

The aim of the current year's research was to further elucidate our earlier discoveries about interactions between briefly flashed lines. In particular, we hoped:

- 1) To connect the apparent motion-detector-like properties of these results with more traditional studies of motion perception.
- 2) To determine whether mathematical vision models, as currently conceived, could account for these data.
- 3) To further study the effect of eccentricity on spatial summation and visual acuity.

The past year has seen us emerging from a difficult period, in that the two major studies of the past few years are finally in press after much difficulty and controversy. These are 1) our study of the effect of criterion on spatial frequency masking, which demonstrates the great importance of cognitive-level factors in a task formerly thought to be very peripheral, and 2) our study of interactions between briefly-flashed lines as a function of spatial and temporal separation.

Our studies of masking (apart from writing and editing) have not changed significantly since our last report, but substantial progress has been made in the area of line interactions. Our earlier work showed that flashed lines showed facilitation over a broad, diagonal area of space-time, which had a slope of about 1.0 degrees per second. We devoted considerable effort to finding correlates between our findings and more traditional measures of motion detectors (e.g. the motion aftereffect). For example, if our line-pair stimuli are being detected by motion-detectors, then a MAE should preferentially reduce detection of line-pairs with the same direction of apparent motion. After a variety of similar experiments -- all negative -- we concluded that despite appearances, our studies of interactions between lines do not measure motion detection in the sense that many, more traditional experiments have done. A second alternative, suggested by the work of Burr, and also by that of Westheimer and McKee, is that we may be measuring mechanisms for the resolution of spatial detail in moving images. We are currently measuring 2-line resolution, as a function of the velocity of the line pairs, hoping to find a preferential velocity comparable to the apparent tuning velocity from our detection data. A final aspect of this work is our efforts in modelling. We devised two spatio-temporal variants of the well-known Wilson and Bergen 4-mechanism model, and found that neither was adequate to fit our data.

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We have begun applying our 2-line detection paradigm to the study of peripheral vision, with significant results. We found that certain visual functions (2-line acuity, single-line luminance thresholds) change with eccentricity in accordance with cortical magnification, while other functions (spatial summation) change much less with eccentricity. We suggest that these two classes of function reflect -- respectively -- the separation and the centre-size of receptive fields, perhaps at the ganglion cell level. These results (in agreement with neurophysiological data) suggest that the spacing between retinal summation areas may be rather larger (perhaps 2x) than the size of an individual area. That is, there may be substantial parts of the peripheral retina which fall "between" the sensitive areas and so are not very responsive. If this is so, then the conditions are fulfilled for the occurrence of aliasing; specifically, at 7° eccentricity, we would expect to observe the effects of undersampling in gratings in the range of 10 to 20 c/deg. Williams has shown that undersampled gratings characteristically lose their orientation. We therefore measured both the detection and the discrimination of grating orientation and found that, in fact, detection was possible at frequencies twice as high as orientation. We take this to be evidence for the detection of an undersampled percept. The most interesting aspect of this observation is not the aliasing itself, but the fact that the aliasing is apparently not occurring at the level of the photoreceptors, but higher in the visual system, perhaps at the level of spatial summation. We draw this conclusion because our aliasing occurs at frequencies about half the Nyquist limit for the receptor mosaic. This type of aliasing has not been observed previously.

We have also used briefly-flashed lines to probe the temporal dynamics of spatial summation. Our paradigm is the familiar one of Kulikowski and King-Smith, in which we present three simultaneously-flashed lines -- a centre and two half-luminance flank lines -- and measure threshold for the three as a function of their separation. To this experiment, we introduce the additional variable of temporal change in the background against which the stimuli are seen. Among the effects we have observed are the following. 1) More lateral inhibition is seen against a bright than a dark background. 2) Spatial summation narrows and lateral inhibition increases immediately after a positive luminance step. 3) The offset of a high contrast grating produces a much stronger effect than the luminance step, but of a similar nature. 4) Briefly-flashed lines do not display lateral inhibition unless they are simultaneous; a 20 msec ISI is sufficient to eliminate inhibition. 5) We are unable to measure any significant amount of lateral inhibition at 7° in the parafovea. Taken in conjunction with our studies of summation and aliasing, we begin to see the outlines of a model of foveal and parafoveal contrast detection which is more detailed, and in some ways quite distinct, from any that has preceded it.

Velocity discrimination was measured in the fovea and over a range of eccentricities. Unlike previous studies, data were collected using contrasts which were always a fixed

Introduction I-3

multiplicative factor (2.25 or 4x) of the contrast threshold of the stimuli. This procedure was intended to: 1. stimulate a minimal number of channels about the test velocity, thereby perhaps revealing the number of velocity channels; 2. Eliminate the use of perceived contrast as a cue for velocity. Stimuli were either gaussian bars or 1 c/d sinusoidal gratings, presented in a 1 sec gaussian temporal window to minimize transients. Velocity discrimination retained the simple u-shaped curve over velocity which is commonly reported (McKee, 1981; Orban et al, 1984), but showed a generally shallower low-velocity decline, and a steeper high-velocity decline. Peak discriminability shifted to higher velocities outside the fovea, but at a fixed velocity (4 d/s) was quite flat over eccentricity. These discriminations do not appear to scale with cortical magnification. These data would be produced by either a very small number of velocity channels bracketing the 4 d/s minimum, or a large number of channels which could not be resolved by the discrimination procedure. Additional experiments measured the apparent velocity of low contrast bars. The results indicated that perception of velocity was veridical virtually down to threshold, suggesting the existence of many, rather than few velocity channels. Additional experiments examined flicker frequency discrimination, which was found to closely resemble velocity discrimination when presentation parameters were comparable. The possibility that flicker and velocity channels are closely related cannot be discounted.

II. The Extended Four Mechanism Models

Does our observation of lateral facilitation between briefly-flashed lines (see previous Progress Reports) require that the detectors underlying this phenomenon also possess lateral facilitation? It is well-known that probability summation between detectors (being a nonlinear operation) can considerably distort direct efforts to measure these underlying detectors (Graham, 1977). We therefore decided to see if lateral facilitation could be predicted by accepted probability summation models, without invoking a fundamentally new detector. An immediate difficulty is that the well-known probability summation models (Wilson and Bergen, 1979; Watson, 1980; Wilson and Gelb, 1984) are essentially spatial models, and a more general spatio-temporal model is needed. In the absence of such a model, we adapted Wilson and Bergen's 4-mechanism model to include the time dimension.

The original Wilson and Bergen (1979) four mechanism model began with receptive fields defined as follows:

$$RF_n(x) = A_{nc} \exp(-x^2/W_{nc}^2) - A_{ns} \exp(-x^2/W_{ns}^2)$$

The subscripts on A and W (Amplitude and Width) are n (= N, S, T, U -- the 4 mechanisms) and c or s (centre or surround).

The Kufflerian Model

In our Kufflerian model, the RF is generalized to the form

$$RF(x,t) = \text{Centre}(x,t) - \text{Surround}(x,t)$$

where Centre and Surround are 2-dimensional, unimodal, roughly bell-shaped functions; with Surround being approximately twice as large as Centre in both space and time. This is shown in Figure II-1. More rigorously,

$$RF_n(x,t) = A_{ncx} \exp(-x^2/W_{ncx}^2) \dagger A_{nct} \exp(-t/W_{nct}^2) - A_{nsx} \exp(-x^2/W_{nsx}^2) \dagger A_{nst} \exp(-t/W_{nst}^2)$$

This introduces an additional 16 parameters, the temporal amplitudes and widths, which are distinguished by a third

subscript, x or t, for spatial or temporal.

In Wilson's original model, the RF parameters were functions of retinal eccentricity. Since our experiments extend no more than 0.5 degrees from the fovea, this effect is small and was omitted. Probability summation between receptors and mechanisms was done with the Quick (1975) probability summation formula using an exponent of 4, as in the original model. The only uncertainty is how to deal with probability summation over time, which certainly occurs, but cannot involve the same processes as summation over space. In the absence of any clear evidence, and because it seemed to work, we generalized Quick's formula to a 2-dimensional sum:

$$\text{Response} = (\text{SUM}_{x,t} R(x,t))^4$$

where $R(x,t)$ is the response of the receptor centered at stimulus coordinates x and t . It will be seen that space and time dimensions are completely equivalent in this model, apart from the different shape of the receptive fields along the two axes.

The Kufflerian model fit the general form of the results very easily, and in most cases our initial guesses for parameter values were adequate. The model gives reasonable predictions to Wilson's 3-line experiments (Figure 6) and to his DOG sensitivity measurements (not shown); we did not fit data for extended stimuli (gratings), since retinal inhomogeneity is not modelled. We also modelled our 2-flash experiment, and found inhibition at approximately the observed time delay. The actual amount of inhibition was rather too small, however. This is apparently due to the broad temporal tuning of the function $t \cdot \exp(-t)$. The function $t \cdot \exp(-t^2)$ yields a much better fit, but we have not yet tried this function for the other simulations. Unfortunately, as shown in Figure II-7, this model does not predict any secondary facilitation. Thus it does not predict our major finding in the interactions of flashed lines, and must be rejected.

The Separable Model

The separable model differed from the Kufflerian model only in the basic equation for the RF, and in some of the parameters. The basic equation now has the form

$$RF(x,t) = SIRF(x) * TIRF(t)$$

which is separable in x and t , as expected. The Spatial IRF (SIRF) and Temporal IRF (TIRF) are a "Mexican-hat" and a temporal biphasic, respectively. Figure II-2 shows this construction graphically. Figure II-3 shows a contour plot of our experiment on the interaction of two lines as a function of spatial and temporal separation (i.e. the LIF), while II-4 shows the same results in wire-plot form. The qualitative similarity between Figures II - 2 and II - 4 is clear, and provides the main

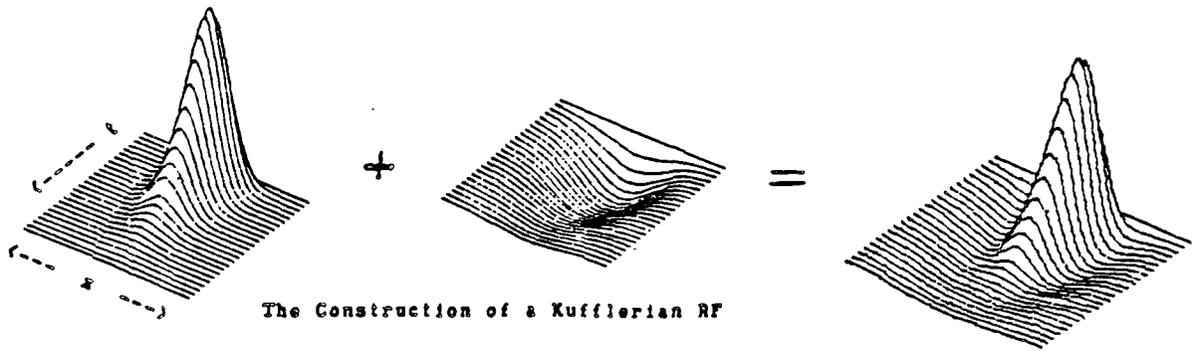
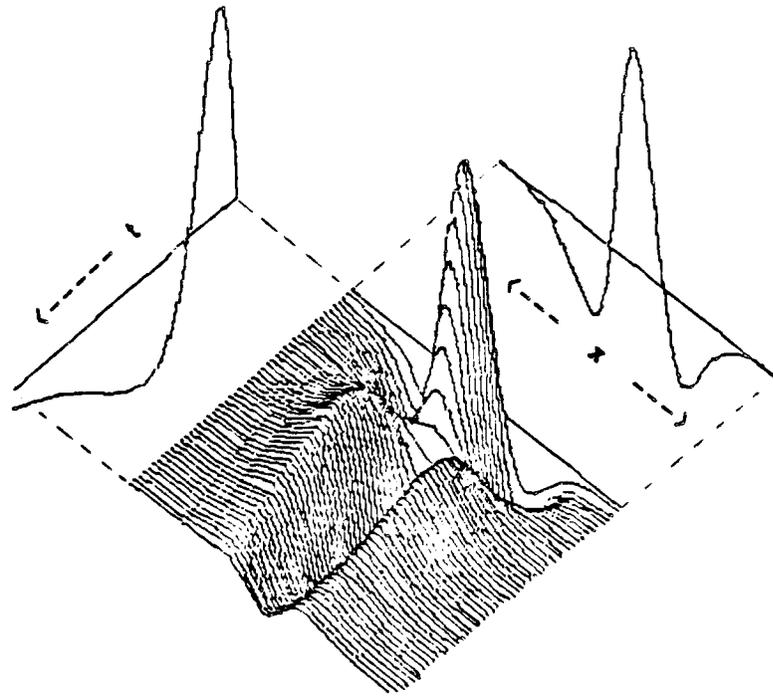


Figure 1



The Construction of a Separable RF

Figure 2

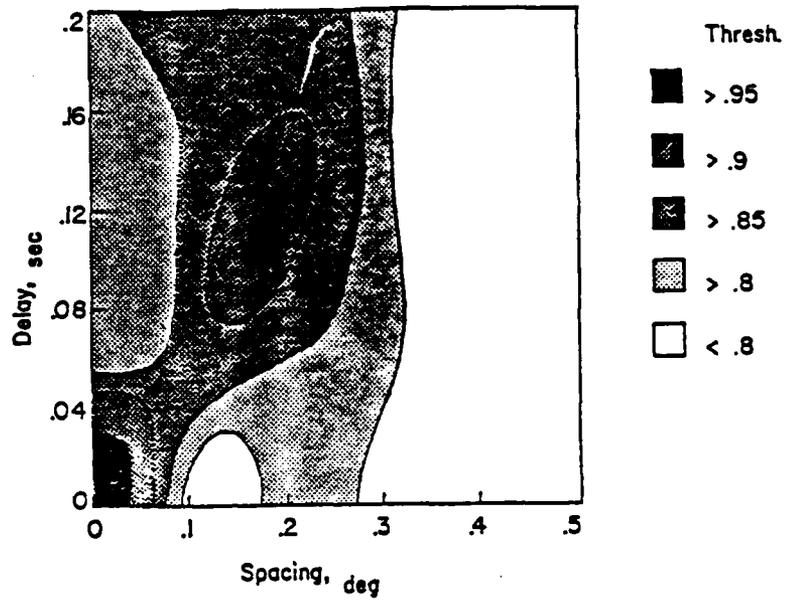


Figure 3. The detectability of a pair of briefly-flashed lines as a function of their separation in space and time.

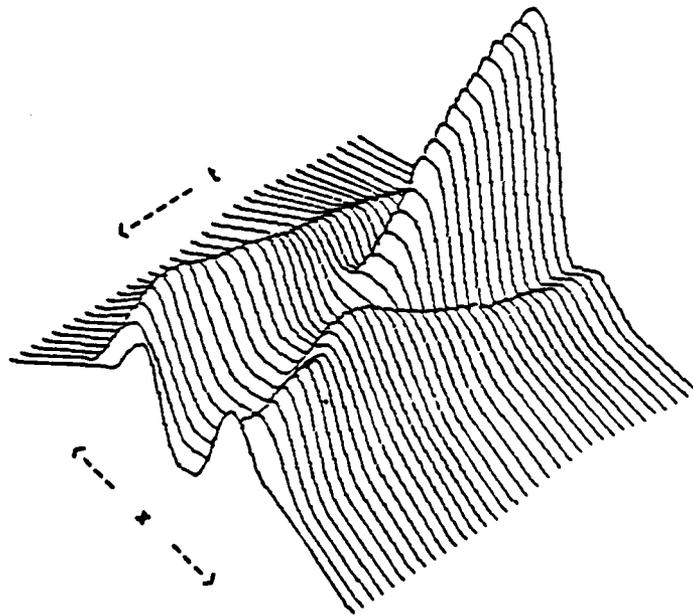


Figure 4. The data of Figure 3 (above), reflected about the time axis, and plotted as a wire mesh. Note the similarity to Figure 2.

S Mechanism

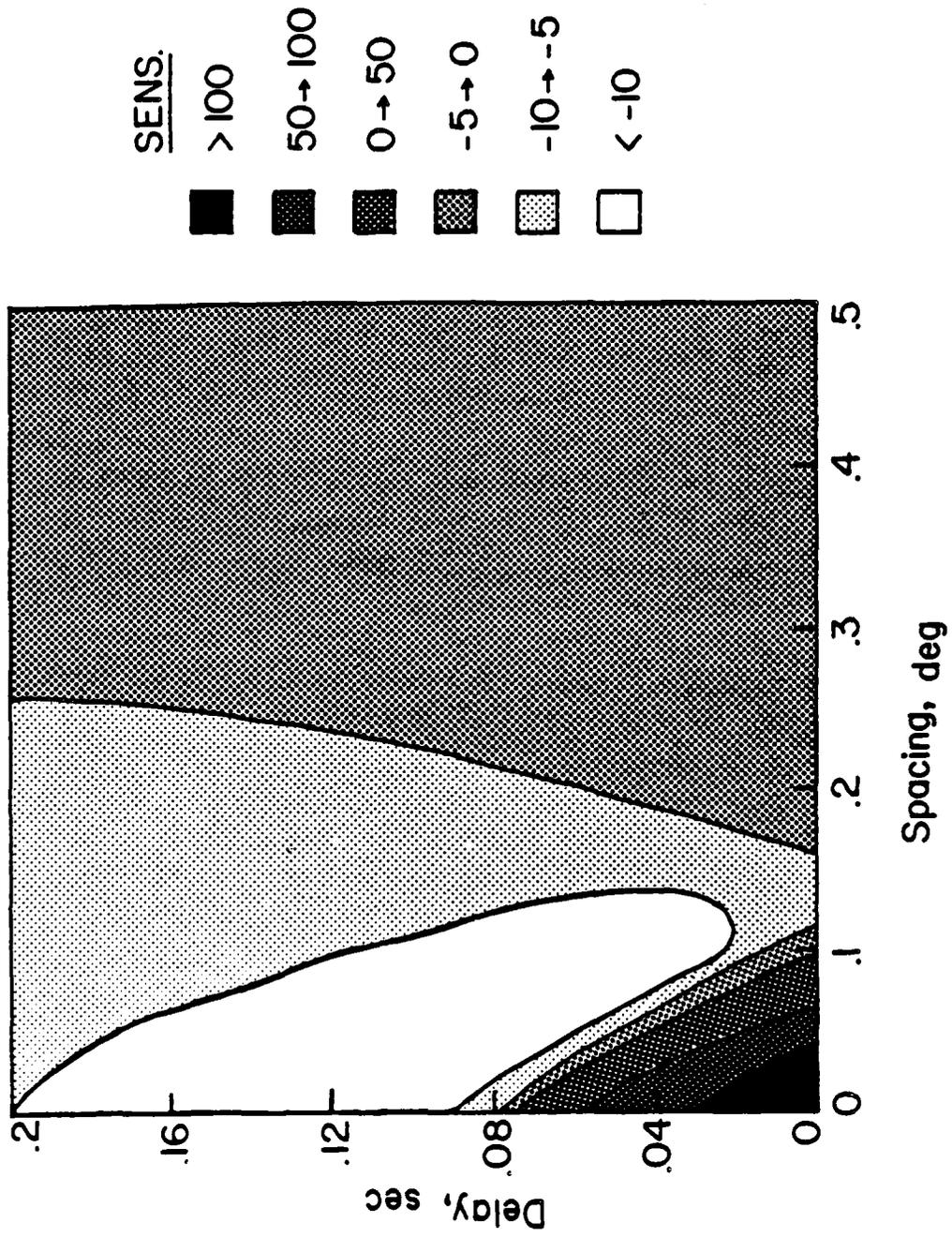
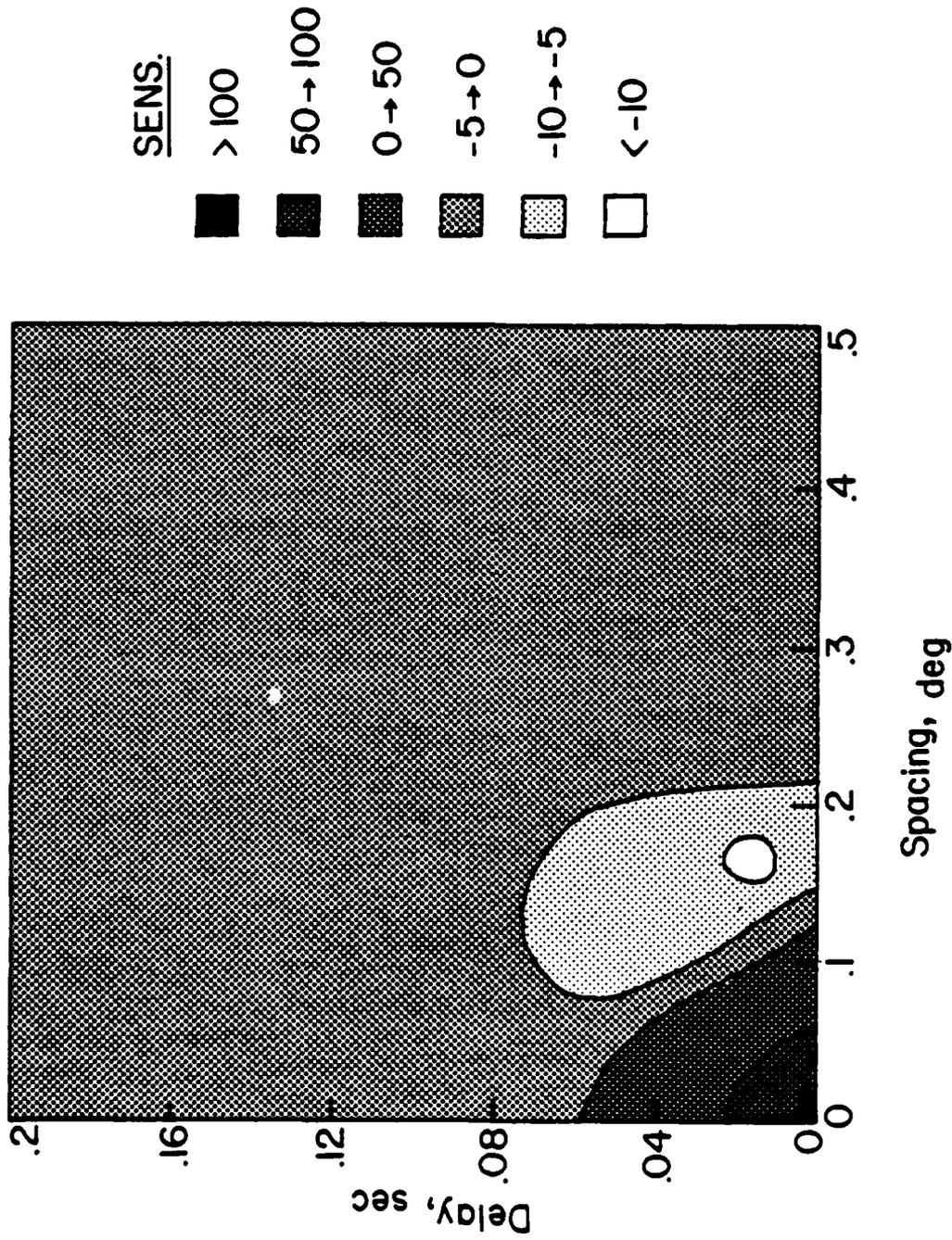


Fig. 5. Contour plots showing the spatiotemporal sensitivity of the S and T mechanisms of the Kufflerian model. Note the 10x decrease in contour separation in the inhibitory regions.

T Mechanism



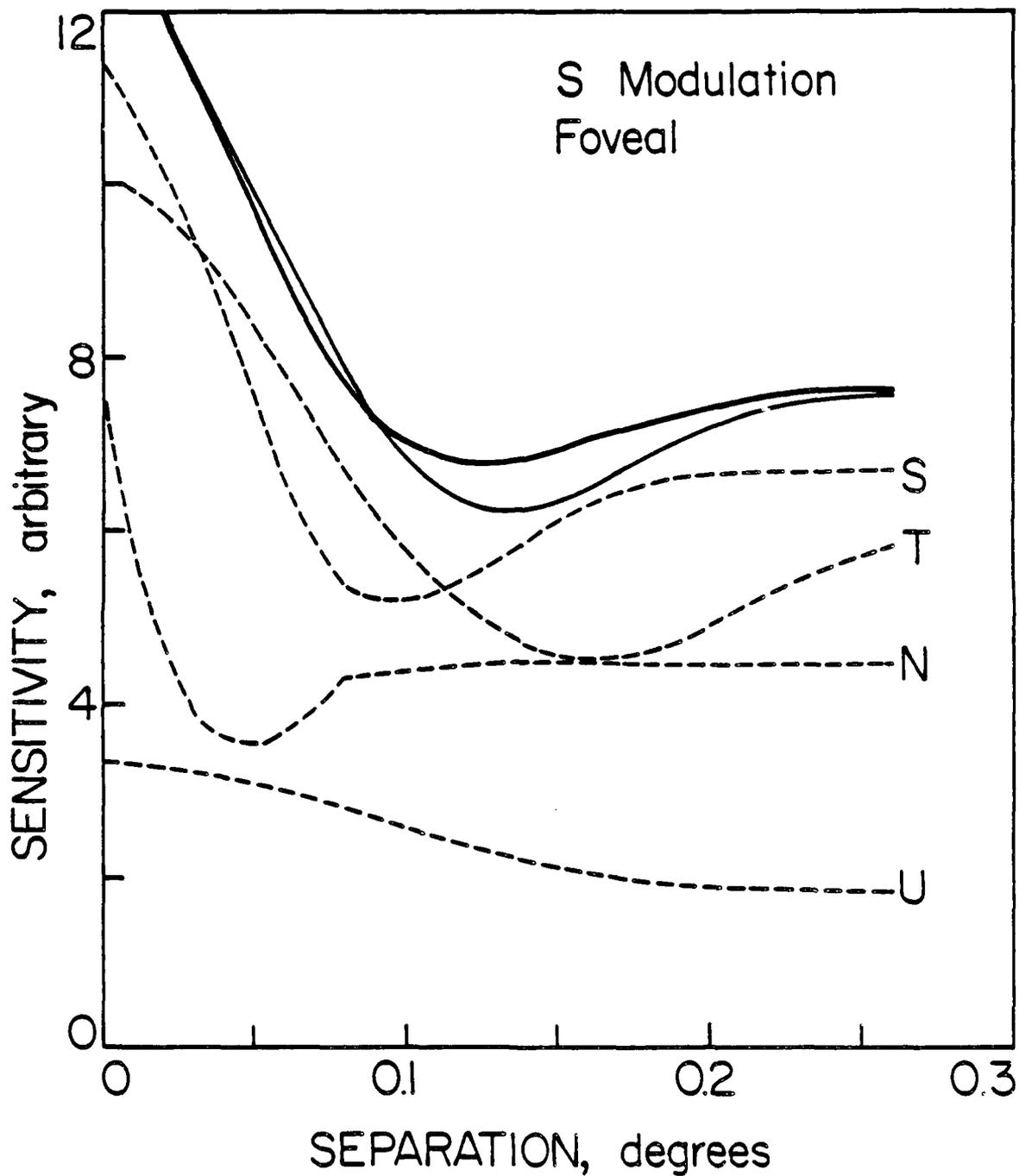
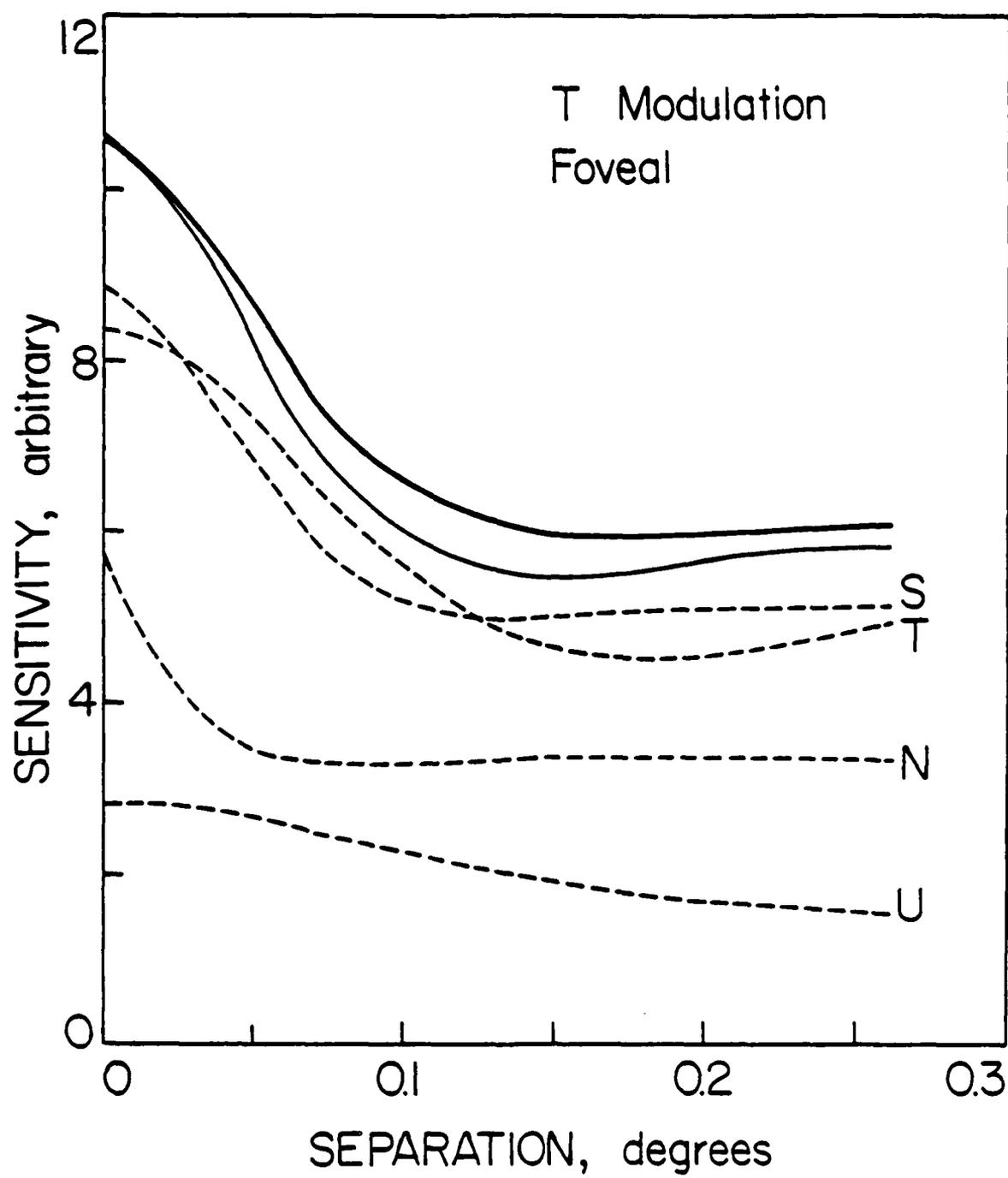


Fig. 6. Kufflerian model replication of Wilson and Bergen's (1979) simulation of the detectability of 3-line patterns under their S and T presentation conditions. The heavy line is our prediction, the lighter line is theirs; the dotted lines are the separate responses of the 4 mechanisms. This figure may be compared directly to Wilson and Bergen's Figure 8.



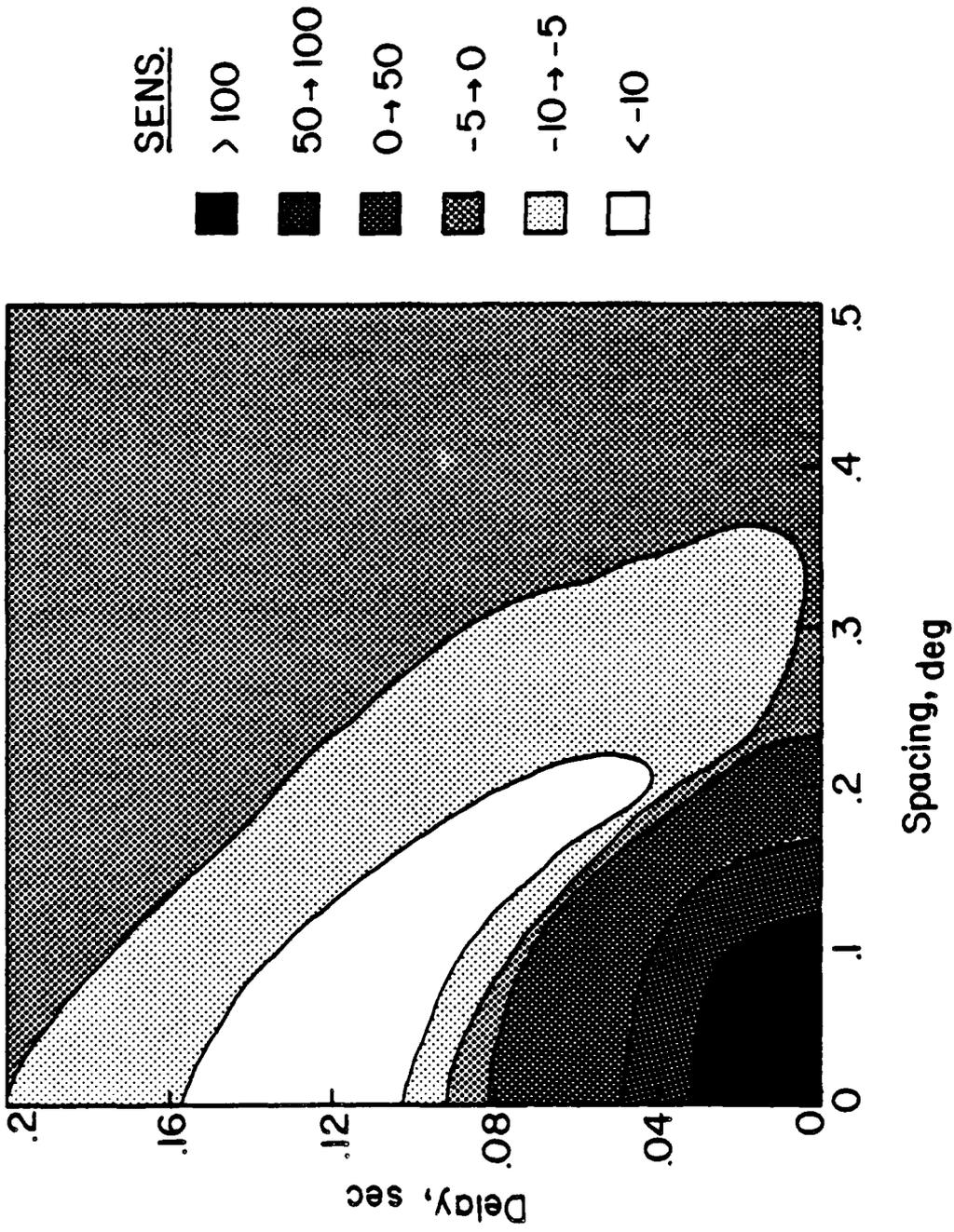


Fig. 7. A simulation of the 2-line LIF experiment with the Kufflerian model. If the model accurately predicted the LIF, then this figure would duplicate Figure 1. In fact, this figure shows no lateral facilitation.

rationale for this approach to modelling. More qualitatively, the separable RF is

$$RF_n(x,t) = [A_{ncx} \exp(-x^2/W_{ncx}^2) - A_{nmx} \exp(-x^2/W_{nmx}^2)] * [A_{nct} \exp(-t/W_{nct}) - A_{nmt} \exp(-t/W_{nmt})]$$

The results of fitting this model are less clear-cut. Since there are 28 free parameters in the model. We placed constraints on the parameters, reducing the number varied to 2 or 3. These constraints must be considered with care, since our conclusions stand largely on their plausibility.

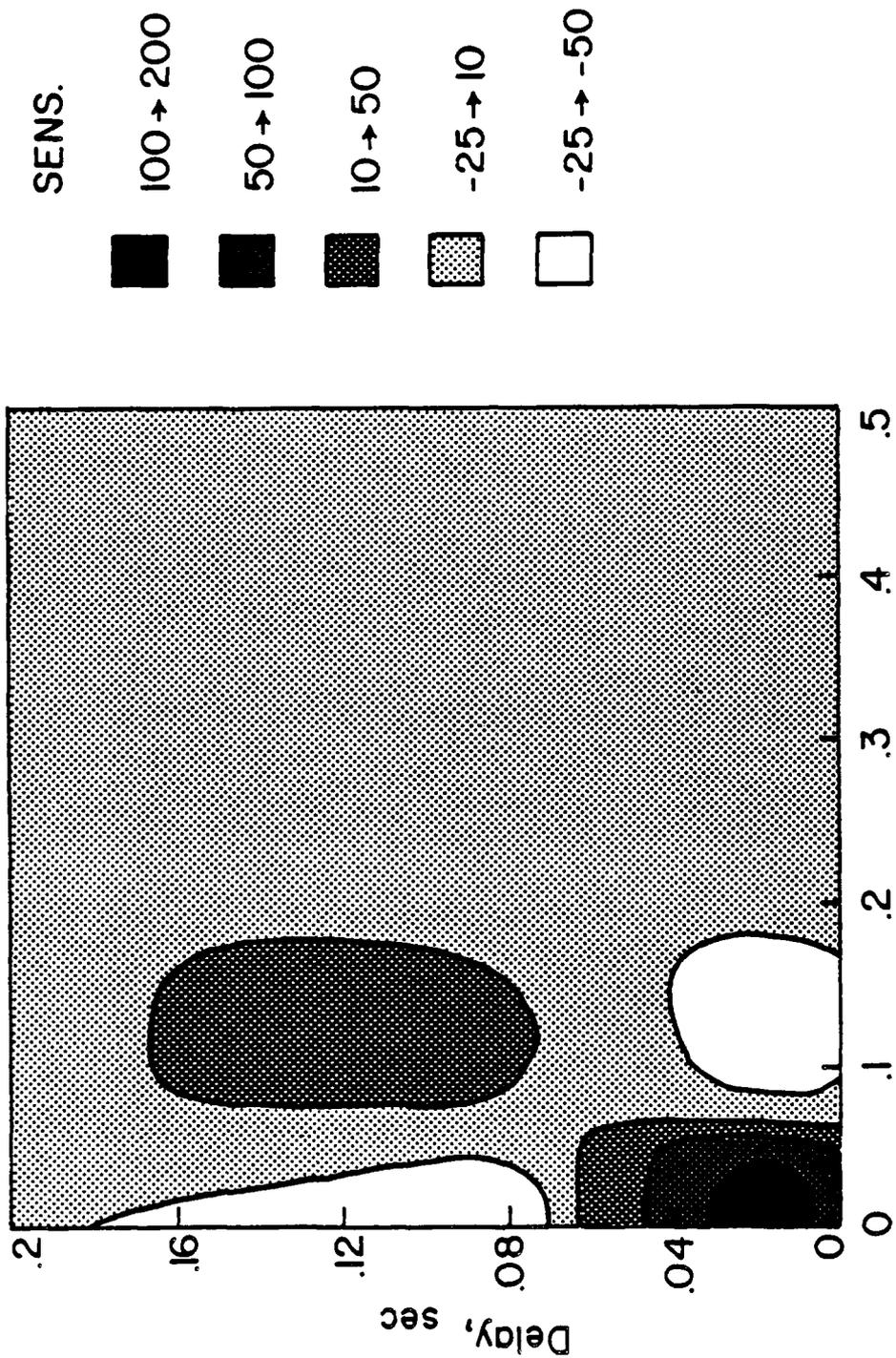
1) We retained the spatial widths given by Wilson and Bergen for each of the 4 mechanisms. We also retained the temporal widths found to work with the Kufflerian model. (Neither model seemed very sensitive to the temporal parameters, provided they stayed within reasonable limits.)

2) While it was not possible to retain Wilson and Bergen's amplitudes (two being given for each mechanism, for the two temporal presentations), we required that the amplitudes remain comparable to those given by Wilson. In particular, the N and U mechanisms have only secondary importance.

3) The mechanisms must be insensitive to static, unpatterned illumination; i.e. they respond only to patterns, not to pure luminous flux.

4) The mechanisms tuned to higher spatial frequencies should have temporal tunings which are both slower and less sharply tuned, and vice versa.

3) and 4) are crucial assumptions, which require some explanation. Assumption 3) requires that the integral of the RF over all space and time be zero, which is readily shown to be equivalent to requiring that at least one of the separate functions integrate to zero over space (or time). This means that we may still choose one of the separate functions to have a non-zero integral, which has profound effects upon the tuning properties of the channel. Consider, for convenience, the spatial function. If this has a zero integral, then the mechanism cannot respond to spatially unpatterned stimuli under any conditions. In spatial-frequency terms, the mechanism is insensitive at zero frequency; it is a band-pass filter. At the other extreme, if the spatial function has no inhibition at all, it will be maximally sensitive at zero frequency (a low-pass filter). In between, there is a continuum of mechanisms with less inhibition than excitation, which are termed "partially band-pass". Thus we can control two important aspects of spatial tuning; changing the overall size of the RF (both centre and



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Fig. 8. Contour plot showing the spatiotemporal sensitivity of the S mechanism in the separable model. Note the somewhat nonlinear contour intervals used to emphasize the various regions. Relative to facilitation at the origin, inhibition has a peak magnitude of about - 0.4 and secondary facilitation peaks at about 0.14. The T mechanism (not shown) has essentially the same "square" geometry, but shifted downward and to the right.

surround) changes the frequency to which it is most sensitive, while changing the balance of excitation and inhibition primarily influences the width of the sensitivity band, especially at its low-frequency end. It is clear that the temporal response may be analyzed in an entirely similar fashion.

Let us apply these considerations to assumptions 3) and 4). Assumption 3) requires that at least one of the separate functions for each mechanism have a zero integral. In Wilson and Bergen's model, the sustained, spatially-narrow mechanisms (N and S) have zero integrals, while the transient, spatially-broad mechanisms (T and U) do not. Thus T and U must have temporal functions with zero integral. This is in good agreement with the psychophysical concept of sustained and transient mechanisms (review in Legge, 1978), which states that high spatial-frequency mechanisms respond in a sluggish, poorly-tuned fashion to temporal variation, while mechanisms which respond rapidly to temporal change have broad, low-spatial-frequency tuning. In a converse fashion, the N and S mechanisms should have temporal functions with non-zero integrals, producing a partially low-pass temporal response. When this is done, each mechanism has one separate function with a zero-integral and one with a non-zero-integral; the sustained mechanisms have a spatial zero-integral, and the transient mechanisms have a temporal zero-integral.

In fact, the theoretical suggestions of the previous paragraph were born out when we began fitting Wilson and Bergen's data for detection of 3-line stimuli under S and T conditions. An RF with a zero-integral temporal function is about 5x more sensitive to T than S stimulation, which is quite out of line with the data. To improve the system sensitivity to S stimulation, it was necessary to give the S mechanism a non-zero-integral temporal function, as suggested above. If the amplitude of the temporal inhibitory term in this function is reduced below about 0.4x the zero-integral value, than a tolerable fit (Figure 9) can be produced. The fit is not affected much by further changes in this parameter, since the S and T fits are now primarily controlled by a single mechanism each.

If we now use these parameters to predict the results of the LIF experiment, we find no secondary facilitation. The reason for this is immediately apparent; with the amplitude of the temporal inhibitory function reduced to this extent, this function never exceeds the value of the temporal excitatory function and their difference is never negative. In short, there is no real inhibition and so no disinhibition as in the LIF. This shows the basic difficulty with this model; the facilitatory effects are much too small. Even if we use a zero-integral temporal S function (optimizing the fit to the LIF at the expense of a factor of 3 misfit to Wilson and Bergen's data), the results (Figure 10) are unsatisfactory in three ways. First of all, the secondary facilitation is roughly 10% of that seen in the LIF. Second, inhibition is apparent along both edges of the predicted

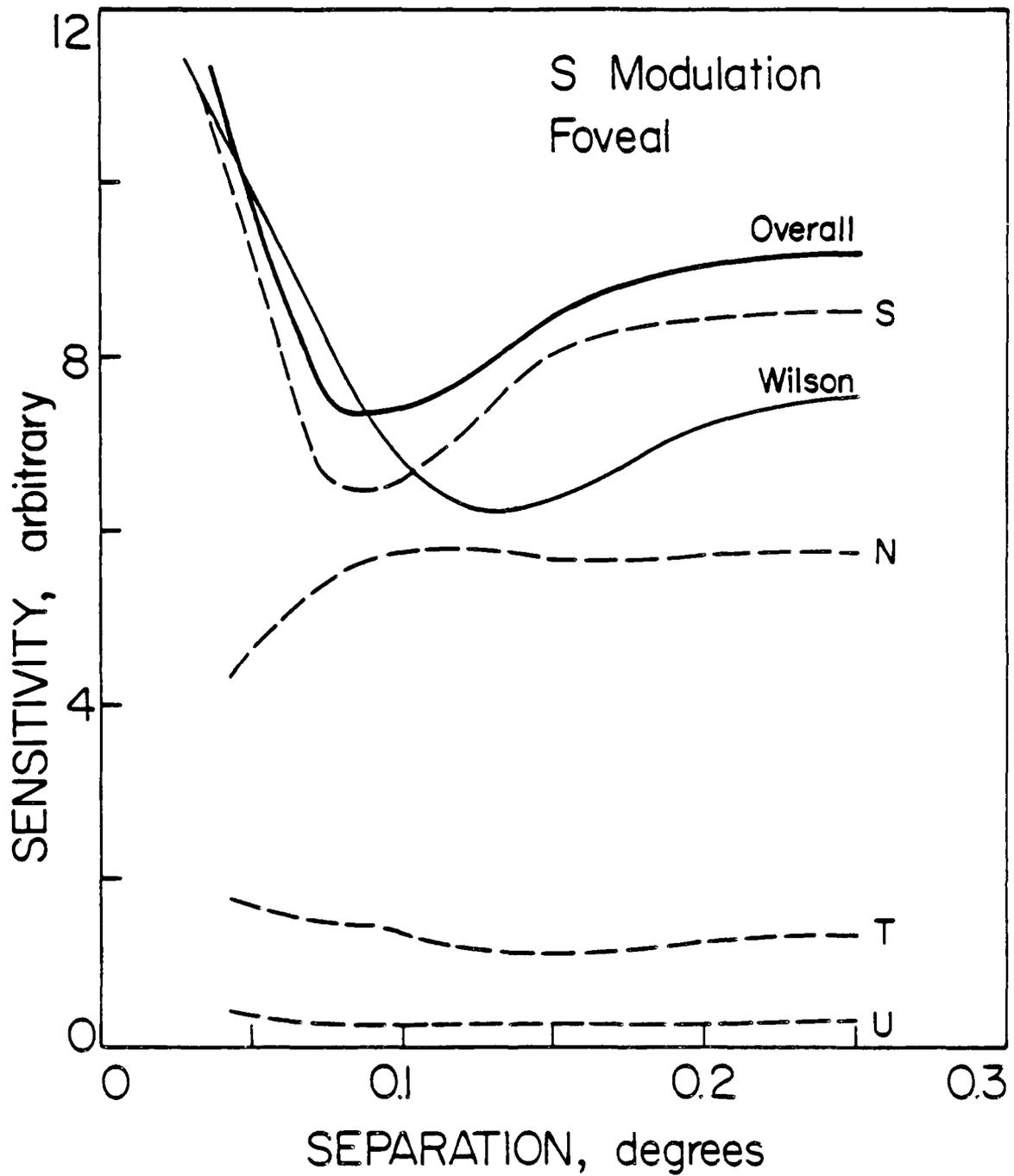
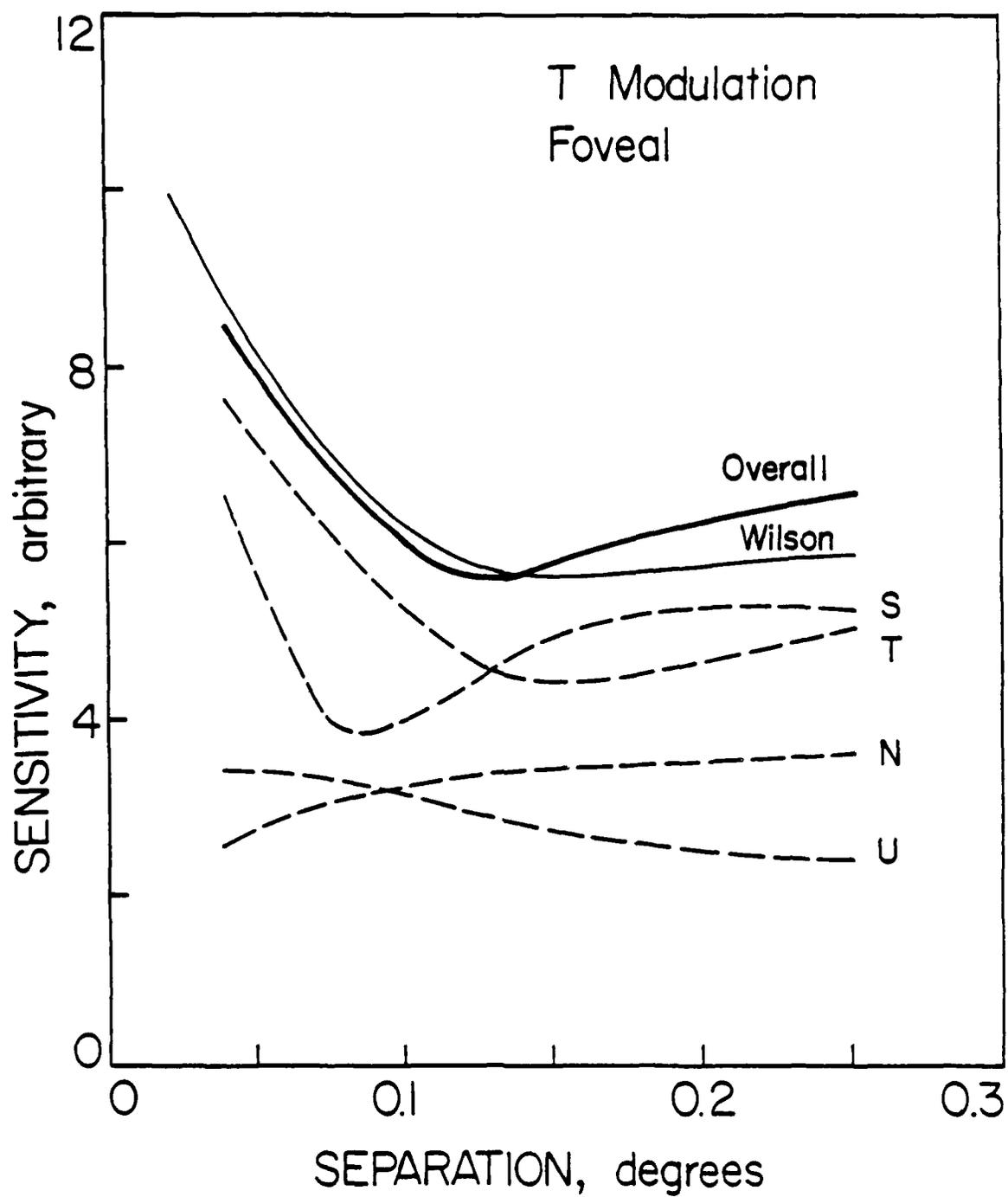


Fig. 9. Separable model replication of Wilson and Bergen's (1979) simulation of the 3-line experiment under S and T conditions. This may be compared to the Kufflerian model (Figure 6) and to Wilson and Bergen's Figure 8. The separate functions were optimized for these data; figures 8 and 10 use somewhat different functions.



LIF, and is several times larger than the secondary facilitation. This is not seen in the data. Finally the secondary facilitation has a definite diagonal configuration, but it is along the wrong diagonal. Where facilitation in the LIF appears to run through the origin, that in Figure 10 runs in the orthogonal direction. This is a direct consequence of the assumption (from sustained and transient channels) that detectors sensitive to high spatial frequencies respond to low temporal frequencies and vice versa; in a velocity detection system, which the LIF more nearly resembles, the two sensitivities would be directly, rather than inversely, correlated.

Our conclusions about the separable model are rather more guarded than those about the Kufflerian model. Given the psychophysical and neurophysiological evidence in its favor we have no desire to dismiss the basic principle of separability. On the other hand, we find basic difficulties with the separable model. One of these is the diagonal organization of the secondary facilitation, described in the previous paragraph. It is difficult to avoid this problem, given current ideas about sustained and transient channels. A second and greater problem is accounting for the amount of secondary facilitation. In this model, the peak of facilitation will be the product of the peaks of the inhibitory portions of the separate spatial and temporal functions. It is difficult to imagine the inhibitory peaks being greater than half the excitatory peaks, which will make the peak secondary facilitation less than one fourth the facilitation at zero separation. This is considerably smaller than is observed in the LIF. Both of these problems arise from relatively basic aspects of the model, and seem to us unlikely to be resolved by simple modifications. At the same time, we must acknowledge that a negative modelling effort is never entirely convincing; the possibility that an unthought-of change in the model might produce positive results will always remain.

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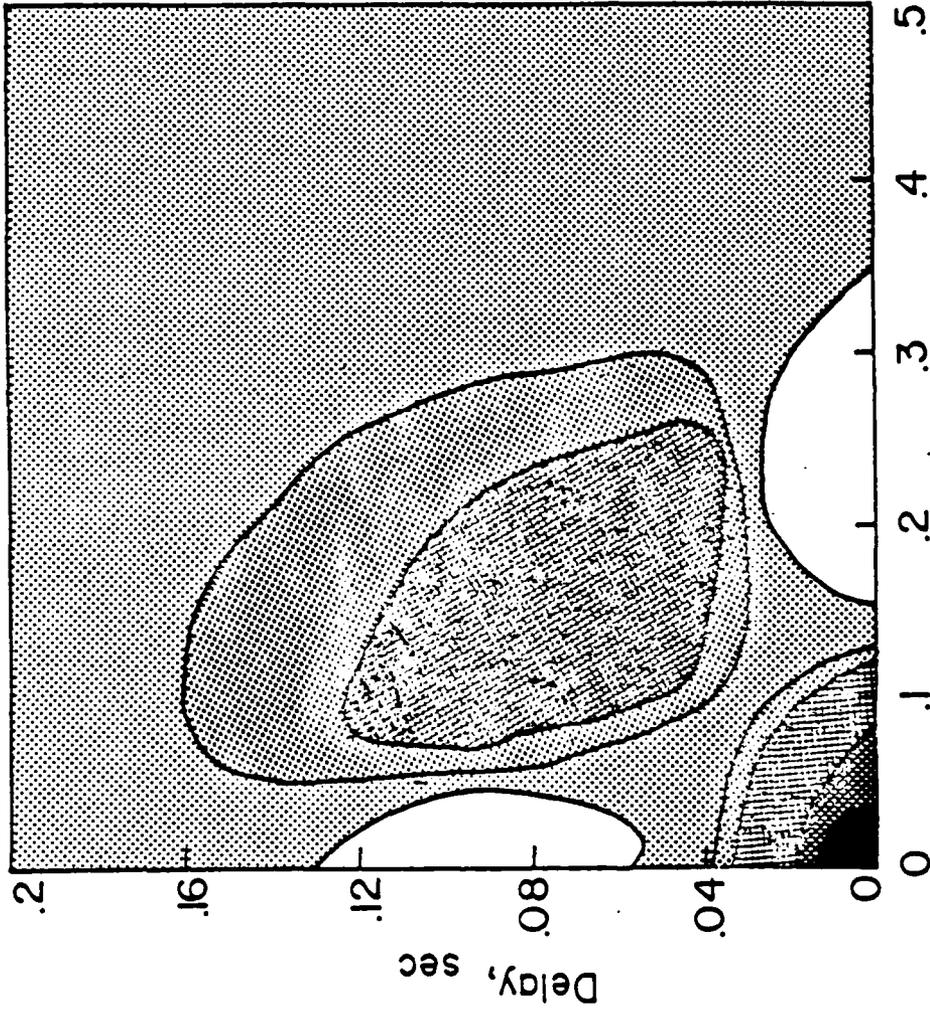
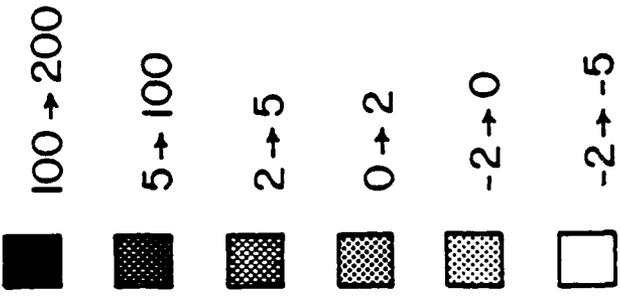


Fig. 10. A simulation of the 2-line LIF experiment with the separable model. This is a limiting case, using fully band-pass temporal functions (also used in figure 8). It gives the greatest amount of secondary facilitation which occurs with this model, but provides a much worse fit to Wilson and Bergen's data than is shown in Figure 9. Peak secondary facilitation is 0.05 times the facilitation at the origin; it is visible only by careful choice of the contour intervals used.

III. Summation, Acuity, and Cortical Magnification

There are two somewhat different ways to look at our data on spatial summation and acuity. In discussing cortical magnification and the theories associated therewith, Westheimer (1982) wrote,

"There is a rather insistent opinion abroad that spatial visual processing has identical properties right across the visual field, save for a multiplicative factor which is a function of eccentricity."

As one might expect from this beginning, Westheimer then proceeded to cite several counterexamples to the "insistent opinion" from the field of visual hyperacuity. Our results offer another two, probably related, counterexamples.

A second aspect of this work involves a less insistent opinion among psychophysicists that a certain cluster of phenomena are all somewhat different ways of measuring the same underlying process. These phenomena include 1) threshold summation between closely-spaced lines, 2) classical acuity, and 3) the size of the centres of receptive fields at various levels of the visual system. We have shown that there are, in fact, at least two distinct mechanisms involved in these phenomena, and that these have quite distinct properties. To do this, we studied the effect of eccentricity on four separate visual functions. These are 1) 2-line summation at threshold, 2) 2-line summation for apparent brightness, 3) threshold for a single line, and 4) 2-line acuity thresholds.

Methods

We used pairs of lines 0.5° high and about $1.5'$ wide, displayed for 1 msec on a CRT screen 3° wide and 4° high with a background luminance of 20 cd/m^2 . Line separation was varied programatically, as was eccentricity by means of a series of 5 fixation points drawn on the screen.

Our psychophysical technique was one we have been developing, and works as follows. The subject is presented with single stimuli, which have a 35% chance of being a catch trial, and he indicates whether he did or did not see the desired stimulus feature. This feature was either simple detection, or discrimination of 2 lines from one. The subject is given feedback on his false alarm rate, and adjusts his criterion to maintain a FA rate of 20%. A simple staircase converges on the 60% correct point of the psychometric function; this is a Wetherill-Levitt type staircase in which intensity drops 1 step for a hit and rises either 1 or 2 steps on alternate misses. A measurement consisted of the mean of 15 reversals of the staircase; this was repeated 5 times and averaged to yield the data presented. Having measured hit-rate with FA-rate controlled, we have a criterion-free measure of detection. d'

Figure 1
The Stimulus

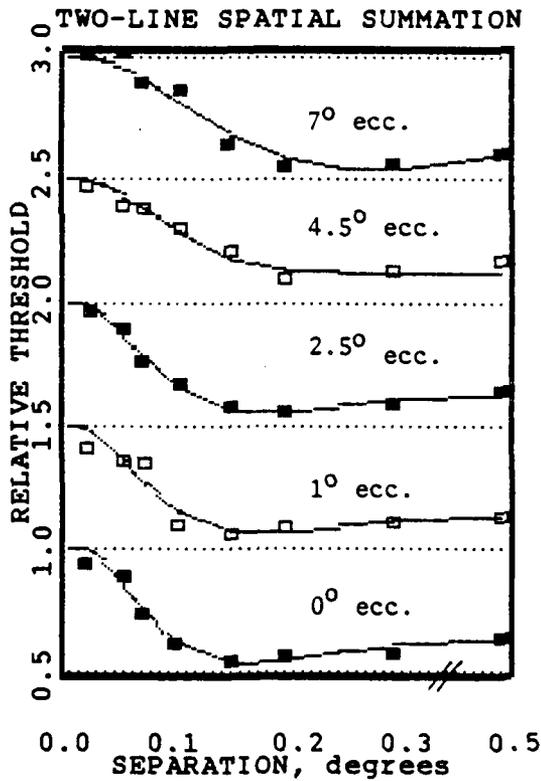
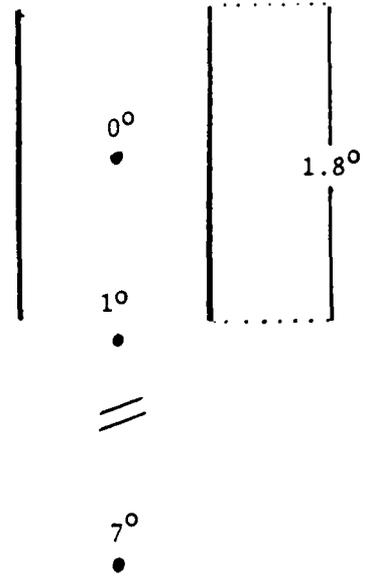


Figure 2

PY's detection thresholds vs line separation for seven eccentricities (0, 1, 2.5, 4.5, and 7 degrees, in ascending order). The curves have been normalized by dividing by the threshold at no separation, and translated upward by 0.5. Smooth curves are fits to a DOG function.

could also be calculated, with additional assumptions, but we have not generally done this.

The brightness-matching experiments used a slightly different paradigm. In these the subject was presented with two pairs of lines, side-by-side, and indicated which was brighter. The standard pair actually had zero spacing (a single, double-width line) and its luminance was adjusted in a simple up-down staircase to match that of the other pair, as a function of the separation between the lines in the second line pair.

Results

Spatial Summation

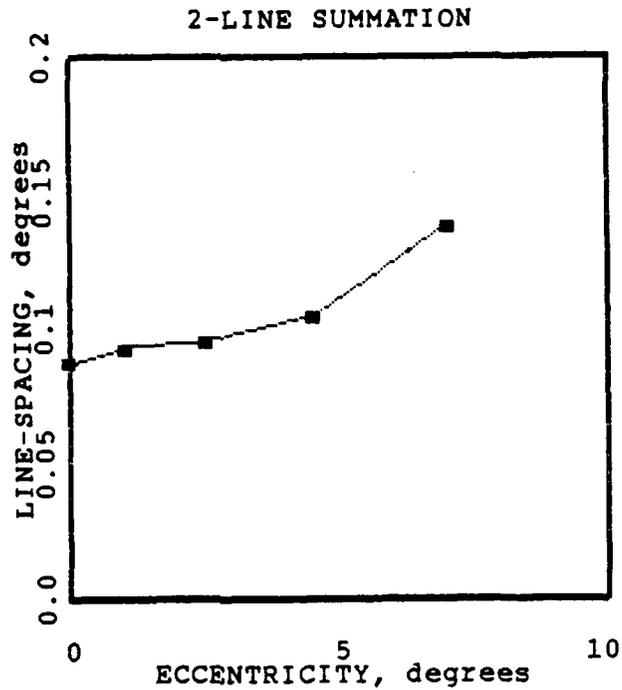
The raw data for spatial summation are shown in Figure III-2, which plots relative sensitivity against line-spacing, for 5 eccentricities. The data show an area of summation for spacings of less than about $10'$, followed by an area of inhibition at larger spacings, with an asymptotic detection level reached by 0.5° separation. The area of summation increases by about a factor of two from 0° to 7° eccentricity. These data are not particularly remarkable; they are in reasonable agreement with those of Limb and Rubinstein, or with those (using 3 lines) of Kulikowski and King-Smith or of Wilson and his associates.

To derive a single measure of the width of the summation area, we fitted the data to the difference of two Gaussians. This function has 5 parameters: 2 widths, 2 amplitudes, and a vertical translation. Three of these parameters were eliminated by the following three assumptions: 1) sensitivities were normalized to 1 by dividing by twice the sensitivity for a single line at each eccentricity (measured as a control condition), 2) the asymptotic sensitivity at 0.5° separation was taken as 0.63, and 3) the width of the inhibitory Gaussian was made 2.5x that of the excitatory Gaussian. The fit was performed on the parameters of width of the excitatory Gaussian and amplitude of the inhibitory Gaussian. Basically the justification for the procedure and its assumptions lies in the quality of the fits (the smooth curves on Figure III-2), which are quite good. The summation area was arbitrarily defined as the width of the centre Gaussian (i.e. the width to a fall-off of $1/e$.) The final results of this experiment -- a plot of summation distance versus eccentricity -- are shown in Figure III-3.

Acuity

It is easier to measure acuity than summation distance. The psychometric function for resolving a pair of closely-spaced lines was found to be monotonic (unlike those in Figure III-2, which are biphasic), so a simple staircase procedure which varied line-spacing will converge to measure acuity directly, acuity being defined as the 60% correct point in resolving the two lines. The lines were all at 2x the threshold for seeing a

Figure 3



PY's overall 2-line summation data

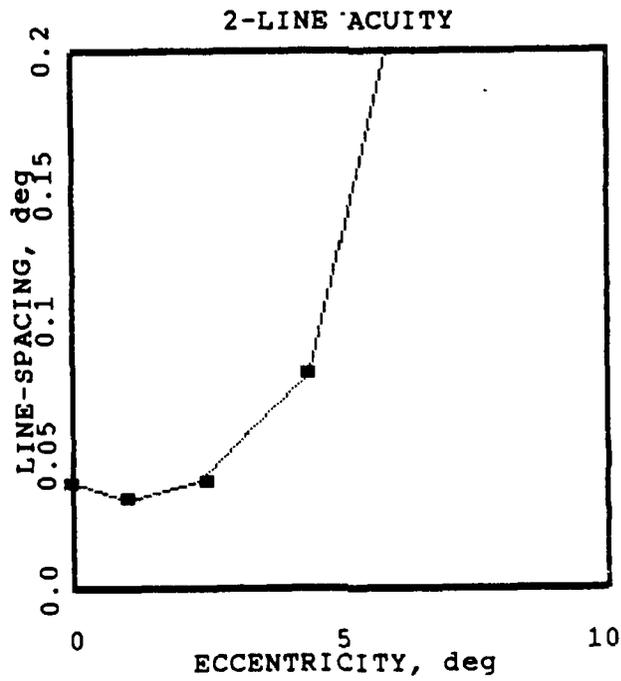


Figure 4

PY's 2-line acuity as a function of eccentricity

single line. The results are shown in Figure III-4, where it will be seen that acuity varies about 8x between 0° and 7° eccentricity (the highest point fell off the graph!) Existing data on the change in acuity between the fovea and 7° eccentricity span a range of about 4x to 10x; our data fall well within that range.

Single-line threshold

As a control condition, we measured the threshold for detecting a single line as a function of eccentricity. These data are plotted in Figure III-5. In their range, they more closely resemble the acuity than the summation data.

Summation for brightness

We quickly observed the well-known phenomenon that the apparent brightness of a pair of lines varies with their separation, even -- to some extent -- when the pair is visually resolvable. We decided to control this effect in the acuity experiment, so that apparent brightness could not be used as a cue. We therefore measured brightness as a function of line separation for all 5 eccentricities, using lines which were at 2x their threshold luminance. The data are in Figure III-6, which bears a considerable resemblance to Figure III-2. These were fit in the same way as the threshold summation data, yielding the final results shown in Figure III-7. (Note that the acuity data, described above, were taken with the luminance of the more widely separated line pairs increased according to the data of Figure III-6, thus producing equally bright stimuli.)

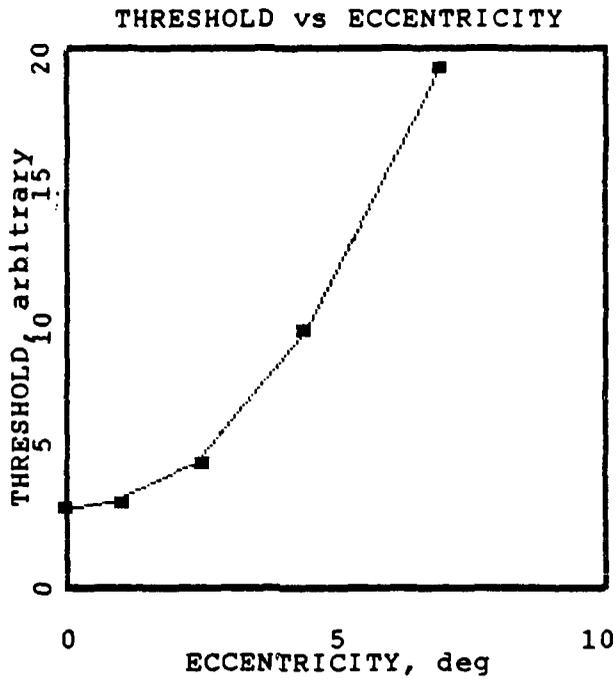
Overall

The 4 sets of results seen are in Figure III-8, where they have been made comparable by normalizing each effect to 1.0 in the fovea. It will be seen that the 4 functions naturally divide into two classes: the two summations, which change by about a factor of 2 with eccentricity, and acuity/threshold which change by almost a log unit. Although it is difficult to propagate errors through our curve-fitting procedure, the internal consistency of the data suggest that the two classes of function are statistically different, while the functions within each class are probably not.

Discussion

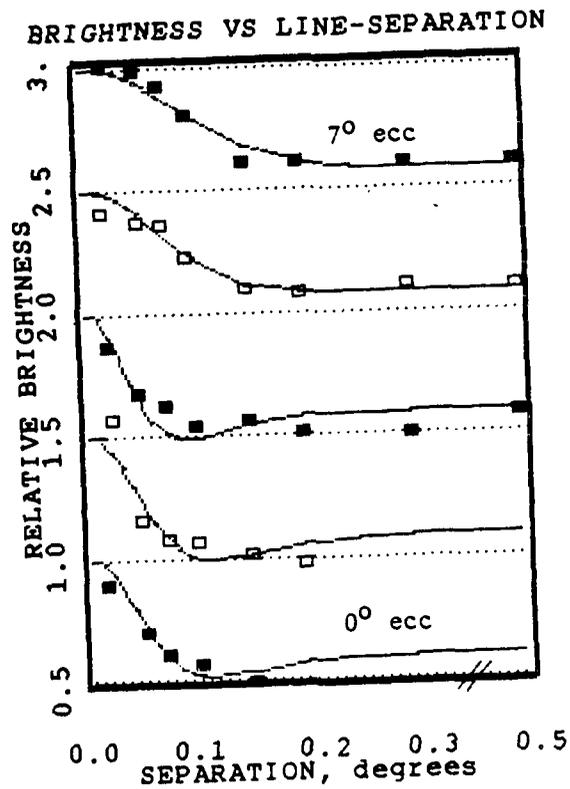
Qualitatively speaking, these data fit nicely with a variety of other results. It is generally accepted that the density of retinal ganglion cells and the cortical magnification factor correlate reasonably well with classical measures of acuity. It is thought that acuity is determined by the dictates of the sampling theorem applied to the retinal mosaic, but this is not readily provable (the sampling theorem cannot strictly be applied to a grating or other quasi-one-dimensional stimulus viewed by a two-dimensional mosaic). In any case, our acuity data are

Figure 5



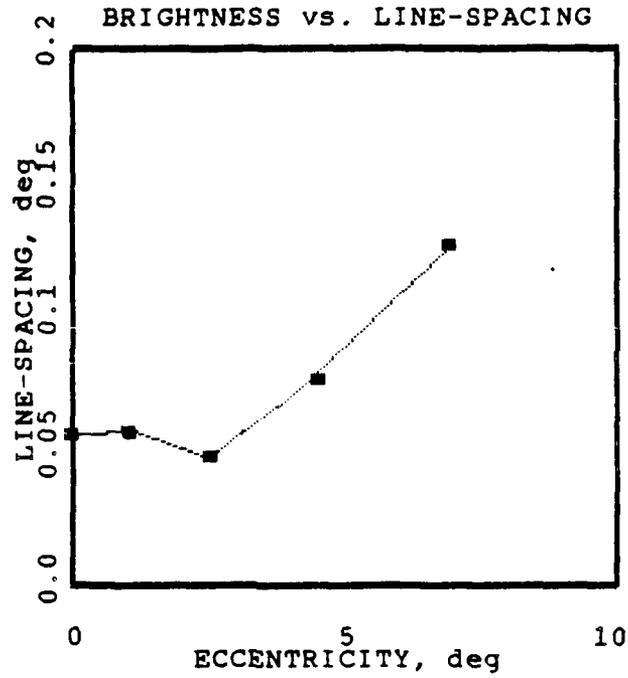
PY's single-line threshold vs. eccentricity.

Figure 6



PY's brightness vs separation for seven eccentricities (0, 1, 2.5, 4.5, and 7 degrees, in ascending order). Smooth curves are fits to a DOG function.

Figure 7



PY's overall brightness summation data

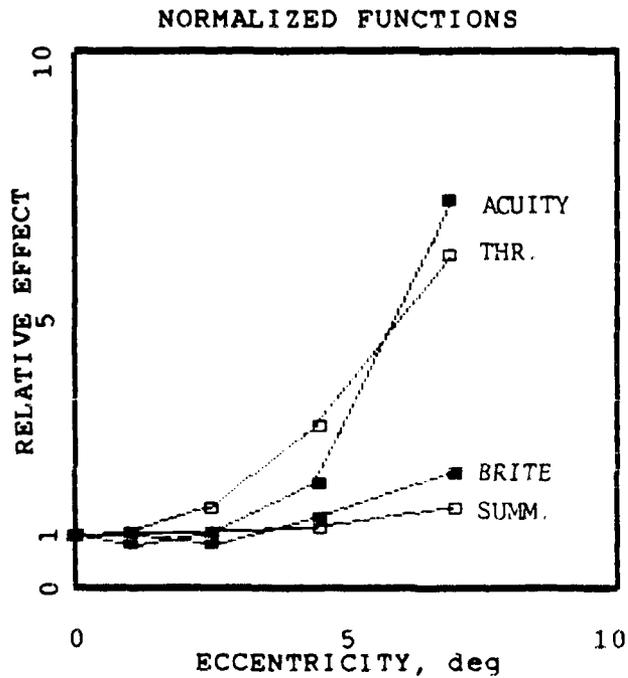


Figure 8

All of PY's data, normalized to 1 in the fovea.
Lower: 2-line (○) summation, and (■) brightness.
Upper: (■) Acuity and (○) Threshold.

consistent with this interpretation. What is somewhat more difficult, however, is to account for our summation data. We suggest that these may be a measure of the size of receptive field centres. Note that these are sometimes considered to represent the limitation on acuity, but that this is not, in fact, true. The theoretical limit is always set by the sampling theorem; even if receptive field centres are much coarser than this, acuity information can -- at least in theory -- always be extracted up to this limit. On the other hand, much evidence suggests that receptive field centres are actually significantly smaller than the spacing of ganglion cells in the peripheral retina. This is shown in direct neuropsychological evidence presented by Lennie, and also by the observation of aliasing at frequencies much higher than the classical resolution limit by Thibos et al. Although there is little quantitative data to compare our results to, these hypotheses provide a good qualitative explanation of our results.

We are somewhat unsure why threshold for a single line covaries with acuity. While it is plausible that single-line-threshold should decrease with sampling density (as does acuity), it would seem that the increasing size of the summation area (less of which -- proportionately speaking -- is therefore excited by a line of constant size) should raise the threshold still further. It is possible that this difference is obscured by experimental error in our current measurements. Perhaps further studies with larger eccentricities (and presumably greater effects) will clarify this point.

Work in Progress

We have briefly considered 2-line summation in scotopic vision. Summation areas are not grossly changed, but there is little fall-off in sensitivity with eccentricity, in marked contrast to the photopic data. We tentatively suggest that sensitivity varies as receptor density (since rod density is about the only density that doesn't fall with eccentricity); this may be confirmed when we have made measurements with 0.5 lines (1.8° lines were used in these pilot experiments), adequately probing the sharp changes in rod density near the fovea.

Sakitt has shown that summation is very different when measured with two separate targets at different spacings, as opposed to a single target of varying width. We have measured thresholds for single bars of different widths at the various eccentricities. Graphed on a log-log, total-flux-vs-barwidth plot, the sensitivities are nearly flat (i.e. near perfect spatial summation!) More specifically, they have a constant slope of about 0.25 from about 2' to nearly 1°. There seems to be a small area of total summation below about 2'. We have, as yet, quite failed to reconcile these results with our 2-line results!

IV. Aliasing in peripheral vision

It is well-known that if a sinusoidal signal is reconstructed from samples taken at regular intervals which are longer than an half-wavelength, then the reconstruction will be a sinusoid of an incorrect (lower) frequency. This falsification of frequency is known as aliasing. Aliasing also occurs with anharmonic signals and irregular sampling intervals, but the reconstruction in this case is more difficult to predict and frequently indistinguishable from noise. More rigorously, aliasing will occur when two conditions are met: 1) the signal must contain substantial energy at wavelengths less than twice the sampling interval, and 2) the aperture over which an individual sample is taken must be significantly smaller than the interval between samples. Condition 2 deserves special note, since it will be of importance in what follows, and since it is less well known, often being implicitly subsumed under condition 1, by treating the sampling aperture as a low-pass filter applied to the input signal.

Williams (1985) and Thibos et al (1985) have recently demonstrated aliasing in central and peripheral human vision, respectively. Their stimuli were interference fringes produced by coherent light. Because such fringes are not blurred by the eye's optics, they were able to produce retinal stimuli whose spatial dimensions were substantially smaller than the spacing between cones. Since the area sampled by a single cone is very small, both of the above conditions are satisfied, and aliasing occurs. Williams argues, and we would concur, that aliasing is rarely observed with real-world stimuli, since optical blur largely removes spatial frequencies which are comparable to the spacing of the receptor lattice, at least in foveal vision. It is well-known, however, that cone spacing drops precipitously with eccentricity in the visual field, while optical blurring -- though somewhat degraded with eccentricity (Jennings and Charman, 1981) -- falls off much less rapidly. Thus it appears that spatial frequencies high enough to undergo aliasing may be visible in the periphery.

For aliasing to occur, however, the second condition must also be met; that is, the sampling aperture of the peripheral visual system must be significantly smaller than the distance between samples. At a physiological level, this condition appears to hold; outside the fovea, monkey receptive field centres are smaller than the separation between adjacent receptive fields (Lennie, 1985). We recently reported an apparently parallel psychophysical phenomenon: the area of spatial summation in human photopic vision increases only modestly between the fovea and 7° eccentricity, while acuity changes about 7x. If we consider spatial summation to be a measure of the sampling aperture, while acuity is limited by the separation between samples, then these results suggest that at 7° eccentricity, there may be a considerable range of spatial frequencies between the limit of ordinary acuity, and what can be

perceived in aliased form.

Williams (1985) observed that the percepts of aliased gratings in the fovea, though grating-like, displayed little preference for the orientation of the original interference fringe. He showed that the slight irregularities found in the foveal cone lattice could account for this. At 7° eccentricity, then, where the receptor arrangement is much more irregular, we may safely assume that the orientation of a grating stimulus will be quite lost in its aliased percept. This percept -- providing its contrast is above threshold -- should nonetheless be detectable. We therefore propose that a task requiring orientation discrimination should measure ordinary (i.e. unaliased) perception, while a simple detection task could be performed with either the ordinary or the aliased percept. Thus if aliasing is present, detection and discrimination data -- though similar in the fovea -- should diverge markedly in the periphery, where detection will become possible at much higher spatial frequencies.

The stimuli used in this study were square-wave gratings produced by a Grinnell 275 image processor on a 14 cm square CRT (P4 phosphor, mean luminance 120 Cd/M^2). To avoid the anisotropy inherent in a raster display, the gratings were all tilted 45° . Gratings were displayed in a square window, also rotated 45° (i.e. a diamond), and surrounded by mean luminance in the rest of the screen. The grating was enclosed in a thin, dark square which consisted of 1) the two outermost dark bars of the grating, and 2) two identical bars at right angles which terminated the ends of the grating. The overall sizes of the grating patches were scaled for equal cortical extent, using the formula given by McKee and Nakayama (1984), though this manipulation has rather little effect upon the results. Data were taken at eccentricities of 0° , 2.5° , and 7° , using field sizes of 0.75, 1.7, and 2.0 degrees square, respectively.

In the discrimination experiment, the subject was shown two gratings at right angles in a successive two-alternative forced-choice paradigm. Each stimulus lasted 0.5 seconds, with a 0.5 second interval between. An audible tone marked the beginning of each stimulus. The task was to determine which interval contained the right-leaning grating. In the detection experiment, the procedure was identical except that one of the two stimuli was a uniform patch with the same mean luminance as the gratings. The uniform patch was surrounded by the same thin, dark square which surrounded the gratings. The detection task was to determine which presentation contained the grating. The just-detectable (or discriminable) spatial frequency was determined by a standard Wetherill-Levitt-type staircase moving down one step and up two (Wetherill and Levitt, 1965). The tasks were quite easy, and standard errors were less than 7%. Two subjects participated: PC (the second author) and LM (a naive subject).

Since we consider any superiority of detection over

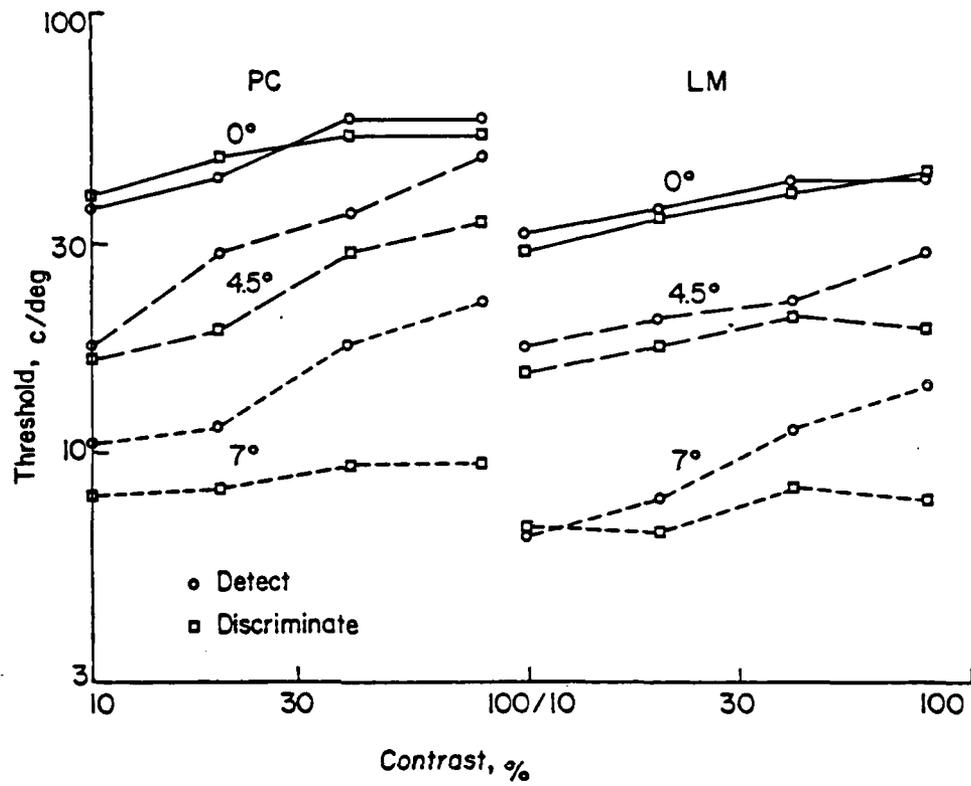
discrimination as evidence for aliasing, it is essential that all artifactual cues be eliminated from the detection task. We considered two potential cues. 1) There might be a detectable temporal transient at the sharp onset or offset of the stimulus. 2) The grating might have a different mean luminance from the uniform field, perhaps due to nonlinearities in the CRT phosphor. We dealt with the possibility of a temporal transient by including the thin, dark square surrounding both fields. This flashed on and off during the uniform-field presentation, just as it did during the grating presentation, masking any other sort of temporal transient. The fact that the gratings and homogeneous fields were not always of exactly the same luminance as the background (vide infra) also contributed to this masking. It was not possible to guarantee that the average luminance of the grating equaled that of the uniform field. The Grinnell offers only 256 brightness levels, and the difference between adjacent levels is marginally superthreshold. To deal with this we 1) adjusted the grating's luminance for the best possible match prior to each session, and 2) added to every field presented a random brightness increment of as much as ± 4 brightness levels. Under these conditions, subjects instructed to perform the task on the basis of apparent brightness alone did not perform better than chance. It should be noted that these precautions seemed superfluous to our subjects, who found the aliased percept -- though less distinct than Williams' -- to be entirely convincing.

In a second experiment we measured contrast sensitivity functions for the two tasks, at different eccentricities. In these experiments the stimuli and procedures were essentially the same, except that spatial frequency was held constant and the staircase instead changed the contrast of the gratings.

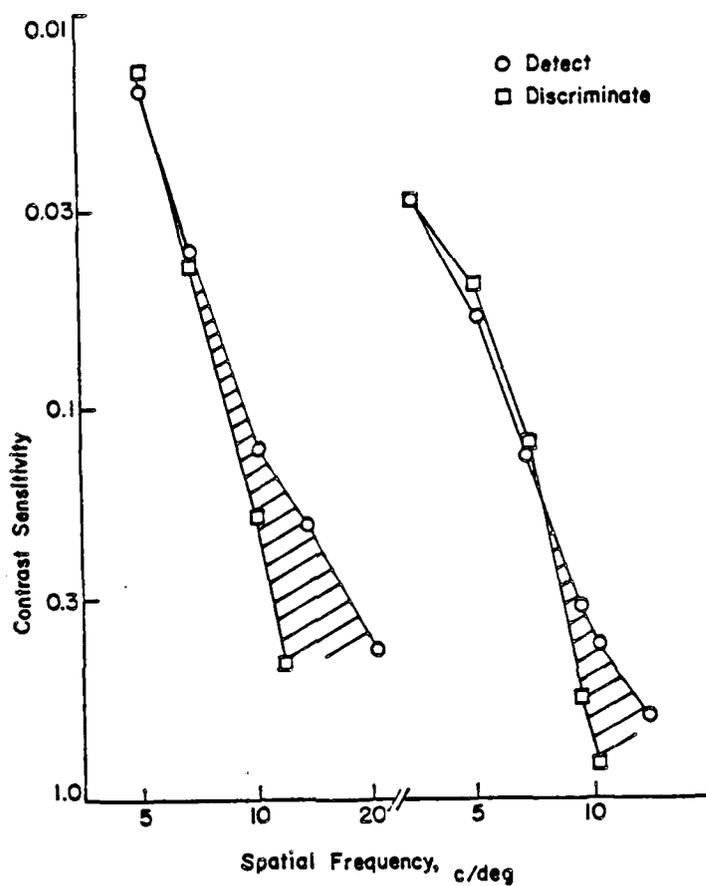
The results are seen in Figure IV-1, which shows the contrast of a threshold grating for the two tasks, as a function of eccentricity and grating contrast. It is clear that our prediction is entirely fulfilled; detection and discrimination thresholds are essentially identical in the fovea, but diverge by a factor of two at 7° eccentricity. The effect is strongest at high contrast (80%), and is nearly absent at 20% contrast.

Figure IV-2 shows contrast sensitivity functions for detection and discrimination at 7° eccentricity. At low contrasts, the two CSFs are identical, but near 20% contrast the detection function shows a moderately well-defined divergence, so that ultimately detection is possible at frequencies about twice as high as discrimination. The shaded area between the curves is the region in which stimuli presumably are detected in aliased form.

It was of some concern to us that earlier workers have not observed this divergence between detection and discrimination in peripheral vision. In particular Rovamo, Virsu, and their associates (1979) have studied detection and orientation discrimination extensively, using paradigms very similar to ours. There are several factors which may, singly or jointly, account



1. Threshold spatial frequencies at three eccentricities as a function of grating contrast. Detection and discrimination thresholds are the same in the fovea (0°), but detection becomes at least 2x better in the periphery at high contrast. (For clarity, the 4.5° eccentricity data are translated up by 1.5x.)



2. CSF's for square-wave gratings at 7° eccentricity. Stimuli falling to the left of the CSFs are always visible; stimuli falling to the right are invisible. Stimuli falling in the shaded region between, however, are detectable only in aliased form.

for this. First of all, Rovamo used a significantly dimmer display than ours (10 cd/m^2 vs. 120 cd/m^2). Although we did not study this directly, it is likely that reducing luminance makes the aliased percepts less visible. Their display had a dark surrounding field, while ours was situated in a isoluminant field. Such a dark surround has been shown to exert a masking effect (Estevez and Cavonius, 1976) whose nature is not well understood. To be sure, this has only been observed at low spatial frequencies and in the fovea; there do not appear to be any studies of the effect in the periphery. Finally (and most convincingly) we have shown that the perception of aliasing is not noticeable at contrasts lower than about 20%. Virsu and Rovamo's detection data (1979) are in the form of contrast sensitivity functions, and show only one or two points with contrasts this high. Thus aliasing may have been present in Virsu and Rovamo's experiments, but it lay outside the range of their observations. In our own contrast sensitivity experiments we could only measure thresholds at high contrast by using tediously small step-sizes to avoid the inevitable biasing of the staircase which occurs with repeated contrast overflows.

Theoretically, we believe the simple observation of aliasing is of less interest than the likelihood that our aliasing is at a different anatomical site from Williams'. The visual system is roughly describable as a hierarchy of processing layers, each receiving input from its predecessor. Aliasing might therefore occur at any stage where the signal is undersampled, relative to the resolution afforded by the preceding stage. In particular, Williams' subjects observed percepts up to about 200 cycles/degree, which is consistent with low-pass filtering by the aperture of an individual receptor. Therefore Williams' aliasing is probably at the receptor level. Our subjects, however, detected percepts only up to about 20 cycles/degree, a very substantial difference. Such a limitation is more compatible with the spatial summation area for line pairs at 7° eccentricity, as discussed in the previous chapter. We tentatively suggest that the spatial summation process limits detection in these experiments, but that the separation between the summation elements is rather larger than their individual widths, so that undersampling occurs. We can plausibly localize these elements in the peripheral visual system. Since the crucial distinction in this experiment was the subjects' inability to discriminate orientation, it is reasonable to assume that orientation-sensitive elements in the visual cortex are not being stimulated by aliased stimuli. This would place the summation elements distal to the visual cortex, perhaps at the ganglion-cell level.

An obvious question is "what does the aliased grating look like?". Williams has presented drawings of the percepts in his experiments, but this is not really possible in our studies. Like most percepts in extra-foveal vision, this one is indistinct and not easily described. The subjects are clearly aware that "something" is there, but it has no clear pattern. It appears to be an irregular and changing texture, with a

reasonably high apparent contrast, but with no discernable orientation. The behavior of subjective contrast is interesting. This decreases monotonically with physical contrast, passing smoothly through the orientation threshold and not reaching zero until near the detection threshold.

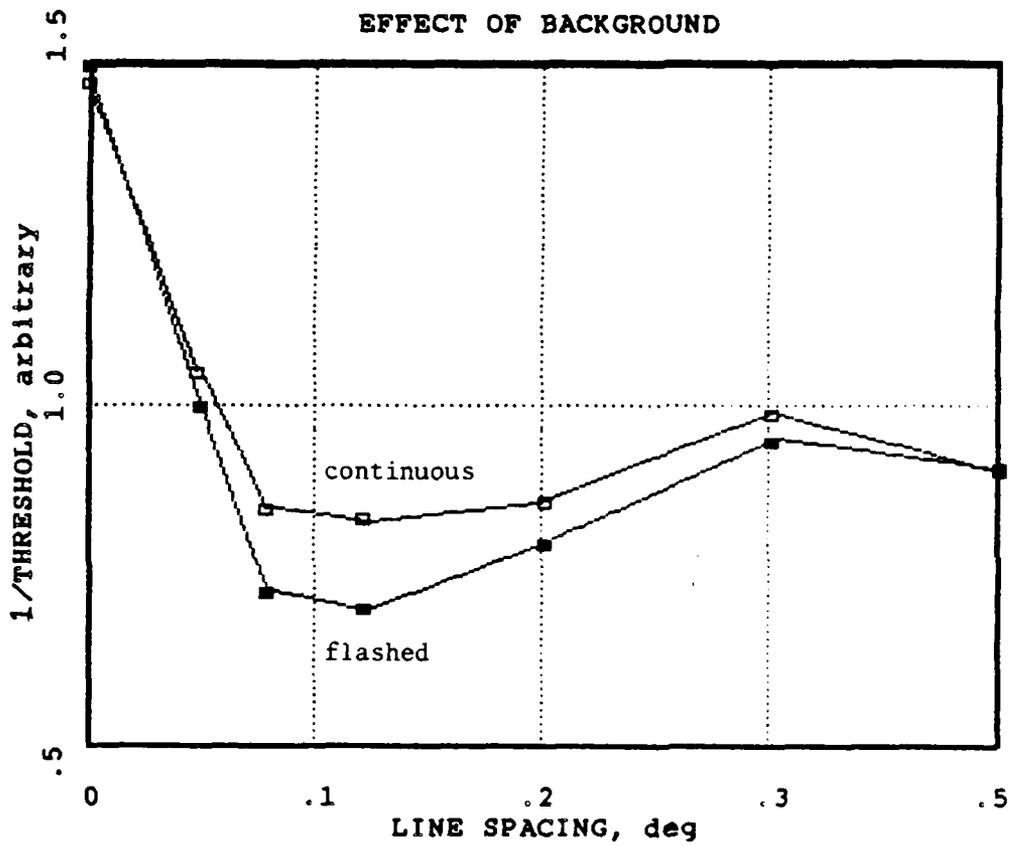
On the basis of our observations, we propose to modify the letter, though not the spirit, of the common assertion that aliasing does not occur in normal visual situations. It appears that there is a significant range of spatial frequencies which are detected only in aliased form in peripheral vision. However aliasing -- in the stronger sense of falsifying a percept -- does not occur. The percept in our studies ("Something is there") is not false, but merely incomplete in that spatial form is lacking. Such percepts, insofar as they occur at all in practical situations, could certainly serve as cues for acquisition and visual tracking which would provide the missing form information. Thus aliasing, as we observed it, is not really an artifact, but a potentially useful part of the visual repertoire.

V. Temporal Effects on Spatial Summation

The possibility that spatial summation may be dynamically modified during the time course of stimulation seems to have first been suggested by Glezer (1965), while Tangney (1980) presented the first convincing demonstration of such effects. Recently Cornsweet and Yellot (1986) have devised a detailed model which qualitatively fits a wide variety of data, though it currently lacks real experimental verification. We came to the study of these phenomena serendipitously. We had been studying summation with 3-line targets, and made a minor modification in our paradigm; we replaced a brief, dark intertrial interval with an interval of uniform time-average mean luminance. This had the effect of significantly reducing the observed lateral inhibition (Figure V-1). We entertained two possible reasons for this. 1) The increased lateral inhibition may be a short-term neural aftereffect of the onset of the background, or 2) it may arise because at the time lateral inhibition is sampled, the retina is illuminated with more than the mean time-average luminance.

To study this further, we placed the 3-line probe at a variety of ISIs after the onset of the bright background. The results (Figure V-2) show a modest but progressive effect. 700 msec after the onset, the perceptive field (PF -- a convenient term for the results of experiments such as these) shows a typical resting configuration, with a broad summation area and only slight lateral inhibition. When the PF is measured progressively closer to the onset of the background (120 msec, 50 msec, 20 msec) the summation area becomes narrower and inhibition more pronounced, the most pronounced change being at about 50 msec. This indicates that at least some of the PF changes are dynamic and short-term. The PF measured before the onset differs only slightly from that measured a long time (700 ms) after; this suggests only a minimal effect of mean luminance. We decided to try a potentially more powerful temporal stimulus, and used the offset of a 3 c/deg, 50% contrast grating to induce PF changes. This frequency was chosen because the mechanism described by a typical PF would have its peak sensitivity at about 3 c/deg. The grating was counterphased at one Hz to avoid afterimages. The results (Figure V-3) show that the grating is indeed more potent; the width of the summation area changes by a full 3x between 20 msec and 700 msec ISI, and inhibition changes from essentially nil to very pronounced. We have verified these dramatic changes with a second subject, and they appear quite real.

In connection with our aliasing studies, we wondered how PFs varied in the parafovea. If summation areas change size under different conditions, then this will change the high-frequency cut-off for detecting aliased gratings. Figure V-4 shows PFs measured at 7° eccentricity. As in the fovea, there is little inhibition in the 700 msec condition, but what is surprising is that there is also little inhibition and little or no narrowing



The effect of background luminance on PPs. The filled squares represent the PF 700 ms after the onset of a 50% duty cycle background. The open squares are taken with a continuous background.

Figure V-1

PERCEPTIVE-FIELD DYNAMICS

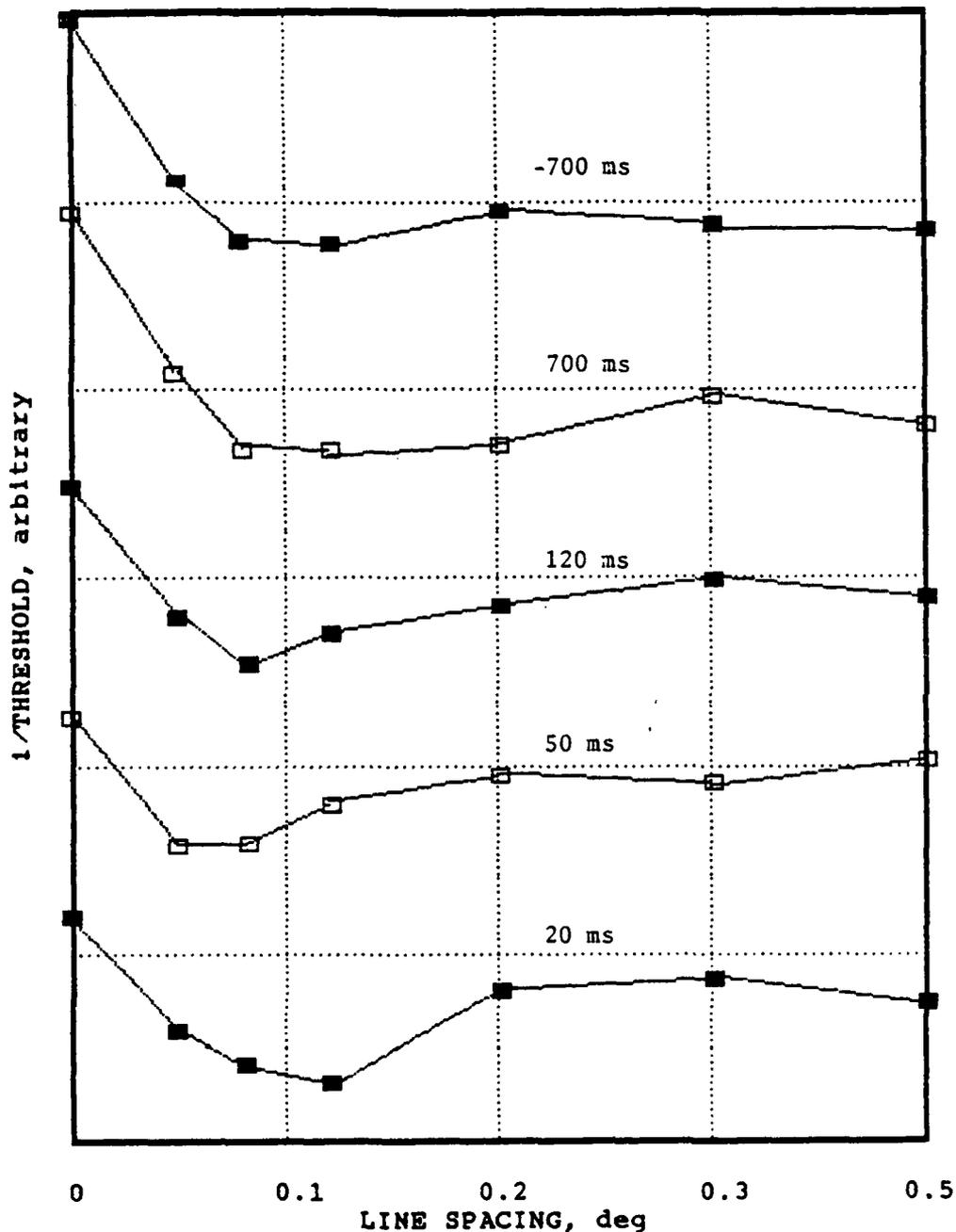


Figure V-2

Perceptive field changes at various intervals around a step increase in background luminance. From the bottom, the tests were made 20 ms, 50 ms, 120 ms, 700 ms, and -700 ms after (before) the brightness step.

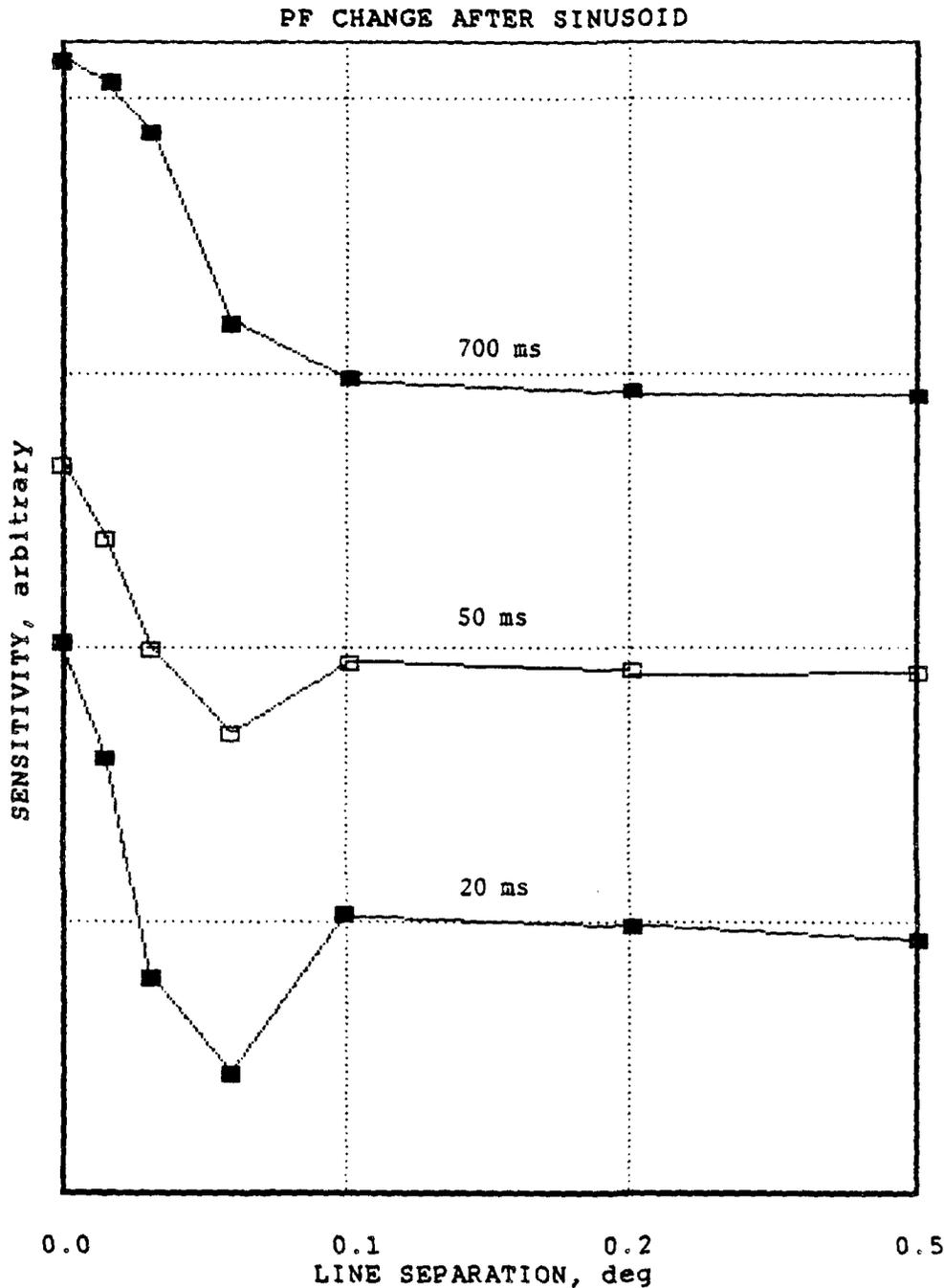


Figure V-3

PC's perceptive fields after the offset of a 3 c/deg sinusoidal grating, 50% contrast. From top to bottom, the ISIs are 700 ms, 50 ms, and 20 ms.

of the summation area in the 20 msec case. Two further conditions shown in Figure V-4 are the beginnings of a search for these effects. A simple luminance flash (similar to Figure V-2) produces increased inhibition at separations between 0.1° and 0.3° . Such a PF would be most sensitive at about 1.5 c/deg. Surprisingly however, the offset of a 1.5 c/deg grating is seen to produce rather little effect. These preliminary results are puzzling, and need to be checked much more completely. For example, we did not increase the field size in the parafoveal condition; it is possible that edge effects spread more broadly in the parafovea, and the edges of the field may be too close to the test stimuli.

It is natural to suppose that much of the lateral inhibition measured in these PF experiments is from the ganglion cells, where lateral inhibition is a prominent part of the receptive field. It was, therefore, quite surprising to discover that this is almost certainly not the case. Kuffler describes lateral inhibition as operating relatively slowly, and only after a delay of about 50 msec. Thus, we might expect that separating the test and flank lines by about this delay would make inhibition more prominent. In fact, we see in Figure V-5 that separating the lines by as little as 20 msec abolishes inhibition altogether! This result has been replicated on three observers, and is quite genuine. Thus we have a very fast-acting form of lateral inhibition. We suggest that this is either 1) a very peripheral inhibition, which occurs before the visual signals have been filtered through the relatively sluggish ganglion cell inhibition, or 2) it is higher level inhibition between fast, excitatory afferents to the visual cortex.

Discussion

Functionally, what produces the change in PF organization? We entertained two possibilities. 1) Organization may change with background level, as originally described by Barlow, Fitzhugh and Kuffler. 2) The observed changes are a dynamic response to the temporal variation of the background stimulus. The first possibility is eliminated by the fact that we get large PF changes after exposure to a grating, which preserves mean time-average luminance. The fact that we find changes from even a simple brightness-flash supports the dynamic response hypothesis, though the nature of this dynamic response is not yet very clear. In practice, viewing any structured field should, by virtue of eye-movements, produce extensive spatial and temporal variation, keeping the PF more-or-less continuously in its narrow, lateral-inhibited condition. Functionally, we suggest that the broadly-summing PF occurs only when the field of view is nearly empty, and that this PF is optimized for detection. When contours are visible, however, the narrower PF may be better suited to acute form discriminations.

What physiological changes seem likely to underly the observed changes in the PF? We suggest three possibilities. 1) The area of summation may actually change, concomitant with

PARAFOVEAL PF CHANGES

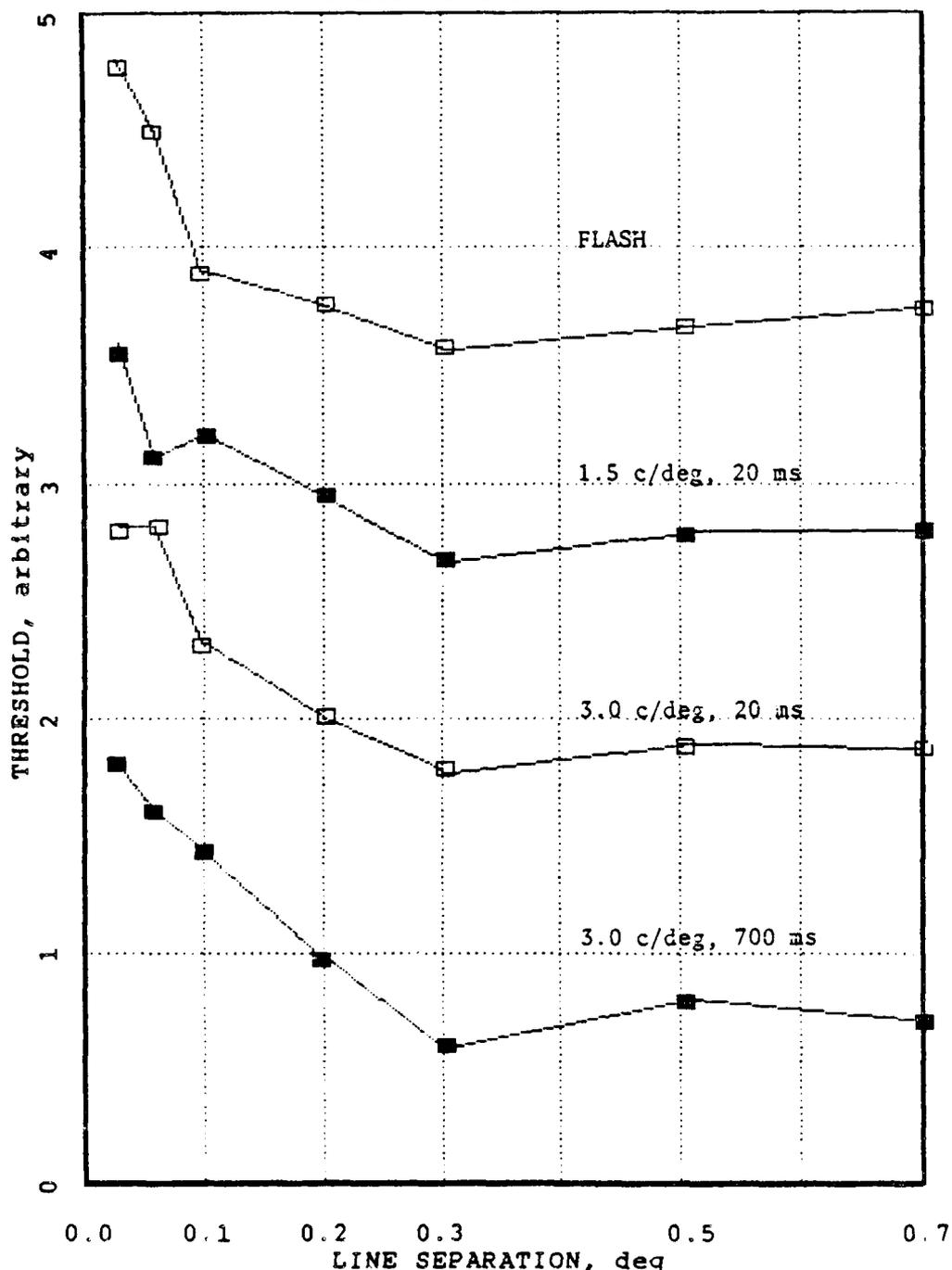


Figure V-4

PY's PFs after the offset of a sinusoid, 7 deg parafoveal. The bottom and 2nd curves are PFs 700 and 20 msec after the offset of a 3 c/deg, 0.5 contrast sinusoid. The next curve is 20 msec after the offset of a 1.5 c/deg sinusoid. The final curve is 20 msec after the onset of a bright, whole-field flash.

FAST-ACTING LATERAL INHIBITION

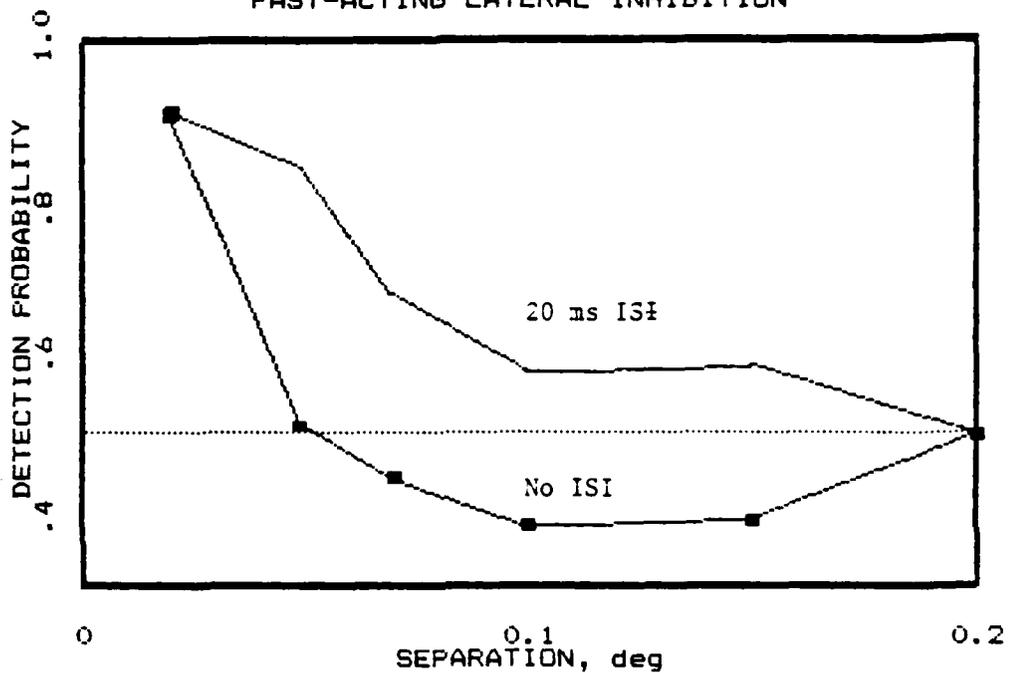


Figure V-5 Detection probability for two simultaneously-flashed lines, as a function of line spacing. The line without symbols shows the results from Figure 6 of the same experiment with a 20 msec delay between the lines.

an increase in lateral inhibition. 2) Lateral inhibition increases, causing an apparent narrowing of summation by subtraction. 3) Individual mechanisms do not change, but the transient stimulation masks the low-frequency mechanisms more than the sustained, high-frequency ones. The apparent changes in organization then merely reflect the changing contributions of various mechanisms. These questions seem experimentally resolvable. The fact that a brief (20 msec) separation between test and flank lines eliminates lateral inhibition may provide a means to study summation in isolation. The experiments described above should be repeated with such temporally offset probe stimuli, to see if the summation region still changes under those conditions. The possibility of switching between mechanisms can be studied by varying the frequency of the pre-exposing grating. If narrowing of the PF is simply a result of stimulation, then grating frequency will have only a modest effect. On the other hand, most multiple channels' models would predict that a high frequency pre-exposure should mask primarily high-frequency channels, and should shift the PF to lower frequencies (i.e. a broader PF). This is the opposite of what we have thus far observed.

We are now able to consider, at least tentatively, a detailed model of peripheral visual interactions, considering the effects of both eccentricity and temporal variation. In the fovea, PFs have the conventional "Mexican Hat" configuration, but they are more sharply tuned and possess more lateral inhibition in the presence of sharp, temporally-varying contours. The tuning of these PFs is roughly commensurate with the tuning of the overall CSF, measured in the fovea. In the parafovea, PFs show a summation area about 2x larger than observed in the fovea, and little lateral inhibition. This implies that they have a low-pass spatial frequency response. At first sight, this difference is puzzling, but in fact it agrees with studies of peripheral contrast sensitivity and cortical magnification. We have already shown that the size of the summation area does not increase as fast as cortical magnification and acuity. Specifically, a variety of published data on peripheral CSFs show that the frequency of peak sensitivity drops at least 4x at 7° in the parafovea, while the PF changes only about 2x in width. If the parafoveal PF included lateral inhibition, and so were bandpass, there would be a mismatch of about 2x between the peak sensitivities of the processes represented by the PF and the overall system (represented by the CSF). A low-pass PF, however, passes the low frequencies to which the system ultimately proves most sensitive. This analysis suggests that lateral inhibition might still exist in the parafovea, but that it would have to be spread over quite a large area (i.e. tuned to low spatial frequencies). Such inhibition might well have been missed in our pilot studies.

This model raises some thought-provoking questions. First of all we wonder why it is that in the fovea the PF is apparently well-matched in spatial frequency response to the CSF of the overall system, yet this match breaks down rather quickly in the

parafovea. Similarly, we ask what is the role of the dynamic changes in the PF with changes in stimulation. It is tempting to assume that acuity is related to spatial summation, but we suggest that the answer to both of these questions lies rather in the recognition that the theoretical limit on acuity is set by the sampling theorem, and that summation (and its variability) may serve a quite different purpose. The most likely purpose would seem to be the reduction (by averaging) of noise within the system. We ultimately hope to study in some detail the constraints on the system (e.g. quantal fluctuations, receptor densities, etc), and demonstrate with a model that the properties we are discovering are actually attuned to the purposes of the overall system.

VI. Velocity discrimination and related experiments

We have in the last year virtually concluded our velocity discrimination studies. These experiments fall into 3 major groups:

1. Velocity discrimination using moving bars and gratings.
2. Flicker frequency discrimination using uniform spatial luminance fields.
3. Velocity matching of a high contrast variable stimulus to a fixed velocity, low contrast standard.

The overall goal of these experiments is to define the characteristics of velocity/motion channels, and determine their relationship to flicker channels. The rationale for these experiments follows:

Discrimination studies allow a crude form of channel counting. If one eliminates artifactual discriminations, differences in discrimination performance may reflect the distribution of underlying channels. Discrimination minima identify where response functions of these channels are changing most rapidly with respect to one another, which in a simple case will be where channel sensitivity functions cross. In a small multi-channel system, counting the number of minima (n) indicates the presence of $n+1$ channels. In a system with a great many channels, the overall discrimination function will be smooth, and the narrow separation of channels will make them difficult to resolve using this (or any) technique. We have conducted velocity and flicker discrimination studies in order to conduct a direct comparison of these behaviors.

Matching the appearance of motion at low contrast is a direct test of channel count. In a multichannel system composed of a small number of channels, well separated in peak sensitivity, a very low contrast stimulus will stimulate only the channel with the most closely matching peak frequency. Since only that single channel contributes to the sensation of velocity, such a system should yield only that number of velocity sensations at low contrast. Stimuli which are at off-peak velocities will be seen inaccurately, with their apparent velocities shifted to those of the channel peak-frequencies. Correspondingly, a system with a great many channels would yield accurate (or at least veridical) sensations of velocity over a wide range of velocities, as no velocity would be greatly off-peak.

Several past studies have investigated velocity discrimination in an attempt to define the visual mechanisms which underly motion perception. Stimuli used have generally been sharp edged bars (McKee, 1984; Orban, 1984; 1985) held at a fixed contrast. Pantle (1978) and Thompson (1984) used sinusoidal gratings. Thompson's stimulus contrasts were a fixed multiplicative factor of detection threshold. McKee (1981, 1984)

Velocity discrimination VI-2

found discrimination to vary smoothly with velocity, with a pronounced low velocity falloff in sensitivity. Orban, using a different apparatus, was able to demonstrate a high velocity decline as well (at >64 d/s), beyond the range which was tested by McKee. Velocity discrimination is dependent on contrast (Orban, 1984). With the exception of Thompson (1984), velocity discrimination experiments have therefore confounded the velocity discrimination function with the variation of contrast sensitivity with velocity.

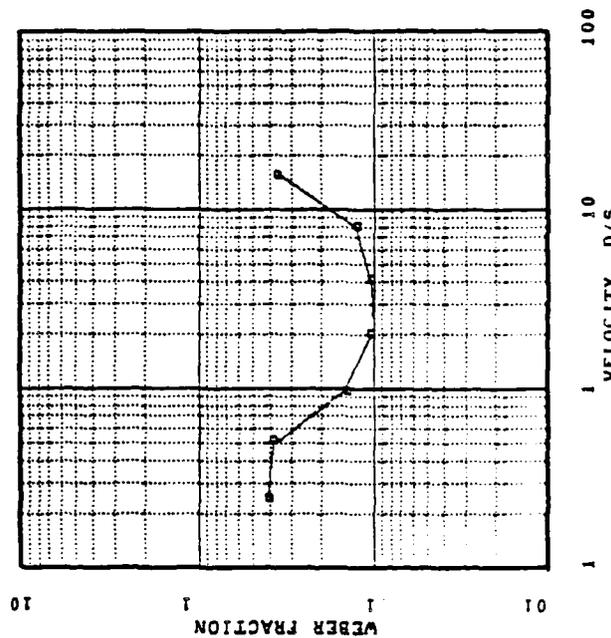
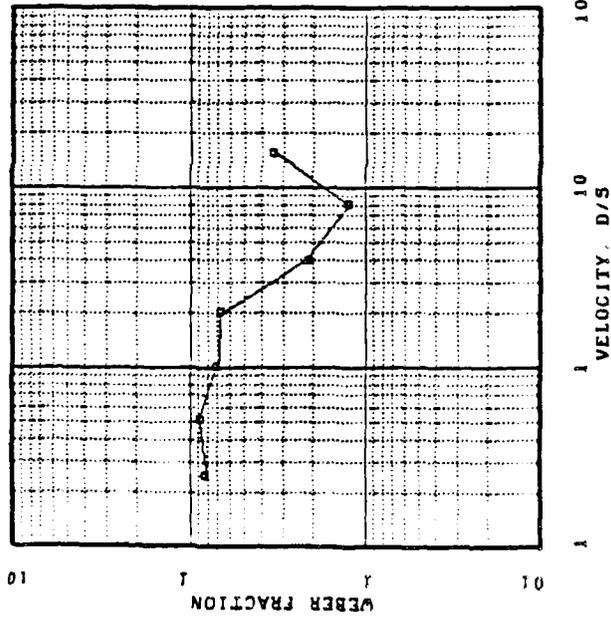
The present experiment demonstrates that this U-shaped velocity sensitivity profile can be seen over much smaller ranges of velocities and has a distinct minimum when the contrast of the stimuli is maintained as a fixed low multiple of contrast threshold. Mandler (1984) used a similarly controlled temporal frequency discrimination procedure to locate temporal-frequency tuned channels.

The first step in each experiment was the determination of the velocity contrast-sensitivity function. Thresholds were determined using a sequential 2AFC staircase procedure. The subjects task was to indicate which interval contained the stimulus. Threshold was taken to be the geometric mean of the reversals. Velocity discrimination was then measured using a staircase procedure. The contrasts of all stimuli in the discrimination experiments were presented at fixed multiples of the previously determined thresholds, approximated by an interpolation procedure incorporated into the staircase. The reversals were converted to Weber fractions.

Experiment 1 - Velocity Discrimination - 1 c/d gratings

The overall form of the curves is u-shaped, with the Weber fractions showing a minimum between 4 and 8 d/s. Velocities below 1 d/s form a plateau of poorest discrimination, which improves with increasing contrast multiple. The curves smooth out at higher contrasts. These data do not show a pattern of small peaks and valleys that would be associated with 3 or more channels tuned to peak velocities within the range tested (.25 \rightarrow 16 d/s). The simple u-shape suggests either 2 channels, most likely bracketing the range of peak sensitivity, or a sufficiently large number of channels to be unresolvable given the spacing of test velocities.

These data and data of the previous experimenters are quite similar in shape, but widely discrepant in sensitivity, with our data virtually at the mean. The shape of the curves taken at 4 x threshold closely resemble the smooth curves of Thompson(1983), which were collected with a similar procedure using contrasts of 4.5 and 12.6x threshold. However, Thompson's data show an order of magnitude less sensitivity than the present data, with Weber fractions falling in the range of 1.3 to 2.8, while data from the present experiment fall between .1 and 1. Thompson's data show best discrimination at 4 Hz., over a spatial frequency range from



Typical grating velocity discrimination functions. Optimal velocity is more sharply defined at lower multiples of contrast threshold. The principal effect of higher contrasts is to improve discrimination at low velocities.

Velocity discrimination VI-3

1-8c/d. Pantle (1978), using an analog driven oscilloscope display, was able to test up to 32 d/s, using .6, 4.8 and 10c/d. His DL functions were bimodal, with minima at 5 and 32 Hz. These minima (0.015) are the lowest in the literature. Pantle used a considerably different stimulus presentation from the other studies, using .25 sec. linear on- and off- ramping with a 2 sec full contrast peak, and roughly 4 deg. square fields with a yellow-green phosphor. Thompson used a physical configuration roughly comparable to the present study, but luminance is not given.

The form of these grating velocity discrimination data are all roughly comparable, showing minimal velocity difference thresholds between 4 and 8 Hz, with Pantle's data showing a secondary minimum above 16 hz. Data from both of the previous studies scaled with temporal frequency. This immediately suggests that the velocity discrimination makes use of temporal frequency. A much different interpretation is that the size of a velocity RF involved in such discriminations scales with velocity, yielding similar temporal frequency sensitivity profiles.

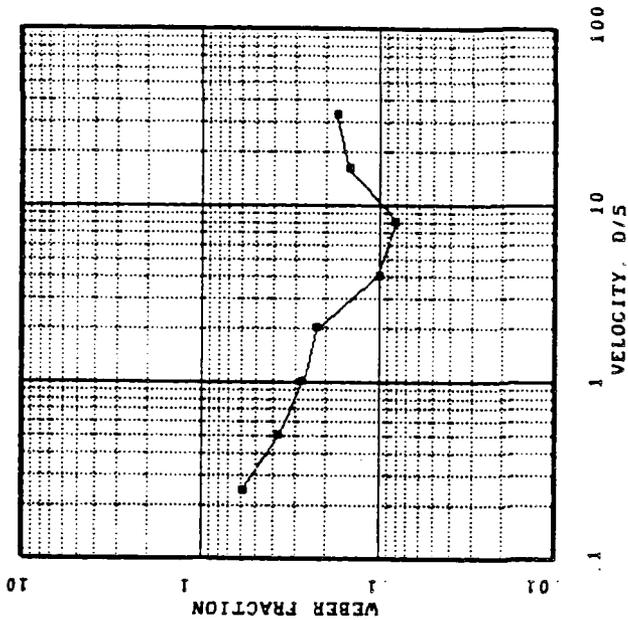
Because these experiments used periodic stimuli, it is difficult to determine whether the channels underlying the discrimination were flicker or velocity sensitive. Additional experiments used non-periodic stimuli to lessen the chances of stimulating flicker sensitive channels.

Experiment 2 - Velocity Discrimination using Gaussian Bars: Central and 7 deg. Peripheral

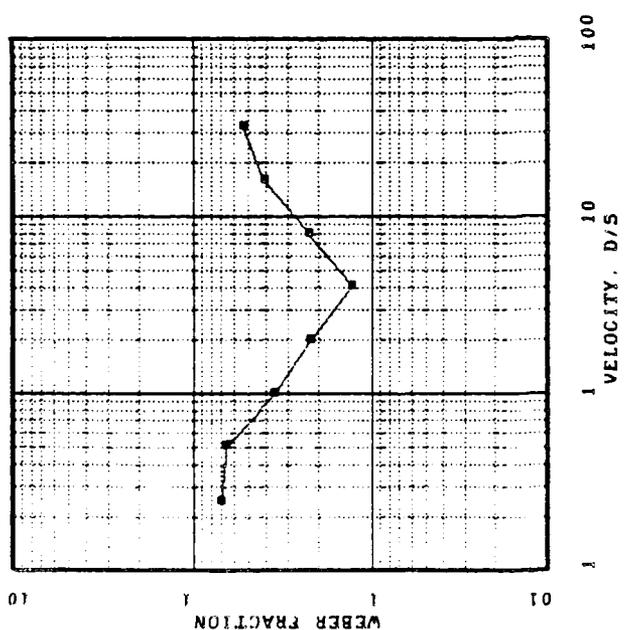
The psychophysical procedure was identical to that of the previous experiment, but all stimuli were gaussian bars with 1 standard deviation equal to .25 degree. These stimuli closely resemble a single positive half-cycle of a 1 c/d grating. The contrast thresholds of these stimuli did not fall off as rapidly as did those of the gratings, allowing velocity discrimination to be tested up to 32 d/s. Data were taken at 2.25 and 4 x threshold, and at a fixed contrast of 80%.

These discrimination functions are very similar to those using grating stimuli. The minima are sharper at 4 x threshold, and the changes between 2.25 and 4 x threshold are considerably greater for the gaussian bars, with lower contrast conditions much more difficult to test than for the gratings. These results suggest that the gratings stimulate spatially parallel mechanisms, allowing summation to improve performance at lower contrasts. Further improvement at fixed high contrast occurs primarily at extreme velocities, and most likely results from the changing apparent contrast of the stimulus being available as an (artificial) cue.

At 7 degrees eccentricity, both subjects showed an increased



RW - GAUSSIAN BAR - 7 DEG ECC
4 X THRESHOLD



RW - GAUSSIAN BAR
4 X THRESHOLD

Typical velocity discriminations, central and peripheral, using gaussian bar stimuli. Note that optimal velocity shifts higher with eccentricity. The overall level of performance is similar at both eccentricities, because all stimuli are equally visible.

Velocity discrimination VI-4

optimal velocity of 8 d/s, and a low velocity plateau is prominent. Overall discriminability was very similar to foveal. The curves flatten at uniform 80% contrast, with the largest changes occurring at extreme high and low velocities, and little change at the optimal velocity.

The shift of optimal discriminability to higher velocities in the periphery is consistent both with data from previous experimenters and known differences between central and peripheral vision. Data from the periphery collected by Orban and McKee show a displacement of the Weber fractions upward and a translation of a range of peak discrimination to higher velocities. That performance decrease was eliminated in the present study by maintaining stimuli at equal multiples of threshold. Given this control, 7 deg. peripheral retina shows performance comparable to fovea. The shift in optimal velocity is clearly visible in the present experiment because our more careful contrast control allows determination of an optimal velocity, rather than the broad range of high discriminability shown by the previous studies.

The next experiment examines changes in discriminability over a wider range of eccentricities, at optimal (foveal) velocity.

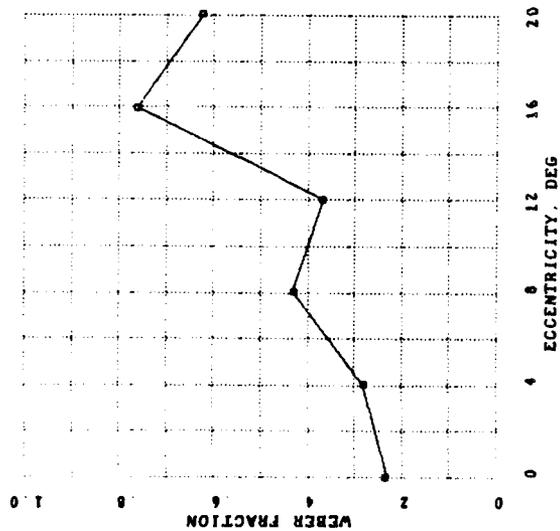
Experiment 3 - Velocity discrimination over eccentricity - Gaussian Bars - 4 d/sc

These experiments were conducted monocularly, such that the 2 degree wide test field never fell in the subjects blind spot. Eccentricities ranged from 0 to 20 degrees. As in all these experiments, contrasts were maintained at fixed multiples of threshold. Weber fractions rose linearly with eccentricity. The slope of this function decreases with increasing contrast, and was flat at fixed, 80% contrast. These data were collected at the optimal foveal velocity. Results would presumably be quite different for higher velocities, which in the previous experiment showed an improvement in discriminability 7 deg. into the periphery. Velocities below 4 d/s, which showed virtually no change with eccentricity, would have slopes of 0. Unlike acuity, the changes in velocity discriminability with eccentricity are complex.

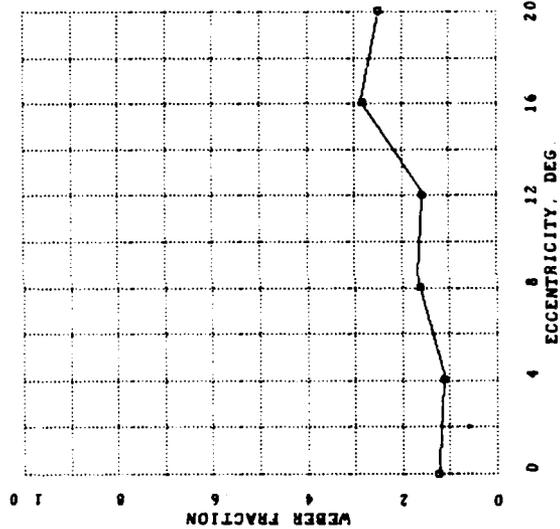
It is also interesting to note that each of the lower contrast curves showed a small improvement in discriminability at 12 degrees eccentricity. This is approximately the location corresponding to that of the blind spot in the untested eye. It is therefore possible that this improved performance compensates for the absence of information from the other eye.

Experiment 4 - Velocity discrimination with stimuli scaled for cortical magnification.

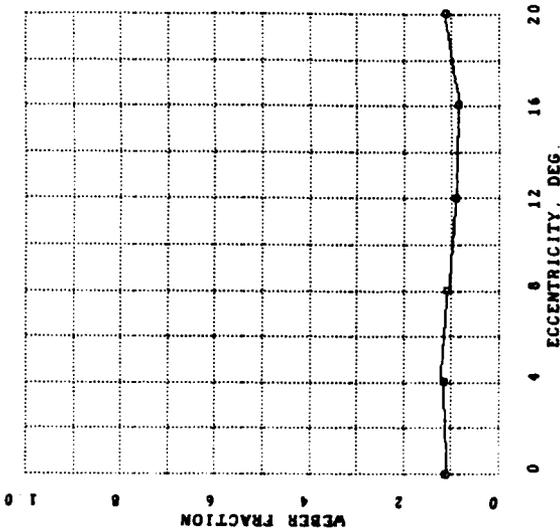
McKee and Nakayama (1985) and Orban have found that scaling for cortical magnification (using the equivalent Minimal Angle of



KR - GAUSSIAN BAR - 4 D/5 STANDARD
VELOCITY DISCRIMINATION OVER ECCENTRICITY
2 X THRESHOLD



KR - GAUSSIAN BAR - 4 D/5 STANDARD
VELOCITY DISCRIMINATION OVER ECCENTRICITY
4 X THRESHOLD



KR - GAUSSIAN BAR - 4 D/5 STANDARD
VELOCITY DISCRIMINATION OVER ECCENTRICITY
80% MODULATION

Effect of increasing contrast on velocity discrimination, at various eccentricities. These data are all taken using a velocity of 4 d/s, the optimal foveal velocity. Significant changes are only seen at low multiples of threshold. The pattern of change would be different at other velocities. The slight, but reliable dip at 12 deg. eccentricity may demonstrate compensation for the blind spot of the contralateral eye.

Velocity discrimination VI-5

Resolution scaling) can decrease some of the disparity between discrimination functions from foveal and peripheral retina. McKee scaled the data, Orban the stimuli. We attempted the latter, using our more elaborate equivalent contrast controls and equating the cortical velocity to that of a stimulus at 4 d/s at 12 degrees eccentricity.

The existence of perfect scaling would have resulted in linear discrimination functions over the conditions tested. One subject was close to linearity, the other not. We do not believe the scaling to be convincing, especially given the difficulty of the task reported at the foveal condition by both subjects. Were the paradigm accurately compensating for intrinsic cortical scaling, the tasks would be expected to be of equal difficulty at all eccentricities. Furthermore, there is considerable disagreement in the literature over the scaling factor. These results are similar to those of McKee(1985) and Orban(1985), although our conclusions differ. Their experiments did not equate all stimuli for visibility, and the effect of the MAR scaling was most likely to render the stimuli more similarly visible across eccentricity. Our data show that differences between foveal and peripheral velocity discrimination are less profound when stimuli are of equal apparent contrast. We do not wish to totally discount the importance of some form of scaling, however. It is clear that at extreme eccentricities the sparsity of receptors must limit discrimination to some extent, but we suspect that that limitation is less severe than previous experimenters' data indicate.

Experiment 5 - Flicker discrimination

For some years there has been controversy concerning the independence of velocity and flicker processing. Both are forms of temporal modulation, are of necessity confounded in any experimental design. Most any mechanism designed to respond to one will also respond to the other. Pantle(1978) and Thompson have found that optimal velocity scales with grating spatial frequency such that the optimal velocity always possesses a temporal frequency of about 4 Hz. (It is not known whether aperiodic stimuli varied in spatial extent would also display this relationship. Moving gratings will stimulate flicker detectors, but it is not obvious how a flicker detector would react to, say, a single bar.) Our previous experiments have shown the primary difference between grating velocity and bar velocity discrimination functions to be the sharper tuning of the bar discrimination data, suggesting a detector optimized for velocity rather than flicker. We therefore wished to compare flicker discrimination under the same conditions.

Experiments were conducted as previously, save that the central 2 degree field was flickered in counterphase, with starting phase randomized at low flicker rates. The range tested was from .25 to 16 Hz., but the 1 second gaussian presentation makes the actual temporal parameters unreliable at low flicker rates, particularly below 1 Hz., where the temporal waveform will

Velocity discrimination VI-6

be undersampled.

The results show the flicker discriminations to be sharply tuned to an optimal frequency of 4 Hz., with the overall form of the discrimination functions above 2 Hz. closely resembling the velocity discrimination functions. No secondary minima were observed. The latter are clearly seen in data from Mandler(1983), who used a procedure similar to our own, but at much higher luminance and with a much longer (5 sec) stimulus presentation. Mandler's data were collected under conditions which are very much different from those typical for velocity investigations. The latter use very short stimulus presentations to minimize the effects of eye movements, typically .2 sec. Our 1 sec. presentations are a compromise between the two paradigms. The similarity between our flicker and velocity data suggest that flicker and velocity discrimination may be tapping closely related or identical mechanisms. We are currently measuring flicker discrimination using a 5 second test presentations to see if the longer temporal presentation will yield the multiple discrimination minima found by Mandler. It is also possible that our data differ from Mandler's because of differences in display luminance and spectral composition, but with our current display hardware we cannot test this possibility.

Experiment 6 - Velocity identification

Our simple u-shaped velocity discrimination functions have two possible interpretations:

1. There exist a very small number of velocity channels, one below and one or two above 4 d/s.
2. There exist many velocity channels over the range of velocities tested, such that the individual channels cannot be resolved by the velocity discrimination procedure.

These two cases generate different predictions in a velocity identification experiment. In this experiment a moving bar is presented at a contrast close to threshold. Its' apparent velocity is determined by matching to it the velocity of a high contrast bar. If there exist a very small number of velocity channels, the low contrast stimulus will only stimulate a single velocity channel, which will provide the velocity percept. There will thus be a limited number of perceived velocities, corresponding to the number of velocity channels, irrespective of actual stimulus velocity. If, on the other hand, there exist a great many velocity channels, the perception of velocity would be veridical down to threshold.

We tested this hypothesis using three levels of apparant contrast, matched in apparant contrast to 2, 1.75 and 1.5 x the threshold of a gaussian bar moving at 4 d/s. Stimuli moving at 0.25, 1, 4 and 16 d/s were matched in contrast to these levels. Moving bars at the resulting contrasts were then used as the standard to which a high contrast bar was matched in apparant velocity. The matches were in fact veridical, supporting the

Velocity discrimination VI-7

many-channel hypothesis.

In conclusion, these experiments suggest that velocity discrimination is mediated by a large number of channels, which may be distinct from the small number of channels found for flicker discrimination. The relationship between flicker and velocity discrimination data remains unclear because of the very different conditions used to investigate motion and flicker.

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