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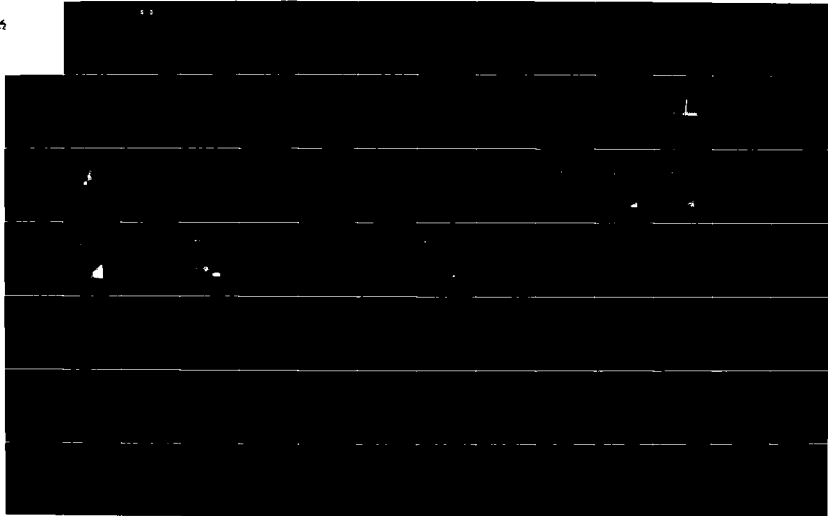
INTERACTIONS BETWEEN BRIEF FLASHED LINES AT THRESHOLD

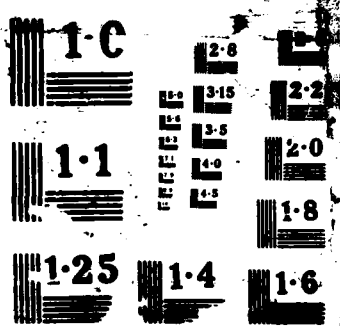
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Our results are concentrated in seven basic areas: 1) We find that masking is subject to considerable learning effects. Weber's Law is only observed--when proper controls are used--in the relatively uninteresting case where it is inherent in the stimulus, and is unaffected by visual physiology. 2) There is a region of space/time separations wherein two flashed lines will show lateral facilitation, rather than inhibition, suggesting the action of a motion-detector. 3) Substantial modelling of line interactions confirmed our conclusion that this facilitation was a nonlinear effect, and not predictable from current probability-summation models. 4) Spatial summation and 2-line acuity change very differently with retinal eccentricity; it may be that one taps primarily receptor size while the other taps receptor separation. 5) It is possible to observe visual aliasing in the parafovea without the use of interference fringes. This aliasing appears to be neural, rather than receptor. 6) Flashed presentations produce a large transient change in the area of spatial summation and in the amount of lateral inhibition. The mechanism of this is (over)

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22a. NAME OF RESPONSIBLE INDIVIDUAL

Dr. John Tangney

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presently unclear. 7) When measured close to detection threshold, velocity discrimination is a broad U-shaped function of velocity. This is consistent with discrimination by a continuum of overlapping tuned mechanisms, and inconsistent with a small number of discrete mechanisms.

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**INTERACTIONS BETWEEN BRIEF
FLASHED LINES AT THRESHOLD**

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**Submitted by: Robert A. Smith PhD
Vision Research Laboratory
University of New Hampshire
Durham, NH 03824**

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Bolling AFB, DC 20332**

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I. Introduction and Summary

In this project, what was originally an investigation of masking between grating stimuli has blossomed into a study of a number of related areas. Early in the work, we considered masking between adjacent parallel lines, which effectively became a study of the spatio-temporal organization of linear receptive elements in the visual system. These elements were found to have motion-detector-like properties, which initiated studies of motion discrimination, aimed at possibly determining if motion perception is subserved by a small number of discrete detectors. We observed two other interesting properties of line interactions: 1) spatial summation dynamically changes after transient stimulation, and 2) summation and acuity do not covary with changes in eccentricity. This latter observation led us to predict, and later observe, aliasing with natural-light stimuli.

Prior to our work, spatial frequency masking was typically (if implicitly) regarded as a peripheral process, treatable with quasi-linear models of the sort familiar in engineering. A modest literature had grown up surrounding the issue of what conditions produced Weber's law behavior as opposed to power-law behavior (exponent about 0.6). We were able to show that the visual system itself displays power-law behavior, and that when Weber's law is observed the subject is being constrained by his unfamiliarity with the stimulus, and not by inherent limitations in his detection apparatus. This situation is a case of Birdsall's Theorem, as described by Lasley and Cohn.

We generalized the common paradigm of measuring lateral interactions by observing variations in the threshold for a pair or triplet of parallel lines as a function of line separation. We used briefly-flashed lines which were separated in both time and space, and found that the most prominent interaction was a propagating lateral facilitation, suggestive of a motion detector. These data show a facilitatory peak at a separation of about 100 msec and 0.1 degrees, suggesting a velocity tuning of about one degree per second.

Despite an enormous amount of work, we found it difficult to convince the vision community of the reality of our detector, or indeed, that our data warranted consideration. At the request of referees, we undertook a major effort at mathematical modelling, to try to show that our results are not predicted by any of the types of probability summation models currently in the literature. This is a somewhat ill-formed question, given the wide variety of models possible, and we were pleasantly surprised that the results were reasonably definitive.

It is often implicitly assumed that a variety of visual functions -- in particular, spatial summation and acuity -- are all more or less closely related to the size of receptive fields somewhere in the visual system. We were somewhat surprised,

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then, to observe that over an eccentricity range of 0 to 7 degrees, spatial summation changes very little, while acuity decreases about seven-fold. From these data we postulated that summation reflects the size of summation areas, probably receptive field centres, while acuity is limited by spatial sampling, that is, by the distance between the summation areas. The fact that acuity falls so much faster than summation suggests that undersampling and aliasing might readily be observed in the parafovea.

To test this prediction, we used a conventional detection/orientation-discrimination paradigm with 7 degree parafoveal gratings, and found that orientation was discriminable up to about 10 c/deg, while the gratings were detectable to about 20 c/deg. Between those frequencies the percept is that of low-frequency visual noise, as would be expected if aliasing were occurring. A serious concern with these results for almost two years was the fact the aliasing began at a frequency which was barely half what would be expected from the geometry of the cone lattice. This led us to offer the widely ridiculed hypothesis that the aliasing was occurring at some neural level proximal to the receptors. This hypothesis was vindicated by Schein (invited address, Optical Society of America, Oct. 1987) who demonstrated that ganglion-cell density begins falling off at much smaller eccentricities than had previously been believed, in good agreement with our results.

Our most enigmatic investigation is the observation of dynamic changes in the areas of summation and inhibition. After a flash of light -- or better still, a flashed grating -- the area of spatial summation shrinks as much as threefold, while lateral inhibition becomes much more pronounced; this effect has a time course of about 100 msec. This could be due to genuine changes in the receptive fields of visual mechanisms, or it could result from the differential masking of sustained and transient channels by the flash. At this point, we have no clear evidence to favor any one explanation over another.

Because our line interaction studies showed a putative motion detector with a velocity of about one degree per second, we examined motion discrimination to see if there was evidence for a mechanism at about this velocity. The logic of this experiment was similar to studies by Mandler with flicker; if there are only a small number of discrete mechanisms, then discrimination should be most acute at those in-between frequencies, where the sensitivities of mechanisms cross over, and worst near the peak sensitivities of individual mechanisms. This was a long study, at least a year being consumed in finding and eliminating all of the extraneous cues (i.e. things other than velocity itself) which have confounded many previous studies of velocity discrimination. Our final result was that discrimination is a broad U-shaped function of velocity, with no indications of discrete sub-mechanisms.

II. The Effect of Criterion on Spatial Masking

INTRODUCTION

In recent years spatial frequency masking has received increasing attention. The basic paradigm is quite simple: a subject sets thresholds for a test grating in the presence of a super-imposed mask grating, typically of a different frequency. Despite masking's apparent simplicity, there have been significant qualitative discrepancies between the results of different investigators. In roughly half the literature it is reported that spatial masking obeys Weber's Law; that is, test threshold rises in direct proportion to mask contrast. In other literature, it is reported that test threshold rises as some lesser power (typically between 0.5 and 1.0) of mask contrast. On the basis of a survey of this literature, we offered the beginnings of an explanation by hypothesizing that a change in threshold criterion may produce functionally different behavior, and by showing that familiarity with a random mask pattern can produce such a criterion change. In this paper we present evidence for the existence of several specific threshold criteria and show that some of these criteria represent detection tasks, while others are more like recognition.

METHODS

Stimuli were generated by a Xitan micro-computer and presented by conventional means on a HP1332A display with P4 phosphor. The experiments were entirely computer-controlled, with the subject signaling responses to the computer via a small hand-held keyboard. The screen was viewed from 75 centimeters, and subtended a visual angle of 10 degrees horizontally by 8 degrees vertically. The screen had a luminance of 55 cd/m²; its surroundings were at least 10x darker. Subjects viewed binocularly with free fixation; head position was maintained by a headrest.

The test stimulus was always a 4 c/d vertical sinusoid. Band limited random noise stimuli were generated by adding together 8 sinusoids of equal amplitude and randomly chosen phase and with frequencies spaced at equal logarithmic intervals across the range of 2-8 cycles/degree. By changing the phases of the constituent gratings, we could generate a variety of noise patterns with identical power spectra -- apart from edge effects -- but with very different appearance.

Three different psychophysical techniques were used in this study: two-alternative forced-choice (2AFC), three-alternative forced-choice (3AFC), and method-of-adjustment (MOA). In the forced-choice experiments the field was always bordered by 1.5 degree mean-luminance edges. The remainder of the field (the

central 7 degrees) was divided into two or three equal test bands separated by narrow black lines. In a typical forced-choice trial, the same mask stimulus would appear in all the test bands; in addition, the test stimulus was added to a single test band. The response indicated which band contained the test stimulus. The observer was given an arbitrary time to respond, in practice responses were always made within 5 seconds. The forced-choice staircase algorithm proceeded as follows. Before the start of each staircase, the subject set the test modulation close to threshold. Thereafter, on each correct trial the test contrast decreased one step (5%). Following an error, the contrast level at which the error occurred was recorded and test contrast was increased by 4 steps (2 steps in 3AFC). The subjects received feedback on error trials. After four errors threshold was taken to be the average of the four contrasts at which errors occurred. We initially used a weighted average for this purpose, but later studies showed that this offers no advantage over a simple average, and this was used thereafter.

In MOA studies, the stimulus filled the entire screen. The subject could increase or decrease the contrast of the test stimulus by one step (6%) by pressing one of two buttons. Trials were continuous, as the change in contrast occurred with no perceptible break. When the subject achieved a satisfactory setting, pressing a third button caused the setting to be recorded and randomly changed the test contrast. The computer averaged 7 such settings to produce a single threshold estimate, and then proceeded to the next set of experimental conditions.

The data presented in this paper are typically test thresholds for a variety of mask contrasts. The various mask contrasts were always presented in order, starting with the lowest contrast, to avoid the possibility that prolonged exposure to the higher mask contrasts might raise thresholds for lower mask contrasts. We have previously shown that prolonged adaptation to a given mask contrast has no effect on masking by that same contrast.

Five subjects were used for different parts of this research, some of which was done in New Hampshire and some in Michigan. The subjects RS, DS, and LA are experienced psychophysicists; MJ and SM are professional subjects who were naive to these particular experiments.

RATIONALE

Our experiment is conceptualized in Figure 1. Here we see the outputs of a variety of spatial channels of different center frequency, viewing a pattern of visual noise which may have a test grating added to it. On the figure are indicated the mean output of all the channels (I_{mean}), a measure (σ) of the variation of these outputs, and the relative output of the channel most sensitive to the test grating (ΔI). The detectability of a signal in this pattern of channel responses reduces to the statistical question of whether ΔI is

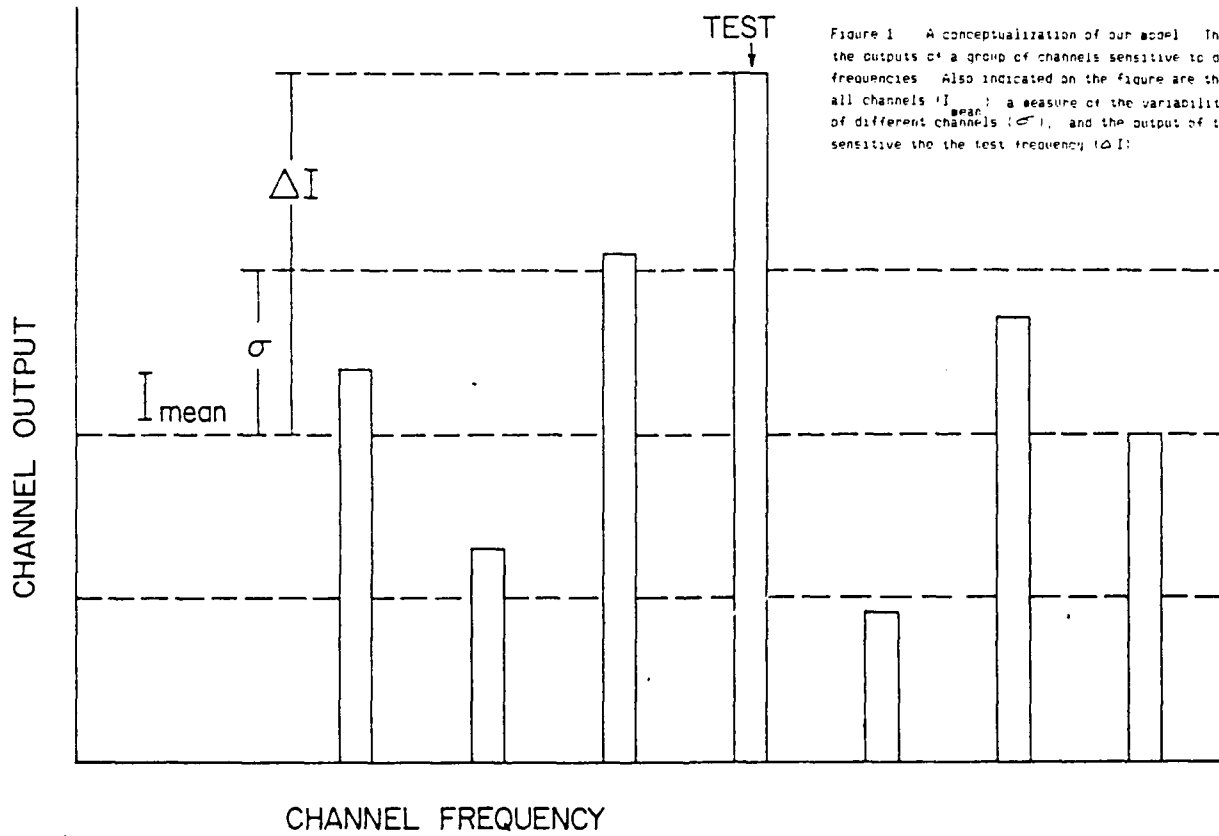


Figure 1 A conceptualization of our model. The bars represent the outputs of a group of channels sensitive to different spatial frequencies. Also indicated on the figure are the mean output of all channels (I_{mean}); a measure of the variability in the outputs of different channels (σ); and the output of the channel most sensitive to the test frequency (ΔI).

sufficiently large that it is unlikely to have occurred by chance in the random mask. For an ideal observer, ΔI is compared to the width of the distribution of channel outputs () by means of a critical ratio ($\Delta I/\sigma$), and if this ratio exceeds some threshold, then detection occurs. This is analogous to the familiar t-test in statistics. Assuming a linear channel response (discussed below), both I_{mean} and σ will be proportional to mask contrast. Substituting for σ , the above critical ratio is seen to be proportional to $\Delta I/I_{\text{mean}}$, which is Weber's Law. We conclude that if detection is limited by external noise, then Weber's Law must hold with the Weber fraction being closely related to the signal/noise ratio.

If the output of the channel is a one-to-one, monotonic, non-linear transform of its input, a surprising result occurs. Such a non-linearity is completely transparent and has no effect upon threshold or upon Weber's Law. A proof of this result (known as Birdsall's Theorem) may be found in Lasley and Cohn (1981). It essentially follows from the fact that determining whether a threshold has been exceeded or not is an ordinal operation on the possible output states of a channel, and the proposed nonlinearity preserves the ordering of these states.

In this paper, we shall develop the following hypothesis. If a test pattern is masked by noise, then Birdsall's Theorem applies and detection must obey Weber's Law. If the mask is not noise, then other, more sensitive detection strategies are available. These strategies are typically observed to obey a power law, though we cannot yet explain this particular functional form. It is essential to define precisely the class of mask stimuli which is considered to be noise, and we propose that this class must have a subjective definition. Whatever its configuration, a stimulus is noise if the subject is unable to predict its appearance and detect deviations therefrom. Commonly this predictive ability depends on previous experience. Nachmias and Rogowitz (1983) present a similar idea.

RESULTS

Figure 2 (taken from our 1983 paper) shows the effect of learning on spatial frequency detection in the presence of a random mask pattern. Consider the column labeled "Pattern #1". All of these data were taken with the same mask pattern, so that the observer gained familiarity with the mask as the trials progressed. The upper-most curve (done first) shows test threshold for a range of mask contrasts. It is essentially linear and the slope is very nearly 1.0 (i.e. Weber's Law is observed). We now selected a convenient pair of mask contrasts and measured thresholds repeatedly, observing the effect of practice. The data are presented in temporal order, descending. These have not been displaced for clarity; thresholds do indeed decrease monotonically with practice. Of more interest, however, is the fact that not only do thresholds decrease but the slope of the masking function also decreases from 1.0 (Weber's Law) to about 0.65 in the lower curves. This shows quite clearly that

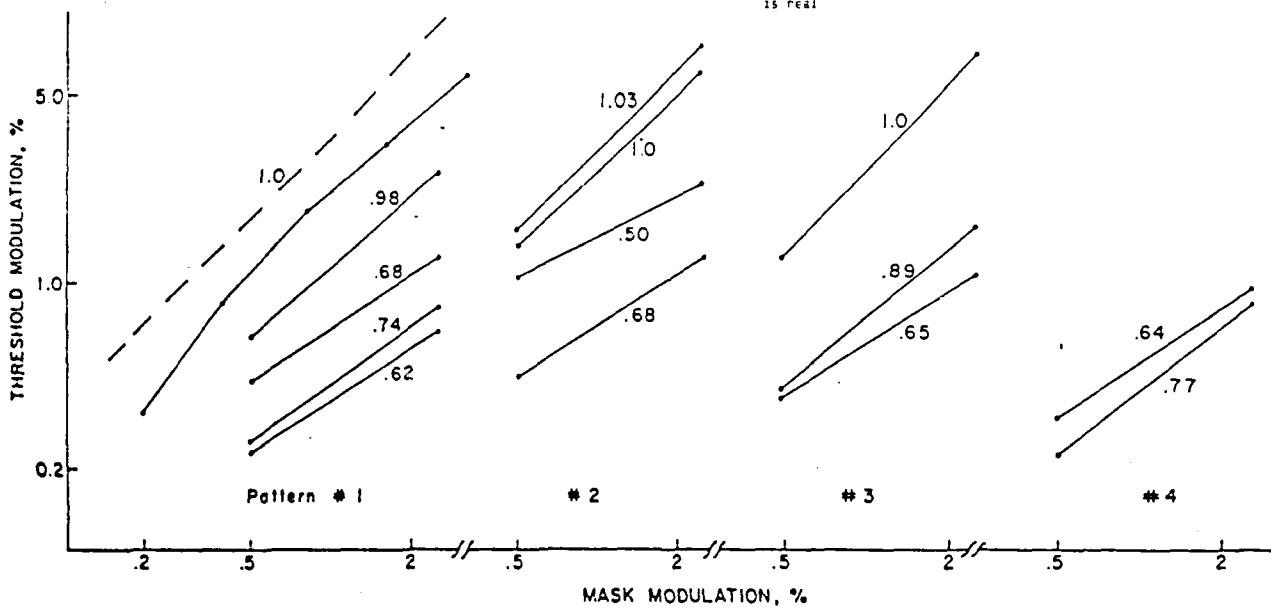


Figure 2 Subject P5 learning to detect the presence of a four cycle/degree test grating with four different random mask patterns. Successive runs with a particular mask pattern are displayed vertically from top to bottom. These data have NOT been displaced for clarity, the change in threshold with practice is real.

the observation of Weber's Law or power law behavior does not depend upon experimental conditions; the same experiment yields either law depending upon practice. It will be seen from the remainder of Fig. 2 that the practice effect is specific to a given noise pattern; when a new noise pattern is introduced (e.g. in the second column of data) the slope of the masking function again rises to 1.0, falling off with further practice.

The remainder of Figure 2 presents a problem. With repeated practice RS' learning becomes faster until in the right-most column he displays power law behavior on the first trial. Is RS actually doing power-law discrimination on new patterns without learning, as these data suggest? If so, it would disprove our hypothesis. In fact, we can show that RS continues to require a period of learning even though that period has become substantially shorter than the duration of a single staircase. Five new noise patterns were presented to RS and thresholds measured in their presence, as in Figure 2. The raw threshold data were now averaged across staircases, specifically we computed the average of the five first errors, the five second errors, etc. These averages are a measure of RS' threshold at different stages of the staircase. It is clear from Fig. 3 that this threshold drops systematically, by more than a factor of 2, as the staircase proceeds. Moreover, there appears to be a decrease in slope with practice as in Fig. 1. Thus RS' learning set does not violate our hypothesis. None of our other subjects has developed such a learning set.

Changing Mask Patterns

If learning the specific configuration of the mask causes the change from Weber's Law to power law behavior, then we might prevent this change by using a different mask pattern on every trial. Learning which involves some other aspect of the task, however, should persist in such an experiment since these other aspects are unchanged. Results from this experiment are seen in Figure 4, showing the slope of the masking function versus number of trials. For comparison, we include data from experiments with an unchanging mask pattern (as in Fig. 2). The results are clear. With an unchanging mask, the slope drops from 1 to about 0.65 in a reasonable number of trials, though this number of trials differs between subjects. For the changing mask condition, however, there is no change in slope. We believe that Weber's Law always holds with changing masks and two-alternative forced-choice. This shows that if the mask is truly noise (i.e. unpredictable), then Birdsall's Theorem applies and Weber's Law is observed.

Three-Alternative Forced Choice

Whether or not a pattern is noise (in the sense of Birdsall's Theorem) depends not upon the regular or irregular appearance of the pattern, or upon the way it is generated, but upon whether the subject is able to predict its appearance and detect deviations caused by the presence of the test. Consider a simultaneous 3AFC discrimination involving two mask-alone and one

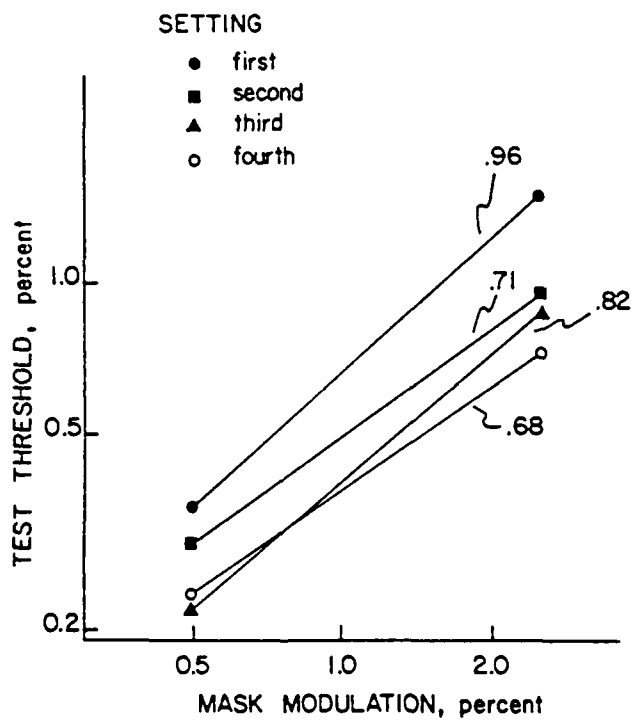


Figure 3 Learning during a single staircase by Subject PC
 This figure presents averages of the four settings in a single staircase averaged over five different staircases (See text)

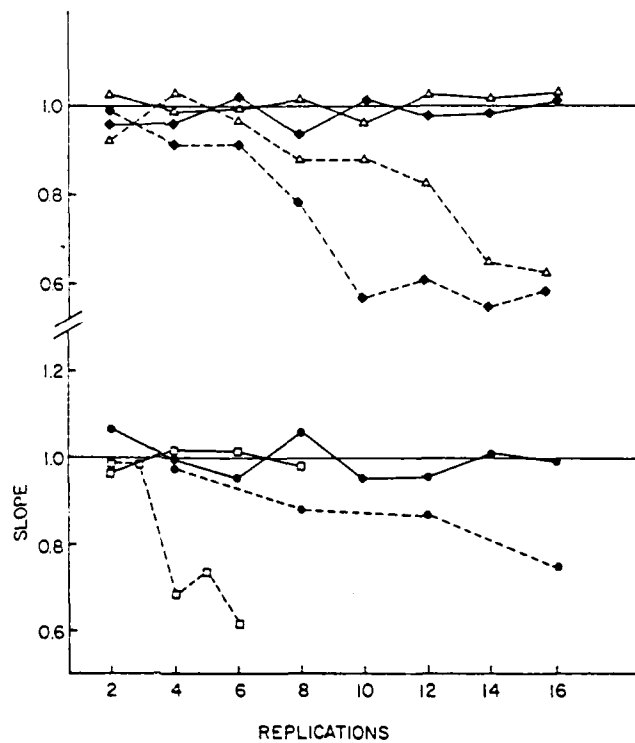


Figure 4. Slope of the 2AFC masking function with a continually changing mask (solid lines). The slope is seen to remain at 1.0 (Weber's Law) over many trials, while the slope with the same mask presented repeatedly (dotted lines) decreases to about 0.65. Subjects: RS (□); DS (●); LA (■); SM (▲)

mask-plus-test stimuli. If the added test stimulus produces any perceptible change in the pattern, then the subject should be able to select the one field which is different, even if the mask is totally unfamiliar. To test this, we repeated the experiment of Fig. 4 with simultaneous 3AFC (rather than 2AFC). As before, a different mask pattern was used on every trial. The results for two subjects are shown in Fig. 5, along with some limited data using 2AFC for comparison. Our prediction is confirmed; the 3AFC results are not only more sensitive, but they clearly obey a power law rather than Weber's Law. There is a decrease in threshold with practice, which suggests some generalized learning effects. Given the difficulty of the task this is not surprising, but it only strengthens our conclusions; neither a power law nor any significant learning are ever observed with changing masks and 2AFC. We attribute the fact that SM's 2AFC data are considerably noisier than the 3AFC data to the greater difficulty of the task, and to the inherently better convergence of a 3AFC staircase. Unfortunately, MJ (like most unpracticed subjects) was totally unable to do the 2AFC task.

Harmonically Pure Stimuli and the Method of Adjustment

The evidence presented so far supports our two-criterion hypothesis for masking by visual noise. Is it possible to apply a similar analysis to the commonly-used sinusoidal mask? Although a sinusoidal mask is mathematically predictable (as indeed were our pseudo-random noise masks) the subject may nonetheless require experience before he can detect small changes in its expected appearance. Fiorentini and Berardi (1979) found that subjects required 100-200 presentations to fully learn to discriminate subtle differences in 2-component complex sinusoids. Thus we might observe (perhaps to a reduced degree) the learning phenomenon of Fig. 2 with sinusoidal masks. Data from such an experiment are shown in Figure 6, which shows SM and LA (both naive to sinusoidal masks) learning to detect a 4 c/deg test in the presence of a 5 c/deg mask using 2AFC. The results are consistent with our hypothesis; discrimination improves with practice, and the slope decreases. Unfortunately this was a one-time observation; after taking these data, both subjects gave slopes of about 0.65 with any harmonically pure mask. We have not found another naive subject whose data are clean enough to interpret.

We can demonstrate the "learning" of a sinusoidal stimulus in another way. It seems probable that certain pairs of mask and test will provide a harder task than others. Specifically if mask and test are in the ratio of 1:2 then detection involves a subtle, second-harmonic distortion in the shape of each sinusoid, while for other ratios (e.g. 3:5) the various bars in the sinusoid will be of different shapes with the same shapes recurring at the period of the beat frequency. Even without knowing the detailed appearance of a single cycle, the subject can still recognize this repetitive beat pattern. Figure 7 shows 2AFC thresholds in the presence of a 2 c/deg mask for several

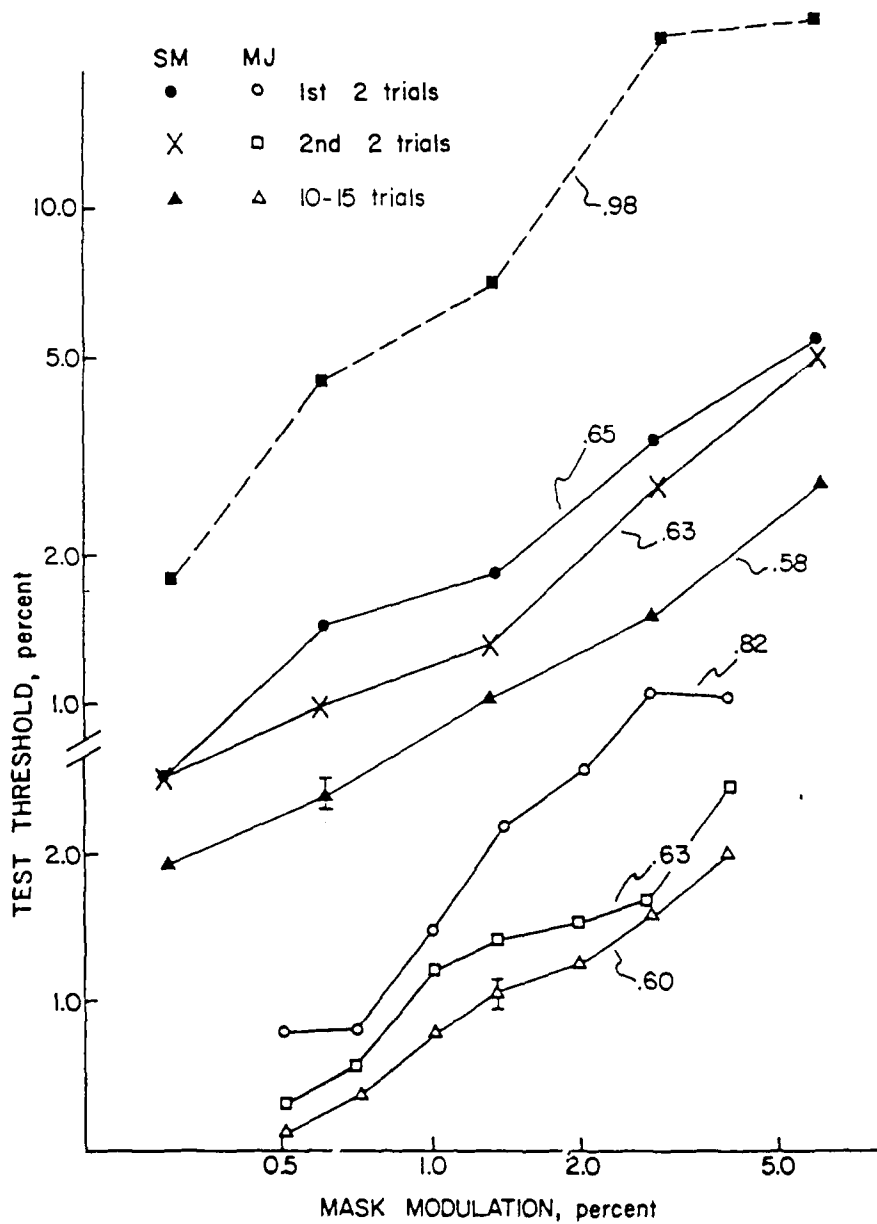


Figure 5. Masking functions for three-alternative forced-choice with continually changing bases. For comparison, the dotted line shows the results of a similar experiment using two-alternative forced-choice for Subject SM, like most naive subjects MJ was unable to do this task at all.

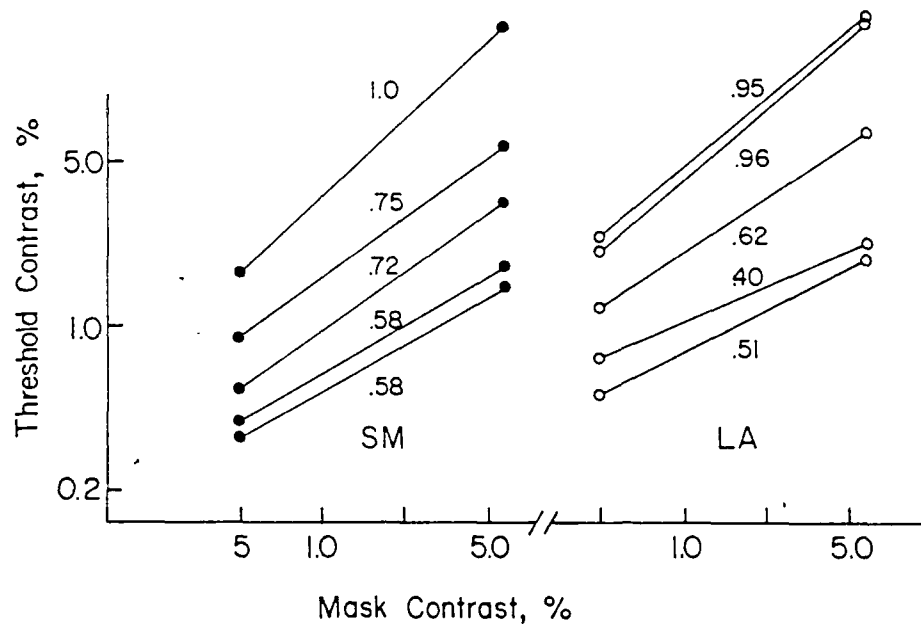


Figure 6. Learning by naive subjects with a sinusoidal mask. This is similar to Figure 2, except that the mask is 5 c/deg, rather than noise.

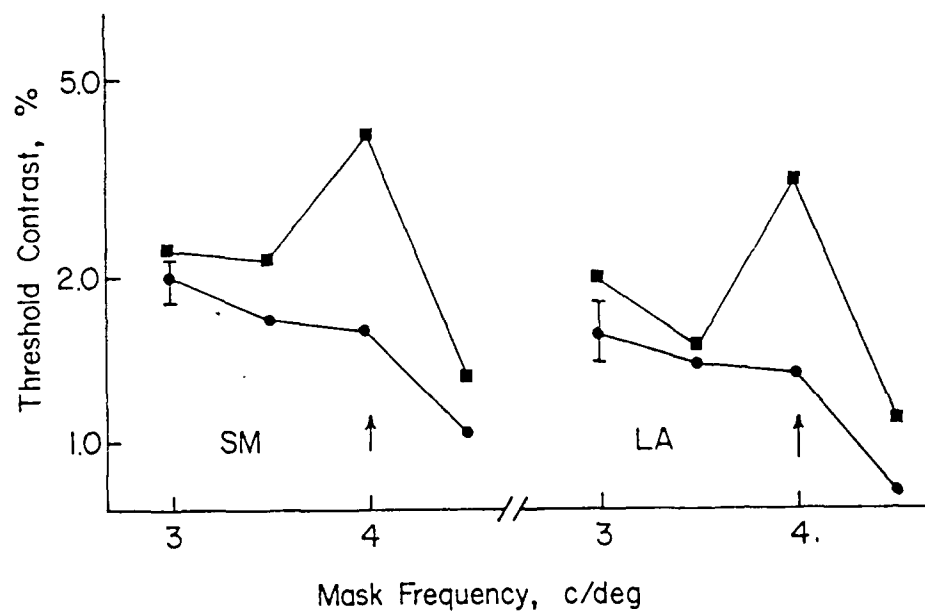


Figure 7. Learning to detect a 2nd-harmonic test. Mask is 2 c/deg, 0.06 contrast, test is 4 c/deg in cosine phase. The upper curves are averages of trials 1-3, the lower are averages of trials 7-9.

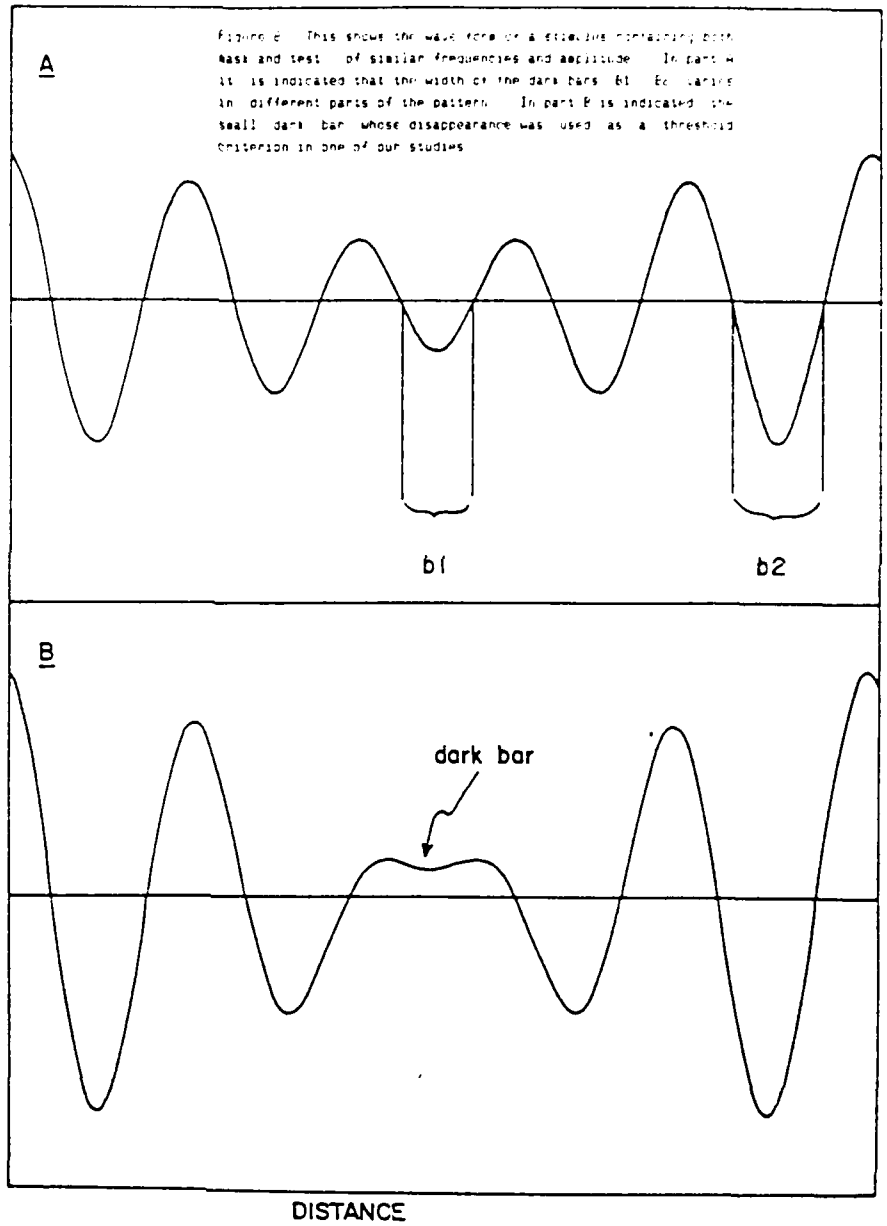
tests which are close to the mask's second harmonic. As expected, the second-harmonic mask is considerably more effective than the anharmonic ones, but loses much of this effectiveness with practice. Thus even the appearance of sinusoidal masks has to be learned. It follows that such masks are, to some extent, noise in the functional sense that the subject cannot detect the test with full sensitivity until he is fully familiar with the mask. Thus Birdsall's Theorem may well apply to non-random masks, particularly with inexperienced subjects and psychophysical procedures (e.g. MOA) which do not encourage maximal sensitivity.

Configurational Criteria

Even if Birdsall's Theorem does not apply, there is a second way in which the subject's choice of criterion may lead to Weber's Law with harmonically pure stimuli. The subject may attempt to identify a particular feature which occurs in the complex test-plus-mask pattern. Since the overall configuration of a complex grating depends solely on the ratio of its components, such a criterion -- rigidly followed -- will lead to Weber's Law. Many such configurational criteria may be devised; in the next experiment we investigate two of these.

For these experiments, we must use a more subjective psychophysical procedure (MOA), instructing the subject to use different criteria under otherwise identical conditions. An advantage of MOA psychophysics is that a significant part of the masking literature has used this method. It has the obvious, but unavoidable, disadvantage that we have no real control -- beyond subjective report -- over what criterion is actually used.

Consider three different threshold criteria. The first we term the absolute criterion; the subject sets thresholds as sensitively as possible, by whatever cues he may find. This is probably not the usual criterion in MOA; even experienced subjects often choose a criterion which is relatively high. The second criterion is the bar-width criterion, shown schematically in Figure 8A. This figure shows the sum of two sinewaves (i.e. mask and test) of similar but unequal frequency and amplitude. The width of the bars in the resulting complex grating is less in the region of destructive interference than in the region of constructive interference. Subjects were asked to set threshold by looking for a just-perceptible change in bar width. Since the subject's JND for bar width will be relatively constant for different contrasts (Smith, 1982), this is a geometrical property occurring at a fixed ratio of mask to test contrast. In short, Weber's Law will apply. The final criterion is exemplified in Figure 8B, where the contrast of the hypothetical test grating has been increased somewhat over Figure 8A, producing a readily detectable feature. This is the small dark bar (indicated by the arrow) which occurs in the middle of an extended bright field. If the contrast of the test grating in Figure 8B were increased slightly, the dark bar would disappear.



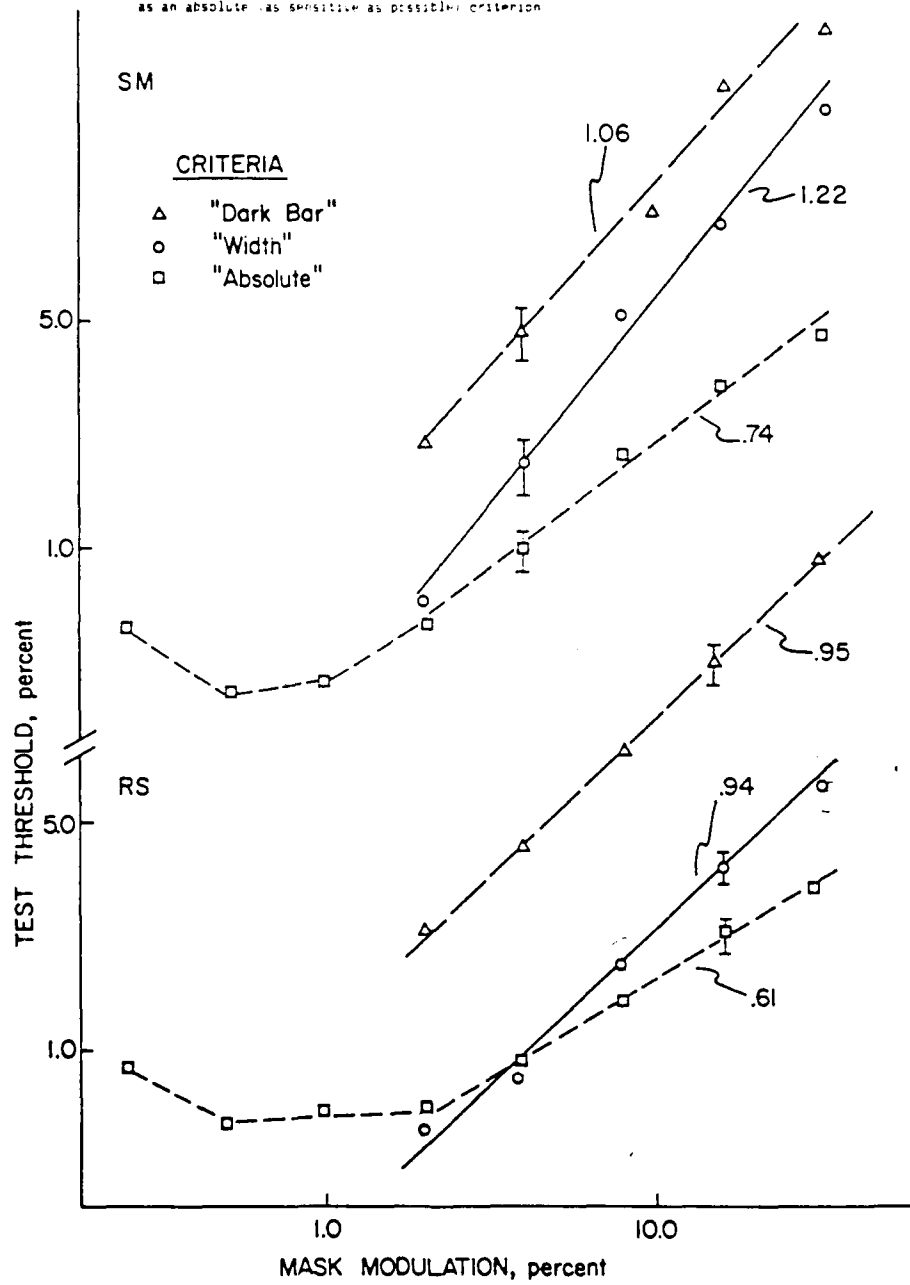
altogether. The disappearance of this dark bar was the final criterion used by our subject. The objective disappearance of the bar is calculable; for sinusoids of 4 and 5 c/deg, it occurs at a Weber fraction of 1.25. The results of this experiment are shown in Figure 9. The data for the two subjects are similar except that EM's slopes are slightly greater than those of RE. Our major expectations are confirmed. The dark bar and bar width criteria display Weber's law. Furthermore the dark bar data show approximately the predicted value of the Weber fraction. The data for the absolute criterion, however, display power law behavior. Thus we see that the adoption of different criteria in method-of-adjustment experiments not only influences threshold but actually changes the power law observed.

DISCUSSION

We have referred to similarities between spatial masking and the processes of detection and identification. In particular, our theoretical explanation (especially Birdsall's Theorem) is in many ways equivalent to that presented by Lasley and Cohn (1981) to distinguish luminance detection and discrimination. We can now make these similarities explicit. Classically detection and identification have been quite distinct paradigms: the former is discriminating a test stimulus from no stimulus, while the latter is discriminating between two different test stimuli. Recent theories based on visual detectors have blurred the distinction somewhat, since "identification" may now be defined as detection by a particular detector. In such a model, "detection" might be the presence of a criterial response from any detector. Under these definitions, our analysis suggests that masking by noise stimuli (involving only one detector -- or a small related set) is an example of identification, while masking by a familiar stimulus (detecting a change from any detector) is detection. Other definitions are possible; in particular it may be objected that masking is not a true identification paradigm, since two test stimuli are not involved. Provided the considerable similarities are recognised, we have no objection to a narrower definition of identification. For this reason, we have referred to noise masking as "identification-like". The essential point is that in noise masking, the observer must know something about the test stimulus, and detect the known feature in the noise. In masking by a familiar pattern, no particular feature need be known; any detectable change is sufficient.

We believe that we are now in a position to explain much of the diversity in the literature on Weber's Law in spatial-frequency masking. Subjects can use at least two quite different threshold criteria in masking experiments. These yield not only different thresholds, but different functional behavior with changes in mask contrast. In some paradigms, we can be sure what criterion was used and understand the results accordingly, but in many paradigms the criterion is uncertain and the results are correspondingly difficult to interpret. Let us therefore survey some common masking experiments from this point of view.

Figure 4. Example of Inversion Thresholds for 4 sided test and 5 sided mask for the two criteria described in Figure 1, as well as an absolute (as sensitive as possible) criterion



When the mask is noise (or equivalently, when the observer is uncertain of mask configuration) then the observer's ability to discriminate is limited entirely by the amplitude of the masking noise, and not at all by the inherent sensitivity of the visual system. Note that Birdsall's Theorem is formulated entirely in terms of the statistical properties of the signal; threshold behavior is largely transparent to the properties of the visual system. Thus such experiments may tell us little about visual physiology.

When the subject is presented with a non-random, sinusoidal mask, Weber's Law may nonetheless be observed. This might occur because the subject still needs to learn the appearance of the mask. From a different point of view, this is equivalent to saying that faced with an unfamiliar discrimination, the subject chooses a very conservative criterion. Another reason for Weber's Law with sinusoidal masks is that there exist configurational criteria which produce Weber's Law even in the absence of visual noise. Of these criteria, we feel that the bar-width criterion deserves attention. This yields thresholds similar to those set by subjects without special instructions. In addition, some of our naive subjects have spontaneously described this as their criterion.

In the literature, MOA psychophysics are almost always associated with Weber's Law. This may be because configurational criteria are easier to use. The fact that we were able to achieve power-law behavior with MOA seems entirely attributable to motivation. Unlike forced-choice, MOA provides no inherent motivation for increased sensitivity. In general, the more we motivated our subjects to set low thresholds, the lower the exponent in their power laws.

The distinction between the two types of criterion is made clear in figure 10, which shows a pair of mask-alone and mask-plus-test patterns from our first experiment. If a subject is asked to detect "any difference", he will do so easily; the added 4 c/deg test grating is readily detected. But if he is asked to which noise pattern the test has been added, his replies will be near chance; he cannot yet identify that particular pattern of channel activation which characterizes a 4 c/deg grating, given the level of masking noise. If, however, he is told which pattern is mask-alone, and asked to determine whether a test has been added to the other, he can easily do so. These changes are not because of any changed performance in his visual system, but because different tasks and/or additional information may convert an apparent identification-type task into a detection-type task. Evaluating the effect of available information (or uncertainty) is not always easy. Our stimuli were relatively well-defined: the masks were spectrally-flat, band-limited noise and the tests were always 4 c/deg at a specified phase. We find that simply randomizing the test phase between trials greatly extends the learning period necessary in our first experiment (Figure 1); undoubtedly relaxing other constraints would have a similar effect. The problem has yet

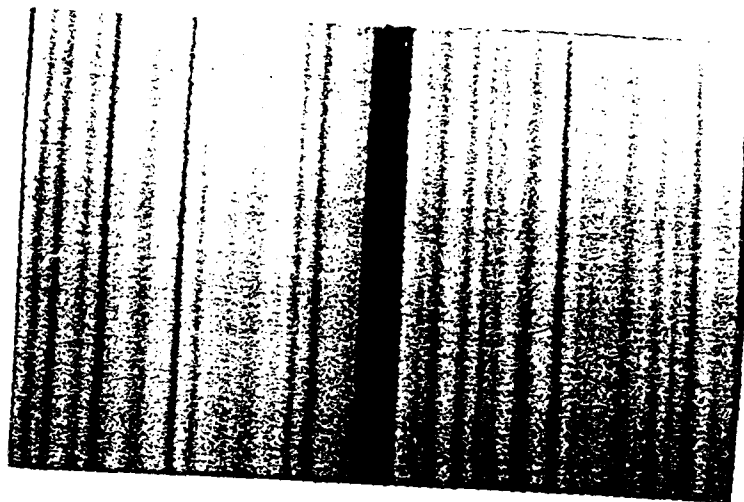


Figure 10 A typical forced-choice random-walk stimulus pair.
It is easy to see that the two stimuli are different, but very
difficult to decide which is base-plus-test, and which is base-
alone.

another dimension. Whatever information may be available to the subject provides only a limit on detectability; we have seen that the subject must often learn to use the information. Unless he is motivated, this may occur slowly, or not at all.

An unfortunate conclusion from this is that many masking studies (especially those using MOA) are effectively unreplicable. We can reproduce the external conditions of an experiment, but only in a few cases (e.g. highly practiced subjects using forced-choice) can we be sure of the detection strategy used. Thus, while the factors we have elucidated seem to us sufficient to account for the diversity of results in the literature, there is no apparent way to show (i.e. by replication) which factors were critical in a particular study, or to show that other factors -- perhaps unknown to us -- were not operative.

Finally, we offer a practical conclusion. We regard 3AFC as a major advance in the study of spatial masking, especially when the issues of detection versus identification are involved. It is the only technique we know (excepting over-learned 2AFC) which largely eliminates variation in detection strategy, by removing the identification-like aspects of the task. This is useful for studying the relationship between detection and identification, and is essential if we desire to isolate the pure detection mechanisms in masking experiments. Another advantage is that a three-alternative staircase converges more reliably than a two-alternative staircase, since the probability of a correct guess is reduced. A final advantage is surprising. The data shown in Figure 5 were taken from naive subjects who had never done masking discriminations before. These discriminations are notoriously difficult; to our knowledge no one has previously obtained reliable masking data from naive subjects without an extensive period of practice. The net result of all of these considerations is that 3AFC yields reliable masking data in much less time than any other psychophysical technique we have used.

III. A Detector for Moving Objects

INTRODUCTION

Studies of lateral interactions in vision date back at least to the discovery of Mach bands but quantitative studies have typically used one of several well-established paradigms. In the spatial domain, Westheimer (1965) studied the increment threshold for a small test spot as a function of the size of a superimposed circular field. Kulikowski and King-Smith (1973) used a comparable technique in which detection of a test line is influenced by subthreshold flank lines of varied spacings. Both of these studies found facilitation for small separations, and inhibition for somewhat larger ones. Interactions over time have been studied with theoretically parallel experiments on the detection of pairs of homogenous light flashes, separated in time rather than space. Recent studies (Rashbass, 1970; Ueno, 1973) measure an impulse response in which closely-spaced flashes summate, while flashes separated by somewhat longer times inhibit. Both spatial and temporal interactions are in qualitative agreement with the dynamics of retinal receptive fields; these display summation between stimuli which are close in space and time, while lateral inhibition occurs at only larger distances and after a brief delay (Kuffler, 1953). The only psychophysical study to systematically study both spatial and temporal interactions used the Westheimer paradigm. Teller et al (1971) varied both the size of the surrounding disk and the IEI between the test flash and the onset of the disk. This more general study confirmed the pattern of Kuffler-like dynamics, in that lateral inhibition occurred only after a delay of about 40 msec. Our experiment is comparable to Teller et al's, except that we used rectilinear stimuli. We measured the detectability of two briefly-flashed lines as a joint function of their separation in space and time.

METHODS

Stimuli were displayed on an HP 1332A CRT, in a 30 cd/m^2 luminous patch 4° wide and 5° high, viewed from 70 cm. Line stimuli 0.8° wide and 1.5° high were flashed for 10 msec in the middle of the field. Fixation was aided by two vertical vernier lines, the test lines being parallel to, and equidistant from, the midpoint of the verniers. The total energy of each test line was equal to that of a 50 cd/m^2 line, 10 msec in duration and 0.8° wide. In a typical trial, the background luminance appeared and awaited a ready-signal from the subject. The test line appeared 700 msec. after the subject's signal, preceded by an audible beep. The screen remained luminous for another 700 msec, and then turned off briefly to process the subject's response. The average duty-cycle was 6 seconds on, one-half second off. The subject was given feedback for incorrect answers.

We used 6 line spacings (0.05, 0.1, 0.15, 0.2, 0.3, and 0.5 degrees) and 6 temporal delays (0.01, 0.02, 0.04, 0.055, 0.07, and 0.1 seconds). These were conceived as a 6 x 7 array; the additional column contained single-line controls. Catch trials were interspersed randomly, making 35% of the total. A single experimental run consisted of one seen/not-seen judgement for each of the 42 (6 x 7) conditions, plus the associated catch trials, presented in random order. Subjects were typically able to perform 5 runs at a sitting, with a complete experiment requiring 100 runs. Thus each experiment involved about 6000 trials. With 100 trials per point, the standard error of estimate was about 0.05. We halved this error by computing a four element boxcar average, averaging two elements along each dimension. Contour plots were calculated by an automated interpolation algorithm, which placed contours at intervals of 1.3 standard errors of the averaged data. The standard error in the placement of a contour varies, being proportional to, and somewhat less than, the separation between adjacent contours. The subjects were given periodic feedback about hit- and false-alarm-rates, and were able to hold these constant within a few percent.

RESULTS

Results are shown in Figure 1; for convenience we refer to these data as an LIF (line interaction function). Unlike the results of Westheimer or Kulikowski and King-Smith there is no suggestion of a lateral-inhibitory or centre/surround organization. The dominant feature is a bimodal area of facilitation with peaks at the origin (no separation) at a separation of about 50 msec. and 0.15 degrees. The existence of this secondary facilitatory region is the major result of this study. Note that the optimum stimulus for the mechanism shown in figure 1 would appear to be a vertical line whose locus (in space/time coordinates) moves diagonally from the origin through the peak of the secondary facilitatory area; this would be a line moving at about 3.0 deg/sec.

To establish the statistical reliability of this effect, we defined the height of the secondary peak as the mean of the data point at 55 msec and 0.15° and its four nearest neighbors. This was then compared with a baseline, defined as the mean of the six data points at maximum spatial separation. We replicated the experiment of figure 1 once with a different subject, and at least four times with other variations. We never observed an effect (as defined above) of less than four standard errors. The secondary peak was always reasonably compact and centered at 50 to 75 msec and 0.12° to 0.16°. Note, however, that the detailed shape of the contours at low levels is generally not significant, as the standard error of the placement of these contours is large. False alarm rates were 0.20 for PC and 0.33 for SM. The intersession variation of these rates was estimated as $\pm .02$ for PC and $\pm .04$ for SM. Single-line hit rates were 0.38 and 0.51, respectively, with intersession variabilities of $\pm .03$ and $\pm .06$.

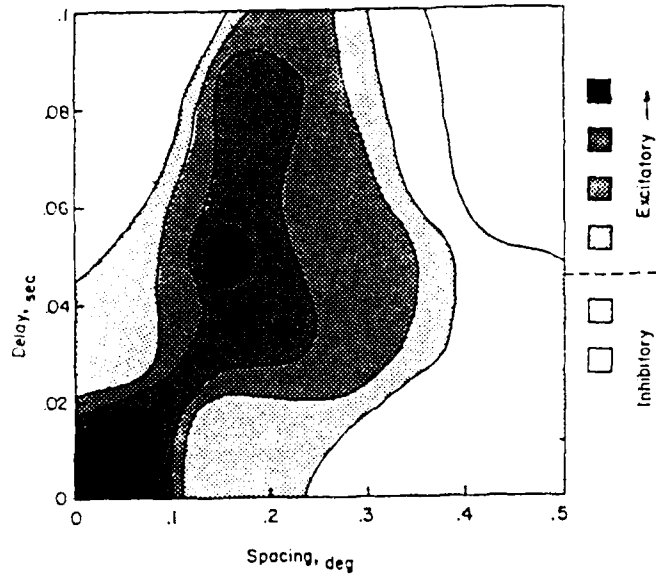


Fig. 1. Contour plot of the probability of detection versus spacing and temporal separation of the two test lines. "Excitatory" and "inhibitory" are relative to the calculated probability of detecting either line independently. The lowest contour line is $p = 0.42$. Higher contours are spaced at 0.03 intervals.

Figure 2 is a replication of Kulikowski and King-Smith's static three-line paradigm. The test and two one-third-luminance flanks were presented simultaneously using a Gaussian temporal presentation with a half-width of 0.5 seconds (as used by Wilson and Bergen, 1979). The results are quite similar to those in the literature: facilitation at small spacings is replaced by inhibition at larger spacings. Similarly, figure 3 is a replication of the two-flash experiment. The subject detected the presence of a pair of 10 msec, whole-field flashes as a function of their temporal separation. These data show a typical pattern of facilitation, followed at longer ISIs by inhibition, followed by disinhibition at still longer ISIs. The temporal parameters of this function (e.g. ISI to peak inhibition) are a strong function of luminance (Ueno, 1977). Our data agree well with Ueno's data for a similar luminance.

DISCUSSION

Attempting to assign a functional interpretation to the LIF raises a number of questions which we cannot yet answer. We will, nonetheless, address the following issues: 1) does the LIF measure the behavior of a single visual detector, or is it a composite; 2) is the underlying mechanism functionally motion sensitive; and 3) why is the LIF so different from the results of other experiments of which it was intended to be a generalization?

Single and Multiple Mechanisms

There do not appear to be any theories of multiple spatio-temporal mechanisms, but an extensive literature on essentially spatial mechanisms is readily generalized. Kulikowski and King-Smith's original measurement of a spatial-only LIF was strongly criticised by Graham and Rogowitz (1978), who showed that probability summation between spatial channels could so distort subthreshold additivity experiments that the results bore little resemblance to the bandwidth or spatial sensitivity of the underlying channels. These concerns seem fully applicable to this experiment. On the basis of present evidence, then, the LIF is only a psychophysical entity; we make no claims about underlying neurophysiology. Note, however, that the actual extent of Graham and Rogowitz' proposed distortion is largely unknown, and may be small. In particular, Hines (1975) and Wilson and Bergen (1979) have used Kulikowski and King-Smith's paradigm to measure a linespread function which was then used in their linear models of spatial detectability. While the physiological reality of their proposed mechanisms is debatable, the considerable predictive success of these models justifies an attempt to generalize this approach to spatio-temporal stimuli.

Motion Detection

It is tempting to equate the mechanism underlying the LIF with a motion detector; the stimulus to which it should be most

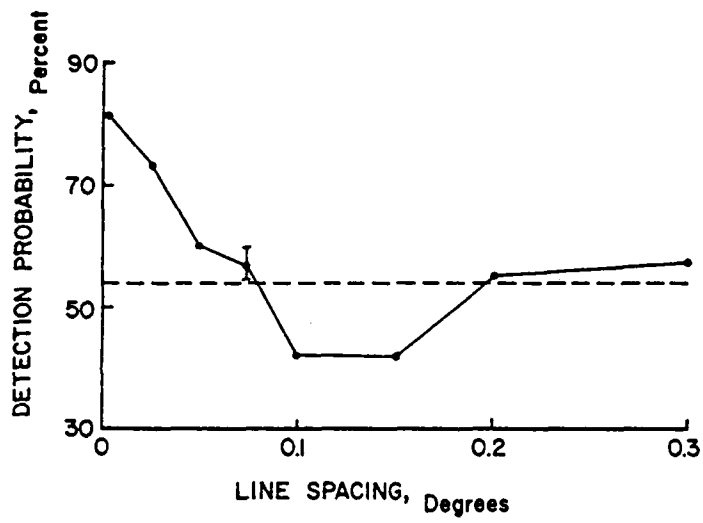


Fig. 2. Visibility of a test line as a function of the separation of two sub-threshold flank lines. Presentation was a 0.5 second half-width Gaussian ramp. The dashed line is the probability of seeing the test line alone.

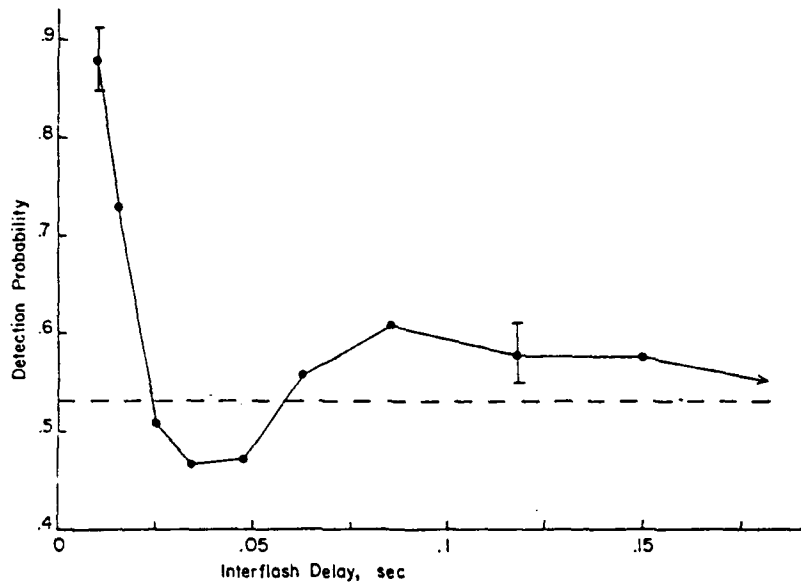


Fig. 3. Visibility of a pair of 10 msec whole-field flashes, as a function of their separation in time. The dashed line is the calculated probability of seeing either flash independently.

sensitive is a line moving with a velocity of about 3 deg/sec. Theoretical discussions of motion detectors (Reichardt, 1961, Barlow and Levick, 1965) describe entities with properties similar to the LIF. We must exercise caution however, since this conclusion involves extrapolating from briefly-flashed lines to quite different stimuli. Such an extrapolation is valid only if the underlying mechanism is linear. Moreover to establish that the LIF mechanism functions as a motion detector will require extensive studies relating its properties to the actual perception of motion. At present, the association of the LIF with motion detection is a tempting but quite unproven hypothesis.

If the LIF taps motion detection mechanisms, why do we find only a single detector, tuned to a single velocity? Given our range of spatio-temporal separations, it would not have been possible to find detectors with a velocity very much different from what we found. It is also possible that detectors tuned for different velocities and spatial patterns exist, but that they are not very sensitive to thin lines and so were unobserved. We are actively searching for such mechanisms.

Related Studies

We have already briefly summarized the better-known literature, and have seen that this generally supports a Kufflerian model of the spatio-temporal dynamics of lateral interactions. A few studies suggest a compatible, but more detailed picture. Smith and Richards (1969) found that lateral interactions appeared to propagate across visual space at about 1.0 degrees/second. Van der Wildt and Vrolijk (1981) also measured propagating inhibition with a velocity of 4 deg/sec in an experiment which is identical to our present experiment with the following exceptions: 1) their data were taken off the fovea, typically at 3° nasal, 2) they used points of light, rather than lines. While the difference in velocity might be explained by retinal locus, we suggest below that the difference between excitation and inhibition is a result of the different stimulus configuration.

It was our original expectation that these experiments would also measure the spatial and temporal dynamics of Kuffler-type lateral inhibition. In fact, the LIF primarily shows delayed lateral facilitation, rather than inhibition. We have replicated some of the experiments showing lateral inhibition (figures 2,3) and our results are in good agreement with those in the literature. Thus the apparent contradiction does not seem to be the result of an artifact or idiosyncrasy in our procedure; rather there appears to be a genuine qualitative difference between our paradigm and these related experiments.

We find only one experiment in the literature which directly tests our result. McGarvey and Cohn (1983) studied the visibility of two flashed, rectilinear LEDs at four space/time separations. Only one of their separations (40 msec and 0.1 degrees) fell within our secondary facilitatory region, but that

point showed clear facilitation.

It is possible to plausibly organize these various results in terms of systems already described in psychophysics and neurophysiology. Results consistent with the lateral inhibitory behavior of retinal neurons are obtained with 1) concentric stimuli, 2) point stimuli, 3) line stimuli in prolonged presentation, and 4) unpatterned light flashes. To obtain secondary facilitation, as in the LIF, it is apparently necessary to use both linear stimuli and rapid temporal presentation. This agrees with the psychophysical concept of the transient visual system. This system is commonly described as being most responsive to motion or rapid temporal variation, and to relatively coarse, rectilinear stimulus contours. We tentatively suggest, therefore, that when a transient, rectilinear stimulus is present, then a set of visual mechanisms is invoked which is wholly inoperative with static stimuli, and that these mechanisms primarily show a facilitation which is offset in both space and time.

IV. 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:

$$RF_{n,c} = A_n \exp(-x^2/W_{n,c}^2) - A_n \exp(-x^2/W_{n,s}^2)$$

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,

$$RF_{n,c}(x,t) = A_{n,c} \exp(-x^2/W_{n,c}^2) - A_{n,s} \exp(-x^2/W_{n,s}^2) \\ - A_{n,c} \exp(-t^2/W_{n,c}^2) + A_{n,s} \exp(-t^2/W_{n,s}^2)$$

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

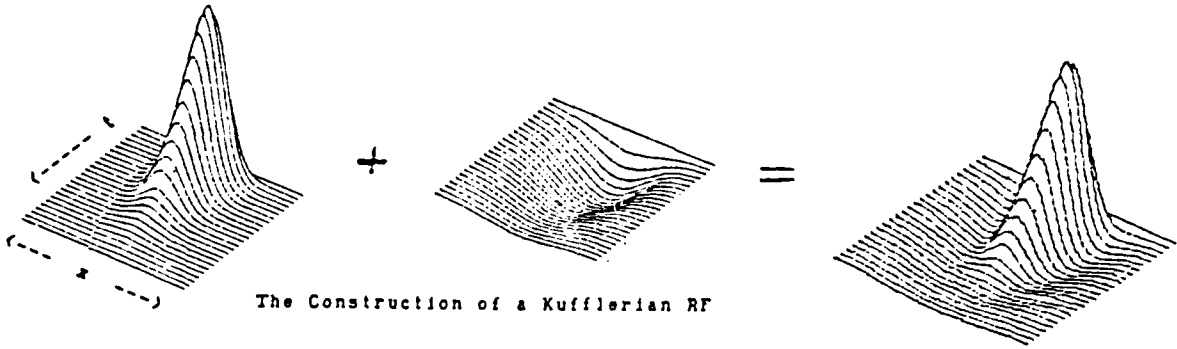
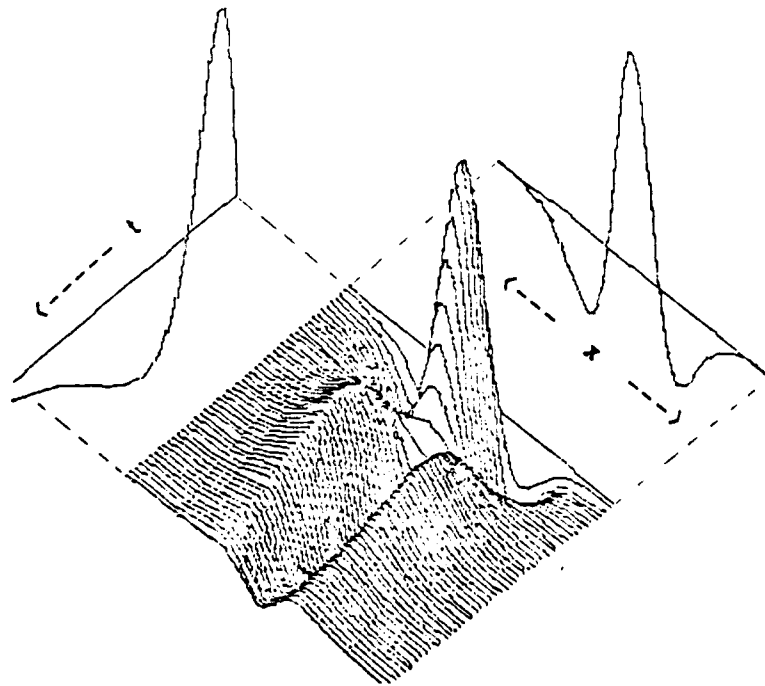


Figure 1



The Construction of a Separable RF

Figure 2

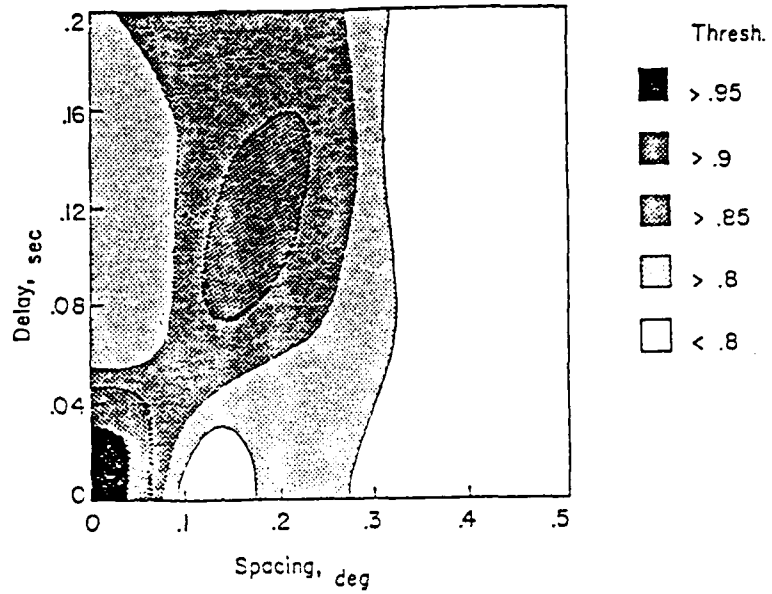


Figure 3. The detectability of a pair of briefly-flashed lines as a function of their separation in space and time.

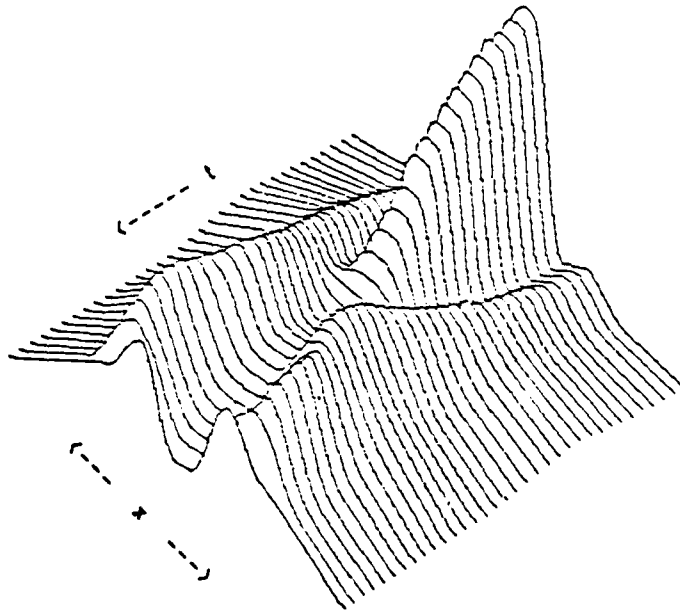


Figure 4. The data of Figure 3 (above), reflected about the time axis, and plotted as a wire mesh. Note the similarity to Figure 2.

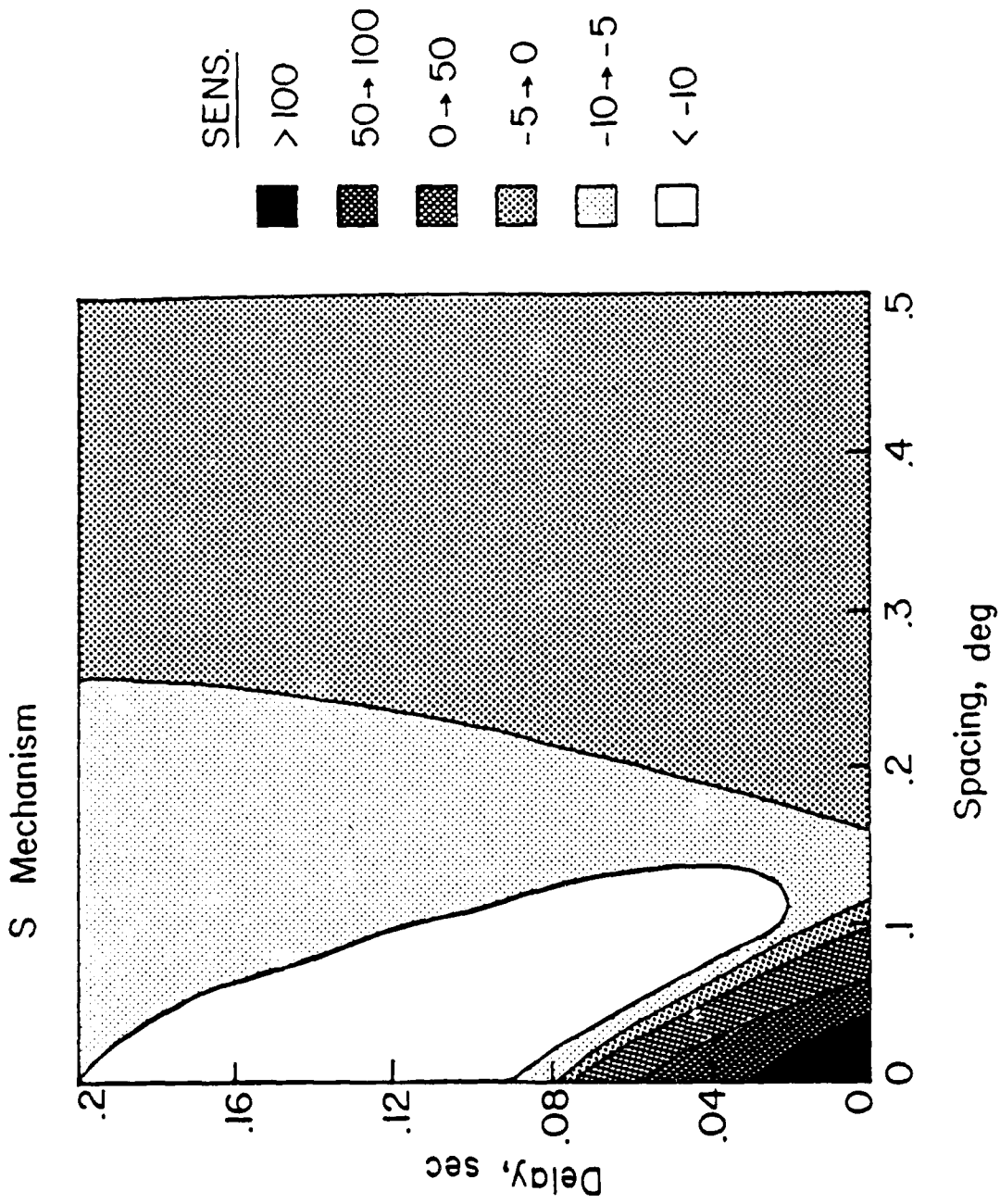
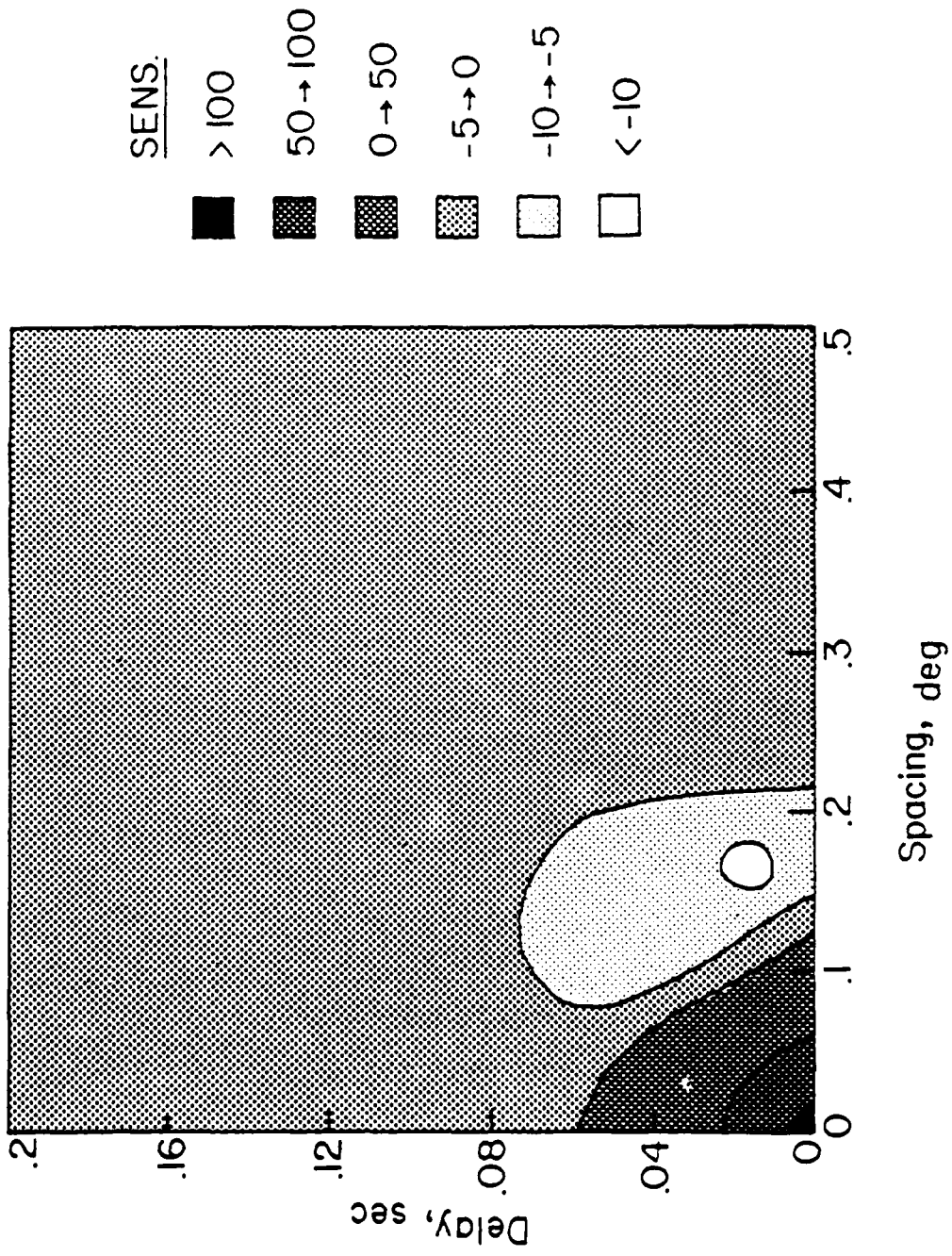


Fig. 5. Contour plots showing the spatiotemporal sensitivity of the S and T mechanisms of the Kufflerian model. Note the 10x decrease in contour separation in the inhibitory regions.

T Mechanism



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:

$$R(x,t) = \sum_{x'} \sum_{t'} R(x',t')$$

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

$$R(x,t) = S\text{IRF}(x) * T\text{IRF}(t)$$

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

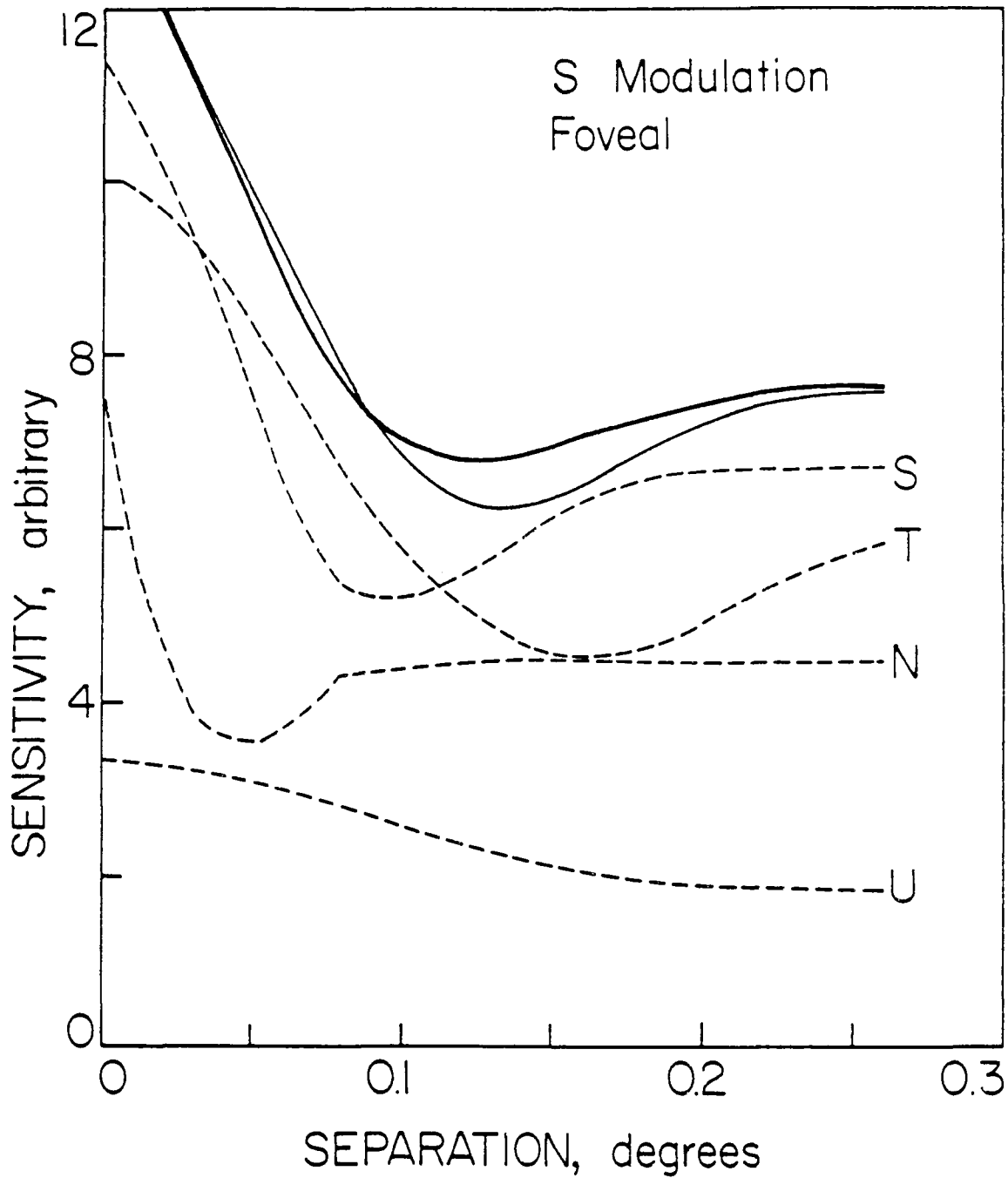
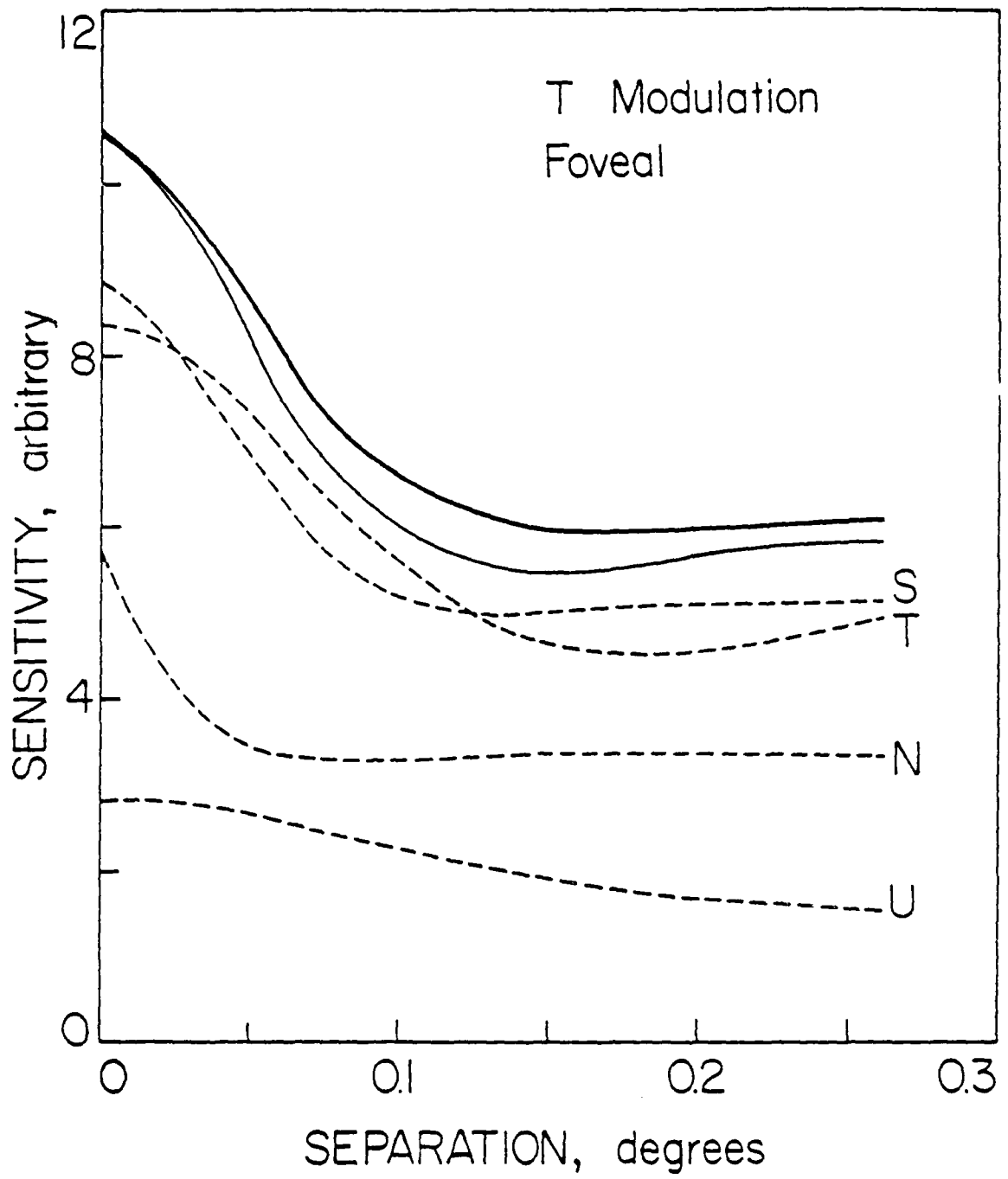


Fig. 6. Kufflerian model replication of Wilson and Bergen's (1979) simulation of the detectability of 3-line patterns under their S and T presentation conditions. The heavy line is our prediction, the lighter line is theirs; the dotted lines are the separate responses of the 4 mechanisms. This figure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



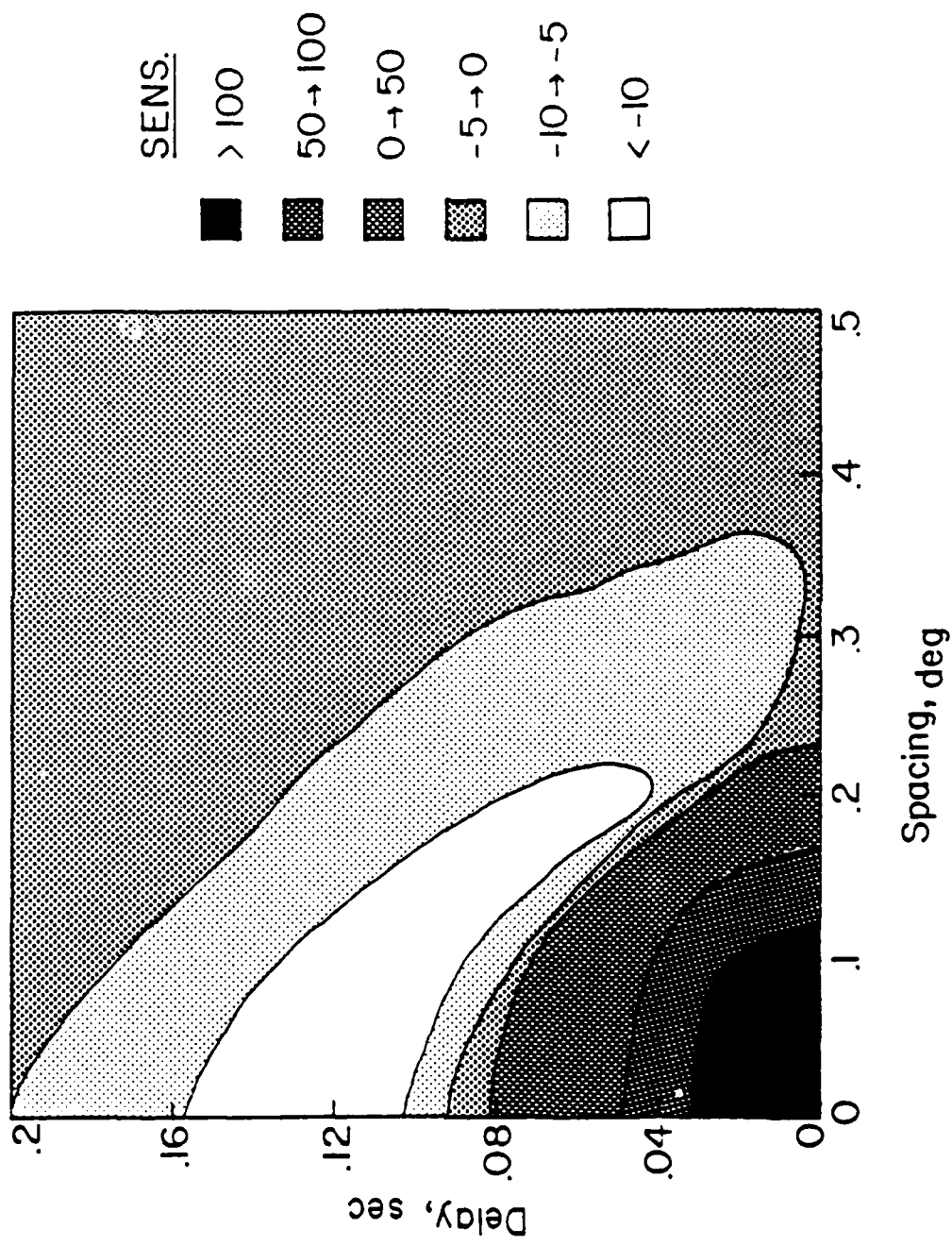


Fig. 7. A simulation of the 2-line IIF experiment with the Kufflerian model. If the model accurately predicted the IIF, then this figure would duplicate Figure 1. In fact, this figure shows no lateral facilitation.

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

$$R(t, x) = \sum_{i=1}^4 \left[\frac{A_i \exp(-t/\tau_i)}{B_i \exp(-x/\lambda_i)} \right]$$

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

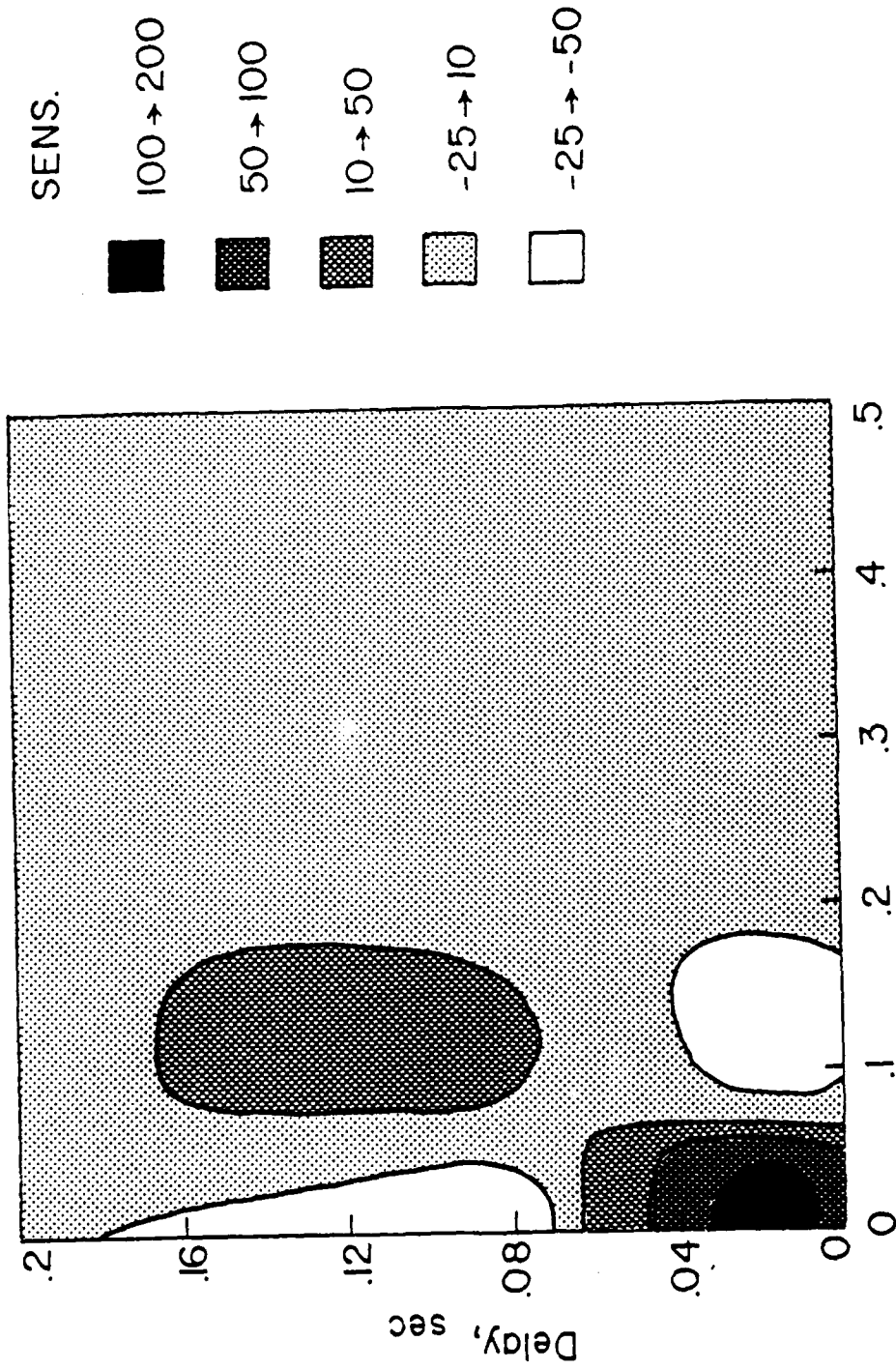


Fig. 8. Contour plot showing the spatiotemporal sensitivity of the S mechanism in the separable model. Note the somewhat nonlinear contour intervals used to emphasize the various regions. Relative to facilitation at the origin, inhibition has a peak magnitude of about - 0.4 and secondary facilitation 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

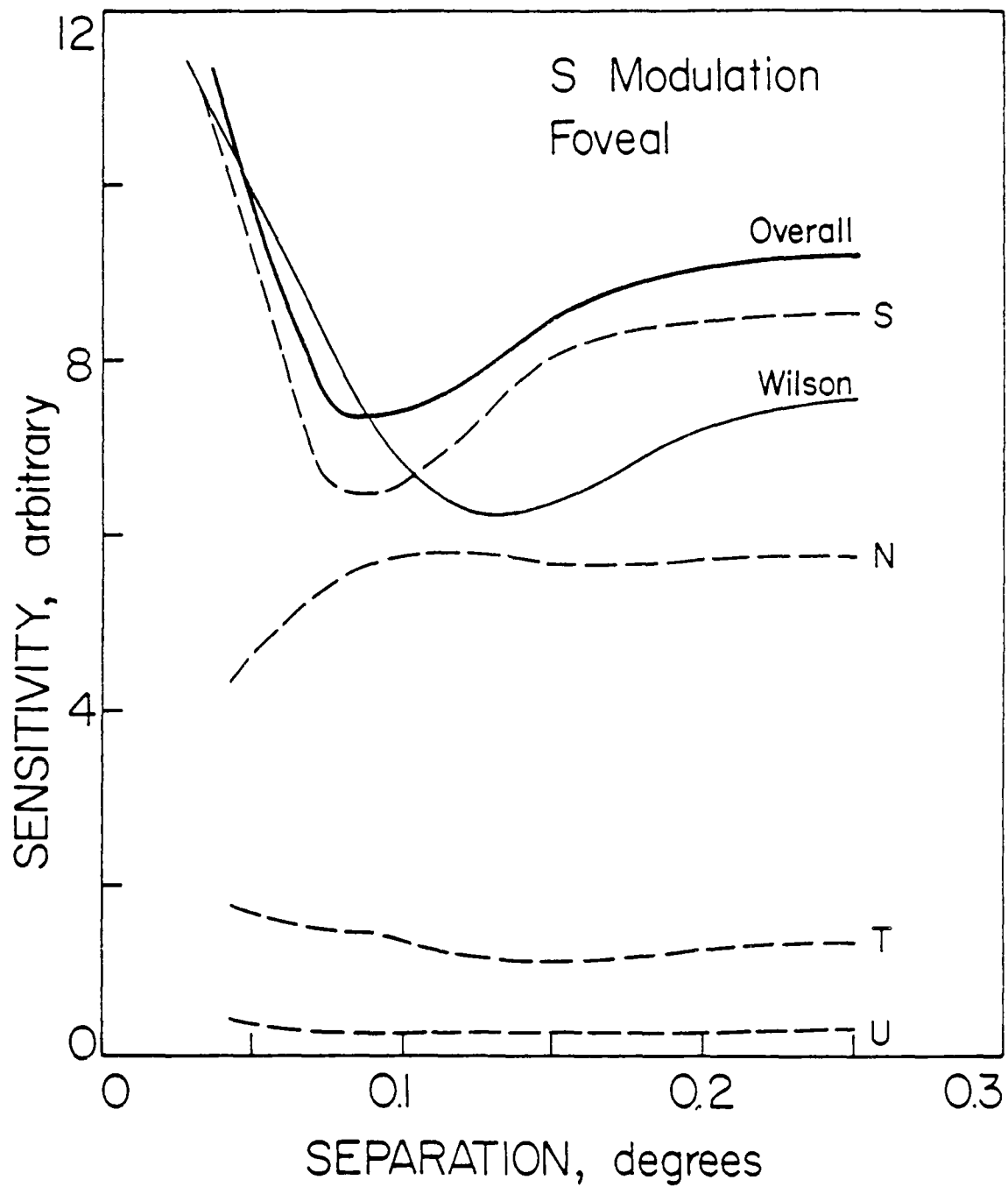
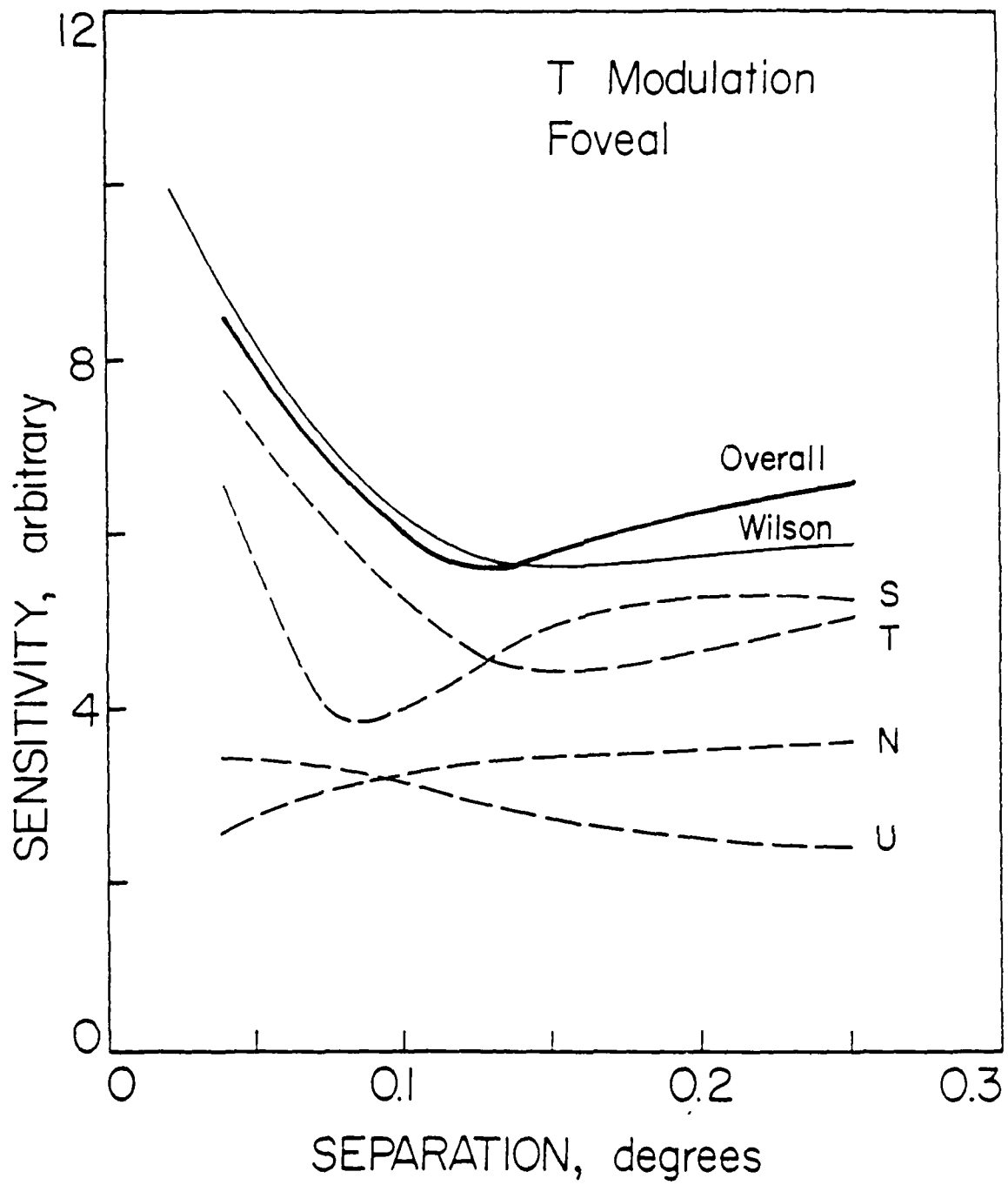
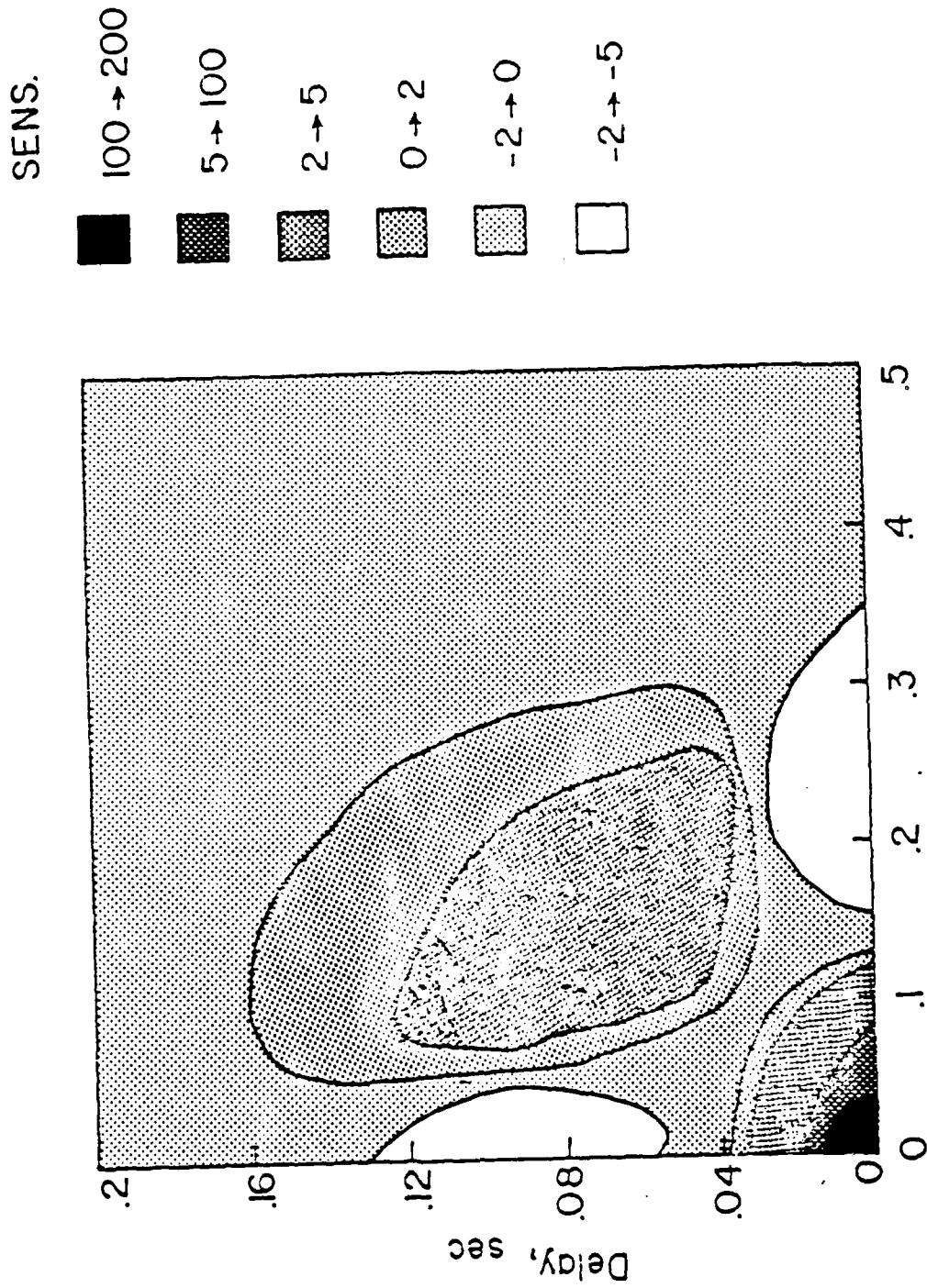


Fig. 9. Separable model replication of Wilson and Bergen's (1979) simulation of the 3-line experiment under S and T conditions. This may be compared to the Kufflerian model (Figure 6) and to Wilson and Bergen's Figure 8. The separate functions were optimized for these data; figures 8 and 10 use somewhat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





Spacing, deg

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.

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.

V. 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'

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 1
The Stimulus

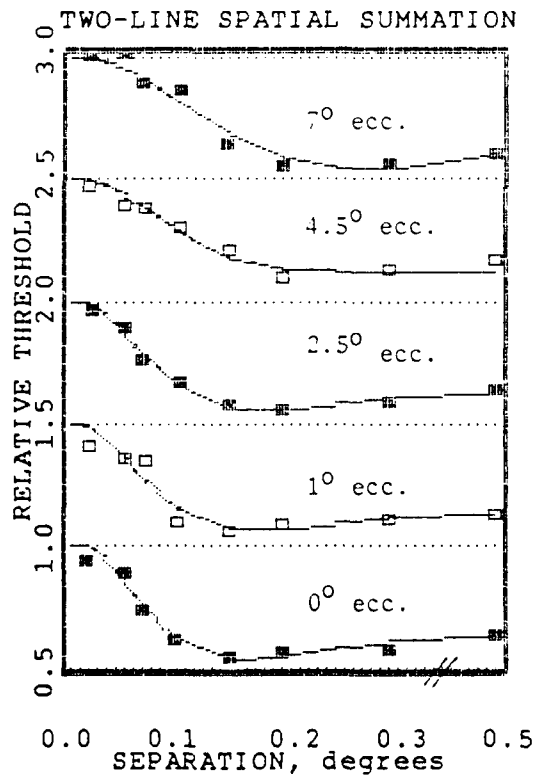
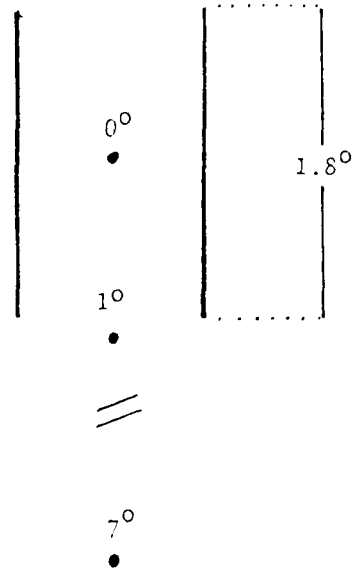
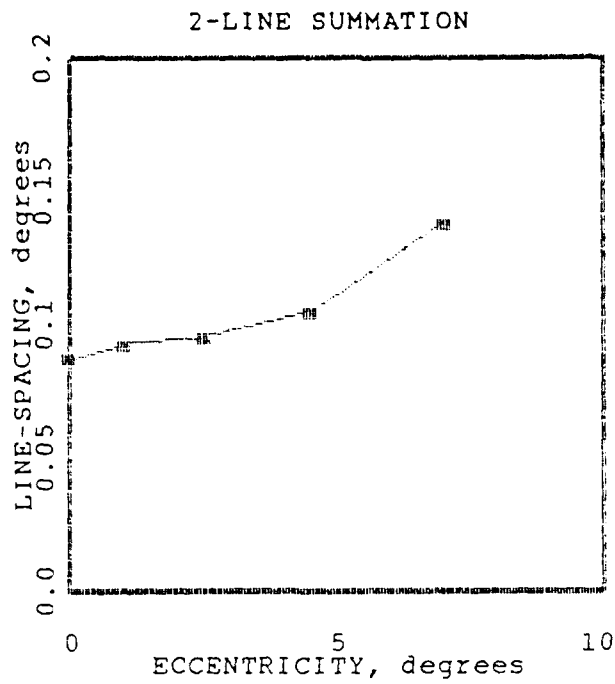


Figure 2

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.

Figure 5



PY's overall 2-line summation data

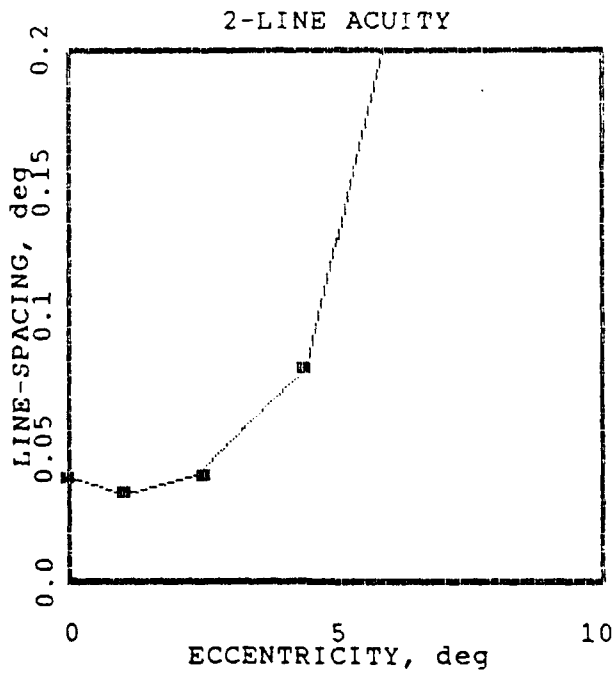


Figure 4

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

Summation V - 3

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.)

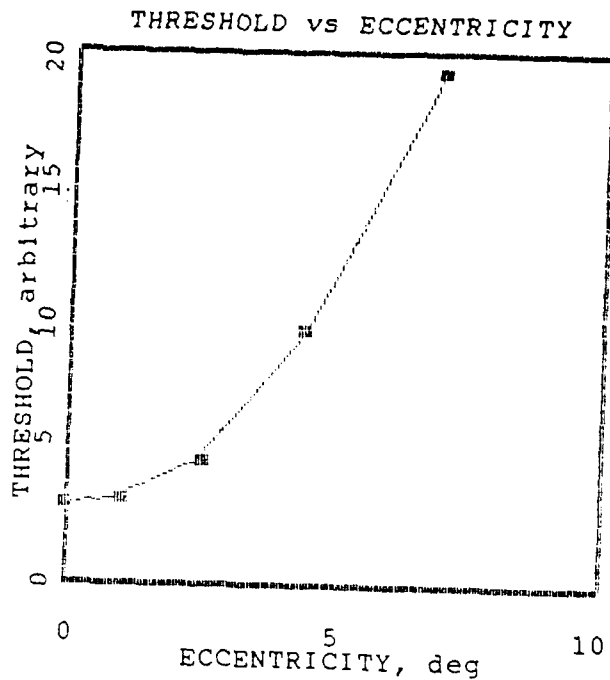
Overall

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

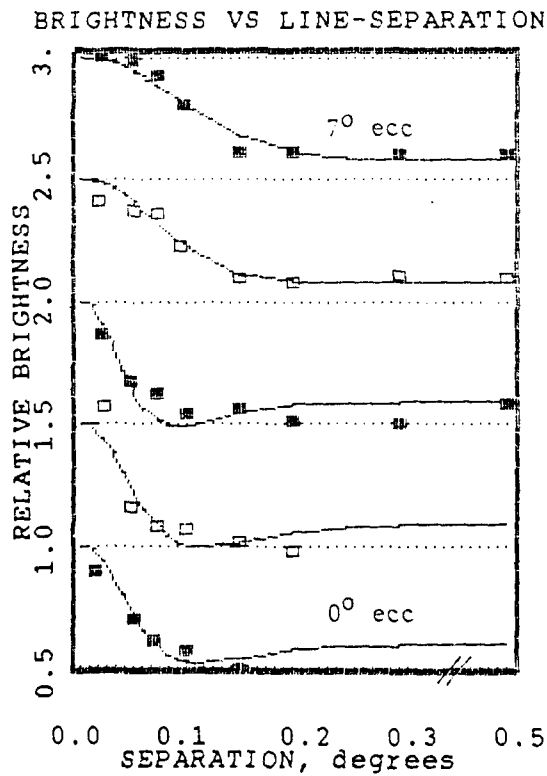
Qualitatively speaking, these data fit nicely with a variety of other results. It is generally accepted that the density of retinal ganglion cells and the cortical magnification factor correlate reasonably well with classical measures of acuity. It is thought that acuity is determined by the dictates 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



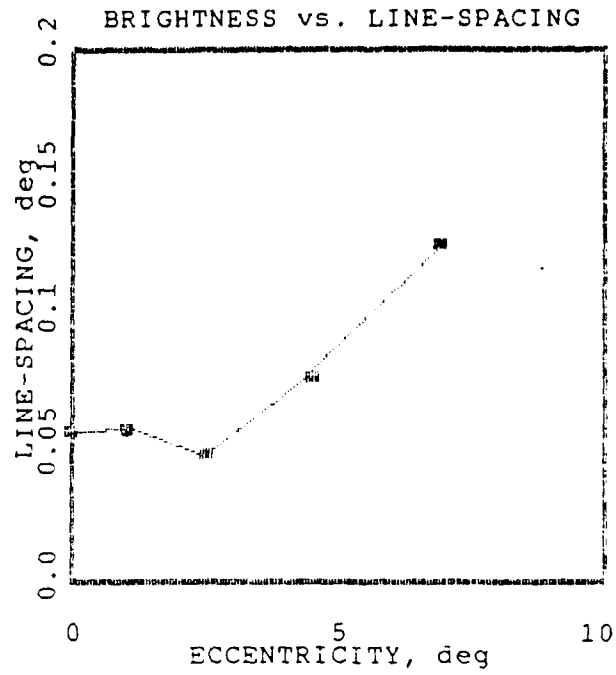
PY's single-line threshold vs. eccentricity.

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

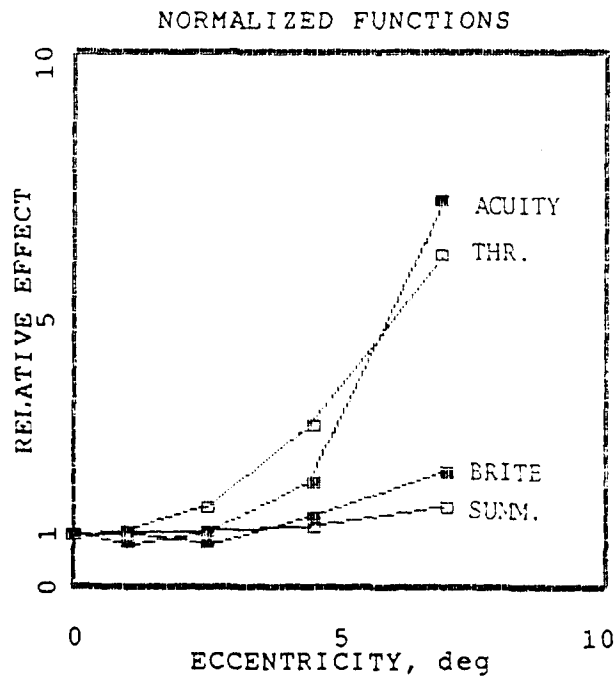


Figure 8

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 unsure why threshold for a single line co-varies 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.

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.

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.

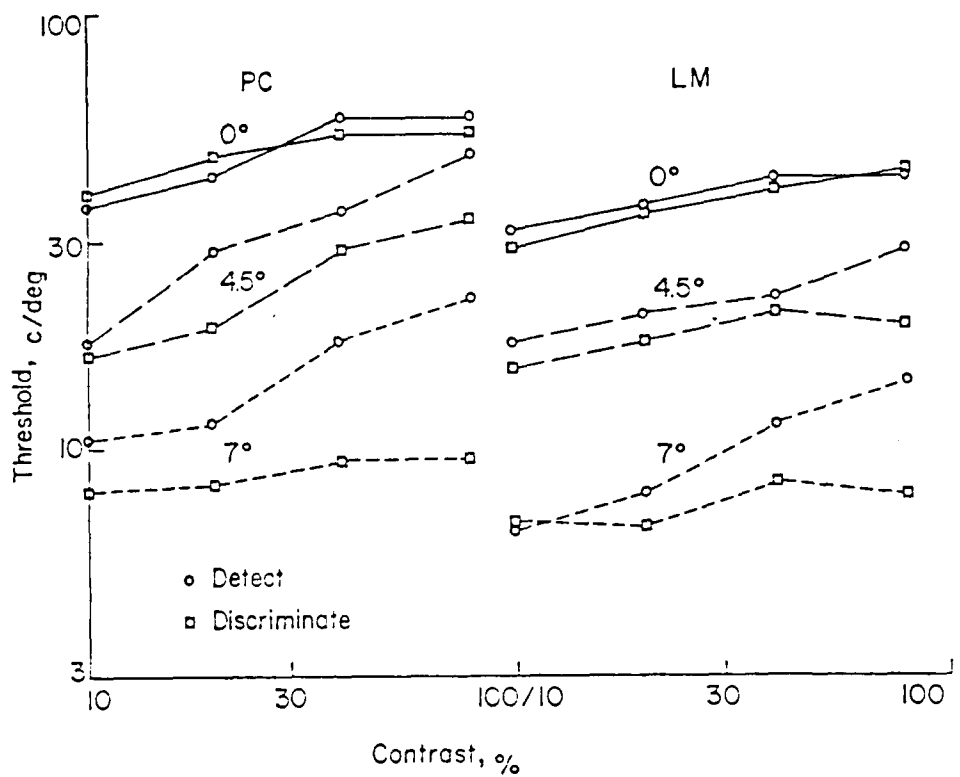
For aliasing to occur, however, the second condition must also be met; that is, the sampling aperture of the peripheral visual system must be significantly smaller than the distance between samples. At a physiological level, this condition appears to hold; outside the fovea, monkey receptive field centres 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.

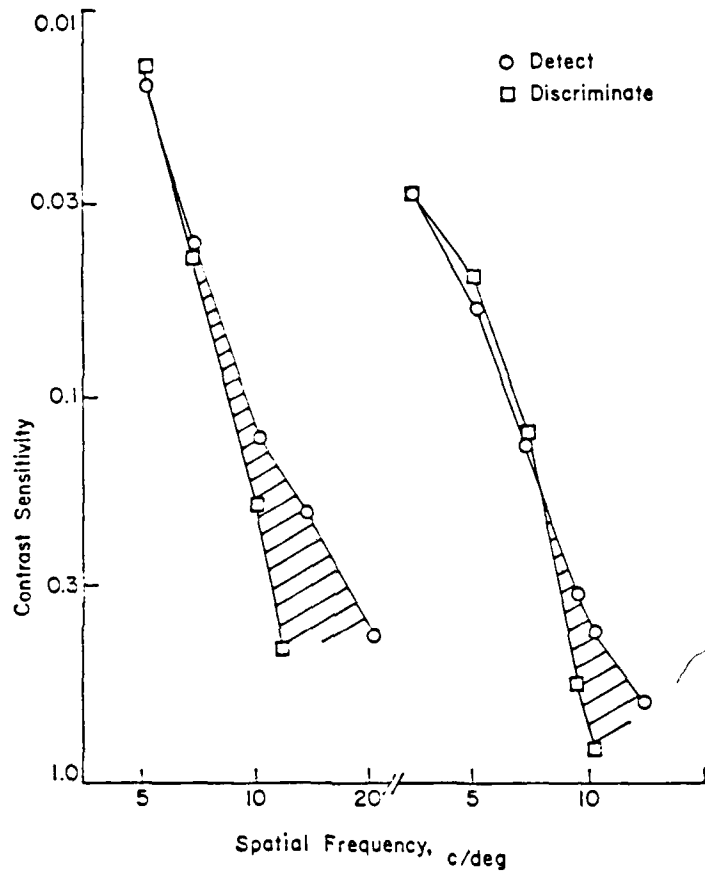
Williams (1985) observed that the percepts of aliased gratings in the fovea, though grating-like, displayed little preference for the orientation of the original interference fringe. He showed that the slight irregularities found in the foveal cone lattice could account for this. At 7° eccentricity, 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 the 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: PD (the second author) and LM (a naive subject).



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.

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 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.

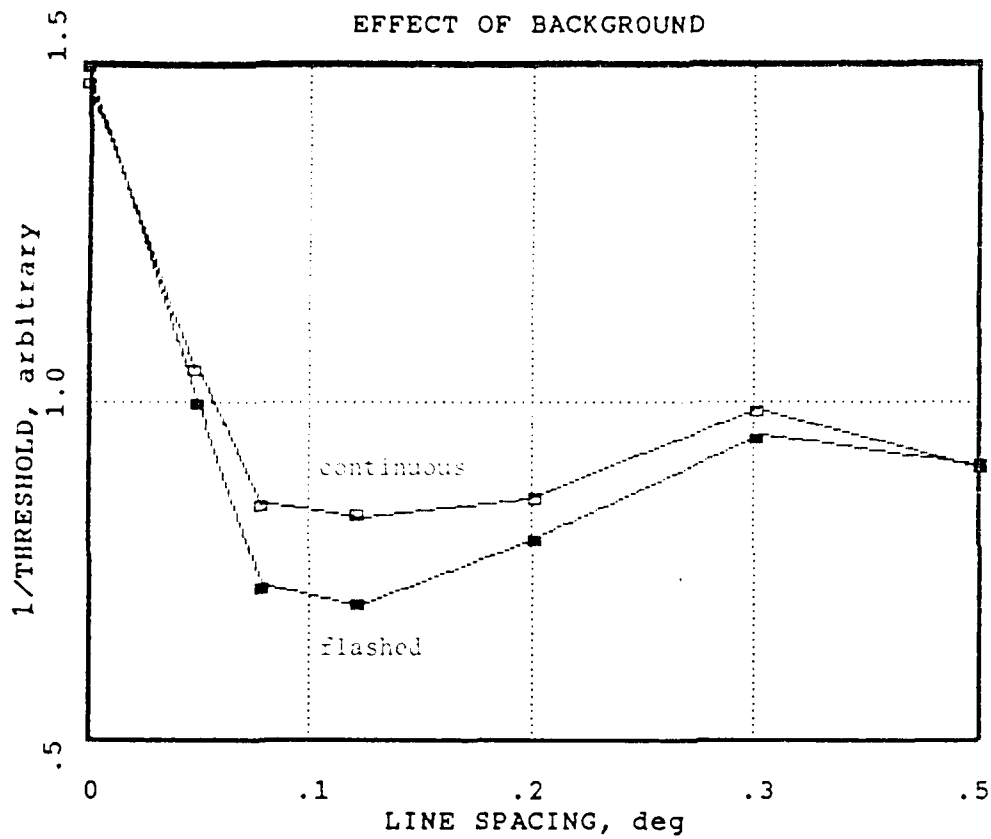
On the basis of our observations, we propose to modify the letter, though not the spirit, of the common assertion that aliasing does not occur in normal visual situations. It appears that there is a significant range of spatial frequencies which are detected only in aliased form in peripheral vision. 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.

VII. 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 PFs. 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

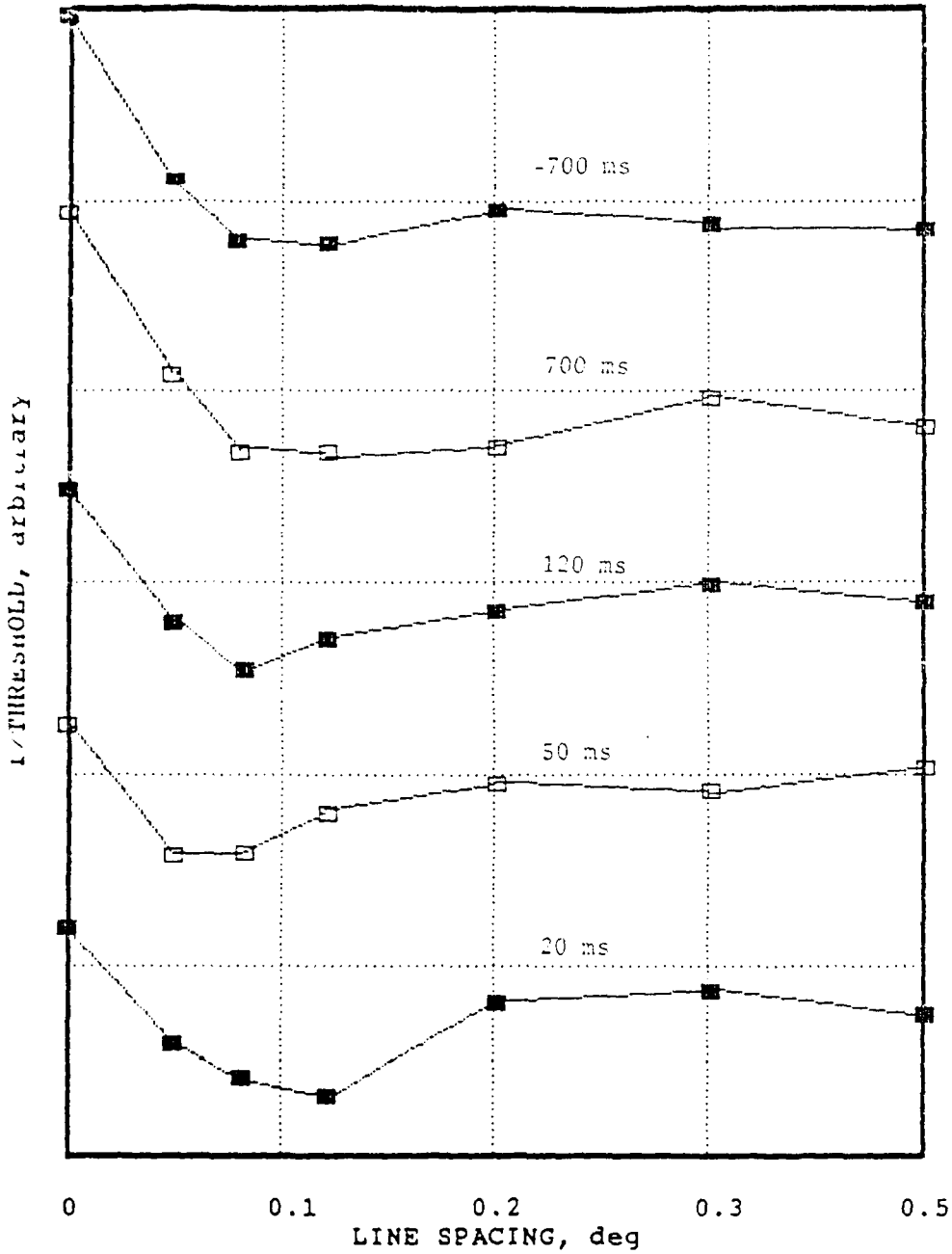


Figure V-2

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.

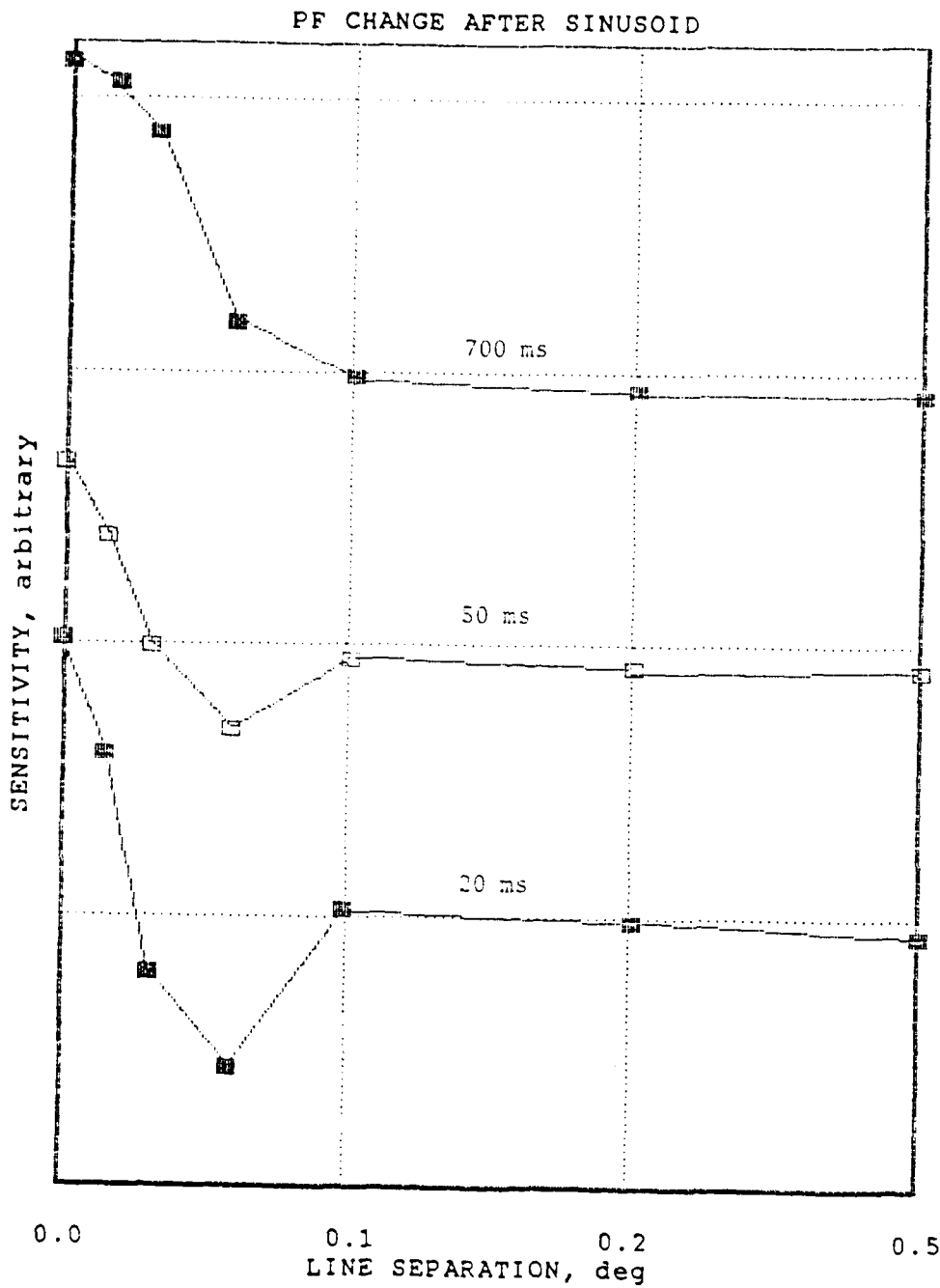


Figure V-3

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

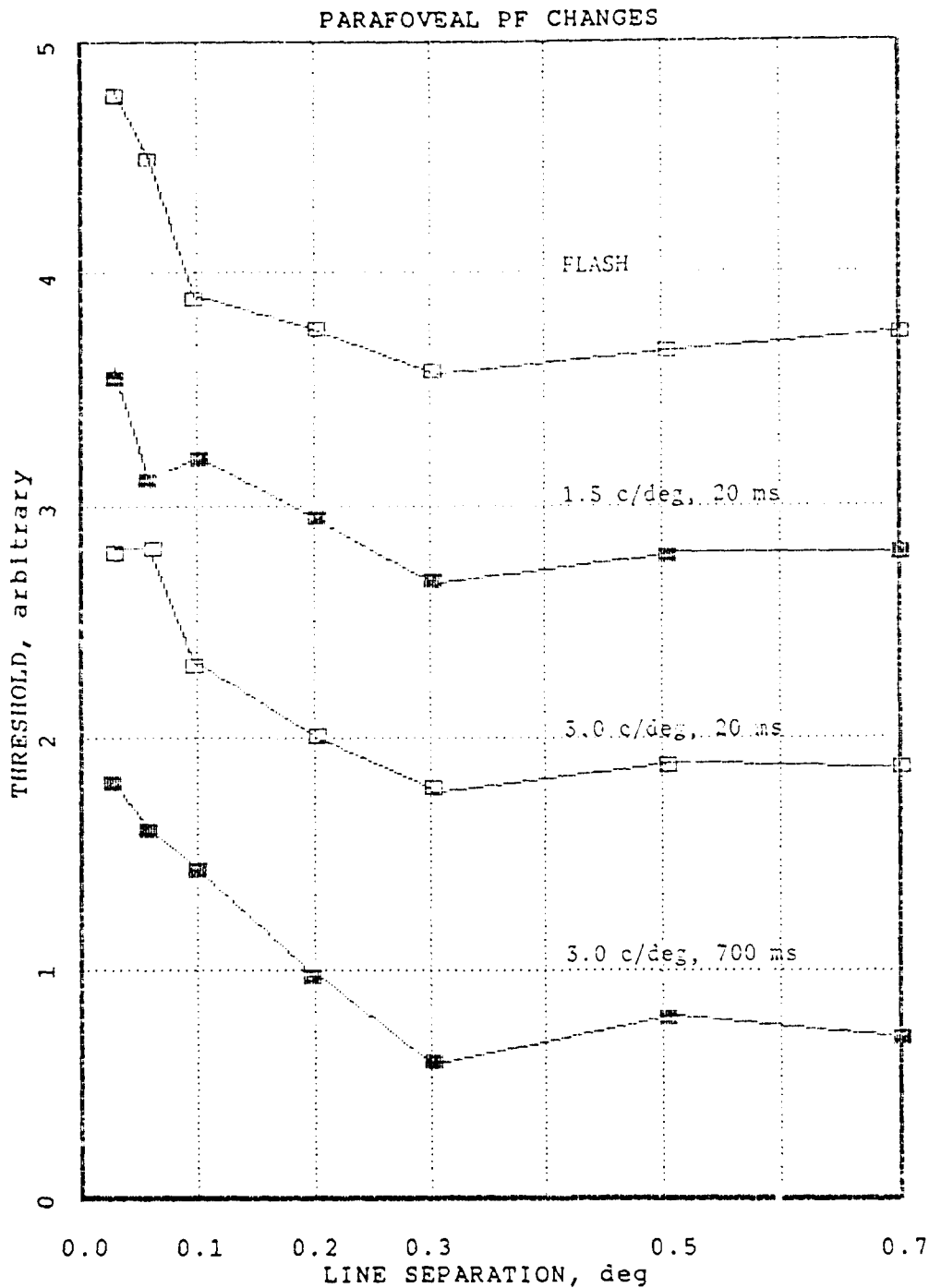


Figure V-4

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

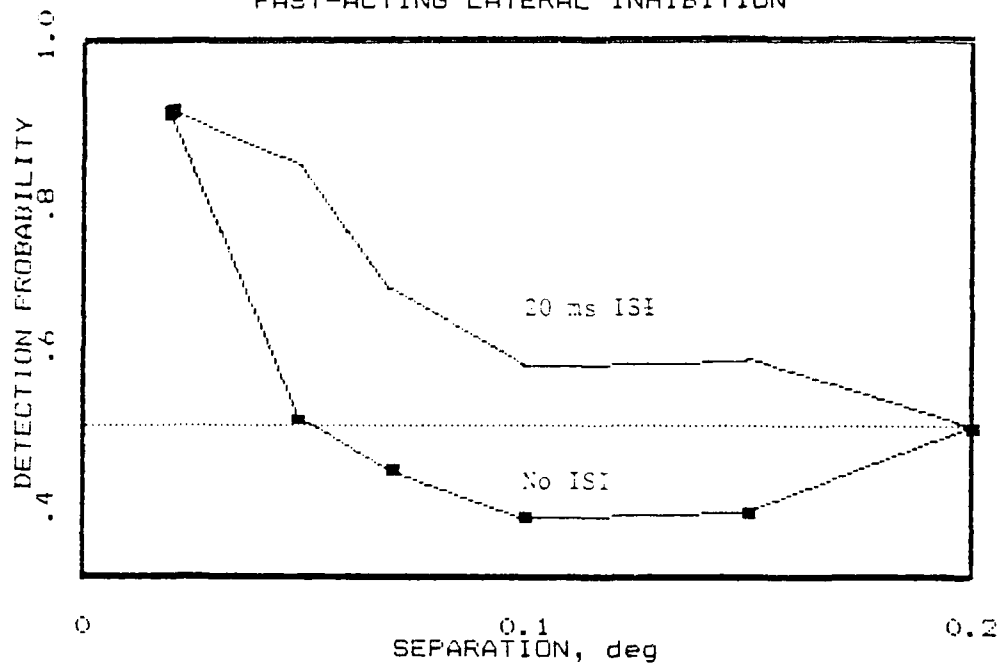


Figure V-5 Detection probability for two simultaneously-flashed lines, as a function of line spacing. The line without symbols shows the results from Figure 6 of the same experiment with a 20 msec delay between the lines.

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 VIII-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.

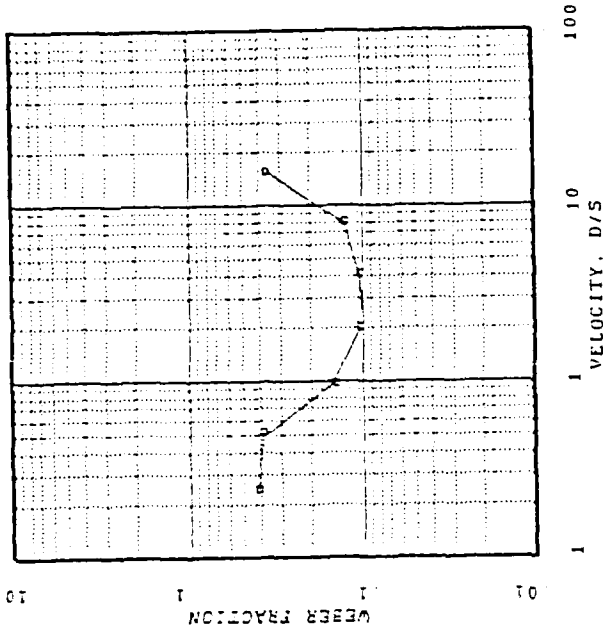
The present experiment demonstrates that this U-shaped velocity sensitivity profile can be seen over much smaller ranges of velocities and has a distinct minimum when the contrast of the stimuli is maintained as a fixed low multiple of contrast threshold. Mandler (1984) used a similarly controlled temporal 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 a interpolation procedure incorporated into the staircase. The reversals were converted to Weber fractions.

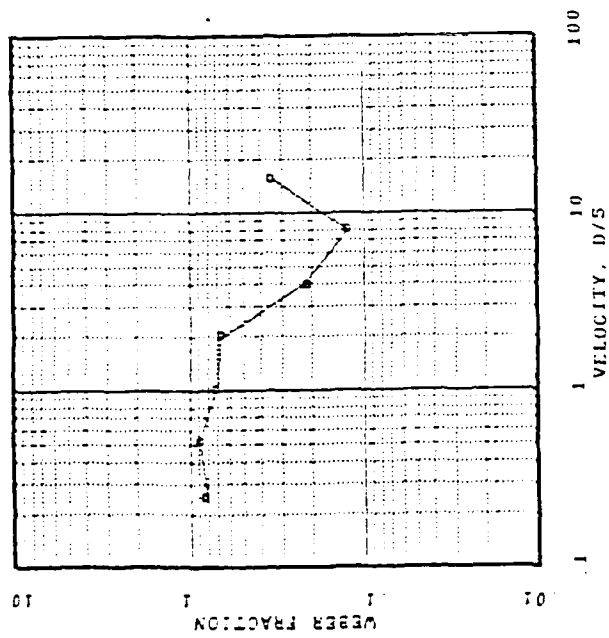
Experiment 1 - Velocity Discrimination - 1 c/d gratings

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 -> 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



KR - 1 G/D GRATINGS
4 X THRESHOLD



KR - 1 G/D GRATINGS
2.25 X THRESHOLD

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 VIII-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.

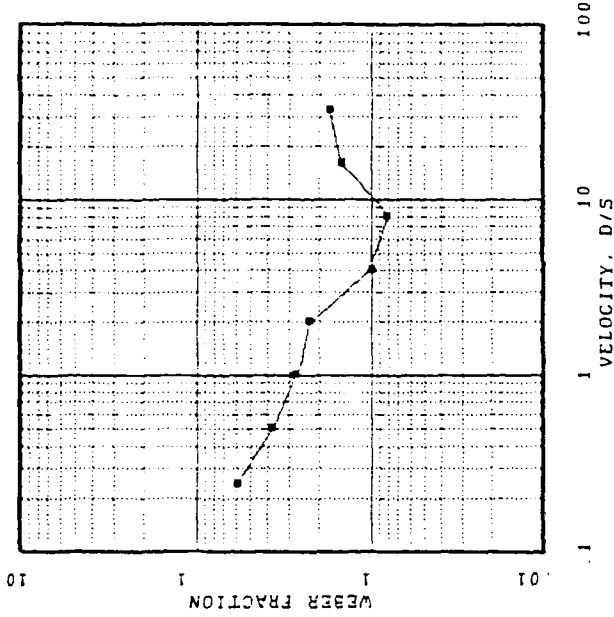
Because these experiments used periodic stimuli, it is difficult to determine whether the channels underlying the discrimination were flicker or velocity sensitive. Additional experiments used non-periodic stimuli to lessen the chances of stimulating flicker sensitive channels.

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

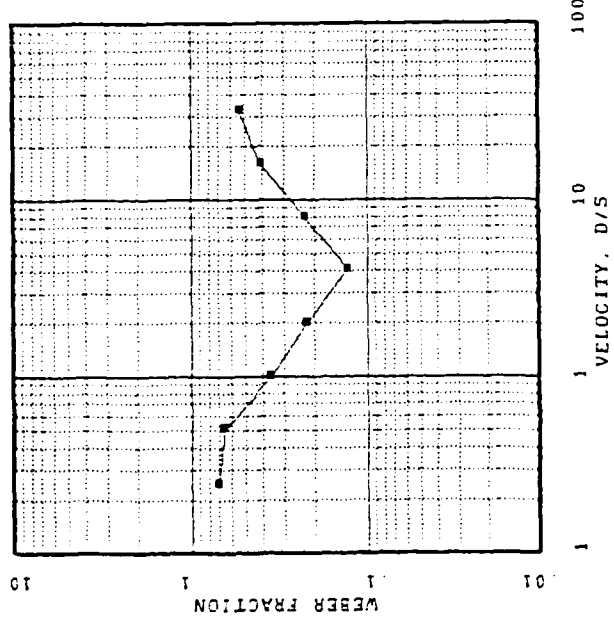
The psychophysical procedure was identical to that of the previous experiment, but all stimuli were gaussian bars with 1 standard deviation equal to .25 degree. These stimuli closely resemble a single positive half-cycle of a 1 c/d grating. The contrast thresholds of these stimuli did not fall off as 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 (artifactual) cue

At 7 degrees eccentricity, both subjects showed an increased

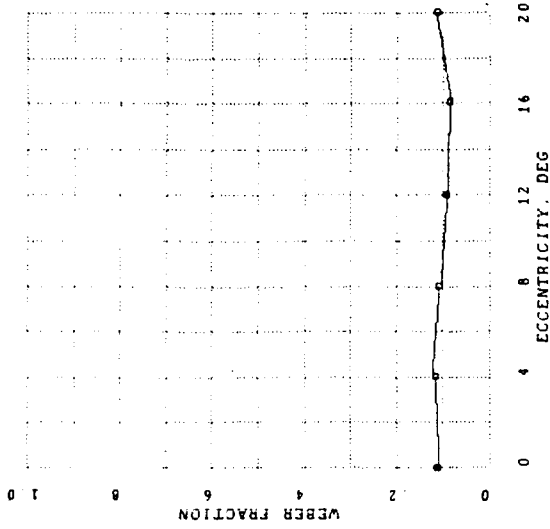


RW - GAUSSIAN BAR - 7 DEG. ECC.
4 X THRESHOLD

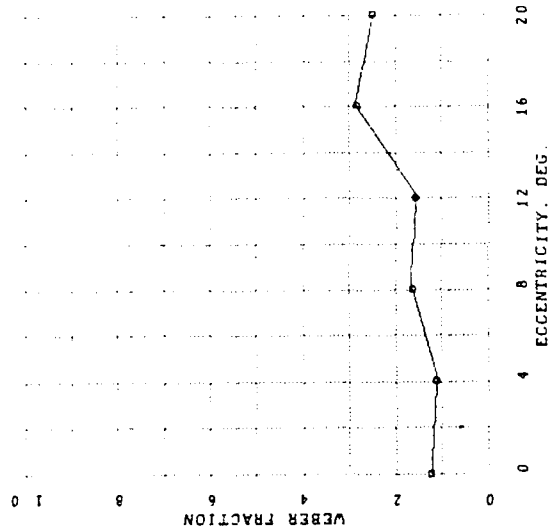


RW - GAUSSIAN BAR
4 X THRESHOLD

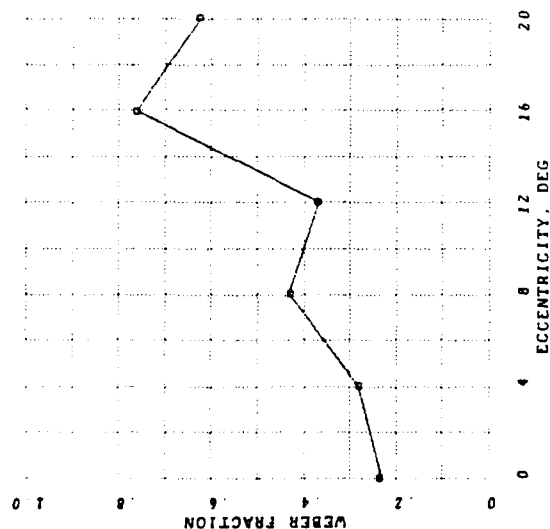
Typical velocity discriminations, central and peripheral, using gaussian bar stimuli. Note that optimal velocity shifts higher with eccentricity. The overall level of performance is similar at both eccentricities, because all stimuli are equally visible.



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



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



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

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 VIII-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 Urban 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 foveal. 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/s

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 Urban have found that scaling for cortical magnification (using the equivalent Minimal Angle of

Velocity discrimination VIII-5

Resolution scaling) can decrease some of the disparity between discrimination functions from foveal and peripheral retina. McKee scaled the data, Urban 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/e 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 Urban(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 VIII-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 VIII-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.

ROBERT A. SMITH, JR.

219 South Road
Deerfield, NH 03037
(603) 463-5503

PERSONAL DATA

Born 4/13/42 6'5" 190 lbs
Married, 2 children
Health - excellent

EDUCATION

Massachusetts Institute of Technology Ph.D 1970 Psychology

Dartmouth College M.A 1969 Physics

Swarthmore College B.A 1964 Physics

PROFESSIONAL AND/OR RESEARCH EXPERIENCE

Research Associate Professor 1984-present Dept. of Psychology
University of New
Hampshire

Research Scientist 1982-1984 Dept. of Psychology
University of New
Hampshire

Adjunct Associate Professor 1973-1981 Depts. of Mechanical
Engineering & Psy-
chology University
of New Hampshire

Research Associate 1970-1973 Dept. of Psychology-
Mass. Inst. of Tech.

PROFESSIONAL SOCIETIES

Optical Society of America
Association for Research in Vision and Ophthalmology

RESEARCH SUPPORT

AFOSR 80-0045 Total \$900,000
"Spatial Frequency Masking and Visibility"
Fall, 1979 - Spring, 1987

NIH EY01475-03 Total \$95,000
"The Motion/Disparity Aftereffect and Tuned Channels"
December 1, 1974 - November 30, 1979

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NIH EY01475-01 Total \$16,397
"The Physiology of Tuned Channels in Human Vision"
September 1, 1974 - September 1, 1976

NSF ENG74-22298 Total \$34,000
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31. The Application of Eirsdall's Theorem to Spatial Frequency Masking. Presented to ARVO, May 1982.

32. Size Discrimination and Fourier Analysis. Presented to ARVO, May 1982.

33. Enhancement of Images in Noise. Presented to AFOSR, May 1982.

34. Space/time interactions between briefly flashed lines Presented to Optical Society of America, Oct. 1983

35. Pixel Flicker: a critical evaluation. Presented to ARVO, May 1984

36. Mapping an elemental motion detector. Presented to AFOSR, May 1984

37. Adaptation to contrast-modulated gratings: evidence for a compressive non-linearity. Presented to ARVO, May 1985.

38. Changes in acuity and spatial summation with retinal locus. Presented to OSA, October 1985.

39. Adaptation to composite gratings: interaction or artifact? Presented to OSA, October 1985.

40. Towards a general model of spatio-temporal contrast sensitivity. Presented to ARVO, May 1986.

41. Foveal and peripheral velocity discrimination near contrast threshold. Presented to ARVO, May 1986.

42. Aliasing with incoherent-light stimuli Presented to OSA, October 1986.

43. Orientation dependence of parafoveal aliasing. Presented to ARVO, May 1987.

44. Two-layer model of visual undersampling. Presented to OSA, October 1987.

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45. Perceived motion reversal in parafoveal aliasing. Presented to OSA, October 1987.

46. Nonlinearities and negative afterimages. Presented to OSA, October 1987.

Steven Chaim Panish
RD #1
Newmarket, New Hampshire 03857
(603) 659-5911

Education: 1974 B.A. Psychology and Fine Arts, Dickinson
College, Carlisle, Pa.
1978 M.A. Psychology, Univ. of New Hampshire,
Durham, New Hampshire
Thesis topic: Psychophysical measurement of
brightness effects in subjective figures
Thesis advisor: Dr. Marty J. Schmidt
1982 Ph.D. Psychology, Univ. of New Hampshire,
Durham, New Hampshire
Dissertation topic: Time course of the
decay of adaptation to spatio-temporal
gratings, with respect to the existence
of spatial and temporal visual mechanisms.
Dissertation Advisor: Dr. Robert A. Smith

HONORS: 1979 Awarded UNH Central University Research Fund
Grant for investigation of the spatial-
frequency shift.
1981 Awarded UNH Central University Research Fund
Grant for investigation of the time-course of
grating adaptation.
1982 Awarded National Institute of Health, Post-
Doctoral Fellowship for study of Behavioral
Effects of Methanol, Ethanol, and Toluene.

RELEVANT EMPLOYMENT:

1975-1977 Research Assistant to Dr. Marty J.
Schmidt, Psychology Dept., UNH
1977-1979 Teaching Assistant, UNH
1976-1980 Project Assistant with Dr. R.A. Smith,
(summers) Mechanical Engineering Dept., UNH
1979-1982 Project Assistant with Dr. R. A. Smith
(academic year)
1982-date Research Scientist II, Vision
Research Lab, Pettee Brook Offices,

TEACHING EXPERIENCE:

1977-1978 Introductory psychology, UNH
 (two semesters)

1978-1979 Perception, Language, and Thought, UNH
 (two semesters - a middle level
 survey course for non-majors)

1980 Manuscript and Thesis Production using
 the DEC-10 System. (a non-credit
 course offered by Academic Computing)

1982 Introduction to BASIC

1982 Wordprocessing with WORDSTAR

PAPERS AND PUBLICATIONS:

Panish, S. and Schmidt, M. Brightness effects in subjective contour patterns: psychophysical measurement. Presented at Eastern Psychological Association, 1978

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Steven Chaim Panish

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DAN J. SWIFT
3812 Hillside Dr.
Ypsilante, Mich. 48197
(313) 572-1226

Born: April 5, 1950

EDUCATION

University of New Hampshire	Ph.D. 1977	Psychology
University of New Hampshire	M.A. 1975	Psychology
Massachusetts Institute of Technology	B.S. 1971	Psychology

HONORS

1968 Received Claire Morton Prince Hanks award for scholarly achievement, M.I.T.

1977 Awarded a Dissertation Year Fellowship from the Graduate School, U.N.H.

PROFESSIONAL AND/OR RESEARCH EXPERIENCE

1981-Present	Assistant Professor,	Behavioral Sciences Univ. of Michigan
1981-Present (summers)	Research Scientist	Vision Research Lab Univ. of New Hampshire
1977-1981	Post-Doctoral Res. Assoc. with Prof. Robert A. Smith	Univ. of New Hampshire
1976-1981	Lecturer	Univ. of New Hampshire
1973-1975	Statistical Consultant	Col. of Liberal Arts Univ. of New Hampshire

PAPERS AND PUBLICATIONS

Panish, S., Swift, D. and Smith, R. Two-criterion threshold techniques: evidence for separate spatial and temporal mechanisms? Vision Research, 23, 1519-1526, (1983).

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