Mach Bands in the Lateral Eye of Limulus

Comparison of Theory and Experiment

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ABSTRACT Patterns of optic nerve activity were computed for stationary step patterns of illumination from theoretical models of lateral inhibition based on revised Hartline-Ratliff equations. The computed response patterns contain well-defined Mach bands which match closely in amplitude and shape those recorded from single optic nerve fibers of the Limulus lateral eye. Theory and experiment show that the amplitude of the Mach bands is reduced by an inhibitory non-linearity, the width of the Mach bands is approximately equal to the lateral dimension of the inhibitory field, but the shapes of the Mach bands are poor indices of the precise configuration of the inhibitory field. Theorems are proved establishing the equivalence of Mach-band patterns for models of different dimensions and a uniqueness condition for solutions of the piecewise linear model.

INTRODUCTION

Neural interactions within a peripheral sensory organ can strongly influence the information transmitted to the brain. Detailed knowledge of the interactions within the organ leads to a better understanding of such information. However, because of the complexity of the sensory organs in most higher animals, such knowledge has generally been limited to the simpler organs of invertebrates. A good example is the lateral eye of Limulus.

The neural interactions among retinal units (ommatidia) in the Limulus eye are predominantly inhibitory (Hartline et al., 1956). The general form of the response pattern of the ommatidia to various patterns of illumination on the retina was predicted by Ratliff and Hartline (1959). They reasoned that retinal inhibition would produce maxima and minima in response to intensity gradients and borders in the visual field and thereby would enhance such stimuli. Their argument was similar to that of Ernst Mach who in 1865 attributed the appearance of light and dark bands at the edges of a penumbra.¹

¹ The light and dark bands are generally called Mach bands (Ratliff, 1965). In this paper the meaning of the term Mach bands is extended to include the patterns of neural activity generated by stationary step patterns of illumination on the retina.

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to reciprocal inhibitory interactions between neighboring units in the human retina. Mach hypothesized that the inhibitory effects were carried with diminishing strength over lateral interconnections of the retina.

The study in 1956 by Hartline et al. clearly established the existence of inhibitory interactions in a physiological system, but did not provide a sufficient basis for analyzing the system in detail. Specifically, the study did not establish the configuration of the inhibitory field, i.e., the relationship between the strength of inhibition and retinal separation. This point was underscored in later work of Ratliff and Hartline (1959). Information on the inhibitory field became available in the interim (Barlow, 1969), and the properties of the inhibitory interactions have been further characterized (Barlow and Lange, 1974). With these data at hand, we decided to investigate further the role of inhibition in processing information in the Limulus eye. It is the purpose of this paper to analyze several forms of a theoretical model describing Mach-band response patterns in the eye of Limulus and to compare the computed response patterns with those measured experimentally. Each of the computed patterns was obtained from calculations performed on an IBM computer at the Watson Research Center in Yorktown Heights, N. Y., and the experimental measurements were made at the Institute for Sensory Research in Syracuse, N. Y.

**THEORY: METHODS AND RESULTS**

**Formulation of the Model**

The theoretical model is based on the following revised form of the Hartline-Ratliff equations for steady-state activity (Lange, 1965):

\[ r_p = [e_p - (1 + a e_p) \sum_{j \neq p}^{n} k_{pj} (r_j - r_p^*)]^+, \quad p = 1, 2, \ldots, n, \quad (1) \]

where the neural response rate \( r_p \) of the \( p \)th receptor unit in an array of \( n \) units is given by the summation of the excitatory and inhibitory influences exerted on it by the other \( n - 1 \) units. The subscript "\( + \)" is an operator defined by

\[ \alpha_+ = \begin{cases} \alpha & \text{for } \alpha \geq 0 \\ 0 & \text{for } \alpha < 0. \end{cases} \]

Barlow and Lange (1974) have given the experimental basis for the nonlinear relationship between the \( r_p \) and the \( e_p \) in the set of equations (Eq. 1). If the constant \( a \) is set equal to zero, Eq. 1 returns to the piecewise linear form derived by Hartline and Ratliff (1958). Both the nonlinear and piecewise linear forms of the equations are used in the following analysis.

We restricted our initial theoretical analysis of the inhibitory system in the
Limbulus eye to a model in which all of the interacting ommatidia were spaced uniformly along a straight line. However, a comparable experimental configuration did not produce measurable changes in response rates because of the weakness of the inhibitory effects exerted among ommatidia in a narrow strip on the retina. Stronger effects with well-defined Mach bands may be elicited from the Limulus eye by illuminating a large region of the retina. To approximate this experimental configuration we developed a two-dimensional model of the inhibitory system. Here we present the results of computations with the two-dimensional model. Results from the one-dimensional model and detailed theoretical treatments of both models are given elsewhere (Barlow and Quarles, 1974).

To compute the desired solutions of Eq. 1 for the two-dimensional model, we prescribed the parameters of that set of equations in the following manner.

**Excitation Pattern** The spatial pattern of excitation simulates a simple step-function distribution of illumination on the retina. The excitation pattern is composed of a "bright" region and a "dim" region separated by a straight-line border and is specified by assigning half of the uninhibited response rates $e_p$ to one constant level and half to another:

$$e_p = \begin{cases} E_1 & \text{for } p = 1, 2, \ldots, n/2 \\ E_2 & \text{for } p = (n/2)+1, \ldots, n, \end{cases}$$

where the even integer $n$ is the total number of receptors for which the response pattern is to be calculated, and $E_1 > E_2 > 0$. The schematic drawing in Fig. 1 illustrates such an excitation pattern for the receptors on a line normal to the border and passing through it.

**Inhibitory Thresholds** We set the thresholds for inhibition $r_{pi}$ in Eq. 1 to zero for all allowed values of $p$ and $j$. This choice was based on preliminary calculations and experimental evidence which indicated that the relatively small thresholds did not play an important role in determining the character of the response patterns for our experimental conditions.

**Inhibitory Field** The spatial distribution of the inhibitory coefficients $k'_{pi}$ characterizes the configuration of the inhibitory field. In a given calculation the configuration of the field was identical for each receptor unit, the coefficients were nonnegative and depended only on the distance, $d_{pi}$, between the $p$th and $j$th receptors. In addition, the coefficients vanished for all sufficiently large distances. We define the radial extent of the inhibitory field as the least positive distance $d$ such that if $d_{pi} > d$, then $k'_{pi} = 0$. It should be noted that each effective coefficient of an inhibitory term in Eq. 1 is represented by the product of a coefficient $k'_{pi}$ with a weighting factor $(1 + ae_p)$ in
in accordance with the inhibitory nonlinearity described by Barlow and Lange (1974).

From the above considerations, Eq. 1 reduces to:

$$ r_p = [e_p - (1 + a e_p) \sum_{j=1}^{n} k'_{pj} f_j] + , \quad p = 1, 2, \ldots, n, \quad (3) $$

in which the summation is taken only over receptors of the model within the radial extent of the inhibitory field from the $p$th receptor.

**INHIBITORY FIELD CONSTRAINTS** Several configurations of the inhibitory field are utilized in the sample calculations described below. In each calculation the inhibitory field is chosen so that the inhibitory coefficient sums $K_p$ and weighted sums $S_p$ as defined by

$$ K_p = \sum_{j=1}^{n} k'_{pj} \sum_{\theta \leq d_{jp} \leq d} \quad p = 1, 2, \ldots, n, \quad (4) $$

$$ S_p = (1 + a e_p) K_p , \quad p = 1, 2, \ldots, n, \quad (5) $$
have prescribed values. From the dependence of the \( k'_{p,i} \) only on distance, the constancy of \( a \), and the specification of the \( \epsilon_p \) in Eq. 2, it follows that \( K_p \) and \( S_p \) must have constant values which we denote by \( K, S^{(1)}, \) and \( S^{(2)} \), where

\[
K_p = K, \quad S_p = \begin{cases} S^{(1)} = (1 + aE_1)K \quad \text{for} \quad \epsilon_p = E_1, \\ S^{(2)} = (1 + aE_2)K \quad \text{for} \quad \epsilon_p = E_2, \end{cases}
\]

for all receptors \( p \) whose distance from the boundary equals or exceeds the radial extent \( d \) of the inhibitory field.

**SPATIALLY-UNIFORM RESPONSE LEVELS** The excitation pattern specified in Eq. 2 contains two uniformly “illuminated” regions. Receptors located in the central part of either region should not be influenced by the border and thus should respond at nearly the same rate. As illustrated in Fig. 1, we denote the spatially uniform response levels of receptors in the bright and dim regions of the pattern by \( R_1 \) and \( R_2 \). From the set of equations (Eq. 1) and the constraints (Eqs. 4–7) we obtain:

\[
R_1 = [E_1 - S^{(1)}R_1]^+, \quad R_2 = [E_2 - S^{(2)}R_2]^+,
\]

which have the solution

\[
R_1 = E_1/(1 + S^{(1)}) \quad R_2 = E_2/(1 + S^{(2)}).
\]

As described below, these relationships specify the numerical values of \( S^{(1)} \) and \( S^{(2)} \) for the calculation of Mach-band response patterns.

**BOUNDARY CONTAMINATION** Our model of the two-dimensional matrix of receptors in the Limulus eye was limited in size. For some calculations, the extent of the inhibitory field was a substantial fraction of the dimensions of the model. Under such conditions boundary effects propagated from one side of the model to the other, and as a result spatially uniform response levels \( R_1 \) and \( R_4 \) were not obtained. Boundary effects are Mach-band phenomena. Receptors located near a boundary of the model respond at relatively high rates because of the relatively small number of neighboring units inhibiting them. The effect decreases for receptors located further from the boundary and disappears only for units separated from the boundary by a distance which is greater than the radial extent \( d \) of the inhibitory field.

Our objective was to compute response patterns produced by a border in the excitation pattern without contamination by boundary effects. In some
cases the direct application of Eq. 3 produced such uncontaminated response patterns, while in other cases the model had to be modified to achieve this result. One way of modifying the model was to enlarge it by increasing the number of receptors, \( n \). This method of modification is limited by the core capacity of the computer. There are, however, several alternative modifications which may achieve the same result without changing the initial choice of \( n \). For example, by choosing only alternate positions in an array of receptors on the retina and correspondingly changing the scale of the inhibitory field, one may form a scaled model for a larger retinal region without increasing \( n \). Any fractional scaling could be performed to reduce the number of receptors in the model required to span a given retinal region, but at the expense of a corresponding reduction in the spatial resolution of the model. A further modification to reduce boundary contamination was to “reflect” the model upon itself at the boundaries. The reflection process in effect equalizes the inhibitory inputs on receptors which are located near boundaries. For the computations described below the reflection process was used in conjunction with fractional scaling. A detailed discussion of the methods for avoiding boundary contamination is given elsewhere (Barlow and Quarles, 1974).

Methods of Numerical Solution

Our main method of numerical solution of Eq. 3 employed standard matrix techniques. To take advantage of these techniques we removed the nonnegativity restriction in Eq. 3. This restriction was met \textit{ex post facto} by selecting only those solutions for which all \( r_p \) are positive. We also required satisfactory solutions to attain the steady levels of response \( R_1 \) and \( R_2 \) in Eq. 8 at positions sufficiently far from the border without contamination of boundary effects. For the range of parameters in our calculations, the solutions for the \( r_p \) are unique due to nonsingularity of the matrices of numerical coefficients.²

A Fourier transform method of solution of Eq. 3 is available for the piecewise linear form of the model, where \( a \) is zero. This method has the advantage of substantially reducing the number of arithmetic operations (Cooley and Tukey, 1965; Dollimore, 1973). We note that Knight (1974) applied the Fourier method to the situation of moving patterns of excitation.

The two-dimensional model we have formulated may be reduced to an equivalent one-dimensional model for certain restricted patterns of excitation and distributions of inhibitory coefficients. Appendix II gives the proof of an equivalence theorem for the models of different dimensions. The theorem may be used to reduce the computational requirements of restricted two-dimensional models.

² In Appendix I we state and prove a uniqueness theorem which provides a necessary condition for the existence of a unique solution of a piecewise linear problem, and demonstrate the incorrectness of a similar result of Melzak (1962).
Mach-Band Response Patterns for Several Configurations of the Inhibitory Field

Before comparing computed response patterns to those measured experimentally, we will first examine the behavior of the model in both its piecewise linear and nonlinear forms. We are particularly interested in any information the Mach-band patterns may contain concerning the configuration of the inhibitory field.

Fig. 2 gives Mach-band response patterns computed for step patterns of excitation where

\[
\begin{align*}
E_1 &= 30 \text{ impulses/s} \\
E_2 &= 10 \text{ impulses/s}
\end{align*}
\]

(9)

Figure 2. Computed Mach-band response patterns. On the left are graphs of the chosen configurations of inhibitory coefficients \( k'_{pj} \) as functions of displacement from a typical \( p \)th receptor. From symmetry considerations, only the values of \( k'_{pj} \) on a line perpendicular to the border of the excitation pattern are shown. The centered Gaussian configuration in A is of the form \( e^{-x^2/60^2} \), and the displaced Gaussian in B can be expressed as \( e^{-(x-5)^2/14^2} \) (Barlow, 1969). The configurations shown above are for unit sums, \( K \), in accordance with Eqs. 4, 6, and 10. On the right are the computed Mach-band response patterns for the piecewise linear (broken curves) and nonlinear (solid) cases. To avoid boundary contamination, the inhibitory fields were scaled by a factor of 0.6 and the model was "reflected" at the boundaries (see text).
were the excitation rates in Eq. 2. The parameters for the inhibitory field constraints (Eqs. 6 and 7) were

\[
\begin{align*}
K &= S^{(1)} = S^{(2)} = 1 \quad \text{when} \quad a = 0 \\
K &= 0.2, S^{(1)} = 1.4, S^{(2)} = 0.6 \quad \text{when} \quad a = 0.2. 
\end{align*}
\]  

(10)

The sums \(K\) for the piecewise linear models were normalized to have the average values of the weighted sums \(S^{(1)}\) and \(S^{(2)}\) for the nonlinear models (when \(a \neq 0\)). The values in Eqs. 9 and 10 are based on the experimental data of Barlow and Lange (1974).

On the left in Fig. 2 are cross sections of the inhibitory fields and on the right are the computed response patterns. The dashed lines were computed with the piecewise linear model and the solid lines with the nonlinear form. The configuration of the inhibitory field in A is a “centered” Gaussian in accord with indirect measurements by Kirschfeld and Reichardt (1964). The field in B is a “displaced” Gaussian based on direct physiological measurements (Barlow, 1969). The annulus in C accentuates characteristics of the displaced Gaussian field. The disk-shaped function in D is similar to that used by Békésy (1960) in his model of the neural unit.

In each computed pattern in Fig. 2 the border between the bright and dim regions of the stimulus is accentuated by maximal and minimal response rates. In most cases, the Mach-band patterns of response undergo damped oscillations between the primary maxima and minima and the steady levels attained far from the border. Such oscillations represent second-order Mach bands which are caused by the differences in response in the neighborhood of each primary maximum and minimum. The appearance of these second-order effects is indicative of the recurrent nature of the inhibitory interactions.

What information, if any, do the Mach bands contain concerning the configuration of the inhibitory field? From Mach's physiological interpretation of human border contrast (see Ratliff, 1965) one might expect the width of the Mach bands (Fig. 1) to be roughly equal to the “diameter,” or twice the radial extent \(d\), of the inhibitory field. Békésy (1960) found this to be true for the Mach bands computed from his relatively simple model of receptor interaction, and this appears also to be true for the computed response patterns in Fig. 2.

Do the Mach-band patterns contain additional information concerning the inhibitory field? Concentrating the inhibition near the center of the field as in A produces patterns in which the response rates tend monotonically to steady levels as the distance from the border increases. Shifting the point of maximum inhibition away from the center of the field as in B and C yields patterns which do not exhibit a monotone behavior but rather contain small second-order effects. Usually strong inhibitory interactions increase the magnitude of these effects (Fig. 3). Thus we conclude that the shape of the Mach-band pattern
contains some information about the configuration of the underlying inhibitory fields, but that the information is indeed limited for the levels of inhibition normally encountered in the Limulus eye preparation.

The inhibitory nonlinearity affects the amplitude of the Mach bands ($\Delta R$ in Fig. 1) but not their shape. For each configuration of the inhibitory field in Fig. 2, the amplitude of the Mach bands is always smaller in the nonlinear case (solid line) than in the piecewise linear case (dashed line). This result might suggest that the nonlinearity decreases the efficacy of lateral inhibition to enhance contrast. However, in each nonlinear case the smaller amplitude is coupled with a smaller difference between the steady levels of response far from the border. If one defines the contrast in a Mach-band pattern as the ratio of the amplitude at the border to the difference of the steady levels of response far from the border, then contrast is little affected by the nonlinearity, the ratio is nearly the same for the corresponding piecewise linear and nonlinear results in Fig. 2.

The inhibitory nonlinearity may, under certain conditions of excitation and inhibition, produce pronounced asymmetries in the Mach bands. For high levels of inhibition and high contrast patterns, the contribution of the “light” band to the total Mach-band amplitude $\Delta R$ is less than that of the “dark” band. Such asymmetries can be detected in the nonlinear cases in Fig. 2. However, the effects are small. We mention them mainly because of their similarity to human psychophysical observations (Lowry and DePalma, 1961). Asymmetries are not observed in the piecewise linear cases. Each broken curve appears to be graphically symmetric about the central point where $r = (E_1 + E_2)/4$ at the border.  

Summary of the Theoretical Results

Solutions were computed for the Hartline-Ratliff equations in both their original (piecewise linear) and revised (nonlinear) forms (Eq. 1). In each calculation the pattern of excitation (Eq. 2) simulated one half of the eye brightly illuminated and the other half dimly illuminated. Parameters (Eqs. 9 and 10) were based on average physiological data. Several configurations of the inhibitory field were chosen, thresholds for inhibition were neglected, and the computations were performed for a two-dimensional matrix of retinal receptors.

The computed solutions contain well-defined Mach bands. The widths of the Mach bands are roughly equal to the lateral dimension of the inhibitory field. The shapes of the Mach bands are relatively insensitive to changes in

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3 Such a symmetry property about the point where $r = (E_1 + E_2)/(2(K + 1))$ may be established for the general linear form of the model equations. A statement and proof of the symmetry theorem, and its corollary which provides border estimates of $E_1 - E_2$ for amplitude and $K + 1$ for contrast, are given elsewhere (Barlow and Quarles, 1974).
the configuration of the inhibitory field: similarly shaped Mach bands can be produced by a variety of field configurations. Apparently, the one necessary condition for border enhancement is that inhibition generally decline with distance on the retina; the exact way it declines is of secondary importance.

The inhibitory nonlinearity reduces the amplitude of the Mach bands and introduces an asymmetry in the response pattern. Neither of these effects strongly influences the physiological contrast in the Mach-band patterns.

EXPERIMENT

Methods

The lateral eye, together with a short length (1 cm) of optic nerve, was excised from an adult Limulus and mounted in a moist chamber. A single active optic nerve fiber, arising from an ommatidium near the center of the eye, was dissected from the optic nerve trunk and placed on a wick recording electrode. The eye was illuminated by a beam of light that passed through a flat Teflon diffusing screen located directly in front of the eye. The diffused light beam illuminated all but the most peripherally located ommatidia. A photographic plate, half of which was blackened to produce a step of 0.6 optical density units, was positioned between the diffusing screen and the cornea. The border of the step pattern was aligned parallel to the dorsoventral axis of the eye. Following the technique of Ratliff and Hartline (1959), the steady-state response of the single unit was recorded and the photographic plate was shifted between records along the anteroposterior axis of the eye so that the one receptor assumed various positions with respect to the step pattern. Records were repeated every 3 min until a detailed response pattern was obtained. A total testing period of 3–4 h was usually sufficient.

One difficulty with this procedure was that only a small percentage of the excised eyes we studied remained stable over a 3- to 4-h period. In most cases the sensitivity of the eye to light declined steadily after the eye was excised from the animal. This problem can be avoided by recording from the optic nerve fibers of the unexcised eye (Barlow and Kaplan, 1971); however, the present study was completed before the intact preparation was perfected. All the results reported here were recorded from excised eyes that elicited stable responses over long enough periods of time to permit accurate measurements of the patterns of optic nerve activity.

Response rates were measured both with and without the effects of inhibition. The inhibitory influences from neighboring ommatidia were eliminated by restricting the illumination to the recorded unit with small aperture (0.3 mm) inserted between the eye and the photographic plate. Response rates measured with and without the effects of inhibition represent the response and excitation rates, respectively, corresponding to the \( r_p \) and \( e_p \) of Eq. 1. This experimental procedure assumes that the recorded unit is representative of all
other units in the eye, an assumption which appears to be reasonable since most receptors in a given eye are similarly affected by light and inhibition.

**Results**

Figs. 3 and 4 compare Mach-band response patterns measured experimentally with those computed from theoretical models. In Fig. 3 the filled circles give

![Comparison of Mach-band patterns measured experimentally with those computed from theoretical models.](image)

the response pattern recorded from a single ommatidium for a step pattern of illumination with no aperture (see Methods). The solid curve is the response pattern computed for the nonlinear form of the revised Hartline-Ratliff equations (Eq. 1), and the broken curve is the pattern computed for the piecewise linear form. Of the two computations, the nonlinear result agrees best with the experimental data.

Fig. 4 gives the response patterns (filled circles) recorded simultaneously from two adjacent ommatidia, A and B. The solid curves are the response
Figure 4. Mach-band response patterns for two adjacent ommatidia, A and B, in a single eye. The filled circles indicate the response rates recorded simultaneously from A and B for three passes of the illumination pattern. The recording from B was lost before completing the third pass. The rectilinear lines give the excitation patterns measured for each ommatidium with a 0.3-mm aperture (see Methods). The curved lines give the Mach-band response patterns computed for the nonlinear form of Eq. 1. Note that theory and experiment correspond well for A but not for B. A possible explanation for this discrepancy is given in the text.

patterns computed for the nonlinear form of Eq. 1. No results for the piecewise linear form are presented in Fig. 4, but excitation patterns are included for both units (see legend). Note that the Mach-band pattern computed for A matches closely the pattern recorded from A. This is not true for B, where the deviation between theory and experiment is significant, especially near the border.

The procedure for computing the response patterns in Figs. 3 and 4 is described in the Theory section. For each experiment the computation required the values of four recorded response rates: the uninhibited rates, $E_1$ and $E_2$, in the bright and dim regions of the pattern, and the response rates, $R_1$ and $R_2$, far from the border in these two regions. The values of $E_1$, $E_2$, $R_1$, and $R_2$ determine from Eq. 8 the weighted sums of inhibitory coefficients, $S^{(1)}$ and $S^{(2)}$. The experimentally measured configuration of the inhibitory field (Bar-
low, 1969) was used in each computation. For the details of a similar computation, refer to the text associated with B of Fig. 2.

The weighted sum $S^{(1)}$ represents the total strength of inhibition exerted on the recorded unit when the unit is located in the brightly illuminated region of the pattern (left-hand side). For example, in the experiment in Fig. 3, $E_1$ is 31.0 impulses/s and $R_1$ is 6.4 impulses/s. The difference of 24.6 impulses/s was caused by inhibition. From Eq. 8 the value of $S^{(1)}$ is 3.9, indicating that the response rate of the recorded unit is reduced 3.9 impulses/s for every 1 impulse/s of response of the neighboring units. $E_2$ is 19.0 impulses/s and $R_2$ is 5.1, giving a value of 2.7 for $S^{(2)}$. These values for $S^{(1)}$ and $S^{(2)}$ are among the highest we have measured from the excised eye. Normally the values range from 0.5 to 2.0 as is the case for the results in Fig. 4. In every experiment $S^{(1)}$ is greater than $S^{(2)}$, furnishing evidence that brightly illuminated ommatidia are more sensitive to inhibition than dimly illuminated units. This property is the basis for the inhibitory nonlinearity (Barlow and Lange, 1974).

Fig. 5 summarizes the results of 11 Mach-band experiments on as many eyes. In each experiment the complete response pattern was measured, but only the amplitudes, $\Delta R$, of the Mach bands are presented in the figure. We chose to display $\Delta R$ because this feature is strongly influenced by the nonlinearity in the inhibitory interactions (see Discussion). The good agreement between the measured and computed values of $\Delta R$ in Fig. 5 provides further support for the revised form of the Hartline-Ratliff equations (Eq. 1).

**DISCUSSION**

Our main objective was to determine a theoretical model that could predict the Mach-band response patterns recorded from the *Limulus* lateral eye. In
most cases the predicted Mach bands agree well with those measured experimentally, as indicated in Figs. 3, 4, and 5. Therefore, we conclude that the revised Hartline-Ratliff equations (Eq. 1), with the inhibitory field measured by Barlow (1969), describe with reasonable accuracy the steady-state interactions among retinal units.

Occasionally the agreement between theory and experiment was poor. We could often ascribe such results to a deteriorated state of the preparation, but this was not always the case. For example, the two Mach-band patterns in Fig. 4 were recorded simultaneously from two adjacent receptors (A and B) in a normal excised eye preparation. Only the pattern recorded from unit A was predicted accurately by the theory. Why did the theory not predict the response of unit B? The answer may be that the configuration of the inhibitory field of the unit B was not adequately represented by the “average” configuration used to compute the response of B. This seems to be a reasonable explanation since not all fields have exactly the same configuration (Barlow, 1969). Another possibility is that the setting of inhibitory thresholds to zero in the computer calculations may have introduced errors for very low response rates such as those recorded from B. However, it appears unlikely that the discrepancy can be satisfactorily explained by threshold considerations, since including nonzero thresholds in several of our model calculations did not change significantly the shapes of the Mach bands but only shifted them vertically on the response axis.

Configuration of the Inhibitory Field

The theoretical results in Fig. 2 show that significant changes in the configuration of the inhibitory fields do not elicit comparable changes in the shapes of the Mach bands. To further investigate this point, we computed two Mach-band response patterns using different field configurations and compared them with the experimental Mach bands shown in Fig. 3. The results are presented in Fig. 6, where the solid curve, A, is based on a displaced Gaussian field (Kirschfeld and Reichardt, 1964). Cross sections of the two fields with different ordinate values are shown in A and B of Fig. 9. Note that the computed Mach bands do not differ markedly in shape from one another or from the experimental data. To judge which theoretical curve best matches the data is indeed difficult, and we conclude that the fine structure of the inhibitory field cannot be readily determined from the shape of Mach bands.

Measurements by Others

Two previous studies have measured Mach bands in the Limulus eye (Ratliff and Hartline, 1959; Kirschfeld and Reichardt, 1964). The results of both studies are in general agreement with ours. Nevertheless, we found that the results of their studies could not be satisfactorily compared with the predictions of the
Mach Bands in Lateral Eye of Limulus

Hartline-Ratliff theory. The Mach bands recorded by Ratliff and Hartline were partially obscured by "edge effects" because the stimulus pattern illuminated less than 10% of the retina. Since the lateral effects exerted by a single ommatidium can extend over 30% of the retina, the response to the border in the stimulus pattern could not be separated from the responses to the edge of the pattern. Such edge effects are the experimental analog of boundary contamination which is described in the Theory. Kirschfeld and Reichardt (1964) eliminated edge effects by illuminating large regions of the retina. However, the variability in their data limited the accuracy of measurement of the shapes of the Mach bands (see Barlow, 1969). Consequently, neither study could serve as an adequate test of the theory.

Mach Bands at Different Levels of Inhibition

That lateral inhibition can produce Mach bands is well established. How the inhibitory interactions govern the characteristics of the Mach bands remains to be determined. One characteristic is the amplitude, $\Delta R$. Figs. 3 and 4 show that small amplitudes are produced by strong inhibition and large amplitudes by weak inhibition. One might therefore conclude that the magnitude of physiological contrast in the Limulus eye is inversely related to the strength of inhibition. This is not the expected result. It is based on the assumption...
that the degree of contrast can be measured by the amplitude of the Mach bands. However, contrast is not an absolute quantity, it is the relative enhancement of the brightnesses of neighboring regions of unequal illumination in the visual field. As described in the Theory, a more appropriate measure of the contrast in Mach bands is the ratio of the amplitude at the border to the response difference far from the border. This ratio is equal to 4.3 for the data in Fig. 3, 2.4 for A of Fig. 4, and 1.8 for B of Fig. 4. By this measure, the degree of contrast is directly related to the strength of the inhibitory interactions. Thus, strong inhibition produces high contrast.

The inverse relationship between Mach-band amplitude and strength of inhibition shown in Figs. 3 and 4 results from the influence of inhibition on the coding of light intensity by the receptor units. Brightly and dimly illuminated ommatidia located far from the border in Fig. 3 respond at about the same rate. The border affects mainly the responses of nearby units. Without a sharp border of separation, regions of unequal illumination may be indistinguishable from one another. The appearance of such regions would depend strongly on the nature of the border. This is a common finding in visual perception (see Cornsweet, 1970; and Ratliff, 1965).

Effect of the Inhibitory Nonlinearity

The tendency for inhibition to equalize the response rates of brightly and dimly illuminated ommatidia results in part from the greater sensitivity of brightly illuminated ommatidia to inhibitory inputs. Such dependence of the sensitivity to inhibition on the incident light intensity introduces a nonlinearity in the Hartline-Ratliff equations (Eq. 1). The nonlinearity has several pronounced effects on the responses of single ommatidia. As mentioned above, one is to reduce intensity coding of units located in uniformly illuminated regions of the eye by "flattening" their intensity functions. An example of this effect is given in Fig. 4 of a preceding paper by Barlow and Lange (1974).

The nonlinearity also reduces the amplitude of the Mach bands. To demonstrate this effect, we begin with the original form of the Hartline-Ratliff equations obtained from Eq. 1 by setting $a$ to zero. We shall assume, as we did in the Theory, that the thresholds for inhibition are also zero. The equations for the responses of two receptors, $u$ and $v$, often take the linear form

$$r_u = v_u - \Sigma k'_{u f j}$$
$$r_v = v_v - \Sigma k'_{v f j},$$

where the summation limits and nonnegativity restrictions are the same as for Eq. 1. Let receptors $u$ and $v$ lie adjacent to one another and on opposite sides of the border in the stimulus pattern in Fig. 1 with $u$ located immediately to the left of the border and $v$ immediately to the right. Under these conditions, the
excitation rates \( e_u \) and \( e_v \) in Eq. 11 equal \( E_1 \) and \( E_2 \), respectively. Subtracting the response of \( v \) from that of \( u \) in Eq. 11 then gives a border estimate of the amplitude of the Mach bands (see Fig. 1):

\[
\Delta R = E_1 - E_2 - (\Sigma k'_{uj} - \Sigma k'_{vj}),
\]

which may be rewritten, with a summation over \( j \) where \( j \neq u \) and \( j \neq v \), as

\[
\Delta R = E_1 - E_2 - \Sigma (k'_{uj} - k'_{vj} r_j).
\]

(12)

Since the inhibitory field of a given ommatidium covers many units and has about the same configuration as the fields of other units (Barlow, 1969) the inhibitory fields of two adjacent ommatidia will be nearly coextensive. Thus \( k'_{uj} \) will approximately equal \( k'_{vj} \) for each value of \( j \), and Eq. 12 reduces to

\[
\Delta R = E_1 - E_2. \quad \text{(Linear theory)}
\]

This is the expected result of the piecewise linear form of the Hartline-Ratliff theory. A more rigorous argument yielding the same result is contained in the corollary of the symmetry theorem (cf. footnote 3).

A different result is obtained from the nonlinear form of the revised Hartline-Ratliff theory. According to this theory, the effective inhibitory coefficients depend not only on the location within the field but also on the excitation rate. The effective coefficients for a brightly illuminated ommatidium are larger than those for a dimly illuminated ommatidium. Thus in Eq. 12, \( k'_{uj} \) is replaced by \((1 + aE_u)k'_{uj}\) and \( k'_{vj} \) by \((1 + aE_v)k'_{vj}\). Since \((1 + aE_u)k'_{uj}\) is larger than \((1 + aE_v)k'_{vj}\) for each value of \( j \), the summation terms corresponding to those in Eq. 12 do not cancel. Consequently, the estimated Mach-band amplitude will be smaller than the step in excitation:

\[
\Delta R < E_1 - E_2. \quad \text{(Nonlinear theory)}
\]

We can carry this analysis one step farther by assuming that the Mach bands are graphically symmetrical about a central point at the border. Then if each \( r_j \) is approximated by the mean of the spatially uniform response rates, \((R_1 + R_2)/2\), we have

\[
\Delta R \cong E_1 - E_2 - \frac{R_1 + R_2}{2} [(1 + aE_1)\Sigma k'_{uj} - (1 + aE_2)\Sigma k'_{vj}].
\]

(13)

From Eqs. 4 to 8 in the Theory, the sums of the inhibitory coefficients can be given in terms of \( E_1, E_2, R_1, \) and \( R_2 \):

\[
\Delta R \cong E_1 - E_2 - \frac{R_1 + R_2}{2} \left( \frac{E_1}{R_1} - \frac{E_2}{R_2} \right).
\]

(14)
This expression relates the response difference of units at the border of the stimulus pattern to the response and excitation rates of units located far from the border. Values of \( \Delta R \) computed from Eq. 14 correspond well with both those measured experimentally and those predicted by the theoretical model and plotted in Fig. 5. Thus, we may conclude that the inhibitory nonlinearity reduces the amplitude of the Mach bands.

**APPENDIX I**

**Existence and Uniqueness of Solutions**

Although we have considerable empirical evidence to support the existence of at least approximate solutions of Eq. 1 for the response rates \( r_p \) when the coefficients \( k'_{pj} \), the constant \( a \), the excitation rates \( e_p \), and the inhibitory thresholds \( r_{pj}^o \) are prescribed in particular ways, little is known concerning necessary or sufficient conditions for the existence of a unique (exact) solution of Eq. 1. What is known regarding such conditions is limited to the piecewise linear form of these model equations which is obtained when \( a \) is zero. Briefly, we shall (a) state and prove a uniqueness theorem which establishes a necessary condition for the existence of a unique solution of a piecewise linear problem, (b) show that the result in (a) proves the incorrectness of a uniqueness theorem of Melzak (1962).

(a) **UNIQUENESS THEOREM** A necessary condition for the existence of a unique solution for the components \( \tilde{r}_p \) of

\[
\tilde{r}_p = e_p - \sum_{j \neq p}^n k'_{pj}(\tilde{r}_j - r_{pj}^o)_+ \quad p = 1, 2, \ldots, n, \tag{15}
\]

when arbitrary nonnegative \( e_p, k'_{pj}, r_{pj}^o \) are prescribed is that the matrix

\[
A = \begin{pmatrix}
1 & k'_{12} & k'_{13} & \cdots & k'_{1n} \\
k'_{21} & 1 & k'_{23} & \cdots & k'_{2n} \\
\vdots & \vdots & \vdots & \ddots & \vdots \\
k'_{n1} & k'_{n2} & k'_{n3} & \cdots & 1
\end{pmatrix} \tag{16}
\]

be nonsingular.

**Proof** Let \( \mathbf{r} \) and \( \mathbf{e} \) denote vectors with components comprised in the order \( p = 1, 2, \ldots, n \) from the \( \tilde{r}_p \) and \( e_p \), respectively, of Eq. 15. Assume that the matrix \( A \) of Eq. 16 is singular. It suffices to show that

\[
AR = e, \tag{17}
\]

does not have a unique solution \( \mathbf{r} \) when some nonnegative \( \mathbf{e} \) and \( r_{pj}^o \) are chosen for which Eq. 15 reduces to Eq. 17. Choose

\[
\begin{aligned}
\begin{cases}
r_{pj}^o = 0 \\e_p = 1 + \sum_{j \neq p}^n k'_{pj}
\end{cases}
\end{aligned} \quad j, p = 1, 2, \ldots, n, j \neq p. \tag{18}
\]
It is easily verified that \( \mathbf{r} \) with components
\[
\mathbf{r}_p = 1 \quad p = 1, 2, \ldots, n,
\]
is a solution of Eq. 15 for the conditions in Eq. 18, and that then Eq. 15 may also be expressed in the form of Eq. 17. Since \( A \) is singular by our hypothesis, \( A \) has a zero eigenvalue and corresponding eigenvector \( \mathbf{e} \) for which
\[
A\mathbf{e} = 0.
\]
(20)

It follows that we may choose a nonzero scalar constant \( c \) such that the vector \( \mathbf{r} + c\mathbf{e} \) has nonnegative components when \( \mathbf{r} \) has the unit components of Eq. 19. Then,
\[
A(\mathbf{r} + c\mathbf{e}) = A\mathbf{r},
\]
and \( \mathbf{r} \) and \( \mathbf{r} + c\mathbf{e} \) constitute two solutions of Eq. 15 or Eq. 17 for the conditions in Eq. 18. The existence of more than one solution establishes the necessity of the condition that the matrix \( A \) of Eq. 16 be nonsingular.

We remark that a sufficient although not necessary condition for the nonsingularity of the matrix \( A \) in Eq. 16 is
\[
0 \leq \sum_{j \neq p}^n k'_{pj} < 1, \quad p = 1, 2, \ldots, n,
\]
which follows from a result of Gerschgorin (1931).

It may be observed that Eq. 1 reduces to Eq. 15 when \( a \) is zero and the \( r_p \) are replaced by the not necessarily nonnegative \( \tilde{r}_p \). Moreover, Eq. 15 is formally the same as the system considered by Melzak. In the notation of the present context, Melzak obtained
\[
\sum_{j \neq p}^n k'_{pj}k'_{pj} < 1, \quad p = 1, 2, \ldots, n,
\]
as a condition for the existence of a unique solution \( \tilde{r}_p \) of Eq. 15 when otherwise arbitrary positive \( k' \) values are prescribed. His conclusion that Eq. 23 is both necessary and sufficient is incorrect, as will be shown below.

(b) INCORRECTNESS OF THE UNIQUENESS THEOREM OF MELZAK

On the basis of our uniqueness theorem and the formal identification of the equations of Melzak with Eq. 15, to show that the result of Melzak is incorrect it suffices to exhibit a singular matrix \( A \) of the form in Eq. 16 with positive entries satisfying the condition in Eq. 23. We shall in fact exhibit two such matrices for the case when the number, \( n \), of receptors is 4. One of these matrices is symmetric \((k'_{ij} = k'_{ji})\) and the other is nonsymmetric, viz.
\[
A = \begin{pmatrix}
1 & 2\varepsilon & \frac{1}{2} + \varepsilon & \frac{1}{2} + \varepsilon \\
2\varepsilon & 1 & \frac{1}{2} + \varepsilon & \frac{1}{2} + \varepsilon \\
\frac{1}{2} + \varepsilon & \frac{1}{2} + \varepsilon & 1 & 2\varepsilon \\
\frac{1}{2} + \varepsilon & \frac{1}{2} + \varepsilon & 2\varepsilon & 1
\end{pmatrix},
\]
(24)
where $\epsilon$ is an arbitrarily small positive number. It may further be verified that when $A$ is the singular matrix of Eq. 24 and the conditions Eq. 18 are prescribed so that $e_p = 2 + 4\epsilon$, then one solution of Eq. 15 or Eq. 17 is given by Eq. 19 and another is

$$ (r + \epsilon\text{p})^T = (2, 2, 0, 0). $$

The same results apply to the singular matrix $A$ of Eq. 25 except that $e_p = 2 + 2\epsilon$, and a second solution is

$$ (r + \epsilon\text{p})^T = (2, 0, 2, 0), $$

instead of Eq. 26.

The examples in Eqs. 24 and 25 show that the requirement of positive data satisfying Eq. 23 is not sufficient to guarantee the existence of a unique solution of Eq. 15, contrary to the conclusion of Melzak in his uniqueness theorem.

**Appendix II**

**Equivalence of Models of Different Dimensions**

We shall show that the particular restrictions imposed upon the prescribed excitation pattern and inhibitory coefficients in our two-dimensional model make possible its reduction to an equivalent one-dimensional model. This result is contained in the following

**Equivalence Theorem** Let $e_p$ be a prescribed step-pattern of excitation as in Eq. 2 over a two-dimensional region $\Omega$ of contiguous receptors, with constant excitation on each parallel to the straight-line border. Assume that, for each receptor $p$ in $\Omega$, the response rate $r_p$ of Eq. 3 satisfies

$$ r_p = e_p - (1 + a e_p) \sum_{j=1}^{n} k'_{pj} f_j, $$

where the distribution of nonnegative inhibitory coefficients $k'_{pj}$ depends only on distance and has radial extent $d$. Then, the $r_p$ are governed by an equivalent one-dimensional model for a subset of $\Omega$ comprising contiguous receptors on a normal to

---

4 "T" denotes transpose.

5 A sufficient condition for the existence of a unique solution of a similar piecewise linear system has been established by Hadeler (1974).
the border. The inhibitory distribution properties of nonnegativity, dependence only on distance, and radial extent $d$ are preserved by the derived equivalent one-dimensional model.

**Proof** From symmetry, $r_p$ has a constant value for the receptors on each line parallel to the border. Therefore, we may replace the sum over a two-dimensional region in Eq. 28 by a sum over a one-dimensional region comprising the receptors on a centrally located normal to the border. This replacement results in the following equations governing the behavior of the $p$th receptor in an equivalent one-dimensional model:

$$r_p^{(1)} = \epsilon_p^{(1)} - (1 + a\epsilon_p) \sum_{j'=1}^{n} k_{p,j'}^{(1)} r_{j'}^{(1)}$$

$$0 < d_{j',p} \leq d,$$

in which the indices $p$ and $j'$ are restricted to the receptors on the centrally located normal to the border contained in the region $\theta$. The superscripts "(1)" in Eq. 29 distinguish equivalent one-dimensional model values defined by

$$\epsilon_p^{(1)} = \epsilon_p / f_p,$$

$$k_{p,j'}^{(1)} = (\sum_{l} k_{p,j',l}') / f_p,$$

$$f_p = 1 + (1 + a\epsilon_p) \sum_{l} k_{p,p,l}'',$$

where a summation with respect to $l$ with an index $q_z$ such as in Eqs. 31 and 32 restricts $k_{p,p,l}'$ to the subset of the $k_{p,j'}'$ of Eq. 28 for the receptors which lie on a parallel to the border through the $q$th receptor. It is apparent from the form of Eqs. 31 and 32 that

![Figure 7](image_url)

**Figure 7.** Configurations of inhibitory fields for equivalent one-dimensional models. The same Mach-band patterns as those displayed in A, B, C, D of Fig. 2 for piecewise linear and nonlinear two-dimensional models may be obtained from one-dimensional models with the configurations A, B, C, D, respectively, of Fig. 7. The equations which relate the excitation levels and inhibitory coefficients for the equivalent models to the corresponding quantities for the two-dimensional models are given in Appendix II.
the coefficients \( k_{p}^{(1)} \) are nonnegative, depend only on distance, and comprise a distribution of radial extent \( d \) as a consequence of the same properties of the \( k'_{p} \). This completes the proof.

In Fig. 7 we display the inhibitory coefficient distributions for the equivalent one-dimensional model which, respectively, correspond to the distributions of Fig. 2 for the two-dimensional model in the case when \( a \) is zero. These \( k_{p}^{(1)} \) values are determined from Eqs. 30 and 31 in terms of the \( k'_{p} \) of Fig. 2. The corresponding excitation levels \( E_{1}^{(1)} \) and \( E_{2}^{(1)} \) for this equivalent model are the values of \( e_{p}^{(1)} \) obtained from Eq. 30 when \( e_{p} \) equals \( E_{1}(=30 \text{ impulses/s}) \) and \( E_{2}(=10 \text{ impulses/s}) \), respectively.

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