Analysis of the Organization and Overlap of the Visual Fields in the Compound Eye of the Honeybee (*Apis mellifera*)

WAYNE WIITANEN and FRANCISCO G. VARELA

From the Biological Laboratories, Harvard University, Cambridge, Massachusetts 02138

ABSTRACT Using the results of an optical analysis, a digital computer technique was developed to analyze the relative excitation produced by arbitrary figures at the rhabdom of the receptors of a compound eye. This technique was applied to several sets of figures for the honeybee (*Apis mellifera*) and a reasonable agreement was found with behavioral data. Similarly, the significance of a fixed cutoff angle for a visual field was investigated. It is concluded that overlap between neighboring ommatidia is highly significant for visual processing in the apposition eye, contrary to the assumptions of the mosaic theory.

INTRODUCTION

The basic assumption of Müller’s mosaic theory of vision (6) is mainly that points of light on the optical axis will excite an ommatidium. Recent workers (5, 13) studying the apposition eye (i.e., an eye in which there is no “cross-talk” between adjacent ommatidia) have indicated that image formation, as in the simple eye, is unlikely because the refractile nature of the crystalline cone would tend to concentrate light onto the rhabdom and would reject off-axis light. In a previous paper (11) we showed that the optical system of the honeybee’s eye does indeed act to reject most off-axis light rays, and that the rhabdom acts as a waveguide. The waveguide nature of the rhabdom in turn implies that image formation, by individual ommatidia, is irrelevant because the incoming energy can be transmitted in only a few discrete modes.

The absence of imaging provides the motivation for defining the light-gathering ability of an ommatidium in terms of an admittance function. By considering the percentage of the lens surface that admits parallel incident rays to the rhabdom, we defined a function that relates the admitting surface area (expressed as a percentage of the entire facet surface) to the angle of incidence of light rays on the surface of the facet. This function is approximated by

\[ f(\theta) = 6.1 \exp(-0.09 \theta), \]
where $\theta$ is the angle of incidence, in degrees. The function is described in detail elsewhere (11).

The bell-shaped form of the admittance function and the symmetry of the field that it describes mean that more points than just those that lie near or on the optical axis of an ommatidium will be able to produce an excitation at the rhabdom. Further, because the optical axes of the ommatidia are, on the average, 1.5° apart, it seems likely that overlap between visual fields is significant. This paper is an attempt to analyze, by means of the admittance function, the significance of the organization and overlap in a given ommatidial visual field.

METHODS

Our approach is a matrix analysis of the excitation pattern produced on the retina by arbitrary figures. This approach is an elaboration of Reichardt's (8) method for one-dimensional excitation in the Limulus eye. Admittedly, the matrix approach is not as accurate as a continuous (or analytical) approach; however, the mathematical difficulties encountered in the latter are severe. In contrast, a matrix analysis is easily done on a high-speed digital computer.

The first problem was to represent the hexagonal array of ommatidial facets as elements in rows and columns of a rectangular array. Because the centers of the facets of alternate rows are aligned over the sutures between the facets of adjacent rows, it is quite easy to make a regular rectangular array out of the intrinsically hexagonal array of the bee's eye. Each row of such a matrix will have two entries for each facet: one for the center of the facet, and one for its (say, left) suture. Similarly, in each column there will be two entries for each facet: the center, and the suture between the two facets in the row above (or below).

In our analysis we used three matrices: (a) a matrix that represented the pattern and intensity of the excitation caused by the stimulus as projected onto the eye—the excitation ($E$) matrix; (b) a matrix that received the final values of the intensity computations, corresponding to a rhabdom—($R$) matrix; and finally (c) a matrix that was used in the transformation from the excitation ($E$) matrix onto the rhabdom ($R$) matrix by means of the admittance function—the filter ($D$) matrix. Each of the matrices will be described in detail below.

Projection of Figures

In describing the excitation matrix, two things must be remembered: there are two spatial coordinates, and there is one intensity coordinate for each stimulus. The first step will be to project an arbitrary surface onto the bee's eye (equivalently, onto the excitation ($E$) matrix). In order to calculate this projection we first have to determine the area encompassed by the projection on the surface of the eye. In order to do so we may capitalize on the solid angle concept.

---

1 We have used $\alpha = 1.5^\circ$ as the interommatidial angle, and have assumed it to be the same in both the horizontal and vertical directions. Del Portillo (7) found that this angle actually increased in the horizontal direction up to $2^\circ 40'$ min. However, we have estimated $\alpha$ directly from electron micrographs, and found that the average interommatidial angle was close to $1.5^\circ$ along any of the three possible axes running through adjacent ommatidia.
Let
\[ x = x(u, v) \]
\[ y = y(u, v) \]
\[ z = z(u, v) \]
be the parametric equations of the surface \( g(u, v) \) under consideration (Fig. 1). Let the pseudocenter of the bee's eye (defined as the center of a sphere whose surface coincides as closely as possible with that of the bee's eye) be taken as the center of a rectangular coordinate system, \( XYZ \). Let the \( Z \)-axis point in the direction of the surface under consideration, passing through the surface of the eye. Since most figures will map onto a limited region of the eye, only a small error is incurred by representing the true surface by a sphere. Let \( S_n \) be the unit sphere \( x^2 + y^2 + z^2 = 1 \) centered at the origin of the coordinate system. By definition, the solid angle \( \Omega(O, S) \), with respect to the origin of the coordinate system \((XYZ)\), subtended by the surface \( S \), is equal to the area \( A_r \) of the portion of the surface of the unit sphere \( S_n \), centered at \( O \), that is cut out by a conical surface with vertex at \( O \) and passing through the perimeter of \( S \). In analytical terms this may be expressed by

\[
\Omega(O, S) = \int_S \frac{\hat{r} \cdot n}{r^2} \, d\sigma
\]

where \( \hat{r} \) is a radius vector from \( O \) to \( d\sigma \) on \( S \), \( r = \| \hat{r} \| \), \( n \) is the outward normal of the surface \( S \) at \( d\sigma \), and \( d\sigma \) is a differential element of the surface \( S \). In terms of the parametric equations for the surface we have (4)

\[
\Omega(O, S) = \int_{R_{uv}} \left| \begin{array}{ccc}
  x & y & z \\
  \frac{\partial x}{\partial u} & \frac{\partial y}{\partial u} & \frac{\partial z}{\partial u} \\
  \frac{\partial x}{\partial v} & \frac{\partial y}{\partial v} & \frac{\partial z}{\partial v}
\end{array} \right| \frac{du \, dv}{(x^2 + y^2 + z^2)^{3/2}}
\]

where \( R_{uv} \) defines the region over which integration is to take place with respect to the parameters of the surface equation. In order to obtain the area, \( A_r \), on the concentric
spherical surface (not necessarily of unit radius) representing the eye, $S_e$, we have

\[ A_e = R_e^2 \Omega(O, S) \]

where $R_e$ is the radius of the bee's eye.

As an example, consider a disc centered on and perpendicular to the $Z$-axis at a distance $a$ from the origin of the coordinate system (at the pseudocenter of the eye). The parametric equations of the disc are

\[
\begin{align*}
  x &= r \cos \theta \\
  y &= r \sin \theta \\
  z &= a
\end{align*}
\]

Then

\[
\Omega(O, S) = \int_0^{2\pi} \int_0^R \begin{vmatrix} r \cos \theta & r \sin \theta & a \\ r \sin \theta & r \cos \theta & 0 \\ -r \sin \theta & r \cos \theta & 0 \end{vmatrix} r \sin \theta \, dr \sin \theta
\]

where $R$ is the radius of the disc. Upon evaluation of the determinant and performance of the integrations it follows that

\[
\Omega(O, S) = 2\pi \left( 1 - \frac{a}{\sqrt{R^2 + a^2}} \right)
\]

Once the area of the surface as projected onto the eye has been determined, elementary trigonometry can be used to obtain any critical dimensions so that the figure may be reproduced accurately on the surface of the bee's eye. By overlaying the pattern thus obtained with a coordinate system corresponding to the rows and columns of the $E$-matrix the spatial matrix representation of the stimulus pattern is obtained.

**The Main Algorithm** When the shape of the stimulus has been transferred from space onto the eye and from there onto the $E$-matrix, only one parameter remains to be evaluated: the intensity. In our studies we assumed that the stimuli were of equal and uniform intensities. We elected to use a normalized admittance function so that all intensities would be relative. This means that the output from the computer may be converted to absolute values by multiplying by a scale factor. We assigned an arbitrary value of 10.0 to each element of the $E$-matrix that belonged to the stimulus pattern.

The filter ($D$) matrix is the crux of the computational method. The dimensions of the $D$-matrix were chosen to be odd (thereby assuring that there is a central element in the matrix) and to be greater than the number of ommatidia and sutures spanned by the entire angular width of the admittance function. For example, the value of our admittance function is virtually zero outside of $8^\circ$ about the optical axis. This $8^\circ$ corresponds to six facets in the horizontal plane and fewer in the vertical. Between facets
are sutures, and those sutures must be included in the D-matrix (because the sutures have been included in the E-matrix—on which the D-matrix will operate). For this reason, the size of the D-matrix for the bee's eye was taken to be 27 X 27, and the central element of the matrix was at $D_{14,14}$. The D-matrix will be filled with weights so that the intensity at the rhabdom, $R_{i,j}$, will be a function of the D- and E-matrices:

$$R_{i,j} = \sum_{k=-14}^{14} \sum_{n=-14}^{14} E_{i+k, j+n} D_{k,n}$$

where elements corresponding to negative values of $i + k - 14$ and $j + n - 14$ are omitted. With this use of the D-matrix in mind we may now interpret its elements: the central element $D_{14,14}$ corresponds to the center of a facet (or suture) at $E_{i,j}$. Other elements of the D-matrix are the weights to be applied to the E-matrix intensity elements in the corresponding positions; the weights measuring the effectiveness of a differential element of area at $E_{i,j}$ in influencing the intensity of the rhabdom at $R_{i,j}$ (Fig. 2).

![Figure 2. Relationship of the matrices used in the computational algorithm to the stimulus.](image)

The weights in the D-matrix are calculated from the angular deviations of each element from the central one and from the admittance function. No attempt has been made to adjust for the small patch of surface area of the admittance function subtended by the equivalent differential of area of the stimulus pattern. Because each element of the D-matrix corresponds to an element of the E-matrix, it follows that each D-matrix element has an angular deviation from the central one ($D_{14,14}$). Along each row (i-axis) the distance between elements is 0.75° (the interommatidial angle is 1.5°). However, the distance along the columns (j-axis) must be derived from spherical trigonometry. Fig. 3 (upper) illustrates the construction used; the formula applied is for a right spherical triangle:

$$\sin d = \sin D \sin \epsilon$$

By substituting $60°$ for $D$ and $1.5°$ for $\epsilon$ we obtain $d = 1°18 \text{ min} (1.3°)$. Thus the facet center to suture spacing in the j direction is $1.3°$. In order to obtain the angular position of an element $D_{i,j}$ with respect to $D_{14,14}$ we use the construction shown in Fig. 3 (lower). Again a right spherical triangle is used, and the formula is

$$\cos \epsilon = \cos a \cos b$$
By letting $u_i$ be the angular distance along the $i$-axis, and $u_j$ be the angular distance along the $j$-axis the formula for $c$ becomes

$$c = \arccos\left[\cos(i'u_i)\cos(j'u_j)\right]$$

where $i' = |i - 14|$ and $j' = |j - 14|$. Once these angles are found they are substituted into the normalized admittance function:

$$D_{i',j'} = \exp[-0.09 \arccos^2(\cos i'u_i \cos j'u_j)]$$

for all $i'$ and $j'$ in the $D$-matrix. This formulation shows that each element of the $D$-matrix is a weight for the corresponding element of the $E$-matrix as it contributes to the total intensity seen at the rhabdom located at $R_{i,j}$.

**Accuracy of the Projection** Because each element of the $D$-matrix is a weight, assigned by treating the element position $(D_{i,j})$ as the equivalent angular deviation of the corresponding $E$-matrix element from the central $D$-matrix element (facet center), it is necessary to show that this correspondence is correct. Fig. 4 is an illustration of the situation in which the point $P$ is the most peripheral point of a stimulus. It is projected down onto the surface of the bee's eye at the point $P'$. We must show that the most distant ommatidium into which $P$ can send rays and have them admitted is the same...
one that would be influenced by the veriest edge of the D-matrix. By the law of sines it follows from Fig. 4 that
\[
\frac{R}{\sin (\pi - \theta)} = \frac{r}{\sin \alpha}
\]
Simplifying we have
\[
\xi = \theta - \arcsin \left[ \frac{r}{R \sin \theta} \right]
\]
For small angles the sine of theta may be replaced by theta (8° is a small angle) and the formula below holds for theta in radians:
\[
\xi \approx \theta - \frac{r}{R \theta}
\]
For large \( R(R \gg r) \) it follows that
\[
\xi \approx \theta
\]
Therefore, a negligible error will be incurred by using the D-matrix and sliding it over the E-matrix as outlined above.

The R-Matrix Rhabdoms are represented by the R-matrix, and receive the results of applying the D-matrix to the E-matrix centered over the facet of the E-matrix corresponding to \( R_{i,j} \). As a practical matter, both the R- and E-matrices must be of the same dimensions, and must be bordered by sufficient zeros to allow the
D-matrix to just reach the edge of the E-matrix when centered at the periphery of the stimulus. In order to obtain values for the intensities in different ommatidia, the i and j indices are selected so as to select each facet in order. This choice of i and j specifies the ommatidium over which the D-matrix is to be centered on the corresponding E-matrix. The process is illustrated in Fig. 2. In this way each ommatidium is given the value of the intensity that it would receive from each element of a stimulus.

Computer Output In order to interpret the results of the computational procedure described above, two types of print-out were obtained: a standard matrix output that gave the intensity of each element in the R-matrix in a tabular format (to eight decimal places), and a matrix of integers from 0 through 9. These 10 classes (0-9) were defined, on a percentage of the maximum intensity found in the R-matrix, as shown in Table I. Subdivision of the intensities into 10 classes was judged to be satisfactory for our purposes. From the integers printed-out we could represent the relative intensity at each rhabdom, due to the specified stimulus figure, in gray tones. The figures in the Results section were obtained by this method.

In order to ascertain quantitatively how different two matrices were, we defined a difference matrix as the difference between the two matrices to be compared. The difference matrix was also printed-out in scaled form on demand. In this case, the integers represent the degree to which the two matrices compared differed in each position, as a percentage of the maximum difference present (see Table I for the integer-percentage correspondences).

RESULTS

The Ommatidial View of Figures The pattern of relative excitation in the bee's ommatidia, produced by several figures, is shown in Fig. 5 (notice that the absolute size of the figures is not relevant here because we may use any arbitrary intensity at the stimulus, and may thus compensate for losses due to distance). As would be expected from the form of the admittance function, the basic shape of the figures is preserved, but distortions are introduced by the overlapping of adjacent ommatidial fields. The star can be clearly distin-
FIGURE 5. Representation of the relative excitations produced at the rhabdoms of an array of ommatidia by the stimulus figures shown. The degree of excitation is indicated by 10 categories of shades, the darkest indicating the highest degree of excitation. (See scale relating the shades used to the integers of Table I.)

Distinguished from the circle, but the circle and the hexagon look remarkably similar. The similarity of the latter two is in good agreement with behavioral evidence: only when there is a difference in the indentation of two figures can bees be trained to distinguish between them (2, 12).

Not all behavioral findings can be explained in terms of the optical properties of the eye alone: bees can hardly distinguish between a striped and an X-shaped figure (12). However, the relative excitation patterns for the two figures are quite different. Thus, it is clear that higher stages in the optic pathway are important for processing information to meet the bee’s needs.
Figure 6. Representation of the relative excitations produced by increasingly more dissected stars (Schnetter series). The difference matrices (star-circle) are indicated in the lowest row. The integers shown represent intensities (see Table I), nine being maximal excitation. (Compare with Fig. 5.)
The Schnetter Training Series In order to obtain more information about the optical basis for shape discrimination, we studied a series of progressively more dissected stars, parallel to the series used in behavioral experiments by Schnetter (9). Schnetter computed the degree of success obtained when bees were trained to discriminate between a star of variable indentation and a circle. The stars differed from one another in perimeter but their surface areas remained the same; they were thus characterized by their degree of indentation, $\Delta K$. Schnetter found that by plotting $\Delta K$ against the number of successes in discrimination (as defined by an appropriate formula), a logarithmic curve was obtained (see inset to Fig. 7).

We studied a parallel series of figures, computing not only the resulting relative excitations, but also the difference matrices between the stars and the circle (see Methods). The results are shown in Fig. 6. The difference matrices provided us with a way of examining the differences of the excitation patterns with respect to the circle for each member of the series of figures. A characterization of the difference matrix was made by simple addition of the entries in it. The lower the value of this sum, $\Delta E$, the less difference there is in the effect of the test figure on the eye relative to the circle. The series of $\Delta E$ values provides a rough optical correlate of the discrimination of figures. When these

---

**Figure 7.** Graph showing three parameters related to the difference matrices in the Schnetter series (see text for details). Abscissa, degree of indentation. Ordinates, left, total excitation measure; right, per cent of maximum excitation, and total number of ommatidia excited. Inset, training success vs. degree of indentation (redrawn after Schnetter [9]).
values are plotted against the degree of indentation, $\Delta K$, the curve shown in Fig. 7 results. The similarity to Schnetter's results is suggestive, and it is reasonable to say, at least in this situation, that the behavioral performance might have a demonstrable basis in the optical properties of the retina.

The increase in $\Delta E$ is not due to an increase in the number of ommatidia that are maximally excited. In Fig. 7 the percentage of the maximum possible

Figure 8 A and 8 B. Representation of relative excitations produced by the two figures at the left when an increasingly larger cut-off angle is used in the computational algorithm. The lowest row shows the difference matrices (star-hexagon). The integers correspond to those in Table I.
excitation of ommatidia is plotted along with the $\Delta E$ values (crosses). This percentage is calculated by (a) replacing all entries in the difference matrix by the maximum grouping value, (b) obtaining by addition a $\Delta E_{\text{max}}$, and, finally, (c) computing the ratio $\Delta E : \Delta E_{\text{max}}$. A similar analysis of the different classes of excitation on the grouping scale showed no striking change in the contribution of any class.

In contrast, the number, $N$, of ommatidia that showed a difference in excitation, that is, the number of nonzero entries in the difference matrix, increases
in parallel with the $\Delta E$ values (Fig. 7, open circles). This indicates that the improvement in the discrimination performance is mainly due to an increase in the number of ommatidia being differently excited rather than to changes in the level of excitation in a fixed group of ommatidia. This increase in the number of ommatidia excited also gives indirect support to the areal component of the form discrimination theory proposed by Wolf and Zerrahn-Wolf (14).

**The Cutoff Series** It is common to find in the literature the term "acceptance angle" referring to a sharp cutoff in the values of the angles that are to be included within the receptive field of an ommatidium. The admittance function (or sensitivity curve) of all the ommatidia investigated so far shows a smooth bell-shaped form (as in the bee) (1, 3, and 10). Much information is discarded by characterizing the visual field by a sharp cutoff, outside of which the ommatidium is essentially blind. However, it is unlikely that the extreme values of the admittance function will be as physiologically significant as the central ones. Presumably, the significance falls as the angle of incidence increases. We approached this problem by calculating a series of $\Delta E$ values based on a series of increasing cutoff values, $1.5^\circ \leq \Delta \theta \leq 8^\circ$, using a hexagon and a star as test stimuli. At each $\Delta \theta$ a $\Delta E$ value was obtained from the difference matrix of the hexagon with the star, as shown in Figs. 8 A and 8 B.

The results of the cutoff series are shown in Fig. 9. The S-shaped form of the

![Graph showing three parameters related to the difference matrices in the cutoff series (see text for details). Abscissa, cutoff angle in degrees. Ordinates, as in Fig. 7.](image-url)
curve (solid circles) suggests that the range (3° to 5.5°) is optimum for discrimination because the changes in the \( \Delta E \) values are largest there. This makes sense from a physiological point of view because it is likely that the extreme values of the admittance function (those greater than 5.5°) will, under most physiological circumstances, produce an excitation too small to elicit a response significant for later stages of information processing.

As in the case of the Schnetter series, the increase in \( \Delta E \) is not due to a change in the general level of excitation. The per cent of the maximum excitation (\( \Delta E: \Delta E_{\text{max}} \)) remains constant (Fig. 9, crosses). The distribution of excitation classes in the grouping system shows no particular trend. No one particular class is mainly responsible for the increase in \( \Delta E \). Again it is the absolute number of ommatidia differently excited that accounts for the increase in \( \Delta E \) (triangles, Fig. 9). This increase in number is mainly due to the number of ommatidia that are differently excited at the edges of the pattern rather than in the center. Thus, in the cutoff series, the fluctuations at the edges seem to constitute useful information and are not just simple random variations.

**Conclusions**

The technique presented here seems satisfactory for studying a compound eye having a known admittance function and geometry. The computer program for actual numerical calculation is included as an Appendix for that reason. It should be emphasized that we have dealt only with relative intensities. For any realistic case the relative values can be transformed to absolute values by simple multiplication. Further, if the relationship between receptor potential and intensity is known then the same multiplicative transformation will yield directly the value of the receptor potential.

The ommatidial view of figures shows that some behavioral data can be explained by the optical organization. However, this does not include the whole behavioral repertoire of the bee. That, behaviorally, discrimination is better for the more dissected figures is correlated with the observation that the number of ommatidia differently excited increases with the degree of indentation of the figure.

The characterization of the receptive field (admittance function) by a simple cutoff value is not satisfactory for the description of the retina—too much information is discarded. However, not all of the range of an admittance function is significant. The central values appear to be the most significant. But, this is not a sharp cutoff and should not be taken as a way of defining a cutoff value. Rather, the visual field should be characterized by the admittance function itself. Consequently, overlap is significant and Müller’s mosaic theory (6) must be rejected as an approximation that, at least for the bee is, simply inaccurate.
The results (and Appendix) presented here should aid in the construction of optically adequate stimuli for electrophysiological studies of visual processing in the bee's nervous system.

Received for publication 1 May 1969.

REFERENCES


W. WIITANEN AND F. G. VARELA  Visual Field Analysis in Honeybee

Appendix

$JOB 101 523700, WIITANEN PATTERN INTENSITIES 12/16/69
$EXECUTE IBJOB
$IBJOB NOLOGIC, NOFILES, MAP
$IBFTC CALLER DECK, FULIST

DISCLAIMER

ALTHOUGH THE AUTHOR HAS TESTED THE FOLLOWING PROGRAMS CAREFULLY,
NEITHER THE AUTHOR NOR THE PUBLISHER MAKE ANY WARRANTY, EITHER
EXPRESSED OR IMPLIED, FOR THEIR CORRECT FUNCTIONING.

AUTHOR.. WAYNE WIITANEN
ADDRESS.. THE BIOLOGICAL LABORATORIES
HARVARD UNIVERSITY
16 DIVINITY AVE.
CAMBRIDGE, MA 02138
DATE.. 5 DECEMBER 1969
LANGUAGE.. FORTRAN IV
MACHINE.. IBM 7094

MAIN PROGRAM TO CALL MATRIX SUBROUTINES

DIMENSION E(50,50), D(27,27), R(50,50)
DIMENSION OLD(50,50)
THIS DIMENSION STATEMENT RESERVES SPACES FOR THE WORKING ROUTINES
CALLED BELOW.

ORDER OF INPUT CARDS

CONTROL CARD -- READ BY THE MAIN PROGRAM (THIS ONE)
TITLE CARD -- READ BY INTENSITY PROGRAM (INTNS)
DATA CARDS -- READ BY INTENSITY PROGRAM (INTNS)

INPUT FORMATS

CARD 1.  DIMENSIONS OF THE E ARRAY I4, IX
NUMBER OF DATA CARDS TO READ I4, IX
DIMENSIONS OF THE OMMATIDIAL FILTER I4, IX
INPUT PRINT CODE I1
0 OR BLANK = DO NOT PRINT E OR D MATRICES
1 = PRINT E MATRIX
2 = PRINT E AND D MATRICES
THIS PARAMETER CONTROLS THE FORMATION OF DIFFERENCE
MATRICES. TO COMPUTE DIFFERENCE MATRICES THE VALUES
OF THE PREVIOUS MATRIX MUST BE STORED AND BE
SUBTRACTED FROM THE VALUES OF THE CURRENT ONE.
SEVERAL OPTIONS ARE AND ARE CODED AS VALUES OF
THIS PARAMETER AS FOLLOWS...
0 = DO NOT COMPUTE THE DIFFERENCE MATRIX, DO NOT
CLEAR THE STORAGE MATRIX.
1 = DO NOT CLEAR THE STORAGE MATRIX, DO NOT
UPDATE THE STORAGE MATRIX, DO COMPUTE THE
DIFFERENCE MATRIX.
2 = DO NOT CLEAR THE STORAGE MATRIX, UPDATE THE
STORAGE MATRIX AFTER COMPUTING THE DIFFERENCE
MATRIX.
3 = CLEAR THE STORAGE MATRIX, UPDATE THE STORAGE
MATRIX AFTER COMPUTING THE DIFFERENCE
MATRIX.
THE ALGORITHMS ARE
(S = STORAGE MATRIX, D = DIFFERENCE MATRIX,
R = RHABDOM INTENSITY MATRIX)
Differencing... \( D(I,J) = R(I,J) - S(I,J) \)

Updating... \( S(I,J) = R(I,J) \)

Admittance cutoff angle \((F8.0)\)

Title card \((12A6)\)

Cards 3 - N.

These cards define the shape of the stimulus and its intensity.

The stimulus is assumed to be rotationally symmetric, and may, for that reason, be confined to the upper left quarter of a pseudo-E-matrix. The center of symmetry is at the lower right corner of the E-matrix.

Format...

\[
\text{IROW,JLO,JHI,VALUE (3(I3,1X),F4.0)}
\]

where:

- IROW = row number of the E-matrix to be assigned values
- JLO = starting column number for assigning values
- JHI = ending column number for assigning values
- VALUE = intensity to be assigned to \( E(\text{IROW,JLO}...\text{JHI}) \)

CONTINUE

READ a control card

READ (5,9001) N,NCARD,NFILTR,ICODE,ICLERS,ANGLE

9001 FORMAT(3(I4,1X),2(I1,1X),F8.0)

IF (NFILTR) 2,2,3

2 NFILTR=27

CONTINUE

CLEAR old matrix

IF (ICLERS-2) 5,5,4

4 DO 10 I=1,N

DO 10 J=1,N

10 OLD(I,J)=0.0

5 CALL INTNS(D,E,R,N,NCARD,NFILTR,ICODE,OLD,ICLERS,ANGLE)

GO TO 1

END

$IBFTC INTENS DECK,FULIST

Main program to analyze intensity patterns at the rhabdom 12/15/69

SUBROUTINE INTNS(D,E,R,N,NCARD,NFILTR,ICODE,OLD,ICLERS,ANGLE)

DIMENSION D(NFILTR,NFILTR),E(N,N),R(N,N)

DIMENSION OLD(N,N)

DIMENSION P(100,100),IP(100,100),TITLE(12)

EQUIVALENCE (P,IP)

READ a title card

READ (5,9000) TITLE

CLEAR E array

DO 4 I=1,N

DO 4 J=1,N

4 E(I,J)=0.0

READ input data
DO 6 K=1,NCARD
READ (5,9002) IROW,JLO,JHI,VALUE
6 CONTINUE
C
C PRINT OUT E MATRIX IF REQUIRED
C IF (ICODE) 12,12,11
11 WRITE (6,9003) TITLE
   WRITE (6,9004) CALL EPC(E,N,N+P,2*N-1,2*N-1,IP,OLD,0)
12 CONTINUE
C
C THIS IS THE MAIN ALGORITHM FOR INTENSITIES
C FIRST SET UP THE D MATRIX (ANGULAR DEVIATIONS ABOUT CENTER)
C IC=NFILTR/2+1
DO 20 I=1,NFILTR
   DO 20 J=1,NFILTR
   D(I,J)=0.O
   Q=COS(O.01309*FLOAT(ABS(J-IC)))*COS(O.02269*FLOAT(ABS(I-IC)))
   Q=ATAN(SQRT(1.O-Q*Q)/Q)
   IF (Q .GT. ANGLE) GO TO 20
20 CONTINUE
C WRITE OUT D-MATRIX IF REQUIRED
C IF (ICODE=1) 21,21,22
21 WRITE (6,9003) TITLE
   WRITE (6,9006) CALL MATOUT(D,NFILTR,NFILTR)
22 CONTINUE
C
C BEGIN EVALUATION OF INTENSITIES VIA SLIDING FILTER
C ITERATE OVER THE R-MATRIX(N..N)
C DO 100 IO=1,N
   DO 100 JO=1,N
      R(IO,JO)=0.O
   IF (MOD(IO+JO,2)).LT.150,100,150
150 IDLO=1
   IF (IO .LT. IC) IDLO=IC-IO+1
   JDO=1
   IF (JO .LT. IC) JDO=IC-JO+1
   DO 200 ID=IDLO,NFILTR
      ...
DO 200 JD=JDL0,NFILTR
   IF (IDLO .GT. 1) IE=ID-IDLO+1
   IF (IDLO .EQ. 1) IE=ID+IO-IC
   IF (JDLO .GT. 1) JE=JD-JDLO+1
   IF (JDLO .EQ. 1) JE=JD+JO-IC
   IF (IE .GT. N) IE=2*N-IE
   IF (JE .GT. N) JE=2*N-JE
200  R(IOtJO)=R(IO,JO)+D(ID,JD)*E(IEJE)
100 CONTINUE

C PRINT OUT THE MATRIX OF INTENSITY VALUES (R MATRIX)
C WRITE (6,9003) TITLE
WRITE (6,9005)
CALL EPC(RNNIP,2*N-192*N-lIPDOLDtICLER)
RETURN

9000 FORMAT(12A6)
9002 FORMAT(3(I3tIX),F4.0)
9003 FORMAT(1H1,31X,21HMATRIX OF INITIAL VALUES FOR PATTERN //)
9004 FORMAT(1H0,31X,36HMATRIX OF INTENSITIES //)
9005 FORMAT(1H0,31X,8HD-MATRIX //)
END

** $IBFTC EPCSR DECK,FULIST
C SUBROUTINE TO EXPAND A QUARTER MATRIX TO A FULL SYMMETRIC MATRIX
C AND PRINT IT.
SUBROUTINE EPC(A,N,M,P,N2,M2,IPOLD,ICD)
C A = MATRIX OF VALUES (QUARTER MATRIX)
C N = NUMBER OF ROWS
C M = NUMBER OF COLUMNS
C P = PRINTOUT MATRIX (SQUARE SYMMETRIC)
C N2 = NUMBER OF ROWS IN P
C M2 = NUMBER OF COLUMNS IN P
C IP = INTEGER NAME OF P
C OLD = NAME OF MATRIX IN WHICH TO STORE PREVIOUS A MATRIX VALUES
C ICD = 0 - NO USE OLD
C 1 -- USE OLD TO FORM DIFFERENCE MATRIX AND PRINT IT OUT
C 2,3 -- USE OLD TO FORM DIFFERENCE MATRIX AND PRINT IT OUT,
C THEN TRANSFER R-MATRIX TO IT.
C
DIMENSION P(N2,M2),IP(N2,M2),A(N,M)
DIMENSION OLD(N,M)

C CHECK FOR EXPANDABILITY
C KSW=0
IF (2*N-1 .LE. N2 .AND. 2*M-1 .LE. M2) GO TO 1
WRITE (6,9000) RETURN

C EXPAND THE QUARTER MATRIX INTO A FULL SYMMETRIC ONE
C
1 DO 10 I=1,N2
 DO 10 J=1,M2
 IP=I
 IF (IP .GT. N) IP=2*N-I
 JP=J
 IF (JP .GT. M) JP=2*M-J

W. WIITANEN AND F. G. VARELA  Visual Field Analysis in Honeybee  323

10 P(I,J)=A(IP,JP)
   IF (KSW) 11,11,12
   C
   C  PRINT OUT MATRIX OF VALUES, P.
   C
   11 CALL MATOUT(P,N2,M2)
   C
   C  SCALE MATRIX FOR CONTOURING
   C
   12 PMAX=-1.0
   DO 600 I=1,N
   DO 600 J=1,M
   600 PMAX=AMAX1(PMAX,A(I,J))
   DO 610 I=1,N2
   DO 610 J=1,M2
   610 IP(I,J)=9.0*P(I,J)/PMAX+0.25
   C
   C  WRITE OUT SCALED MATRIX IN COMPRESSED FORM
   C
   WRITE (6,9001) PMAX
   DO 100 I=1,N2
   WRITE (6,9002) (IP(I,J),J=1,M2)
   100 CONTINUE

9000 FORMAT(1H1,40X,50HMATRIX CANNOT BE EXPANDED DUE TO SPACE LIMITATION
9001 FORMAT(1H1,27X,45HSCALED SYMMETRIC MATRIX OUTPUT FOR CONTOURING
9002 FORMAT(66(1X,I1))

END

$* SIBFTC MATOU DECK,FULIST
C MATRIX OUTPUT SUBROUTINE FOR SINGLE PRECISION MATRICES
SUBROUTINE MATOUT(A,N,M)
DIMENSION A(N,M)
DIMENSION ICOLNO(8)
INTEGER HI
DATA CTL/IH /,BLNK/1H /EJCT/1H1/
C
C  M=NUMBER OF COLUMNS IN THE MATRIX
C  N=NUMBER OF ROWS IN THE MATRIX
C
C  SET PRINT CONTROL CHARACTER TO A BLANK, FIRST TIME THROUGH
CTL=BLNK
C DO WE HAVE TO PARTITION THE MATRIX
IF (M-8) 10,10,20
C NO
10 MM=1
HI=M
GO TO 30
C YES, DETERMINE NUMBER OF SEGMENTS OF COLUMNS
20 MM=M/8
C TEST FOR REMAINDER TO GET RIGHT NUMBER
IF (MOD(M,8)) 24,26,24
C THERE IS AN EXCESS OF COLUMNS - INCREASE MM
24 MM=MM+1
C NUMBER OF COLUMNS IS AN EXACT MULTIPLE OF 8
26 HI=0
30 LO=-7
C DO THE NUMBER OF SEGMENTS REQUIRED
DO 1000 ISEG=1,MM
C SET LINE AND PAGE PARAMETERS
IPAGE=1
ILINE=55
LO=LO+8
C WE ARE NOW IN POSITION TO OUTPUT A SEGMENT OF THE MATRIX
IF (ISEG-MM) 100,200,100
C THIS TAKES CARE OF THE LAST CASE TO SET THE PROPER UPPER LIMIT
200 HI=M
GO TO 300
100 HI=HI+8
300 CONTINUE
DO 2000 IROW=1,N
IF (ILINE-51) 40,50,50
C A NEW PAGE IS REQUIRED
50 ILINE=1
ICOLNO(1)=LO
DO 60 K=2,8
60 ICOLNO(K)=ICOLNO(K-1)+1
WRITE (6,9001) CTLt(ICOLNO(K),K=1,8),IPAGE,ISEG
9001 FORMAT(A1,9X,8I4,4X,6HCOL 13,3X),5HPAGE 12,1H12/4HOROW/)
CTL=EJCT
IPAGE=IPAGE+1
GO TO 42
C INCREASE LINE COUNTER
40 ILINE=ILINE+1
42 IROW=IROW
W. Whitman AND F. G. Varela  Visual Field Analysis in Honeybee

325

WRITE (6,9000) IROW,(A(IROW,ICOL),ICOL=LOHI)
9000 FORMAT(1X,I3,6X,8(I1X,E12.5,1X))

2000 CONTINUE
1000 CONTINUE
RETURN
END

$DATA
0031 0010 0027 0 2 0 026180 CONTROL CARD
STAR DATA -- ADMITTANCE ANGLE = 1.5 DEGREES
022 022 022 10.0
023 023 023 10.0
024 023 025 10.0
025 023 027 10.0
026 024 029 10.0
027 024 031 10.0
028 025 031 10.0
029 025 031 10.0
030 020 031 10.0
031 014 031 10.0

on June 19, 2017 Downloaded from
Published March 1, 1971