Mosaic Arrangement of Ganglion Cell Receptive Fields in Rabbit Retina

STEVEN H. DEVRIES AND DENIS A. BAYLOR
Department of Neurobiology, Stanford University, Stanford, California 94305

DeVries, Steven H. and Denis A. Baylor. Mosaic arrangement of ganglion cell receptive fields in rabbit retina. J. Neurophysiol. 78: 2048–2060, 1997. The arrangement of ganglion cell receptive fields on the retinal surface should constrain several properties of vision, including spatial resolution. Anatomic and physiological studies on the mammalian retina have shown that the receptive fields of several types of ganglion cells tile the retinal surface, with the degree of receptive field overlap apparently being similar for the different classes. It has been difficult to test the generality of this arrangement, however, because it is hard to sample many receptive fields in the same preparation with conventional single-unit recording. In our experiments, the response properties and receptive fields of up to 80 neighboring ganglion cells in the isolated rabbit retina were characterized simultaneously by recording with a multielectrode array. The cells were divided into 11 classes on the basis of their characteristic light responses and the temporal structures of their impulse trains. The mosaic arrangement of receptive fields for cells of a given class was examined after the spatial profile of each receptive field was fitted with a generalized Gaussian surface. For eight cell classes the mosaic arrangement was similar: the profiles of neighboring cells approached each other at the 1-σ border. Thus field centers were 2 σ apart. The layout of fields for the remaining three classes was not well characterized because the fields were poorly fitted by a single Gaussian or because the cells responded selectively to movement. The 2-σ center-center spacing may be a general principle of functional organization that minimizes spatial aliasing and confers a uniform spatial sensitivity on the ganglion cell population.

INTRODUCTION

A retinal ganglion cell “peers out” at a small patch of the visual scene through its receptive field and encodes local features with action potentials that pass through the optic nerve to higher centers (Barlow 1953; Kuffler 1953). An entire scene is encoded piecewise by many ganglion cells whose receptive fields are distributed over the image plane at the retinal surface. These cells can be divided into classes on the basis of differences in morphology and function. The somata of ganglion cells within a class are evenly spaced and the dendrites of neighboring cells fill the available space with minimal overlap (Dacey 1989, 1993; Wassle et al. 1981a–c). This anatomic “tiling” of the retinal surface suggests that each class of ganglion cell independently processes the entire visual scene. Thus the arrangement of receptive fields for cells of a given class is likely to determine many properties of vision. For example, the distance between field centers fixes the maximum spatial resolving power of the representation. Excessive overlap in the fields may lead to undesirable redundancy in the neural representation, whereas too little overlap may lead to local impoverishment or frank blind spots.

The physiological consequences of anatomic tiling have been studied for several ganglion cell classes by measuring the width of the receptive fields and the distance between cell somata. From work on cat β-cells in the area centralis, Wassle and coworkers (Peichl and Wassle 1979; Wassle and Boycott 1991) proposed that the receptive field diameter was well matched to the resolving power of the cell lattice, being large enough to prevent gaps yet small enough to preserve spatial resolution. A similar arrangement of receptive fields was described for cat α-cells (Peichl and Wassle 1981) and rabbit direction-selective (DS) cells (Amthor and Oyster 1995). The lack of population-specific markers and the technical limitations of single-cell recording have prevented extending these findings to other types of ganglion cells, however. Thus it is not known whether the receptive field arrangement inferred for cat α- and β-cells and rabbit DS cells is characteristic of all classes of ganglion cells.

The purpose of this work is to determine whether there is a common arrangement for receptive fields of cells in all classes. The experimental strategy was to monitor the simultaneous activity of up to 80 ganglion cells in the isolated rabbit retina with a multielectrode array (Meister et al. 1994). The cells were classified into 11 groups on the basis of their functional properties. We then examined the spatial extent of the receptive fields and their placement on the retinal surface.

METHODS

The methods for recording with the multielectrode array and analyzing the activity of individual ganglion cells have been described (DeVries and Baylor 1995; Meister et al. 1994, 1995). In brief, pigmented New Zealand white rabbits, 12–18 wk of age, were maintained in darkness overnight and killed in accordance with institutional guidelines. After enucleation under dim red light, the eyecup was hemisected just inferior to the optic nerve head and its radiations and the superior retina was discarded. The remaining eyecup was divided into four pieces of approximately equal area consisting of central, inferior, temporal, and nasal retina. The retina was separated from the pigment epithelium and mounted ganglion cell side down on a glass substrate bearing 61 closely spaced extracellular electrodes. A piece of transparent dialysis membrane pulled taut across a weighted plastic ring was used to hold the retina in place. The exact position and orientation of the retina relative to the array could not be controlled because the retina often shifted laterally when the dialysis membrane was lowered. Most recordings were obtained from the central piece of retina within a region that was ~1–5 mm below the visual streak. Recordings from the other retinal regions gave similar results, with the excep-
tion that receptive fields were generally larger in inferior retina. The retina was stimulated by a Macintosh high-resolution RGB color monitor imaged onto the photoreceptor layer. The stimulus intensity was adjusted by monitor controls and neutral density filters. Mean stimulus intensity in units of \( \text{Rh}^* \cdot \text{rod}^{-1} \cdot \text{s}^{-1} \) was calculated as described in DeVries and Baylor (1995). During stimulation, voltage spikes occurring at each electrode were continuously recorded and their amplitudes, widths, and times of occurrence were stored in a computer. At the end of a recording session the spikes were sorted and assigned to individual neurons (Meister et al. 1994). The retina was continuously superfused with bicarbonate-buffered Ames medium (Sigma) and maintained at 35°C.

Neurons were classified into functional groups by two criteria. The first was the shape of the autocorrelation function of the spike train (Fig. 2B). The autocorrelation function plots a cell’s mean firing rate as a function of time after the occurrence of a spike. In the autocorrelation functions shown, the spike at 0 ms was omitted for clarity and the plots were normalized by the maximum firing rate. Pilot experiments indicated that a dim, randomly flickering stimulus (mean intensity \( \sim 1 \text{Rh}^* \cdot \text{rod}^{-1} \cdot \text{s}^{-1} \)) elicited many spikes from the preparation before leaving the shape of the autocorrelation function very similar to that observed in darkness and dim, diffuse, steady light. The second criterion for cell classification was the time course of the mean effective stimulus, which was obtained by analyzing responses to random flicker stimulation. In this method, the retina was stimulated with a randomly varying checkerboard whose squares were made green or black according to a pseudorandom sequence. A square was 100–150 µm on a side at the retinal surface (35–58 min of visual angle) (Hughs 1971), and the entire pattern was updated continuously at 13.3 or 16.7 Hz. The sequence of patterns imaged on the retina was cross-correlated with a ganglion cell’s spike train to obtain the cell’s mean effective stimulus. This is the stimulus, a function of space and time, that on average preceded the occurrence of a spike. It has units of light intensity. Figure 4A illustrates the spatial dependence of an on center cell’s mean effective stimulus at the temporal maximum. In Fig. 4, intensity was normalized such that +1 and −1 correspond to the high and low intensities in the checkerboard, the average normalized intensity being zero. Actual intensities can be obtained by adding 1 to the normalized value and then multiplying by the mean intensity of the checkerboard stimulus. Thus squares outside the receptive field have an intensity equal to the average intensity of the stimulus. A plot of the time course of the mean effective stimulus (Fig. 2A) was obtained by spatially averaging the stimulus intensity over the center of the profile, with the use of squares whose intensity at the temporal maximum exceeded by a factor of 2.5 the SD of the squares in the background. For comparison, the time courses were scaled so that the background intensity equaled zero and their maxima (or minima) coincided.

A quantitative description of a ganglion cell’s receptive field profile was obtained by fitting the mean effective stimulus, at a time near its peak, by a generalized two-dimensional Gaussian with the use of least-squares minimization. This description ignores the surround, which was weak or absent at the relatively dim intensities used in the experiments. Moreover, with the exception of DS cells, there was no evidence that the form of the spatial profile changed as it scaled up and down in time. The equation for the Gaussian was

\[
f(x, y) = A \exp \left\{ -\frac{1}{2} \left( \frac{(x-h) \cos \theta - (y-k) \sin \theta}{\sigma_x} \right)^2 + \left(\frac{(y-k) \cos \theta + (x-h) \sin \theta}{\sigma_y}\right)^2 \right\}
\]

(1)

where \( x \) and \( y \) are positions on the stimulus grid, \( h \) and \( k \) are the horizontal and vertical coordinates of the receptive field center relative to the origin of the stimulus pattern, \( \theta \) is the angle between the major axis of the receptive field and the pattern grid, \( \sigma_x \) and \( \sigma_y \) are the Gaussian widths along the major and minor axes of the Gaussian, and \( A \) is the maximal receptive field amplitude.

Gaussian fits of receptive fields were diagrammed by plotting the borders of their 1-σ ellipses. The spacing ratio, \( s \), used to express the distance between receptive fields is defined by

\[
s = \frac{d}{r_1 + r_2}
\]

(2)

where \( d \) is the distance between receptive field centers and \( r_1 \) and \( r_2 \) are the center to 1-σ border distances for each receptive field as measured along the line connecting the field centers. Use of the dimensionless parameter \( s \) allowed the layout of receptive fields in different preparations to be compared despite differences in the spatial scale of the field mosaic. The distribution of spacing ratios was examined by constructing a histogram of number of occurrences per unit area versus \( s \). It was necessary to normalize for retinal area because for a random distribution of points in a plane the probability of finding a given point-to-point distance increases linearly with distance in the same way that the area of an annulus of width \( \Delta x \) increases with increasing radius \( r \).

In some experiments we tested the generality of the mean effective stimulus as a measure of the spatial profile of receptive fields. Receptive field diameters obtained from the mean effective stimulus were compared with those obtained with contrast reversal spatial sine wave gratings (Enroth-Cugell and Robson 1966). The gratings had a contrast, \( I_{\max} - I_{\min}/I_{\max} + I_{\min} \), of 1 where \( I_{\min} \) and \( I_{\max} \) are the peak and trough intensities. The mean intensity was 1.5 \( \text{Rh}^* \cdot \text{rod}^{-1} \cdot \text{s}^{-1} \). The spatial intensity profile of the grating was periodically reversed by a temporal sinusoid at 0.5 Hz. Monitor intensities were corrected for the nonlinear relation between command voltage and phosphor emission. At each spatial frequency the retina was stimulated for two 60-s intervals, between which the phase was shifted by 90°. Time histograms of each ganglion cell’s spike train were analyzed by measuring the area under their Fourier transforms at the fundamental frequency. By determining the linear component of a cell’s response at the two different phases, it was possible to calculate the linear component expected at the phase that would produce the maximal response (i.e., centered on the receptive field) (Hochstein and Shapley 1976a). The areas under the 0.5-Hz peak for the 0° and 90° phase-shifted stimuli were used to calculate the area expected for a centered stimulus with the use of the simultaneous equations

\[
A_1 = A_{\max} \cos (\theta)
\]

\[
A_2 = A_{\max} \sin (\theta)
\]

(3)

where \( A_1 \) and \( A_2 \) are the areas of the fundamental for 0° and 90° phase-shifted stimuli, respectively, \( A_{\max} \) is the area for the centered stimulus, and \( \theta \) is the unknown position of the receptive field center relative to the origin of the stimulus. \( A_{\max} \) was then plotted as a function of the spatial frequency of the stimulus. Unlike contrast sensitivity ver-
sponse versus spatial frequency plots may be subject to distortions when the stimuli are weak. For X and Y cells in cat, these distortions are reportedly not significant (So and Shapley 1981).

The effective diameters of the center and surround of the receptive field were obtained by fitting plots of $A_{\text{max}}$ versus spatial frequency with a sum of two Gaussian curves

$$y = k + A_1 \exp\left[ -0.5(s/\sigma_1)^2 \right] + A_2 \exp\left[ -0.5(s/\sigma_2)^2 \right]$$

where $y$ is the center/surround profile of the receptive field measured along the sine wave axis, $k$ is a constant offset, $A_1$ and $A_2$ are the amplitudes and $\sigma_1$ and $\sigma_2$ are the Gaussian widths of the center and surround mechanisms, respectively (in units of spatial frequency), and $s$ is spatial frequency.

The profile of the field center obtained with sinusoidal gratings was compared with that obtained by fitting the spatial part of the mean effective stimulus. For this comparison, the checkerboard stimulus had the same mean intensity as the sine wave stimulus. Because the axes of the Gaussian surface fitted to the mean stimulus were usually not orthogonal to the sine wave grating, it was necessary to calculate the effective “aperture,” $\sigma_{\text{eff}}$, that the Gaussian presented to the sine wave by integrating the receptive field along the $Y$-axis of the sine wave

$$f(x) = \int F(x, y) dy$$

where $F(x, y)$ is $\text{Eq. 1}$ and $f(x)$ is a one-dimensional Gaussian curve of width $\sigma_{\text{eff}}$.

**RESULTS**

We characterized the mosaic arrangement of receptive fields for ganglion cells of different functional types. Evidence that different types of cells were recorded by the array is presented in Fig. 1, which shows the diverse response patterns of 16 simultaneously recorded neurons in a preparation stimulated with a dim, full-field pulse of light. Cells 1–7 (Fig. 1, left) fired at increased rates during the light pulse. Cells 1–4 fired a burst of spikes only at the onset of the pulse, whereas cell 6 fired at a high rate throughout the pulse. Cells 9–14 (Fig. 1, right) fired at an increased rate in the dark. Cells 9–11 gave a burst at pulse off, whereas cells 12–14 fired at a low rate in the dark, were suppressed during the pulse, and fired at slightly increased rates at pulse off. A few cells gave only weak responses to the full-field pulse (e.g., cells 8, 15, and 16), as observed previously where $y$ is the center/surround profile of the receptive field for several types of rabbit ganglion cells (Levick 1967). Although some rabbit amacrine cells may generate spikes (Bloomfield 1992), we could not distinguish between spikes generated by ganglion cells and displaced amacrine cells, which make up 20% of the neurons in the ganglion cell layer (Vaney 1980). We assume that a majority of the recorded cells were ganglion cells. Responses similar to those illustrated in Fig. 1 were observed in >50 retinas.

**Cell classification**

We classified cells with the use of the mean effective stimulus from random flicker stimulation and the autocorrelation function of the spike train. The mean stimulus time courses and autocorrelation functions of cells within a class had nearly identical shapes and were distinct from those of other classes. Of the 11 classes derived, 9 are apparently similar to those reported previously (Amthor et al. 1989a,b; Caldwell and Daw 1978; Levick 1967), and for simplicity we have adopted the previous terminology. Because we used different criteria for classification than earlier studies, the class name assignments are tentative. The classes identified and the percentage of cells in each class are shown in Table 1. The properties of 10 of these classes are described below. The properties of ON center $\eta$-cells, a newly identified class, will be described in a later paper.

**FIG. 1.** Responses of 16 ganglion cells recorded simultaneously. Bar below traces: timing of light stimulus, which was spatially uniform and produced $\sim1$ Rh+·rod $^{-s}$·$^{-s}$. Each response histogram is normalized by peak spike rate (shown at left). Bin-width: 50 ms. Average of 10 repetitions. *Inset:* positions of ganglion cells on array estimated by triangulation (Meister et al. 1994). Eighteen other cells (not illustrated) were recorded at same time in this preparation.
Figure 2, A and B, shows the mean effective stimulus time courses and autocorrelation functions of three simultaneously recorded ON center cells. The cells had relatively biphasic time courses that superimposed closely after normalization. The time course suggests that the cells fired, on average, ~160 ms after a dark-to-light transition in the center of their receptive fields. For comparison, the photocurrent in isolated rabbit rods also reaches its peak ~160 ms after a very dim flash (measured at 38–41°C) (Nakatani et al. 1991). As shown in Fig. 2B, the autocorrelation functions of the three cells had similar shapes when vertically scaled. Consistent with the shape of the autocorrelation function, spike trains contained doublets or triplets with an interspike interval of ~3 ms, often followed by another doublet 15–35 ms later. At the onset of a light pulse, these cells fired a high-frequency burst of spikes (see Fig. 1, cells I and 2) and thus are likely to correspond to the previously described ON brisk transient (ON BT) cells (Amthor et al. 1989a; Caldwell and Daw 1978). Another class of ON center cell had a more monophasic time course and an autocorrelation function that rose after a brief interval to a single peak followed by a plateau. Results from three simultaneously recorded cells are shown in Fig. 2C and D (different retina from that shown in Fig. 2, A and B). These cells fired at a high maintained rate throughout a light pulse and at a reduced rate in the dark (see Fig. 1, cell 6), suggesting that they correspond to the previously described ON brisk sustained (ON BS) cells (Amthor et al. 1989a; Caldwell and Daw 1978).

Figure 2, E–H, shows the properties of two types of OFF center cells. The three cells whose time courses and autocorrelation functions are shown in Fig. 2, E and F, typically fired a transient, high-frequency burst of spikes following a light pulse (see Fig. 1, cells 9–11). These cells apparently correspond to the previously described OFF brisk transient (OFF BT) cells (Amthor et al. 1989a; Caldwell and Daw 1978). The cells whose time courses are shown in Fig. 2G and whose autocorrelation functions are shown in Fig. 2H typically fired at a moderate rate (5–40 spikes/s) in the dark, and firing was suppressed by a light pulse (see Fig. 1, cells 12 and 13). Both the pulse response and the relatively monophasic time course suggests that these cells may correspond to the previously described OFF brisk sustained (OFF BS) cells (Amthor et al. 1989a; Caldwell and Daw 1978).

A third type of OFF center cell (Fig. 2, I and J) had a biphasic time course whose peak was delayed relative to that of the other two types of OFF cells. The autocorrelation function had a characteristic shape, declining from a peak value to baseline over 40 ms. These cells fired at moderate rates in the dark (<30 spikes/s), and firing was suppressed by a light pulse (see Fig. 1, cell 14). These cells could not be associated with a previously described cell type in the rabbit retina and will be termed OFF center delayed cells. Figure 2, K and L, illustrates the behavior of a class with unusually small receptive fields. The mean effective stimulus time courses were much more prolonged than those of other types of ON and OFF center cells (note the change in time scale) and the minimum interspike interval obtained from the autocorrelation function was considerably longer than those of the other cell types. A full-field light pulse produced a weak response during the pulse, followed by a stronger response beginning ~1 s after the pulse. The small spatial extent of the receptive field suggests that this class may correspond to the local edge detector (LED) cell of Levick (1967) (Amthor et al. 1989b), although some properties, including responses to full-field stimuli, are not typically associated with LED cells.

Figure 3, A and B, illustrates the behavior of a cell whose response properties are similar to those of ON-OFF DS cells (Barlow et al. 1964; Oyster 1968; Oyster and Barlow 1967). The mean effective stimulus profile indicated that this cell preferentially responded following a darkening in the center of its receptive field. The dark region appeared to move across the retinal surface. The approximate contours of the region are shown at 30-ms intervals in Fig. 3A (see also Fig. 8B). The peak velocity, calculated from the profile centers, was ~1.25 mm/s or 7.5°/s. If the envelope of all of the contours is used as a measure of receptive field area, the receptive field size is comparable to that previously found for ON-OFF DS cells (Amthor et al. 1989b; Yang and Masland 1992). The arrow in Fig. 3B shows the correspondence between the direction of movement of the mean stimulus profile and the direction of best response to drifting sine wave gratings. Altogether, >200 ganglion cells exhibited the behavior illustrated in Fig. 3, A and B. The mean effective stimulus profiles were usually OFF center at the dim stimulus intensities used (DeVries and Baylor 1995), although fields with both ON and OFF components, moving one after the other in the same direction, were sometimes observed. Figure 3C shows a plot of preferred direction for all the members of this class in a single preparation. Four orthogonal directions of motion sensitivity are apparent. The response properties and arrangement of preferred directions are characteristic of ON-OFF DS cells (Barlow et al. 1964; Oyster 1968; Oyster and Barlow 1967).

In addition to ON center η-cells, three other classes of ganglion cells were identified. The properties of ON center DS cells and putative ON and OFF center sluggish cells (Cleland and Levick 1974) will be briefly described. The drifting sine wave stimulus revealed a second type of DS cell that was distinguished from ON-OFF DS cells by having an ON center profile that did not traverse the retinal surface. ON DS cells (Oyster...
FIG. 2. Functional properties of ON-OFF direction-selective (DS) cells. A: superimposed, normalized mean effective stimulus time courses of 3 ON brisk transient cells in 1 preparation. Mean stimulus intensity was 4.1 Rh−rod−1 s−1 (—). Peak amplitudes before normalization: 4.75 (red), 6.62 (green), and 6.48 (blue) Rh−rod−1 s−1. Mean time-to-peak: −161 ms. B: normalized autocorrelation functions for same cells. Peak rates before normalization: 264 (red), 536 (green), and 396 (blue) spikes/s. C: superimposed, normalized time courses of ON brisk sustained cells. Mean stimulus intensity: 2.3 Rh−rod−1 s−1. Peak amplitudes before normalization: 2.45 (red), 2.43 (green), and 2.46 (blue) Rh−rod−1 s−1. Mean time-to-peak: −147 ms. D: normalized autocorrelation functions for same cells. Peak rates before normalization: 69 (red), 87 (green), and 31 (blue) spikes/s. E: superimposed, normalized time courses of OFF brisk transient cells. Mean stimulus intensity: 2.4 Rh−rod−1 s−1. Peak amplitudes: 2.13 (red), 2.17 (green), and 2.10 (blue) Rh−rod−1 s−1. Mean time-to-peak: −164 ms. F: normalized autocorrelation functions for same cells. Peak rates: 289 (red), 175 (green), and 153 (blue) spikes/s. G: superimposed, normalized time courses of ONN brisk sustained cells (mean stimulus intensity: 2.4 Rh−rod−1 s−1). Peak amplitudes: 1.69 (red), 1.79 (green), and 1.86 (blue) Rh−rod−1 s−1. Mean time-to-peak: −178 ms. H: normalized autocorrelation functions for cells. Peak rates: 446 (red), 528 (green), and 336 (blue) spikes/s. I: superimposed, normalized time courses of OFF delayed cells (mean stimulus intensity: 2.4 Rh−rod−1 s−1). Peak amplitudes before normalization: 2.04 (red), 2.06 (green), and 2.07 (blue) Rh−rod−1 s−1. Mean time-to-peak: −225 ms. J: normalized autocorrelation functions for cells. Peak firing rates: 247 (red), 209 (green), and 126 (blue) spikes/s. K: superimposed, normalized time courses of 3 local edge detector cells (mean stimulus intensity: 4.9 Rh−rod−1 s−1). Peak amplitudes: 3.82 (red), 3.72 (green), and 3.32 (blue) Rh−rod−1 s−1. Mean time-to-peak: −320 ms. L: autocorrelation functions for same cells. Peak rates: 38 (red), 41 (green), and 43 (blue) spikes/s.

1968; Oyster and Barlow 1967) could be reliably distinguished from ON-OFF DS cells by the ability of the metabotropic glutamate receptor agonist 2-amino-4-phosphonobutyric acid to block their responses at midscotopic to mesopic light intensities (DeVries and Baylor 1995). The time courses of ON and OFF center sluggish cells were biphasic, like those of ON and OFF BT cells, but more extended in time, with times-to-peak that were intermediate between those of the brisk and LED cells. The autocorrelation functions of sluggish and LED cells had a similar shape, but the minimum interspike intervals were also intermediate between those of the brisk and LED cells.

Ganglion cells from all 11 classes were frequently observed in a single retina, allowing their mean stimulus time courses and autocorrelation function shapes to be directly compared (Table 2). Within a retina, mean stimulus time-to-peak for a given cell class was reduced by a factor of 2 as mean stimulus intensity was increased from 1 to 104 Rh−rod−1 s−1. However, at each intensity, the time courses of cells in a class were tightly grouped in a manner similar to that illustrated in Fig. 2. In a sample of >50 retinas, the mean stimulus time-to-peak for a cell class could vary by as much as 25% from one preparation to the next at the same stimulus intensity. However, the relative ordering of peak times for the various classes was maintained across preparations. The shapes of autocorrelation functions of the cells within a class were strikingly similar within a preparation but varied somewhat between preparations.

Quantitative characterization of receptive field position and extent

A generalized Gaussian surface was fitted to the peak of the mean effective stimulus to obtain a quantitative index of the position and extent of a ganglion cell’s receptive field. As viewed along the Z-axis, the Gaussian was allowed to have elliptical contours and was specified by parameters describing the amplitude of the peak, its width along the major and minor axes, and the inclination and position of the Gaussian relative to the checkerboard grid. A Gaussian fit to the mean stimulus profile of an ON BT cell is illustrated in Fig. 4. Figure 4A shows a plot of light intensity versus retinal position at the peak of the mean stimulus. Cross-sectional views (Fig. 4B) compare the fit and the experimental results at higher resolution. Contour plots (not shown) revealed that the experimental profile had an elliptical shape and was well fitted by the Gaussian. The profiles of 9 of the 11 classes of ganglion cells were similarly well fitted by the generalized Gaussian surface (Fig. 5). The Gaussian failed to provide a good fit, however, in the following cases. 1) The profiles of ON-OFF DS cells moved across the retina. Although a single generalized Gaussian provided a good fit...
TABLE 2. Properties of mean effective stimulus and autocorrelation functions of ganglion cells in one retina

<table>
<thead>
<tr>
<th>Cell Type</th>
<th>Time-to-Peak, ms</th>
<th>Minimum Interspike Interval, ms</th>
<th>Field Area, μm²/10⁹</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean</td>
<td>Range</td>
<td>Mean</td>
</tr>
<tr>
<td>ON BT</td>
<td>176</td>
<td>172–185</td>
<td>2.4</td>
</tr>
<tr>
<td>ON BS</td>
<td>171</td>
<td>160–182</td>
<td>5.3</td>
</tr>
<tr>
<td>OFF BT</td>
<td>157</td>
<td>153–162</td>
<td>2.5</td>
</tr>
<tr>
<td>OFF BS</td>
<td>189</td>
<td>187–191</td>
<td>2.9</td>
</tr>
<tr>
<td>ON sluggish</td>
<td>204</td>
<td>194–213</td>
<td>9.5</td>
</tr>
<tr>
<td>OFF sluggish</td>
<td>229</td>
<td>224–237</td>
<td>7.7</td>
</tr>
<tr>
<td>LED</td>
<td>286</td>
<td></td>
<td>1.3</td>
</tr>
<tr>
<td>off delayed</td>
<td>226</td>
<td>224–227</td>
<td>3.5</td>
</tr>
<tr>
<td>ON η</td>
<td>177</td>
<td></td>
<td>3.3</td>
</tr>
</tbody>
</table>

Values are given for time-to-peak of mean stimulus, minimum interspike interval of autocorrelation function, and area within 1 σ boundary of mean effective stimulus profile at its peak. For comparison, receptive field areas measured by Amthor et al. (1989a,b) are included. Comparison is qualitative because areas were measured with different techniques and at slightly different eccentricities. In addition to cells tabulated, 12 ON-off DS and 3 ON DS cells were identified in this preparation. Five cells were not classified. Areas were not calculated for OFF BS cells due to poor fit by single Gaussian.

Receptive field mosaics

Our purpose was to determine how the receptive fields of ganglion cells of a given class are laid out. This was examined by plotting the 1-σ ellipses from the Gaussian fits. Figure 6, A–D, shows plots for ON BT, OFF BS, OFF delayed, and OFF sluggish cells in seven different preparations. The plots show that the receptive fields frequently met near their 1-σ borders, the receptive field centers being ~2 σ apart. This result is not an artifact of the regular placement of electrodes in the array, because the interelectrode spacing is narrow (70 μm) compared with the center-center spacing of the receptive fields in Fig. 6, A–D (250–500 μm). More-

FIG. 5. Characterization of fit of mean effective stimulus profile by generalized Gaussian surface for several ganglion cell classes. Stimulus profile amplitude is plotted against fit amplitude for 8 representative classes. For 7 of the 8 classes, plot closely approximates straight line with slope of 1 (——). Profiles of all cells in given class in retina were first normalized by maximum amplitude of their Gaussian fit. Individual plots of profile vs. fit amplitude were combined and profile values (means ± SE) were calculated for each 0.1-unit bin of fit amplitude. Each of the 8 plots was obtained from a different retina. Cell class, number of cells in each plot, and mean stimulus intensity (Rh⁺·rod⁻¹·s⁻¹), respectively: OFF BT, 3, 2.2; OFF BS, 5, 2.2; OFF delayed, 4, 0.66; LED, 7, 4.9; ON BT, 6, 0.66; ON BS, 3, 1.6; ON sluggish, 3, 2.2; ON-off DS, 10, 1.6. Successive plots are displaced by 0.7 units along abscissa for clarity.
over, a similar pattern of receptive field overlap was seen for LED cells (Fig. 6E), which had very small receptive fields.

The plots in Fig. 6 suggest that the centers of neighboring receptive fields were separated by $2\sigma$. This impression was confirmed by plotting the distribution of center-center spacings for ON BT, ON BS, OFF BS, and OFF delayed cells in 35 retinas (Fig. 7). Here, the center-center spacing was normalized according to Eq. 2, so that a ratio of 1 indicates that neighboring receptive fields met at their $1\sigma$ borders. As is evident from the histogram, a cell’s $1\sigma$ border extended past the center of the neighboring receptive field (ratio $\leq 0.5$) only twice in 122 pairs of ON BT cells and never for the other three cell types. Spacings $>1.5$ were frequently encountered because all receptive fields in a class were included in the histogram plot, and many were not nearest neighbors (e.g., a regular trigonal array will have spacings of $\sqrt{3}A3$ and 2). If we assume that a spacing of $<1.5$ is produced by adjacent cells and exclude all pairs with a greater spacing, then the first peak in the histogram can be approximated with a normal distribution. For the cell classes shown, the mean spacing was close to 1 (range of means = 0.93–1.06). The spacing histogram for pairs of OFF BS and OFF delayed cells is shown in Fig. 7 as a control (inset). The distribution declines monotonically, consistent with two independent mosaics (Wassle et al. 1981a, c).

Spacing histograms were also plotted for ON and OFF center sluggish, ON center $\eta$, and LED cells. These cells all had relatively small receptive fields and were less frequently encountered than cells with large receptive fields. Figure 6, D and E, illustrates that small field size and lower recording percentages decreased the chances of recording from nearest neighbors, and this in turn skews the spacing histogram toward larger values. Nonetheless, the spacing histograms (Table 3) were consistent with a ratio of 1. Thus the receptive fields of 8 of the 11 recognized ganglion cell classes had a $2\sigma$ center-center spacing. Overlap in the three remaining classes was not analyzed because the receptive fields of OFF BT and ON-OFF DS cells were not well fitted by a single Gaussian surface. Although ON DS cell profiles were well fitted by the Gaussian surface, the existence of subclasses responding to specific stimulus orientations and the low overall probability of recording from these cells made it difficult to characterize the mosaic arrangement of their receptive fields.

**Receptive field mosaics of ON-OFF DS cells**

In histological preparations, ON-OFF DS cells can be distinguished from other retinal ganglion cells by their bistratified morphology (Amthor et al. 1989b). Tracer injections into neighboring ON-OFF DS cells typically show extensive over-
lap of dendritic trees. However, on occasion, tracer injected into one ON-OFF DS cell passes into neighboring ON-OFF DS cells through putative gap junctions, revealing a population of cells whose processes tile the area with minimal overlap (Vaney 1994). The interpretation is that the tracer-coupled cells all respond to motion in the same direction and that there are four independent mosaics corresponding to the four directions of motion selectivity. Experiments in which the direction selectivities of tracer-injected cells were characterized were consistent with Vaney’s interpretation (Amthor and Oyster 1995), although the sample of cells was small.

Figure 8 shows the mean effective stimulus profiles of four simultaneously recorded ON-OFF DS cells with similar directional selectivity. The movement of the cells’ mean effective stimuli is apparent in the plot of the 1-σ ellipses of the Gaussians fitted to successive frames of the mean stimulus. These ellipses may give only an approximate measure of field width, because ON and OFF center components in an ON-OFF DS cell’s receptive field may cancel each other when the mean effective stimulus is calculated. Moreover, although the profile of each stimulus frame is well fitted by a single generalized Gaussian surface (Fig. 5), it has been reported that the receptive field profiles of ON-OFF DS cells fall off rather steeply (Yang and Masland 1992). Nevertheless, it is evident that the profiles of adjacent fields approach each other near their 1-σ borders. The receptive fields of ON-OFF DS cells sensitive to the other three directions of motion were characterized in the same preparation and overlap those shown in Fig. 8. Partial mosaics were obtained for each of the other subclasses.

Measurements of receptive field diameter with spatial sine wave gratings

Determining the mean effective stimulus provided a rapid method to find the position and size of many receptive fields. The generality of the results obtained with this method was tested by stimulating with a series of contrast reversal spatial sine wave gratings (Enroth-Cugell and Robson 1966) whose single Gaussian or because the cells responded selectively to the fundamental sine wave gratings (Enroth-Cugell and Robson 1966) whose single Gaussian or because the cells responded selectively to the fundamental sinusoid reversed sinusoidally in time at a frequency of 0.5 Hz. Figure 9 plots the area under the peak at the fundamental temporal frequency as a function of the spatial frequency of the sinusoid (filled circles) for two cells in the same retina (Hochstein and Shapley 1976a). The dashed line is the least-squares fit to the sum of two Gaussian curves (Eq. 4) representing the center and surround (with widths \( \sigma_c \) and \( \sigma_s \)). The thick gray line plots the profile of the center component alone (\( \sigma_c \)), whereas the solid black line plots the center obtained by fitting the mean effective stimulus (Eq. 5, \( \sigma_{eff} \)) scaled to the same maximal amplitude. The center profiles obtained with both methods agree quite well. Values for \( \sigma_c \) (center) and \( \sigma_s \) (surround) obtained with sinusoids, and values for \( \sigma_{eff} \) obtained from the mean effective stimulus are shown for five simultaneously recorded cells in Table 4, which includes results from the two cells shown in Fig. 9. Differences in \( \sigma_c \) and \( \sigma_{eff} \) were <15%. Similar results were obtained in a total of 18 cells in four retinas. The agreement in the results obtained by the two methods is satisfactory.

Effect of background light intensity on receptive field size

In the cat retina, increasing the background light intensity increased the strength of the antagonistic surround in a ganglion cell’s receptive field (Barlow et al. 1957), reducing the apparent diameter of the center. Clearly, receptive fields could not continue to meet at the 1-σ points if their diameters changed significantly. With the use of the spatial profile of the mean effective stimulus, the receptive field diameter was measured over a 4-log-unit range of background intensity from midscotopic to low photopic. This range was limited at lower intensities by the ability to obtain receptive field profiles with the use of the checkerboard stimulus and at higher intensities by the maximum intensity available from the stimulator. OFF BT and ON-OFF DS were excluded from the sample because their fields were not well fitted by a Gaussian surface. In one retina, center diameters decreased by an average of 12.2% (range = -33.0 to +4.0%, \( n = 6 \) fields) when background light intensity was increased over a 4.2-log-unit range. These results and those from three additional retinas in which mean stimulus intensity was varied over a 2.8- to 4.2-log-unit range beginning at midscotopic intensities showed that receptive field center diameter shrank by \(-3.7 \pm 1.8\%\) (mean \( \pm \) SD, total of 21 cells) with each log unit increase in mean stimulus intensity. Most of the decrease likely resulted from strengthening of receptive field surrounds at higher light intensities (Barlow et al. 1957). These measurements suggest that receptive field centers maintained their 2-σ center-center spacing up to low photopic light intensities.

Discussion

The receptive fields of cells in 8 of the 11 functional classes we have identified shared a common mosaic arrangement: the fields had Gaussian sensitivity profiles and their centers were spaced at 2-σ intervals. The mosaic arrangement of the fields of cells in the other three classes did not fit this pattern because their profiles were poorly fitted by a single Gaussian or because the cells responded selectively to motion.

It seems unlikely that sampling bias can explain the 2-σ spacing that we observed. Over 250 pairs of neighboring ganglion cells were studied in four classes (Fig. 7), yet only twice did the receptive fields show extensive overlap (e.g., spacing ratio \( \approx 0.5 \)). Low ratios should have been observed more frequently if greater overlap were characteristic of the underlying population. Furthermore, the observed cell densities suggest that on some occasions we recorded from all of the neighboring ganglion cells of a given type in the region. Thus the average density of ON BT cells from two preparations in which an apparently full mosaic was observed was 19.5 mm\(^{-2}\) (Fig. 6A), whereas that for OFF BT cells in a single retina was 16 mm\(^{-2}\). Anatomically determined densities of ON and OFF \( \alpha \)-cell somata of 4–10 mm\(^{-2}\) have been reported at eccentricities 1–5 mm below the visual streak (Peichl et al. 1987), where most recordings were obtained. Similarly, the density of ON-OFF DS cells, estimated from the outlines of the profiles in Fig. 8, was 16 mm\(^{-2}\), whereas the anatomic density of ON-OFF DS cells with a given preferred direction varies between 20 and 55 mm\(^{-2}\) at eccentrici-
FIG. 8. Mosaic arrangement of time-dependent receptive fields of 4 simultaneously recorded ON-OFF DS cells with same directional selectivity. A: fits of generalized Gaussian surface to mean effective stimulus profiles of 4 cells at 30-ms intervals, 1-σ border of Gaussians being shown. Profiles moved in rightward direction. Time of stimulus frame relative to spike is color coded as follows: −435 ms, gray; −405 ms, blue; −375 ms, light blue; −345 ms, turquoise; −315 ms, green; −285 ms, light green; −255 ms, yellow; −225 ms, pink; −195 ms, orange; −165 ms, red; −135 ms, purple. Stimulus frames fitted with Gaussian surface ranged (top to bottom) from −345 to −135 ms, from −435 to −255 ms, from −375 to −195 ms, and from −435 to −255 ms before spike. Width of hexagon showing borders of array: 545 μm. Profiles moved at maximum velocities corresponding to 5–10° of visual angle per second. Mean stimulus intensity: 1.6 Rh* rod s−1. B: mean effective stimulus frames for bottom cell at −435, −375, −315, and −255 ms before spike. Normalized intensities are shown (scale bar at right). Stimulus frames were smoothed by cubic spline interpolation (DeVries and Baylor 1995).
Functional consequences of 2-σ spacing

The mosaic arrangement of receptive fields described here may have two useful functional consequences.

PROTECTION AGAINST ALIASING. The highest spatial frequency that can be faithfully represented by a 1-D array of uniformly spaced detectors is determined by the requirement that there be at least two detectors per period. Frequencies above this limit will be aliased, indistinguishable from lower frequencies. Somewhat similar considerations apply for sampling by 2-D arrays of detectors. In the primate fovea, potential aliasing in the cone array is minimized by optical blur, which attenuates high spatial frequencies prior to sampling (Williams 1986).

What additional aliasing of the visual image is introduced as the retinal ganglion cells sample the output of the photoreceptor array? In the foveal region of the primate retina there are one-to-one connections between cones and ganglion cells, so that no additional aliasing should be introduced. In the retinal periphery, however, the photoreceptor spacing is much smaller than that of the ganglion cells, and optical blur remains similar to that in the central region (Jennings and Charmin 1981), so that high-frequency spatial information is present at the output of the photoreceptors. Additional aliasing due to sampling by the ganglion cells will, however, be opposed by spatial low-pass filtering by the ganglion cell receptive fields, at least those in which linear spatial summation occurs. The filtering and sampling expected for an idealized version of the field mosaic described here is illustrated in Fig. 10. The Nyquist frequency for the trigonal lattice is $1/2\sqrt{3}$ (Fig. 10A). Figure 10B shows that at this frequency the signal amplitude is reduced about fivefold by low-pass filtering by the ganglion cell receptive field. Thus potential aliasing in the neural representation of the input is significantly lowered.

LEVEL SENSITIVITY PROFILE FOR A CELL POPULATION. Although ganglion cell tiling implies that there are no gaps in the sensory surface formed by a cell class, the 2-σ spacing observed here has a more specific benefit: the 2-σ spacing is the widest that still gives a “level” sensitivity profile for the summed receptive fields. This is illustrated in Fig. 11. In Fig. 11A, left are the idealized Gaussian field profiles belonging to one ganglion cell class in a patch of retina. The spacing between adjacent receptive field centers is 2 σ. The surface on the right was obtained by summing the heights of the Gaussians on the left. The summed profile is level to

![Fig. 9](image91x552 to 268x729)

**TABLE 4.** Comparison of diameters of receptive field centers determined by two methods

<table>
<thead>
<tr>
<th>Cell Type</th>
<th>Sine Wave Grating</th>
<th>MES Center</th>
<th>% Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Center</td>
<td>Surrounded</td>
<td></td>
</tr>
<tr>
<td>ON BT</td>
<td>157</td>
<td>1,165</td>
<td>167</td>
</tr>
<tr>
<td>ON BT</td>
<td>152</td>
<td>3,191</td>
<td>174</td>
</tr>
<tr>
<td>OFF BS</td>
<td>155</td>
<td>549</td>
<td>156</td>
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<tr>
<td>OFF BS</td>
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<td>442</td>
<td>220</td>
</tr>
<tr>
<td>ON BS</td>
<td>151</td>
<td>298</td>
<td>149</td>
</tr>
</tbody>
</table>

Widths of receptive field centers (μm) were obtained by fitting mean effective stimulus (MES; Eq. 5, $a_{\sigma}$) and by analyzing responses to spatial sine waves (Eq. 4, $a_\sigma$). Surround width (Eq. 4, $a_\sigma$) is also shown. Percent differences are for center widths. Results are for all ON BT, ON BS, and OFF BS cells in one preparation.

![Fig. 10](image354x132 to 531x224)

**FIG. 10.** Properties of population of Gaussian-shaped ganglion cell receptive fields separated by 2 σ. A: for idealized trigonal array of receptive fields, Nyquist frequency is determined by distance spanned by 2 rows of fields. This distance is $2\sqrt{3}$, where σ is radius of border indicated by circles. B: signal attenuation vs. frequency plot for sinusoidal signal filtered by one of the component Gaussian-shaped profiles in A. Vertical bar: distance that determines the Nyquist frequency for array of detectors.
We conclude that the mosaic arrangement of receptive fields for ganglion cells of most classes is governed by a distribution of preferred directions. Distances are in units of \( \sigma \).

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**REFERENCES**


**FIG. 11.** Theoretical plots showing formation of level sensory surface by summation of Gaussian receptive field profiles with interfiber spacing of \( 2 \sigma \). A: diagram showing individual field profiles (left) and summed profile (right). B: minimum amplitude (\( a \)) of summed Gaussian surface is plotted as function of spacing ratio. Maximum amplitude was normalized to 1. Spacing ratio of 1 implies that centers are \( 2 \sigma \) apart. Inset: cross section through surface profile when adjacent Gaussians were separated by \( 2 \sigma \). Distances are in units of \( \sigma \). Minimum height is given by \( a \).