# Receptive-field microstructure of blue-yellow ganglion cells in primate retina

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**We examined the functional microcircuitry of cone inputs to blue-ON/yellow-OFF (BY) ganglion cells in the macaque retina using multielectrode recording. BY cells were identified by their ON responses to blue light and OFF responses to red or green light. Cone-isolating stimulation indicated that ON responses originated in short (S) wavelength-sensitive cones, whereas OFF responses originated in both long (L) and middle (M) wavelength-sensitive cones. Stimulation with fine spatial patterns revealed locations of individual S cones in BY cell receptive fields. Neighboring BY cells received common but unequal inputs from one or more S cones. Inputs from individual S cones differed in strength, indicating different synaptic weights, and summed approximately linearly to control BY cell firing.**



Individual neurons in the central nervous system typically integrate inputs arising from many other neurons. Such pooling operations are thought to contribute importantly to sensation and perception, but, even in the visual system, current understanding is largely macroscopic or based solely on anatomical observations. How are visual receptive fields assembled from individual photoreceptor inputs?

We exploited the wide spacing of S cones in the peripheral primate retina to make the first physiological measurements of individual cone inputs to blue-ON/yellow-OFF (BY) ganglion cells[1], which may have a role in opponent color perception. The morphology of BY cells and the retinal neurons that provide input to them have been examined in detail. The bistratified dendritic trees of BY cells[2] integrate inputs from ON bipolar cells that receive S-cone input[3,4,5,6] and OFF diffuse bipolar cells that receive mixed L and M cone input[6]. The BY cell pathway thus provided a unique opportunity to examine the way in which anatomically defined circuits shape receptive field microstructure. Here we report differing weights of individual cones in BY cell receptive fields, divergence of individual cone signals to more than one BY cell, and linearity of S-cone signal summation in BY cells.

## Results

To characterize cone inputs to BY cells, we made multielectrode recordings[7] from multiple ganglion cells in peripheral regions of the isolated retina of the macaque monkey while stimulating the photoreceptors with the optically reduced image of a computer monitor. BY cells were identified by stimulating with a spatially uniform, randomly flickering colored display and calculating the average stimulus on the display before a spike (spike-triggered average, STA). The STA, a measure of the time course of monitor gun intensities that effectively triggered spikes, unambiguously revealed BY cells. This is shown for three simultaneously recorded BY cells (**Fig. 1a**). These cells demonstrated color opponency[1,8]: firing was stimulated by transient increases in the intensity of the blue gun, which primarily stimulated the S cones, and suppressed by the red and green guns, which primarily stimulated the L and M cones. This blue-ON/yellow-OFF spectral signature contrasted with that of simultaneously recorded nonopponent ON cells (**Fig. 1b**) and OFF cells (**Fig. 1c**) that were driven by all three guns with the same polarity and time course. Based on their receptive-field sizes, these nonopponent cells may have been parasol cells[9].

The origin of the yellow-OFF signal in BY cells was determined by stimulating the retina with spatially uniform cone-isolating stimuli in which gun intensities covaried in a ratio that stimulated one cone type but not the other two cone types[10]. STAs for L, M and S cone-isolating stimuli are shown for three BY cells from different preparations (**Fig. 2**). In each case, transient decreases in both L- and M-cone photon absorption caused firing, indicating that yellow-OFF signals originated in both cone types. This finding confirms earlier physiological[11,12] and anatomical[2,6] evidence. The time courses of the blue-ON and yellow-OFF signals (**Fig. 1a**) were similar, also consistent with previous findings[13]. This suggests that the poor temporal resolution of the S-cone system[14,15] does not reflect sluggish responses of S cones or differential retinal filtering of S-cone signals[16,17,18] but instead may arise in the brain[13]. However, the time to peak of the blue component of the STA (**Fig. 1a**) was approximately 10–20 ms shorter than that of the red and green components (42 cells, 11 preparations), indicating that yellow-OFF signals in BY cells were delayed relative to blue-ON signals. Previous studies did not find such a delay[13].

To examine the microstructure of cone inputs to BY cells, the retina was stimulated with a display in which 240 square pixels, each 20–30 μm on a side, flickered randomly and independently of one another. The STA from a single BY cell is shown (**Fig. 3a**, central panel). Six distinct blue pixels are visi-

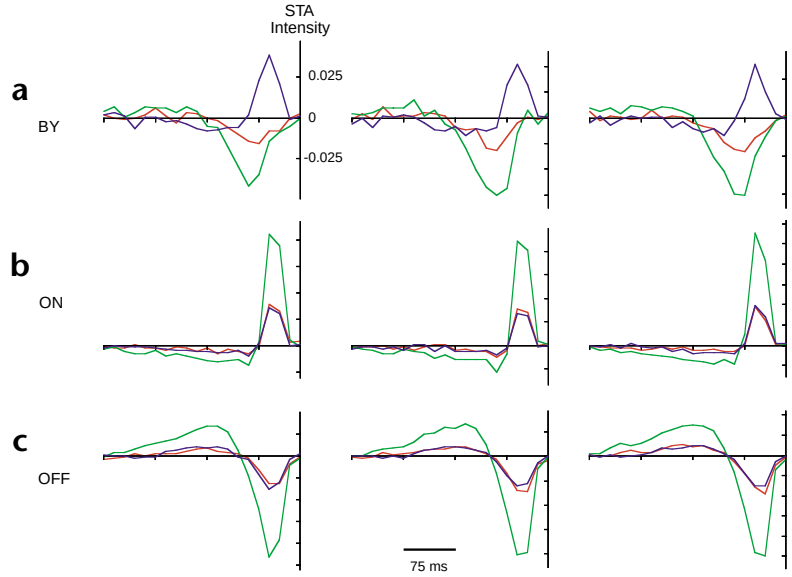



**Fig. 1.** Spike-triggered average stimulus intensity time course for nine simultaneously recorded macaque ganglion cells. Each panel shows the average red, green and blue gun intensity over 300 ms preceding a spike in one cell. Spike time is indicated by the placement of the vertical axis. STA intensity is expressed in normalized units with 1 indicating maximum achievable intensity for each gun. It is plotted as a difference from the mean intensity during stimulation, which was 0.5 (half maximum for each gun). Thus 0, which is indicated by the placement of the horizontal axis, corresponds to the mean intensity during stimulation. This is the STA intensity expected if changes in the stimulus did not influence firing. Positive STA intensity values correspond to intensities above the mean, and indicate that the cell tended to fire after increases in gun intensity; negative values indicate that the cell tended to fire after decreases. Each vertical axis tick represents 0.025 normalized intensity units. (**a**) STA time course of three BY cells. (**b**) STA time course of three nonopponent ON cells. (**c**) STA time course of three nonopponent OFF cells. During stimulation, the red, green and blue guns of the spatially uniform display flickered independently, with new intensity values drawn randomly from a Gaussian distribution every 15 ms.

ble. The STA time course at two of these pixels (left insets) shows that a transient increase in blue gun intensity at these locations produced spikes in the BY cell. Each blue pixel is surrounded by a region whose STA time course (right insets) lacks this blue-sensitive ON signature and instead shows a weaker red- and green-sensitive OFF signature. The distance between nearest locations of blue sensitivity is about 56 μm, similar to the average spacing between S cones in the peripheral retina[19]. We take these punctate islands of blue sensitivity to represent the locations of individual S cones in the photoreceptor mosaic. It is unlikely that more than one S cone was located under a given blue pixel because the S cones are fairly regularly spaced[19]. A total of 53 BY cells with 2–11 isolated locations of blue sensitivity, similarly spaced, were observed in 16 preparations. In comparison, the receptive-field structure of simultaneously recorded nonopponent ON and OFF cells resembled classical descriptions[20] (**Fig. 3b** and **c**). Measured at this spatial scale, nonopponent cell receptive field centers consisted of a diffuse region apparently representing many L and M cones. (In normal viewing conditions, chromatic aberration blurs the short-wavelength component of images on the retina[21], so that the functional receptive field of a BY cell is effectively smoother than the anatomical receptive field shown in **Fig. 3a**.)

The strengths of different S-cone inputs to a given BY cell were very different. Examples from two BY cells are shown (**Fig. 4**). Bright spots in the central panel indicate presumed locations of individual S cones. Assuming that BY cell spike rate depends on a linear combination of cone inputs over space and recent time (see below), the amplitude of the STA time course at different locations (insets) reflects the relative strength of cone inputs. The strongest S-cone input to a given cell was often several-fold more powerful than other S-cone inputs, consistent with anatomical evidence[6]. Though the data in Fig. 4 suggest that cone inputs to BY cells may be quantized, this possibility could not be supported statistically.

Individual S cones often provided input of different relative strength to more than one BY cell. In each of three groups of

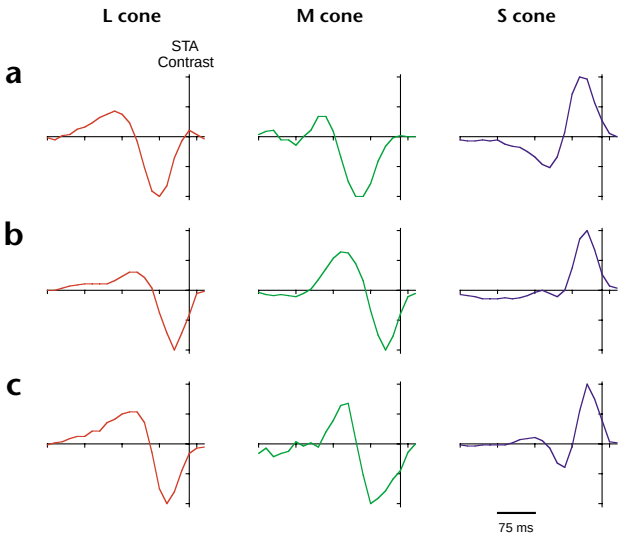



**Fig. 2.** STA cone contrast time course for L, M and S cone-isolating stimuli in three BY ganglion cells from different preparations (**a**, **b**, **c**). Spike time is indicated by the placement of the vertical axis. STA cone contrast indicates the difference between the mean photon absorption rate before a spike and the mean rate during stimulation, divided by the mean rate during stimulation. Thus 0, which is indicated by the placement of the horizontal axis, corresponds to the mean rate during stimulation. Positive cone contrast values indicate that the cell tended to fire after increases in photon absorption; negative values indicate that the cell tended to fire after decreases. For cell (**a**), each tick on the vertical axis represents 0.25 of the maximum cone contrast achievable on the display (cell **b**, 0.125; cell **c**, 0.05). The maximum achievable cone contrast on the display for each cone type was L, 0.127; M, 0.134; S, 0.794. The spatially uniform stimulus consisted of a random choice between two colors every 45 ms, with gun intensities covarying in a ratio that selectively stimulated one cone type but not the other two cone types. Because the STA is calculated at single frame resolution (15 ms) but the stimulus changes only every third frame (45 ms), spikes can be correlated with stimuli occurring up to two frames later, causing the nonzero component of the STA to extend beyond the time of the spike.

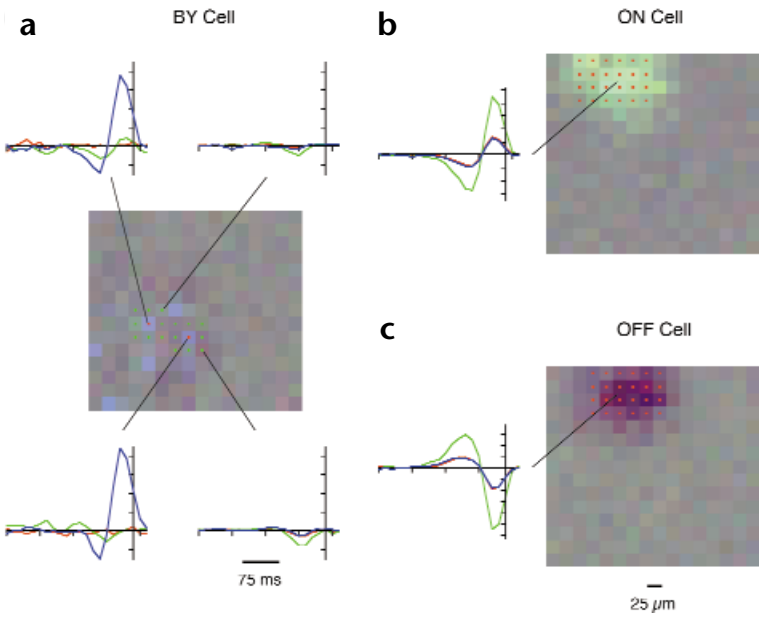
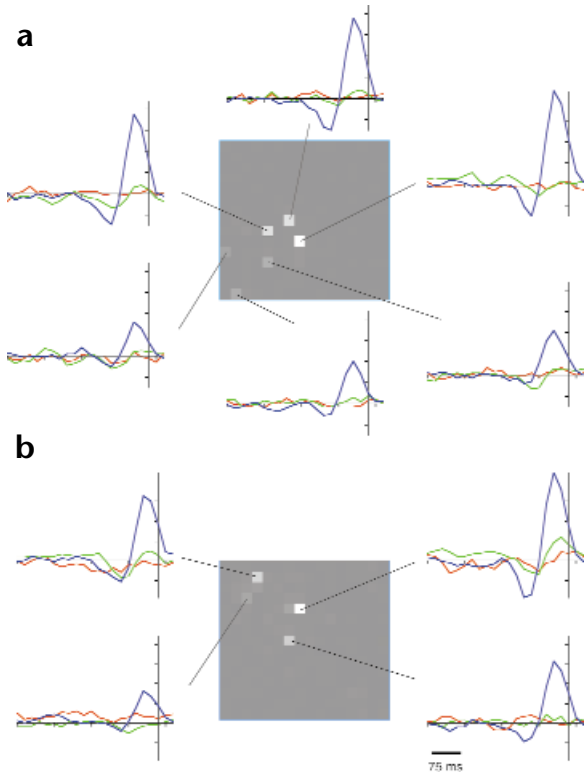



**Fig. 3.** Receptive field of a BY cell, a nonopponent ON cell and a nonopponent OFF cell recorded simultaneously. For each cell, the central panel shows the average stimulus present on the display 30 ms before a spike. Insets show the STA time course (see **Fig. 1**) summed over specified locations. Each vertical axis tick represents 0.01 normalized gun intensity units. (**a**) BY cell. STA time course at each of the two locations marked by red dots is shown in the left insets. Right insets indicate STA time courses averaged over the nine surrounding pixels marked by green dots. (**b**) Nonopponent ON cell. Inset indicates STA time course averaged over the 24 pixels indicated by red dots. (**c**) Nonopponent OFF cell, otherwise same as (**b**). During stimulation, each monitor gun at each pixel location flickered independently, its intensity randomly selected from two levels every 45 ms.

BY cells shown, two or three BY cells shared input from at least one S cone (circles, **Fig. 5**). Shared S cones sometimes provided the dominant input (arrows) to one BY cell and secondary input to another (**Fig. 5a** and **b**), but in no case of shared input observed (14 pairs of cells) did a single S cone provide dominant input to more than one BY cell. In the case of Fig. 5b, the first two cells shared inputs from two S cones; for one cell, the strength of the input from the two S cones was similar, for the second cell, one S cone provided stronger input than the other. These observations suggest that the differing strengths of S-cone inputs to a given BY cell cannot be attributed to different sensitivity of the cones themselves or to optical artifacts, but instead reflect differences in the gain of synaptic connections that transmit S-cone signals to BY cells[6].




Shared input from a single S cone stimulated in isolation could drive spikes in two BY cells. This was demonstrated for one pair of cells by randomly flickering a single 25 μm pixel at the circled location while all other pixels retained the mean background level (**Fig. 5c**). The STA time course for single-pixel flicker shown in the insets indicates that a single shared cone drove spikes in both BY cells.

How strongly must a single S cone be stimulated to cause a reliable change in BY cell firing? The effect of brief stimulation of the S cone providing strongest input was estimated from the responses of 8 BY cells to random flicker stimulation (see Methods). During the 75 ms duration of the BY cell's impulse response, a stimulus causing about 700 additional S cone photoisomerizations was estimated to add 1 extra BY cell spike to the 1 spike expected from maintained discharge. Assuming that spike counts from maintained discharge are Poisson distributed, this stimulus therefore represents the classical threshold for reliable detection. Psychophysical measurements suggest that just ten photoisomerizations in a single dark-adapted perifoveal S cone can be reliably detected[22]. The higher threshold obtained here may reflect the fact that the present experiments were performed on the isolated peripheral retina exposed to low photopic backgrounds.

Do inputs from individual S cones combine linearly in BY cells, or does the retinal circuitry integrate them in a more complex fashion? If signals from two cones sum linearly, then only the sum total cone stimulation, irrespective of how much each cone is stimulated individually, should influence BY cell firing. This was tested by examining firing rate as a function of the time-varying individual

**Fig. 4.** Strengths of individual cone inputs to two simultaneously recorded BY cells (**a**, **b**). Central panels show blue gun energy at each pixel location summed over the peak 75 ms of the STA for each cell. Bright spots indicate regions where increases in blue gun intensity correlated strongly with firing, and are assumed to represent locations of individual S cones in the photoreceptor mosaic. Insets indicate STA time course (see **Fig. 1**) at marked locations. Each vertical axis tick represents 0.0125 normalized gun intensity units. Stimulus as in Fig. 3. Cell (**a**) same as in Fig. 3a.

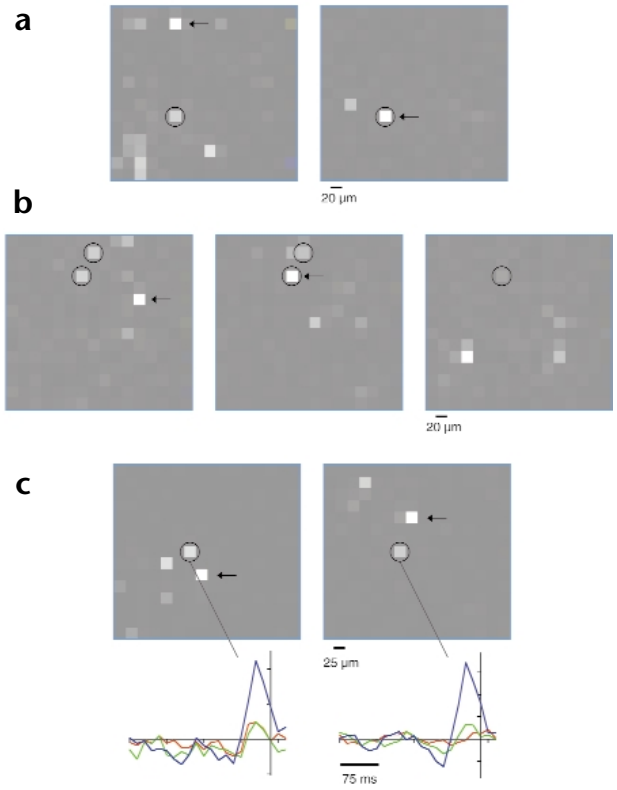



**Fig. 5.** Locations of S-cone input to three groups of BY cells (**a**, **b**, **c**). Each group of cells was recorded simultaneously; different groups were recorded in different experiments. Central panels as in Fig. 4. Circles indicate shared input to two or three BY cells from a single presumed S cone. Arrows indicate location of strongest S-cone input to each BY cell. Stimulus as in Fig. 3, except for (**b**), in which the stimulus refresh interval was 15 ms. Insets in (**c**) indicate STA time course (see **Fig. 1**) obtained by flickering the single circled pixel alone. Each vertical axis tick indicates 0.0125 normalized gun intensity units. Cells in (**c**) same as in Fig. 4.

and summed S-cone stimulation during random flicker presentation. The average spike rate in one BY cell is shown as a function of the stimulation of one S cone averaged across many values of the stimulation of the other S cone, and as a function of the summed stimulation of both cones in varying relative amounts (**Fig. 6**). If signals from the two S cones combined linearly, then only the total S cone stimulation should affect firing, so all three plots of firing rate versus cone stimulation in Fig. 6 should superimpose. Conversely, models in which either or both cone signals must cross a threshold to generate a spike predict that the individual and/or summed curves should not superimpose. (The curve in **Fig. 6** need not be straight for linear summation of cone signals to hold. For example, if cone signals combined linearly to influence postsynaptic current in the BY cell, but firing rate depended nonlinearly on the summed postsynaptic current, this curve would not be straight.) The superposition of all three sets of points in each panel of Fig. 6 suggests that signals from individual S cones combined linearly. Similar results were obtained from nine other BY cells.

## Discussion

Microscopic analysis of S-cone inputs to BY cells provides several insights into how photoreceptor inputs create visual receptive fields. First, what creates receptive field overlap in neighboring ganglion cells? The finding that one cone can drive activity in more than one BY cell shows that overlapping receptive fields of ganglion cells can arise from common cone inputs in the overlap region, as suggested by anatomical observations (for example, ref. 6). By this arrangement, a ganglion cell may sample all photoreceptor signals in its receptive field. The alternative possibility, less elegant, would have been that receptive field overlap arises from separate cone inputs interleaved at a spatial scale too fine to be resolved by macroscopic measurements.

Second, what creates the tapering light sensitivity profile of retinal ganglion cells? A ganglion cell could integrate inputs from fewer cones per unit area in regions farther from the receptive field center. This would create a tapering sensitivity profile even if inputs from all synaptically connected cones were equally strong. Alternatively, ganglion cells could receive weaker inputs from cones farther from the center due to differences in the strength of the intervening synaptic connections[6,23]. Microscopic analysis shows that the strengths of the circuits conveying S-cone signals contribute to the shape of the BY cell receptive field.

Third, how do inputs from individual photoreceptors combine to create ganglion cell light responses? Macroscopic measurements support roughly linear summation of cone inputs between widely separated areas of the receptive field in several types of ganglion cells (for example, ref. 24; see also ref. 21). However, linear pooling of signals from distant cones could mask local nonlinearities, and pooling of signals from individual nearby cones has not been examined previously. The present results indicate that the BY cell's excitatory receptive field is constructed by linear superposition of the input signals from individual cones, consistent with recent hypotheses[23,25].

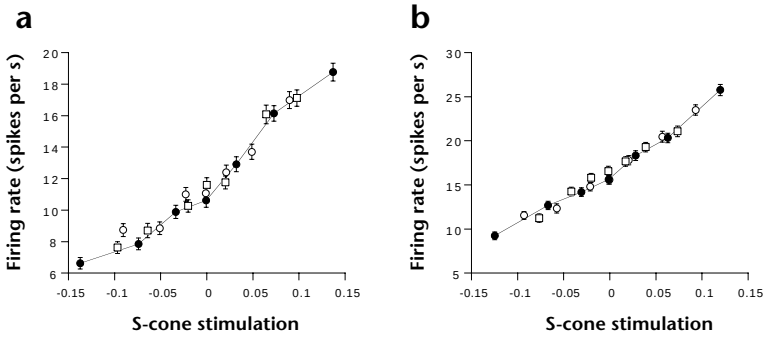



**Fig. 6.** Firing rate as a function of S-cone stimulation (arbitrary units) for two simultaneously recorded BY cells (**a**, **b**). Open circles and squares indicate firing rate as a function of stimulation of the S cone that provided the strongest and second strongest inputs, respectively, to the BY cell, averaged over many values of the stimulation of the other S cone. Filled circles indicate firing rate as a function of the summed stimulation of both S cones in varying relative amounts. Lines connect filled circles. Stimulus as in Fig. 3 but with a refresh interval of 15 ms. Time-varying firing rate was computed in 15 ms time bins over the 45-minute duration of random flicker stimulation. Time-varying S-cone stimulation was computed in 15 ms time bins by convolving the STA at selected S-cone location(s) with the stimulus. Each point in each graph was obtained by averaging S-cone stimulation and firing rate over about 25,000 time bins during which S-cone stimulation fell within a small range. Error bars indicate ±1 s.e. of the average firing rate over these time bins.

Receptive field microstructure suggested a quantitative connection between anatomical properties of the circuits conveying S-cone signals and the shape of BY cell receptive fields. Viewed at single-cone resolution, BY cell receptive fields had irregular sensitivity profiles (**Figs. 4** and **5**), and neighboring BY cells often received inputs of different relative strength from a single S cone (**Fig. 5**). The known connectivity of S-cone ON-bipolar cells, which relay S-cone signals to BY cells, may help to explain these findings. The number of synapses from different bipolars onto single BY cells varies widely, at least in the fovea[6]. Also, each bipolar usually contacts only 1–3 S cones[4,5] and may receive the majority of its input synapses from a single S cone[6]. Thus signals from individual S cones might provide inputs of different strength to one or more BY cells by passing through distinct bipolar cells via different numbers of synapses whose effects sum linearly[6,23,25]. The finding that individual S cones do not always contact more than one S-cone ON-bipolar cell[4] may explain why shared S-cone input to neighboring BY cells was not always observed. These parallels suggest that the microstructure of visual receptive fields measured physiologically may be predicted quantitatively from the connectivity and number of synapses in retinal circuits[25,26].

## Methods

Eyes were obtained from anesthetized adult male *Macaca fascicularis* monkeys that were donors in lung transplant experiments. Immediately after enucleation, the anterior portion of the eye and vitreous were removed. Under infrared illumination, pieces of retina 2–3 mm in diameter were cut from regions 20–50° from the fovea, separated from the pigment epithelium, and placed flat against an array of 61 extracellular microelectrodes[7]. These electrodes monitored action potentials in ganglion cells as the preparation was superfused with oxygenated Ames' solution (Sigma) at 36°C, pH 7.4. Spikes from individual cells were segregated offline by identifying clusters of spike height and width recorded on each electrode. The retina was stimulated with the optically reduced image of a CRT display refreshing every 15 ms. The photon absorption rate for the L (M, S) cones caused by each monitor gun at half-maximum intensity was approximately equal to the rate that would be caused by a 561 (530, 430) nm monochromatic stimulus with intensity (photons per $\mu m^2$ per s) given in Table 1.

Photoisomerization estimates assume that the effective collecting area for primate cones is 0.37 $\mu m^2$ when the outer segment is stimulated directly by nonaxial illumination[16]. Because stimuli were delivered from the photoreceptor side of the preparation, the orientation of the cones in the light path probably had little impact on photoisomerization rates. Cone-isolating stimuli were created using the measured monitor phosphor spectral power distributions[21] and the spectral sensitivities of monkey cones[27]. The effectiveness of this procedure was verified by using a calibrated photodiode to measure the power of the stimuli transmitted through three groups of glass filters, each with a transmission that approximated the spectral absorption of one cone type. Stimuli intended to isolate each filter group yielded photodiode power measurement ratios in excess of 10:1, indicating good cone isolation. Estimated BY cell responses to stimulation of a single S cone by a brief flash were calculated as follows. The firing rate of a BY cell was assumed to depend on linear summation of cone signals over space and time, followed by a mild nonlinearity in spike generation (for example, see **Fig. 6**). On this model, the linear weighting of cone inputs is simply the STA obtained with random flicker, and the nonlinearity can be obtained from the dependence of the time-varying spike rate on the convolution of the STA with the flicker stimulus. This model was used to calculate the response to a brief flash delivered to a single S cone in the presence of a uniform gray background.

**Table 1.**

| Equivalent intensities | L (561 nm) | M (530 nm) | S (430 nm) |
|---|---|---|---|
| Red gun | 1,030 | 380 | 40 |
| Green gun | 3,110 | 3,240 | 190 |
| Blue gun | 860 | 1,320 | 2,370 |

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