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The Spectral Sensitivity of Dark- and Light-adapted Cat Retinal Ganglion Cells

Elke Guenther and Eberhart Zrenner

Department of Pathophysiology of Vision and Neuroophthalmology, Division of Experimental Ophthalmology, University Eye Hospital, 7400 Tübingen, Germany

The spectral sensitivity of cat retinal ganglion neurons (RGNs) was determined by means of extracellular recordings under scotopic and photopic conditions, in both receptive field center and surround. Test stimuli were presented either as square-wave single flashes or as flicker stimuli. Chromatic adaptation was achieved by a large steady monochromatic background field. In the dark-adapted state the spectral sensitivity of the majority of ganglion cells (92%) was rod mediated (peak sensitivity at 501 nm). Under photopic conditions all neurons received input from a long-wavelength-sensitive (L-cone) system with a peak sensitivity of 550 nm. Input from a short-wavelength-sensitive (S-cone) system (peak sensitivity at 450 nm), however, was found only in 15% of the ganglion cells.

A small cell population (8%) located within the area centralis revealed a different receptive field organization. In these cells, spectral sensitivity in the field center peaked at 520 nm in the dark-adapted state and response threshold was about 1 log unit higher than in cells with a peak sensitivity of 501 nm. Critical flicker fusion was reached at 60–70 Hz, a frequency that usually is mediated by cones.

We therefore postulate an additional input of a midspectral receptor system (M-system) other than rods in cat retinal ganglion cells. This input was found only in the receptive field center of some ganglion cells in the dark-adapted state, whereas the surround sensitivity was mediated in all cells by rod signals under scotopic and predominantly by L-cone signals under photopic conditions.

[Key words: adaptation, cat, spectral sensitivity, retinal ganglion cells, trichromaticity, middle-wavelength system]

Although the visual system of the cat has been extensively investigated, it is still contentious whether the animal has a di- or trichromatic vision. In early behavioral studies of cat photopic vision, problems arose in training the animals to perform chromatic tasks (Gunter, 1954; Meyer et al., 1954). The difficulty for brightness matching with an animal is that one already needs to know something about the animal's spectral sensitivity. Only then it is possible to reinforce it when it is correct (Gunter, 1954; Bonaventure, 1962). When brightness and other cues were carefully eliminated, cats could be trained to distinguish between red and green lights (Sechzer and Brown, 1964; Meyer and Anderson, 1965) and also between red and blue or yellow lights (Mellow and Peterson, 1964).

Based on the finding that rod and cone signals converge upon retinal ganglion cells, as demonstrated morphologically (Polyak, 1941; Walls, 1942; Rodieck, 1973) as well as physiologically (Granit, 1943, 1947; Donner, 1950), various authors have suggested the cat's ability of color discrimination in the mesopic range to be mediated by an interaction between rods and long-wavelength cones (L-cones) only (Daw and Pearlman, 1969; Andrews and Hammond, 1970a,b). However, some years earlier Granit (1943) already had postulated in his dominator-modulator theory the existence of various cone systems. This idea was strongly supported by the experiments of Daw and Pearlman (1970), who found color-opponent cells with spectral maxima at 450 nm (short-wavelength, or S-cones) and 556 nm (L-cones) in the LGN of cat.

While neurophysiological evidence for both cone systems is now established (Hammond, 1978), there is little agreement on the relative influence of S-cones (Daw and Pearlman, 1969, 1970; Hammond, 1978; Zrenner and Gouras, 1979; Crocker et al., 1980). To confuse the picture even more, some studies revealed a photopic trichromaticity (Lennox, 1956; Ringo et al., 1977; Crocker et al., 1980; Schuurmans and Zrenner, 1981a,b; Wienrich and Zrenner, 1983) with a cone system peaking in the midspectral region near 500–510 nm. The existence of a such photopic active mechanism, however, was disputed in recent behavioral (Loop et al., 1987) and electrophysiological (Rodieck and Dineen, 1985; Jacobs and Neitz, 1986) work.

We attempted to elucidate the problem about cat's photopic mechanisms measuring the spectral sensitivity of retinal ganglion cells electrophysiologically in the dark-adapted state and under various conditions of chromatic adaptation. Extracellular recordings were restricted on the area centralis and the near surround (+5°).

The antagonistic center–surround components were separately analyzed in both on- and off-center cells. Spectral sensitivity curves were derived from response versus intensity functions (R/log I functions, R in numbers of action potentials per second) that were determined without a background light and in the presence of large-field chromatic backgrounds.

We found that rods provide the most sensitive input to the receptive field in the majority of ganglion cells. However, the most sensitive input in a small population of cells (8%) located within the area centralis had a spectral sensitivity peak of 520 nm, which is clearly different from rods. Thus, our data indicate an additional photoreceptor input to cat retinal ganglion cells

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Correspondence should be addressed to Elke Guenther, Department of Experimental Ophthalmology, Ob dem Himmelreich 9, 7400 Tübingen, Germany.

in the midspectral region (M-system). Additionally, the critical fusion frequency (cff) of a flickering test stimulus in these cells was reached at 70 Hz, a value too high to be mediated by rods (fusion around 40 Hz). Under photopic conditions, all ganglion cells received input from L-cones whereas input from S-cones was found in only 15% of the ganglion cells.

Part of this work has been published in abstract form (Guenther and Zrenner, 1990).

Materials and Methods

Extracellular recordings from retinal ganglion cells were performed in adult cats (*Felis catus*). After initial anesthesia, the animals were artificially respirated and sodium pentobarbital (60 mg/ml stock solution, diluted 1:11 in 0.9% saline) was given intravenously in a continuous flow of 0.4 ml/kg•hr during the whole experiment. To suppress eye movements, alcuronium chloride was administered by continuous intravenous infusion at rates of 0.09 mg/kg•hr. All vital parameters were continuously monitored. To dilate the pupil and paralyze accommodation the eye was atropinized, and phenylephrine hydrochloride was applied to retract the lids and the nictating membrane. A contact lens of +0.5 diopters was used to prevent drying of the cornea.

The cat's head was fixated in a stereotaxic instrument so that the focus of the Maxwellian view system (Westheimer, 1966) was on the vertex of the cornea. A tungsten-in-glass electrode (Levick, 1972) was inserted into the eye and advanced to the region of the area centralis under optical control by a modified fundus camera (Gouras and Zrenner, 1979).

The present results are based upon records from 189 cells in 15 cats, male and female. In 111 cells receptive fields had an off-center; 78 were on-center cells. No classification in terms of X/Y-cells was carried out because only limited recording time was available and the aim was directed at spectral sensitivity. However, the location within the area centralis or nearby, the small diameters of the receptive field centers, as well as the sustained response over a wide range of light intensity indicate that most of them were X-cells.

Stimulation. The dual-beam optical stimulator was energized from a xenon arc lamp (900 W) that ran at constant current from a stabilized DC supply. Test stimulus duration and interstimulus interval could be changed independently. Light was projected onto the retina via Maxwellian view. Test spot size matched either the receptive field center of a slightly light-adapted ganglion cell (see below) or covered the entire receptive field (8° stimulus). The adaptation background always subtended an angle of 25°.

Variation in the chromaticity of the test beam (λ) was achieved by narrow-band interference filters (12 nm half-width, Schott) in a range of 402–704 nm (steps of 20–25 nm). The transmission of each filter was measured spectrophotometrically. Two different chromatic filters were interposed in the adaptation beam (μ). A blue-green broad-band filter (BG 28) with a transmission maximum at 456 nm provided a light particularly effective for rods and S-cones, whereas a steep yellow cutoff filter (OG 580, tolerance of cutoff ± 6 nm) mainly adapted L-cones.

Light intensity could be varied by means of neutral density filters (Schott). As neither the outputs of the xenon arc lamp and neutral density filters nor the spectral distribution of the photodiode was flat, we had to measure the light intensity for each possible filter combination. Light intensities were measured by means of a photodiode at the position of the retina. In eight cases, a cat lens was removed from the untreated eye and interposed at its relative distance from the retina in the eye. The lenses were prevented from drying out by superfusing them with 0.9% saline.

We corrected all measurements for the influence of the tapetal reflection (see Weale, 1953) and the absorption of the cat's lens. The maximal difference in absorption was 0.08 between 500 nm and 550 nm but went up to 0.28 at 400 nm (see Guenther and Zrenner, 1989). Irradiance (E) of test beam was determined radiometrically (PIN 1223, UTD) and had its maximum (10^7 quanta•sec^{-1}•μm^{-2}) at a wavelength of 613 nm. The orange and blue-green adaptation lights provided by the OG 580 and BG28 filters were measured photometrically (PIN AP-10 diode, UTD; V_λ characteristic). The maximal illuminance that could be reached in the adaptation beam was $1.2 \cdot 10^4$ lumens•m^{-2} for a blue-green light generated by means of a BG 28 filter.

Presentation. The test stimulus was presented as a 500 msec square wave with an interstimulus interval of 1.3 sec or as equal duty rectangular flicker in the range of 30–100 Hz produced by a spinning windmill. It was superimposed onto a steady background light that subtended an angle of 25°. To determine the receptive center of an individual ganglion cell, position and size of a test spot (irradiance 2.5 log quanta•sec^{-1}•μm^{-2}) were varied across the retina until a maximal center response (either on or off) could be recorded. The animals were kept in darkness for 40 min before starting the experiment.

Data analysis. The action potentials recorded extracellularly from single ganglion cells were amplified, monitored on an oscilloscope, and stored on a FM tape (HP 3968A) together with the stimulus signal for off-line analysis. The "threshold for detection" refers to the weakest irradiance of a test stimulus producing a discernible, stimulus-related change in the discharge rate of an individual cell as it was perceived over a loudspeaker. Measurements of the response behavior of a cell were started at this irradiance level. For data analysis the amplified action potentials were fed into a window discriminator and a frequency analyzer. The thereby processed analog signals were digitized and averaged by a Nicolet Averaging System (1072, Fabri-Tec) to obtain post- and peristimulus time histograms (PSTHs). In most experiments PSTHs had a bin width of 20 msec and were averaged from eight responses. The average discharge 300 msec prior stimulus onset was taken as the baseline for the response amplitude measurements. The response of on-center cells was evaluated at the appearance and the response of off-center cells at the disappearance of the same stimulus. Five bins (i.e., 100 msec) around the peak amplitude were averaged and plotted as response frequency (in hertz) against the test spot irradiance that was increased in steps of 0.125 or 0.25 log units (log E, quanta•μm^{-2}•sec^{-1}). Such response versus intensity (R/log I) functions were determined for 5–12 chromatic different test stimuli (between 400 nm and 704 nm) under scotopic and photopic conditions. Spectral sensitivity functions were derived from R/log I functions by plotting the test irradiances necessary to elicit a criterion response of 40 Hz against the different stimulus wavelengths. Since we were interested in the absolute shape as well as the absolute sensitivity, we normalized the spectral sensitivity functions of all cells at the peak wavelength, averaged them, and plotted the peak of the thereby obtained functions at the mean peak sensitivity averaged from all cells' absolute values. Therefore, the functions can be compared on an absolute scale. The standard deviations were calculated after normalization. Additionally, we included the standard deviations obtained for the mean peak of spectral sensitivity in order to give an estimation for the variability of its position within different cells.

To investigate which photoreceptors are involved in the generation of the spectral sensitivity of a given cell, Dartnall nomograms (Dartnall, 1953) that describe the spectral characteristics of photoreceptors were fit to the data. The nomograms were first shifted in the wave number domain to the different peak values and transferred afterward into the wavelength domain to examine the quality of fit.

All experiments were performed according to the ARVO resolution of animal experiments and the laws applicable in Germany.

Results

Figure 1 shows R/log I functions of the center response of a ganglion cell recorded under scotopic conditions in the presence of various chromatic test stimuli. The response is given as the number of spikes per second. Data points for each wavelength are fit by a modified Naka–Rushton function (Naka and Rushton, 1966):

$$R = \frac{R_{max} \cdot E^n}{(E^n + s^n)}. \quad (1)$$

R is the peak-to-peak amplitude of the center response, E the irradiance of the test stimulus, s is the half-saturating test stimulus irradiance, and n is a parameter determining the steepness of the intensity response relationship. R_{max} and s^n were determined from linear regression of E/R versus E, and the resultant SE of estimate was minimized by iteratively adjusting n. In Figure 1 R_{max} ranges from 135 to 145 Hz, and n, from 0.95 to 1.1. The constancy in slope of the R/log I functions indicates a high degree of univariance and argues for a single receptor mechanism generating the center response at different test stimulus wavelengths. To derive the spectral sensitivity distribution in

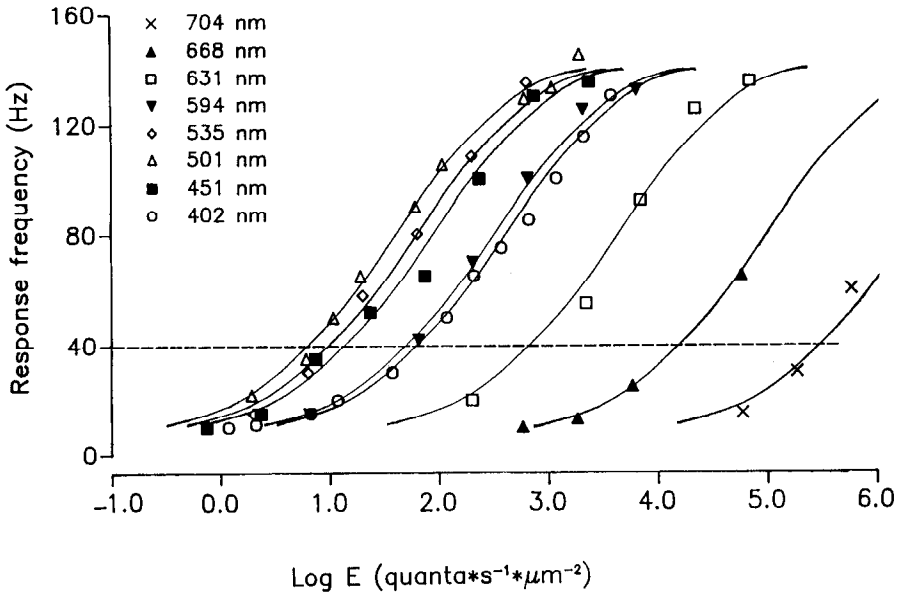

Figure 1. Response versus intensity functions for an off-center ganglion cell (3° parafoveally) at different test stimulus wavelengths. Test stimulus diameter is 0.4°; stimulus duration, 500 msec; interstimulus interval, 1.3 sec. Data points for each wavelength are fit by a modified Naka–Rushton equation (Eq. 1; *solid lines*). R_{max} ranges from 135 Hz to 145 Hz; n, from 0.95 to 1.1. The most sensitive stimulus wavelength is 501 nm (*open triangles*). Based on a threshold criterion of 40 Hz (*broken line*), spectral sensitivity functions were determined.

the field center from these R/log I functions, a threshold criterion was set for a response frequency (40 Hz) in the lower range of the limb (broken line in Fig. 1.). A criterion position at low irradiance levels further ensures that the cell's activity is only mediated by the most sensitive receptor mechanism (Naka and Rushton, 1966). Curves at 501 nm, 535 nm, and 451 nm are leftmost (solid triangles, diamonds, and solid squares, respectively), and the center response is most sensitive for a stimulus wavelength of 501 nm. Measurements of R/log I functions were restricted to only a few wavelengths under prebackground condition, due to the difficulty in maintaining the rods dark adapted while investigating the upper limb of the functions. In the range of 450–550 nm, however, R/log I functions were determined in steps of 15 nm to obtain a good resolution of the peak spectral sensitivity. For clarity, not all curves are shown in the graph.

In Figure 2, results for the interpolation of test stimulus irradiance necessary to produce a 40 Hz criterion were plotted against different wavelength. A Dartnall nomogram (Dartnall, 1953) that represents the rod pigment absorption function (peak at 501 nm) fits the data best (solid line). Thus, rods provide the most sensitive receptor input to the field center of these dark-adapted retinal ganglion neurons (RGNs). This result was confirmed for the majority (92%) of ganglion cells (type I cells in Table 1) recorded and is in good accordance with the dominance of this receptor type in the cat retina.

In about 8% of the ganglion cells (type II cells in Table 1) within the area centralis the spectral sensitivity data in the dark-adapted state did not fit the rod pigment absorption function. The broken curves in Figure 3 represent the rod nomogram curve (see Fig. 2*A,B*); the solid curves, a Dartnall nomogram with a peak sensitivity at 520 nm that fits the data best. The

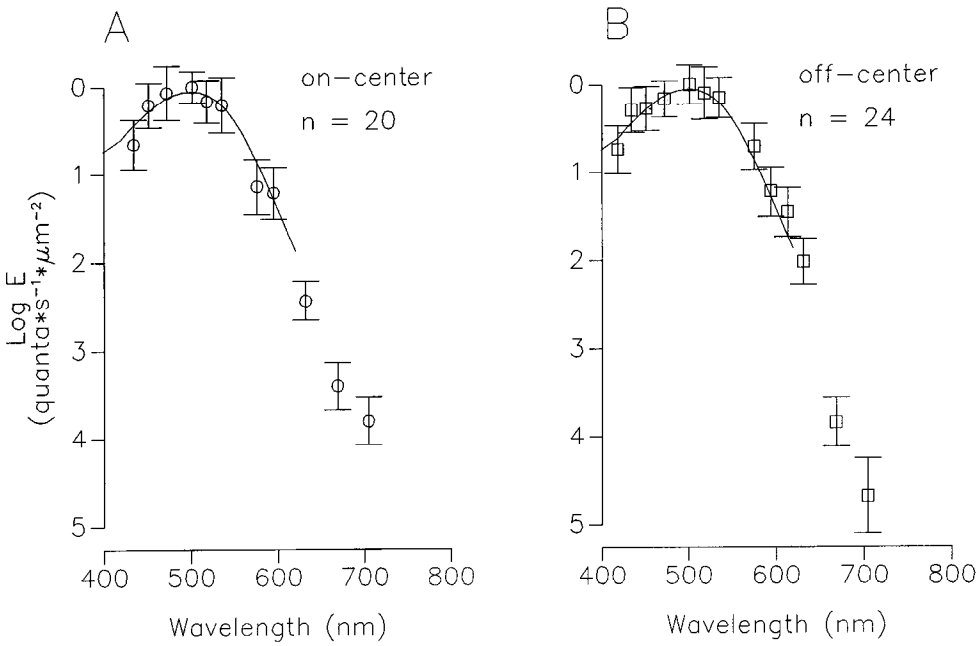

Figure 2. Center spectral sensitivity functions in the dark-adapted state, based on a threshold criterion of 40 Hz. Mean values for 20 on-center cells (*A, circles*) and 24 off-center cells (*B, squares*). Test stimulus diameter varies from 0.5° to 0.95°. Irradiance of test stimulus (quanta•sec^{-1}•μm^{-2}) is plotted against wavelength (nm). Mean peak sensitivity at 501 nm is reached at 0 log units in on-center and 0.05 log units in off-center cells. Data are fit by a Dartnall nomogram (*solid line*) that represents the rod pigment absorption curve (peak at 501 nm).

Table 1. Distribution of photoreceptor inputs to the receptive field center and surround of retinal ganglion cells under various conditions of adaptation

	Receptive field center (189 cells)			Receptive field surround[a]		
					72 of 189 cells	
	Dark-adapted	Yellow-adapted	Green-blue–adapted	79 of 189 cells, dark-adapted	Yellow-adapted	Green-blue–adapted
Peak spectral sensitivity generated by	Rods	S-cones	L-cones	Rods	S-cones	L-cones
Total number of cells found with this peak sensitivity	189	18	189	79	11	72
Type of center response in cell type[b]						
I	72 on, 101 off	4 on, 11 off	72 on, 101 off	49 on, 19 off	3 on, 3 off	46 on, 15 off
II	7 on, 9 off	1 on, 2 off	7 on, 9 off	6 on, 5 off	3 on, 2 off	5 on, 6 off

[a] In the receptive field surround, only 79 out of 189 were tested in the dark-adapted state; 72 out of these 79 cells were additionally tested under yellow and blue-green adaptation.

[b] Cell type I refers to the rod-dominated RGNs; cell type II, to RGNs with an input from the M-system in the dark-adapted state. Type of center response indicates the center–surround response characteristic.

stimulus threshold is about 1 log unit higher than in RGNs, with a peak sensitivity of 501 nm. The position of the spectral sensitivity peak indicates that a receptor system different from rods but also in the midspectral region provides the most sensitive input to the field center of these cells. We further refer to this system as the M-system. Interestingly, all cells of this type had small (0.15–0.5°) receptive fields and were located within the area centralis.

In order to characterize further the nature of the M-system, we determined the cff of the 520 nm cells presenting a square-wave flicker in the range of 30–100 Hz. The existence of an additional midspectral but not rod-mediated mechanism in cat was demonstrated earlier in studies where the rod system was saturated by a bright background light (Crocker et al., 1980; Schuurmans and Zrenner, 1981a,b; Wienrich, 1983; Olsen et al., 1986). One observation suggesting it as a separate cone mechanism was its cff of 40–50 Hz; rods were reported to reach the critical point already at a response rate of 30–40 Hz (Dodt and Walther, 1958).

The temporal characteristics of two on-center ganglion cells with peak sensitivities of 501 nm and 520 nm in the dark-adapted state were compared in Figure 4. Center response is shown for flicker stimulation of 40 Hz, 50 Hz, and 60 Hz, respectively. A wavelength of 510 nm was chosen for the test stimulus, the irradiance of which was set 1.0 log unit above the criterion threshold of 40 Hz in each ganglion cell. A strong correlation between light onset and spike response for flicker frequencies of >40 Hz is only obvious for the 520 nm cell. The correlation weakens at 60 Hz but spike rate still follows the time course of flicker. In contrast, the cff for the 501 nm cell is already reached at a frequency of 40–50 Hz.

Under scotopic conditions, all of the 520 nm cells found in the present study (n = 16) showed significantly different (t = 0.001) temporal response properties (64.4 Hz ± 5.8) in the field center than rod-mediated cells (46.8 Hz ± 5.5; n = 14). We therefore conclude that the former do not have any or only a very weak rod input in the dark-adapted state and that the spectral sensitivity under this condition is mediated by an additional receptor system peaking in the midspectral region.

Next, we assessed the question of whether the M-system also

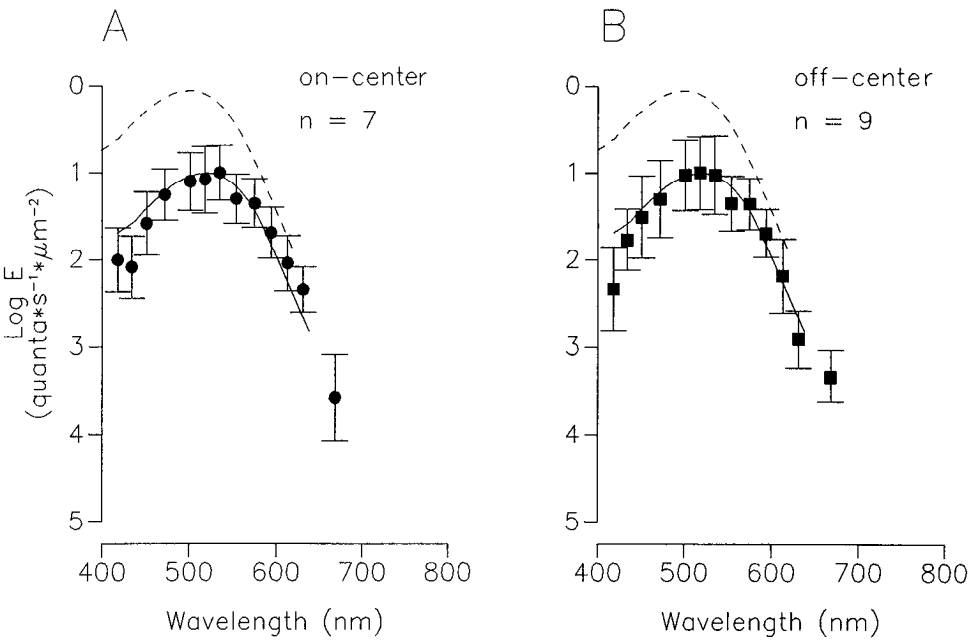

Figure 3. Spectral sensitivity curves for the center response in the dark-adapted state for a subpopulation of RGNs. Mean values for seven on-center cells (*A, circles*) and nine off-center cells (*B, squares*) are presented. Test stimulus diameter varies from 0.15° to 0.5°. Data are best fit by a Dartnall nomogram peaking at 520 nm (*solid curve*), which points to an input of a receptor system other than rods. For comparison, the rod pigment absorption curve is plotted (*broken curve*). Threshold of a midspectral test stimulus is about 1 log unit higher in the 501 nm–peaking ganglion cells.

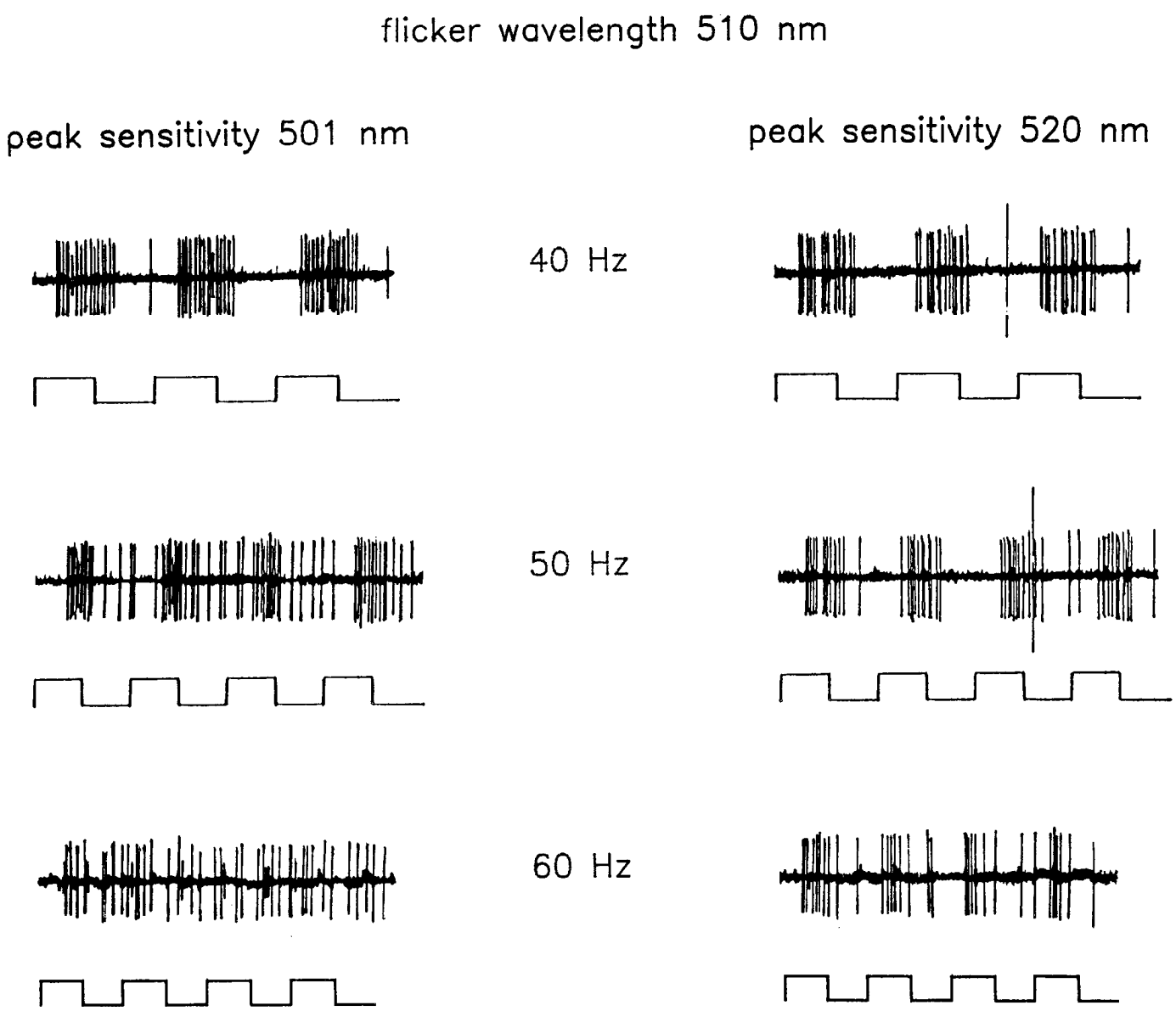

Figure 4. Spike response of the receptive field center as a function of flicker frequency. On the *left* are data for a ganglion cell with a peak sensitivity of 501 nm; on the *right*, for one peaking at 520 nm. Test stimulus is presented as flicker in the range of 30–100 Hz at a wavelength of 510 nm. Test stimulus irradiance was set 1.0 log unit above threshold in both cell types (0.9 log units for the 501 nm cell, 2.0 log units for the 520 nm cell). Cff is reached at about 50 Hz in the 501 nm cell. The 520 nm cell still can follow this flicker frequency and reaches cff at values of >60 Hz. As a cff for rods of 40–50 Hz is reported in cat, the result points to a "non-rod" mechanism in the 520 nm peaking ganglion cells that determines the spectral sensitivity in the dark-adapted state.

provides inputs to the receptive field surround. As no anular stimulation with continuously variable diameters could be produced by means of our Maxwellian view system, we had to test the receptive field surround under conditions where no center contribution was obvious. In order to perform this, we completely light adapted the receptive field center by means of a bright test stimulus (4 log units above its absolute threshold) that was matched to the center's diameter. Due to this preadaptation, no response could be produced when the irradiance of the test stimulus was decreased to its absolute threshold. In general, the threshold of detection was raised about 1–2 log units by this procedure. If now the test irradiance was decreased to its absolute threshold while, in parallel, the stimulus diameter was enlarged to 8°, only the receptive field surround could generate a discharge in response to the test stimulus. This surround response was antagonistic to the center response; that is, the surround response of an on-center cell was measured by the off-discharge and vice versa.

Only ganglion cells with a distinct spatially antagonistic response were analyzed in their surround. We never could observe any other than the rod system to be most sensitive in the surround of both 501 nm and 520 nm cells (see Figs. 5, 6). The difference in response threshold between the center and its antagonistic surround in 501 nm cells was 0.3 log units in average. Notice, that the data for the surround in Figure 5 are translated 1.5 log units downward along the y-axes only for clear graphical presentation. In contrast, data in Figure 6 reflect the absolute mean difference (0.9 log units) of the peak sensitivity between the center and surround in 520 nm cells.

Thus, our data demonstrate a "spectrally homogeneous," al-

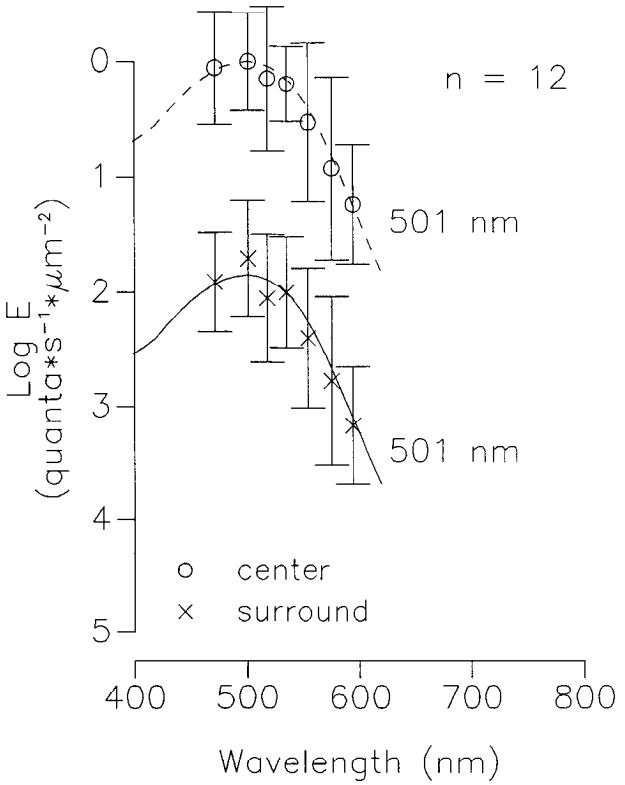

Figure 5. Center (*circles*) and surround (*crosses*) spectral sensitivity functions. To analyze the surround response, test spot diameter was enlarged to 8°. Only data for on-center ganglion cells (here $n = 12$) that show a distinct center–surround antagonism are pooled. Both center and surround have a peak sensitivity at 501 nm and are best fitted by the rod pigment absorption curve. Notice that the data points and Dartnall fit for the surround response are translated 1.5 log units downward along the irradiance axis for better graphic presentation.

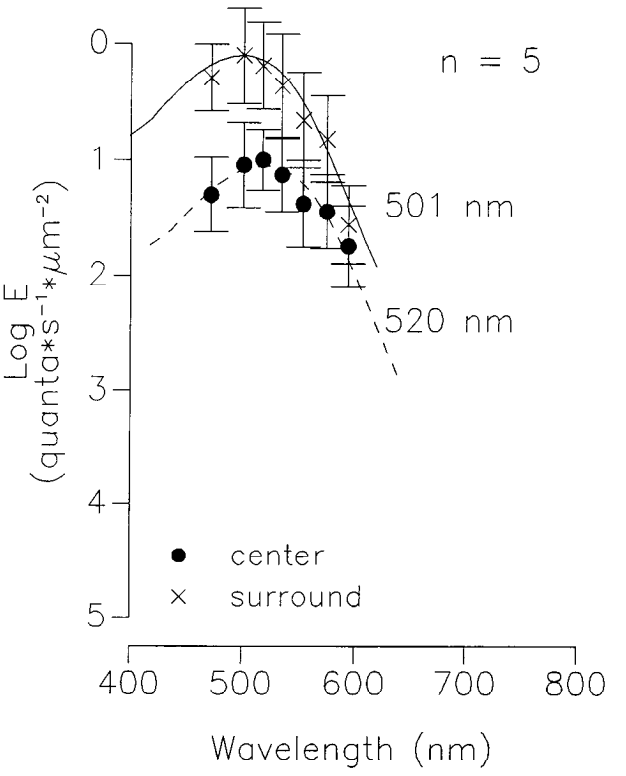

Figure 6. Center (*circles*) and surround (*crosses*) spectral sensitivity of ganglion cells with a peak sensitivity of 520 nm in the field center ($n = 5$). As in Figure 5, the surround response peaks at 501 nm and is best fitted by the rod pigment absorption curve (*solid curve*). Peak response threshold for the surround is reached at an irradiance of 0.05 log E (quanta•sec^{-1}•μm^{-2}); for the center, only at 0.95 log E.

though spatially antagonistic, receptive field organization under scotopic conditions in most RGNs (92%). In 8% of RGNs within the area centralis, a difference of 20 nm in the position of the sensitivity peak between the center and surround results in a "spectral inhomogeneity" of the receptive field.

In order to determine which photoreceptors provide inputs to RGNs under photopic conditions, we preadapted them with steady Ganzfield backgrounds, either blue-green (BG 28) or yellow (OG 550). As no differences were found in the spectral composition data, both on- and off-center RGNs were summed for the two different cell types respectively (Fig. 7). Superposition of a bright blue-green background reduced test stimulus sensitivity and yielded a shift to longer wavelengths (triangles) no matter whether the center response in the dark-adapted state was mediated by rods (Fig. 7*A*) or by the M-system (Fig. 7*B*). A Dartnall nomogram peaking at 550 nm (dashed curve) fits the data best and indicates that the center response is mediated by L-cones.

In a few ganglion cells, chromatic adaptation with a yellow background shifted the center sensitivity function to shorter wavelengths (diamonds). Data could be fit best by a Dartnall nomogram with a peak sensitivity of 451 nm (dotted curve). Such an S-cone input to the field center could only be observed in 18 RGNs ($n = 4$ in Fig. 7*A*, 3 in Fig. 7*B*). In the majority of cells, the spectral sensitivity still shifted to 550 nm in presence of photopic yellow adaptation.

Analysis of the surround responses yields comparable results and spectral sensitivity functions are not shown separately. Detailed information about the photoreceptor inputs to the two cell types under various conditions of adaptation is given in Table 1.

The fact that S-cone input was only observed in 29 of 189 or 15% of all RGNs tested (see Table 1) is in accordance with the finding of other authors that most retinal ganglion cells only have L-cone input in their receptive fields, besides a highly sensitive rod input (Daw and Pearlman, 1969, 1970; Andrews and Hammond, 1970a,b). Interestingly, in the present study S-cone input was restricted to either the receptive field center or surround but was never observed in parallel.

Discussion

Based on the results in the dark-adapted state and under different conditions of chromatic adaptation, our results point to at least two spectrally different major cell classes within the area centralis in cat retina that differ in the spectral characteristics of their photoreceptor inputs. In the majority of RGNs only rods were active in the dark-adapted state, whereas in a small subpopulation of cells the visual signals were mediated by a mid-spectral receptor system different from rods.

In earlier studies, chromatic adaptation was required to reveal any middle-wavelength input in addition to rods (Ringo et al., 1977; Crocker et al., 1980; Schuurmans, 1981; Wienrich, 1983; Wienrich and Zrenner, 1983; Schuurmans and Zrenner, 1981a,b). Although the M-mechanisms of these studies differed with re-

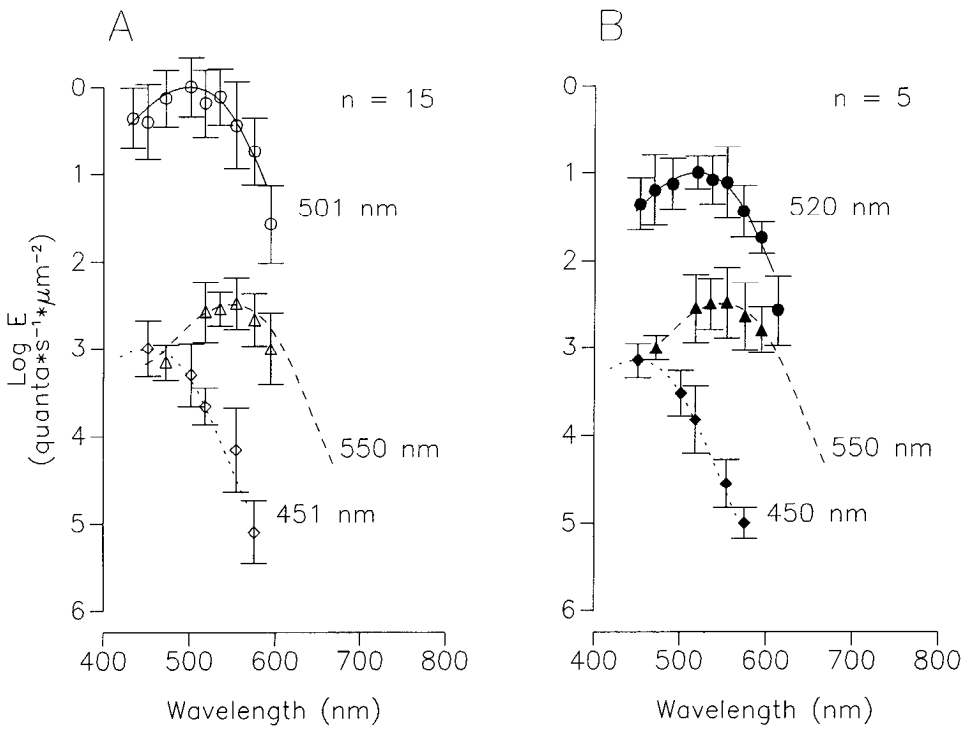

Figure 7. Cone-mediated spectral sensitivity of the receptive field center revealed by different conditions of chromatic adaptation for cells with a sensitivity peak of 501 nm in the dark-adapted state (*A, circles*), and 520 nm cells (*B, circles*). Bright chromatic adaptation with a steady, blue-green Ganzfield (25°) background (BG 28, −1.5 log *I* in lumens•m^{-2}) reveals L-cone input (*triangles*), which is indicated by a 550 nm Dartnall nomogram fit (*dashed line*). S-Cone input (*diamonds*) was obvious only in a few RGNs (n = 4 in *A*, 3 in *B*). Data are best fitted by a 451 nm Dartnall nomogram (*dotted line*). Comparable results were obtained for the spectral sensitivity functions of the surround response both in 501 nm and 520 nm peaking ganglion cells.

spect to the position of their sensitivity peak, all had properties usually attributed to cones. They were active under conditions of adaptation where rods were clearly saturated and followed flicker light of 40 Hz (Schuurmans and Zrenner, 1981a,b), while rods show a cff of 30 Hz (Dodt and Walther, 1958). Moreover, a midspectral input could be demonstrated in the cone-dominated visually evoked cortical potential (Schuurmans and Zrenner, 1981). It was therefore concluded that the cat is a photopic trichromat having in addition to L-cones and S-cones (a cone system with a peak sensitivity around 500–510 nm).

We now could demonstrate inputs of an M-system without the necessity of rod light adaptation. This is a crucial fact regarding the problem of the position of its peak sensitivity within the midspectral region, its absolute sensitivity, and its functional properties. The small discrepancy in peak position of the M-system reported here and that described by others might be explained by the strength of the chromatic adaptation they had to use for its isolation. This also might be the reason for the differences in threshold sensitivity. Since the action spectra of different receptor systems overlap over a wide range, it is impossible to light adapt only one system without influencing the others. Especially in rods and M-cones, where the peak sensitivities are so close together, light adaptation yields in a sensitivity reduction in both. Thus, the exact position of the threshold sensitivity of the M-system could not be determined in earlier studies in adaptation experiments and an input was obvious only under photopic conditions. In contrast, the M-system reported here has a peak threshold that is only about 1 log unit higher than that of rods, indicating that it is already active at high scotopic to mesopic light levels.

There has always been doubt as to whether the M-system originates from rods instead of representing a separate, midspectral cone system. Recent findings suggest that the rod system is physiologically not producing univariant responses in the retina but can transmit its signals via two retinal pathways. This hypothesis is based on anatomical studies that showed a direct rod–cone contact via gap junctions at the axon terminals (Raviola and Gilula, 1975; Kolb, 1977). Rod signals might be transmitted to the ganglion cells via the cone and cone–bipolar cell, and this pathway probably is used at higher ambient light levels (Nelson, 1977; Smith et al., 1986; Stockman et al., 1991). At lower light levels the rod signal might then be transmitted via the rod–bipolar/AII amacrine cell pathway (Kolb, 1977; Steinberg et al., 1983). Analysis of the temporal properties indicates that the former pathway had a higher temporal resolution (Green and Siegel, 1975; Hess et al., 1989).

One can argue now that a shift from one rod pathway to the other, as light adaptation proceeds, might mimic a rod–cone-like sensitivity change at the ganglion cell level (Loop et al., 1987) and that the M-system could be related to the low-sensitivity rod system with high temporal resolution. However, it would be very difficult to conceive how such a rod system's sensitivity can be changed from a peak value of 500 nm to a peak value of 520 nm. It also would be very difficult to imagine a mechanism that makes a particular rod pathway form a spectrally homogeneous small receptive field center that excludes the high-sensitivity, low-temporal-resolution pathways of rods. Therefore, our data support the hypothesis of a separate M-receptor mechanism.

Nothing can be said at the moment about the population of RGNs that receive input from the M-system. In common, they all are located within the area centralis and have small receptive fields (0.4–1.3°). They respond to a test stimulus with a sustained discharge over a wide range of light intensities that might indicate that they are X-cells.

Although the spectral and temporal properties of the M-system point to a separate cone, or at least "cone-like" mechanism, a participation in color vision does not necessarily follow. Each individual cone mechanism can transmit information only about the number of photons absorbed, and an interaction between

two different receptor mechanisms is necessary for good color vision. Wienrich and Zrenner (1983) reported the number of color-opponent RGNs in cat to be small compared to the primate retina. Opponency between the red- and middle-wavelength-sensitive receptor mechanisms was only obvious under certain conditions of chromatic adaptation in only a few ganglion cells (Wienrich and Zrenner, 1984). Since we did not investigate color-opponent mechanisms, we cannot say whether there is any of such a hidden opponency in the ganglion cells presented in this study. However, the overall distribution of celis receiving input from the M-system (see also Wienrich and Zrenner, 1983) seems to be too sparse to mediate a powerful signal in color-coding processes. This might be the reason why the M-system is not easily revealed to a behavioral observer investigating color discrimination capability in cat.

One can then only speculate about the possible role of the cells with the 520 nm receptor input. They might be involved in fixation processes where high spatial acuity is required in the low mesopic range. It possibly could be an advantage for a nocturnal animal like the cat to possess a receptor system within the area centralis that has relatively high sensitivity at light levels where the rods are already at the end of their linear range and the cone systems still are not fully involved.

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