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INFLUENCES OF CONES UPON CHROMATIC- AND LUMINOSITY-TYPE HORIZONTAL CELLS IN PIKEPERCH RETINAS

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SUMMARY

1. The spectral sensitivity and spatial organization of cones and horizontal cells have been analysed by intracellular recording in pikeperch retinas.

2. The vast majority of cone recordings were obtained from orange-sensitive cones. They have an action spectrum which peaks at about 605 nm. Recordings from several green-sensitive cones have also been obtained.

3. The results of action spectrum measurements and spectral screening tests indicate that the vast majority of luminosity-type horizontal cells receive predominant input from the orange-sensitive cones.

4. Chromatic-type horizontal cells were recorded at more proximal levels of the retina than luminosity-type cells and were the classic red-depolarizing, green-hyperpolarizing (R/G) type.

5. The action spectra of the depolarizing and hyperpolarizing responses of chromatic horizontal cells peak at about 650 and 530 nm, respectively. When the depolarizing mechanism is selectively depressed by a red background field, the action spectrum of the hyperpolarizing mechanism shows an enhanced sensitivity, peaks at 530–540 nm, and may approximate the action spectrum of the green-sensitive cones.

6. Small red fields evoke depolarizing responses from chromatic-type horizontal cells but do not seem to significantly activate the depolarizing surround mechanism of cones.

7. These and other results suggest that the colour-opponent properties of the chromatic-type horizontal cells are not fundamentally dependent upon feed-back to cones but rather originate from antagonistic interactions generated in post-receptor networks.

INTRODUCTION

It is rather well established that cones are the receptors upon which vertebrate colour vision depends but it is less certain exactly how they influence the colour-discriminating networks of the visual pathway. It is now known that some colour-discriminating networks are established quite distally, since there is clear evidence in fish and turtle that the polarity of the response of certain bipolar and horizontal cells varies with the wave-length of the stimulating light (Kaneko, 1970, 1973; Yazulla, 1976*a*). In contrast, the first systematic study of cones by intracellular recording (Tomita, Kaneko, Murakami & Paulter, 1967) indicated that all spectral

classes of cones in the carp retina generate simple hyperpolarizing responses to lights in all regions of the spectrum. This suggests that cones satisfy the principle of univariance (Naka & Rushton, 1966*a*). Thus, the amplitude but not the polarity of the response is free to vary with stimulus wave-length, and if an equal number of photons is absorbed, a cone will generate identical responses to light of any wave-length. This means that an individual cone has no capacity for colour discrimination.

The generality of this simple view of cone function may now be questioned since some green-sensitive cones in the turtle retina can show wave-length dependent variations in response polarity (Fuortes, Schwartz & Simon, 1973; Fuortes & Simon, 1974). This raises the possibility that the colour-opponent responses of bipolar and chromatic-type horizontal cells might largely be a reflexion of colour-opponent responses already elaborated by cones. The colour-opponency in turtle cones is a consequence of an antagonistic centre-surround receptive field organization in which the surround mechanism is mediated by luminosity-type horizontal cells which feed back a depolarizing influence upon cones (Fuortes *et al.* 1973). It has been assumed that feed-back to cones acts similarly in fish retinas and plays a pervasive role in shaping the colour-opponent responses of chromatic-type horizontal cells (Gouras, 1972; Stell, Lightfoot, Wheeler & Leeper, 1975).

The first physiological evidence for feed-back and centre-surround receptive field organization in fish cones has recently been reported for two species of pikeperch (Burkhardt, 1977). Because these fish have remarkably large cones and horizontal cells, they provide favourable preparations for further analysis of retinal function by intracellular recording. Here we extend the study of pikeperch retinas by charting some relations between the responses of cones and horizontal cells. From this, we advance some conclusions about mechanisms of colour vision in the distal retina.

METHODS

Preparation and recording

Intracellular recordings were made from eyecup preparations as described in detail elsewhere (Burkhardt, 1977). The recordings were obtained within a circular area about 10 mm in diameter centred about the point where the optic nerve head ends in the central retina. Spectral lights were obtained from a grating monochromator (7 nm half-band pass) or an interference wedge (12 nm half-band pass). Spectral energy calibrations were made at the plane of the retina with a photomultiplier whose spectral sensitivity had been precisely determined with a thermopile. All action spectra in this paper are based on the relative number of photons required to evoke a fixed (criterion) response.

The walleye (*Stizostedion vitreum*) and the sauger (*Stizostedion canadense*) are closely related species which together constitute the luciopercinae subfamily (pikeperch) of the perch family of North American fishes (Eddy & Underhill, 1974). Their retinas appear very similar when analysed by light microscopy (D. A. Burkhardt, unpublished; Zyznar & Ali, 1975) or by electrophysiology. Thus, although most of the present work comes from the walleye, all essential results have also been observed in the sauger. For brevity, we will therefore generally use the inclusive term, pikeperch, in this paper and make no distinctions between the two species.

RESULTS

Properties of cones and luminosity-type horizontal cells

The vast majority of recordings from cones in pikeperch retina were maximally sensitive to orange light. The closed circles of Fig. 1 show the mean action spectrum for eleven of these cones when responses were evoked by a small spot of light flashed in the centre of the receptive field. The action spectrum is well fit by the smooth curve which is the absorption spectrum of a visual pigment with maximum absorbance at 605 nm, as given by the A_2 pigment nomogram of Ebrey & Honig (1977). The responses of these orange-sensitive cones were univariant, as would be expected for a response depending on a single pigment (Naka & Rushton, 1966*a*).

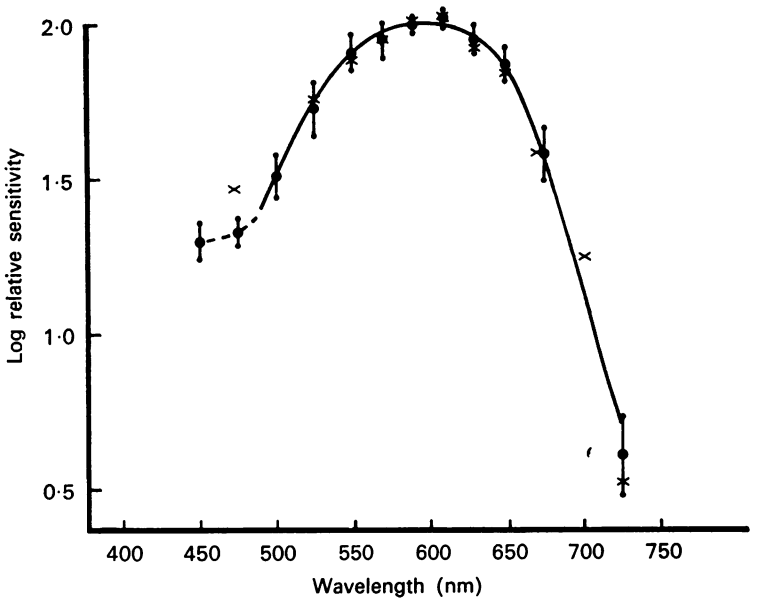

Fig. 1. Action spectra of orange-sensitive cones and luminosity-type horizontal cells in the walleye retina. The large filled circles show the mean action spectrum for eleven cones and the small filled circles indicate the standard deviations. The continuous curve is the absorption spectrum expected for an A_2 cone pigment with maximum absorption at 605 nm (Ebrey & Honig, 1977). The crosses show the mean action spectrum for fourteen luminosity-type horizontal cells. Sensitivity is the reciprocal of the relative number of photons needed to evoke a constant response. Stimulus diameter is 0·10 mm for cones and 2 mm for horizontal cells.

Recordings from luminosity-type horizontal cells (L cells) were distinguished from recordings from cones by functional criteria of relative depth of recording and degree of spatial summation (Burkhardt, 1977). These criteria have recently been confirmed by dye injection (D. A. Burkhardt and G. Hassin, unpublished). Spatial summation was assessed by determining the dependence of response amplitude upon the diameter of a centred spot of light flashed at a constant level of illuminance. For each cell, the illuminance level was selected so that the largest diameter stimulus would evoke a response of about half-maximum amplitude. The dotted curve in Fig. 2 shows

results for a cone. There is little increase in peak amplitude for stimuli larger than 0·10 mm. This is typical of cones (Burkhardt, 1977). L cells, by contrast, showed summation over much larger areas and the area of summation varied considerably from cell to cell. The filled circles in Fig. 2 show data for five L cells. Analysis of such data from about eighty L cells showed a rather continuous range of receptive field size from about 0·5 mm to at least 5 mm with no clear evidence for discrete subgroups. Although we have attempted no statistical analysis of variations of receptive field size with location on the retina, no striking variations seemed apparent over the region sampled (see Methods). Moreover, L cells with widely different sizes of receptive fields were sometimes recorded in successive penetrations of points separated by 200–500 μm on the retina.

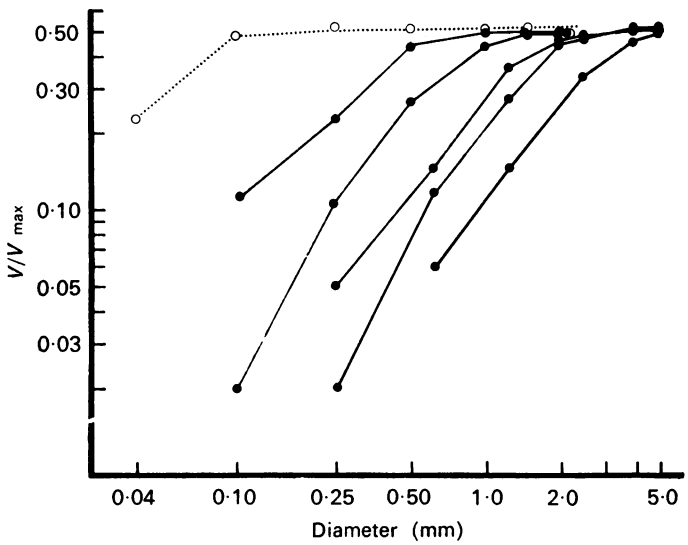

Fig. 2. Relation between peak amplitude and stimulus diameter for a cone (open circles) and five L cells (filled circles). The ordinate gives the measured response amplitude (V) relative to the maximum amplitude ($V_{max.}$) which can be evoked by a high intensity flash. See text for other details.

The mean action spectrum for fourteen L cells is shown by the crosses in Fig. 1. It agrees closely with the action spectrum of the orange-sensitive cones. A further comparison between the spectral properties of cones and L cells was obtained by a two-colour screening test. By varying flash intensity in fixed steps, the relative number of photons needed to evoke equivalent responses at 530 and 630 nm was determined. Thus, the 630/530 nm sensitivity ratio was specified for each cell. Fig. 3 shows the distributions of the logarithm of this ratio for a large sample of cones and L cells. The distributions are similar; both show a prominent peak around +0·20 log unit. This suggests that the majority of L cells receive predominant input from the orange-sensitive cones.

There are clearly a few cells in both distributions of Fig. 3 which have significantly negative values of the logarithm of the 630/530 nm ratio and are therefore more sensitive to green than red light. It is not possible to reach very precise conclusions

about these cells from the few recordings obtained so far. None of the cones were held long enough to complete action spectrum measurements. The few spectra obtained from L cells showed a range in their peak sensitivity from about 530 to 580 nm. This suggests that there may be a few L cells which receive strong input from green-sensitive cones.

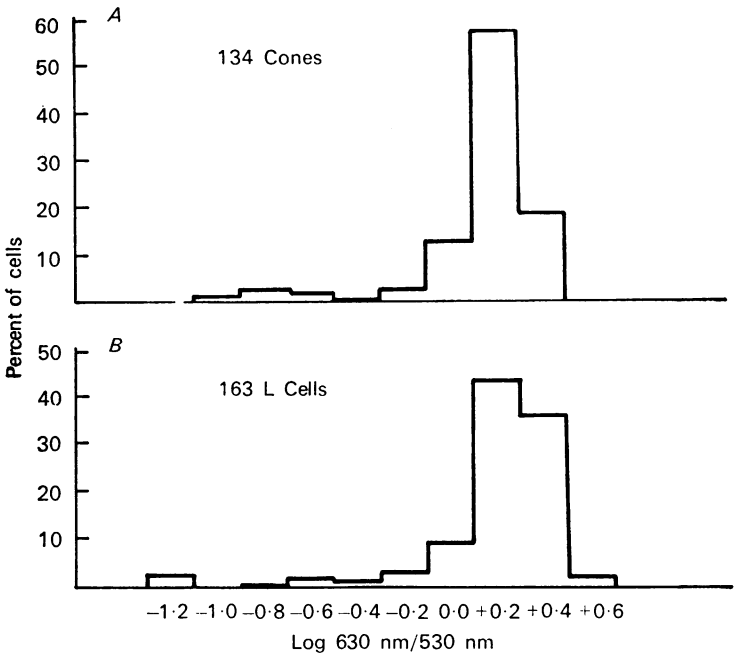

Fig. 3. Distributions of the 630/530 nm sensitivity ratio for a sample of 134 cones (*A*) and 163 L cells (*B*).

As a rule, pikeperch L cells conformed closely to the principle of univariance. This was evident in both the action spectra and two-colour measurements. Fig. 4*A* shows a representative example. In the upper trace, the relative intensities of a 680 and 530 nm flash have been adjusted to yield equivalent (superimposed) responses. When the 680 and 530 nm intensities are then increased by equal factors, the responses remain equivalent (lower traces). Thus, in this and most other L cells, it seems quite clear that univariance holds almost exactly. In about 10 % of the L cells sampled, slight departures from univariance were detectable. These were subtle, variable in detail, and usually introduced less than 0·10 uncertainty in specifying the logarithm of the 630/530 nm sensitivity ratio. Hence, these L cells must receive input from more than one class of cone but the resulting interactions seem minor.

The wave form of the response of many L cells contained a transient on-response component. As Fig. 4*A* suggests, the transient was most prominent for large diameter stimuli of intermediate intensity and was not dependent on the spectral content of the flash. Fig. 4*B* shows that the transient was effectively eliminated by reducing the stimulus diameter and could not then be re-established by increasing the stimulus intensity. Thus, the transient is fundamentally dependent upon stimulus diameter. About 90 % of the eighty L cells studied had receptive fields of 1 mm or greater in

diameter. About 75 % of these cells displayed the transient component. It was clearly developed when the stimulus diameter was 1–2 mm or greater but undetectable or greatly attenuated when 0·5 mm diameter stimuli were used. Thus, Fig. 4*B* is representative of the typical properties of the L cell transients seen in our experiments. To judge from our small sample of L cells with receptive fields in the 0·5–0·9 mm range, it appears that on-transients may be less common and, when found, are less prominent than in L cells with larger receptive fields.

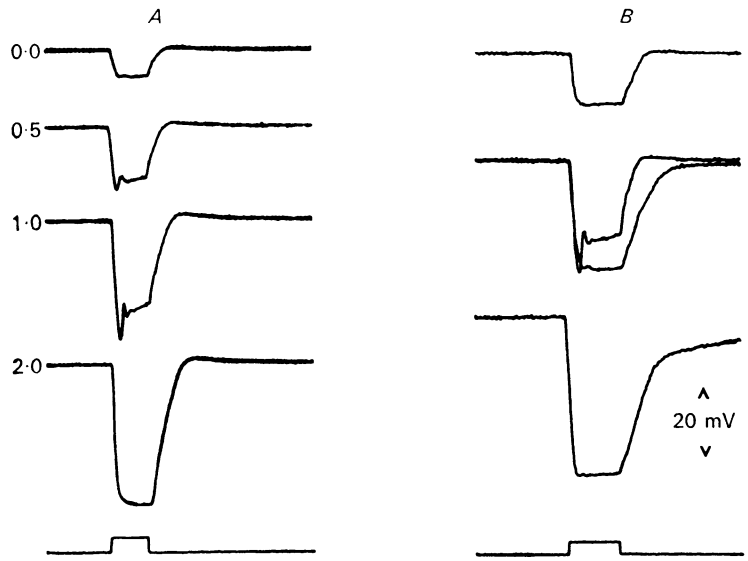

Fig. 4. Response properties of L cells. *A*, univariant responses. The top left trace shows superimposed responses to 680 and 530 nm flashes when the latter is 1·4 times more intense than the former. In successively lower traces, the 680 and 530 nm flashes are increased by equal factors indicated in log units to the left. In each case, the responses continue to superimpose almost exactly. An intensity of 1·0 log unit at 530 nm is equivalent to $1{\cdot}5 \times 10^4$ photons/μm^2.sec. Stimulus diameter is 2·2 mm. *B*, effect of stimulus diameter on response wave form. In the middle trace, the on-response shows a transient component when the stimulus diameter is 1 mm and the intensity is 5×10^3 photons/μm^2.sec at 630 nm. In the upper trace, the diameter is reduced to 0·5 mm and the transient is abolished. When the diameter then remains at 0·5 mm and the flash intensity is increased so that the peak amplitude matches (middle trace) or exceeds (lower trace) that evoked by the 1 mm stimulus, the on-transient is not re-established. The intensities of the 0·5 mm stimuli in the middle and lower traces are, respectively, $15{\cdot}8 \times 10^4$ and $75{\cdot}8 \times 10^5$ photons/μm^2.sec. Trace durations are 2 sec in *A* and *B*. The voltage calibration applies to all records.

There are three layers of horizontal cells in pikeperch retinas (P. Witkovsky and D. A. Burkhardt, in preparation). Procion Yellow dye injection experiments show that both the distal and middle layers are L cells with similar properties, although L cells of the middle layer are impaled with much greater frequency (G. Hassin, unpublished).

Properties of chromatic-type horizontal cells

Recordings from chromatic-type horizontal cells (C cells) were invariably obtained proximal to those from L cells, which suggests that C cells comprise the most proximal layer of horizontal cells. This has recently been confirmed by dye injection (G. Hassin, unpublished). In general, C cells were more difficult to penetrate than were L cells. To date, about 100 C cells have been impaled. All depolarized to a standard red test light (630 nm) and hyperpolarized to a green test light (530 nm).

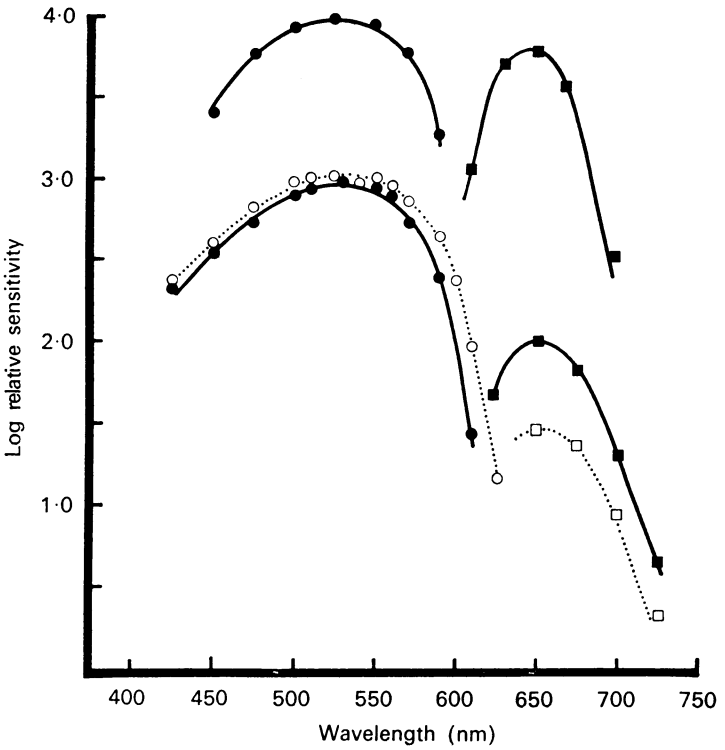

Fig. 5. Action spectra for two R/G C cells. The hyperpolarizing mechanism is represented by circles and the depolarizing mechanism by squares. Measurements for one cell in the absence of background illumination are given by the two curves at the top of the Figure by filled circles and squares. Measurements for a second cell under the same conditions are shown by the lower set of filled symbols. For clarity, maximum sensitivity of this cell is arbitrarily displaced one log unit below that of the other cell. The open symbols and dotted lines show the action spectrum of the second cell when the retina was exposed to a red background field of 646 nm dominant wave-length. This depresses the sensitivity of the depolarizing mechanism and elevates the sensitivity of the hyperpolarizing mechanism.

Complete action spectra were obtained for fifteen cells in the absence of background illumination. All spectra were fundamentally like that shown for two cells by the filled symbols in Fig. 5. The hyperpolarizing response was maximally sensitive around 530 nm and the depolarizing response was maximally sensitive around 650 nm. Thus, pikeperch C cells resemble the biphasic R/G type previously described in other vertebrates (Gouras, 1972).

When action spectrum measurements were made in the presence of a steady red background field of appropriate intensity, the depolarizing mechanism was selectively depressed, whereas the hyperpolarizing mechanism showed an enhancement in sensitivity. The region of maximum sensitivity was not clearly changed; it remained around 530–540 nm. An example of these effects of chromatic adaptation is shown by the lower set of curves in Fig. 5. On the simple assumption that pikeperch C cells receive input from two classes of cone, the orange-sensitive class of Fig. 1 and a class maximally sensitive to shorter wave-lengths, the results of chromatic adaptation imply that the latter class are green-sensitive cones which contain a photopigment which absorbs maximally at about 535 nm. Such cones would have a log 630/530 nm

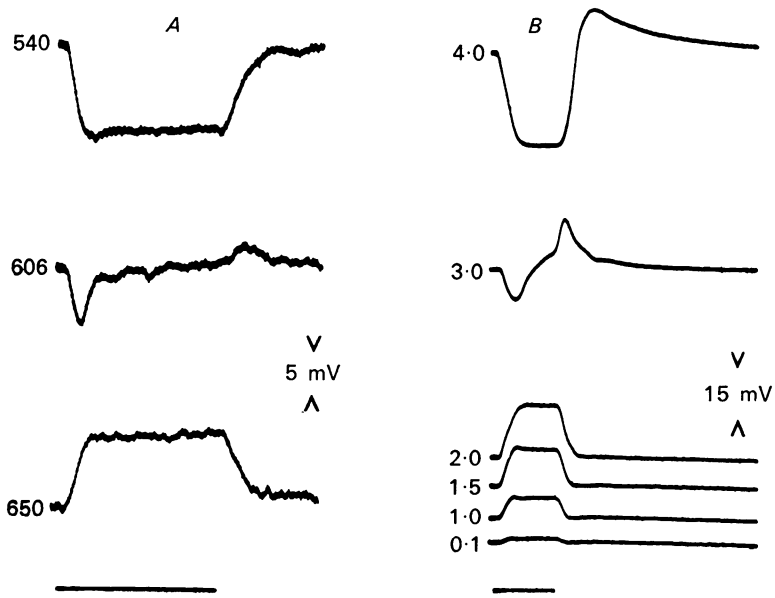

Fig. 6. *A*, responses of an R/G cell to flashes of 650, 606, and 540 nm. The flashes are approximately equated for a photon level of 6×10^3 photons/μm^2.sec. *B*, responses of an R/G C cell to flashes of 630 nm over a wide range of intensity indicated in $\log_{10}$ units to the left of each trace. An intensity of 1·0 log unit is equivalent to $2{\cdot}4 \times 10^3$ photons/μm^2.sec. Stimulus diameter is 2 mm in *A* and *B*.

sensitivity ratio of about $-0{\cdot}80$ (Ebrey & Honig, 1977). This is in reasonable agreement with the range of values found for the small cluster of cones which have significantly negative sensitivity ratios in Fig. 3*A*. We have made some preliminary calculations in which signals derived from 535 and 605 nm cones are differentially weighted, given opposite signs, and then summed. When the signal from the 535 nm cones is weighted some 2–3 times more heavily than that from the 605 nm cones, the calculated action spectra show a long wave-length peak in the 640–650 nm range and also approximate the over-all form of the action spectra which we have measured experimentally for pikeperch C cells.

All action spectrum measurements in the absence of background illumination were made with low intensity flashes. In this range, which spanned some 1·5 log units above threshold, the wave form of the responses and the action spectra were largely

independent of the amplitude used for the criterion. For stimuli near 600 nm, the maintained response was small since the maintained potentials of the red and green mechanisms tended to cancel each other. There remained, however, a prominent hyperpolarizing transient at stimulus onset and a depolarizing transient at stimulus offset, as shown in Fig. 6*A*. This implies that the response of the depolarizing mechanism has a somewhat slower onset and decay than the response of the hyperpolarizing mechanism.

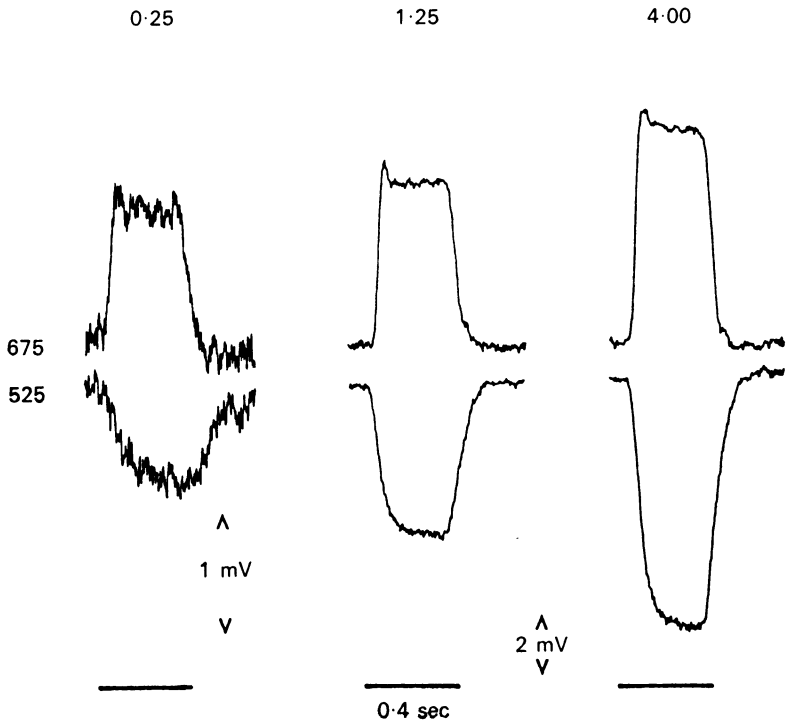

Fig. 7. Response of an R/G C cell at 675 and 525 nm at three values of stimulus diameter shown above in mm. The intensity levels are approximately 2×10^3 and 9×10^1 photons/μm^2.sec at 675 and 525 nm, respectively. Calibration marker at the right applies to responses evoked by 1·25 and 4 mm fields.

When responses to high intensities were investigated, appreciable differences in the maximum (saturated) amplitude of the response of the red and green components were usually evident. Although in a few cells, the maximum depolarization exceeded the maximum hyperpolarization, usually, the maximum response of the hyperpolarizing mechanism exceeded that of the depolarizing mechanism by a factor of 2–5. As a result, low to moderate intensities of red light evoked simple depolarizing responses, as shown in the lower traces of Fig. 6*B*. With further increases in flash intensity, complex biphasic waves were generated when both mechanisms were activated and differences in the time course of their responses came into play. At even higher intensities of red light, the hyperpolarizing component was maximally stimulated and largely masked the depolarizing component, as shown in the upper trace of Fig. 6*B*. In a few extreme cases, cells were found in which the maximum

hyperpolarization was some 20 times larger than that of the maximum depolarization. Without extensive tests, such cells could be mistaken for green-sensitive L cells. Hence, it is possible that some cells nominally classified as green-sensitive L cells in pikeperch (Fig. 3*B*) and other retinas could be R/G C cells in which the red mechanism was abnormally insensitive and not detected.

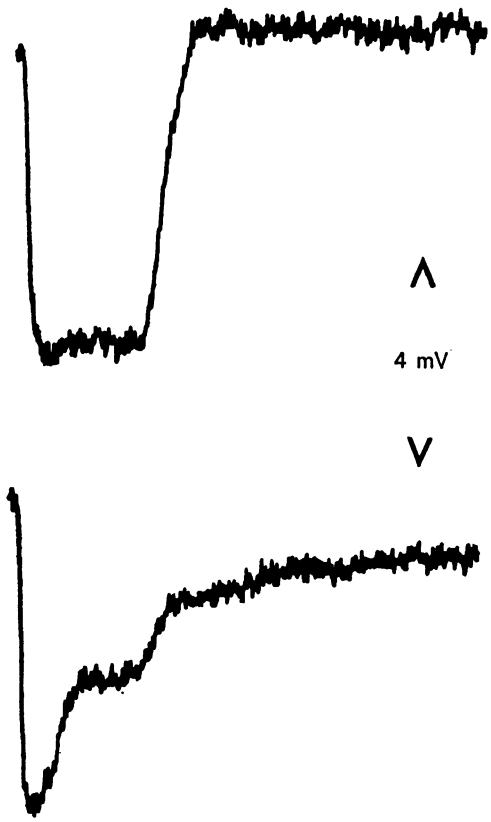

Fig. 8. Responses of a green-sensitive cone to 630 nm flashes of 0·25 and 2·2 mm diameter. Flash intensity is approximately 2×10^5 photons/μm^2.sec. With a tenfold reduction of flash intensity, response amplitude was considerably reduced but the effect of stimulus diameter was qualitatively similar to that illustrated here. Duration of traces is 2 sec. The 630/530 nm sensitivity of this cell was −0·60 log unit.

From experiments in which flash illuminance was held constant and stimulus diameter varied, the diameter of the receptive field of pikeperch C cells was found to range from about 1 to 5 mm, depending on the cell. No striking differences in the behaviour of the hyperpolarizing and depolarizing components were observed. Thus, as Fig. 7 shows, response amplitude increased markedly with stimulus diameter but the colour-opponent nature of the C cell response was clearly evident for small (0·25 mm diameter) as well as much larger stimuli. The use of brief flashes (25 msec)

or annuli also produced no differential effects upon the components. Hence, the only identified factor which disrupts colour-opponency is the use of high stimulus intensities (Fig. 6*B*).

Analysis of the receptive field organization of more than seventy orange-sensitive cones shows that feed-back is undetectable for spots of 0·25 mm or less, as previously shown (Burkhardt, 1977). Although recordings from green-sensitive cones are rare (Fig. 3*A*), we now have similar evidence for the four cones in our total sample which satisfied the joint criterion of showing clear evidence for feed-back and also being green-sensitive (the log 630/530 nm sensitivity ratios ranged from −0·60 to −1·00). Thus, the lower trace in Fig. 8 shows that a 2·2 mm spot of 630 nm evokes an initial hyperpolarization from a green-sensitive cone followed by a significant decline which is characteristic of the delayed depolarizing influence of feed-back from the surround. When the stimulus is reduced to 0·25 mm, the response is a simple maintained hyperpolarization (upper trace). Thus, feed-back is undetectable for the 0·25 mm spot and even when the feed-back mechanism is strongly activated by enlarging the stimulus to 2·2 mm, the cone remains hyperpolarized for the duration of the flash. Taken together, the results illustrated in Figs. 7 and 8 indicate that small red fields which evoke hyperpolarizing responses from pikeperch cones without significantly activating the feed-back mechanism are nevertheless capable of evoking depolarizing responses in C cells. Furthermore, large red fields which provide strong feed-back to cones and evoke large depolarizing responses in C cells still evoke a net hyperpolarizing response in cones. It thus seems evident that there is a polarity-inverting mechanism between the level of the cone output and the generation of the C cell response to red light.

DISCUSSION

The results described suggest that the spectral organization of pikeperch retinas is relatively simple. There is evidence for two cone types, orange- and green-sensitive. The action spectrum of the orange-sensitive cones seems based on a photopigment which absorbs maximally at about 605 nm (Fig. 1) and may be identical to the orange-sensitive pigment identified by microspectrophotometry in the teleost, *E. plumieri* (Laufer & Milan, 1970). The results of Figs. 3*A* and 5 suggest that the green-sensitive pigment absorbs maximally around 530–540 nm.

The experimental evidence accumulated over the last two decades strongly suggests that luminosity-type horizontal cells in vertebrates are not monotypic: functional variants may occur in a given retina as well as across species (Gouras, 1972). In the spectral domain, the simplest type of L cell seems to be largely driven by a single cone system and therefore is not selectively adapted by chromatic backgrounds and shows no obvious wave-length dependency in response wave form. The present results indicate that the vast majority of L cells in pikeperch are of this simple type and receive their predominant input from orange-sensitive cones. An analogous type is common in turtle (Yazulla, 1976*b*). These L cells may be contrasted with more complex types which show wavelength dependencies in wave form (Fuortes *et al.* 1973; Fuortes & Simon, 1974; Yazulla, 1976*b*), or action spectra which are strongly dependent upon the response amplitude or the chromatic aspect

of background fields (Naka & Rushton, 1966*c*; Witkovsky, 1967). No striking examples of such complex L cells have yet been demonstrated in pikeperch.

In the spatial domain, pikeperch L cells have large receptive fields comparable to those found in other species. Although transient on-responses have often been demonstrated in L cells, the present findings (Fig. 4*B*) may be the first to indicate that large fields (1–2 mm) are necessary for generating such transients. This might be the consequence of feed-back to cones since large fields are also necessary for evoking feed-back and on-transients in pikeperch cones (Burkhardt, 1977), but the present observations do not rule out alternative mechanisms.

The action spectra of Fig. 5 and the wave form variations of Fig. 6 show that the R/G cells of pikeperch are prototypical since very similar results are characteristic for such cells in other species (Svaetichin & MacNichol, 1958; Naka & Rushton, 1966*a*; Gouras, 1972; Yazulla, 1976*b*). If feed-back to cones plays the pervasive role in shaping the colour-opponent properties of C cells as recently suggested (Gouras, 1972; Fuortes & Simon, 1974; Stell *et al.* 1975), conditions which markedly alter feed-back to cones would be expected to affect the hyperpolarizing and depolarizing components differentially. Moreover, in the special case where feed-back is eliminated, the C cell should hyperpolarize to red as well as to green light, and thus lose its colour opponency. When put to the test, pikeperch C cells do not conform to these expectations. Thus, the relative amplitudes of the depolarizing and hyperpolarizing components were not markedly altered by variations in stimulus diameter which are known to markedly alter feed-back to pikeperch cones. Furthermore, small red fields which do not significantly initiate feed-back to cones are still quite capable of evoking depolarizing responses from C cells (Figs. 7 and 8). Thus, the present results suggest that feed-back to cones is not essential for generating colour-opponent responses in pikeperch C cells.

There seem to be only two previous studies which deal with spatial-spectral interactions in C cells in any detail. Both were done in carp and support the present findings by showing that the colour-opponent properties of C cells are detectable with small spots and are not fundamentally modified by variations in the diameter or configuration of the stimulating flash (Norton, Spekreijse, Wolbarsht & Wagner, 1968; Hashimoto, Kato, Inokuchi & Watanabe, 1976). Moreover, in these and many other reports, well developed C potentials have been routinely recorded from isolated fish retina preparations which, in contrast to the eyecup preparations used here, have yet to yield evidence for feed-back to cones and probably fail to achieve the physiological conditions necessary for maintaining the feed-back mechanism (Pinto & Pak, 1974). Hence, from the evidence now available, it seems likely that the primary mechanism of the R/G C cell response in pikeperch and other fish retinas involves relatively simple post-receptor circuitry like that proposed by Naka & Rushton (1966*b*, Fig. 2*A*). In this scheme, independent pathways arising from red- and green-sensitive cones converge upon the C cell and there modulate the liberation of transmitters which evoke post-synaptic potentials of opposite polarity. The apparently slower onset of the response to red light relative to that to green (Fig. 6*A*) should not then be attributed to the delay of feed-back on cones, as recently suggested (Gouras, 1972; Stell *et al.* 1975). It could well arise from differences in the dynamics of the actions of the transmitters which impinge upon the C cell, since it is now

known that the latency of the response of the depolarizing bipolar cells in the mudpuppy is significantly longer than that of the hyperpolarizing bipolars (Nelson, 1973; Frumkes & Miller, 1978).

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