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COLOUR-DEPENDENCE OF CONE RESPONSES IN THE TURTLE RETINA

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SUMMARY

1. Responses to monochromatic lights were recorded intracellularly from red cones, green cones, and luminosity horizontal cells (L-cells) in the retinae of turtles.

2. Both types of cones responded to small fields of illumination with graded hyperpolarizations. Red cones were only moderately more sensitive to deep red (680 nm) than to green (550 nm) light while green cones were much more sensitive to the green light than to the red. L-cells produced small responses for flashes of either colour covering small fields.

3. Stimulation of large fields with monochromatic lights of moderate or high intensity evoked large L-cell responses and composite responses in cones. These latter include the hyperpolarizing action of the light absorbed by the cone itself (direct response), its enhancement by illumination of the near surround, and the depolarizing effects of L-cell feed-back.

4. L-cells respond primarily to the activity of red cones; with sufficient intensity of the light, however, their responses are influenced also by green cones. As a result, if a red and a green light stimulate red cones equally, the L-cell response is larger for the green stimulus.

5. Green cones were depolarized by deep red lights of moderate intensity applied over large fields. These depolarizing responses include oscillations which follow closely oscillations in L-cells. Green light applied to the same large fields produced hyperpolarization of green cones.

6. Red cones were hyperpolarized by red or green light covering large fields, but the time course of their responses differed for the two colours, reflecting a corresponding difference in L-cell activity.

7. Red light in the form of an annulus produced large responses in central L-cells without eliciting direct responses in central green cones.

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In these conditions green cones developed depolarizing waves which included a large, sharp transient.

8. It is concluded from these and other results that the direct response of each cone is modified by two interactions: enhancement only from nearby cones of the same colour and depression controlled (through L-cell feed-back) by cones of all colours. In this way the response of any cone will change as the proportion of responses in cones of different colours changes, this proportion being a function of the wave-length of the light.

INTRODUCTION

Photoreceptors in the vertebrate retina are usually hyperpolarized by light (Tomita, 1965; Bortoff & Norton, 1967). It has been noted, however, that luminosity horizontal cells (L-cells) exert a depolarizing action upon cones (Baylor, Fuortes, & O'Bryan, 1971). If a flash of light is applied to a small retinal area, L-cells develop a negligibly small response, and cones produce a smooth hyperpolarizing wave. The amplitude of this wave increases when a circle of light centred on a cone is enlarged from 4 to about 70 μm radius. This enhancement is due in part to scattering of light in the retina and in part to coupling between cones (Baylor *et al.* 1971; Baylor & Hodgkin, 1973). When the stimulus is further enlarged, the horizontal cell response increases, and the response of the cone is shortened by a prominent depolarizing deflexion. The response to illumination of large retinal areas is then interpreted as a combination of the hyperpolarizing action of the light absorbed by the cone itself (to be called the 'direct response' of the cone), the enhancement due to light scattering and to coupling between cones, and the depolarizing action exerted by the horizontal cells. This action has been called 'feed-back' in previous work. The term will be used in this article even when it is not entirely appropriate, namely when one type of cone initiates L-cell activity and different cones receive the depolarizing impingement.

To study the properties of the action of L-cells upon cones it is desirable to evoke it without the complication of a coexisting direct response. This was achieved in previous experiments in which a horizontal cell and a cone were simultaneously impaled (Baylor *et al.* 1971). It was seen then that hyperpolarizing currents through a horizontal cell can produce depolarization of a nearby cone.

In the present study the feed-back was elicited in the absence of direct cone responses by a simpler method involving the use of monochromatic lights. It is known that the cones of the turtle contain pigments which absorb maximally red, green or blue light (620, 520 and 450 nm respectively, according to Liebman & Granda, 1971). Red light is absorbed

poorly by 'green' cones (namely by cones containing the pigment which absorbs maximally green light) but is an effective stimulus for L-cells which, in the turtle, are maximally sensitive to wave-lengths around 600 nm (Simon, 1973). Thus, red light applied to a large area may produce sizeable responses of red cones and L-cells without appreciable direct activation of green cones. The results reported in this article show that in these conditions the feed-back evokes pure depolarization of green cones. In addition they demonstrate that the feed-back modifies the time course of receptor and L-cell responses making them different for different colours of illumination.

METHODS

The methods used for stimulating and intracellular recording from retinal cells of the turtle, *Pseudemys scripta elegans*, have been described by Baylor & Fuortes (1970). Temperature was approximately 21° C in all experiments. Cones and horizontal cells were identified by the properties of their responses as set forth by Baylor & Fuortes (1970) and Simon (1973). Since blue cones were never penetrated satisfactorily in this study, only red and green cones (which form the large majority of all photoreceptors) were studied. The L-cells considered had the large receptive field characteristic of 'type I' horizontal cells (Simon, 1973). In a number of experiments, very small responses evoked by dim flashes were investigated. In these cases they were summed on a Mnemotron computer and displayed on an $X-Y$ plotter.

Narrow-band interference filters were used to obtain monochromatic lights. Intensity was measured as the number of photons delivered by the flash over 50 μm^2, which is approximately the cross-sectional area of the inner segment of one cone. It is difficult, however, to estimate what fraction of the light impinging over an inner segment is absorbed by the visual pigment. Its value depends on the wave-guide properties of the cone, the direction of the beam of light relative to the axis of the cone (Stiles & Crawford, 1933; Toraldo Di Francia, 1948), the absorption spectrum of the visual pigment, and the transmission of the associated oil droplet. Baylor & Hodgkin (1973) recently have described how the fraction of absorbed photons can be estimated taking these factors into account, but their interpretations were not known when the present experiments were performed.

RESULTS

Responses of cones and L-cells to small and large fields

Peak heights of the responses of cones and L-cells evoked by flashes of red or green light are plotted in Figs. 1 and 2. A red cone, a green cone, and an L-cell from a sample of eighteen red cones, seven green cones and eighteen L-cells are illustrated. Although the selected cells are fairly typical of the sample, it should be pointed out that the absolute sensitivity of cones as well as their relative sensitivity to different colours showed considerable variation (see Baylor & Hodgkin, 1973). Because of this variability quantitative comparison of responses of cells from different preparations to the same stimuli (as in Figs. 1 and 2) should be interpreted

with some caution. Qualitatively, however, the results illustrated are representative of the sample.

Stimuli for the experiments shown in Fig. 1 were flashes of red or green light covering a circle of 55 μm radius centred over the impaled cell. When the light was deep red, there was a wide range of intensities over which red cones produced responses but green cones remained inactive. In contrast, sensitivity to the green light was only moderately higher in

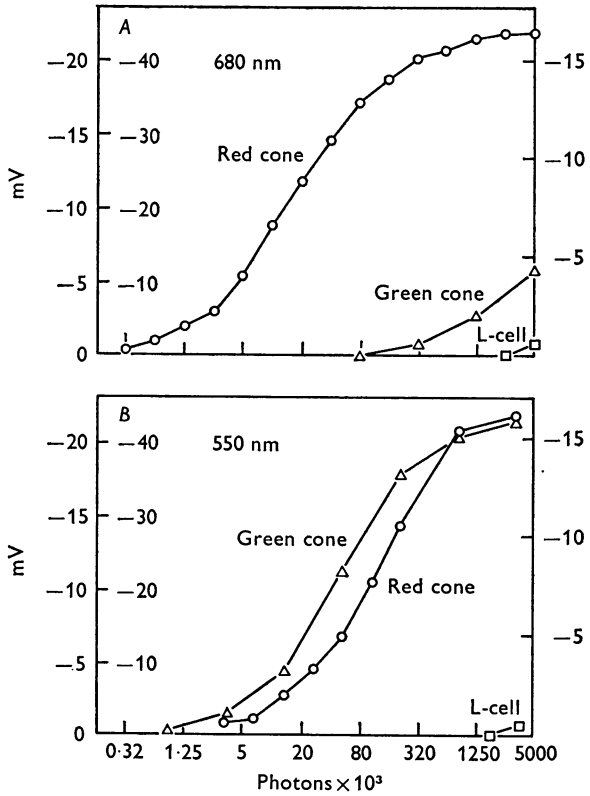

Fig. 1. Responses of cones and L-cells to small fields. Peak amplitudes of responses of a red cone (circles), a green cone (triangles) and an L-cell (squares) are plotted as a function of the number of photons incident over a retinal area of 50 μm^2 during a flash. Cells were from different retinae. Flashes were 10 msec in duration and covered a circle of 55 μm radius centred over the impaled cell. Wave-length was 680 nm in *A* and 550 nm in *B*. Different scales were used in ordinates to facilitate comparison. From left to right they apply to the red cone, the L-cell, and the green cone respectively. The red cone was much more sensitive than the green cone to the red light (*A*), but the green cone was only slightly more sensitive than the red to the green light (*B*). The L-cell gave very small responses to either colour.

green than in red cones; it was less than threefold in the two cones illustrated and it never exceeded a factor of ten in the sample. (Sensitivity to a flash is defined as the peak height of the response divided by the quantity of light in the flash.) Consequently, green lights which produced sizeable responses of green cones excited the red cones also. L-cell responses to these small fields were negligibly small for either colour.

When the illuminated area was enlarged to cover a circle of 1250 μm radius, the responses changed as shown in Fig. 2. Red lights of dim or moderate intensities evoked large hyperpolarizing responses in red cones

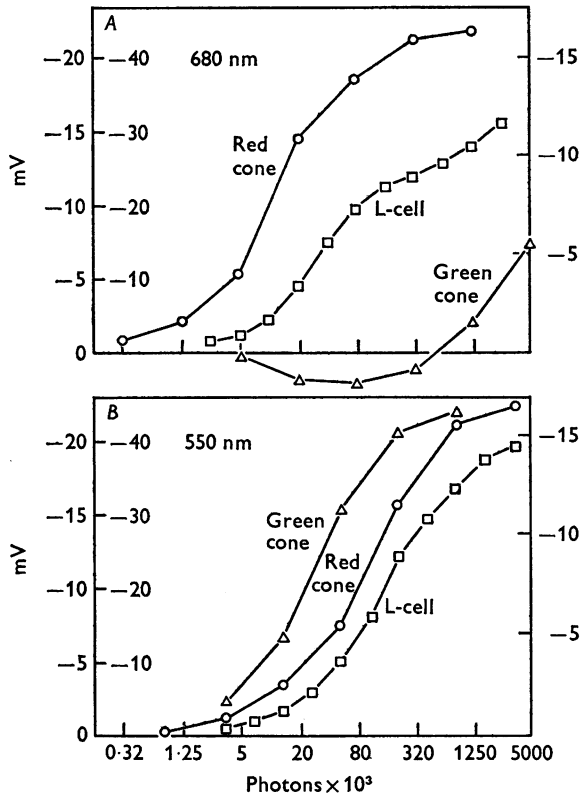

Fig. 2. Responses of cones and L-cells to large fields. Cells were the same as in Fig. 1. Experimental conditions were also the same, but the stimulus was enlarged to cover a circle of 1250 μm radius. The L-cell generated large responses which grew differently with stimulus strength for the two colours (see Fig. 6). The green cone produced depolarizing responses (points below the abscissa in *A*) for red flashes of moderate intensities but hyperpolarizing responses for brighter red flashes. The responses of the red cone to either colour and of the green cone to the green light were slightly larger than with the small field.

and L-cells, but in green cones they elicited purely depolarizing responses. Since the red light does not activate the green cones directly until it is very bright (Fig. 1*A*), this depolarization can be interpreted as the result of the feed-back from L-cells acting in the absence of a direct response. When the light was sufficiently bright to activate the green cones directly, their responses to the large field became first diphasic and then hyperpolarizing.

As seen in Fig. 2, with green flashes no appreciable response developed in L-cells in the absence of red cone activity. Therefore, these flashes will not be expected to initiate the feed-back without eliciting direct responses in red cones.

Depolarizing responses of green cones

The results of Fig. 2 indicate that the depolarizing action of L-cells can be studied best in green cones where it can be observed in the absence of direct responses. The time courses of cone and L-cell responses to flashes of red light are illustrated in Fig. 3. The tracings show the average of responses recorded from two green cones, four red cones, and four L-cells. Averaging was done by superposing photographic records of responses from different preparations. In the green cones no detectable depolarization was evoked by the dimmest flash illustrated even though red cones and L-cells produced sizeable responses with this stimulus. This result would be obtained if the depolarizing effect became appreciable only when the L-cell response exceeded a certain amplitude. It is also possible, however, that the green cones illustrated (or perhaps their connexions) were somewhat damaged and did not respond as they would in the living animal (see Discussion).

With flashes of intermediate intensities, the responses of green cones were purely depolarizing waves. Their amplitude was small but still much larger than the extracellular potentials evoked by the same stimuli (local electroretinogram). In fact, when these stimuli were applied while the electrode was just outside a cone no appreciable potential change was recorded, indicating that the depolarizing wave occurs across the cone membrane.

The depolarizations of the green cones include prominent oscillations which follow with slight delay similar oscillations of opposite polarity in L-cell responses. These oscillations of green cones can be explained as a consequence of the impingement from L-cells; however, the origin of L-cell oscillations is not clear. With deep red light L-cell responses can be initiated only by red cones. Yet, at certain intensities of the flash, large oscillations appear in L-cells but not in red cones (Fig. 3*C*, *D*; see also Fig. 6), suggesting that the later phases of L-cell responses are influenced by the activity of other retinal cells.

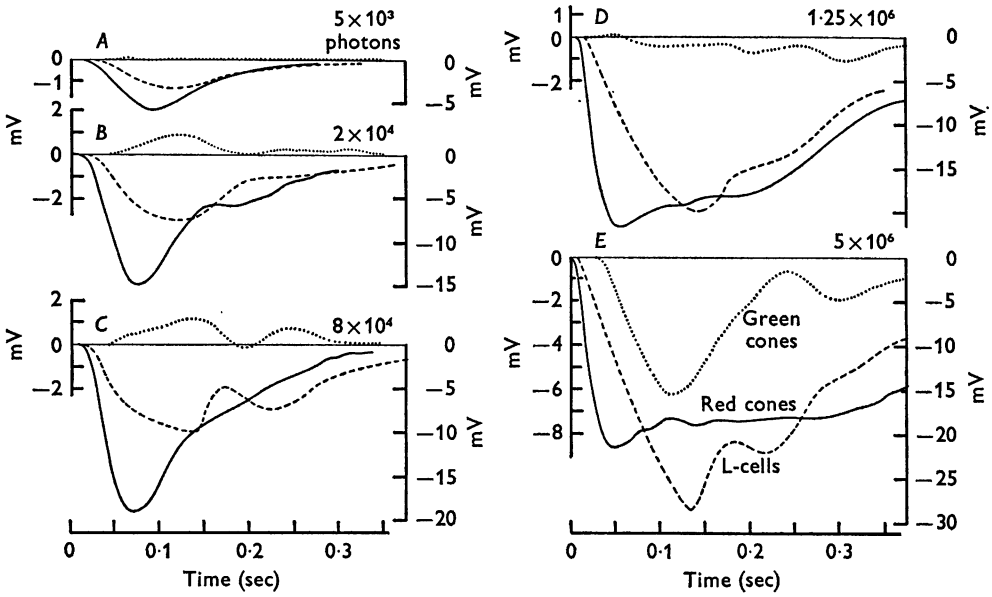

Fig. 3. Comparison of cone and L-cell responses. Tracings show the average responses of two green cones (dotted lines), four red cones (continuous lines), and four L-cells (dashed lines) to large red fields. The stimuli were 10 msec flashes of red (680 nm) light covering a circle of 1250 μm radius applied at time zero. The figures at the right give the number of photons delivered by the flash over 50 μm^2. With dim lights (*A*) L-cells generated small responses, and no depolarization was seen in the green cones. Moderate lights (*B*, *C*) produced larger responses in L-cells and evoked purely depolarizing waves (upward deflexions) in green cones. These waves contain oscillations which, with slight phase delay, reflect opposite polarity oscillations in the L-cells. When the light was brighter (*C*, *D*), the green cones were activated directly (see Fig. 1), and their responses changed from depolarizing to hyperpolarizing. Oscillations in responses of red cones are much less prominent than in the L-cells or green cones. Voltage scales at the left apply to the responses of green cones; those at the right apply to red cones and L-cells.

Responses of cones and L-cells to coloured lights

The results described so far compare responses of cells from different preparations. It is useful to compare in addition the responses elicited in the same cells by different stimuli (Figs. 4–6). In green cones, green flashes produced the usual hyperpolarizing responses (Fig. 4) while red light, which was too dim to be absorbed significantly by the green photopigment, elicited purely depolarizing waves mediated by activation of L-cells via

red cones. These results are a striking example of colour-dependence of cone responses.

In red cones this dependence is less conspicuous, but it is often appreciable as illustrated in Fig. 5. In this cell the responses to brief steps of green or red light covering a small field were essentially identical when the intensity was about sixfold higher for the green than for the red stimulus (Fig. 5*A*). When the field was enlarged (Fig. 5*B*), the response was shortened for either colour, but more for the green light.

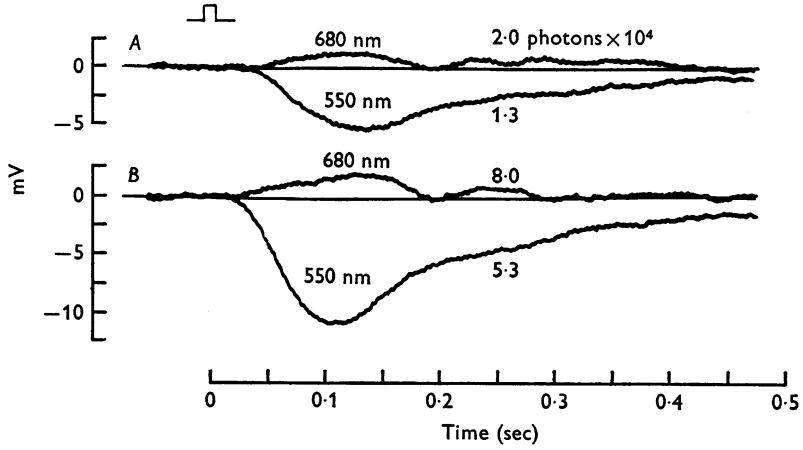

Fig. 4. Reversal of green cone responses with colour. Responses were evoked in a green cone by flashes (monitored at top) of red or green light covering a circle of 1250 μm radius. The wave-length of the stimulus and the number of photons it delivered to an area of 50 μm^2 are indicated near each record. Superposition of responses to stimuli delivering a similar number of photons to the retina shows that the depolarization evoked by the red lights is not negligible as compared to the hyperpolarization produced by the green flashes.

To explain these results it is necessary to examine the responses of L-cells to the same stimuli. When the light was restricted to a small circle (Fig. 5*C*), the L-cell response was small for both colours, and the feed-back on the cone was negligible. For a large circle, however, it was consistently observed that the L-cell response was larger for the green than for the red light (Fig. 5*D*). Consequently, the feed-back on the red cones should be stronger for the green light giving the result illustrated in Fig. 5*B*.

Closer examination shows that the time course of L-cell responses depends strongly upon colour except when the light is very dim. With these dim stimuli, the responses were approximately proportional to light intensity, and their shape was quite similar for green or red flashes

(Fig. 6*A*, *B*). The responses to brighter stimuli, instead, changed in a complicated manner with both light intensity and colour. With red light they reached peak in two phases, rapidly at first and more slowly thereafter (arrow in Fig. 6*A*). This abrupt change of slope did not occur or was less apparent with green stimuli; correspondingly, the peak height of the response grew more rapidly with light intensity for the green than for the red flashes causing crossing of the two curves in Fig. 6*C*.

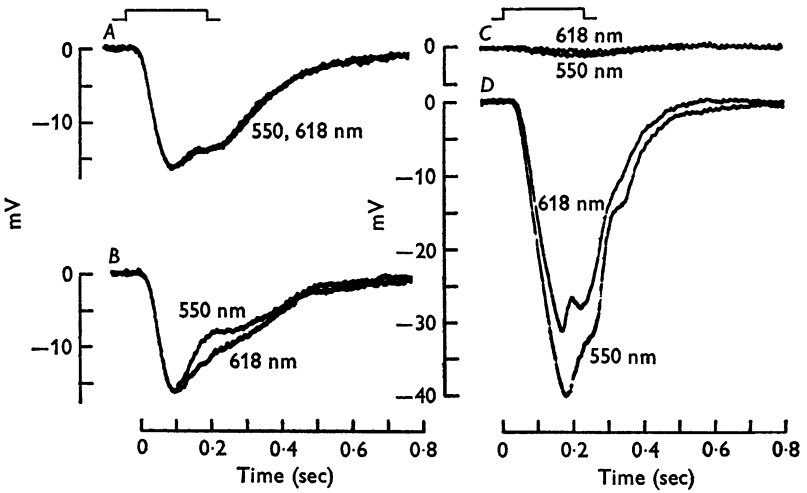

Fig. 5. Colour dependence of red cone responses. The records were taken from a red cone (*A* and *B*) and from an L-cell (*C* and *D*) in different retinae. Stimuli were brief steps (monitored at top) of 618 or 550 nm light. Photon flux over 50 μm^2 was $3{\cdot}0 \times 10^6$ sec^{-1} for the red and $2{\cdot}1 \times 10^7$ sec^{-1} for the green light. The stimuli covered a circle of 55 μm radius in *A* and *C* and of 1250 μm radius in *B* and *D*. The responses of both the cone and the L-cell were very similar when the field was small but conspicuously different when it was large.

These results indicate that L-cell responses can be influenced by the activity of cones of different colours. The mechanisms subserving this colour-mixing in L-cells were not determined in this study. Nevertheless, it follows from the results that, if a green and a red light of moderate or bright intensity are adjusted to give the same direct response of a red cone, L-cell responses will be different for the two colours, and the resulting feed-back will be different – the ultimate shape of the cone response will then change as a function of colour.

It is difficult to state whether colour-mixing occurs when the stimulating lights are dim. It is safe to conclude that red cones contribute to small L-cell responses because they can be elicited in the absence of direct excitation of green cones (Fig. 2). To establish whether green cones also affect the L-cells when the light is dim, it

would be necessary to show that the spectral sensitivity of L-cells under these conditions differs from that of red cones. Due to the variability of results in individual cells, this question could not be decided with certainty.

Mixing of enhancement and depression

Direct activation and feed-back are not sufficient to explain all the features of cone responses to small or large fields; it is necessary in addition to take into account the hyperpolarizing action of cones in the near surround described by Baylor *et al.* (1971) and Baylor & Hodgkin (1973). If the depolarizing feed-back were the only important action intervening

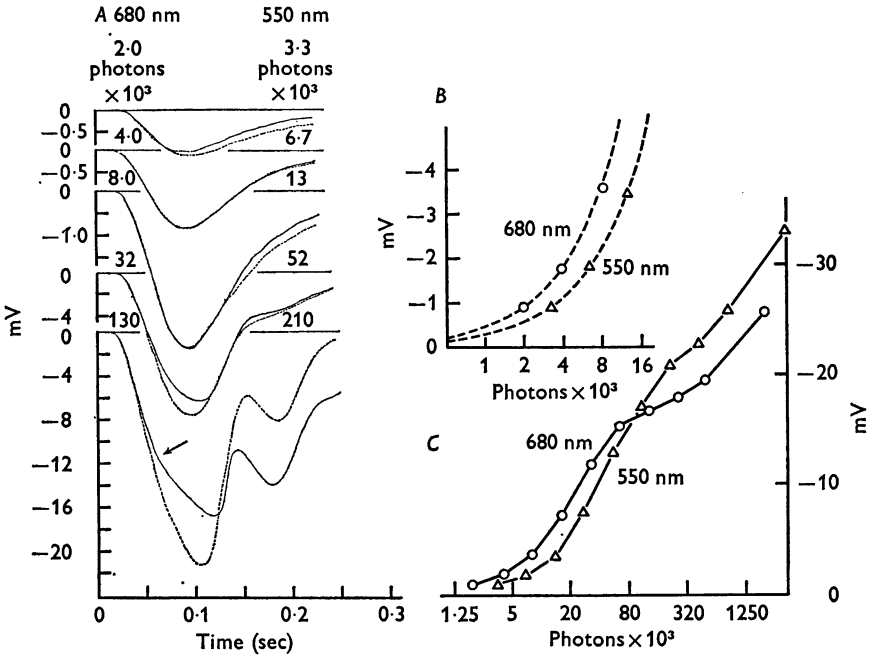

Fig. 6. Responses of L-cells to monochromatic lights. Flashes of 10 msec duration were delivered at time zero over a circle of 1250 μm radius. The number of photons incident over 50 μm^2 is indicated. *A*, Mnemotron averages of twenty responses to red (continuous curves) or green (dashed curves) flashes. In the first three pairs of tracings, the responses were roughly linear with light intensity and were similar for the two colours. With brighter lights peak amplitude was greater for the green stimulus. The arrow points to a sudden change of slope in the rising phase of the response to the red flash. Note change in ordinate scales. *B*, peak height of responses to dim flashes of red (circles) or green (triangles) light. With logarithmic scale in abscissa, the points fall on exponential curves (dashes) showing that the peak of the response grows linearly with light intensity. *C*, similar plot over a wider range of light intensities shows that the increase of peak amplitude with stimulus strength is different for the two colours (see Fig. 2).

to modify cone responses when the illumination is enlarged from 55 to 1250 μm, the responses should be smaller for the larger stimulus. Instead, it is often observed that (at peak) they are conspicuously larger.

Fig. 7 shows averaged responses of a red cone and an L-cell to flashes covering small or large areas. Red and green flashes were applied, and their intensities were adjusted to give similar small-field responses of the cone. When the illuminated area was enlarged, the peak of the response increased for both colours but less for the green than for the red light, while

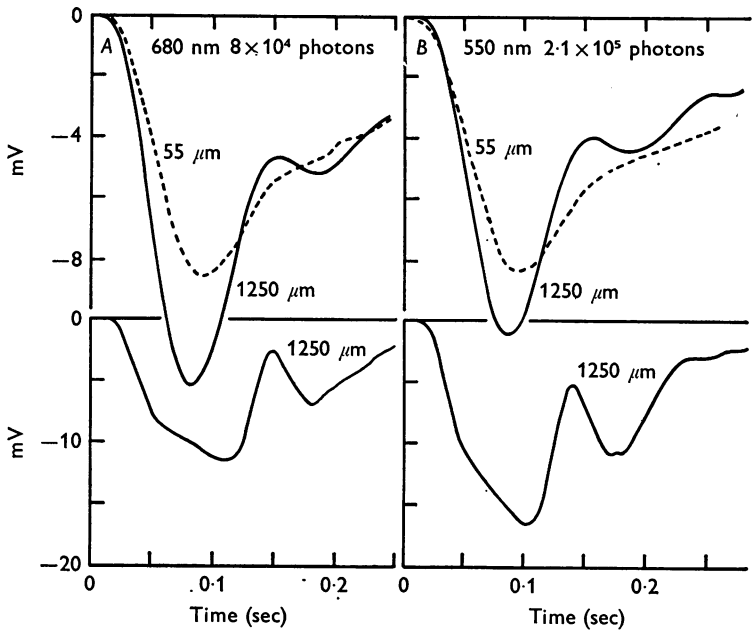

Fig. 7. Mixing of enhancement and depression. Responses of a red cone to 10 msec flashes covering circles of 55 or 1250 μm are superposed in the upper tracings. Each tracing is the average of two records. The intensities of a 680 nm (*A*) and a 550 nm (*B*) flash were adjusted to produce responses of equal peak height for the small field; the time course of the response was then the same for the two colours. The peak height of the cone response increased in both cases for the large field, but this increase was less for the green flash. Conversely, the late depolarizing wave was greater. L-cell responses to the large field (lower tracings) were larger for the green stimulus.

the L-cell response was larger for the green stimulus. These results can be interpreted assuming that (1) the depolarizing feed-back operates with short delay (as indicated by the results of Fig. 3), is already effective at the peak of the response, and is stronger for the green than for the red stimulus, and (2) the enhancement increases as the area of the stimulus is

enlarged but is approximately equal for red or green lights (see Discussion). With this organization the direct responses to red and green lights will be equally augmented by cone to cone interactions, but the response to the green stimulus will be more effectively depressed by the feed-back, leading to the final outcome illustrated in Fig. 7.

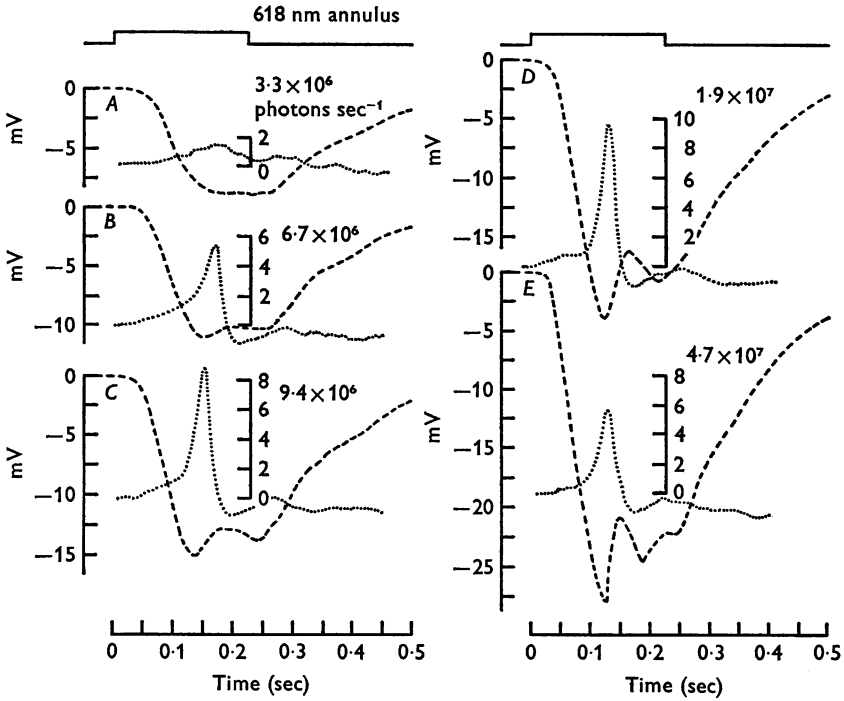

Fig. 8. Depolarizing transients in green cones. Responses were elicited in a green cone (dotted lines) and an L-cell (dashed lines) by steps of red light (618 nm) in the shape of an annulus centred about the cells (radii: 1250–500 μm). A dim annulus (*A*) produced a response of about 8 mV in the L-cell and a depolarizing wave in the cone similar to those of Fig. 3*B* and *C*. With brighter intensities (*B*, *C*, *D*) the L-cell response increased, and the cone generated a sharp depolarizing transient. L-cell responses continued to increase for still brighter lights (*E*), but the depolarization of the cone now decreased. Voltage scales for the L-cell are on the left and for the cone are on the right.

Responses to annuli

Since horizontal cells are electrically coupled (Naka & Rushton, 1967; Kaneko, 1971; Simon, 1973), large responses can be produced in L-cells at the centre of an annulus of light. With red lights the red cones at the centre may generate appreciable direct responses due to scattering and reflexions, but such responses will be negligible in green cones unless the

light is very bright. Hence, annuli may be more effective than circles in evoking large feed-back actions uncomplicated by direct responses.

As seen in Fig. 8, a dim red (618 nm) annulus evoked in a central green cone a depolarizing wave similar to the responses which were produced by the large red circle in Fig. 3. With brighter annuli, however, a sharp depolarizing transient developed which reached a peak amplitude of 10 mV (depolarizing transients of over 20 mV have been recorded by O'Bryan (1973) under different experimental conditions). With the

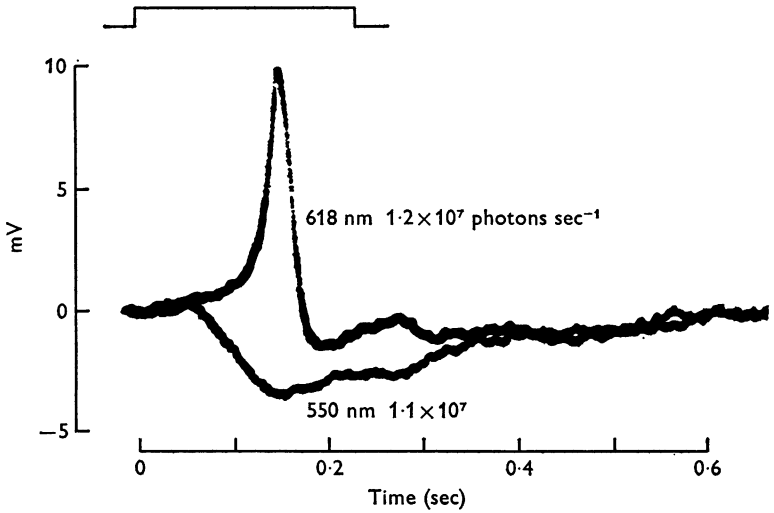

Fig. 9. Responses of a green cone to annuli. Steps (monitored at top) of red or green light were applied to an annulus of 1250–500 μm radii. The green cone at the centre developed a large depolarizing transient for the red stimulus and was hyperpolarized when the light was green. Photon flux over 50 μm^2 is indicated near each record.

brightest lights the depolarizing wave decreased possibly due to addition of the direct hyperpolarizing response evoked by scattered and reflected light. L-cell responses to brighter stimuli include oscillations, but these cannot be the cause of the sharp transients of the cones because the oscillations follow the transients.

L-cell responses should be at least as large with green as with red lights (see Fig. 6) and should produce even stronger feed-back actions. Green annuli, however, evoked hyperpolarization of the central green cone (Fig. 9), probably because sufficient absorbable light reached the cone to elicit sizeable direct responses. This result again illustrates the remarkable colour-dependence of green cones and suggests that the depolarizing action of the feed-back can be masked easily by the direct response.

DISCUSSION

The notion that photoreceptor cells act independently of one another was disproved by Hartline, Wagner & Ratliff (1956) in their classical work on the inhibitory interactions of *Limulus*. When it became possible to record intracellularly from vertebrate photoreceptors, it was noticed that cones in the turtle are also subject to interactions: synergistic from neighbouring cones and antagonistic (feed-back) from luminosity horizontal cells (Baylor *et al.* 1971).

In the present work, the feed-back was studied by using monochromatic lights. The results obtained clarify some properties of the interactions and lead to the conclusion that their organization provides a mechanism by which photoreceptor responses may become colour-dependent.

Delay of the feed-back

When the feed-back is evoked by white light, its effect on the co-existing direct response of a cone becomes evident only after a long delay – the decay of the response is accelerated but its rising phase and peak are not appreciably changed (Baylor *et al.* 1971). Instead, when the feed-back is produced in isolation by monochromatic lights (Figs. 3 and 4), it elicits a purely depolarizing wave which starts with short delay. These results suggest that the feed-back is rapid; but, when it is superposed on a direct response, its early effects remain undetected. This observation may be explained assuming that, when a circle of light is enlarged from 55 to 1250 μm radius, the early depolarizing action is initiated by the horizontal cells but is compensated by the hyperpolarizing effects of the near surround. Thus, two antagonistic interactions may operate on a cone when the illuminated field is large: enhancement from nearby cones and depression from L-cells.

Organization of the interactions

Feed-back and enhancement are organized differently with respect to colour. In red cones the depression (measured as the proportion of the direct response) is greater for a green than for a red stimulus (Fig. 5) with the possible exception of very dim lights. This finding is explained by the observation that, if a red and a green stimulus give equal direct responses in red cones, the green gives larger L-cell responses and thereby more depolarizing feed-back. Similarly, the depression is greater on green cones for red lights because these stimuli evoke negligibly small direct responses but produce strong activation of L-cells.

In contrast, the enhancement is effective only between cones of the same colour (P. M. O'Bryan, unpublished; Baylor & Hodgkin, 1973); therefore,

its action on the response of a given cone is the same for either red or green stimuli.

O'Bryan demonstrated that the responses of a red cone to green or red flashes covering very small circles (12 μm radius) can be made to coincide by appropriate adjustment of intensity. When the field was large enough to cause conspicuous enhancement (65 μm radius), the stronger activation of surrounding green cones which is brought about by the green stimulus did not increase the enhancement, implying that coupling between cones of different colours is not appreciable. Baylor & Hodgkin (1973) reached the same conclusion by analysis of the spectral sensitivity curves.

Given this organization of enhancement and depression, the time course of cone responses to large fields of illumination will change as the proportion of the responses of red, green, and (presumably) blue cones is altered, this proportion being in turn a function of the wave-length of the stimulus. Other cells in the retina are known to generate depolarizing responses to certain patterns or colours of retinal illumination. It seems probable that the effects of L-cell feed-back are important in the generation of these responses, in particular those of chromatic horizontal cells, which are depolarized by long and are hyperpolarized by short wave-lengths (Svaetichin & MacNichol, 1958) as is the case for green and (presumably) blue cones.

Oscillations

Purely depolarizing waves evoked in green cones by red flashes follow closely the oscillations of L-cell responses (Fig. 3) as would be predicted by the suggested interpretations. The origin of L-cell oscillations, however, is unclear since at certain light intensities sudden inflexions appear in L-cell responses, but no corresponding waves are generated by the cones (Figs. 3 and 6). This disparity suggests that the neural circuit controlling L-cell activity involves more than the feed-back loop linking these cells with cones.

Conversely, sharp depolarizing transients can be produced in cones with no counterpart in the activity of L-cells (Fig. 8). Although their origin is uncertain, they reveal a form of receptor activity which may be important in producing transient responses in other retinal cells.

Experimental limitations

In considering the discrepancies between receptor and L-cell responses, it is important to keep in mind that these may be due, at least in part, to damage to the impaled cone. Micro-electrodes introduced from the vitreal surface of the retina may injure the connexions between horizontal cells and cone pedicles before reaching the receptor layer. Further damage may be caused by penetration of the cone membrane. Two observations suggest

that the responses of impaled cones may be seriously distorted. First, although the peak hyperpolarizing response may reach 30 mV in some cones, it is usually less than 20 mV in otherwise typical cells. Secondly, cones that show large feed-back effects when first impaled frequently lose much of the depolarizing wave even though the direct response remains unchanged. This rapid degredation of the effects of the feed-back is illustrated in Fig. 10.

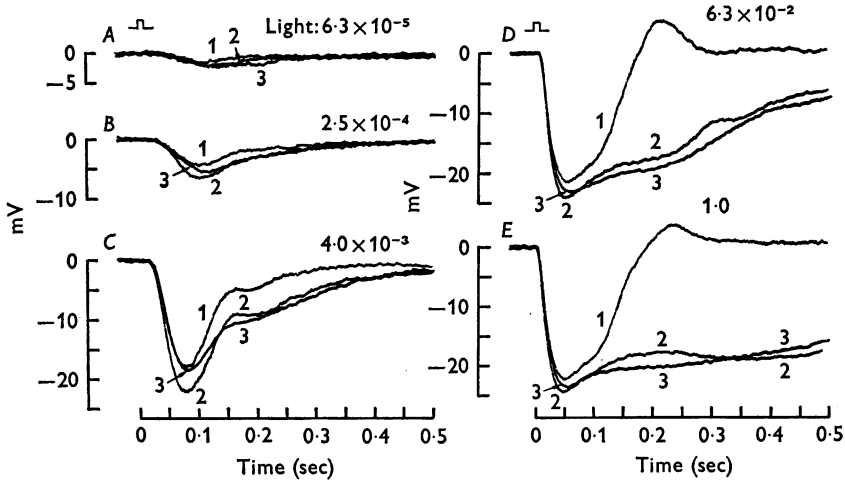

Fig. 10. Deterioration of the feed-back. Responses to 10 msec flashes of white light were recorded from a red cone. Dark adaptation was the same throughout the experiment. Records 1 were taken immediately after impalement and were evoked by stimuli covering a circle of 1250 μm radius. After a few minutes the responses to the same stimuli changed as shown by records 2. Responses to a small circle (55 μm radius) were tested after the series labelled 2 and gave records 3. Light intensities are indicated in relative units.

Records 1 show the responses of a red cone immediately after its impalement. The stimuli were flashes of white light covering a circle of 1250 μm radius. With bright intensities a large depolarizing wave made the response short and diphasic. A few minutes later (records 2) the same stimuli produced responses of slightly larger peak height, but the late depolarizing phase was markedly reduced. These responses remained stable throughout the remainder of the experiment. Flashes covering small fields now gave the responses labelled 3 with peak heights slightly larger than in records 1 and smaller than in records 2. This suggests that peak height was reduced by the strong feed-back operating at the beginning of the experiment; later the feed-back was weaker, and its early effects were overcome by the enhancement of the near surround.

The responses indicated by 2 and 3 are similar to those recorded from most impaled cones. It seems reasonable to conjecture that the responses of normal cones may be more similar to records 1 than to records 2. Similarly it is possible that normal green cones respond to red lights with larger depolarizations than were recorded in the present sample. Since horizontal cells are considerably larger than cones, they may be less subject to experimental injury. The responses recorded from them could reflect the activity of undisturbed receptors while bearing faint resemblance to the responses of impaled cones.

Univariance

The results of the present paper impose some limitation on the rule known as the principle of univariance (Naka & Rushton, 1966). This principle states that the response of a photoreceptor depends only on the number (or rate) of photons it absorbs but does not depend on their wave-length. According to the interpretations offered above, the principle of univariance is valid only for the direct response of a cone. It may fail in the presence of short-range interactions even though these operate only between cones with the same visual pigment because differently-coloured oil droplets may be associated with the same pigment (Liebman, 1972). However, this failure has not been detected in experiments performed so far. The principle is certainly not valid when the feed-back action intervenes because the response of a cone is then a function of the wave-length as well as of the number of photons absorbed.

It may be concluded that the retinal photoreceptors of the turtle are not a mosaic of independent units; rather, due to the interactions described in this and in preceding papers, their responses are affected by the activity of neighbouring cells and change with both the pattern and the colour of the stimulus.

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