

## PROXIMAL NEGATIVE RESPONSE IN THE PIGEON RETINA

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### SUMMARY

1. The proximal negative response (PNR) of the inner plexiform layer of the pigeon retina was recorded intraretinally.
2. The PNR can be distinguished from the local b-wave by its area dependence, and its depth profile in the retina.
3. The 'on' and 'off' transients of the PNR have differing depth profiles in the retina: the 'on' transient is distributed vitreal to the 'off', and both are distributed vitreal to the b-wave.
4. As spot diameter is increased, so the amplitude of the PNR decreases, and the threshold rises.
5. Ganglion cells fire at 'on' and 'off' during the PNR and like the PNR, are suppressed as spot size is increased.

### INTRODUCTION

The present experiments investigate with extracellular micro-electrodes the response to visual stimulation of the inner plexiform layer of the pigeon retina. In the pigeon this layer is one of the most highly developed among vertebrates. In it take place the interactions between bipolar cells, amacrine cells and ganglion cells, with amacrine cells acting as interneurons between bipolar cells and ganglion cell dendrites (Dowling, 1968).

This paper describes the proximal negative response, a new component of the electroretinogram, recently given an elegant characterization in the frog retina by Burkhardt (1970), and also observed in the avian retina by Ogden & Wylie (1971). The response is an extracellular field potential, and is essentially a population measure of neural processes in the inner plexiform layer. In the present experiments the proximal negative response (PNR) is investigated under conditions where it can be distinguished from the local b-wave. The experiments are intended only to characterize the proximal negative response. An analysis of the electro-

retinogram of the deeper retinal layers is not attempted, for a full description has recently been presented by Ogden & Wylie (1971). A preliminary account of these experiments has been published (Holden, 1970).

#### METHODS

The experiments were carried out on twenty-five adult feral pigeons, anaesthetized with 3–5 ml. 20% urethane, injected intraperitoneally.

The feathers were trimmed from the head and neck, and the pigeon was fixed in a headholder which was designed to leave the visual field of the left eye unobstructed. Fixation points were ear-plugs and a beak bar 25 mm anterior to it in a horizontal plane. Intraretinal recordings were made in the left eye.

A small incision was made into the skin overlying the dorsal pole of the left eye, and the conjunctiva removed over 2 mm. A slit was made into the outer coats of the eyeball, at latitude 30°, some 2 mm below the dorsal pole. The slit was 1 mm long and was made with a sharp iridectomy knife. The cannula of one channel of a Brown (1964) retinal manipulator was pushed into the slit, and advanced into the vitreous chamber until it could be seen with an ophthalmoscope. The cannula was an '0'-gauge syringe needle which could accommodate 1 mm o.d. micropipette electrodes with a smooth fit. The micro-electrodes were 4½–5 in. long. They were loaded backwards into a glass sleeve, which fitted on to the end of the cannula and maintained accurate alignment. The electrodes were pushed by hand 2 in. into the cannula, and the sleeve was withdrawn. The shaft of the micro-electrode was held by a spring clip on the cannula. The electrode was further advanced by hand until it could be seen with an ophthalmoscope to emerge from the tip of the cannula. The cannula was mounted on a ball joint close to the point of entry to the eye, and could be directed to parts of the central and lower retina. Usually it was aimed at the lower retina which views visual space 15° above the horizontal meridian in the anterior visual field.

The electrode was advanced into the retina on the hydraulic drive until a negative going penetration transient and the abrupt appearance of pulse beat signalled contact with the retina.

The pigeons were fitted with zero power contact lenses, and were refracted. The optical system projected visual stimuli to a white screen 4 ft. from the eye. Experiments were conducted with the room lights on, when the screen was illuminated with a background of 27 cd/m<sup>2</sup>, or in the dark, when stray light produced a background of approx. 0.03 cd/m<sup>2</sup>.

The head stage for the recording system was initially a double cathode follower valve, and in later experiments an FET input stage. The cathode follower was used with Tektronix 122 and 502A amplifiers, and the FET stage was used with the 502A alone. Film records were taken with a Shackman camera. Considerable use was made of a Devices two channel pen recorder, fed from the upper beam of the 502A. While this limited the frequency response to 100 Hz, it was adequate for measuring amplitudes of the components of the local electroretinogram, and provided quick and permanent records which could be measured during each experiment. Light intensities were measured with an SEI photometer.

## RESULTS

Local responses in the pigeon retina were recorded between the penetrating micro-electrode and the vitreous cannula. They were local in that the receptive areas of the electroretinogram components and of unit responses were sharply circumscribed in visual space, and generally centred at the point of micro-electrode entry.

Smooth penetrations through the retina were often not achieved, for the internal limiting membrane constituted a strong mechanical barrier, and would often be penetrated abruptly. When measuring depth profiles observations were usually made on withdrawals. Micrometer readings were converted to percentage depth criteria, following Ogden & Wylie (1971). The depth at which the a-wave and b-wave declined was taken as 100 %, and the depth on withdrawal at which the proximal negative response and retinal pulse-beat disappeared was taken as 0 %. The angle of entry was usually oblique to the retinal surface, and traverse through the retina took place over 350–400  $\mu$ .

*Distinction between the intraretinal b-wave and the proximal negative response*

Fig. 1 illustrates the local electroretinogram at a depth of 50 %, corresponding to the middle of the inner nuclear layer. In this and all subsequent Figures negativity is displayed as a downwards deflexion. In sweep 3 the stimulus was an unattenuated spot, 10° in diameter, centred on the micro-electrode. There is a brief positive-going a-wave at a latency of 19 msec, followed by the transient negative-going b-wave. In the first sweep the spot diameter is reduced to 1°, and the b-wave cannot be detected. In sweep 2 spot diameter is 5°, and the b-wave is present, though smaller in amplitude than in sweep 3. Thus the local b-wave increased in amplitude as spot diameter was increased from 1 to 10°.

The proximal negative response showed an opposite area dependence when investigated under comparable conditions. In Fig. 2 the proximal negative response is recorded at a depth of 30 %. The first sweep shows the response to an unattenuated 1° spot, and the second and third sweeps show responses to a 5° and 10° spot. Response is maximal to the 1° spot and is suppressed or attenuated as spot diameter increases. Thus a small centred spot producing a maximal PNR would produce a minimal b-wave, and a large spot producing a large b-wave would produce a minimal PNR. This behaviour provided a simple test to determine whether the micro-electrode had passed deep to the PNR level, and enabled the depth profiles of the two components to be measured on the same track with spots of different sizes.

A depth profile measured in this way is shown in Fig. 3. The local b-wave was in response to an unattenuated  $10^\circ$  spot, and the PNR was in response to a  $1^\circ$  spot. The open circles represent the peak amplitude of the 'on' component of the PNR, and the filled circles represent the amplitude of the b-wave. The amplitude maximum of the b-wave occurs at a retinal depth of 50%, close to the depth found by Ogden & Wylie (1971). The

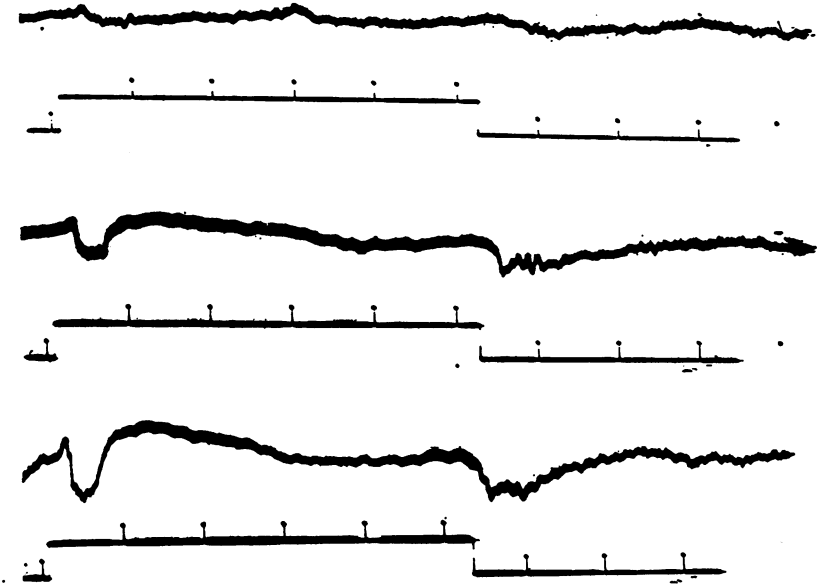


Fig. 1. Intraretinal ERG at 50% retinal depth. In this and all subsequent Figures negativity is displayed as a downwards deflexion. In each pair of sweeps the upper trace shows the response and the lower trace shows the output of a photocell monitoring the flash, and 100 msec time marks. For the first record the stimulus was an unattenuated  $1^\circ$  spot. For the second, spot diameter was increased to  $5^\circ$ ; for the third, spot diameter was  $10^\circ$ . The b-wave is large in case three, of intermediate size in case two, and scarcely discernible in case one. The amplitude of the b-wave in case three was approximately 1 mV. Intensities used were: spot,  $108 \text{ cd/m}^2$ ; background,  $0.03 \text{ cd/m}^2$ .

amplitude maximum of the PNR occurs at 30%, in the inner plexiform layer. It was found when plotting depth profiles that ganglion cell activity would be recorded in the vitreal half of the PNR zone, at depths of 15–20%, and never in the deeper retina where the b-wave was maximal.

Finally, there were qualitative differences between the wave forms of the PNR and b-wave. The b-wave was a large transient occurring only at 'on', while the PNR consisted of negative going responses at both 'on'

and 'off'. While the b-wave would not extend for more than 250 msec, the PNR would decay more slowly, over 1-1.5 sec.

*Receptive field of the proximal negative response*

The receptive area from which the proximal negative response could be obtained was usually some 3-4°. Fig. 4 illustrates a plot of a receptive field obtained by moving a  $\frac{1}{2}^\circ$  unattenuated spot through the centre of the receptive area along a vertical line. The responses are to flashing the spot at

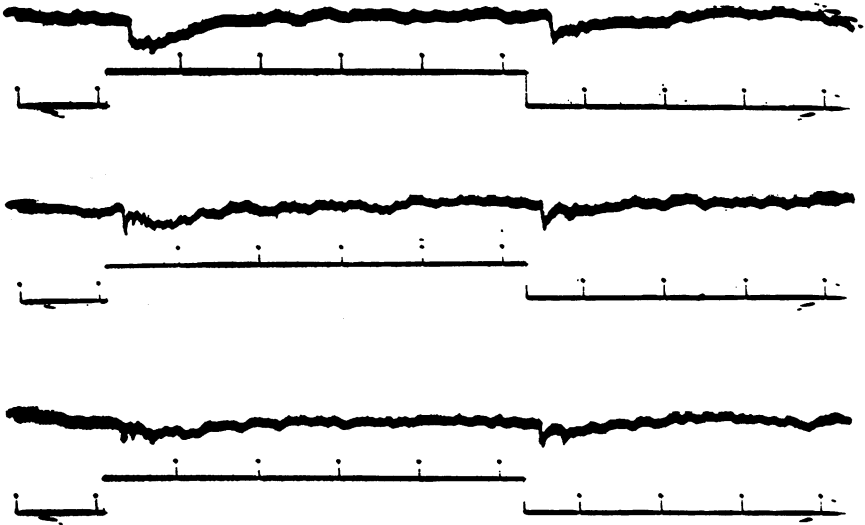


Fig. 2. Intraretinal ERG at 30% retinal depth. General conditions as for Fig. 1. The first record shows the response to an unattenuated  $1^\circ$  spot; the second to a  $5^\circ$  spot, and the third to a  $10^\circ$  spot. The response is the proximal negative response; it is maximal to a  $1^\circ$  spot, and declines as spot diameter is increased. The amplitude of the 'on' PNR transient to a  $1^\circ$  spot was approximately 0.5 mV. Intensities used were: spot 108 cd/m<sup>2</sup>; background 0.03 cd/m<sup>2</sup>.

successive  $\frac{1}{2}^\circ$  displacements. The 'on' and 'off' processes are maximal in the central three positions across  $1.5^\circ$ , while slow responses of reduced amplitude can be obtained  $2^\circ$  from the centre of the field. In general the latency of response was minimal and the amplitude was maximal in the centre of the field, and the oscillatory components were often greatest in the centre of the receptive field. Comparable plots of the receptive area of the b-wave, made deep to 50%, needed a spot at least  $2^\circ$  in extent to produce measurable responses, and would extend for  $7^\circ$ . The radius of the receptive field of the proximal negative response sets an upper limit to the joint effects

of stray light and tangential spread of current; for a field of radius  $2^\circ$  this limit is approximately  $200 \mu$ .

When the peak amplitudes of the 'on' and 'off' transients were plotted against position it was generally the case that they were distributed symmetrically about the receptive field centre, though variants with an asymmetrical second hump were recorded.

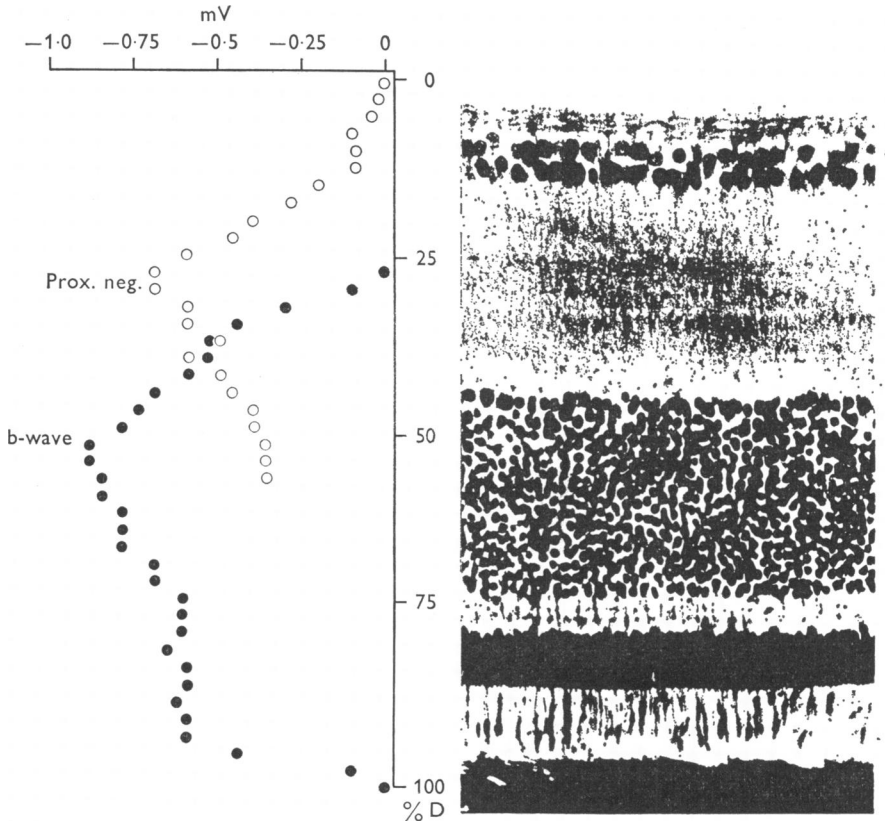


Fig. 3. The intraretinal depth profile of the PNR (open circles) and of the b-wave (filled circles). The PNR was in response to an unattenuated  $1^\circ$  spot; the b-wave in response to an unattenuated  $10^\circ$  spot. A cross-section of the pigeon retina is included, vitreal surface upwards. The amplitude maximum of the PNR 'on' transient falls at 25-30%, in the middle of the inner plexiform layer, while the amplitude maximum of the b-wave falls at 50%, in the inner nuclear layer. Both profiles were recorded on the same withdrawal, using spots of differing diameter. Intensities were: spot,  $108 \text{ cd/m}^2$ ; background  $0.03 \text{ cd/m}^2$ .

*Distribution of PNR voltage radially in the retina*

Early in the experimental series it was noted that at any one recording depth the 'on' and the 'off' components of the PNR could vary in their relative amplitude. When the depth profiles of the two components were

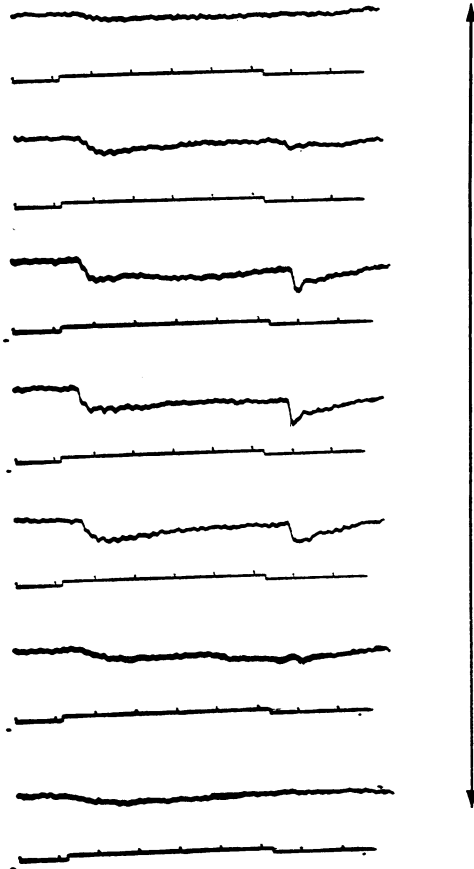


Fig. 4. From top to bottom the records illustrate the PNR to a stationary unattenuated spot of diameter  $\frac{1}{2}^\circ$ , exposed at successive  $\frac{1}{2}^\circ$  positions along a vertical line through the centre of the receptive field. The arrow corresponds to  $3^\circ$  of visual space (approximately  $300 \mu$  on the retina). Response is maximal across the central three positions, and is attenuated in more peripheral locations. Spot intensity was  $108 \text{ cd/m}^2$ ; background  $27 \text{ cd/m}^2$ .

investigated it became clear that this variation depended on depth. Superficial in the inner plexiform layer the 'on' component was greater than the 'off' component, while deeper in the inner plexiform layer the 'off' component was greater than the 'on' component. This finding provided a

useful physiological measure of retinal depth, both for withdrawing to the ganglion cell level, or advancing to the depth of the maximum PNR. Fig. 5 illustrates four depth profiles, all recorded on one withdrawal from 75% retinal depth. The upper set illustrate the PNR to an unattenuated 1° spot, and the lower set to the same spot attenuated by 1.2 log units. The

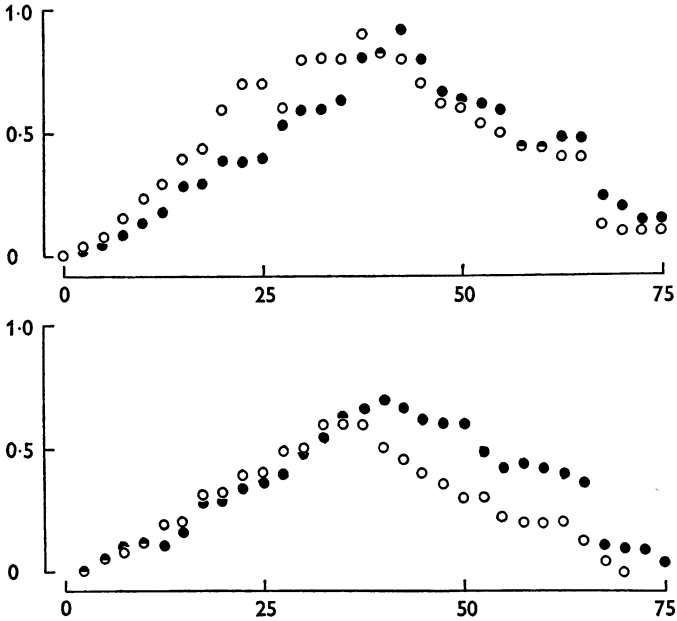


Fig. 5. Depth profiles of the 'on' and 'off' transients of the proximal negative response on withdrawal from 75% retinal depth. Ordinates: response amplitude in mV. Abscissae: % retinal depth. All sets of measurements were taken on one withdrawal. The upper profiles represent the response to an unattenuated 1° spot; the lower profiles represent the response to a spot attenuated by 1.2 log units. The open circles represent the amplitude of the 'on' transient, and the closed circles represent the amplitude of the 'off' transient. Both sets show that the 'on' transient is greater than the 'off' vitreal to the amplitude maximum, and the reverse holds deep to the amplitude maximum. Spot intensity was: unattenuated 108 cd/m<sup>2</sup> (upper profile) and 7 cd/m<sup>2</sup> (lower profile). Background intensity was 0.03 cd/m<sup>2</sup>.

open circles represent the amplitude of the 'on' component, while the closed circles represent the amplitude of the 'off' component. The same pattern is displayed by each set, despite the discontinuities due to uneven electrode movement. The 'on' component is greater than the 'off' component superficial to 33% depth, while the reverse holds deep to 33%. Thus the amplitude maximum of the 'on' component is vitreal to that of the 'off' component.



This difference entails that the generators of the 'on' and 'off' transients are not spatially coincidental in the retina. A geometrical consideration can only be tentative because electrode entry was oblique to the retina in the vertical plane. If the difference in amplitude maxima were due only to oblique electrode entry and a concentric (tangential) difference in the distribution of the 'on' and 'off' transients, then it could arise only if the 'off' process had a wider tangential distribution than the 'on' process, and if the 'on' process had a higher current density in the centre of the receptive field. Under these conditions electrode entry normal to the retina surface would produce no difference in the amplitude maxima of the two transients, and the 'on' transient would exceed the 'off' transient in amplitude at all depths.

On the other hand, if the 'on' and 'off' transients had a different laminar (radial) distribution in the retina, this would be a sufficient condition for the different amplitude maxima and for the change in relative amplitude of the 'on' and 'off' transients observed in the depth profiles, both for entry of the electrode normal to the retina and for oblique entry.

An attempt to test these possibilities was made by plotting the amplitude of the 'on' and 'off' transients at fixed positions in their receptive field at four depths in the inner plexiform layer. The plots are shown in Fig. 6, where the ordinates represent response amplitude, and the abscissae represent position in visual space. The results show that with minor exceptions the relative amplitude of the two transients are maintained for each receptive field plot, though an averaging technique would be necessary to establish this for positions near the boundaries of the receptive fields. The 'off' transient does not have a wider tangential distribution than the 'on' transient. The greatest tangential spread is for the 'on' transient at 33% retinal depth. While these results need to be supplemented with observations made with an averager, they suggest that the depth profiles of the 'on' and 'off' transients are due to a laminar separation of their generators. This need not imply that different cells generate the two components, but only that the relative amplitude of the two components varies systematically on a laminar basis.

This finding provokes the question of whether the response described in this paper as the 'off' PNR is homologous with the off response or 'd' wave recorded in the mammalian retina. The most direct argument that the two responses are distinct is that the amplitude maximum of the 'off' PNR is vitreal to that of the b-wave; it occurs in the proximal retina. In contrast the amplitude maximum of the 'd' wave in the *Cynomolgus* retina occurs at 87% retinal depth, distal to the b-wave maximum, and at the depth where the a-wave is maximal (Brown, 1968).

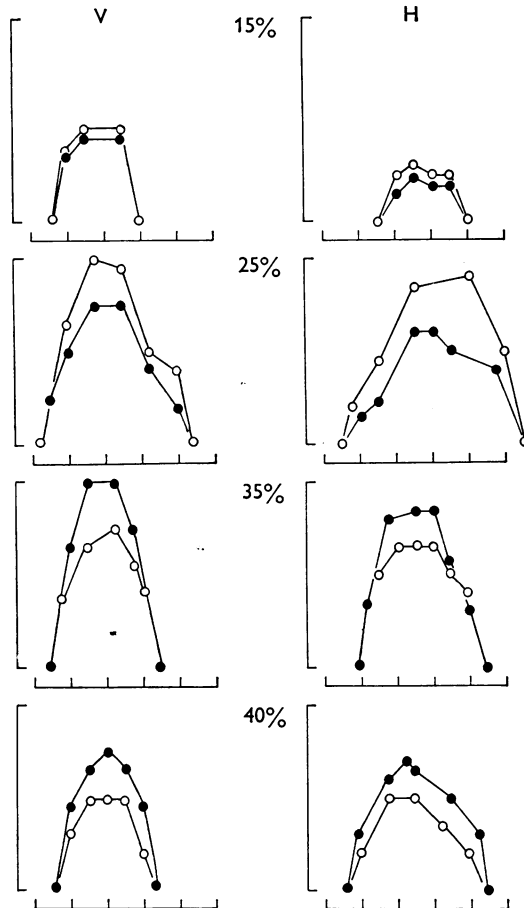


Fig. 6. Receptive field plots of the PNR at four retinal depths on one penetration (15, 25, 35 and 40%). The amplitude of the 'on' transient is shown by the open circles, and the 'off' transient by filled circles. The left-hand column (V) shows a vertical scan through the receptive field of the type illustrated in Fig. 4: left to right on the abscissa represents top to bottom in visual space, and is marked at  $1^\circ$  intervals. The ordinate represents 1 mV. The right hand column (H) shows a horizontal scan through the receptive field, with left to right on the abscissa representing posterior to anterior in visual space. The plot was made with a  $\frac{1}{2}^\circ$  spot of intensity  $108 \text{ cd/m}^2$  on a background of  $0.03 \text{ cd/m}^2$ .

#### *Effects of intensity and area on the proximal negative response*

When the intensity of a  $\frac{1}{2}$  or  $1^\circ$  spot centred in the receptive field of the PNR was varied there was a steep rise in response amplitude over a dynamic range of 1-1.5 log units followed by saturation of response. A

similar relation held for the 'on' and 'off' transients, as is illustrated in Fig. 8*b*. The same type of relationship held for the response to a moving spot passing through the centre of the receptive field, as is illustrated in Fig. 8*a*. The b-wave usually showed a similar threshold to the PNR, but did not saturate over the same limited dynamic range.

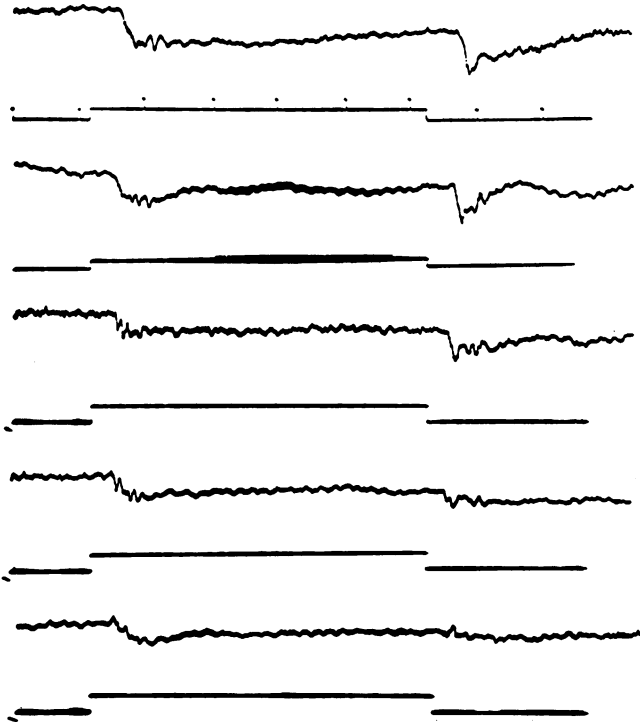


Fig. 7. Proximal negative response to unattenuated spots of increasing diameter. From top to bottom spot diameter was 1.75, 2.5, 5, 7.5 and 14°. The records were taken at 30% retinal depth with a time constant of 3 sec. As spot diameter increases from 1.75 to 14° so the latency of the 'on' response shortens from 40 to 31 msec. There is a graded reduction in the amplitude of the 'on' and 'off' transients. A small positive going response appears to the 14° spot, shown in the bottom record. The spots were 108 cd/m<sup>2</sup>, on a background of 0.03 cd/m<sup>2</sup>.

Fig. 7 illustrates the proximal negative response to unattenuated spots of diameter 1.75, 2.5, 5, 7.5 and 14°, recorded at 30% retinal depth with a time constant of 3 sec. As spot diameter increases so there is a reduction in the amplitudes of the 'on' and 'off' transients, and a shortening of their latency. In response to a 14° spot there is a small reversal of the polarity of these transients,

Fig. 8b and c illustrate a set of measurements which combine variations in spot diameter and variations in intensity, showing the intensity-amplitude relations for spot diameters of 1.75°, 5, 7.5 and 13.5°. In general the same effect is seen for both 'on' and 'off' transients: as spot diameter is increased so there is a reduction in response amplitude. In addition, an increase in spot diameter causes a rise in the threshold for the response.

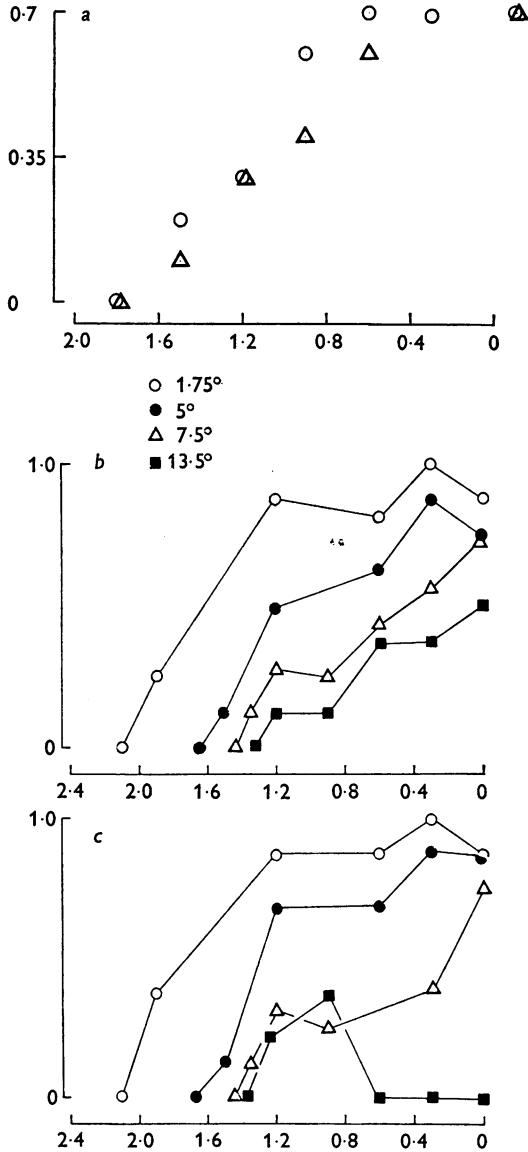


Fig. 8. For legend see opposite page.

The threshold for a  $13.5^\circ$  spot is approximately 1 log unit higher than for a  $1.75^\circ$  spot. In this series the 'off' transient in response to a  $13.5^\circ$  spot was completely suppressed at attenuations less than 0.8 log units.

Several phenomena could underly the suppression and threshold rise of the PNR accompanying an increase in spot area. There could be a masking by tangentially distant proximal negative response, or by other e.r.g. components: there could be surround inhibition in the pathway generating the response. It can be argued from Fig. 8 that a passive masking by source currents of tangentially distant proximal negative response cannot be a sufficient explanation, for if this were operating the source currents would not produce shifts in threshold. Since surround inhibition has been shown in the bipolar cells of the *Necturus* retina (Werblin & Dowling, 1969), there is good reason to expect it in the more complex pigeon retina, and could account both for suppression and for the rise in threshold.

#### *Relation to ganglion cell firing*

Eighty ganglion cell spikes were recorded during retinal penetrations. They were diphasic action potentials, positive-negative in conformation, and rarely exceeding 1.5 mV in amplitude. Their receptive areas were usually centred where the proximal negative response could be recorded, and most were between 1 and  $4^\circ$  in diameter. From this region small spot stimulation would produce uniform 'on' 'off' firing. They could be identified as ganglion cells by the depth at which they were recorded, which was generally at 15–20% retinal depth, and by the criterion that most could be antidromically invaded following electrical stimulation of the contralateral optic tectum.

Fig. 9 illustrates the firing of a ganglion cell recorded simultaneously

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#### Legend to Fig. 8.

Fig. 8. (a) The amplitude of the PNR (ordinate) in mV against log intensity (abscissa) for a  $1^\circ$  spot. The triangles show the amplitude of the 'on' transient to a flashed spot, the circles show the amplitude of the response to a  $1^\circ$  spot moving through the receptive field at a linear velocity of  $20^\circ/\text{sec}$ . In each case there is a limited dynamic range of approximately 1 log unit. The unattenuated intensity was  $108 \text{ cd/m}^2$ , the background intensity was  $0.03 \text{ cd/m}^2$ .

b. Amplitude/intensity plots under the same general conditions as in a, for the 'on' transient of the PNR in response to spots of 1.75, 5, 7.5 and  $13.5^\circ$  (symbols shown in Figure).

c. Amplitude intensity plots for the 'off' transient of the PNR in response to spots of 1.75, 5, 7.5 and  $13.5^\circ$ .

In both b and c response amplitude at a given intensity is reduced as spot size is increased, and the threshold rises as spot diameter increases.

with the proximal negative response, in response to spots of diameter  $\frac{1}{2}$ , 1, 3 and  $5^\circ$ . There is vigorous firing to the smaller spots, and a gradual suppression as spot diameter exceeds  $3^\circ$ . The firing is phasic at 'on' and 'off', and is correlated with the PNR transients. This particular ganglion cell

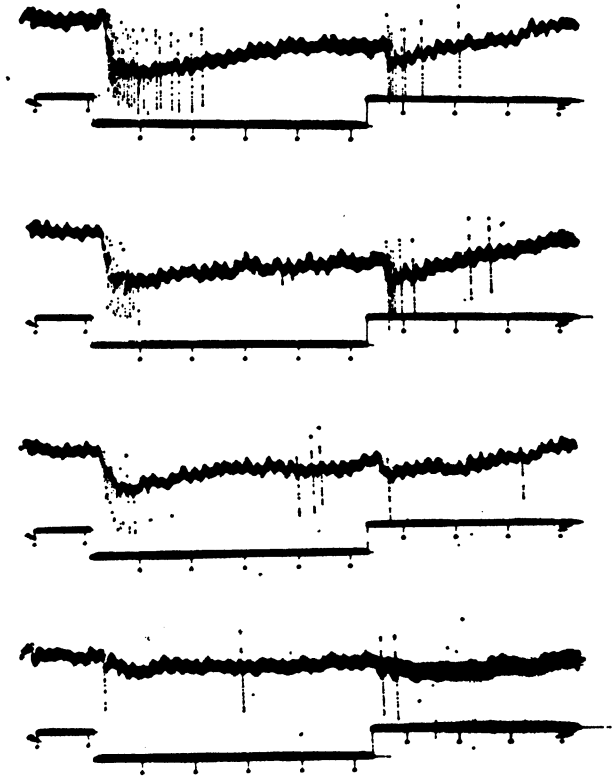


Fig. 9. Simultaneous recording of ganglion cell firing and the proximal negative response. Retinal depth 15%. Spots were unattenuated and centred in the receptive field of the ganglion cell and the PNR. From top to bottom the spot diameter was 0.5, 1, 3, and  $5^\circ$ . The PNR 'on' transient is greater in amplitude than the 'off' transient, as is typical vitreal to 33% retinal depth. Both ganglion cell firing and the proximal negative response show a reduction as spot diameter exceeds  $3^\circ$ . Spot intensity  $108 \text{ cd/m}^2$ ; background  $27 \text{ cd/m}^2$ .

was directionally selective, and movement of a spot in the null direction produced a smaller proximal negative response than movement in the preferred direction. If the pigeon retina is closely comparable to the *Necturus* retina, where ganglion cells but not amacrine cells are directionally selective (Werblin, 1970) this entails that the proximal negative response contains a contribution from ganglion cell dendrites,

## DISCUSSION

These experiments have shown that the proximal negative response in the pigeon retina is localized nearer the vitreal surface than the b-wave, as has also been shown in the frog retina by Burkhardt (1970). They have also shown that the 'on' and 'off' transients of the PNR have a different spatial distribution, with the 'on' component being localized vitreal to the 'off'.

Burkhardt (1970) has suggested that the amacrine cells are likely to be the main generators of the PNR on three chief grounds. First, as an extracellular potential the PNR corresponds in polarity and time course to the intracellular records obtained from amacrine cells by Werblin & Dowling (1969) in the *Necturus* retina and by Kaneko (1970) in the goldfish retina. Secondly, the PNR does not reverse polarity as the retina is penetrated, suggesting that it is not generated as a simple radial dipole in the retina. Thirdly, annular stimuli can reverse the polarity of the PNR in the frog, which suggests, if local post-synaptic inhibitory potentials are not present, that it is generated as a tangential dipole.

There are obvious similarities in the results described here. The chief difference has been in the inability to date to demonstrate a full polarity reversal of the pigeon PNR. Experiments with annuli and large spots have not produced a greater reversal than the small positive-going notch illustrated in Fig. 7. The reason for this difference between frog and pigeon is not clear, but it could be explained if the pigeon inner plexiform layer is under surround inhibition. Two observations made in this paper support this possibility. First, the threshold for producing a PNR increases as spot diameter increases, as was illustrated in Fig. 6. Secondly, both ganglion cell discharge and the PNR are suppressed by large spot stimulation. Where the PNR and ganglion cell discharge have been observed in the frog retina (Burkhardt, 1970) stimulation producing a reversed PNR is accompanied by vigorous ganglion cell firing.

The results of this paper do not add new evidence to the question of which cell types generate the PNR, except to suggest a liminar separation of the 'on' and 'off' generators in the inner plexiform layer. Since in the pigeon the majority of ganglion cells fire transiently at 'on' and 'off', the time course of their synaptic potentials must correspond closely to that of the PNR and of amacrine cell responses. Furthermore, since the disposition of their dendritic trees is almost co-extensive with that of amacrine cell processes, one would expect both cell types to contribute to the field potentials in the inner plexiform layer.

The proximal negative response in the pigeon retains the interest of a slow potential closely related to the output from retina to brain. It is generated

in a receptive field similar to those of the ganglion cells, and shows an area dependence similar to the ganglion cells. It is generated in the retina at a level proximal to the termination of centrifugal fibres, and is therefore a candidate for possible centrifugal actions produced through the isthmo-optic system.

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