The Electrical Field in the Retina and Pattern Vision

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(Received for publication, September 19, 1962)

INTRODUCTION

It was shown by Motokawa et al.1,2) that the effect of local illumination is not restricted to the illuminated part of the retina, but spreads physiologically into the surrounding areas. Evidence has been provided that the discharge pattern of some retinal ganglion cells depends on the electric field caused by slow potential activity (Motokawa et al.3)). In the carp's retina the slow potential which occurs within and immediately surrounding an illuminated area is of positive polarity; slow negative potentials can be recorded from the surrounding areas. These slow potentials of opposite polarities have opposite effects on the spike activity of the ganglion cells, one being facilitatory, and the other inhibitory. This provides evidence that the effects of the electrical fields associated with these slow potentials can be imposed upon the information transferred to the central nervous system.

The present paper reports on the distribution of electrical fields within and surrounding various patterned stimuli which were projected upon the retina; the possible significance of these potential fields in pattern vision is also discussed.

METHODS

The carp's retina was isolated and mounted, the receptor side upwards, on a small piece of Ringer-soaked black cloth which covered a small silver plate, the indifferent electrode. Slow potentials were recorded with a silver wire, 20 to 100 μ in diameter, insulated except at the tip, which was placed at the receptor surface. For some records 3 M KCl-filled micropipettes, 1–2 μ in tip diameter, were used.

Responses were amplified with a RC-coupled amplifier with cathode follower input and displayed on a dual-beam cathode-ray oscilloscope. The overall time constant of the recording system was 0.9 sec.

The optical arrangement is illustrated schematically in Fig. 1. The light source
S was a tungsten filament lamp run by 100 V house line. The filament was focused onto a slit Sl by lens $L_1$. An electromagnetic shutter Sh was driven by an electronic pulse generator synchronously with the sweep of the cathode-ray beam and gave a flash of variable duration. A small mirror $M_1$ reflected a small portion of the light into a photocell Pt to provide a stimulus mark. A black patch P with a stimulus figure cut in it was placed immediately behind a diaphragm D which served to block scattered light. The stimulus pattern was focused onto the retina by a lens $L_3$.

The distribution of potentials within and surrounding a projected test pattern was mapped by scanning the test pattern across the retina as the electrode was maintained in a fixed position. The test pattern was first moved horizontally from one side of the field to the other. The movement was in discrete steps, and the test pattern was illuminated for 0.2 sec after each increment of horizontal displacement.

At the end of each horizontal sweep, the test pattern was returned to the starting side, and displaced vertically; then a second horizontal sweep was begun, in the same direction as and parallel to the first sweep. This process was continued until the entire field had been scanned. The spatial relations between the potentials evoked during the scanning was preserved by synchronization of the scanning program and the sweep of the recording oscilloscope.
The stimulus flashes occurred at constant spatial and temporal intervals along the horizontal sweep at the test pattern. Thus the distances between response deflections on the horizontal sweep of the cathode-ray tube corresponded to horizontal distances between successive displacements of the test pattern. Furthermore, the vertical position of the cathode-ray sweep was moved synchronously with vertical displacement of the test pattern sweep so that the correspondence of vertical distances was on the same scale as horizontal distances. The form of the data derived from such a procedure is shown in Figs. 3 and 4 in which the spatial distribution of the responses recorded corresponds to relative distances between the active electrode and the test pattern.

It took about 20 minutes to scan the whole field, and this was the shortest possible time, because a long interval of at least 2.5 sec had to be allowed between successive test flashes to keep the adaptation state of the retina constant.

RESULTS

Interaction of positive and negative slow potentials

The polarity of responses is referred to the microelectrode placed on the receptor surface of the isolated retina. Therefore, so far as polarity is concerned, the positive potential recorded from the illuminated part corresponds to the a-wave (or the PIII component) of the usual ERG, and the negative one recorded from the surrounding area corresponds to the b-wave (or the PII component). In the retina of the frog or the toad the negative potential is so predominant that a sustained positive potential such as recorded from the carp's retina cannot be obtained in most cases. This is probably because the recorded potential in the retina of the frog or toad is an interference product of a weak positive and strong negative potential.

According to a histological investigation by Ogawa the population of nerve cells in the inner nuclear layer is much greater in the retina of the frog or toad than in the carp's retina. In view of the fact found by Tomita et al. and confirmed by Brindley and by Ogawa that the b-wave of the frog's ERG changes its polarity in the bipolar cell layer when the potential is explored by advancing a microelectrode through the retinal layers, Ogawa attributed the observed difference in the electrical behavior of the retinæ of frog and carp to the structural difference, especially in the development of the bipolar cell layer.

The difference is, however, only quantitative, but not qualitative, because it was shown by Brindley that under some favorable conditions the frog's retina showed a positive potential at an illuminated locus, but a negative one in the surrounding areas in much the same way as the carp's retina.

On the other hand, it is possible to make the negative potential predominant over the positive one at an illuminated part of the carp's retina by using stimuli of sufficient intensity and area and also by other ways, for example, by cocainiza-
tion of the receptor surface; as was shown in the previous paper, the positive potential recorded from an illuminated part changed to a negative one, when a droplet of 1% cocaine solution was applied to the illuminated locus of the receptor surface. This finding suggests that the positive component of potential which is predominant within an illuminated area must originate in the more distal, superficial layer, while the negative component is produced in the more proximal, deeper layer. Ogawa maintains that the positive and negative potentials originate in the receptor layer and the bipolar cell layer respectively. As has been stated above, increases in stimulus area are favorable for obtaining a negative potential at the site of illumination; this fact may be accounted for in terms of spatial summation of negative slow potentials. Evidence was provided in a preceding paper that the negative potential is induced from the illuminated part into the surrounding area and propagates at a rate of about 110 mm/sec on an average. From the above-mentioned effect of cocainization it is apparent that the negative potential is induced not only into the surrounding area, but also into the illuminated area. Because of the physiological spread of the negative potential the degree of spatial summation is much greater for the negative potential than the positive one for which there is no evidence of physiological lateral spread.

Examples of the area effect are illustrated in Fig. 2 in which the illuminated areas were 0.34, 1.7 and 3.7 mm in diameter for the upper, middle and lower records respectively (see the left records). The potential was recorded with a microelectrode placed at the center of the illuminated area. As can be seen in these records, the sustained positive deflection during illumination showed no increase with increasing stimulus areas (compare the upper record with the middle one).

When the stimulus area was sufficiently large, the on-response became biphasic, first positive, then negative, and the negative off-response increased in amplitude, as is shown in the lower record. The biphasic property of the on-response may be attributed to the difference in the properties of the positive and negative components. The positive component is a direct effect of illumination at the site of stimulation and develops more quickly, while the negative one represents a summation product of the local and propagated effects and develops more slowly. The larger off-response with increasing illuminated area is explained by a slower dissipation of the negative component. As is shown in the right records in Fig. 2, a square cut was made with a blade of razor so as to isolate the central part from the surrounding area and the retina was subjected to illumination as before. The responses obtained were almost identical with the respective controls, when the illumination was restricted to the inside of the square cut (see the upper and middle right records), but a conspicuous effect was observed, when the cut was included within the illuminated area. The major effect consisted
of a marked decrease of the negative component; the on-response was monophasic instead of diphasic, and the amplitude of the negative off-response was much smaller (see the lower right record). These effects cannot be attributed to possible deterioration caused by the cut, because no such effect could be seen when an area completely inside of the square cut was illuminated. The observed decrease of the negative component is probably due to the circumstance that the illuminated part lying outside the cut would not contribute to the response recorded at the center, because the propagating negative potential from this part would be blocked by the cut and unable to reach the recording electrode at the center.

Motokawa, Yamashita and Ogawa\textsuperscript{8}) reported that the slow potential recorded at the central part of a large illuminated area is generally more negative than that recorded in the periphery of the illuminated area; this fact was accounted for in terms of summation of negative potentials. The summation must be more marked at the center, because propagating negative potentials come from all of the areas stimulated around it, while there is no such contribution to the potential recorded in the periphery from the non-illuminated neighboring areas.
Electric fields of the retina caused by stimuli of various patterns

In the following experiments the distribution of electric fields caused by various stimulus figures was mapped by means of the scanning procedure described above. In Fig. 3 the vertical distance between sweeps and the horizontal distance between successive response deflections both correspond to a distance of 0.2 mm on the retina. A, B and C refer to the fields caused by a circular, square and triangular stimuli respectively. The illuminated part is stippled in each figure. The margin of the illuminated part was determined accurately by a microscopic examination. The image was not strictly square, but a rectangle in B, and it was not an equilateral triangle in C because of some distortion caused by defects of the optical system used.

The outermost continuous line was drawn manually connecting points of zero-potentials; the polarity of response is positive within the area enclosed by the zero-potential line, but negative outside it. It will be seen that the zero-potential line surrounding a circular retinal image is circular, and that the line...
surrounding a triangular image is roughly triangular. It is to be noted that the line around the rectangle is not rectangular, but cruciform. These findings agree very closely with the results which were obtained from the human eye by Motokawa\textsuperscript{9}) using his method of retinal induction; in the Motokawa's experiment the contours of "equi-inductive lines" around a circle, a triangle and a square were found to be circular, roughly triangular and cruciform respectively.

Within the halo around the retinal image, responses are positive just as inside the retinal image, but smaller in amplitude. The area of the halo relative to the image area decreases with increasing stimulus areas and with increasing intensities of the background illumination. These properties of the halo may be correlated with the well-known sensory phenomenon, irradiation, which causes an overestimation in size of a visual object.

\textit{The electrical field in the retina and optical illusion}

Fig. 4 illustrates the famous Müller-Lyer figures and the electrical fields caused by these stimuli. The horizontal lines of both figures are of equal length, but that of A appears longer than that of B. It is also seen that the contour of the zero-potential line shows a greater horizontal extent in A than in B.

It is not difficult to regard the observed difference as one of the physiological factors responsible for the Müller-Lyer optical illusion; it is conceivable that the
positive field or the halo around the retinal image would contribute to judgement of the figure-size, because the responses within the halo are the same in polarity as those in the retinal image and are expected to have a similar effect upon the discharge pattern of retinal ganglion cells.

Next, the electrical field caused by a set of two concentric circles was investigated, for it is known that optical illusion concerning size perception occurs with such a stimulus pattern. In these experiments the distribution of positive and negative potentials was determined along a straight line passing through the center of the circles, and it was found that the point of maximum positivity in the field did not always coincide with the illuminated part of the retina which corresponded to the circumference of each circle, but that the maximally positive point was often displaced either towards the center of the circle or in the reverse direction depending upon the relative sizes of both concentric circles. Such displacement was generally more marked for the inner circle than the outer one. This situation is schematically illustrated in Fig. 5. Fig. 5A represents the potential distribu-

![Diagram A](image1)

**Fig. 5.** Electrical field caused by a set of concentric circles (schematic representation). Curve represents distribution of positive and negative potentials measured along straight line passing through center of circle.
tion along a straight line passing through the center of the circles of which the inner one is relatively small. It is seen that the right positive peak of the potential field is a little displaced from the circumference of the inner circle towards the center of the circle, while there is no such marked displacement of the left positive peak from the circumference of the outer circle.

When the inner circle was relatively large, the displacement of the positive peak due to the inner circle occurred in the reverse direction, that is, outward from the circumference, as is illustrated in Fig. 5B. Another conspicuous difference between A and B is that in A the two positive peaks are separated by a deep negative field, whereas in B they are separated only by shallow depression. Examples of actual records are shown in Fig. 6A and B. In this figure each response is represented by a vertical bar, positive responses being directed upward.

![Fig. 6. Actual records of potential distribution caused by concentric circles. Because of low rate of sweep each response is represented by a vertical bar. Upward deflection is positive. Positions of two stimuli are indicated by vertical bars under record; right mark is for inner circle and left one for outer circle.](image)

The positions of the circumferences of the outer and inner circles are marked by
vertical bars under the record, where the left and right marks refer to the outer and inner circles respectively.

It is to be noted that the size of the inner circles was the same in both cases. The type of responses at the illuminated parts appears diphasic in these cases, because each positive on-response was followed by a negative off-response.

In psychology it is a well-established fact that the relatively small inner circle tends to appear smaller than its actual size, while a relatively large one is apt to appear larger. It does not appear unreasonable to suggest that the above-mentioned displacement of the positive peak in the electrical field of the retina is at least a partial basis of the perceptual illusion. The displacement occurs in such a way that the positive peak for the relatively small inner circle is shifted towards the center, which would correspond to a perceptual contraction of the circle. For the relatively large inner circle the displacement is in the reverse direction, which would correspond to a perceptual expansion of the circle.

A number of experiments have been made to establish a quantitative relation between over- or underestimation of the inner circle and the size-ratio of the two concentric circles, but this phenomenon has proved too complicated to be expressed as a simple function of the ratios. In the present experiment no attempt has been made to determine a quantitative relationship between the displacement of the positive peak and other variables, but it seems safe to conclude that such displacement would correspond to over- or underestimation of the inner circle.

DISCUSSION

For the present experiment, the stimulus figures were made as small as possible in view of the physiological heterogeneity of the retina reported by Hamasaki and Marg. The positive fields within such small retinal images were found to be nearly uniform (see Fig. 3).

The use of small stimulus figures also has the advantage that the halo around the illuminated area is relatively large. However one shortcoming of such small test patterns is that there appears little or no border contrast such as has been observed in a previous report.

To correlate the electrical field in the fish retina with a psychological phenomena such as optical illusions might seem too speculative, but it has been shown by Herter that some kinds of optical illusions, for example those of Müller-Lyer type, can be observed in some species of fish.

In addition to the possible significance of the retinal electric field in pattern vision, it must also be noted that some of the findings of the present study fail to conform to the classical concept of physiological optics which assumes a correspondence between the response pattern and the distribution of retinal illuminance. This concept was found to hold for small simple figures for which the
greatest positive potentials coincided with the illuminated area. With more complicated figures, however, the maximum positive potential was not always found at the illuminated area, but was sometimes displaced into a neighboring non-illuminated area (see Fig. 5 A). A previous report\(^8\) on the distribution of potentials across a uniformly illuminated large retinal area is also consistent with the perceptual phenomenon (in this case border contrast), but fails to correspond to the concepts of physiological optics.

Such findings, however, can be accounted for in terms of an interaction between positive and negative potentials the properties of which differ greatly from each other. The field pattern caused by concentric circles can be explained from this point of view, for example. As can be seen in Figs. 5A and 6A, the amplitudes of negative potentials are generally greater between the two concentric circles than in the other areas. This fact is due to summation of the negative potentials induced by the two stimulus figures. Inside the inner circle and outside the outer circle less summation will take place, because these areas are remote from one of these stimuli.

In general, the field strength of the negative potential is greater within a circle than outside of it, because within the circumscribed area negative potentials arriving from all directions summate well, while outside the circle negative potentials come only from one side. This is supported by the finding that in Fig. 6A the amplitude of the negative potentials is larger on the right side of the right vertical mark than on the left side of the left vertical mark.

This general law of summation accounts for the above-mentioned displacement of the positivity maximum due to the inner circle: The negative potential field exerted by the outer circle upon the inner circle is greater than the negative potential field exerted by the inner circle upon the outer circle, thus the center of gravity of the summed negative field in the intervening area between both circles are displaced towards the inner circle. In consequence the negative potential field in this area interferes with the positive potential field caused by the inner circle more severely than with that caused by the outer one. This must be reason for the more marked displacement of the positive field caused by the inner circle. When the inner circle is relatively large as is shown in Fig. 5B, the two circles collaborate in making a strong field of negative potential within the inner circle. In agreement with this interpretation is the observation that the amplitude of the negative potentials on the right side of the right mark (inside of the inner circle) is much greater in Fig. 6B than in Fig. 6A, since in the latter case the contribution by the outer circle must be only slight because of its remote distance. The strong negative field thus established interferes with the positive field caused by the inner circle so that it is displaced outward.

The interaction between the positive and negative potentials cannot be regarded as a mere physical event occurring in a volume conductor, but must be a
physiological phenomenon for the following reasons: 1. The effect of the positive response is usually so predominant that interaction of positive and negative responses of equal magnitude yields always a positive resultant. 2. Only little interaction takes place between these responses and artificially produced electrical fields of opposite polarity.

**SUMMARY**

1. In the carp’s isolated retina a positive potential was produced within and very closely around an illuminated area, and a negative one in the surrounding area.

2. The configuration of the potential recorded at the center of the illuminated part varied with the area of illumination in such a manner that the negative component increased with increasing areas of illumination. This effect was attributed to the summation of negative potentials coming from all parts of the illuminated area. When the central part was isolated from the surrounding area by a mechanical cut, the negative component decreased so that the recorded potential became more positive.

3. The distribution of positive and negative potentials in the retina subjected to stimuli of various patterns was mapped, and the zero-potential line separating the positive field from the negative one was determined for each stimulus. The contour of the zero-potential line was circular for a circle, about triangular for a triangle, but cruciform for a square.

4. The potential fields around Müller-Lyer figures were mapped, and the extent of the positive field was correlated with the perceptual effect of these figures.

5. The electrical field caused by a set of two concentric circles was mapped. The positive field of the inner circle of definite diameter was found to be displaced towards the center, when the outer circle was relatively large, and displacement occurred in the reverse direction when the outer circle was relatively small. These phenomena were correlated with under- and overestimation of the size of the inner circle when viewed within large and small outer circles, and accounted for in terms of interaction between positive and negative potentials.

**References**

7) Brindley, G. S., Ibid., 1956, 134, 360.