LETTERS TO THE EDITORS

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Inhibition and the Polarity of the Retinal Elements

THE retinal elements in the cat's eye[1], as isolated by the micro-electrode technique, are, like those of the frog's eye[2], of three types: pure on-elements discharging merely to onset of illumination, pure off-elements inhibited by light and discharging merely to cessation of illumination, and on-off-elements combining the two properties. If a polarizing current of some 0·7–1·0 mA. is passed through the retina between electrodes stuck in vertically into the nasal and temporal cavities outside the bulb, it is possible to elicit on- and off-effects also by polarization[3]. In such experiments it is necessary always to place the micro-electrode in the same part of the retina, so as to preserve a constant relation to the polarizing source. Threshold responses to polarization can be measured with an accuracy of 5 per cent. In the following description of the polarities of the retinal elements, the terms 'cathodal' and 'anodal' refer to threshold responses at the nasal polarizing electrode.

The pure on-elements reproducing the simple receptor properties respond to cathodal stimulation with an on-effect. An increase of current strength by some 30–40 per cent is necessary to elicit the anodal off-effect (as in many peripheral nerves). The more complex pure off-elements (inhibited by light) have, however, opposite polarity. They respond to the threshold cathodal stimulation with an off-effect. Current reversal, *without increase of strength*, brings forth the anodal on-effect that light cannot elicit. The on-off-elements (80 per cent of the population[4]) respond with a threshold on-effect to either cathode or anode. Those that give cathodal on-effects respond to the anode with an off-effect; those with anodal on-effects respond to the cathode with an off-effect. The elements with anodal on-effects (cathodal 'off') are highly off-sensitive when tested by illumination (high off/on ratio); those with cathodal on-effects are mostly on-sensitive when tested by threshold illumination (low off/on ratio). Cathodal and anodal effects again occur at the same current strength. Except for the electrical symmetry of all the on-off-elements, a greater on-sensitivity thus makes them behave more like pure on-elements, and a greater off-sensitivity makes their properties exactly like those of the pure off-elements. This statement is based on measurements on 71 well-isolated on-off-elements.

In a very large material of isolated spikes the off/on ratio (to light) has varied from 0·001 to 10·000. This enormous variation is coupled with differences in colour sensitivity of the on- and off-components of the on-off-elements[4,5]. These two facts can only be explained by assuming the off-path to start in different receptors and join the direct on-path over internuncial neurones such as amacrines and horizontal cells[4]. The path that is inhibited by light and set free by cessation of illumination is therefore an indirect path to the fibre isolated by the micro-electrode. The polarization results can accordingly be explained in the following manner: the indirectly excited path turns its anode (source) towards the direct path and blocks it, with consequent release at 'off'. With respect to the polarizing electrode, this off-effect will be cathodal. Current reversal leads to indirect excitation (on-effect) at the same converging focus, because in this case the indirect path has turned its cathode (sink) towards the direct path. With respect to the polarizing electrode this means an anodal on-effect. The inner stimulus, however, is cathodal. Hence the perfect electrical symmetry. The anodal and cathodal foci may generate slow potentials of opposite sign, as in the isolated axon of *Sepia*[6], because it is well known that excitation and inhibition in the retina are accompanied by opposite slow potentials[1]. Inhibition is thus a function of the existence of an indirect path which can be picked out by its opposite polarity in the polarization test, and which responds to illumination with a block, followed by an off-effect when the light is turned away. The instantaneous character of the inhibition, when compared with excitation, is due to the rapid establishment of the electrical field in the short axons of the amacrines and horizontal cells which serve as 'internal commutators'. The on-off-elements are a mixture of direct and indirect paths and thus combine anodal and cathodal responses.

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[1] Granit, "Sensory Mechanisms of the Retina" (Oxford Univ. Press, 1947).
[2] Hartline, *Amer. J. Physiol.*, **121**, 400 (1938).
[3] Granit, *J. Physiol.*, **105**, 45 (1946).
[4] Granit and Tansley, in the press.
[5] Gernandt, see following communication.
[6] Arvanitaki, *J. Physiol. Path. gén.*, **38**, 147 (1941–43).

Colour Sensitivity, Contrast and Polarity of the Retinal Elements

SINCE the time of Purkinje and Ritter, it has been known and often confirmed that a galvanic current passed through the eye elicits a sensation of bluish-violet when the electrode on the bulb is an anode, of greenish-yellow when it is a cathode. Kravkov and Galochkina[1] have recently shown that the anodal pole (on the eye) enhances the sensitivity to short wave-lengths and depresses that to long wave-lengths, whereas the cathodal pole has opposite effects. In view of the results on different polarity in retinal elements isolated by the micro-electrode technique, reported above[2], it was thought to be of interest to combine polarization of the retina with measurements of the colour sensitivity of such elements. The micro-electrode technique and the cat's eye were used, as above[2]. The strength of the current was 1·0 mA.

The pure on-elements (cathodal 'on'[2]) responded as shown in Fig. 1. Cathodal polarization increased the sensitivity to short wave-lengths; anodal polarization caused a corresponding but smaller depression. The majority of the pure on-elements in the cat's eye are blue- and green-sensitive[3]. The pure off-elements, which have opposite polarity[2], gave an increase in the long wave-lengths during cathodal polarization, with a corresponding depression during anodal polarization (Fig. 1). The majority of these elements are actually red-sensitive[3]. The on-off-elements vary a great deal in colour sensitivity,