dark adaptation is determined neurally rather than at the receptor level[7,8], it is likely that the dark deafferentation occurs between the bipolar and the ganglion cell.

This research was sponsored jointly by the Office of Scientific Research, OAR, through the European Office, Aerospace Research, United States Air Force, under grant *AF–EOAR* 63–9, and by the Rockefeller Foundation.

G. W. Hughes*
L. Maffei
Istituto di Fisiologia Umana della Università di Pisa
e Centro di Neurofisiologia del C.N.R.,
Sezione di Pisa, Italy.

* Under Special Fellowship of the National Institute of Neurological Diseases and Blindness, U.S. Public Health Service.

[1] Granit, R., in *Sensory Mechanisms of the Retina* (London: Oxford Univ. Press, 1947).
[2] Kuffler, S. W., Fitzhugh, R., and Barlow, H. B., *J. Gen. Physiol.*, **40**, 683 (1957).
[3] Arduini, A., and Pinneo, L., *Arch. ital. Biol.*, **100**, 415 (1962).
[4] Batini, C., Moruzzi, G., Palestini, M., Rossi, G. F., and Zanchetti, A., *Arch. ital. Biol.*, **97**, 12 (1959).
[5] Rushton, W. A. H., *Nature*, **169**, 743 (1949).
[6] Hecht, S., *Physiol. Rev.*, **17**, 239 (1937).
[7] Rushton, W. A. H., *J. Physiol.*, **149**, 327 (1959).
[8] Rushton, W. A. H., *J. Opt. Soc. Amer.*, **53**, 104 (1963).

Intracellular Action Potentials associated with the Beating of the Cilia in Ctenophore Comb Plate Cells

In ctenophores the tall columnar cells which bear the large cilia are about 100μ × 8–12μ, arranged in groups along the combs[1]. The large size of the cells makes it possible to record intracellular potentials which occur at each beat of the cilia. Although there is a good deal of previous work on the relations between membrane potential and ciliary activity in Protozoa[2], no accounts of intracellular potentials from metazoan ciliated cells have come to hand.

Pieces of comb plate are cut from specimens of the Venus's girdle, *Cestus veneris*, about 50 cm long, and firmly held down in a wax dish by means of fine cactus spines. Usually the cilia then beat slowly at regular intervals and can also be aroused to give a single beat by a very gentle tap to the bench. Under direct observation a KCl-filled glass microelectrode (which must be 30–100 M ohms to be successful) is lowered into the cushion of ciliated cells just at the region of the ciliary basal bodies. Negative-going extracellular potentials, in the form of small peaks of a few millivolts and about 0·1 sec duration, are recorded before the electrode enters a cell. They vary greatly in height as the electrode presses to different extents against the cell. Resting potentials up to 40 mV are recorded as the electrode enters; at the same time the action potentials reverse in sign and now have a long falling phase (Fig. 1). The maximum height of action potentials was 27 mV at 15° C. The action potential is similar whether the beat is spontaneous or set off by a minute vibration. At this first attempt technical difficulties prevented successful recording of the mechanical movement and it is not possible to say whether the electrical change starts before or after the beat of the cilia. The beat is, however, terminated in 0·2–0·4 sec and the potential change lasts much longer. Action potentials are graded, the smaller ones corresponding with weaker beats and larger ones with stronger beats. When two beats occur in quick succession the action potential of the second stands on the first as in Fig. 1*b*, although the two mechanical beats are quite separate. All cells have similar responses. No pacemaker or generator potentials have been seen. Depolarization of the cell by damage with the electrode causes the cilia of that cell, and of neighbouring cells, to beat rapidly. This can lead to a continual quivering of a small group of cilia. Although it is impossible to identify individual cells from which recordings are made in these circumstances, the quivering of cilia is found when the resting potential declines away to nothing. These small movements are not propagated.

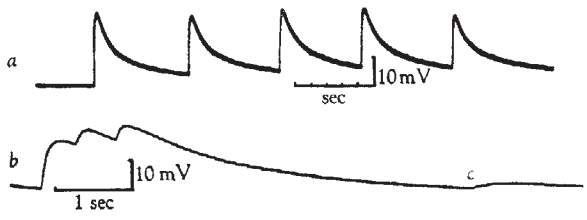

Fig. 1. Intracellular records from ciliated comb plate cells. *a*, At each beat there is a positive-going action potential with a rapid rising phase and a slow falling phase; *b*, at 5 times the recording speed, three beats, artificially initiated by small vibrations, follow each other rapidly, forming a staircase; *c*, the graded nature of the action potentials is shown by a small spontaneous potential, which was accompanied by a weak beat of the cilia

This is the tissue for which the term "neuroid transmission" was first coined[3], meaning propagation from cell to cell, but the results reported here fail to elucidate the mechanism by which the groups of ciliated cells are coordinated among themselves or between groups. It seems reasonable to conclude that the depolarization of the cell sets off the beat of the cilia of that cell. The ciliated cells lie close against each other, and their closely apposed membranes in some places closely resemble electrical synapses without vesicles[4], as do some muscle fibre contacts in ctenophores. The beat of the ciliated cells is inhibited by a nerve net which spreads over the whole ectodermal surface and the ciliated cells have synapses on them only at their basal ends, far from the cilia[4], showing that the whole cell must be electrically active for them to be effective. Post-synaptic potentials are presumably so attenuated that they are not observable in records from the ciliated ends of the cells.

This work was carried out at the Stazione Zoologica, Naples, and I thank the director, Dr. P. Dohrn, for the facilities which made it possible. Among his staff, I particularly thank Dr. R. A. Chapman, whose apparatus was used for the intracellular recordings.

G. A. Horridge
Gatty Marine Laboratory and
Department of Natural History,
University of St. Andrews.

[1] Heider, K., *Z. Morph. Ökol. Tiere*, **9**, 638 (1927).
[2] Naitoh, T., *Ann. Zoo. Jap.*, **31**, 59 (1958).
[3] Parker, G. H., *J. Exp. Zool.*, **2**, 407 (1905).
[4] Horridge, G. A., and Mackay, B., *Quart. J. Micr. Sci.*, **105**, 163 (1964).

Metabolic Effect of Epinephrine on the Q_{O_2} of the Arrested Isolated Perfused Rat Heart

Sympathetic amines increase the oxygen consumption of the myocardium and it has usually been assumed that this is related primarily, if not exclusively, to the increase effected in rate and contractility. The present investigation demonstrates an increase in myocardial oxygen consumption due to epinephrine during potassium-induced cardiac arrest, that is, in the absence of any chronotropic or inotropic effect. This metabolic increase in oxygen consumption is accompanied by an increase in glycerol release into the perfusion medium, suggesting that the rate of utilization of endogenous lipids rises.

Fed male albino rats were decapitated, and their hearts removed and perfused following the method of Morgan *et al.*[1]. 15–30 c.c. of modified Krebs' bicarbonate buffer[2] was used, equilibrated with 95 per cent O_2 and 5 per cent CO_2. Q_{O_2} was calculated from arterio-venous pO_2 differences, measured with a Clark O_2 macroelectrode, and from the O_2 solubility constant, flow rates being measured directly. Perfusions were carried out at 37·5° C.

In the first series of experiments, using beating hearts (Series *A*, Table 1), Q_{O_2} was measured at 20 min in 11

© 1965 Nature Publishing Group