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Physiology of the Nervous System

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BY

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PREFACE TO FIRST EDITION

'. . . The antithesis sometimes made between the science and practice of medicine is false and mischievous.'

G. W. Pickering

One purpose of this book is to place before those interested in clinical neurology an account of the physiology of the nervous system. In the text will be found numerous examples in which it is clear that a profound understanding of common clinical problems can be achieved only by thinking in neurophysiological terms. The opportunity has also been taken of offering to the psychologist a description, in some detail, of the physiology of the sense organs and of the cerebral cortex. The advanced student of physiology may find it useful to have a summary of neurophysiology in one volume and should use the book as a guide to the original literature. It is not to be expected that the medical student will, at first, find all of the sections easy to comprehend but much will become clearer as his years of training proceed, and the volume will afford a link between the preclinical and clinical years.

E. G. W.

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January 1956

PREFACE TO SECOND EDITION

This work has now been subjected to very substantial changes. Besides numerous alterations in the text there are some 82 new illustrations and 2 wholly new chapters. For many of the ideas as to appropriate material I am indebted to my colleagues in Edinburgh. The volume has involved the publishing staff in a great deal of trouble; it must have been unusually trying to produce.

E. G. W.

Edinburgh, *June* 1963

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UNITS

LENGTH

1 m. = 1 metre

1 cm. = 1 centimetre

= $\frac{1}{100}$ metre

1 mm. = 1 millimetre

= $\frac{1}{10}$ centimetre

= $\frac{1}{1000}$ metre

1 μ = 1 micron

= $\frac{1}{1000}$ millimetre

= $\frac{1}{1000000}$ metre

TIME

1 sec. = 1 second

1 msec. = 1 millisecond

= $\frac{1}{1000}$ second

1 μsec. = 1 microsecond

= $\frac{1}{1000}$ millisecond

= $\frac{1}{1000000}$ second

VELOCITY (as in nerve conduction or rate of stretching)

1 m./sec. = 1 metre per second

1 mm./sec. = 1 millimetre per second

ACCELERATION (as stimulus to vestibular apparatus)

1 cm./sec./sec. = 1 centimetre per second per second

1 G. = 981 cm./sec./sec.

FREQUENCY (of sound vibration or other oscillation)

1 c/s or 1 c.p.s. = 1 cycle per second (of spike discharge)

1/s. = 1 (spike) per second

PRESSURE

1 dyne/sq. cm. = 1 dyne acting on 1 square centimetre

SOUND INTENSITY

Absolute units—dyne/sq. cm. (*vide supra*)

Comparative units—decibel or db. (*vide* pp. 304 and 305)

VOLTAGE

1 V. = 1 volt

1 mV. = 1 millivolt

= $\frac{1}{1000}$ V.

1 μV. = 1 microvolt

= $\frac{1}{1000}$ millivolt

= $\frac{1}{1000000}$ volt

CURRENT

1 amp. = 1 ampère

1 mA. = 1 milliampère

= $\frac{1}{1000}$ ampère

1 μ A. = 1 microampère

= $\frac{1}{1000}$ milliampère

= $\frac{1}{1000000}$ ampère

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CHAPTER 1

NERVE AND MUSCLE

Who, when Galvani touched the muscles of a frog with different metals, and noticed their contraction, could have dreamt that eighty years afterwards, in virtue of the self-same process, whose earliest manifestations attracted his attention in his anatomical researches, all Europe would be traversed with wires, flashing intelligence from Madrid to St. Petersburg with the speed of lightning? In the hands of Galvani, and at first even in Volta's, electrical currents were phenomena capable of exerting only the feeblest forces, and could not be detected except by the most delicate apparatus. Had they been neglected, on the ground that the investigation of them promised no immediate practical result, we should now be ignorant of the most important and most interesting of the links between the various forces of nature.—HELMHOLTZ (1893).

THE ACTION POTENTIAL

THE brain can be regarded as a signalling system; to understand the ways in which information may flow within it, and in the periphery, it is necessary to know something of the messages that can be transmitted along individual nerve fibres. A knowledge of the properties of individual nerve fibres allows a number of aspects of the form and function of the nervous system to be understood that otherwise would be unintelligible. The brain has been likened to a telephone exchange and the nerve fibres to telegraph wires; one function of this first chapter is to examine the extent to which this 'telegraph wire' analogy is valid, another is to demonstrate that certain pathological processes affecting nerve and muscle can only be evaluated intelligently by a knowledge of the processes of excitation in single fibres.

It is over a hundred years since the *action potential* was discovered. By this term neurophysiologists refer to the electrical disturbance which signifies that a message is being transmitted through nerve fibres and the corresponding disturbance that is normally found in muscles preceding contraction. A related type [1] of disturbance in the plates of the *electric organ* of a fish is responsible for the shocks that these structures can deliver. In the electric eel potentials of several hundred volts may be developed by the summation, in series, of the small currents produced by the numerous plates.

'The essential component of an electrical organ is a disc, upon one surface of which a nerve twig ramifies, while the other surface is vascular. The electrical organ consists of piles of such discs, surface to surface, like

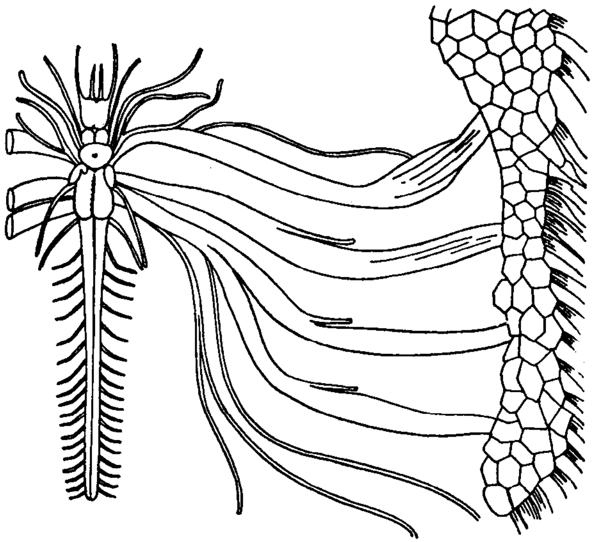

FIG. 1.1.—Diagram of an electric organ in the torpedo with its large extrinsic nerves. (After Feldberg, 1951)

the elements of an old-fashioned voltaic pile; its structure, as well as the great electro-motive force of the discharge, suggests that it is actually a battery of which the elements (discs) are disposed in series' (Waller, 1903).

John Walsh (1773) was able to demonstrate the electrical nature of the shock produced by the torpedo and he interested John Hunter in its anatomy (Fig. 1.1). These electric discharges have since that time attracted a good deal of attention (*vide* Fessard, 1952); one interesting problem concerns the ways by which the component

[1] The electric organs of different animals show a good deal of diversity in their reactions. In some cases the electric potentials produced by the plates may be of the nature of an end-plate potential (p. 31) rather than homologous with a propagated action potential.

plates, situated at considerable distances from one another, are brought into play at the same moment in order to allow their short-lasting voltages to summate effectively.

Mammalian nerve fibres are of small diameter, rarely being larger than 20μ in diameter, whilst the majority are much smaller. It is a matter of considerable technical difficulty to approach directly the problems of excitation in such filamentous structures. Much of our information about the details of nervous action have for this reason been obtained by studying the much larger nerve fibres that are found in some invertebrates. There is reason to believe that the processes are fundamentally rather similar throughout the nerve fibres that are found in the animal kingdom.

Nerve fibres may be obtained from the squid that are nearly 1 mm. in diameter. When a fine electrode is inserted into the interior of the cell it is found to be some 60 mV. negative with respect to the outside. This potential difference is a reflection of the chemical differences between the inside and the outside of the fibre and of the properties of the *cell membrane*. In introducing this term we are accepting the view that the chemical differences that distinguish the axoplasm from the extra-cellular fluid are found on either side of a fine boundary. It is on the properties of this membrane that the processes of excitation largely depend.

In exciting a nerve, mechanical or perhaps thermal stimuli (Laget & Lundberg, 1949) could be used, but for ease of control electrical shocks are preferable. On excitation of the squid axone a disturbance travels down the fibre at a velocity of some 25 m./sec. By inserting a fine electrode into the core of the axone it can be shown that this disturbance is associated with a reversal of the direction of polarisation of the cell membrane. The internal electrode becomes momentarily positive with respect to the outside of the fibre. The disturbance is abrupt and of short duration (1 msec.) at any given point. Each wave of excitation is similar; indeed if the stimuli are not repeated too rapidly, the size of the electrical disturbances is constant. Nerve fibres are therefore said to obey the 'All-or-None' law. Excitation is an explosive process, and a second stimulus arriving at the moment of excitation is ineffective; the nerve fibre is said to be in an *absolutely refractory state*. As the action potential declines the nerve is found to respond to strong stimuli by discharging an action potential that is smaller than normal; it is in the *relative refractory state*. The 'All-or-None' law is of the greatest importance in understanding the