A Handbook of
ANIMAL
PHYSIOLOGY

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PREFACE

STUDENTS are often introduced to several branches of science within the period of one academic year and the amount of information covered is constantly increasing. There is a place, therefore, for books providing a brief but coherent first approach to various subjects. There is something to be said for acquiring a framework of the main facts and an idea of the scope of a new subject before settling down to a more thorough and detailed study of its parts.

This applies perhaps with more force to animal physiology than to other subjects, and the present book was written with the above aim in mind. It is impossible, of course, to include, in a handbook of this type, any exhaustive discussions of the research background to each topic. Conflicting viewpoints and unsolved problems are, however, underlined again and again. In the selection of material there has been a bias towards topics appearing in examination papers for biological, agricultural and veterinary degrees.

The above features will, it is hoped, make the book particularly valuable in its introductory role. At the same time, it should be clear to the student that he will need to proceed from this to detailed textbooks, reviews and original papers. The Reading List includes on the one hand recent accessible and comprehensive articles, and on the other hand papers which are not covered by the former or are particularly useful for the understanding of techniques or theories outlined briefly in the text.

I am greatly indebted to Dr. F. B. Billett, who revised thoroughly the manuscript of Section II. I am also indebted to many editors, publishers and authors for generous permission to include illustrations from original papers and books. Acknowledgement to the authors and journals is made in the legends of the illustrations. I wish to express here my thanks to the following publishers:

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PART ONE
RESPONSE AND RESPONSE MECHANISMS

1. SIMPLE TYPES OF RESPONSE

Stimulus and Response

Changes in environmental conditions often elicit from living organisms activities described as *responses* or *reactions*. The changes, which must be more or less sudden, are described as *stimuli*. Stimuli utilized in experiments for the study of response include: light, electric current, mechanical forces, osmotic pressure, temperature, chemicals.

It should be noted that it is difficult to arrive at a concise definition of a stimulus. Gravity, for instance, elicits responses from animals (and plants), but it is not, normally, a sudden or changing influence. It would not be more accurate to describe a stimulus as a factor eliciting a response, since similar difficulties apply to defining response. (See Heilbrunn, L. V.: *An Outline of General Physiology*, ch. 35.)

There are, of course, many types of responses; one of the easiest to record is movement.

Simple Types of Locomotory Responses

KINESIS consists in an increase or decrease of the amount of locomotory activity, with indiscriminate changes in the direction of movement. In a Paramecium culture increased activity can be induced by dim light or moderate rise of temperature; decrease of activity results from bright light or extreme temperatures. If dim light be applied at one corner of the container only, an increase in the number of individuals in that corner is usually observed; this is not the result of many individuals proceeding towards that corner but the statistical result of the fact that individuals finding themselves in that corner respond to light by increased activity.

TAXIS consists in maintaining the line of movement at a certain angle with the direction of a stimulus. The phototaxis of Euglena is an example. This flagellate has at the anterior tip an eye-spot sensitive to changes in light intensity and screened (on one side only) by a red stigma. Euglena constantly rotates round its longitudinal axis. If it moved in a direction at an angle other

than 0° to the direction of the light, the stimulation of the eye-spot would be interrupted at the moments when the screen is opposite the light source. By orientating itself as it moves, so that the light stimulus is not interrupted, the cell, in fact, follows the line towards the source of light.

In a similar way, insects turn in relation to light so that both eyes are equally illuminated. This means, normally, moving towards the light but, in experiments, conditions can be devised under which it means moving towards the shadow. Blackening of one eye is found to lead to circular movement on a plane, or to spiral movement on climbing; the uncovered eye is constantly stimulated by light in excess of the other, and the insect constantly turns as if to bring the covered eye also into the light.

TROPISM is the orientation, by differential growth, of sessile organisms at a certain angle to the direction of certain stimuli.

Many patterns of behaviour can be analysed into component taxes. Young turtles move instinctively from their nests towards the sea and it was found that this is the result of positive taxes to the following stimuli: (a) gravity—moving down slopes, (b) optic stimuli—moving towards uninterrupted horizon, and (c) colour—moving towards the blue colour of the sea.

However, these three types of response cannot cover, even in Protozoa, the whole repertory of reactions. The sequence of responses of the stalked ciliate, Stentor, for instance, cannot be analysed in terms of the above types: when this protozoan is first stimulated by touch, its stalk bends towards the opposite side; if stimulation is persistent, it repeats the same response several times up to a point beyond which it also reverses its ciliary beat; if stimulation is continued still further, it contracts and, finally, it may break off its stalk altogether.

It should be noted that the response to a certain stimulus can be different under different physicochemical conditions, or age, etc. Arenicola larvae are negatively geotactic and swim upwards even in the dark. They swim however in the opposite direction if the water in which they are placed contains an excess of calcium or magnesium ions.

2. MECHANISMS OF LOCOMOTORY RESPONSES IN PROTOZOA

Amoeboid Motion

Pantin investigated this on *Amoeba limax*, the whole cell of which acts as a single pseudopodium of a constant shape. There is, centrally, a streaming of endoplasm *sol* in the direction of the movement. On reaching the tip of the cell the endoplasm diverges out to the periphery on both sides and becomes part of the ectoplasm *gel*. This streaming is kept up by reconversion of the ectoplasm *gel* to endoplasm *sol*, at the posterior end of the cell. Gelation is combined with contraction whilst the *sol* extends passively and swells the pseudopodium, thus forcing it to advance (Fig. 1).
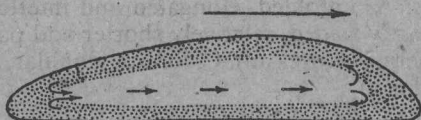

Fig. 1. Direction of cytoplasmic streaming in *Amoeba limax*. Dotted layer: ectoplasm. Clear layer: endoplasm (sol).

It was observed that deprivation of oxygen causes suspension of movement (after 6 hours) and, finally, death. Decrease of osmotic pressure of the medium causes water-loading and speedier conversion of ectoplasm to endoplasm with consequent swelling of the cell. Increase of osmotic pressure has the opposite effect, the cell shrinking and assuming a star-like shape. In both cases the cell stops moving. The uptake of water and swelling in the advancing pseudopodium has been attributed to a more acidic local reaction, detectable by the use as an indicator of the vital stain, neutral red.

The mechanism described for *A. limax* does not seem applicable to other amoebæ.

A recent hypothesis (Goldacre-Lorch) attributes pseudopodial movement, and cytoplasmic streaming in general, to a reversible change of the protein molecules from an unfolded to a globular form: in the ectoplasm (*gel*) the protein molecules are unfolded, elongated and interlocking (Fig. 2). Where the ectoplasm contracts (posterior end of the *A. limax* cell) they are partly folded and

Note. The word 'cell' is used in this and later chapters to denote an individual, although the two terms are not strictly synonymous for all protozoan groups.
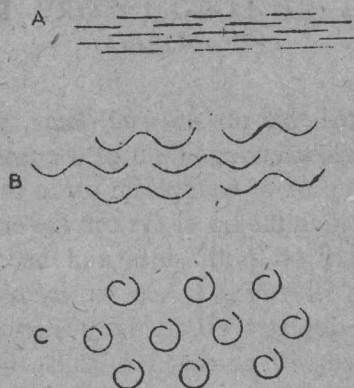
Fig. 2. Diagrammatic representation of the changes in shape of protein molecules. A, unfolded, elongated and interlocking molecules (ectoplasm). B, partly folded, relatively shorter and partly interlocking molecules (contracting ectoplasm). C, folded, globular, non-interlocking molecules (endoplasm).

still interlocked. When the folding is completed and molecules are no longer interlocked, the *gel* has become a *sol* (endoplasm) which is squeezed forth by the contracting ectoplasm. The folding of the molecules is set off by an enzyme localized at the posterior tip of the cell (tail organizer). The reconversion of endoplasm to ectoplasm is assumed to be caused by the nucleus acting on the endoplasm as it streams by. The tail organizer would be produced by the nucleus at mitosis (one for each daughter cell) and cytoplasmic movement would stop when the enzyme is eventually used up; the cell then rounds itself up and has to undergo a new mitotic division in order—among other things—to renew its tail organizer.

Flagellar Motion

A flagellum consists of an axoneme and a sheath spirally wound round it, and is attached to a *basal granule* or *blepharoplast*. The beat of a flagellum ceases if it is severed from its basal granule.

A flagellum which would move to each side of its rest-position like a pendulum (i.e., remaining straight and with constant speed), would produce equal forces in both directions and no movement of the cell would result. But, in fact, the forces produced are unequal because (*a*) the speed is different in the two directions;

(b) the flagellum bends during movement in one direction, so that less resistance is met from the medium—the movement in this direction is called the recovery beat, the movement in the opposite direction, with the flagellum straight, the effective beat; (c) the flagellum undulates by waves of curvature passing from its basal end to the tip.
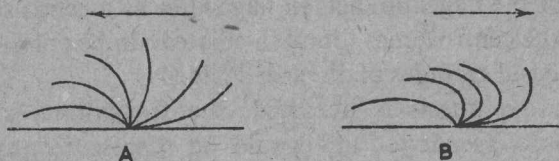

Fig. 3. Phases of ciliary movement. A, effective beat, quick. Cilium nearly straight. B, recovery beat, slow. Cilium bent.

Ciliary Mechanisms

As in a non-undulating flagellum, there are two phases in the motion of each cilium: (a) a forward, effective beat, during which the cilium is more or less stiff, and (b) a backward recovery beat, at the beginning of which the cilium is limp but stiffens gradually, starting from the base (Fig. 3). Energy derived from chemical energy stored in metabolites is expended during the effective beat. The water is pushed by the cilia in the direction of the effective beat. If the organism is floating, it will be propelled in the opposite direction; if it is sessile, a water current flows past it, in the direction of the effective beat.

The beat of all cilia is co-ordinated so that regular metachronal waves are produced. Certain stimuli, such as some drugs, or contact with a solid object, can bring about a reversal of the ciliary beat and of the direction of locomotion in some Ciliates.

A special mechanism has been described, occurring in many complex ciliates, such as Euplotes, the cilia of which are grouped in tufts. Cytoplasmic fibrils, the *neuronemes*, connect the tufts to a single centre for the whole cell, the *motorium*. It has proved possible to sever these neuronemes by microdissecting instruments; the co-ordination of the tufts or cirri was abolished as a result.

Comparison of the Locomotory Organelles of Protozoa

The primary importance of movement was probably that it brought the cell into contact with new portions of the medium,

thus facilitating the diffusion of substances through the cell membrane.

Of the locomotory organelles found in Protozoa, the flagellum is considered the most primitive, because: (a) it is found in animals as well as plants; (b) since some follow a holophytic mode of nutrition, flagellates are the most primitive group of Protista; (c) the basal granule of the flagellum acts in flagellates as a centrosome during mitosis; the centrosomes found in ciliates can be considered as the retained basal granules of discarded flagella.

If this hypothesis is accepted, the transitional stages from flagellum to pseudopodium would be represented by : (a) the *axopodia* of the Heliozoa (ex. Actinophrys) each of which includes an axoneme, resting on the nuclear membrane; the bending of these axopodia could be considered as a slow-motion flagellar beat; (b) the pseudopodia of the Foraminifera, which have no axial filament and are used for the capture of food particles rather than for locomotion.

3. THE NEURONE AND THE TRANSMISSION OF IMPULSES

The Neurone

A constituent cell of nervous tissue, i.e., a *neurone* (Fig. 4) has three parts: (a) a cell body, or *cyton*, containing the nucleus, (b) receptor fibres, *dendrites*, which can be short and branch profusely; they receive impulses (from other neurones or from sensory cells or, in cases where their endings are free, by direct stimulation) and convey them towards the cyton; (c) a more or less long single effector fibre, the *axon*, which conveys the impulses away from the cyton to other neurones or to effector organs, i.e. muscles or glands. The axon also branches so that, through it, an impulse can reach a large number of muscle fibres simultaneously. An axon and the muscle fibres supplied by it constitute a *motor unit*.

Neurones are linked to each other at *synapses*, where an impulse is relayed from an axon branch to the dendrites of one or more other neurones. The axons do not, however, become continuous with the dendrites at a synapse; a minute gap separates them.
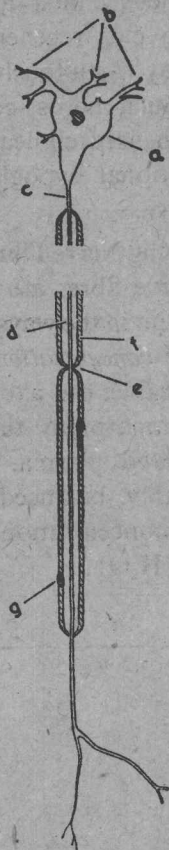
Fig. 4. Diagrammatic representation of a neurone with a myelinated axon. a, cyton. b, dendrites. c, axon. d, myelin or medullary sheath; consists of lipoid material and surrounds the axon except for its base and terminations; it is also interrupted at: e, the nodes of Ranvier, at regular intervals (of 1 mm. in man, 3 mm. in frog). f, neurilemma or Schwann's sheath round the myelin sheath. g, nucleus of a neurilemma cell.

As neurones develop in the embryo, the cyton and the dendrites grow towards the positions from which stimuli are or will be originating, whilst axons grow in the opposite direction. There is as yet no explanation for the mechanism of this *neurobiotaxis*.

If a nerve is transected, the parts of the fibres severed from the cyton degenerate simultaneously throughout their lengths (*Wallerian degeneration*). The parts proximal to the cyton also degenerate, but gradually, starting from the distal end (*retrograde degeneration*).

Nerve fibres possessing a neurilemma may, if severed, regenerate. If the neurilemma is also cut, regeneration is slower and the growing proximal part may fortuitously connect with the distal part of another cut fibre. Such a cross-connection or anastomosis of different fibres has been used clinically, by anastomosing the proximal end of the functional hypoglossal nerve to the distal end of a paralytic facial nerve.

Transmission of Impulses along Nerve Fibres

RESTING POTENTIAL. Nerve fibres are found to differ from the interstitial fluids bathing them in the ways described below.

(a) *The proportions and concentrations of ions.* Although the fibre membranes are permeable, the axoplasm, i.e. the semi-fluid material of the axis, contains many times more K^+, and less Na^+ or Cl^-, than the blood plasma. The excessive K^+ inside the membrane is, presumably, balanced by organic anions. The following are some of the concentrations measured, in m. equiv. (milli-equivalent) per kg. of H_2O:

	Na^+	K^+
Frog:		
myelinated nerve	37	173
plasma	108	2·6
Sepia:		
nerve, fresh	44	369
nerve, washed in sea water	101	321
sea water (as Sepia plasma)	498	13

(b) *Electrical potential.* It is possible, by using the giant nerve fibres of Sepia which have a diameter of about 1 mm., to introduce into the axoplasm a micro-electrode (insulated, except at its tip, by a layer of glass). This electrode is connected with another, immersed in the saline medium bathing the fibre, with a volto-meter interpolated. A potential difference (P.D.) across the fibre membrane is thus traced, of the order of 50 mV. This P.D., attributed to the high K^+ content of the axoplasm, is known as the *resting potential* of the fibre. On the basis of the difference in K^+ concentration, a P.D. of 85 mV. would be theoretically expected, i.e., a higher one than the values obtained. The discrepancy could be accounted for by short circuits and damage to the fibre.