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SYMPOSIA
OF THE SOCIETY FOR
EXPERIMENTAL BIOLOGY

NUMBER XVI

BIOLOGICAL
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MECHANISMS

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BIOLOGICAL RECEPTOR
MECHANISMS



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PREFACE

The sixteenth Symposium of the Society started its career under the title of 'Sense Organs'; it was soon appreciated that it would be of value to embrace an exchange of information between parallel problems in botany and in zoology. Plants do not, in general, have discrete structures which can have this designation, and the title 'Receptor Mechanisms' has been used to overcome the difficulty. The contributors to the Symposium were invited with this advice: the subject includes all aspects of mechanisms whereby living organisms transform or transduce the information in their environment into that form to which they respond internally; but central phenomena are excluded.

The Symposium is largely concerned with mechanisms resulting in information within the organism in an electrical or chemical form; it is, however, clear that such internal information does not necessarily bear a one-to-one relationship to the corresponding information in the environment. Thus, many of the contributions include some discussion of peripheral systems above the level of the unit receptor, and the Symposium concludes with a discussion of coding in primary receptors.

The Conference was held in the Department of Physics, University of Birmingham from 10 to 16 September, and enjoyed many facilities made available by that University through Professor O. E. Lowenstein. Dr R. W. Murray undertook the duties of Local Secretary.

I am much indebted to contributors and colleagues for their advice during the planning of the Symposium, particularly acknowledging the help of Professor J. W. S. Pringle and Dr K. E. Machin. Finally, it is a pleasure to record the help and co-operation of the Cambridge University Press in the preparation of the volume.

J. W. L. BEAMENT

*Editor of the sixteenth Symposium of the
Society for Experimental Biology*

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PROLOGUE: THE INPUT ELEMENT

By J. W. S. PRINGLE

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The function of a Prologue at a scientific symposium is, I think, to give the participants an outline bill of fare. Without knowing exactly what the speakers are going to say, he has to try to circumscribe the range of topics to be discussed and suggest how they relate to one another. This, at any rate, is what I shall be trying to do. I have no new experimental results to communicate but I do intend to put forward one or two ideas which may be new.

It is only about 40 years ago that the electrophysiological investigation of impulses in sensory nerves opened the door on the modern phase of investigation of receptor mechanisms. Before that, much had been learnt about sense organs by behavioural and subjective methods but electrical recording of impulses in sensory nerves provided for the first time a method of isolating the sense organ from the rest of the behavioural machinery of the organism and so increased greatly the exactness of analysis. From his results obtained by the use of such methods Adrian (1928) was able to formulate the principles of sensory action which provide the starting-point for most modern investigations. It is accepted as axiomatic that the impulses in sensory nerves provide the sole channel for the passage of information from sense organs to the central nervous system and that the specificity of sensory information depends on the anatomical connexions of the sensory fibres. If it is stated in this simple form there is really no evidence at all which conflicts with this doctrine, but it is now clear (Davis, 1961) that some of the widely accepted extensions of the doctrine are more in doubt. At the end of this symposium Professor Gray will be discussing this problem of the coding of information in systems of receptor neurons and we shall no doubt hear more about it from the several speakers who are talking about eyes. The point is, of course, that the information received by the organism about events in the external world is subject to elaborate processing in the nervous machinery before being used to control effector actions, and the impulses in sensory nerves which are the intermediate events which we can monitor with the greatest precision contain information which may already have been subjected to a considerable amount of processing. In other words, we fully realize now that this valuable technique of electrophysiological detection of impulses does not enable us to study

the primary processes of reception, at any rate not without a great deal of careful analysis and interpretation. Sometimes the impulse monitoring point lies near the beginning of the chain of events and sometimes it is much later; sometimes, that is, the information is passed relatively unchanged to the central nervous system and processed there, and sometimes it is processed in the sense organ itself. During this symposium we shall be considering a range of sense organs which differ very widely in this respect and the differences must be continually borne in mind when drawing comparisons.

Until about 40 years ago, the starting-point for any analytical study of sense organs was the subjective classification of sensations into the broad categories of sight, hearing, touch, etc. Then came what one may call the Sherringtonian epoch and the currency of more objective terms like exteroceptor, interoceptor, proprioceptor, based on function, or mechanoreceptor, photoreceptor, chemoreceptor, based on the nature of the stimulus. I believe we are now entering on a third phase, in which the biologist, sometimes consciously but more often unconsciously, is looking at the organism in much the same way as an engineer looks at a complex piece of machinery and has no use, except as a form of convenient shorthand, for terms of classification which imply less than a full understanding of physico-chemical mechanism. After all, we only have to give special biological names to things and processes when we cannot relate them fully to other things and events in physical and chemical science. It is for that reason that I have chosen an engineering term for the title of my introductory talk.

Most of the problems of an engineer involve the building up of complex systems with the required properties from simple, known elements. The task for the biologist is to explain the functioning of complex systems in terms of simpler elements which he has first to identify before they can be described. In both subjects the analysis of a dynamic mechanism involves the basic idea of a *sequence of control*. Information about the value of some particular parameter is fed into the system and used through a sequence of events to control some action which influences that feature of the environment. Let me now quote from the introductory chapter of an engineering textbook (Macmillan, 1951):

'The first element of the sequence is the *input element*. This feeds out information, which may be a pointer reading, fluid pressure, shaft rotation or electrical voltage signal, regarding the desired value of the controlled variable. This signal is then amplified and used to control some source of power such as a motor or other *output element*; this in turn acts directly on the load or process in such a way as to make the desired alteration of the controlled variable.' It does not require much imagination to translate this

into biological language and to identify the receptor mechanisms with which we are concerned with the input element of a control system. If, unfortunately, parts of the amplifier and the control machinery have got mixed up with the input element in some of our biological systems that is just our misfortune; organisms do not seem to have been designed so as to make it easier for the biologist to find out how they work.

I do not want to dwell unduly on this comparison with engineering practice, but before leaving it I believe there is one lesson which we can learn and which has not yet been fully appreciated by most biologists. Engineers have to be good mathematicians and they are always concerned with the quantitative as well as with the qualitative performance of their components. Biologists have not always tried to give that rather precise quantitative description of the properties of the elements into which a behavioural system must be analysed if the over-all performance of the intact system is ultimately to be understood. Certainly it is not an easy task, particularly when the identification of the element is uncertain and when its performance appears to be very non-linear. But the objective should be to describe a transfer function for each element in the control sequence, that is, an exact quantitative description of the relationship between input and output. An example will make my meaning clear. Nearly all sense organs show to a greater or less extent the property of adaptation and in some mechanical sense organs, for example the muscle spindle, the crustacean stretch receptor and the insect tactile hair (Wolbarsht, 1960), it has been possible to investigate the extent to which this is due to mechanical properties of the supporting tissues or to physiological properties of the neural elements. The adaptation curve of the sense organ as a whole is known not to be a simple exponential decline but, so far as I am aware, no one has tried to determine whether this adaptation curve can be fully and quantitatively explained in terms of the properties of the mechanical and neural elements of the sense organ. To do so would involve expressing the results in the language of an engineer rather than of a biologist. Until that has been done the analysis of the properties of the sensory element is not complete and we have to take merely the empirical determination of the adaptation curve as the information to be used in the synthesis of an understanding of the performance of the control system as a whole at the next higher level.

Accepting then that we are concerned this week primarily with the mechanism of operation of the input element of the biological control system, what are the different ways in which this element can be studied? In sense organs, energy in various forms is absorbed and used to control the output of electrical energy in the form of nerve impulses. There is a control

sequence even within the working of the input element itself and I think there is now a very generally accepted scheme for this finer analysis (Fig. 1). Working backwards from the nerve impulse it is clear that in most and perhaps all cases the all-or-none, propagated impulse is triggered by a maintained depolarization of the neuron at or near its point of origin. This depolarization can be measured either intracellularly or extracellularly as a graded potential depending on the strength of the stimulus and conducted electrotonically for a certain distance along the neuron, its cell body if present and its dendrites. Starting now from the other end, the beginning of the control sequence, it is clear that in all cases there must be a primary process of energy capture by which the external stimulus (light, chemical, mechanical, etc.) influences the biological system. Sometimes this primary process has been thought to occur in the actual sensory neuron and sometimes in accessory cells of the receptor organ and again the result of the

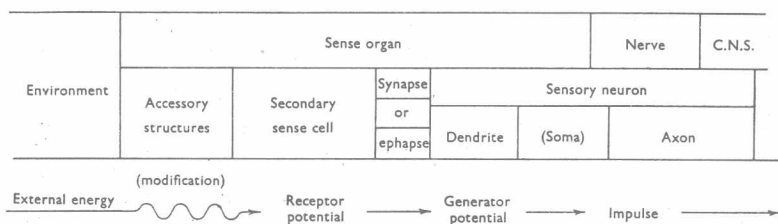


Fig. 1. Scheme for analysis of electrical events in a sense organ. (Redrawn in simplified form from Davis, 1961.)

primary process can often be detected as an electrical change. Unfortunately, there is a considerable confusion of terminology about these two sorts of electrical measurement. The two terms *generator potential* and *receptor potential* have been used by different authors to mean different things. Davis (1961) calls the potential which immediately gives rise to the nerve impulses the generator potential, and the potential immediately derived from the receptor process he calls the receptor potential. This usage appears to be the exact opposite to that of Bernhard, Granit & Skoglund (1942), who originally coined the terms, and it is certainly the opposite of that which was specifically proposed by Murray (1958) at the International Congress of Zoology and indeed earlier (Murray, 1956) in his paper on the lateral line organs of *Xenopus*. I think that Gray (1959) uses the terms in the same sense as Dr Murray so that this could become one of these transatlantic divergences. In some types of sense organ where there is thought to be no secondary sense cell forming part of the receptor mechanism, it probably does not much matter that the two terms are used

in different senses, since the potentials across different parts of the membrane of the same cell will be related electrotonically in a reasonably precise manner; but when there is a separate cell (and I shall argue later that this is more widespread than has been generally recognized) there is a danger of misunderstanding unless these terms are used carefully.

One very fundamental aspect of the study of receptor mechanisms which is not, I hope, yet confused by terminological differences is the primary process of energy capture. We shall have contributions to this aspect of the subject from Professor Wald, Dr Rushton and Dr Burkhardt in relation to visual reception and from Professor Heath, Professor Whittingham and Professor Ingold on the closely related problems of the reception of radiant energy by plants. We shall have papers from Dr Kuiper and from Drs Burt and Catton on optical problems which are closely related to this problem of the primary process of visual reception. The primary processes of chemoreception will be discussed by Professor Dethier and Professor Davies and, maybe, the primary processes of temperature reception and electrical reception by Dr Murray and Dr Machin. I am not sure to what extent those speakers who are going to talk to us about various forms of mechanoreception are going to be concerned with the primary process, but I should guess that it will form an important part of the problems to be discussed by Professor Audus, Dr Trincker and Dr Inman. At this first point in the control sequence of the receptor itself there may be little common ground between the different modalities but any common ground that there is will no doubt emerge in the course of this Symposium.

Whatever the form of the energy received and whatever the primary process of energy reception, the activity of the receptor mechanism soon manifests itself (or at any rate can be detected) as an electrical potential difference. I want to deal in rather more detail with this part of the problem and to make one or two tentative generalizations. Electrical potential differences in living organisms arise across membranes which have a considerably higher electrical resistance than the protoplasm of the cell or the extracellular fluid. Electron micrographs appear to be able to identify these membranes across which potentials arise and which, in other words, form the barriers to the movement of ions, as the electron dense lines of the unit membrane which forms the plasma membrane of the cell. There is therefore a great need for correlation between electrophysiological and electron microscopical investigations of receptors, in order to identify positively the membranes responsible for the generation of the observed potential differences. Histological observations with the light microscope are of very little use in this connexion since the membranes forming the ionic barriers are often too fine to be resolved except by the electron beam.

We are only at the beginning of this sort of combined physiological and fine structure study but I expect that we shall hear of some exciting discoveries of this sort during the week. The general point which I myself wish to make is this. We know from many studies of the fine structure of peripheral nerve that the external plasma membrane of the axon is always (that is, in so-called non-medullated as well as in medullated nerves) closely invested by the plasma membrane of the Schwann cell. Where the axon enters the sense organ, it emerges from this Schwann cell sheath but is then immediately invested by the membrane of some other type of cell. Some examples are shown in Fig. 2. The so-called free endings in the corneal epithelium are in

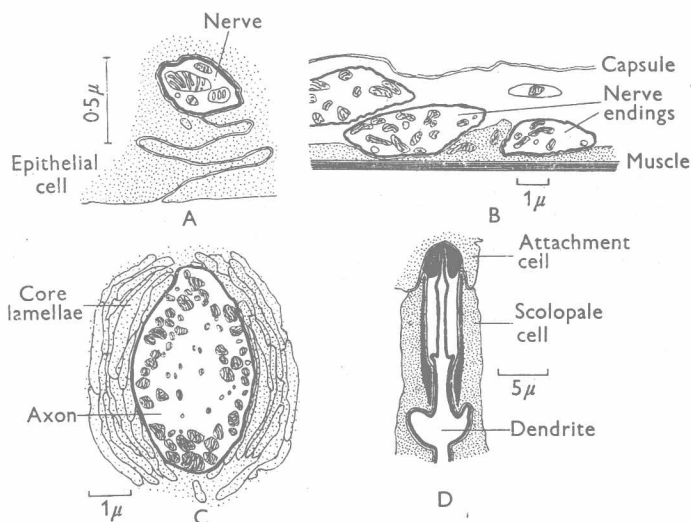


Fig. 2. Semidiagrammatic drawings from electron micrographs of four types of mechanosensory ending, to show the relationship between the plasma membranes of nerve ending and adjacent cells. A, Endings in corneal epithelium (from Whitear, 1957); B, endings in frog muscle spindle (from Katz, 1961); C, Pacinian corpuscle (from Pease and Quilliam, 1957); D, insect chordotonal sensillum (from Gray, 1961).

fact deeply embedded in the cells of the basal layer of the epithelium. The so-called free endings in the Pacinian corpuscle are in fact closely invested by the inner lamellae from the perikaryon. The endings in the frog muscle spindle are closely apposed to the membrane of the muscle fibre and otherwise enclosed in the capsule. The distal process of the sense cell in the insect chordotonal organ is invested by the scolopale cells. Is it a safe generalization to say that there is no such thing as a naked nerve ending, that, in fact, all parts of the mature neuron including its fine terminations are either invested by the membrane of another cell or, if they appear to be free, are surrounded by a specialized fluid space which in its turn is bounded

by specialized cell membranes? I wish to suggest as a hypothesis that the external surface of the functioning neuron is never in direct contact with the general extracellular fluid, and that so far as the properties of the sensory ending are concerned we have to deal either with the properties of a double membrane formed by the closely apposed surfaces of the neuron and the accessory cell, or with the properties of the neuron membrane separating the axoplasm of the neuron from a specialized extracellular space which may have a different electrical potential and a different ionic composition from that of the general body fluid. If one looks at the structure of sense organs with this idea in mind there seems to me to be less difference between different sense organs than at first sight appears. For example, it ceases to be so important whether there appears to be an accessory receptor cell there or not. In cases like the ending of the neuron in the Pacinian corpuscle, the corneal ending and the muscle spindle, where it is generally thought that the primary process of reception takes place in the dendrites themselves, we are dealing in fact with the properties of a double membrane, the axonic half of which is dominant in controlling the electrical properties. The presence of a dense concentration of mitochondria in the axoplasm suggests that this is the case, but it is not ruled out that the plasma membrane of the accessory cell may make some contribution to the total electrical and ionic permeability properties of the double membrane. In the case of the lateral line receptors, where it is known that accessory sensory cells play an important part in the over-all mechanism, we have merely a specialization of different parts of the accessory sense cell, so that the portion immediately reacting to the stimulus (the hair) is different from the portion forming part of the double membrane with the neuron cell. The measured microphonic activity of the lateral line organs is then the extracellular component of the mutual activity of sensory cell and neuron. The inner ear gives yet a further complication, where a second-order accessory tissue, the stria vascularis, contributes to the over-all operation of the receptor mechanism by establishing a specialized extracellular environment for the first-order accessory cells (the hair cells) at a positive potential with respect to the general body fluids. The mechanism of this receptor system will be discussed by Professor v. Békésy, who has done so much to give us our present understanding of it.

A type of sensory ending which appears at first sight to invalidate my suggested generalization that the plasma membrane of the axon is never free in the body cavity is the epithelial ending like, for example, the insect mechanoreceptors investigated by Wolbarsht (1960). Sensory neurons which penetrate the basement membrane of the epithelial layer often appear to have a free plasma membrane in contact with the extracellular

space surrounded by epithelial cells. I would suggest that this extracellular space outside the basement membrane is distinct from the extracellular space inside it. Electrodes placed on cut insect hairs or on the chemoreceptive hairs have always recorded a maintained potential difference across the basement membrane, usually with the external fluid positive to that in the body cavity. This system is then analogous to that found in the inner ear and the potential difference across the basement membrane, presumably maintained by activity of the epithelial cells, can act as an additional driving voltage which adds to the potential across the membrane of the axon and increases the current flow through the ending of the axon when there is a resistance change in the membrane of the axonic ending. In a mechanism of this sort it is not easy to identify a receptor potential and a generator potential, whichever way round the terms are used. If we can identify histologically the membranes across which the various potential differences arise and describe them in this way, that is surely a more satisfactory method than to try to give abstract names to the various phenomena.

It may be that a generalization of this sort has little value, or that it is too early to try to find common ground between the various receptor mechanisms. In any case I feel sure that electron microscope evidence about the fine structure of sense organs is going to make us pay more attention in future to the properties of the accessory cells at sensory endings, including tissues which have not been classed as nervous at all, such for example as the Müller cells of the retina. The recent work of Svaetichin *et al.* (1961) seems to confirm the view that closely apposed cell membranes must be considered as a single functional unit, and that current flowing inside the accessory cells is at least as important as current supposed to flow through the narrow extracellular clefts or channels between axon and accessory cell and between the different accessory cells.

Electrophysiologists have been tolerating for too long the inconsistency of their attitude to these channels, the best-known example of which, the 'mesaxon', has been so extensively reviewed by Robertson (1960). Sometimes, as with the tortuous channels between the Schwann cells of the squid giant axon, the 60 Å. space between the unit membranes is assumed to be electrically conducting (Villegas & Villegas, 1960). At other times, for example between the hair cells and the cells of the reticular lamina in the organ of Corti, a space apparently much greater than 100 Å. is assumed to be non-conducting in order to maintain the potential difference between the scala media and the scala tympani (Tasaki, Davis & Eldridge, 1954; Smith & Dempsey, 1957). It needs emphasizing (as indeed did Fränkenhäuser & Hodgkin, 1956) that the equally likely possibility must be seriously considered that the Schwann cell and other accessory cell membranes have

a much lower resistance than those of axons and that the extra-axonic current flows through these cells.

I have assumed in what I have said so far that the interaction between accessory cells and the ending of the neuron is an electrical one—either direct so that the two membranes act as a unit or indirectly by current flowing through a specialized extracellular space. The possibility also exists that some of the interactions between accessory cells and the neuron or between one set of accessory cells and another may be chemical as at the neuromuscular junction and at many synapses in the central nervous system. So far as I know there is only one experimental result which points clearly to a chemical transmission in a sense organ, and that is the recent demonstration by Ruck (1961) in the insect dorsal ocellus that there is chemical transmission between the reticular cells and the ocellar axons which, in this case, have their cell bodies in the central nervous system. In the dark there is a spontaneous discharge of impulses in the ocellar nerve fibres and this discharge is inhibited by illumination of the ocellus which produces a depolarizing response in the rhabdomere cells. The evidence for chemical transmission comes from the fact that Ruck could record irregular small hyperpolarizations at the origin of the ocellar nerve fibres which were accompanied by a temporary cessation of the impulse discharge. He points out that these irregular spontaneous hyperpolarizations resemble the miniature end-plate potentials found in muscle where they have been explained as the result of the release of quantal amounts of chemical transmitter into the junctional space. This is much better evidence for chemical transmission than that on the basis of which Fuortes (1959) postulated this mechanism for coupling of the reticular and eccentric cells in the eye of *Limulus*. There are some grounds for expecting the separation of the two unit membranes to be greater in chemically transmitting synapses than in electrically transmitting ephapses, and it would be interesting to know if a separation considerably greater than the usual 100 Å. is found in the eye of *Limulus* and the ocelli of insects.

I now turn to a different aspect of receptor biophysics where I have another general suggestion to make. Professor v. Békésy, Dr Machin and possibly some others are concerned with the problem of the ultimate sensitivity of receptors. There appears to be a real problem in understanding how animals are able to receive signals which are well below the noise level for the operation of their sense organs. I was struck some years ago by the great differences which there are in records of impulses in single sensory neurons in the regularity of timing of the impulses in the rhythmic pattern. Receptor mechanisms which are working at or near the noise level in the ending would be expected to have a very irregular discharge since, if the

sensitivity is set at a very high level, the threshold for firing will often be reached simply on the fluctuations of potential due to thermal noise (Katz, 1950). If a sensory neuron gives a very regular discharge one can therefore say that it is not set near to maximum sensitivity. I believe that one can make the following generalizations. Since it is advantageous to an animal to have its exteroceptors as sensitive as possible, the triggering mechanism in these endings will be set at maximum sensitivity and there will be the greatest irregularity of discharge. As a result either a long time or a large number of nerve fibres operated in parallel will be required for the central detection of changes in the amplitude of the measured parameter. On the other hand, proprioceptive and interoceptive endings, where there is available a large amount of energy of which only a fraction need be tapped for the operation of the sensory mechanism, are likely to be set well below maximum sensitivity so that the discharge is regular and a rapid detection of changes of intensity can be achieved with only a small number of nerve fibres. These predictions are borne out in practice. The discharge pattern in chemoreceptive fibres (Pffaffmann, 1955) and in fibres from the lateral line system (Katzuki, Yoshino & Chen, 1950) is extremely irregular, whereas impulses in fibres from muscle spindles (Matthews, 1933), ampullae of the semicircular canals (Lowenstein & Sand, 1940) and from the carotid body (Landgren, 1952) are very regular. An apparent exception are the impulses from the eye of *Limulus* (Hartline, 1935) which are as regular as any that I know, in spite of the fact that this is an exteroceptor in which one might have expected maximum sensitivity. The answer in this case is to be found, I believe, in the nature of the stimulus. The energy available in a quantum of light is so much greater than that of the thermal noise at body temperature that there is no point in setting the triggering mechanism of a photoreceptor at maximum sensitivity. This sort of functional interpretation of the difference between various receptor mechanisms does not, of course, tell us anything about the way in which triggering thresholds are set at different levels. For an understanding of this we may have to wait for much more detailed knowledge of the processes which go on in the molecular structure of plasma membranes.

Now for a Prologue I have talked for long enough. We have before us a most interesting programme and I am sure that in spite of the apparent variety we shall find many things which we can discuss in common. I will conclude with the words put by Shakespeare into the mouth of a famous predecessor in my present role

'Gentles, perchance you wonder at this show;
But wonder on, till truth make all things plain.'

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