

SYMPOSIA
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EXPERIMENTAL BIOLOGY

NUMBER IV

PHYSIOLOGICAL MECHANISMS
IN
ANIMAL BEHAVIOUR

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PREFACE

This number contains the papers read at a Symposium of the Society for Experimental Biology, which was held at Cambridge in July 1949. It is the fourth of an annual series of Symposium Reports. The Symposium for 1950 will be on 'The Fixation of Carbon Dioxide'.

The Society is deeply indebted to the Rockefeller Foundation and to the British Council for financial aid. We must also thank the British Council and the Foreign Office for assistance in making travelling arrangements for European visitors to the Symposium.

The editors wish to thank the members of the advisory committee which prepared the symposium programme; thanks in particular are due to Dr R. J. Pumphrey and Dr W. H. Thorpe. The Symposium was held in collaboration with the Institute for the Study of Animal Behaviour. We also wish to thank the Cambridge University Press for the kindness with which we have been assisted in producing this report.

J. F. DANIELLI

R. BROWN

*Honorary Symposium Secretaries
Society for Experimental Biology*

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THE RANGE OF CAPABILITIES
OF SENSE ORGANS

HEARING

By R. J. PUMPHREY

Zoological Laboratory, Cambridge

I. INTRODUCTION

Everyone will be conscious that the senses of touch and hearing are quite different in man. In fact, the differences are so many and so obvious, that definitions of tactile and auditory senses based on them lead only to confusion unless a careful selection is first made.

If the term 'hearing' is to have any place at all in descriptions of the behaviour of any animal other than man, the definition of 'hearing' must be based on primitive and persistent attributes of the sense and not on structural or functional features peculiar to man or to primates or to terrestrial animals or to any other limited category of animals. Neglect of this obvious precaution has led different authorities to definitions of hearing which are unsatisfactory because they are arbitrary and exclusive and because, in consequence, a host of new terms with arbitrary and restricted meanings have to be invented to describe sensory responses which by definition are not 'hearing' but which are nevertheless obviously related to it. Thus, for example, 'hearing' has been defined as an attribute of animals possessing a cochlea, or a tympanic membrane or the capacity of frequency analysis or the capacity to respond to air-borne vibrations. None of these definitions is inclusive and none is free from ambiguity. Moreover, all must be complemented by other terms, *Fernstastsinn*, vibrational sensitivity, phonoreception, etc., to describe sensory responses excluded by the definition of 'hearing'.

It must be agreed that both touch and hearing belong to Parker's system of mechano-receptors. The end-organs of both senses are primarily sensitive to mechanical deformation. I want to suggest to you that an absolute distinction can nevertheless be made between tactile and auditory senses. The primitive function of touch is the location of moving objects in contact with the animal. The primitive function of hearing is the location of moving objects not in contact with the animal. So we can define hearing as follows. an animal *hears* when it *behaves as if* it has located a moving object (a sound source) not in contact with it. And *sound* can be defined as any mechanical disturbance whatever which is potentially referable to an external and localized source.

This definition of hearing has at least the merit of being objective.

Hearing is an attribute whose existence in a particular case can be checked by observation. Moreover, it is consistent with our knowledge of the evolution of hearing. It is true that man is degenerate compared with many other animals in his ability to locate a sound source, and in civilized life other functions of hearing are much more important. Probably this is the reason for the reluctance of physiologists to recognize directional sensitivity to sound as the fundamental and primitive property of hearing. But it is nevertheless true that when we both hear and feel a loud sound, we feel it at the stimulated point, we hear it outside ourselves, and though we may locate it incorrectly, we do locate it. A man's first response to an unexpected sound is to turn his eyes towards the source.

I cannot refrain from a slight digression at this point, because it occurred to me only recently that a very close analogy existed between the evolution of hearing in the mammalian line and the evolution of radar during the war.

Radar, as you know, is an electromagnetic device for (a) finding a target, (b) determining its position in polar co-ordinates, i.e. by determining its distance from and its direction from a datum point which is the position of the radar installation. The accuracy of range-finding depends on irrelevant considerations which we can ignore. The accuracy of direction-finding is directly proportional to the frequency and to the size of the aerial. And because the earliest radar employed only relatively low frequencies, the directional accuracy was rather low, although the installations were huge. The evolutionary pressure was at first wholly towards the employment of higher frequencies in order to increase the accuracy and reduce the size of the outfits. And at the same time subsidiary devices were employed to cheat the disabilities of low frequencies. One of these devices consists in principle of a null comparison of the signals received on two directional aeriels which could be rotated together through a wide angle and rotated through a small angle with respect to each other. Now the earliest mammals, we believe, were nocturnal creatures with indifferent eyes which must have depended on their ears for directional warning, much as man has learned to depend on radar in bad visibility. And we can note in mammals: (i) an extension of the range of frequency sensitivity upwards far above the reptile limit, (ii) the development of directional aeriels, the pinnae, and (iii) the development of the necessary musculature and reflexes for directing the pinnae together but with some degree of independence. The nocturnal bats seem to represent the pinnacle of achievement in this line. Their upper limit of frequency sensitivity is said to be in the neighbourhood of 0.25 Mcyc./sec.

But there is a limit beyond which there is nothing to be gained by the employment of higher frequencies in a single radar installation, because as

the directional accuracy increases, the time taken to find a target in the first instance also increases inconveniently. When extreme accuracy was required, as in the control of long-range artillery, this difficulty was circumvented by the use of two sets. The first could keep a continuous all-round watch and indicate immediately the approximate direction of an approaching target. The second, the fire-control set, could then search the indicated sector, single out the target from other objects and put the guns on to it with high directional accuracy.

Now consider the evolution of the primates. At first nocturnal, the higher primates are now diurnal and, alone among mammals, have developed foveate eyes and elaborated the oculo-motor reflexes for keeping the fovea on a moving target. Such an eye has precisely the properties which we were striving to give to fire-control radar, and it suffers from the same disadvantage, that it takes a long time to search a wide solid angle. The ear has taken over the functions of warning radar, it serves to put the eye on to the target; but great accuracy is no longer needed, and the devices associated with it, the large mobile external ears, the extrinsic muscles and associated reflexes, are in a fair way to disappear.

The parallel is curiously close and, I think, illuminating. It has, I hope, given point to my argument that the primitive function of the ear was direction-finding, and that our poor performance in this respect is directly related to our diurnal habits and our perfected eyes. It would be wrong therefore to judge the auditory powers of animals (except perhaps the higher apes) by our own standards.

Consider the following examples: a female cricket moves directly to a chirruping male, an aquatic toad springs at a wriggling insect several centimetres away, an ichneumonid wasp lays eggs on a *Sirex* larva through an inch of bark and wood, a whirligig beetle detects and avoids sources of disturbance in the water-air interface, a scorpion turns towards and threatens a moving object on its substrate, a spider locates and identifies living prey in its web, a blinded fish in a water current maintains its position with respect to other fixed objects in the current, a bat avoids obstacles and catches moths in the dark. By my definition and provided stimulation in other modes can be excluded, as, in fact, it can, these are examples of hearing.

II. THE EVOLUTION OF HEARING

In any endeavour to trace the evolution of a highly specialized organ, a difficulty often arises in the application of what may be called the principle of continuity. It is repugnant to reason to suppose that eye or ear appeared suddenly in evolutionary history. Their evolution must have been a

continuous process, and there must certainly have been antecedent organs which were potential eyes and ears and which, however crude and inadequate compared with their successors, were at every stage functional. But it is often not by any means self-evident what the functions were, and in consequence there may appear to be an awkward discontinuity. In such cases it is frequently illuminating to consider what functions are physically conceivable, and then to try to relate physical inference with evidence from other sources.

Although palaeontological evidence is of little direct assistance, a fairly clear plan of the evolutionary sequence can be constructed from the wide variety of auditory structures in living animals. This is particularly true of the vertebrates. The origin of the acoustico-lateralis system is lost, but it is clear on several grounds that the labyrinth is a specialized and structurally modified part of the lateral line and not conversely. The implications of this have not always been appreciated, and it will be useful to consider them from a physical point of view, for it will, I think, become apparent that the lateral line is functionally the missing link between the tactile sense and the ears proper of vertebrates.

An aquatic animal, since it is largely composed of water, has necessarily nearly the same compressibility and density as the medium it inhabits, at least so far as its soft tissues are concerned. As a consequence the mechanical discontinuity at its boundary is far less abrupt than it would be for an animal living in air. And a body moving close to the surface of an animal in water will deform that surface to an extent comparable with the deformation produced by bare contact.

If we assume that a tactile system capable of localizing contacts already existed, it is easy to see how hearing could have begun. Moving objects very close to the surface can be localized with sufficient accuracy, merely by determination of the point of maximum stimulation.

Now consider that some moving object, let us say a wriggling worm, is moved progressively away from the sensitive surface. A wriggling worm, considered as a source of sound, is physically equivalent to a doublet. It may be represented as a sphere oscillating about a mean position without change of volume. The frequency of this oscillation is unlikely to exceed 10 cyc./sec., equivalent to a wave-length of 140 m., so that all the dimensions of the system we are considering are small compared with a wave-length. At distances greater than a wave-length from a source of sound, the displacement amplitude of particles of the medium due to the sound is inversely proportional to the distance of the source, but at distances from a doublet much less than a wave-length the amplitude is inversely proportional to the *cube* of the distance. Fig. 1 illustrates the change of

amplitude at a surface and the change of gradient along it as the distance of the source changes. It will be noted that both maximum amplitude at the point nearest to the source and the gradient along the surface fall

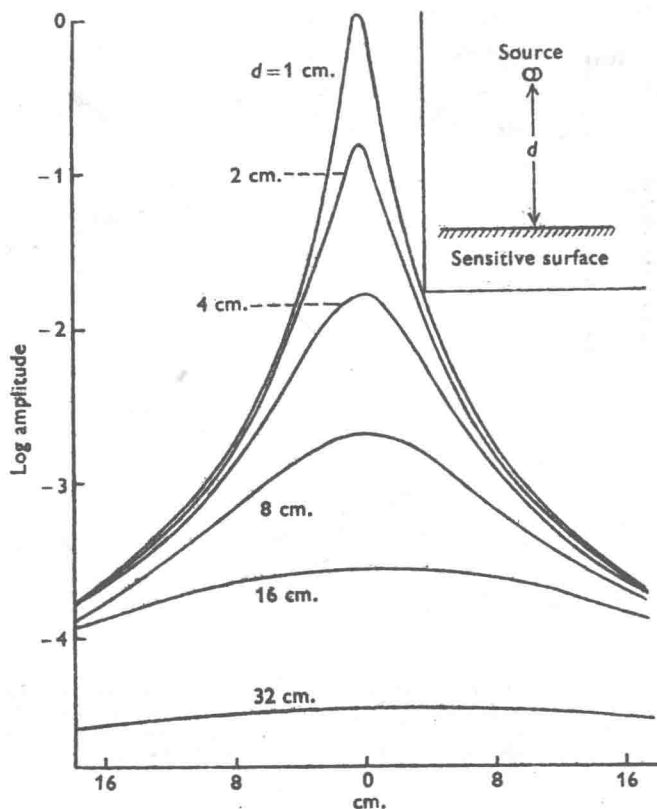


Fig. 1. The graph shows the change on the displacement amplitude along a surface for varying distances (d) between the surface and a doublet source of constant frequency and power ($d \ll \lambda$).

rapidly with increasing distance. But the source can still be located accurately if three conditions are satisfied, namely, (1) the range of sensitivity at sensitive points is sufficiently increased, (2) the extent of surface over which simultaneous comparisons of amplitude can be made is sufficiently increased, (3) the sensitivity of the most sensitive elements is sufficiently increased.

These three conditions seem to be fulfilled by the lateral line of fishes as far as is theoretically possible.

(1) The end-organs are grouped so that a considerable number of hair cells of widely different threshold are included in each group. This arrange-

ment is characteristic of *all* known auditory organs. Fig. 2 shows that in the optimum case, if there are n end-organs each of a working range m , the working range of the group is m^n . So that if a single end-organ has a working range of $30/1$ in intensity, a group of six may have a working range of $10^9/1$.

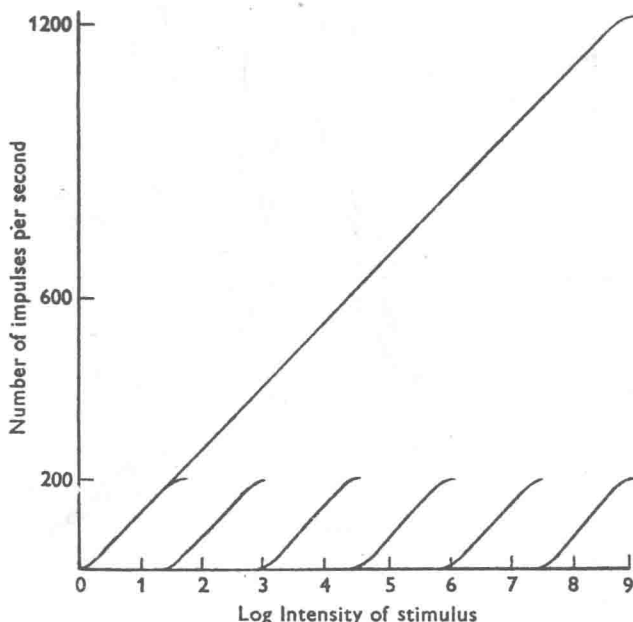


Fig. 2. Explanation in text. It is supposed that the six end-organs are independently innervated and that the afferent fibres reach a common centre in which the impulses from the group produce an additive effect. $10^9/1$ is perhaps a fair average range for auditory organs. For the human ear in the middle of its frequency band the range is about $10^{12}/1$.

(2) It is evident from inspection of a fish that the lateral-line system utilizes the whole length, height and breadth though the density of groups of hair cells varies. And unlike the tactile system which has segmental innervation, the lateralis fibres all enter the same nucleus in the medulla, so that simultaneous comparison of the degree of excitation over the whole surface is possible (Fig. 3).

(3) I have mentioned that the sensitivity of the most sensitive end-organs of the lateral-line system is extraordinarily high, so improbably high in fact, that doubt has always existed about the accuracy of estimates in the minds of those who have not actually worked on them. So a brief parenthesis summarizing recent indications about the origins of this sensitivity may not be out of place, although the story properly starts at the other end of the evolutionary scale. Gold & I (1948) have recently shown that the

selectivity of the resonant elements of the human cochlea is about two orders of magnitude higher than could reasonably be expected of a passive system. It has been known for about twenty years (Wever & Bray, 1930) that sounds impinging on the mammalian ear excite not only impulses in

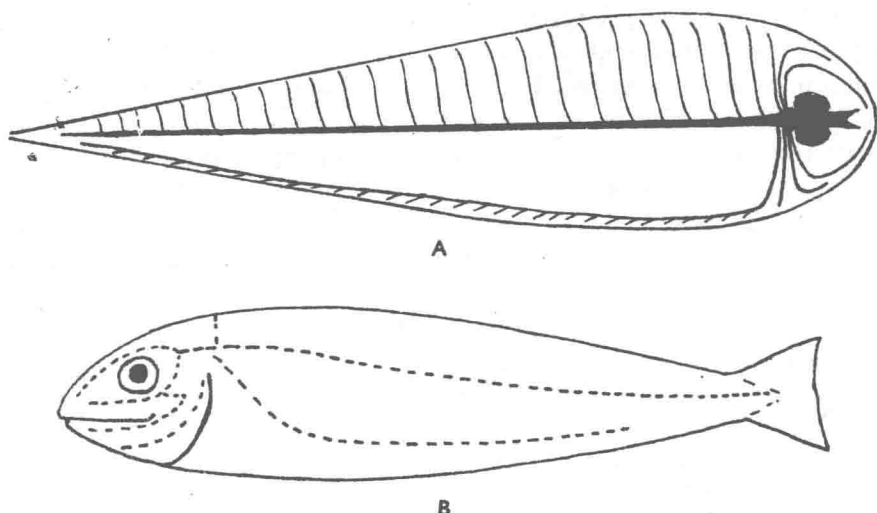


Fig. 3. Diagrams to show (A) that the lateralis system utilizes the whole available extent of the surface of a fish, (B) that, though the tactile innervation is segmental, the lateralis innervation has a common centre in the medulla, so that simultaneous central comparison of nerve signals from the whole extent of the surface is feasible.

the auditory nerve but also an additional electrical effect arising apparently from the cochlear hair cells and nowadays generally referred to as the microphonic potential. Conversely, Gersuni & Volokhoff (1936) showed that direct stimulation of the cochlea by alternating electric currents caused an auditory sensation as if the current was equivalent to an acoustic stimulus of the same frequency. Gold (1948) has suggested that these observations are consistent with the action of the cochlear hair cells as regenerative amplifiers, an action which would provide a reasonable explanation not only of their selectivity in the cochlea but of their sensitivity. (The minimum audible energy for the human ear is about 10^{-12} erg, the minimum *visible* energy is about 10^{-10} erg.) If this view is correct, my own 10-year-old observation (1939) that the microphonic potential is not, in fish, confined to the auditory part of the labyrinth acquires a new significance, as does the recent claim by de Vries (1948) that a microphonic potential can be recorded from lateral-line organs. In default of evidence to the contrary, it is reasonable to suppose that *all* end-organs of the acoustico-lateralis system are regenerative, and that their maximum sensitivity is consequently only