HEARING MECHANISMS IN VERTEBRATES

A Ciba Foundation Symposium

Edited by
A. V. S. DE REUCK
and
JULIE KNIGHT

J. & A. CHURCHILL LTD.
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Contents

Section I Structure and function of hearing organs in non-mammalian vertebrates

Section II Structure and function in mammals

Section III Afferents and efferents in the auditory nerve

Section IV Spatial localization

Section V Central mechanisms

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Symposium on Hearing Mechanisms in Vertebrates, held 26th–28th September, 1967

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The Ciba Foundation

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The Foundation's house at 41 Portland Place, London, has become well known to workers in many fields of science. Every year the Foundation organizes six to ten three-day symposia and three to four shorter study groups, all of which are published in book form. Many other scientific meetings are held, organized either by the Foundation or by other groups in need of a meeting place. Accommodation is also provided for scientists visiting London, whether or not they are attending a meeting in the house.

The Foundation's many activities are controlled by a small group of distinguished trustees. Within the general framework of biological science, interpreted in its broadest sense, these activities are well summed up by the motto of the Ciba Foundation: *Consocient Gentes*—let the peoples come together.

Preface

In this, the fourth in a series of symposia on sensory function held at the Ciba Foundation, we turn to vertebrate hearing mechanisms—having previously dealt with *Colour Vision* (1965), *Touch, Heat and Pain* (1966) and *Myotatic, Kinesthetic and Vestibular Mechanisms* (1967). Included in the volume are both formal papers, providing a survey of current research in a range of aspects of hearing in vertebrates, and the informal discussions of the papers by the group of twenty-four specialists who attended the meeting. It is hoped that this combination of the formal and informal, the factual and speculative, may give readers a perspective not only of current developments in the field but also of areas where further investigation may be most rewarding.

The Ciba Foundation is once again much indebted to Professor Otto Lowenstein, for his guidance of the meeting itself and for his continuing help over the preceding months of planning. Our thanks are also due to Dr. I. C. Whitfield for valuable advice during the preliminary stages.

Shortly after the symposium we were shocked to learn of the sudden death of one of the members, Professor Dwight W. Batteau, whose outstanding contribution and personality had made a deep impression on the meeting. We are most grateful to Dr. Sanford J. Freedman, also of Tufts University, Massachusetts, for his help in editing Professor Batteau's often highly condensed comments in discussion, and also for reading his paper in proof.

CHAIRMAN'S INTRODUCTION

Professor O. Lowenstein

This is the fourth in the Ciba Foundation's series of symposia on sensory function, and the third on mechanoreceptive mechanisms, a fact which should assure us of the great importance of mechanoreception. It is curious that whereas there has been hardly any difficulty in defining "vision"—when we talk about vision everybody, quite naturally, knows that what is being discussed is something performed by the eyes and what is being perceived is light—when we come to hearing, unfortunately the history of the subject has turned out differently, and the literature is full of often rather meaningless disputations about what is "hearing". Very often one finds circular definitions, such as "hearing is the perception of sound", and when one wonders what sound is, one is told that sound is what is perceived by the ears. I fervently hope that this sort of scholastic dispute will be avoided during the present meeting. Let us be naïve and take hearing at its face value. I know that this will not be completely possible, because contributors dealing with hearing in fish will have some difficulty in proving that what they are studying is in every instance genuinely hearing. However, the less arguing about the concept of hearing, the better, I feel.

We shall begin quite fittingly with an account of hearing in fish. However much emphasis we may finally place on the mechanism of hearing as found in the mammalian ear, we must never lose sight of the comparative aspect, a thread which has run through all three of the earlier symposia. From hearing in fish we shall follow the great adventure of life in its emergence on to dry land and the adaptations connected with terrestrial existence. Then, with the exception of a paper on hearing in birds and one on orientation through sound in fish, the rest of the symposium will be devoted to mammalian hearing, fittingly culminating in contributions dealing with central nervous phenomena. This in outline is the scope of the symposium which now follows.

SECTION I

STRUCTURE AND FUNCTION OF HEARING ORGANS IN NON-MAMMALIAN VERTEBRATES

HEARING IN FISH

Per S. Enger

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For the purposes of presentation the topic of hearing can conveniently be divided into descriptions of (1) The range of sound frequencies perceived by the animal, and the auditory thresholds; (2) The power of pitch discrimination; and (3) The ability to determine the direction of a sound source. (The last topic will not be discussed here, since Professor Kleerekoper will present a paper on orientation through sound in fish; see p. 188.) A presentation of hearing in aquatic animals, however, should start with a discussion of the acoustic stimulus and the so-called near-field and far-field effects.

NEAR-FIELD AND FAR-FIELD

In reports of sound perception in fish there has been some disagreement and controversy about the auditory stimulus (cf. Harris and van Bergeijk, 1962; Dijkgraaf, 1963*a*), simply because the physical parameters of this stimulus have been unknown or at least not fully understood. Harris and van Bergeijk (1962) clarified some of these difficulties in an important study of the lateral line organ and introduced the terms near-field and far-field. In short, an underwater sound source produces two effects: one is a compression and rarefaction of water particles—that is, a change of pressure; the other is a displacement of water particles around the source. The pressure changes represent the actual propagated sound wave whose pressure amplitude decreases linearly with distance, whereas the displacement amplitude of the near-field decreases with distance to the second or third power. In the case of a spherical, pulsating sound source, the relation between far- and near-fields is given by the equation

$$d = \frac{p}{2\pi f \rho c}\left(i - \frac{\lambda}{2\pi r}\right)$$

where d = displacement amplitude, p = sound pressure, f = frequency, ρ = density, c = sound velocity, λ = wavelength, r = distance from sound source, $i = \sqrt{-1}$ (meaning a 90° phase shift). The propagated sound wave obeys the equation $d=p/2\pi f\rho c$ and the factor $\lambda/2\pi r$ is the correction for near-field displacements. It can be seen that for low frequencies in particular, the near-field effect extends for a considerable distance from the source. For example, for 100 Hz the wavelength is 15 m. and at 2·4 m. distance the displacement amplitudes of the two effects are equal.

Harris and van Bergeijk (1962) did not study sound reception in fish, but pointed out the difficulties one might encounter in such studies. Most experiments on hearing in fish have been performed in relatively small tanks and therefore the acoustic stimulus from an underwater speaker has been a mixture of far- and near-field effects. Inasmuch as the sound pressure is the physical parameter measured with ordinary hydrophones, the distance between the fish and the underwater loudspeaker also becomes a parameter in the auditory stimulus under such circumstances. The total displacement amplitudes at threshold, however, calculated from the formula given, are independent of distance (Olsen, 1965; Enger, 1966).

The near-field effect can stimulate the lateral line receptors and also the auditory receptors directly. The far-field effect can stimulate auditory receptors through the swim bladder, which is caused to vibrate. The net effect in both cases is a displacement of the auditory receptors.

In tanks of a reasonable size there is only one way of avoiding the near-field effect for low frequencies, namely by producing the sound in air (Parvulescu, 1964) in such a way that the aquarium is inside a closed chamber in which the loudspeaker diaphragm constitutes part of the wall. Increased (or decreased) pressure in the air will immediately produce increased (or decreased) pressure in the water in the aquarium.

Enger (1966), using this information from Parvulescu, found considerable differences in pressure thresholds in goldfish exposed to sound from a water loudspeaker and an air loudspeaker, respectively, but the experimental conditions were far from ideal. The system was "open" instead of "closed", so that sound in air was not necessarily transmitted as sound pressure to the water, but could produce displacement on the water surface. In spite of the technical short-comings, there was a clear indication that displacement is a better parameter than pressure in determinations of auditory thresholds.

Jacobs and Tavolga (1967) were closer to creating a pure sound pressure, but the lowest auditory threshold obtained was about the same as that found by Enger (1966), namely about −40 db re 1 μbar at 1,000 Hz. However, for low frequencies (below 800 Hz) they found considerably lower thresholds than did Enger.

In order to avoid using small aquaria, the acoustics of which are little understood, Enger and Andersen (1967) performed some experiments at sea. Reflections from aquarium walls and standing waves can thereby be avoided and, most important, free field acoustic conditions can be obtained. Through implanted electrodes, saccular microphonic potentials were recorded. The fish was held at distances of up to 10 m. from an underwater loudspeaker—that is, in the acoustic far-field. In the codfish (*Gadus morrhua*) —which has a swim bladder—the potential amplitude was clearly a function of sound pressure and not of distance, implying that the swim bladder transforms pressure into displacement. In the sculpin (*Cottus scorpius*)—which lacks a swim bladder—the amplitude varied with distance as well as with pressure, but beyond 1 m. distance no microphonics could be recorded at all. The conclusion drawn from this has been that the swim bladder in teleosts is essential for hearing in the acoustic far-field.

SOUND FREQUENCY RANGE AND AUDITORY THRESHOLDS

The range of sound frequencies perceived by fishes has been determined for a large number of species. As far as hearing was concerned, teleosts were previously put roughly into two major groups: (1) The Ostariophysi, perceiving frequencies up to several thousand Herz; and (2) The non-Ostariophysi, perceiving frequencies up to 1,000 Hz. The former group comprises the Cyprinidae, Characinidae and Siluridae, and the basis for their well-developed sense of hearing is the so-called Weberian ossicles connecting the swim bladder to the labyrinth. Vibration of the swim bladder, due to the passage of sound, will then be directly transmitted to the ear. The extirpation of the malleus of the Weberian ossicles reduces the sensitivity by 30–40 db (Poggendorf, 1952) in the catfish, and mutilation of the swim bladder reduces the sensitivity by 13 db at low frequencies (330–750 Hz) and by 30 db at high frequencies (1,500 Hz) (Kleerekoper and Roggenkamp, 1959). The few audiograms published for ostariophysid species show that their lowest threshold is for frequencies around 1,000 Hz at an intensity of about -40 to -45 db re 1 μbar. These values were determined and found to be the same whether the fish was within the acoustic near-field (Poggendorf, 1952; Enger, 1966) or the far-field (Jacobs and Tavolga, 1967). This value was roughly 20 db higher with the fish in essentially a pure near-field (Weiss, 1966).

Among the non-Ostariophysi the situation is not quite as clear as stated above. Very many species no doubt respond to frequencies below 1 kHz only, but some species with swim bladder extrusions contacting some part of the labyrinth (Sparidae) can perceive frequencies up to 1,250 Hz (Dijkgraaf, 1952). Tavolga and Wodinsky (1963) also obtained responses to higher frequencies than 1 kHz in several species, but found no systematic relation between a close swim bladder–ear connexion and perception of relatively high frequencies, and the converse situation. Thus, the auditory threshold of *Holocentrus ascencionis* which has a swim bladder–ear connexion, is higher than that of *Equetus*, which has no such connexion. The lowest thresholds in most non-ostariophysids are found for frequencies below 500 Hz, although there are species with 600–800 Hz as their best frequency range. The accuracy of the threshold values reported for low frequencies, however, is probably poor. First of all, the near-field effect must have been rather pronounced in most experiments and therefore large variations in the threshold determinations in different reports are to be expected. Secondly, individual differences in auditory sensitivity among several specimens of the same species may be 10–20 db or even more for frequencies below 300 Hz (Tavolga and Wodinsky, 1965). Thirdly, threshold values depend on the duration of the stimulus. In goldfish, the threshold is found to be lowest for continuous tone stimulation (Offutt, 1967), but this does not necessarily have to be so for all fish. (Incidentally, this is in contrast to man, whose threshold for a series of tone pips is lower than for a continuous tone.) Finally, the threshold varies with the background noise. Nelson (1966) reported that an increase in the background noise by 20 db resulted in a corresponding rise in the auditory threshold of the lemon shark (*Negaprion brevirostris*).

Species in which the ear is more or less surrounded by air-filled cavities do perceive considerably higher frequencies than most other non-ostariophysids. Thus, the Mormyridae perceive tones of pitch up to 3,100 Hz (Stipetic, 1939), and the Anabantidae up to 4,700 Hz (Schneider, 1942). There is still another group of fish, the Clupeidae, which on anatomical grounds have long been suspected of possessing a relatively acute sense of hearing. In these fish a thin duct from the swim bladder expands into two air-filled bullae close to each labyrinth (Tracy, 1920; Evans, 1932; Wohlfahrt, 1936). The anterior one, the pro-otic bulla, is aimed directly at the sensory epithelium of the utricle. A membrane in this bulla separates the air from the endolymph, and pressure changes produced by sound would presumably cause the membrane to vibrate. Recently, Enger (1967) published a tentative audiogram for the herring (*Clupea harengus*) based on recordings of the nervous activity in auditory neurons in the medulla oblongata. The threshold is probably low (less than − 20 db) for frequencies up to about 1,200 Hz, after which it increases rapidly, but nervous responses were obtained for frequencies up to 4,000 Hz at moderate intensities.

All reports on hearing in teleosts support the notion that some kind of air bubble enclosed within the animal greatly improves hearing, and perhaps is even necessary to make hearing possible in the acoustic far-field.

Although a swim bladder or some other air-filled cavity may be the most effective transducer in the perception of underwater sound, it is not the only way propagated underwater sound can be received. Elasmobranchs have no swim bladder, but there are numerous reports of the perception of sound in these fishes. Thus, Kritzler and Wood (1961) trained bull sharks (*Carcharhinus leucas*) to respond to pure tones and obtained responses in the 100–1,500 Hz frequency range, with the lowest threshold for 400–600 Hz. The distance between fish and loudspeaker in these experiments was approximately 6 m., meaning perhaps that the fish detected far-field sound waves. More convincing in this respect are later publications (Nelson and Gruber, 1963) where sharks are reported not only to hear low frequency pulsed sounds at distances beyond 15–25 m., but also to detect the direction of the source. Observations from aircraft (Nelson, 1966) showed that sharks detected and orientated to sounds in the acoustic far-field from distances as great as 600 feet.

Auditory thresholds obtained are fairly high (above 1 μbar), except in the report of Kritzler and Wood (1961), and there is good evidence that in spite of the sharks being in the acoustic far-field, the displacement rather than pressure is the stimulus for the receptors (Banner, 1967).

Whether the lateral line organ responds to low frequency auditory stimuli in the far-field (which might be suspected, since these fish orientate in the acoustic far-field) is not known. Dijkgraaf (1963*b*) found in the dogfish (*Scyliorhinus caniculus*) that the inner ear was responsible for the detection of a tone of 180 Hz. His experiments were performed in the near-field, but it may well be that the difference in acoustic properties between water and cartilage is sufficient for elasmobranchs to detect low frequency sound in the far-field as well.

PITCH DISCRIMINATION

Studies on the power of pitch discrimination in fish are rather few. Among the Ostariophysi, Stetter (1929) found minnows (*Phoxinus laevis*) able to discriminate two tones an octave apart (100 per cent frequency difference) and in one case even a minor third apart (19 per cent). These values are for absolute pitch, since the fish in these conditioning experiments was not presented with the two tones in immediate succession, but had to "remember" the first tone for some time before the next one sounded. Wohlfahrt (1939) investigated relative pitch discrimination in minnows and found it to be about 6 per cent for tones around 1,000 Hz.

Dijkgraaf and Verheijen (1950), using a better technique, found these fishes able to distinguish two tones differing in pitch by 3 per cent in the 400–800 Hz range. With the same method, Dijkgraaf (1952) found the best pitch discrimination for non-ostariophysids to be 9 per cent. For elasmobranchs, the only report known to the present author is that of Nelson (1966), who found discrimination ability in lemon sharks (*Negaprion brevirostris*) to be half an octave or a little better in the 40–60 Hz range. This refers to absolute pitch, however, since the time-interval between the presentation of the two tones was about one minute.

For animals which have no obvious morphological frequency analyser such as a cochlea, this accuracy in pitch distinction is certainly quite remarkable. One can think of two possible mechanisms for pitch discrimination in these animals; either that a synchronization between sound frequency and the frequency of impulse discharge takes place, or that different sensory units respond to different sound frequency ranges. The first possibility was formulated by Wever (1933) in his so-called volley theory, and in recordings from the elasmobranch nerve the impulse discharge is indeed synchronized with the sound (Lowenstein and Roberts, 1951). The second possibility implies that some kind of frequency analyser is present after all, and Enger (1963) showed that even in fish this possibility cannot be excluded. An analysis of the nervous activity of single auditory neurons in the sculpin (*Cottus scorpius*) revealed four types of neurons, classified according to their spontaneous activity, but at the same time with different properties in respect of their responsiveness to sound: (1) Units with a regular spontaneous discharge did not respond to sound stimulation. This agrees well with the results of Lowenstein and Roberts (1949, 1951), who found that labyrinthine neurons (in the ray, *Raja clavata*) with a regular spontaneous discharge responded to positional changes, but not to vibratory stimuli. (2) Units with no spontaneous discharge responded to low frequencies only (below 200 Hz). (3) Units with an irregular spontaneous discharge pattern responded to all frequencies which the animal presumably can hear. (4) Units with a burst-like spontaneous discharge responded to sound frequencies up to around 300 Hz with a discharge characterized by being synchronized with the stimulating sound and without showing any adaptation.

There is no indication that any frequency analysis is taking place by, for example, the lagena and sacculus covering different sound frequencies. All types of units were found in these two structures as well as in the utriculus. This is in contrast to the situation in rays, in which no sound responses were recorded from the lagena (Lowenstein and Roberts, 1951).

Units of type (4), and to a certain extent also of type (3), support the volley theory insofar as pitch discrimination is concerned. On the other hand, a comparison of the information received by the central nervous system through neurons of type (2) and (3), respectively, should give a rough discrimination of frequency regardless of the eventual information received by the synchronization between sound frequency and discharge rate. From these results one would expect frequency distinction in the sculpin to be at its best for frequencies below 200 Hz, fairly good between 200 and 400 Hz and virtually absent above 400 Hz. Data from conditioning experiments on *Gobius niger* (Dijkgraaf, 1952) compare well with these expectations, inasmuch as the discriminating ability is 9 per cent around 150 Hz and 12 per cent for 300 Hz. In *Sargus annularis*, which is responsive to higher frequencies than *Cottus scorpius*, the values reported are for 150 Hz, better than 9 per cent; for 300–450 Hz, 15 per cent; and for 600 Hz, over 30 per cent.

SUMMARY

An underwater sound source produces a propagated sound pressure wave and a local water displacement. The latter can stimulate auditory receptors directly and will at close range interfere with determinations of sound pressure thresholds. Perception of propagated sound is accomplished by air bladders or vesicles in teleosts. A swim bladder will undergo volume changes in response to pressure changes. These volume changes produce local particle displacements which in turn stimulate the auditory receptors.

Species having a chain of ossicles connecting the swim bladder to the labyrinth (Ostariophysi) perceive frequencies up to at least 4,000 Hz. Non-ostariophysids with air cavities close to the labyrinth (Mormyridae, Clupeidae) have an upper limit of 3,000–4,000 Hz; other non-ostariophysids have upper limits ranging from less than 1,000 Hz to 2,000 Hz. Teleosts without a swim bladder are perhaps unable to perceive propagated sound. Elasmobranchs do hear propagated sound although air-filled body cavities are lacking.

Pitch discrimination in fish may be as good as 3 per cent. The neurological basis for this is in part a frequency analysis taking place in the peripheral auditory system. Not even in fish, therefore, is pitch discrimination based solely on discharges in auditory nerve fibres having the same frequency as the stimulating sound.

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DISCUSSION

Fraser: Dr. Enger, you have shown that the Ostariophysi which have a swim bladder seem to have a better perception of sound than those non-Ostariophysi which do not have a swim bladder. Is it not a question of the opportunity of transferring a molecular vibration into a molar vibration on going from water into air that gives the better performance in the Ostariophysi?

Enger: The difference between the Ostariophysi and non-Ostariophysi is that the former have a swim bladder *and* a chain of ossicles connecting it to the inner ear, which compare functionally to our middle-ear ossicles. The non-Ostariophysi have no such connexion but they may have swim bladders.

An ostariophysid of course has a good mechanism for transferring vibrations of the swim bladder to vibrations of the endolymph of the inner ear. A non-ostariophysid with a swim bladder is still not at a complete loss, because vibrations of the swim bladder produce a secondary near-field effect which goes through the tissues of the fish and also to the auditory receptors. That is how I see it. Without a swim bladder you may be in difficulty, and from the data presented here I think you will agree that sound perception in the far-field is impaired, to say the least. On the other hand, sharks have been shown to perceive sound in the far-field, but it was concluded that in these fish also the actual stimulus is displacement or shearing and not pressure (Nelson, D. R. [1966]. *Diss. Abstr.*, **27**, no. 1); there is no pressure receptor.

Fraser: Among the non-Ostariophysi you mentioned the Mormyridae which have air spaces in the labyrinth, which again indicates that it is better to have an air space than not to have one.

Enger: Yes. And of course the closer this air space is to the labyrinth, the stronger are the near-field effects, so that when you get right next to the sensory cells, the displacement will produce large effects on them.

Lowenstein: When you recorded the saccular microphonics, Dr. Enger, where exactly were the electrodes implanted?

Enger: The electrodes were rather thick (0·1 mm. diameter) and they were placed between the saccule and the brain, but not so far ventrally as to destroy the sensory cells.

Lowenstein: Secondly, did you try tilting the fish to see whether the units which did not respond to sound were sensitive to changes of position?

Enger: No: my set-up did not allow that.

Schwartzkopff: The microphonics that you recorded showed the double wave very clearly, which has also been seen in the lateral line system. My co-worker Miss B. Grözinger and I ([1967]. *Naturwissenschaften*, **54**, 446) found the same to be true occasionally even at midbrain level, which means that this double response goes up through the neural pathways and is not only a microphonic effect from the periphery. We have no explanation for this but we would like to know more about it. We have considered the possibility that one could influence the double wave by tilting the fish, but we have not done experiments to this effect. We thought that by changing the position of the fish, vestibular effects might come in and one or other part of the auditory events might become stronger. Have you any ideas about that?

Enger: Not really. But one can change the relative amplitudes of the two components of the microphonic response very much, for example by touching the receptors. The microphonic potentials from fish can be completely sinusoidal, yet the frequency is double that of the stimulating sound. On the other hand you can also get different distorted wave-forms with a fundamental frequency equal to that of the stimulus. I am surprised that you can record these double potentials in the brain, but of course with sinusoidal stimulation, in fish as in other animals, you can have two spikes on each wave, if the sound intensity is high enough.

Schwartzkopff: We certainly found the double spikes on these waves, though not at very high intensity, and they change with the relative amplitude of the wave. However, this is not a microphonic in the sense of being produced by the hair cells, but some potential of the nervous brain structures which is not exactly sinusoidal, but shows two peaks and spikes may appear on top of both peaks, or sometimes only on one.

Tumarkin: Å. Flock ([1964]. *Acta oto-lar.*, Suppl. 199) also found in the lateral line organ that the microphonic had double the frequency of the stimulus. He related this to the fact that alternate hair cells are orientated in opposite directions, so that a displacement that hyperpolarized one would depolarize the other, and *vice versa.* He confirmed this by recording the effect on the microphonic of a static displacement of the cupula. This would appear to be exactly the experiment that Professor Schwartzkopff suggests. A. Zalin ([1967]. *J. Lar. Otol.*, **81**, 119–135), discussing the function of the hair cell, has suggested that the kinocilium is a true motile organ exactly as it is elsewhere and that its function is to bias the stereocilia so as to set up a resting discharge. This would explain the double microphonic and also the effects produced by static displacement of the cupula. I would go further and suggest that the hair cells may turn out to be coupled in pairs so that they act in push-pull. This might considerably improve not only sensitivity but also directionality.

Lowenstein: In the sacculus of all the forms I have seen (cyclostomes and elasmobranchs), the hair cells point in two opposite directions (see also Wersäll, J., Gleisner, L., and Lundquist, P.-G. [1967]. *Ciba Fdn Symp. Myotatic, Kinesthetic and Vestibular Mechanisms*, pp. 105–116. London: Churchill). There are always two populations, divided by a midline, and it is quite likely that the two peaks are created by the two populations responding alternately.

Batteau: Dr. Enger, I was interested to learn that you feel that displacement is the dominant stimulus, rather than pressure, because my colleagues and I at Tufts University have looked at the problem of sensing pressure and have found that biochemical reactions are very insensitive to pressure—as opposed to temperature, for example. We suggested that if there was shear, produced by pressure gradients or motion, the strong forces produced by the shearing of surfaces would be sufficient to disturb the biochemical rates, whether they be shifts in energy levels or actual reactions. I did not then know anything about the actual structure, and I would be very interested if it is so constructed that shearing is produced in the sensory regions.

Lowenstein: Shearing is apparently the *only* stimulus that affects the hair cells. My slight bewilderment has always been in connexion with this question of pressure *versus* displacement as the stimulus, because I do not know of a pure pressure receptor. There is always displacement in the last instance.

Fex: Since we do not actually know what the mechanical transducer is, at what level do we speak about the shearing force as the *critical* force? We do not know where it is critical that something changes.

Lowenstein: It is at the hair cell itself, which has processes—one kinocilium with a root, and a group of stereocilia. There are ancillary structures over the hair cell, either otolith organs or cupulae, which undergo displacement, and the shearing force then acts somewhere at the base of the hair processes. So the shearing force acts right at the point where transduction must begin.

Fex: We do not really know that transduction does begin at the base of the hair processes.

Lowenstein: This is surmise, but the mechanical events certainly involve the bases of the hairs and therefore it is plausible that mechano-electric transduction begins there. In the organs of dynamic and static equilibrium shearing forces are bound to act on the bases of the cilia.

Hallpike: Dr. Enger, have you any idea to which half-cycles of the sinusoidal sound stimulus the evoked action potentials correspond?

Enger: I do not know.

Schwartzkopff: They respond to both; we found a double response.

Enger: In your case, yes, but I found a discharge rate corresponding to the frequency of the sound. The spikes were phase-locked to the sound waves, but I do not know to which half-cycle.

Johnstone: Recent work of Furukawa (Furukawa, T., and Ishii, Y. [1967]. *Jap. J. Physiol.*, **17**, 572–588) in the goldfish might throw light on this. He was able to record intracellularly from giant primary nerve fibres to the macula which multiply innervate hair cells. The macula is divided into hair cells which have different directional sensitivity; their kinocilia point in opposite directions. A certain number of the nerve fibres branch and innervate cells pointing in both directions. He records intracellularly from them; hence he can pick out the microphonic and postsynaptic potential. It is also possible to bias the whole mechanical system by putting a collar around the animal's head and increasing the pressure on one side or the other.

He obtains microphonics of three kinds, depending upon where the nerve that he is recording from terminates. Some nerves give responses for the positive half-cycles of pressure, some for the negative half-cycles, and some give responses for both—that is, twice per cycle. Hence it is possible to obtain action potentials at double the input frequency.

A nerve that gives single spikes goes wholly to one side or the other. Those that give double the input frequency go to both sides. For such a nerve, the response can sometimes be changed to a single-frequency type by compressing or decompressing part of the fish.

Engström: In the maculae of most mammals there are at least three separate regions, one in the striola region and one on each side of this, which all seem to have different morphology (Lindeman, H. [1968]. *Acta oto-lar.*, in press). It would be most interesting to know what can be recorded from the striola region; whether a small population of exceptionally sensitive cells can be found there, or of cells with a different kind of response. Also on the cristae ampullares, at the top of the crest there is a population of exceptionally richly innervated sensory cells.

Davis: I am glad that the concept of the "sensory unit"—the single nerve fibre and the receptor transducer mechanisms which excite it—has already been introduced, because this is the fundamental concept for analysing the activity of the ear and the laws of its sensitivity to differences of frequency and intensity. For example, the overall threshold is the envelope of the response areas of the different sensory units.

I want to call attention to the fact that for a single sensory unit there is a relation between frequency and intensity that describes its sensitivity; the curves that bound the response area are sloping curves. It becomes an interesting question whether the important change in the acoustic stimulus should be considered as a change of frequency or a change of intensity. The important point is that it crosses a contour. I would like to know whether the effective percentage difference in intensity at a single frequency has been investigated in fish. If we want to be anthropocentric, we can ask how the fish hears a change in sound. Does it perceive the change as a difference of frequency, meaning some different *kind* of source, or simply as a difference of intensity, meaning a changing intensity from the *same* source?

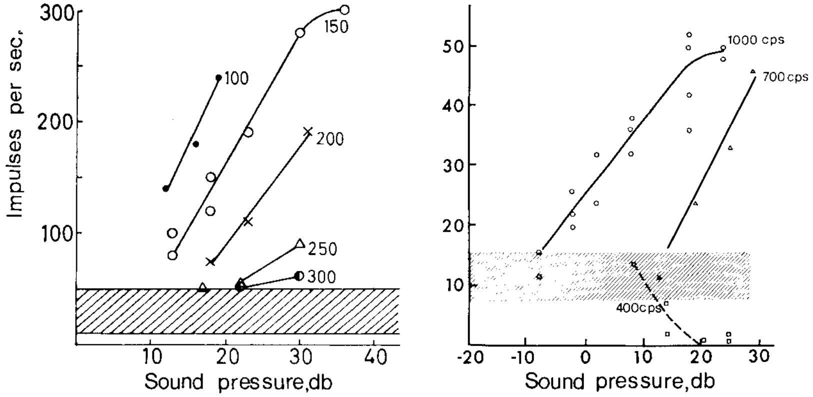

FIG. 1 (Enger). Plots of intensity (sound pressure) against number of impulses per second, for single units from the sculpin (*Cottus*; left) and the herring (*Clupea harengus*; right).

Enger: In my experiments the thresholds of single units were estimated for different sound frequencies by plotting the intensity (sound pressure) against the number of impulses. In Fig. 1 (to the left) are shown data from *Cottus*. For a given sound pressure there was a certain discharge rate for a given frequency, and this discharge rate falls as the sound pressure is decreased.

The crossing points between the curves and the level of spontaneous activity are what I estimated as thresholds. For 300 Hz this is some 20–25 db; for 150 Hz it is around 10 db. The right half of the figure gives data from the herring (*Clupea harengus*) (Enger, P. S. [1967]. *Comp. Biochem. Physiol.*, **22**, 527–538), probably from the second-order auditory neurons, and again the threshold depends on the frequency. For 1,000 Hz the estimated threshold is −8 db, for 700 Hz, +14 db. For 400 Hz it is also +14 db, but estimated as a threshold for inhibition. What I am pointing out is that even in this primitive ear, the fish ear, there is a possibility of peripheral frequency discrimination, but I also think that more work should be done in fish on the spectrum or critical bandwidth, as we know really nothing about that. We know only the sinusoidal frequency ranges, and nothing about the envelopes.

Lowenstein: Dr. Davis, would you find it easy to imagine that absolute pitch discrimination—remembered pitch on consecutive occasions (the minor third is the best a minnow can do in this way)—is possible on a memory of intensities?

Davis: Definitely not; this is very good evidence that there is frequency selection. The response depends on which unit or group of units is being activated. My intention was to bring out just this point.

Schwartzkopff: I could add a little information in answer to the question posed by Dr. Davis. Miss B. Grözinger has studied the intensity function at different levels of the fish's brain, and in some cases, in the midbrain, the intensity slope was less pronounced than at the level of the lower centres, which is opposite to what Katsuki reported in higher vertebrates. We therefore do not feel that intensity becomes better evaluated at higher levels of the brain. If any difference exists, it is worse at higher levels because there is less discrimination. Certainly we have never found better transformation. (See Grözinger, B., and Schwartzkopff, J. [1967]. *Naturwissenschaften*, **54**, 446; Grözinger, B. [1967]. *Z. vergl. Physiol.*, **57**, 44–76.)

On the question of frequency differentiation, we failed to find evidence of this, but perhaps this was because, working in the tench, we could only occasionally hold units. In about a dozen different places in the brain we found auditory activation but only one of these, in the medulla, showed different frequency contours with a maximum at 300 cyc./sec. Generally, for a certain auditory area or auditory fibre bundle, we found almost identical envelopes, which in the tench had a maximum at about 600 cyc./sec. We supposed that this one maximum at 300 cyc./sec. might have come from the lateral line, or from one of the parts of the peripheral organ which we cannot discriminate, but according to your experiments, it would not be expected to come from the peripheral organ—that is to say, not from the lagena.

Spoendlin: Dr. Enger, if you find different central units responding to different frequency ranges in fish, do you find them mixed throughout the whole nerve or are they arranged according to topographical principles, as for instance in the acoustic nerve of mammals?

Enger: I cannot answer that, because I cannot say whether particular units are on the top of the nerve or deep in it.

Bosher: Some work at Princeton University (Weiss, B.A. [1966]. *J. aud. Res.*, **6**, 321–335) seems to show that 100 cyc./sec. stimulation may be of importance for fish, and I was interested to note that in the present investigation such low