MECHANISMS FOR DIRECTIONAL HEARING IN THE SEA CATFISH (*ARIUS FELIS*)

By WILLIAM N. TAVOLGA*

Department of Biology,
City College of the City University of New York,
and Department of Animal Behavior,
American Museum of Natural History, New York

SUMMARY

The marine catfish (*Arius felis*) uses directional hearing for the acoustical detection of obstacles, and is primarily dependent on the vector components of near-field acoustics. Directional sound, detected as lateral line action potentials, produces the strongest response on the side toward the stimulus. Responses are maximal in the 50–150 Hz range. The swim bladder is asymmetrical as a sound generator (7 dB front-to-back ratio). As a sound receiver, the swim bladder is even more directional (24 dB front-to-back ratio at 100 Hz). It is concluded that directional response to sound in fishes can involve the interaction of at least two mechanisms, in this case the lateral line and the swim bladder.

INTRODUCTION

Sound production by the estuarine sea catfish, *Arius* (= *Galeichthys*) *felis*, has been described and is well known (Breder, 1968; Tavolga, 1962). Recently, however, a function has been ascribed to these sounds which is unusual for fishes. Reflexions and reverberations from nearby obstacles were found to interact with the sound output, so as to create changes in timbre (Tavolga, 1971 a). Since the sounds and their harmonics are well within the hearing range of the catfish, it was suggested they could be used in a form of echolocation. Observations of the behaviour of blinded and muted individuals swimming through plastic mazes further demonstrated acoustical orientation in this species (Tavolga, 1976 a).

The next question concerns the mechanisms by which these animals localize sound images. This question is part of the larger problem of directional hearing in fishes (Popper & Fay, 1973; Tavolga, 1971 b, 1976 b). There are two pathways available to fish for obtaining acoustic directional information: the lateral line and swim bladder-inner ear complex. The present study attempts to evaluate the amount and quality of information available through the two pathways during the course of sonic obstacle detection in this species of catfish.

* Present address: Mote Marine Laboratory, Sarasota, Florida.

The lateral line pathway

Van Bergeijk (1964) suggested that only the lateral line system, being an array of displacement sensitive sensors, could provide directional information within the near-field. More recent studies, however, have shown that it is possible for the inner ear mechanism in fish to respond to the directional acoustic energy (Schuijf & Buwalda, 1975). In either case, it is the vector component (i.e. displacement or velocity) of near-field acoustic energy to which either system must respond. It is also evident that the catfish acoustical orientation is dependent upon the obstacles being well within near-field range.

Although van Bergeijk (1964) provided a theoretical model, there is little experimental evidence of directional hearing through the lateral line. The experiments reported here were designed to discover whether the lateral line system can respond differentially to directional acoustic displacements.

The basic experimental design was to provide a directional sound source, which impinged asymmetrically on the two sides of the animal, and to record action potentials simultaneously from the lateral line nerves on the two sides.

The swim-bladder pathway

Sound is produced in the marine catfish by a pair of thin flanges of bone, which are attached to the anterior–dorsal surface of the swim bladder, and are vibrated by a pair of specialized sonic muscles (Tavolga, 1962). The swim bladder is also involved in sound reception and four pairs of small bones (the Weberian ossicles) couple the swim bladder to the inner ear. The bladder itself is composed of soft, inelastic connective tissue, with a number of partial transverse septa toward the posterior end (Fig. 1). The construction of the bladder resembles the internal architecture of some high-fidelity loudspeaker enclosures, which suggests that the swim bladder possesses some directional acoustic characteristics that would be advantageous in acoustical orientation.

To test the above hypothesis, the animal was suspended, at various angles to a hydrophone, and stimulated to produce sounds. Conversely, the swim bladder was tested for any directional capacities in acoustical reception.

MATERIALS AND METHODS

The lateral line pathway

The fish used were all mature individuals of the sea catfish (*Arius felis*), ranging in size from 25 to 35 cm in standard length. Twenty-five animals were used in this study. Recordings were made with the animals under anaesthesia (MS-222) or after severing the spinal cord just anterior to the dorsal fin.

The electrophysiological equipment was conventional, except that two amplifiers (W-P Instruments, differential preamplifiers) were used whose gain characteristics were carefully matched. The potentials were observed and photographed on a dual-beam oscilloscope (Tektronix).

The electrode needle (Transidyne, platinum-coated tungsten) was placed into the lateral line nerve at about the level of the pectoral fins. Here the nerve is readily
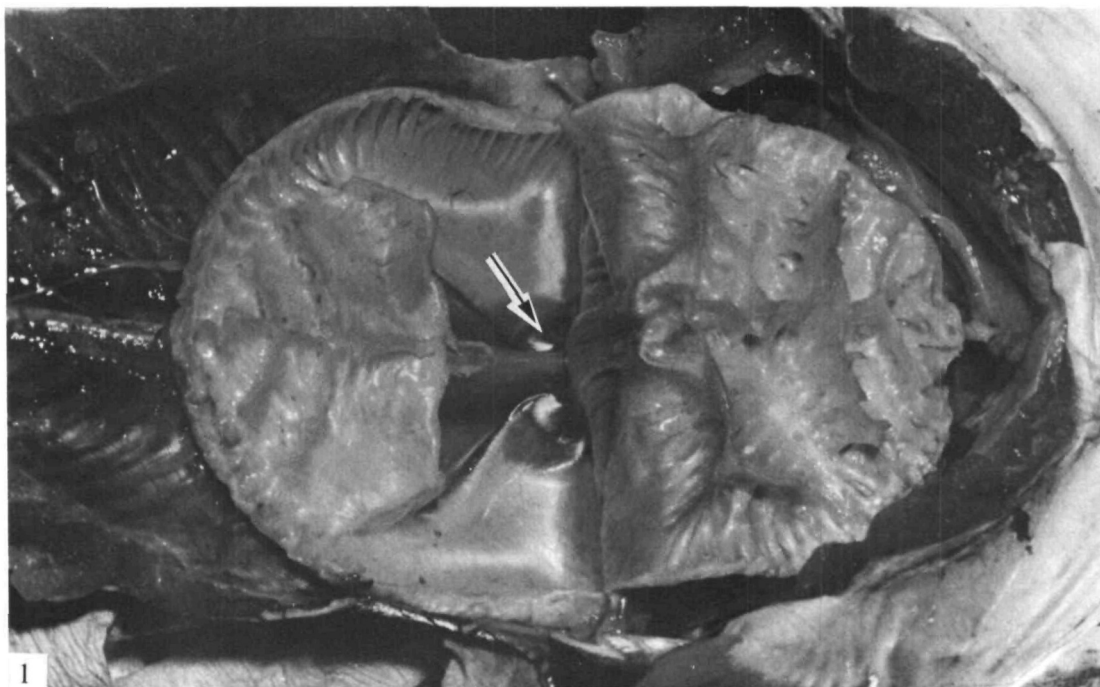
Fig. 1. Swim bladder of *Arius felis*, exposed and opened by removal of ventral surface, showing internal partitioning. Arrow points to the tripus, which is set in the dorsal wall of the anterior chamber of the bladder. Ventral surface shown reflected forward.
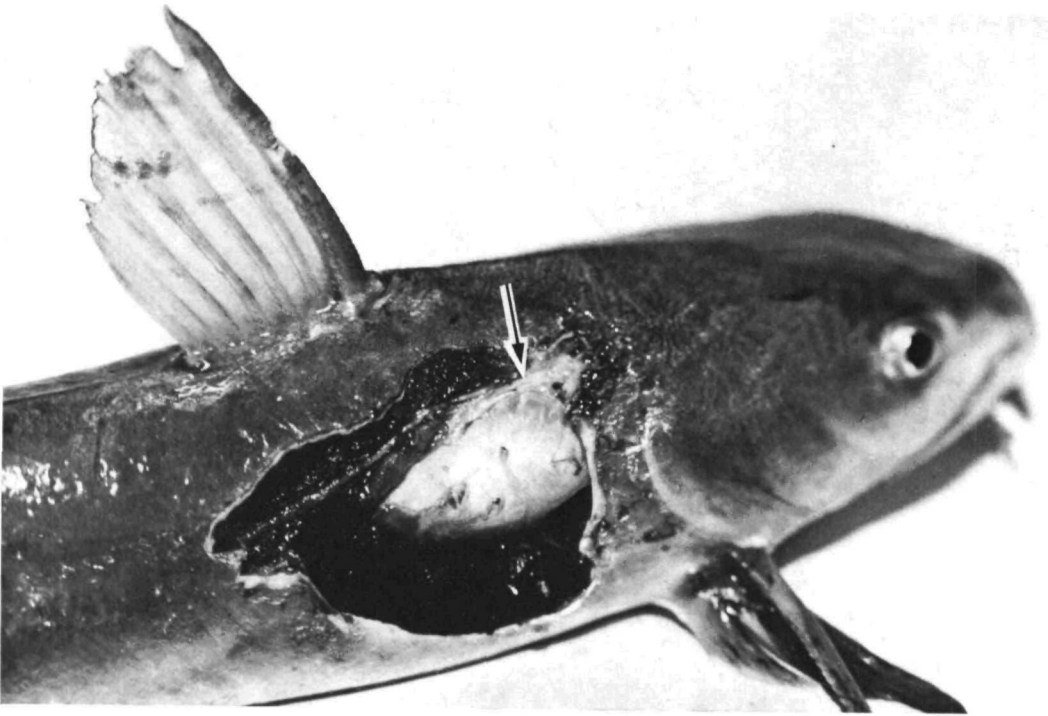
Fig. 2. Exposed lateral line nerve of *Arius felis*. Arrow indicates usual site of action potential recording. Here the nerve runs along the edge of the 'elastic spring'. The swim bladder is ventral to the 'elastic spring'. For anatomical details, see Tavolga (1962).
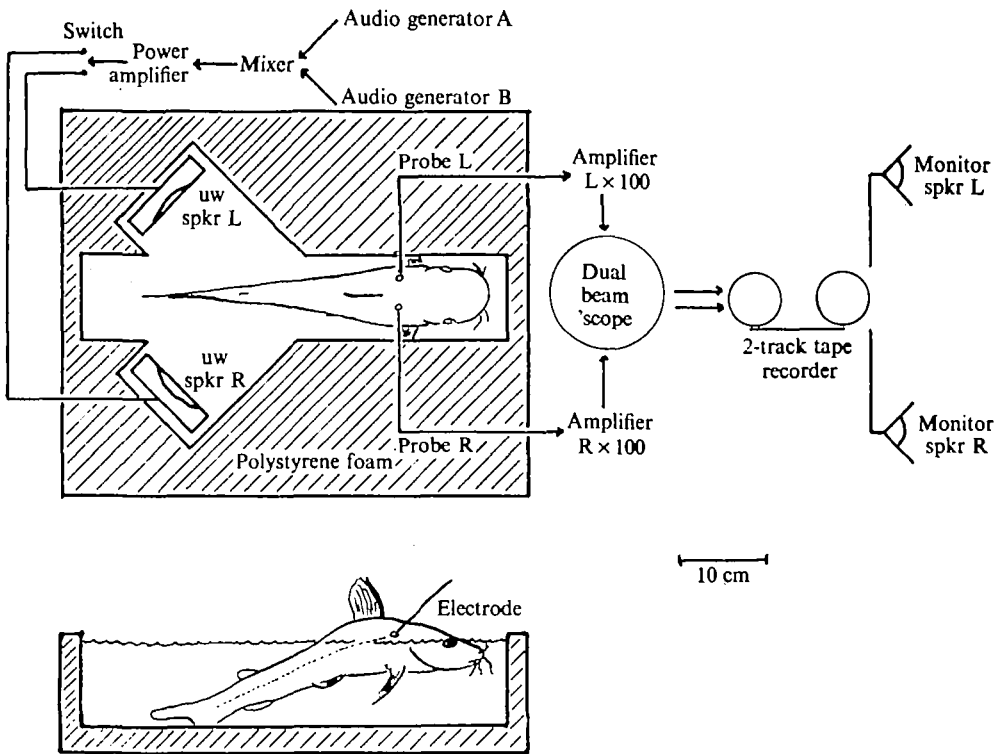
WILLIAM N. TAVOLGA

Fig. 3. Diagram of experimental tank used for lateral line nerve recordings, with a block diagram of the electronic apparatus.

available, just under the skin, and it runs along the dorsal edge of the flange of bone formed by the fusion of transverse processes (Fig. 2). This structure is involved in sound production and the skeletal details are more fully described elsewhere (Tavolga, 1962). The nerve fibres were teased apart, so as to obtain as few recorded fibres as possible. In the figures of the oscilloscope tracings, the polarity of the action potentials is always negative, but an inverting operational amplifier was used in obtaining some of the records. The indifferent electrode was usually placed in the dorsal musculature about 1 or 2 cm dorsal and posterior to the recording site. The nerve was severed anterior to the recording site to prevent the possible inhibiting effect of efferent units, as reported for some species (Russell & Roberts, 1972).

The animal was placed in the experimental tank (Fig. 3) so that the base of the lateral line nerve was above and the rest of the trunk and tail beneath the water. Underwater loudspeakers were placed to direct the sound stimulus toward one side of the fish. The sound stimulus could be switched to either of the two loudspeakers (Electrovoice DU-30), both of which were tested to ensure that their acoustic and impedance characteristics were matched. A conventional 30 W power amplifier was used to drive the speakers. An opto-electric switch provided a rise time of about 10 ms and eliminated switching transients.

The sound generation system was devised to obtain maximum directionality. The frequencies used were below 200 Hz. The propagation of such low frequencies is

normally non-directional, especially in water. By using the principles of non-linear acoustics, however, directional propagation could be achieved. Two audio oscillators were used: one set at 20 kHz and the other at 20 kHz plus the desired output frequency (e.g. generator A at 20 kHz and generator B at 20·1 kHz). These were heterodyned and then power-amplified. Only the 100 Hz sideband was effectively generated into the water. Because of the non-linear acoustic characteristics of water, a low frequency generated in this fashion has the directional characteristics of 20 kHz, and, in addition, the speakers were able to deliver a considerable amount of power without any damage. This technique was first suggested to me by Dr C. Scott Johnson (Naval Undersea Center, San Diego, Cal.), and the theoretical principles involved were summarized by Westervelt (1957, 1963).

The speaker output was measured at a point in the experimental tank about 15 cm from each speaker. Both a hydrophone (Chesapeake Instruments, SH-102) and an accelerometer (Geophone: Geo Space Corp., HS-1) were used. The hydrophone responds primarily to pressure, although pressure generated by a near-field would also be detected. The instrument showed an ambient noise level of +6 dB re 1 microbar (μb). The addition of a low-pass filter, that attenuated all frequencies above 250 Hz at about 24 dB per octave, showed that the low-frequency noise level was about −10 dBμb under the conditions of the experiment.

The geophone, whose response above 300 Hz was not significant, was calibrated in terms of particle velocity and showed an ambient noise level of −47 dB re the 1 cm sec^{-1} reference level. Most of this near-field noise was probably generated by air conditioners and other equipment in the laboratory building. This could not be eliminated even by placing the experimental tank on a thick layer of polyurethane foam-mattress material.

To make particle velocity and acoustic pressure units more comparable, Siler (1969) coined the unit *microvar*. This is equivalent to a particle velocity of 1 cm sec⁻ × 1/ρc, with the ρc value assumed to be about 150 000 acoustic ohms. This assumption, however, is not necessarily valid in small, enclosed, water masses such as in aquarium tanks. Parvulescu (1967) suggested that caution should be exercised in using standard acoustic energy formulas in such containers of water, and even in shallow-water field conditions, since the actual acoustic impedance can approach that of air and be orders of magnitude lower than under free-field conditions. As will be seen later, this warning is of considerable significance in the present study.

The effects of surface waves generated in this apparatus were considered, but at the small volumes of water used the separation of surface from internal waves is not possible. In this instance, the displacement produced by the loudspeakers is probably the same, at least in amplitude, on the surface and below the surface by a few centimetres.

The measurements given here (obtained from hydrophone output) are in terms of pressure, dB re 1 μb (dBμb), or in microbars directly (1 μb = 1 dyne/cm^2). Using the following formula (Harris, 1964), the particle displacement could be calculated:

$$d = \frac{p \times 10^7}{\omega \rho c}\left(1 + \frac{1}{(kr)^2}\right)^{\frac{1}{2}};$$

d = particle displacement in nanometers (nm),

p = acoustic pressure in microbars (μb),

ω = $2\pi f$, at 100 Hz (this equals 628),

k = ω/c (c = acoustic velocity), and at 100 Hz in water this equals 0·00419,

r = distance from sound source to hydrophone in cm,

ρc = the characteristic acoustic impedance of the medium, usually taken as 150000 in water, but this applies only to free-field conditions.

Particle velocity, as obtained from the geophone output, is given here in terms of cm sec^{-1} or in terms of dB re 1 cm sec^{-1}. If the frequency is known, then the near-field particle displacement can be calculated easily:

$$d(\text{nm}) = \text{cm sec}^{-1} \times 1/\omega \times 10^7.$$

These formulae and calculations were also used in the course of the next section on swim bladder function.

Swim bladder directionality

The tests were conducted in a circular concrete pool, 4·5 m in diameter and 1·5 m in depth. The receiver (hydrophone) or projector (J-9) was placed near the centre of the tank at a depth of about 0·5 m. The fish was immobilized by severing the spinal cord just behind the skull, and suspended on a rotatable plastic rod at a depth of 0·5 m. The fish was about 2 m from the hydrophone or projector, and the inner face of the tank in back of the fish was lined with a layer of polyurethane foam 2 cm thick. This lining slightly reduced acoustic reflexions from the tank surface immediately in back of the fish.

In transmitting tests, the animal was induced to produce sounds by short electric shocks. Since the innervation of the sonic muscles is spino-occipital (Tavolga, 1962), the animal could still produce its species-typical sounds although the body was immobilized. The sounds were recorded and observed by means of an oscilloscope. The fish was rotated and tested every 45°. Average peak-to-peak levels of the sounds were determined from oscilloscope photographs.

The fish was also induced to emit artificial sounds at various frequencies by stimulating its sonic muscles directly with a pulse generator set to different frequencies. The subject was rotated with respect to the hydrophone and peak-to-peak levels were measured as before.

In receiving tests, the J-9 sound projector was suspended in the same position as the hydrophone, and the sound output monitored with a hydrophone placed next to the suspended fish. The sounds produced by the projector consisted of (*a*) recordings of catfish sounds; (*b*) short, 100 Hz, pulses of 20 msec duration generated by a sine-wave oscillator; (*c*) pulses and long-duration emissions at frequencies from 30 to 2000 Hz; and (*d*) directional low-frequency sounds generated by the heterodyning technique described above. Projected sound levels were maintained at 0 dBμb as measured by the hydrophone.

The reception characteristics of the swim bladder were monitored by a number of different devices: (*a*) a miniature ceramic microphone, waterproofed and applied against the swim-bladder surface in different areas; (*b*) a heart catheter microphone (American Electronics) inserted into the body cavity and pressed against the swim bladder surface; (*c*) a guitar-type contact microphone (Turner), dismantled except

for magnet and vibrating element, waterproofed and inserted against the bladder wall. To test if these devices were actually detecting the bladder wall vibration, their sensitivity was tested when they were simply suspended in the water or placed inside a fish with its swim bladder totally deflated. Each of the devices mentioned showed at least a 20 dB drop in sensitivity under these conditions and it was concluded that the major part of the received signal could be assumed to come from the swim bladder. Several other microphones were tested, but were found to be too large, not sensitive enough to the bladder wall displacements, or too sensitive to the near-field displacements of the water.

<div align="center">RESULTS</div>

Lateral line directionality

The figures (Figs. 4–9) present samples of oscilloscope recordings of lateral line action potentials. Fig. 4A and B was from the same preparation, and shows the effects of reversing the direction of impinging sound. The side opposite the stimulus showed no response other than a spontaneous background. In the preparation illustrated in Fig. 5, there was a considerably higher background of potentials, but the side towards the sound source showed a clear response from several units. Fig. 6, from another preparation, illustrates a response that differentiated the two sides less clearly. In this case, with the sound source on the left, the left side continued to respond as long as the stimulus remained on, while the right side dropped off quickly. Fig. 7 illustrates a preparation in which inhibition appeared to occur. In this case, an irregular background of strong units was inhibited. This was especially distinct when the sound source was on the right, and the opposite side potentials were strongly inhibited but recovered when the sound went off (Fig. 7B). This inhibition was not observed in any other preparation, and the significance of the phenomenon cannot be evaluated at the present time. Since the nerve was severed anteriorly, this inhibition could not be caused by any efferent fibre activity.

The figures show only a small sample of the results, which were not always so clear-cut or repeatable. It is evident that the lateral line system is capable of responding differentially to directional sound in the frequency range of 50–150 Hz. Above 150 Hz, the responses were scarcely detectable, and at 200 Hz, no responses could be noted.

Since the main frequency used as a stimulus in these experiments was 100 Hz, some sample measurements will be given. At a signal level of 0 dBμb, this provided a stimulus about 10 dB above the ambient noise level in that low-frequency band. With the hydrophone placed about 15 cm from the vibrating speaker cone, the particle displacement was calculated to be about 1·7 nm, a value very close to the supposed threshold of the lateral line receptors (van Bergeijk, 1964). The geophone placed in the same receiving position as the hydrophone, and pointed toward the speaker, provided a very different reading: -22 dB re 1 cm/s, or 0·079 cm/s. At 100 Hz this gives a particle displacement magnitude of 1257 nm. As predicted by Parvulescu (1967), this indicates that the ρc value (as used in the formula given earlier) probably approaches that of air because of the small volume of water confined in a rigid container. In this instance, the acoustic impedance of the
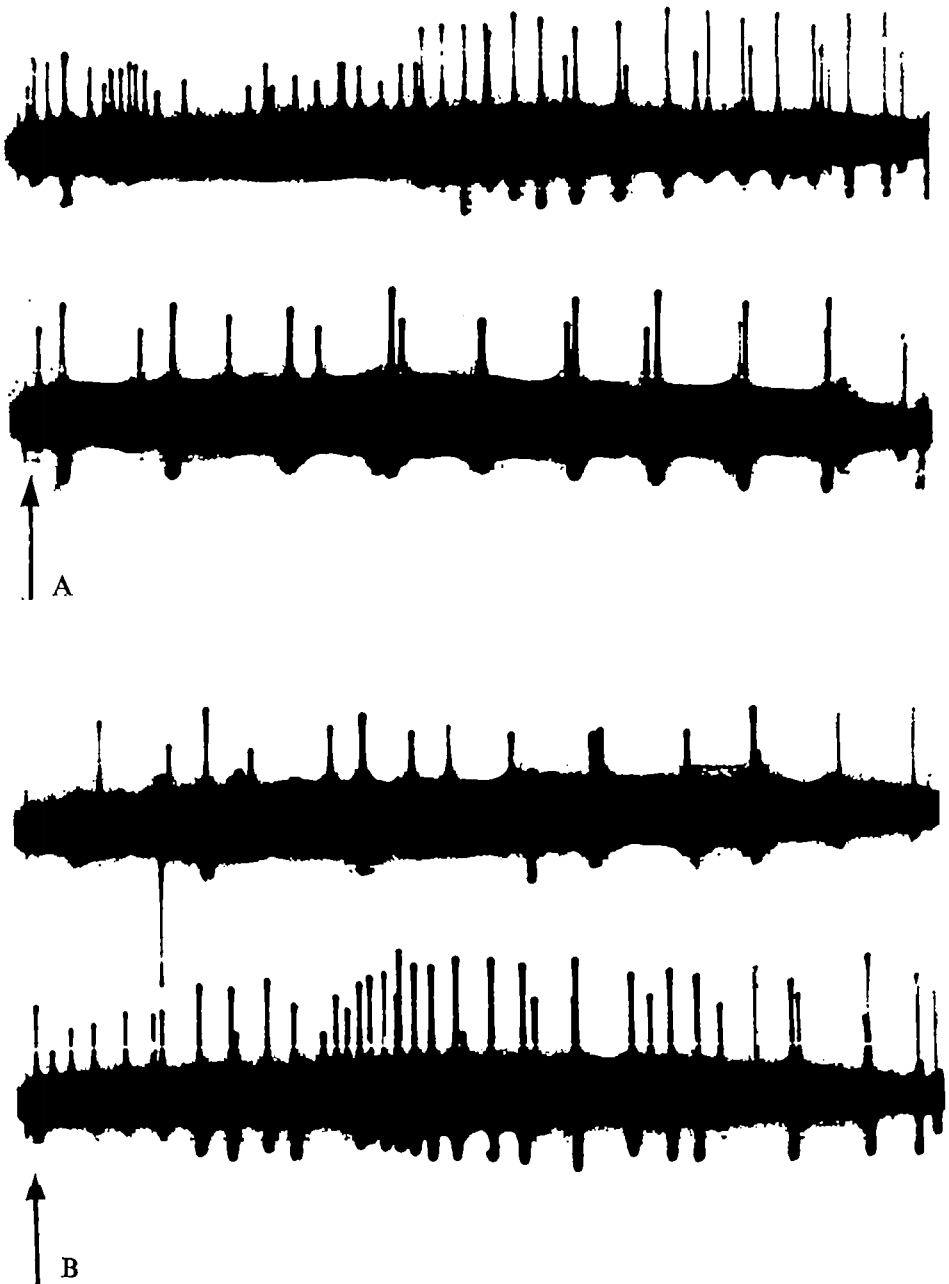
Fig. 4. Simultaneous recordings from both lateral line nerves when stimulated by a sound frequency of 50 Hz at an intensity of 0 dBμb. Sweep speed 0·5 s cm^{-1}. (A) Sound from left speaker. (B) Sound from right speaker. In these and in all subsequent figures, the upper trace is from the left side recording site and the lower trace from the right side. Arrow indicates time of onset of stimulus. Inverting amplifier used.
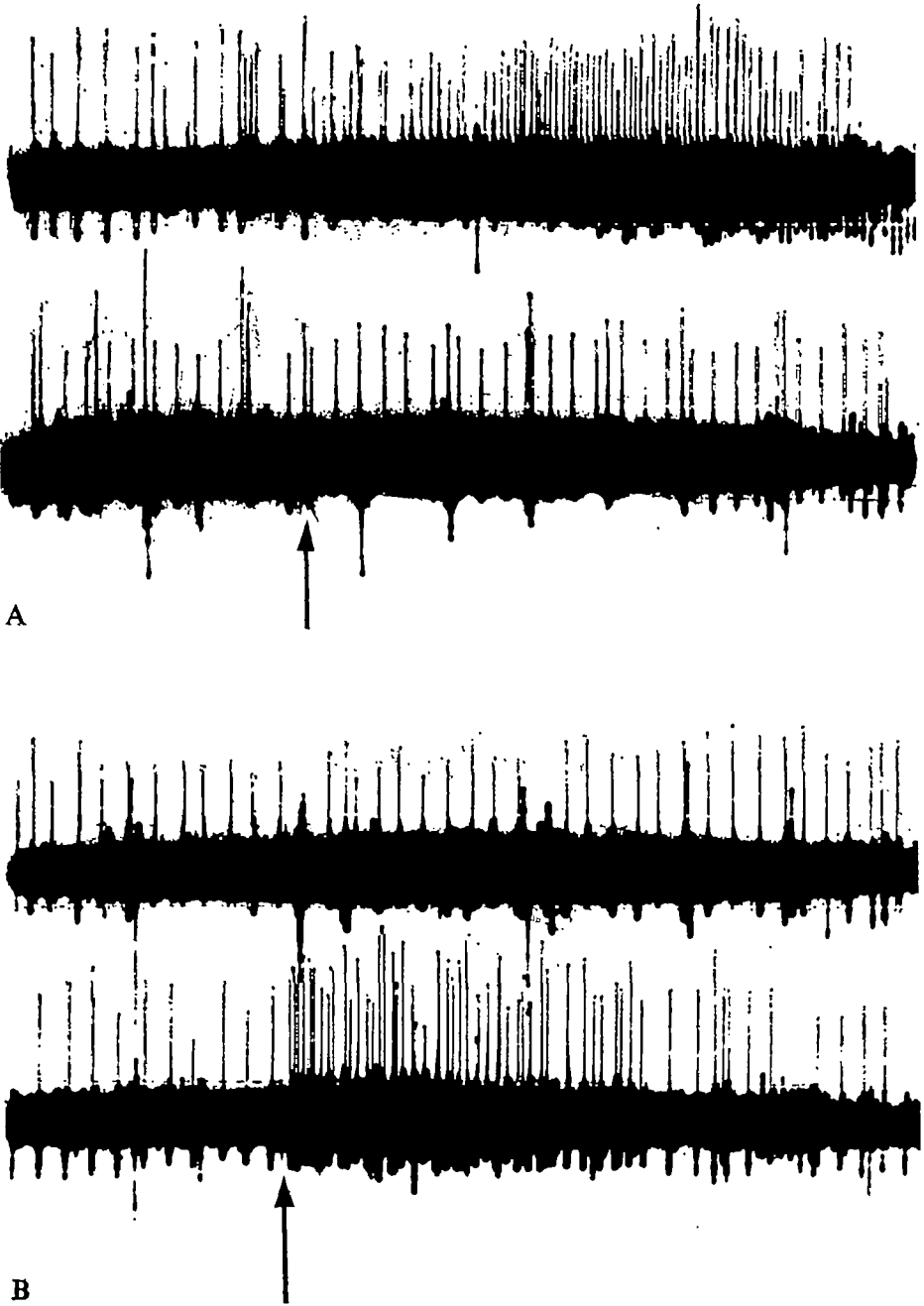
Fig. 5. Simultaneous recordings as in Fig. 4, and in the same preparation. Stimulus frequency was 100 Hz at an intensity of 5 dBμb. Sweep speed 0·2 s cm⁻¹. (A) Sound from left speaker. (B) Sound from right speaker. Inverting amplifier used.

Fig. 6. Simultaneous recordings as in Fig. 4, but from a different preparation. Stimulus frequency 150 Hz at an intensity of 8 dBμb; sweep speed 0·2 s cm^{-1}. Sound from left speaker. Note equal response on both sides.

experimental tank can be calculated to be about 2000, instead of the 150 000 as usually assumed. For this reason, the microvar units, as defined by Siler (·1969), are not appropriate here,

It is apparent, however, that the near-field generated by the stimulus was of considerable intensity, but no attempt was made to obtain threshold measurements. In this particular situation, the background noise was high, and if the stimulus level were substantially reduced, the response disappeared. This may be because of the masking noise, but it is also possible that this system can respond only to strong stimuli, either because of its high threshold or the particular arrangement used in which only a portion of the trunk and tail of the animal was immersed in water.

The background activity of most of the preparations was initially low, when the electrode first penetrated the nerve. Shortly after, however, the nerve was severed anterior to the electrode, and activity increased distinctly. It is now known that there is a significant supply of efferent fibres that can inhibit the sensory response in the lateral line system (Russell & Roberts, 1972), and this appears to be so in this species.

Occasional background activity was so strong that it masked any responses to sound stimuli, and some preparations generated extremely rapid bursts. Sometimes the rapid bursts were in response to the sound signal (Figs. 7, 8). A similar burst from the same preparation shown in Fig. 8 is illustrated in Fig. 9. The large, slow pulses (Fig. 9A) have a repetition rate of about 100/s. The smaller, fast pulses (resolved in Fig. 9B) appear to have a repetition rate of at least 1200/s, although many units are involved as can be seen from differences in pulse height. Such fast bursts were never observed in response to the sound stimulus. Their origin and significance are unknown.
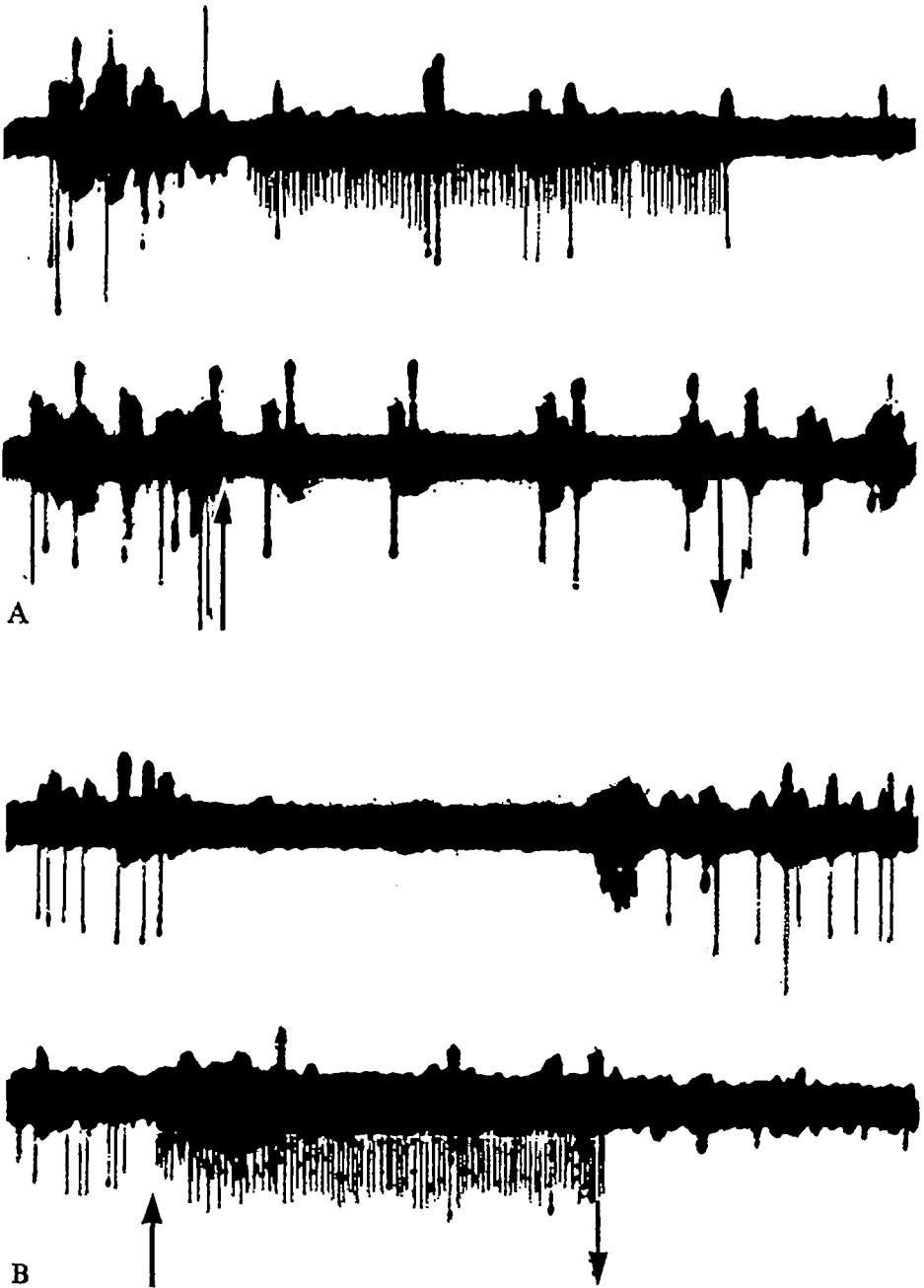
Fig. 7. Simultaneous recordings as in Fig. 6, but from a different preparation. Stimulus frequency 100 Hz at 0 dBμb; sweep speed of 0·2 s cm⁻¹. (A) Sound from left speaker. (B) Sound from right speaker. Note increase in action potentials on the stimulated side and simultaneous inhibition on the contralateral side.

Fig. 8. Recording sample from same preparation as shown in Fig. 7, but the response to the 100 Hz signal is displayed on a faster sweep speed of 50 ms cm^{-1}. A repetition rate of 80 s^{-1} can be seen, although the potentials may not all be from the same unit.
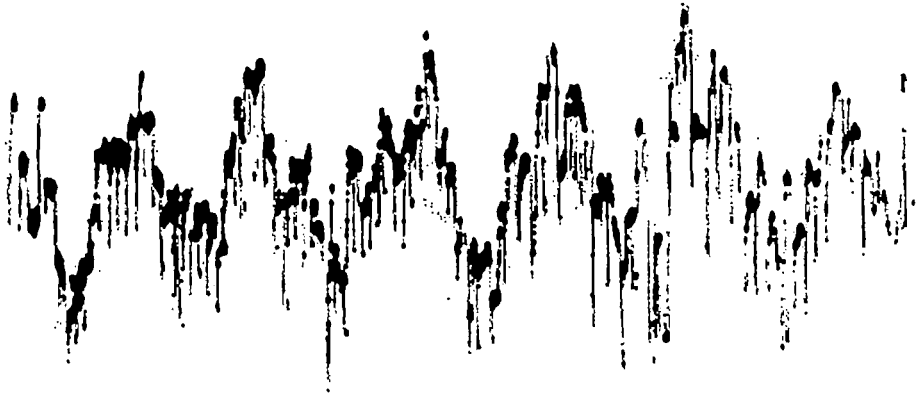
A

B

Fig. 9. Recording from same preparation as in Fig. 7 showing a spontaneous pulse burst of a rapid repetition rate superimposed on slower firing fibres. (A) Sweep speed of 10 msec cm^{-1}. (B) The tape recording was slowed to one-eighth normal speed and the oscilloscope sweep speed was 10 ms/cm.

Table 1. *Sound-propagating characteristics of catfish swim bladder*

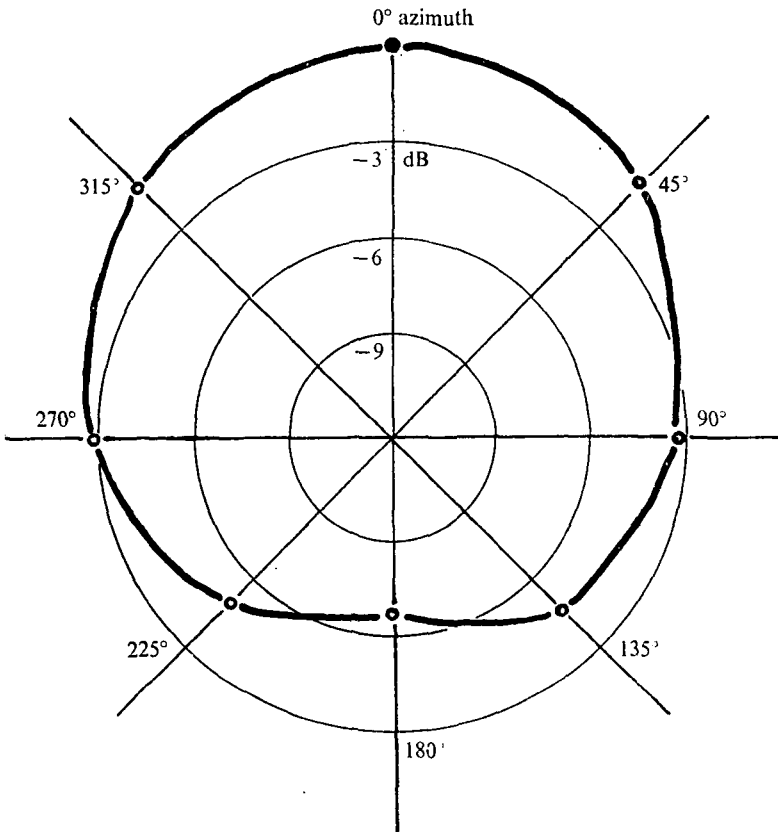| Azimuth to the right of centre (deg)	Mean relative sound level (peak-to-peak) re zero azimuth position (±standard deviation) (dB)	
	Natural evoked pulses	Artificially stimulated
0	$0 \pm 1\cdot8$, $N = 24$	$0 \pm 0\cdot5$, $N = 10$
45	$-1\cdot2 \pm 1\cdot6$, $N = 28$	$-1\cdot1 \pm 0\cdot4$, $N = 10$
90	$-3\cdot1 \pm 1\cdot7$, $N = 32$	$-3\cdot2 \pm 0\cdot3$, $N = 10$
135	$-4\cdot6 \pm 1\cdot0$, $N = 30$	$-4\cdot5 \pm 0\cdot4$, $N = 10$
180	$-6\cdot8 \pm 2\cdot9$, $N = 22$	$-6\cdot5 \pm 0\cdot2$, $N = 10$
225	$-4\cdot9 \pm 1\cdot5$, $N = 23$	$-4\cdot5 \pm 0\cdot3$, $N = 10$
270	$-2\cdot9 \pm 1\cdot5$, $N = 20$	$-3\cdot1 \pm 0\cdot4$, $N = 10$
315	$-1\cdot1 \pm 0\cdot9$, $N = 30$	$-1\cdot0 \pm 0\cdot2$, $N = 10$

Fig. 10. Polar coordinate graph of the output of the swim bladder as a sound projector. Data from Table 1 (natural evoked pulses).

Swim bladder directionality

In general, the results (summarized in Table 1 and Fig. 10) showed that the catfish swim bladder is directional in its sound propagating characteristics. In spite of considerable variability in the sound level of individual pulses which were spontaneously produced by the fish, there was a detectable difference in the received level which was correlated with the position of the fish. Artificially induced vibrations

Table 2. *Sound receiving characteristics of catfish swim bladder*

Azimuth to the right of centre (deg)	Mean peak-to-peak sound level received re zero azimuth position (dB) Frequency (Hz)					
	50	100	200	500	1000	2000
45	−1·2	−1·0	−1·2	−1·2	−1·9	0
90	−4·5	−4·5	−4·6	−4·3	−3·5	−0·3
135	−7·2	−7·1	−7·4	−7·0	−5·8	−1·2
180	−12·4	−12·5	−12·6	−12·0	−8·3	−2·5
225	−7·5	−7·4	−7·4	−6·9	−5·4	−0·9
270	−4·6	−4·8	−4·7	−4·3	−3·6	−0·4
315	−1·4	−1·3	−1·4	−1·0	−2·1	0

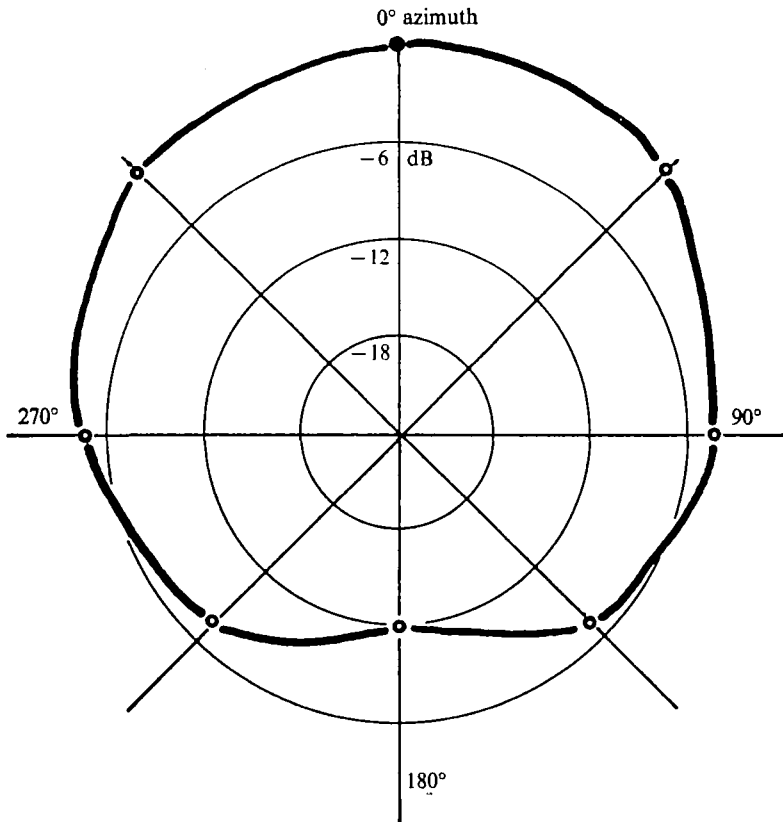$N = 25$ at each azimuth position. Standard deviation not over 0·2.

Fig. 11. Polar coordinate graph of the directional receiving characteristics of the swim bladder at 100 Hz. Data from Table 2.

of the sonic muscles provided more consistent information, especially at frequencies from 50 to 200 Hz. Table 1 shows the average results obtained at different azimuth positions of the fish with respect to the hydrophone at a distance of 2 m.

The directional characteristics of the swim bladder in receiving sounds was most evident at low frequencies. Above about 500 Hz the reception sensitivity varied

Table 3. *Sound-receiving characteristics of catfish swim bladder to 100 Hz sounds of directional nature*

Azimuth to the right of centre (deg)	Mean peak-to-peak sound level received re zero azimuth position (dB)
45	−1·0
90	−8·4
135	−12·0
180	−24·5
225	−13·2
270	−7·8
315	−1·5

$N = 30$ at each azimuth position. Standard deviation not over 0·4.
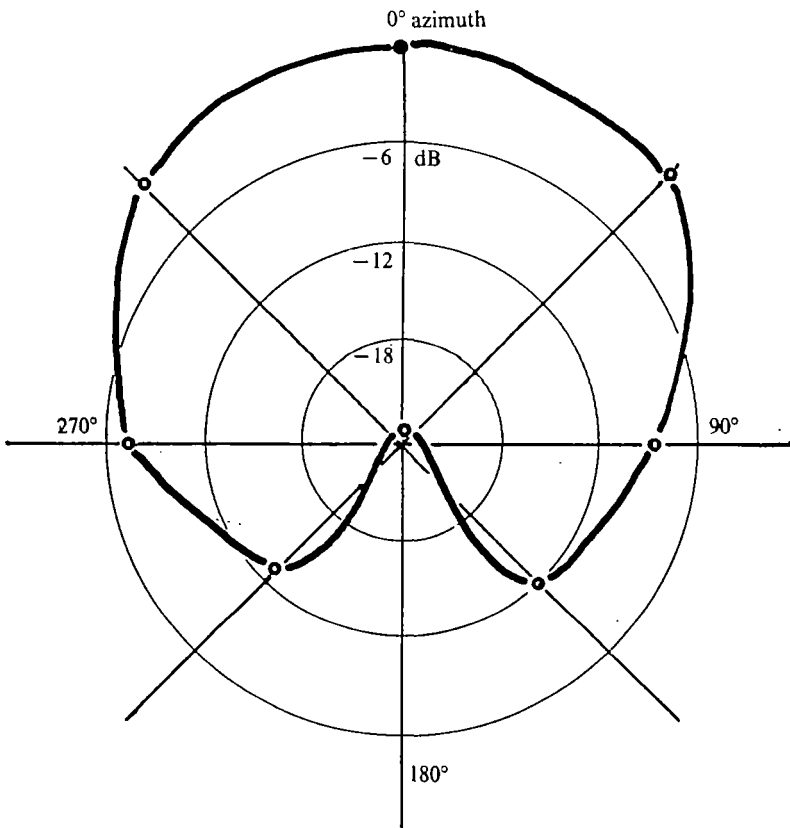

Fig. 12. Polar coordinate graph of receiving characteristics of the swim bladder to directional 100 Hz sound. Data from Table 3.

Table 4. *Intensity of catfish sounds as measured by a hydrophone*

	Hydrophone distance (cm)				
	10	25	50	100	200
Average sound level peaks (dBμb)	35	22	10	−3	−13
Particle displacement values as calculated from Harris formula (*d*, nm)	142	12·9	3·2	0·7	0·2

Ambient noise in band below 250 Hz = −20 dBμb.

Table 5. *Intensity of catfish sounds as measured by a geophone*

	Geophone distance (cm)				
	10	25	50	100	200
Average sound velocity peaks re 1 cm/sec (dB)	−1·0	−20	−41	Masked by noise	
Calculated particle displacement (nm)	14172	1560	143	—	—

Ambient noise = −55 dB re 1 cm/s.

significantly less with the position of the fish with respect to the sound projector. Above about 2000 Hz the directivity appeared to be lost, at least in the present testing conditions. Differences resulting from the characteristics of the various receiving devices used were negligible, at least as far as relative values were concerned. The results obtained with the different microphones and projected sounds were therefore combined (Table 2, Fig. 11).

When the sounds generated by the projector were produced by heterodyning of two frequencies (20000 and 20100 Hz) the directional response of the swim bladder was significantly improved. Table 3 and Fig. 12 summarize the results giving the mean values.

As a sound projector, the swim bladder appears to be only slightly directional, with a front-to-back ratio of 6·5–7 dB. As a receiver, however, especially with a directional sound source, the swim bladder in the catfish is significantly directional at low frequencies, with a front-to-back ratio of up to 24·5 dB at 100 Hz.

This experiment also provides an estimate of the intensity of normal catfish sounds. Under field conditions, and even in captivity, single animals rarely produce sounds, while in a group it is impossible to determine which animal is producing the sounds. Even with a single intact animal in a school of muted ones (Tavolga, 1976a) it is difficult to estimate sound intensity for its distance from the hydrophone at a given utterance was not possible to estimate.

In the above situation, the spinal-severed and tethered animals produced sounds spontaneously, and the output intensity could be measured readily. Because of the slow response of a dB meter to the short pulses that constitute the catfish sounds, the sounds were observed on an oscilloscope and photographed. At least 20 sound pulses were measured at each hydrophone or geophone distance, and the peak values were averaged, with little variation. Table 4 shows the values obtained with

the hydrophone, and the calculations of particle displacement were made with the assumption of the main energy being at 100 Hz and the usual pc value of 150000.

By contrast, Table 5 shows the same sounds as measured by the velocity-sensitive geophone. Beyond a distance of 50 cm, the masking effect of background noise prevented measurements, but it is obvious that calculated particle displacement values (assuming dominant energy at 100 Hz) are much higher. In effect, this concrete tank of water (containing almost 24000 l of water) was acting as if it had an acoustic impedance of only 15000.

In both cases, the rate of signal attenuation with distance approaches the condition characteristic of displacement energy (i.e. the amount of displacement attenuates as the square of the distance or the cube if power terms are used (van Bergeijk, 1964; Harris, 1964)).

DISCUSSION AND CONCLUSIONS

As stated earlier, there are two sensory pathways through which fishes can obtain directional information about acoustic energy: the lateral line, and the inner ear. The inner ear obtains most of its acoustic input from the nearby swimbladder.

Lateral line pathway

As part of his model for fish audition, van Bergeijk (1964) proposed that the swim-bladder/inner-ear complex was not adequate for directional hearing. Since this complex is essentially a far-field detector only, it follows that the fish effectively has only one ear. Pressure being a scalar rather than a vector form of energy, there is no mechanism for determining the position of a sound source relative to the swim-bladder transducer. Sound localization, therefore, could only take place in the near-field in which adequate displacement energy was present. This energy has direction (vector), and according to the physics of acoustical phenomena, the range of effective near-field energy was limited to about one-sixth of a wavelength. Obviously, low frequencies would have the greatest near-field range. This range could be extended in situations where the source energy was so high as to generate strong-pressure-induced displacements. The mathematics of these phenomena were discussed by Harris (1964).

Van Bergeijk (1964) argued, further, that the lateral line system was the only receptor that was adequately sensitive at low frequencies and specifically adapted for detection of displacement energy. He visualized the lateral line as an array of minute displacement detectors with their axes of sensitivity in different directions and sufficiently widely distributed over the body of the fish to provide all the directional data necessary for the central nervous system to correlate and to obtain range and bearing information.

One of the critics of this model was Dijkgraaf (1964), whose work was a pioneering contribution to our understanding of fish audition. He pointed out that all the studies on acoustical function of the lateral line were based upon neurophysiological and not behavioural experiments, and he expressed strong doubts that the lateral line was an acoustic receptor. The kind of stimuli to which the lateral line responds are slow, relatively massive water displacements, as exemplified in his concept of 'distance-touch-sense' (Ferntastsinn) (Dijkgraaf, 1947).

Some workers, including Dijkgraaf, prefer to limit the concept of 'acoustic' energy to pressure (far-field) phenomena, and exclude near-field displacements from the definition. In this view, the lateral line is not an 'acoustic' sense. Van Bergeijk (1967) took the broader view, based on the fact that displacement energy and pressure energy are not truly separable and one can obtain pressure measurements from near-field 'sound' and yet all pressure oscillations include some particle displacement. In addition, all acoustic detectors, lateral line and saccular hair cells included, are fundamentally displacement detectors. Whether the lateral line is considered an acoustic detector or not is a matter of definition.

Neurophysiological evidence does support the function of the lateral line as a low-frequency-vibration detector (Suckling, 1962, 1967; Suckling & Suckling, 1964). Horch & Salmon (1973), in their report on sound production and detection in squirrelfish, observed lateral-line microphonics in response to sounds of 300 and 400 Hz. By using an arrangement in which pressure and displacement amplitudes could be varied independently, the lateral-line response was found to be primarily to the displacement component, as expected. The critical observation was made by shifting sound source position and the lateral-line microphonics were significantly stronger with the sound source behind the fish than in front.

Inner-ear pathway

There has been an accumulation of recent data to show that the swim-bladder/inner-ear complex can serve as a directional sound detector. The techniques used in these studies included conditioned heart and respiration rate changes, behavioural changes, and saccular microphonics, and most of the data were obtained from open water, field conditions (see chapters in Schuijf & Hawkins, 1976).

Evidence is now available that shows that the inner ear can receive acoustic stimuli directly, and that it can detect displacement direction without the necessity of a swim-bladder transducer. This notion is based on the fact that hair cells in the saccular maculae are organized in groups with their axes of sensitivity in different directions. In addition, Schuijf & Buwalda (1975) proposed a model for directional sound detection based on discrimination of phase differences within the sacculus.

CONCLUSIONS

The results reported here confirm the role of the lateral line in detecting low-frequency near-field displacements. The system can respond differentially to directional stimuli, and this lends support to the idea that the lateral line can operate as a directional array, as proposed by van Bergeijk (1964).

The swim-bladder study, however, indicates that the Schuijf inner ear model could operate with enhancement by the directional characteristics of the swim bladder. It is likely that the directional transmitting characteristics of the bladder may aid in the acoustic orientation that is exemplified by the catfish, *Arius felis*.

The resolution of the problem may come with the realization that both models can operate simultaneously and, perhaps, synergistically. As is the case with most orientational systems in animals, several sensory modalities are used together. In bird navigation, for example (Keeton, 1974), it is becoming clear that one need not

postulate any one mechanism with a high degree of accuracy. Instead, several modalities of low accuracy tend to correct each other so as to increase the probability of correct orientation. In fishes, similarly, it is not a case of one system *or* another, it is a case of the lateral line information being correlated with swim bladder and inner-ear inputs.

With recent advances in our understanding of fish audition, one thing is clear: the auditory system in fishes is a highly specialized and complex receptor system – much more so than was ever imagined a few years ago.

The present data emphasize the fact that the acoustic orientation or echolocation that the catfish possesses is entirely dependent upon the near-field particle displacement energy. In the observations on orientational behaviour (Tavolga, 1976*a*) it appeared that the ability of the animals to detect obstacles was limited to a range of only a few cm. Considering the rapid attenuation of particle displacement energy this range limitation is understandable. It may well be that the acoustic conditions in the observation tank were such as to increase the range because of the lowering of the acoustic impedance.

Future studies will examine the limits of sensitivity of the catfish to particle displacement energy, and will test the relative contributions of lateral line, swim bladder and inner ear to the acoustic orientational (echolocation) behaviour in this species.

REFERENCES

BREDER, C. M., JR (1968). Seasonal and diurnal occurrences of fish sounds in a small Florida bay. *Bull. Am. Mus. Nat. Hist.* **138**, 325–78.

DIJKGRAAF, S. (1947). Über die Reizung des Ferntastsinnes bei Fischen und Amphibien. *Experientia* **3**, 206–16.

DIJKGRAAF, S. (1964). The supposed use of the lateral line as an organ of hearing in fish. *Experientia* **20**, 586.

HARRIS, G. G. (1964). Considerations on the physics of sound production by fishes. In *Marine Bio-Acoustics* (ed. W. N. Tavolga), pp. 233–47. Oxford: Pergamon Press.

HORCH, K. & SALMON, M. (1973). Adaptations to the acoustic environment by the squirrelfishes *Myripristis violaceus* and *M. pralinius. Mar. Behav. Physiol.* **2**, 121–39.

KEETON, W. T. (1974). The orientational and navigational basis of homing in birds. In *Advances in the Study of Behavior*, vol. 5 (ed. D. S. Lehrman, J. S. Rosenblatt, R. A. Hinde and E. Shaw), pp. 47–132. New York: Academic Press.

PARVULESCU, A. (1967). Acoustics of small tanks. In *Marine Bio-Acoustics*, vol. 2 (ed. W. N. Tavolga), pp. 7–13. Oxford: Pergamon Press.

POPPER, A. N. & FAY, R. R. (1973). Sound detection and processing by teleost fishes: a critical review. *J. Acoust. Soc. Am.* **53**, 1515–29.

RUSSELL, I. J. & ROBERTS, B. L. (1972). Inhibition of spontaneous lateral-line activity by efferent nerve stimulation. *J. exp. Biol.* **57**, 77–82.

SCHUIJF, A. & BUWALDA, R. J. A. (1975). On the mechanism of directional hearing in cod (*Gadus morhua* L.). *J. comp. Physiol.* **98**, 333–43.

SCHUIJF, A. & HAWKINS, A. D. (1976). *Sound Reception in Fish.* Amsterdam: Elsevier.

SILER, W. (1969). Near- and far-fields in a marine environment. *J. Acoust. Soc. Am.* **46**, 483–4.

SUCKLING, E. E. (1962). Lateral line in fish – possible mode of action. *J. Acoust. Soc. Am.* **34**, 127.

SUCKLING, E. E. (1967). Electrophysiological studies on the trunk lateral line system of various marine and freshwater teleosts. In *Lateral Line Detectors* (ed. P. Cahn), pp. 97–103. Bloomington, Indiana: Indiana University Press.

SUCKLING, E. E. & SUCKLING, J. A. (1964). Lateral line as a vibration receptor. *J. Acoust. Soc. Am.* **36**, 2214–16.

TAVOLGA, W. N. (1962). Mechanisms of sound production in the ariid catfishes, *Galeichthys* and *Bagre. Bull. Am. Mus. Nat. Hist.* **124**, 1–30.

TAVOLGA, W. N. (1971*a*). Acoustic orientation in the sea catfish, *Galeichthys felis. Ann. N.Y. Acad. Sci.* **188**, 80–97.

TAVOLGA, W. N. (1971*b*). Sound production and detection. In *Fish Physiology*, vol. 5 (ed. W. S. Hoar and D. J. Randall), pp. 135–205. New York: Academic Press.

TAVOLGA, W. N. (1976*a*). Acoustic obstacle detection in the sea catfish (*Arius felis*). In *Sound Reception in Fish* (ed. A. Schuijf and A. D. Hawkins), pp. 185–204. Amsterdam: Elsevier.

TAVOLGA, W. N. (1976*b*). Recent advances in the study of fish audition. In *Sound Reception in Fishes* (ed. W. N. Tavolga), pp. 37–52, Benchmark Papers in Animal Behavior, vol. 7. Stroudsburg, Pa.: Dowden, Hutchinson and Ross.

VAN BERGEIJK, W. A. (1964). Directional and nondirectional hearing in fish. In *Marine Bio-Acoustics* (ed. W. N. Tavolga), pp. 281–99. Oxford: Pergamon Press.

WESTERVELT, P. J. (1957). The scattering of sound by sound. *J. Acoust. Soc. Am.* **29**, 199–203.

WESTERVELT, P. J. (1963). Parametric acoustical array. *J. Acoust. Soc. Am.* **35**, 535–7.