PROGRAM AND ABSTRACTS

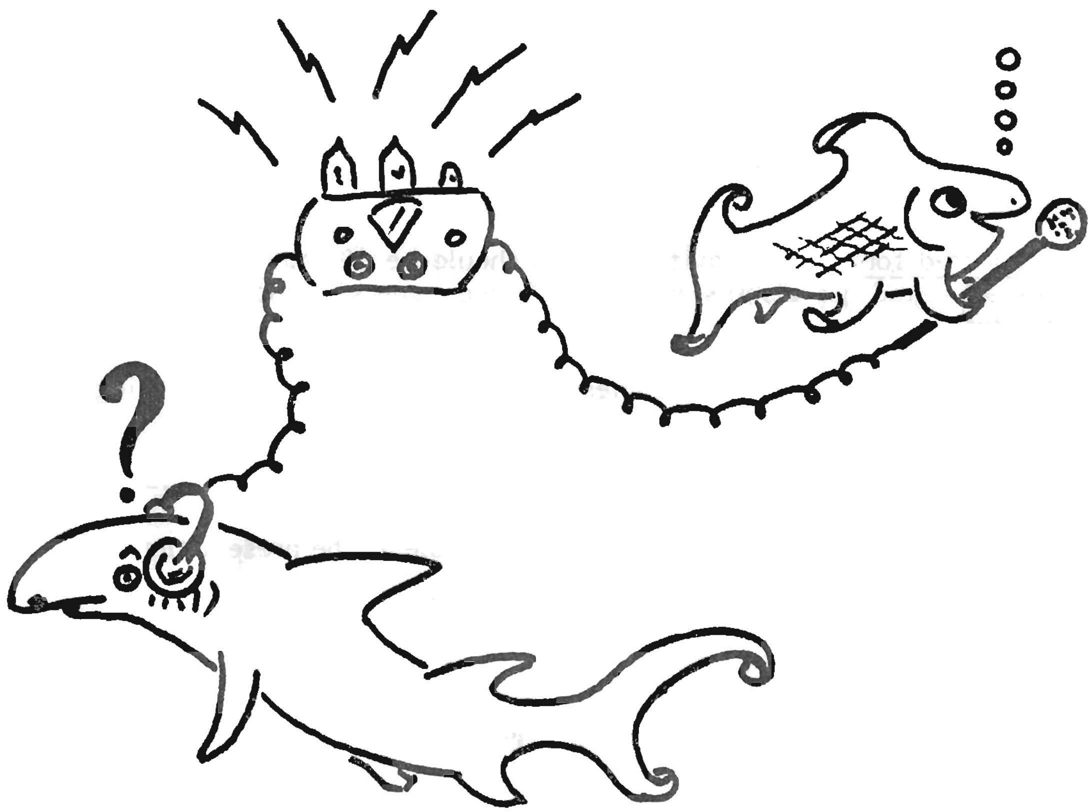
# HEARING AND SOUND COMMUNICATION IN FISHES

MOTE MARINE LABORATORY, SARASOTA, FLORIDA

April 22 to 26, 1980


Organizing Committee

Richard R. Fay
Arthur N. Popper
William N. Tavolga

## Meeting Information

Address: Mote Marine Laboratory
1600 City Island Park
Sarasota, Florida 33577

Phone: (813) 388-4441

Hotel: Sarasota-Lido Beach Holiday Inn
233 Ben Franklin Drive
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Note: People who arrive before 5:30 pm on April 22nd (Tuesday) should feel free to call Mote Marine Laboratory and come out to the lab to visit. There will be space available at the lab to get together informally. The lab will provide rides or you can take a cab.

When you check in to the hotel please check for a message indicating who has already arrived and room assignments for all participants. There will be a hospitality suite available to participants at the hotel.

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Times allotted for papers: Invited papers should be 30 minutes long with an additional 10 minutes allocated for discussion. Contributed papers should be 15 minutes long with five minutes for discussion.

Please remember to bring three copies of your manuscript to the meeting.

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Not all abstracts are available at the present time.

These abstracts are not for citation.

# PROGRAM*

22 April (Tuesday): Participants Arrive

23 April (Wednesday)

9:00 am to 12:30 pm - R. R. Fay, presiding

Welcoming remarks: W. H. Taft, President, Mote Marine Laboratory

1. Fine Structure and Function of the Auditory System.
   C. Platt & A. N. Popper
2. Acoustico-Lateralis System in Clupeid Fishes.
   J. H. S. Blaxter, E. Denton & J. A. B. Gray

Coffee Break

3. Auditory Physiology in Elasmobranchs.
   J. T. Corwin
4. Audition and Central Nervous Function in Fishes and Sharks.
   R. G. Northcutt

Lunch

2:30 to 5:30 pm - A. N. Popper, presiding

1. Stimulation of the Lateral Line Sensory Cell.
   D. Strelioff
2. The Lateral Line Organ and Sound Reception.
   O. Sand

Coffee Break

3. Central Processing of Acoustico-Lateralis Signals in Elasmobranchs.
   B. L. Roberts
4. Auditory Psychophysics and Behavior in Fishes.
   A. D. Hawkins

6:00 - Evening barbeque - Mote Marine Laboratory

*As of 12 March.

24 April (Thursday)

9:00 am to 12:30 pm - W. N. Tavolga, presiding

1. Auditory Physiology and Signal Processing in Fishes.
   R. R. Fay
2. Frequency Discrimination in Teleost - Central or Peripheral?
   P. S. Enger

Coffee Break

3. Models of Acoustic Localization.
   A. Schuijf & R. J. A. Buwalda
4. Segregation of Directional and Non-Directional Information in Teleosts.
   R. J. A. Buwalda

Lunch

2:30 to 5:30 pm - Contributed Papers - R. G. Northcutt, presiding

1. Sound Production in the Naked Goby, *Gobiosoma bosci*.
   M. Mok
2. Mismatch Between Sound Production and Hearing in the Oyster Toadfish.
   M. L. Fine
3. Comparative Hearing Capabilities in Teleost Fishes.
   S. Coombs
4. Neurophysiological Mechanisms of Intensity Discrimination in the Goldfish: E. H. Weber's Other Contibution to Hearing.
   L. Hall, M. Patricoski & R. R. Fay
5. Frequency Characteristics of Single Units from the Ear of the Codfish, *Gadus morhua*.
   K. Horner & A. D. Hawkins
6. The Directional Properties of the Codfish Ear.
   A. D. Hawkins & K. Horner

Coffee Break

Discussion Session - To be arranged

25 April (Friday):

9:00 am to 12:30 pm - A. D. Hawkins, presiding

1. Sound Communication in Fishes.
   A. A. Myrberg
2. Neural Control of Sound Production.
   L. Demski

Coffee Break

3. Comparative Physiology of Audition and Electroreception.
   T. H. Bullock

Discussion of Dr. Bullock's paper

Lunch

2:30 to 5:30 pm - Contributed Papers - J. T. Corwin, presiding

1. The Utricle in *Ictalurus punctatus*.
   D. B. Jenkins
2. Lateral Line Function and Schooling.
   B. L. Partridge
3. The role of the Swimbladder in Sound Detection.
   J. H. S. Blaxter
4. Central Auditory Pathways in Fishes.
   C. A. McCormick
5. Connections of Eighth Nerve Medullary Centers in a Mormyrid Fish.
   C. C. Bell

Coffee Break

Retrospect and Prospect - Listening Through a Wet Filter.
W. N. Tavolga

Discussion Sessions and Topics on Future Research Directions.
(To be arranged)

Final Evening Session - Banquet - Mote Marine Laboratory

23 April (Saturday) - Participants Depart

## PARTICIPANTS

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**William N. Tavolga***, Mote Marine Laboratory, 1600 City Island Park, Sarasota, Florida 33577.

*Presenting Papers

# FINE STRUCTURE AND FUNCTION OF THE EAR.

**Christopher Platt** and **Arthur N. Popper**

One of the most striking features of the auditory system of fishes is the extensive structural diversity in the inner ear that extends from gross structures to ultrastructural features.

While there is substantial inter-specific variability in the structures of the ear, some generalizations can now be made both about gross and ultrastructural features of the otolithic organs of fishes from different taxonomic groups. For example, among all bony fishes so far examined, the utrricular otolith is far less variable in form than the otoliths of the saccule or lagnea, while the saccular otolith is much smaller than the lagenar otolith in the Ostariophysi but not in the non-ostariophysines. Another case of inter-specific variation occurs in the directional orientation of the sensory hair cells, particularly on the saccular macula; to a lesser degree on the lagenar macula; and least of all in the utricular macula. The most striking differences in hair cell orientation patterns are seen when comparing the sacculus in the Ostariophysi which only have two opposite oriented hair cell groups, and the sacculus in most non-ostariophysines where hair cells are oriented in four directions. There is also extensive inter-specific variation in the non-ostariophysines.

Substantial variation has also been observed with regard to the lengths of the ciliary bundles on the sensory cells of the various maculae. The bundles can be classified into seven known types, based on the relative length of the kinocilia and stereocilia. The variation in ciliary bundle pattern may occur within a single otolithic macula where cells with different bundle lengths may reside in different regions.

The ultrastructural and gross morphological data has led to the tentative suggestion that there may be substantial intra-macula variation in the function of the otolithic organs as well as variations in function when comparing the same organs in different species. However, physiological data are yet too sparse to make any major generalizations about the specific function of the otolithic organs in fishes.

In light of the substantial variation in the otolithic organs between fishes, several major points may be made. First, we feel that a division of function (e.g. auditory and vestibular) between the different otolithic organs of the ear may not be as absolute as has often been implied, so it may be necessary to reconsider some of the basic "classical" assumptions of auditory organ functions, at least with regard to the teleost ear. Second, we suggest that the notion of a functionally and structurally "typical teleost ear" is no longer tenable since the breadth of interspecific structural variation in teleost ears may imply significant functional variation.

# ACOUSTICO-LATERALIS SYSTEM IN CLUPEID FISHES

**J. H. S. Blaxter, E. Denton** and **J. A. B. Gray**

The clupeid acoustico-lateralis system differs from that of other fish in having partly gas-filled bullae which are mechanically linked with the utriculi and the lateral lines. These bullae are connected by exceedingly fine gas-filled tubes to the swimbladder. With change of depth the volumes of the gas-filled parts of the bullae are maintained constant by exchanges of gas with the swimbladder. The time constant of the movement of gas is about 15 sec. Measurements of the mechanical displacements of the bulla membrane, the utricular floor and the lateral recess membrane show that the perilymph movements which excite the receptors of the utriculus and lateral line are linearly related to pressure up to 5 x $10^4$ N $m^{-2}$ and are almost independent of frequency from 0.01 Hz to 1 K Hz. There are phase delays between stimulating pressure and mechanical responses which reach about $180^o$ at 900 Hz. At an intensity of sound of $10^{-12}$ W $m^{-2}$ (the absolute threshold of the human ear) the utricular floor is displaced at least as much as the mammalian cochlea. Two kinds of liquid displacement affect the sense organs of the lateral line and utriculus, one arises from particle displacements in the vibrational field, the other from pressure acting on the bulla. From estimates of their absolute values we conclude that clupeids have the potentality of estimating the distances and the directions of vibrating objects. As a step in analysing this system we have studied the anatomy and fine structure of the utriculus and its gross electrophysiological responses (microphonics) to oscillating stimuli.

The major part of each of the anterior and middle utricular maculae is backed by a tough plate of collagenous tissue and must behave mechanically as a single unit. Each of these maculae is divided into two areas distinguishd by having their hair cells orientated in opposite directions. In response to sinusoidal pressures the utricular electrical 'microphonics' show frequency doubling. We attribute this to the two groups of hair cells responding asymmetrically to displacements and forming a large back-to-back system of the type first analysed by Flock. One group of utricular receptors responds to movements of the maculae towards the fenestra of the bulla whilst the other responds to movements away from the fenestra: These reponses are immediate and almost independent of frequency between 30 and 900 Hz. Experiments with mixed frequency stimulation show that the behavior of the utricular microphonics to complicated waveform stimulation can be explained by assuming that, over wide frequency ranges the displacements of the utriculus act on a single large back-to-back system of receptors. There is no sign that the utriculus can perform Fourier analysis of complicated waveforms. The implications of this system in the handling of information will be discussed.

We show that the simplest type of response, the startle response, responds only to the onset of a maintained stimulus (i.e. the first half cycle). It has remarkably constant thresholds and is directional.

# AUDITION IN ELASMOBRANCHS

**Jeffrey T. Corwin**

Behavioral studies by Nelson, Myrberg, and others have described many aspects of sound sensitivity in a few species of sharks, and the ear's mechanisms for detection have recently been examined in several families of elasmobranchs.

In sharks and rays, as in most fishes, the ear contains seven distinct sensory epithelia; one crista associated with each of three semicircular canals, three otolithic maculae, in the sacculus, the lagena, and the utriculus, and a non-otolithic macula neglecta in the posterior canal duct.

Unlike the other maculae, the neglecta is not associated with a dense otolithic mass; instead a light collagenous cupula rests above its sensory cells and mearly fills the lumen of the posterior canal duct. It's sensory hair cells lie in the walls of that duct forming a single patch of epithelium in rays and two separate patches in sharks. In rays and some sharks the hair cell populations are loosely polarized and small, but in other, actively piscivorous sharks the patches of the neglecta contain exceptionally large popluations of hair cells, completely aligned within each patch, and oppositely polarized in the two patches.

In contrast to the neglecta, the sacculus is a true otolithic detector, with a dense mass of either sand or otoconia lying above its single sensory epithelium. Its hair cells are like those of the neglecta and are distributed with the same spatial density, but here two aligned populations of hair cells with opposite directions of polarization are present in one epithelium. A line of polarity reversal runs longitudinally along the middle of the epithelium with the cells on either side oriented so that their kinocilia ends face outward from the line. Until recently the macula neglecta of carcharhinid sharks was thought to contain the largest hair cell population described in any vertebrate ear, 260,000 cells in a 25 kg adult, but the saccular macula, forming a long s-shaped patch on the anterior and ventral walls of that organ, occupies more than six times the area of the neglecta, and contains over 300,000 hair cells in a 1-kg juvenile and problably several million cells in an adult.

Electrophysiological recordings from the statoacoustic nerve in the lemon shark have frequency and threshold characteristics that fit well with behavioral data from studies by Nelson and Banner, suggesting that the ear has a primary role in that sensitivity. Local recordings have also demonstrated acoustic sensitivity of both the sacculus and the macula neglecta, and ablation experiments suggest that they are the only acoustic detectors in that shark's ear.

Thus two dissimilar channels appear to function in parallel in that ear's detection of sound. The anatomy and acoustical theory suggest that the non-otolithic macula neglecta should sense sound as relative motion between its hair cells anchored to the skull, and the overlying cupula, which should have particularly good acoustic coupling to the ambient sound field above and in front of the animal, via the parietal sound channel. The otolithic saccular macula should detect sound as relative motion between its dense, acoustically reflecting otolithic mass and the skull, which should be somewhat coupled to the surrounding sound field in all directions. Together they should provide at least carcharhinid sharks with unambiguous combinations of outputs for localization of prey and other acoustic detection.

## AUDITION AND THE CENTRAL NERVOUS SYSTEM OF FISHES

**R. Glenn Northcutt**

The sensory organs, cranial nerves, and primary medullar nuclei that constitute the octavolateralis complex of fishes will be briefly reviewed. These data reveal three distinct organizational patterns in fishes and their descendents. Given these patterns, the origin(s) and evolution of audition among anamniotic vertebrates will be discussed. Finally, information on higher order auditory pathways in anamniotes will be summarized and current problems relating to central auditory pathways in fishes will be identified.

# STIMULATION OF LATERAL LINE SENSORY CELLS
**D. Strelioff**

During normal physiological stimulation all sensory hair cells are exposed to both mechanical and electrical stimuli. Mechanical deflection of the hair cell cilia is achieved through direct coupling to the stimulating medium. Extracellular potential variations are produced by mechanically-induced electrical impedance variations at the apical surfaces of neighboring hair cells. The excitatory roles of these two stimuli in the process of neural transduction in hair cell systems have been cosidered previously (Honrubia et al., Ann. Otol. Rhinol. Laryngol. 85:697-710; Strelioff and Honrubia, J. Neurophysiol. 41:432-444, 1978). This report presents the results of recent electrophsiological and modeling studies to test and improve current heuristic models of hair cell function.

The electrophysiological studies were conducted in an in vitro preparation of the Xenopus laevis (African clawed toad) lateral line organ. The specific objective was to determine the characteristics of the neural responses to mechanical and electrical stimuli, and thus to gain insight into the transduction process with a particular emphasis on the excitatory role of potentials. The neural responses of the two afferent fibers innervating each organ or stitch were recorded during accurately controlled mechanical, electrical and combinations of mechanical and electrical stimulation.

Electrical stimulation with sinusoidal potential variations produced sinusoidal variations of instantaneous firing rate (IFR) of the fibers. In contrast, mechanical stimulation with sinusoidal water movements produced asymmetric IFR variations. A frequency-dependent phase lag of the neural responses reslative to the stimuli were found for both types of stimuli. The responses to combinations of mechanical and electrical stimuli indicate that a multiplicative interaction as opposed to an additive interaction occurs between the two stimuli. This latter finding indicates that mechanical and electrical stimuli interact at a stage of the transduction process which precedes the generation of action potentials.

The results of the electrophysiological experiments are consistent with the notion that neural excitation in hair cells can be cosidered a two-stage process. The first stage consists of the generation of receptor potentials by mechanically-induced impedance changes that modulate continuous resting currents through the hair cells. The second stage of the process consists of a current-induced modulation of neural transmitter release at the synapses between hair cells and afferent nerve endings.

The results of modeling studies aimed at estimating the amplitude and phase of current variation through the hair cells for various stimulus combinations are qualitively consistent with the experimental fidings. Nonlinearities in stimulus-response relations and differences between the predicted and experimentally measured phase of neural responses are the main quantitative discrepancies. These discrepancies indicate that electrophysiological features such as membrane capacitance, voltage-dependent membrance impedance and synaptic properites will have to be included in future models in order to improve valuable insight into the process of coding of acoustic information by hair cell systems.

This research was supported by grants from the Deafness Research Foundation and the National Institutes of Health.

# THE LATERAL-LINE ORGAN AND SOUND RECEPTION

**Olav Sand**

Is sound an adequate stimulus for the lateral-line organ? A critical review of the relevant literature does not lead to an unambiguous answer to this question, in spite of numerous experiments in the field.

Previous reports have showed the lateral-line organs to be sensitive to near field vibrations, with optimal frequency range between 50 and 100 Hz and threshold values down to $10^{-7}$ cm. Particle displacements of this magnitude in the far-field for 70 Hz correspond to a sound pressure of about +15 dB, which is far above the reported auditory thresholds in this frequency range in most fish. Furthermore, elimination of the lateral-line system does not elevate auditory thresholds or abolish directional hearing in the far field. However, most biologically significant sounds perceived by fish are certainly well above threshold intensity for the inner ear, and it is important to clarify if it is possible for fish to detect intense sound with the lateral-line system at some distance from the sound source. If this was the case, the fish could extract more information from the sound and the directional hearing might be improved.

In previous electrophysiological experiments testing lateral line sensitivity to vibrational stimuli, the organ was either vibrated directly or the stimulus caused relative movements between the water and the fish. However, if the fish is freely positioned a few body lengths from a sound source, the fish and surrounding water will vibrate with approximately the same phase and amplitude. The dense otoliths will vibrate with a phase lag, creating shear movements between otoliths and maculae, whereas the lateral-line organs lack similar dense structures. It is thus difficult to imagine how these organs may be stimulated by the gross vibration of fish and surrounding water in a sound field at some distance from the source. However, the swimbladder will be the center for a local nearfield which could possibly stimulate the lateral-line system when the fish is exposed to sound.

In an attempt to elucidate these questions, I record from the trunk lateral-line nerve in the roach (Rutilus rutilus) with implanted electrodes. The degree of synchronization between the multi-unit nervous activity and the sinusoidal stimuli is used as a measure for the response. Three different experimental situations are compared. 1) Near-field stimulation caused by a vibrating sphere close to the organ. 2) Sound stimulation with low p/v ratio, causing simultaneous vibration of the fish and the neighboring water column. 3) Sound stimulation with high p/v ratio.

The two latter situations are obtained using a rigid walled metal tube with a sound projector at each end. Several previous authors have also utilized the possibility to vary the ratio between particle motion and sound pressure within wide limits in such a tank by altering the phase difference between the driving voltage to the projectors.

The experiments are not finished yet, and I have therefore chosen to present only the background for the study and not to give any detailed results in this summary.

# CENTRAL PROCESSING OF ACOUSTICO-LATERALIS SIGNALS IN ELASMOBRANCHS

**B. L. Roberts**

A feature that is believed to unite the various sense organs of the acoustico-lateralis system is the projection of the primary afferent fibres to a common hindbrain centre, the 'acoustic tubercle'. For elasmobranch fishes detailed information on the organization of this part of the hindbrain has become available in the last few years so that it is now possible to determine the characteristics of the central analysers of the various sensory modalities. In contrast to this structural detail there is little information on the neuronal activity of these regions so another aim of this presentation will be to define those questions that can be pursued by future experimentation.

The sensory fibres of all components project as parts of nerves VII, VIII and X to the ipsilateral hindbrain, to reach rostrally as far as the cerebellar peduncle and caudally to the medulla/spinal cord junction. In their passage the head and body lateral-line fibres make synaptic termination on neurons that occupy much of the lateral wall of the medulla, the dorsal surface of which is covered by a layer (the 'cerebellar crest') of fine unmyelinated fibres. These axons come from granule cells of the lateral portions of the auricles which are, in turn, driven by lateral-line input. The neurons that are adjacent to the crest (in the dorsal and intermediate nuclei) are large multipolar cells which have dorsally-directed dendrites that connect with the crest axons, while the ventral dendrites receive primary lateral-line fibres. The output of these nuclei is channelled forward to midbrain centers.

The neurons that are driven by VIII fibres lie deeper in the medulla and for the most part are not associated with crest axons. Much of their output goes to the spinal cord: some of these cells are electrotonically coupled to vibration-sensitive afferents.

Thus the anatomical organization indicates several features: the separate projection areas for the different sensory modalities; the possibility of interaction at this level because of overlap of dendritic fields with adjacent terminal fields; the absence of bilateral interaction; the considerable projection of nerve VIII centers to the spinal cord in contrast to the ascending lateral-line projection; and, most striking of all, the fact that lateral-line centers (both electro- and mechano-) involve a cerebellar-like organization which is totally absent from most of the centers related to nerve VIII. The possible features of lateral-line analysis that require such complexity will be considered in relation to current ideas of cerebellar function.

At present we have only limited data about second-order neuronal activity but it appears that lateral-line centers act as low-pass filters that project low-frequency signals; that they retain the directional responses of the peripheral end organs and that, perhaps surprisingly, they incorporate considerable convergence of the primary input. This will limit spatial resolution but will improve signal to noise ratio and overall sensitivity.

Much of the 'noise' in acousticolateral signals comes from an animal's own movements and it has been suggested that it is the role of the efferent system to counteract this. This concept will be examined tha the importance of the efferent impact will be reconsidered.

## PHYSIOLOGY OF THE SACCULAR AND LAGENAR NERVE.

**Richard R. Fay**

The literature on the discharge patterns of single units of the saccular and lagenar branches of the 8th nerve in fishes is reviewed, and new published and unpublished data from my laboratory on the goldfish 8th nerve are summarized.

Single units are "tuned" in the sense that the best excitatory frequency and the bandwidth of response varies among cells within an individual animal. There appear to be two distinct populations of saccular neurons, one tuned in the 300-800 Hz range, and one tuned to frequencies below 200 Hz. These tuning and bandwidth measures vary considerably, however, depending upon: 1) the response measure used, 2) the criteria for a response, and 3) the impedance of the impinging signal. Regarding the latter point, it appears that a cell's frequency selectivity for "acoustic" stimulation largely disappears for direct vibratory stimulation.

The sensitivities of goldfish saccular and lagenar units to direct vertical vibration of the the head are similar and show a monotonic increase between 20 and 200 Hz. Behaviorally measured sensitivity under nearly identical conditions corresponds well to the single unit data, but is from 20 to 60 dB above that measured for cod (Chapman and Hawkins, 1973) in a free field.

Both saccular and lagenar units appear to be directionally sensitive to a vibratory stimulus with a distribution of "best directions" which is wider than predicted on the basis of hair cell orientation patterns for the saccule. The phase relations between stimulus and response also show wide variation among saccular and lagenar neurons which is not easily predictable from the hair-cell orientation patterns. In response to acoustic stimulation, saccular neurons tuned to high frequencies show the predicted bimodal distribution of stimulus-response phase angles only at frequencies near 400 Hz. At higher and lower frequencies, the distributions broaden and tend to become flat.

Saccular neurons differ considerably in spontaneous activity rates and patterns, in adaptation rates, and in their ability to "follow" temporal variations in envelope. While some neurons follow 20 Hz amplitude modulation rates best, others may follow best at other rates up to 300 Hz. The ability to follow envelope structure is related to the neuron's bandwidth of sensitivity to pure tones. Some neurons may clearly respond to amplitude fluctuations in continuous tones as small as 0.1 dB, illustrating a case of temporal contour enhancement. For certain complex harmonic signals, some neurons discharge at a rate which is clearly related to phase relations among the harmonics, and not to the signal's amplitude spectrum.

Generally speaking, it is apparant that the inter-neuron variation in response properties in the goldfish saccular nerve is far greater than that observed in the 8th nerve of mammals and birds, and, in fact, is more like that seen in mammalian cochlear nucleus. A significant challenge now exists to specify the cellular morphological correlates of this variation. In any case, it is now clear that the "simple" otolithic ear of the fish somehow codes a wide variety of stimulus features and dimensions in the spatial and temporal discharge patterns of its innervating neurons.

# FREQUENCY DISCRIMINATION IN TELEOSTS - CENTRAL OR PERIPHRAL?

**Per S. Enger**

In previous conditioning experiments, the ability for pitch discrimination has been found to be around 3% and 9% for Ostariophysi and non-ostariophysine fish species, respectively. Experiments performed on the sculpin (Cottus scorpius) will be reported. This species lacks a swimbladder, therefore, the adequate stimulus is particle displacement or velocity, not sound pressure. The particle velocity was measured. A pitch discrimination ability of about 8% for the optimal frequency of 100 Hz was found. Control experiments have ascertained that the training was performed on frequency differences, not on differences in particle displacement or sound pressure.

Pitch discrimination in fish is based either 1) on the volley principle where the analysis is performed in the central nervous system or 2) on the existence of a crude frequency analyzer in the ear, or 3) on a combination of these two possibilities. Studies in progress on the degeneration of hair cells in the codfish ear after intense sound exposure, give support to the second or third of these possibilities. Various sound frequencies give cell degeneration in different -although overlapping - areas of the sensory maculae.

# MODELS OF ACOUSTIC LOCALIZATION

**A. Schuijf** and **R.J.A. Buwalda.**

In this presentation the general traits of systems for acoustic localization by fishes will be considered, rather than the detailed relationships between the function and morphology of the labyrinthine parts and their functions. Only models of localization involving the labyrinths are considered in view of the complete lack of evidence that the lateral line participates in localization of sound sources at distances over a few decimeters.

One objective of the model building is to select a model of the greatest possible generality which describes the common principles of directional preception of sounds in different kinds of fishes. To synthesize such a model the psychoacoustic data, i.e. the dynamic interrelationships between the acoustic input variables and directional responses, must be given for some representative species of fish: fishes with swimbladders -specialized coupling (ostariophysines) or not - or without swimbladder (in particular sharks). The general model presented here - called the "coherent detection model" - should concisely summarize information from the whole body of behavioral data in such a way that predictions can be made as to the responses of the system on "new" stimulus conditions. For fishes with swimbladders the external particle acceleration $\vec{a}(t)$ in the sound wave provides directional information and the external acoustic pressure acts as the non-directional, coherent reference signal input. This frame of thought will be elaborated during the lecture.

A second objective of the modelling is to generate possible solutions of the functional organization of the acoustic oreintation system consistent with the behavioral data and the morphology. The selection of likely solutions will be discussed. Topics concerning subsystems of the directional detection process to be discussed are: swimbladder models, otolith mechanics and transduction processes (see Hawkins and Horner), bilateral and unilateral aspects of the processing, and extraction of relative timing.

# SEGREGATION OF DIRECTIONAL AND NON-DIRECTIONAL INFORMATION IN TELEOSTS

**R.J.A. Buwalda**

A generally accepted theory of hearing in fish has it that the teleost swimbladder promotes an efficient coupling of acoustic energy into the labyrinths. The involved pressure-to-motion transformation renders both ears effectively a single pressure-sensitive receptor and should thus severly impair the bilateral labyrinth's capacity of extracting directional information from the incident particle motions. Recent proof of directional hearing in fish via the labyrinths has cast doubt on this argument. Further experiments have disclosed that, far from impairing acoustic localization, the essentially non-directional pressure input is even necessary for eliminating the $180^{\circ}$ directional ambiguity conveyed by the particle motion input, via a phase comparison between these inputs. Such findings indicate that teleost fish possess, on the one hand, ways of segregating the directional and non-directional information, and, on the other hand, interactive processing of these inputs for phase analyzing purposes.

The present contribution reports on perceptual segregation between pressure and motion by the codfish under conditions that permit extensive, independent manipulation of the relevant acoustic variables. Cross-modality masking experiments provide in sound detection thresholds and angular discrimination thresholds that indicate a very high degree of segregation, compatible with the notion of selective peripheral pressure- and motion-sensitive detectors. As the limited available physiological evidence provides no clue to this problem as yet, the various mechanisms that could explain this peripheral selectivity for one input over another are discussed from a theoretical point of view. A comparative point of view is taken when the situation in codfish is compared to that in ostariophysine fishes, where both morphological and physiological evidence seems to validate the idea of peripheral segregation of directional and non-directional information through a functional organization of the labyrinth.

# SOUND PRODUCTION IN THE NAKED GOBY, GOBIOSOMA BOSCI (GOBIIDAE)

**Michael H. K. Mok**

Male Gobiosoma bosci emits clicking sounds under diverse interacting conditions including agonistic and non-aggressive interactions with other males. Sounds are also produced during interactions with females which lead to further spawning activities even if courtship does not eventually take place. Sound emission synchronizes with either sideward shaking of the head or backward pulling of the body associated with slightly upward flipping of the tail. The average duration of the sounds is 27.0 msec. Repetition rate, intensity, and distribution of the major portion of the sound energy are variable. The sounds are non-harmonic and most sound energy is distributed from 2 to 4 KHz. The high frequency levels of the sounds suggest the stridulatory producing mechanism. The recipients of these acoustic signals do not respond immediately in most cases but remain stationary in a non-aggressive posture. The sounds produced toward the ripe females are usually associated with slight body shaking, pectoral flipping, and head down. This performance frequently allows the male to approach the ripe females to a short distance. In some instances, it attracts the ripe female, a response which in turn increases the repetition rate of sound production in the male. The behavioral patterns and the sounds considered as a whole are not performed toward a male recipient. The acoustic signal alone or the signal associated with the stereotyic behavior of the male may serve as an attractant to the ripe females. The observed response of the recipients to these signals make it plausible that they do not act as a threatening signal.

# MISMATCH BETWEEN SOUND PRODUCTION AND HEARING IN THE OYSTER TOADFISH

**Michael L. Fine**

It is generally accepted that a match exists between the spectral properties of an animal's mating call and the most sensitive range of its hearing. Such correspondance will maximize the distance over which individuals can communicate. Extracellular recordings from the saccular branch of the VIII nerve, indicate that the oyster toadfish displays no such match. Neurons are tuned to low frequencies between 25 and a 90 Hz, with a strong modal peak at 40 Hz. The boatwhistle, the male mating call, has a fundamental frequency ranging from under 150 Hz to over 250 Hz depending on temperature and assumed hormonal state. Thresholds of the most sensitive neurons to 200 Hz tone bursts are more than 20 dB down compared to sensitivity at 40 or 90 Hz. The boatwhistle, however, is a loud call (40 dB re: 1 dyne/$cm^2$ at 1 meter) and the fish appears to hear it using the tails of tuning curves of neurons tuned to lower frequencies.

## HEARING VARIABILITY AMONG DIFFERENT FISH SPECIES

**S. Coombs**

Behavioral techniques have been used to measure basic hearing capabilities as well as more complex analytical capabilities for several teleost fish species chosen on the basis of anatomical differences in their peripheral auditory systems. Threshold sensitivity and frequency range of hearing in addition to the masking effects of tones on the detection of pure tone signals have been characterized with standard psychophysical functions -- the audiogram and the psychophysical tuning curve (PTC). Both qualitative and quantitative differences in auditory functions generated for the different species demonstrate significant interspecific variability in hearing capabilities which, in some cases, may tentatively be correlated with anatomical differences in the auditory system.

Data were obtained for two marine fish from the family Holocentridae, Adioryx Xantherythrus and Myripristis kuntee, plus one freshwater fish from the family Notopteridae, Notopterus chitala. Peak sensitivity for Adioryx was found to be around -28 dB re: 1 dyne/$cm^2$ between 500 and 600 Hz, whereas best sensitivity for Myripristis was as low as -50 dB over a much broader range of frequencies (300 - 2000 Hz). Similarly, while the low frequency end of the auditory range was at least 100 Hz for the two marine species, the high end extended only up to 800 Hz for Adioryx, but up to 3000 Hz for Myripristis. On the average, hearing sensitivity and frequency range of hearing for Notopterus appeared almost identical to that of Adioryx, although there was substantially more inter- and intra-individual variability in threshold values for Notopterus than for either of the two marine species.

PTC's generated with a 500 Hz signal for Notopterus were similar to those reported by Fay et al. (J. Exp. Biol. 1978, 74:83-100) for the goldfish, Carassius auratus, with peak masking occuring in two separate frequency regions: at the same frequency as the signal, 500 Hz, and also at 300 Hz. The sharply tuned, multi-peaked curves seen for Notopterus and Carassius are quite different from the rather broadly tuned, uni-peaked curved generated for Adioryx. While data for Adioryx show that masking of a 500 Hz signal is a relatively simple, inverse function of the frequency separation between masker and signal, masking in Notopterus appears more complex.

While all three species tested differ in both gross and ultrastructural features of the peripheral auditory system, both Myripristis and Notopterus have in common a non-homologous specialization of the anterior end of the swimbladder which results in a physical coupling between the swimbladder and the saccular endorgan of the inner ear. This condition differs markedly from that found in Adioryx, where the anterior end of the swimbladder effects no such connection and is situated some distance away from the ear. It is possible that differences in the swimbladder/inner ear relationship may in part account for differences in hearing sensitivity between Adioryx and Notopterus. Although sensitivity data for Notopterus appears to be inconsistent with this possibility, an unusual configuration of the saccular macula in this fish in relation to the swimbladder connection may explain this anamoly.

# NEUROPHYSIOLOGICAL MECHANISMS OF INTENSITY DISCRIMINATION IN THE GOLDFISH: E.H. WEBER'S OTHER CONTRIBUTION TO HEARING

**L. Hall, M. Patricoski** and **R. Fay**

The detection of changes in sound intensity ($\Delta$ I) is one of the fundamental auditory capacities for which auditory systems have presumably been "designed" throughout evolution. Questions of the neural representations of sound intensity, and the ways these are processed by the brain are basic to an experimental analysis of sensory coding. The literature contains two major observations on the capacities of human observers to make intensity discriminations: 1) The ratio $\Delta$ I/I is approximately constant for noise signals within a wide range of I values (i.e., Weber's law holds). 2) For tone signals, a slight deviation from $\Delta$ I/I constancy exists such that the ratio declines somewhat at larger I values (i.e., that there is a "near miss" to Weber's law). The questions which have arisen from these observations are: 1) What aspect of neural activity accounts for Weber's law behavior? and 2) Why is there a "miss" to this law for tones? In this paper, we report a combined behavioral and physiological approach to these questions using the goldfish auditory system as a model. Hypotheses advanced to explain the human behavior may be partially evaluated to the extent that both Weber's law and the "near miss" are thought to arise from the mechanical response patterns of the mammalian cochlea. These mechanisms are thought not to operate the same way in the goldfish ear, and the relations between the ear's structure, the psychophysical capacities and the neurophysiological coding of intensity differences in the goldfish may shed some light on the processes operating in man and other species. These experiments, therefore, measure the goldfish's capacities for auditory intensity discrimination under a variety of conditions, and charactrize the response of single neurons of the auditory nerve to intensity changes under identical stimulus conditions.

Goldfish were classically conditioned to suppress respiration upon presentation of sinusoidal amplitude modulation (2.5 Hz) impressed upon continuous carriers (wideband noise or an 800 Hz tone) at 15, 25, 35, 45, and 55 dB abve threshold. Intensity difference limens (dB) were measured as a function of sound pressure level for the two carrier types.

In physiological studies, goldfish were restrained in a similar acoustic field and activity of single neurons of the saccular nerve was recorded. Measures of spike rate modulation were compared with the modulation depths of the stimulus to characterize the "gain" of the transduction mechanism at a variety of sound pressure levels for both tones and noise.

For noise carriers, the goldfish I measures averaged between 3 and 4 dB and were independent of sound pressure level (SPL). This independence indicates that Weber's law holds under these conditions. For tonal carriers, $\Delta$ I is a steadily declining function of increasing sound pressure level, with values below 0.5 dB for SPL's of 45 and 55 dB, a figure well below that measured for other vertebrates. The neurophysiological results show that the coding of amplitude changes for tones is enhanced at the periphery, and that the degree of enhancement increases with SPL. This enhancement does not occur for noise carriers. This correspondence between the behavioral and neurophysiological results indicates that discharge patterns within neural channels can account for the discrimination acuity, for the fact that Weber's law holds for noise signals, and for the fact that Weber's law misses for tonal signals. This correspondence occurs in the absence of a mammalian cochlea and shows that a cochlea-like frequency analysis may not be necessary for theoretical explanations of intensity discrimination behavior.

# SOUND COMMUNICATION IN FISHES

**Arthur A. Myrberg, Jr.**

One of the most intriguing aspects of studying the social behavior of animals is that sooner or later the topic of communication is confronted. The term, confrontation, appears accurate here since the topic centers on an extremely elusive concept. Although a voluminous literature has been devoted to the concept, one becomes rapidly confused if that literature is perused to obtain the meaning of communication. The term apparently means totally different things to many people.

My charge for the present symposium forced to seek a clear and useful definition of communication since to define the process is to establish its boundaries; and if such boundaries are diffuse or lack meaning, any effort relative to review will most likely be meaningless as well.

Upon completing that task, I turned to the bio-acoustical literature on fishes and found that few studies actually tested directly facts of the communication process. Although many studies had mentioned communication, most dealt with it in terms of suggestions, speculations, possibilities, or reasonable, but as yet untested, interpretation. Thus, I faced a dilemma, to provide an extremely brief review, using for the most part examples already included in the recent review by Fine et al. (1977), as well as those by Tavolga (1968, 1971) or attempt something else - that being to describe a reasonable framework upon which analysies of communication might develop in the future. I selected the latter goal.

To accomplish this, three points had to be made: 1) explain my view of communication, 2) provide a framework consistent with that view, and 3) illustrate that framework by examples from the available literature.

The paper will begin with a brief introduction, emphasizing the confusion that the concept of communication presently 'enjoys'. That will be followed by a discussion of the various constraints or criteria which have been used by workers in defining the communication process. I will then attempt a definition of the process which is based on adaptation and function. This will be followed by a description of a theoretical framework which hopefully will aid not only in analyzing specific communication systems but also in providing an impetus for renewed interest in bio-acoustical studies of the process, as a whole. The paper will conclude by illustrating that framework by example from the literature on fishes and by suggesting, as well. areas where future study appears warranted.

# NEURAL MECHANISMS OF SOUND PRODUCTION

Leo S. Demski

This paper will review available information on brain mechanisms underlying the production of sounds used in fish communication, including some recent results on electrically evoked croaking in Micropogon undulatus. For purposes of discussion, neuronal mechanisms of sound production will be considered under several different functional categories (lower motor, higher motor, motor initiation, sensory integrative and motivational systems).

Lower motor refers to primary sonic motor neurons and the muscles they innervate. Most of the systems studied in fishes involve occipital nerves. Only the sonic muscles in the Sciaenids appear to have a different nerve supply, in this case derived from branches of spinal nerves. This poses an interesting question concerning the mechanims of development of these seemingly very different motor pathways in animals such as toadfish and croakers in which the same area of the midbrain appears to be controlling sound production (brain stimulation evokes sounds from areas in the torus semicircularis near acoustical-lateral lemniscus in both species). It can be suggested that this sonic midbrain area (SMA) developed in connection with midbrain acoustic mechanisms which appear to be at least partly homologous throughout the vertebrates. The SMA probably receives direct input from the adjacent auditory areas and may be thought of as the next link in a sensorimotor pathway for acoustic communication. Presumably the SMA triggers sound production by controlling motor systems that have evolved independently in several groups of vertebrates.

Recent findings in birds and amphibians indicate that sonic motor neurons concentrate radiolabeled androgens. The suggestion is made that the sex hormones directly influence the production of sounds at the lower motor level and that this may account for many seasonal and sex related differences in bird songs and from mating calls. It is not known if a similar system is present in fishes such as toadfish in which only males produce courtship sounds (boatwhistles) under natural conditions but in which females maintain the neural mechanisms for the calls since it can still be evoked using brain stimulation.

Higher motor areas or "call pattern generators" are virtually unknown in fishes. Based on brain stimulation experiments and some of Bennett's electrophysiological data, I have suggested that the call duration and frequency control mechanisms in toadfish were located somewhere in the medulla and lower midbrain tegmentum. Precise electrophysiological and anatomical studies are needed to better define these higher motor areas in fishes. There is a good possibiity that mapping using labeled androgens might also help to identify these areas in toadfish since the duration and posibility also the frequency of the boatwhistle call has a seasonal variation that is not attributable to temperature effects but rather more probably to hormonal changes.

The major motor initiation areas or "trigger zone" appears to be the SMA. This is based mostly on the results of brain stimulation studies in fishes and a vareity of lestion, stimulation and anatomical studies in other vertebrates. Perhaps the strongest support for this idea comes from studies on squirrel monkeys which indicate that the caudal periaqueductal grey and adjacent midbrain tegmentum (a probable homolog of the fish SMA) must be intact for species-typical calls to be evoked by electrical stimulation in sonic areas both rostral and caudal to this region of the midbrain. It is also noteworthy that sonic midbrain regions contain androgen-concentrating neurons in both songbirds and amphibians. Thus, male sex hormones could affect the level of singing or calling by perhaps changing the thresholds for activation of calls that normally trigger the lower motor mechanisms. It remains to be determined whether or not androgen-concentrating neurons are present in the midbrains of sound producing fishes.

Based on brain stimulation experiments, the sensory integrative regions most involved in the control of sound production in fishes include the auditory areas in the midbrain and medulla and perhaps the nucleus isthmi and certain regions of the thalamus. It is likely that these areas mediate their effects via connections with the SMA. So-called motivational systems may also influence sound producition by modulation of the activity of cells in the SMA, in this case as part of a complex neural pattern underlying such behaviors as courtship or territorial defense. The preoptic area and hypothalamus fall into this catagory. The preoptic area in particular is known to cotain numerous androgen-concentrating neurons and may therefore represent one of the substrates for the seasonal regulation of sonic activity in male teleosts.

# THE UTRICLE IN ICTALURUS PUNCTATUS

**David B. Jenkins**

Light microscopy and scanning electron microscopy were utilized to study the utricle in the channel catfish, Ictalurus punctatus. The utricle lies ventrolaterally to the brain in a shallow depression in the cranial floor; its anterior end angles laterally, approximately $45^{\circ}$ from the mid-sagittal plane. Within the utricle the lapillus, separated from the utricular macula by an otolithic membrance, fills most of the anterior part of the chamber. A deep groove on the anterior and anterolateral parts of the undersurface of the lapillus extends dorsolaterally to form a notch in the lateral edge of the otolith. The underlying otolithic membrane, which covers the entire macular surface, is thickened anteriorly and fills the groove in the lapillus. Posteriorly the membrane is thinner. Only the taller processes of the hair cells appear to be attached to the otolithic membrane (most obvious on the periphery of the macula where the membrane has a trabecular appearance). More centrally the bundles project into cavities in the undersurface of the membrane.

The macula covers most of the floor of the utricular recess. The neuroepithelium on the anterior and lateral margins is higher than that of the remainder of the macula; the lateral continuation of this region, the lacinia, extends onto the wall and passes dorsally to the utricular roof. This entire area is associated with the thickened region of the otolithic membrane. The morphological polarization of the macula is similar to the "typical" pattern reported in other fish with the line of opposition (cells polarized toward the line) lying parallel to the anterior margin of the macula and extending into the lacinia. Several different types of hair cell bundles (determined by relative length and number of processes) were evident in this study.

Due to speculation in other reports that specific regions of the macula may respond to different stimuli (in particular the lacinia), the hair cell bundle types and their distribution in I. punctatus will be compared with data from the utriculi in other fish and with other sensory regions of the nner ear. In addition regional variations of the relations of the otolithic membrane and lapillus to the macula will be discussed.

# ROLE OF THE LATERAL LINE IN FISH SCHOOL STRUCTURE AND DYNAMICS

**Brian L. Partridge**

A number of studies have investigated aspects of the sensory basis of fish schools and their internal structure or have speculated about the function (survival value) of schooling. Most authors have concluded that vision is the primary sensory modality employed in schooling and that other modalities such as the lateral line are relatively unimportant. In this paper, I shall demonstrate that the role of the lateral line in schooling is far greater than has been previously recognized. Aditionally, I shall tie together results from a number of recent studies to show that the structure of schools results from the constraints posed by the sensory capabilities of the fish and, ultimately, from the function of schooling as an anti-predator device.

Experimental evidence does not support the suggestions that fish school structure results from fish packing into the smallest possible space or from the hydrodyanmics of schooling. Fish take up those positions at which they can most rapidly respond to velocity or heading changes by neighbors thus facilitating collective decision making by the school. Altering the sensory input to a fish by lateralis-section or temporary blindfolding causes large changes in the positions the fish takes up with respect to their neighbors. Separate experiments on the sensory capabilities of saithe (Pollachius virens) demonstrate that the changes exhibited by sensorily deprived fish result in their taking up those positions with respect to their neighbors at which they can best determine their headings and velocities by vision or lateral line alone.

# THE SWIMBLADDER AND SOUND DETECTION

**J. H. S. Blaxter**

The importance of the swimbladder in sound perception is shown by experiments where hearing is impaired after withdrawing swimbladder gas or enhanced by placing gas-filled structures near the head of a fish lacking a swimbladder. The wider frequency response and greater sensitivity of the Ostariophys and some holocentrid fishes, which posses various types of coupling between the swimbladder and inner ear, or of clupeoids with otic bullae, provide further circumstantial evidence for the value of gas-filled structures in improving hearing.

Swimbladders reradiate sound pressures as particle displacements. Although these may exceed the amplitude of particle displacements received directly from the source, expecially in the far field, the loss of a directional sense is not complete. The natural resonance frequency of the swimbladder is often above the upper frequency limit of the fish. This may result from a number of factors such as available space within the body cavity or from the need for the swimbladder to perform other functions in buoyancy, sound production or as a gas reservoir.

Many fish make regular diel vertical migrations of tens to hundreds of meters and undergo hydrostatic pressure changes of several atmospheres. In such circumstances most swimbladders change in volume roughly according to Boyle's Law. Nevertheless they seldom act as simple gas-filled, compliant structures. They are usually attached along most of their dorsal surface to tissue underlying the rigid vertebral column and they are constrained by a muscular body wall. They are usually angled within the body cavity being higher at the anterior end.

Probably few fish can compensate by gas secretion or resorption for the volume changes experienced by the swimbladder diel vertical migrations. There will always be a substantial lag. There is evidence that fish have some control over swimbladder function during changes of hydrostatic pressure which is unrelated to the speed of gas exchange. Some fish can maintain pressures above ambient within the swimbladder, others show changes in resonance frequency with depth which cannot be related to the expected changes calculated on the basis of Boyle's Law. Hydrostatic pressure sensitivity in gadoids is thought to lie in stretch receptors in the swimbladder wall or overlying structures; yet the loss of pressure sensitivity after a dive is very short-lived and returns to normal long before gas secretion could have restored the volume and tonus of the swimbladder wall.

X-ray studies and other experiments on a gadid the saithe, and two clupeids the menhaden and herring, show that the longitudinal axis of the swimbladder is important in determining how it contracts after an increase of hydrostatic pressure. If the fish is horizontal or in a shallow dive gas collects at the anterior end of the swimbladder. During steeper dives the whole swimbladder may flatten or gas may collect posteriorly. On assuming a horizontal position the gas moves anteriorly again. There is thus a strong tendency for gas, if limited in volume, to collect near the head. This ensures that the gas is in the best place for stimulating the labyrinth in fish like saithe and that it is available as a reservoir for the otic bullae in clupeoids. There is an interesting difference in the swimbladders of herring and menhaden. That of the herring lies at a shallow angle but has a very tough non-compliant anterior end. This ensures, after a pressure increase, the preferential location of gas at the point nearest the ducts to the otic bullae. The shorter, deeper-bodies menhaden has a more steeply-angled swimbladder with a thin-walled compliant anterior end. During an increase in pressure, gas will tend to collect anteriorly, near the ducts to the otic bullae, even if the dive is quite steep. The need for the toughened anterior swimbladder wall as found in the herring is therefore obviated.

# THE OCTAVUS NUCLEI IN ACTINOPTERYGIANS

**Catherine A. McCormick**

In a previous study of the octavolateralis area in the bowfin, Amia calva (Holostei) it was reported that this area is organized into dorsal and ventral longitudinal cell columns which receive lateral line and eighth nerve input, respectively (McCormick, in press). The dorsal cell column contains two first order lateral line (lateralis) nuclei, whereas the ventral cell column contains four first order octavus nuclei. The octavus nuclei were designated, in an antero-posterior direction, the anterior, magnocellular, descending, and posterior octavus nuclei.

A normal cytoarchitectural study of the octavus area in other actinopterygians was undertaken in order to define the patterns of variation that occur within this portion of the octavolaterali area. Species belonging to each actinopterygian superorder were examined: Polypterus palmas, Calamoicthyes calabaricus (Polypteriformes); Scaphirhynchus platorynchus (Chondrostei); Gymnothorax moringa, Osteoglossum bicirrhosum, Salmo gairdneri, Carassius auratus, Ictalurus melas, Ictalurus punctatus, Sorubim lima, Lepomis cyanellus (Teleostei). The four octavus nuclei experimentally defined in Amia are found in all of the fish examined. In teleosts an additional octavus nucleus, nucleus tangentialis, is also present and lies lateral to nucleus magnocellularis. Among many actinopterygians the octavus area thus appears to have a common organizational scheme, although relatively few teleosts have been examined. This finding contrasts with older notions of the evolution of the actinopterygian octavus area, and indicates that this area is more complexly organized than was previously recognized.

In addition to containing afferent fibers coursing to the central nervous system, trhe eighth and lateralis nerves also contain efferent fibers coursing to the periphery. It is possible to localize the cell bodies of these axons by means of the retrograde transport of horseradish peroxidase (HRP) subsequent to its injection into the eighth or lateralis nerves. In Amia, the majority of the efferent octavus cells are located at the floor of the fourth ventricle at and medial to the sulcus limitans (McCormick and Braford, 1979). A few efferent cells are also present within the caudal portion of nucleus magnocellularis. The larger population of efferent cells has a diffuse organization, and extends from a level just caudal to the entrance of the posterior ramus of the eighth nerve to a region just caudal to the entrance of the glossopharyngeal nerve. In Amia, the efferent cells of the posterior lateralis nerve lie among this latter population of octavus efferent cells, although the majority of these cells are clustered near the entrance of the posterior lateralis nerve. Thus, it is not certain whether a single efferent cell can contribute axons to both the posterior lateralis nerve and the eighth nerve, or whether separate octavus and lateralis efferent cells are present. Efferent lateralis and octavus cells are typically fusiform or multipolar in morphology, have large diameters (50-80u), and large dendritic extents. It is likely that efferent lateralis and octavus cells form a population distinct from the motor nuclei of the facial, glossopharyngeal, and vagus nerves. This has been experimentally confirmed in the case of the motor cells of the glossopharyngeal nerve, which occupy a position ventral to that of the lateralis and octavus efferent population.