Central and Peripheral Mechanisms of Teleost Sound Production

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SYNOPSIS. Fishes have a variety of peripheral mechanisms for sound production. These can be categorized as: (i) hydrodynamic mechanisms related to swimming; (ii) stridulatory mechanisms in which portions of the body strike against each other; and (iii) swim bladder mechanisms which produce sounds by contraction of muscles which alter swim bladder volume. The sounds produced by hydrodynamic and stridulatory methods usually consist of broad-band noise while swim bladder sounds generally contain a fundamental frequency which is related to the rate of muscle contraction. Harmonics can be present in swim bladder sounds, but they may be a function primarily of the environment rather than the sound-producing mechanism. The precise role of the swim bladder is not clear although it probably acts as a broadly tuned sound amplifier. In this regard, the contribution of the swim bladder as a vibrating sphere is discussed. The central mechanisms controlling sound production in fishes are best understood in toadfish of the genus *Opsanus*. As a synthesis of the findings in this field, a model of the neurological control of toadfish sound production is presented. Neuromuscular, central motor, and central integrative mechanisms are discussed.

INTRODUCTION

In considering the sonic mechanisms in the vertebrates, it must first be realized that the methods of sound production in aquatic species (with the exception perhaps

of marine mammals) differ considerably from those in terrestrial vertebrates. While the most common sonic mechanisms in tetrapods are based upon movement of air past a taut membrane, teleost sounds are produced by movement of bones or contraction of special sonic muscles. In many teleosts the sound produced by the particular sonic mechanism sets an air-filled taut membranous chamber, the swim bladder, into motion and this acts as an impedance-matching device between the fish and the water and "amplifies" signals. However, unlike the vibrating vocal cords and the various oral and nasal cavities, the swim bladder does not seem to significantly affect the spectral content of the signals (Skoglund, 1959; Tavolga, 1962, and others).

Perhaps as a consequence of limitations in the sonic mechanisms, the sounds produced by most teleosts are not nearly as complex as those found in tetrapods and no known sound-producing species produces the variety of sounds found in birds, mammals, or amphibians.

Sound production has been reported for a wide variety of teleosts (see Fish, 1954; Fish and Mowbray, 1970; Moulton, 1958, 1963; Tavolga, 1958, 1960, 1965, 1971) although the biological significance of the sounds is only known in a few cases (for example see Tavolga, 1958; Delco, 1960; Winn, 1964, 1967). In fact, many of the sounds produced by fish may have no biological significance but may be incidental to other aspects of the fish's behavior.

Sonic communication is of considerable importance to teleosts since in many cases it is the only effective means of relatively long-range, directional communication, especially where visibility is poor. Emphasizing the importance of sounds in fish behavior is the fact that many species of fish possess a well-developed sound detection system and are capable of detecting sounds up to several thousand Hz (Tavolga and Wodinsky, 1963; Popper, 1970; Tavolga, 1971; Popper and Fay, 1973. In addition, fishes can discriminate frequency (Jacobs and Tavolga, 1968; Fay, 1969, 1970) and intensity (Jacobs and Tavolga, 1967) and the goldfish is capable of detecting very short pulses with as great a threshold sensitivity as long duration signals (Popper, 1972). Although there is some speculation that fish cannot localize sounds over large distances (von Frisch and Dijkgraaf, 1935; van Bergeijk, 1964), recent evidence indicates that at least some species can home on a sound source from beyond a few meters (Richard, 1968; Myrberg et al., 1969; Popper et al., 1973).

Sound production mechanisms in fishes have generally been divided into several categories depending upon the mechanism involved (Fish, 1954; Tavolga, 1960, 1965, 1971). In order to maintain clarity we will use basically the same classification as used by the previous authors. Briefly the

first group of sounds, called swimming or hydrodynamic sounds, are broad-band noise (Moulton, 1960) resulting from turbulence produced as the fish swims and changes direction (Moulton, 1960; Tavolga, 1964) and also from internal movements in the fish (Moulton, 1960). The second group of sounds, stridulatory sounds, are produced by the striking of two hard objects such as teeth on coral or teeth against one another. The stridulatory sounds may also be produced by movement of specialized body parts such as spines in the dorsal fin or portions of the pectoral girdle against one another. The sounds generally consist of pulses produced by a striking together of the appropriate structures. In some cases the amplitude of these sounds may be increased by interaction with the swim bladder. Tavolga (1971) has called these sounds indirect swim bladder sounds. The third group of sounds are produced by highly specialized sonic muscles which contact, or are in close proximity to, the swim bladder. These swim bladder sounds are generally harmonic, with the fundamental frequency being the frequency of contraction of the sonic muscle. There are two subgroups within swim bladder mechanisms. In the intrinsic mechanisms, muscles involved are totally on the swim bladder. This is contrasted to the extrinsic systems where the muscles arise either on the cranium, pectoral girdle, or lateral body musculature and insert on the swim bladder or on some structure in very close proximity to the swim bladder.

The characteristics of fish sounds depend to a considerable degree upon which of the several sonic mechanisms are involved in the production of a particular sound. In cases where specialized fast-contracting muscles are involved, the sounds may have a fundamental frequency with or without several harmonics as in the boat-whistle sound of the toadfish, *Opsanus tau* (Fig. 1A). In other species with special musculature, the sounds may be rapidly pulsed as in the Atlantic croaker, *Micropogon undulatus* (Fig. 1B). In species where the sonic mechanism involves movement
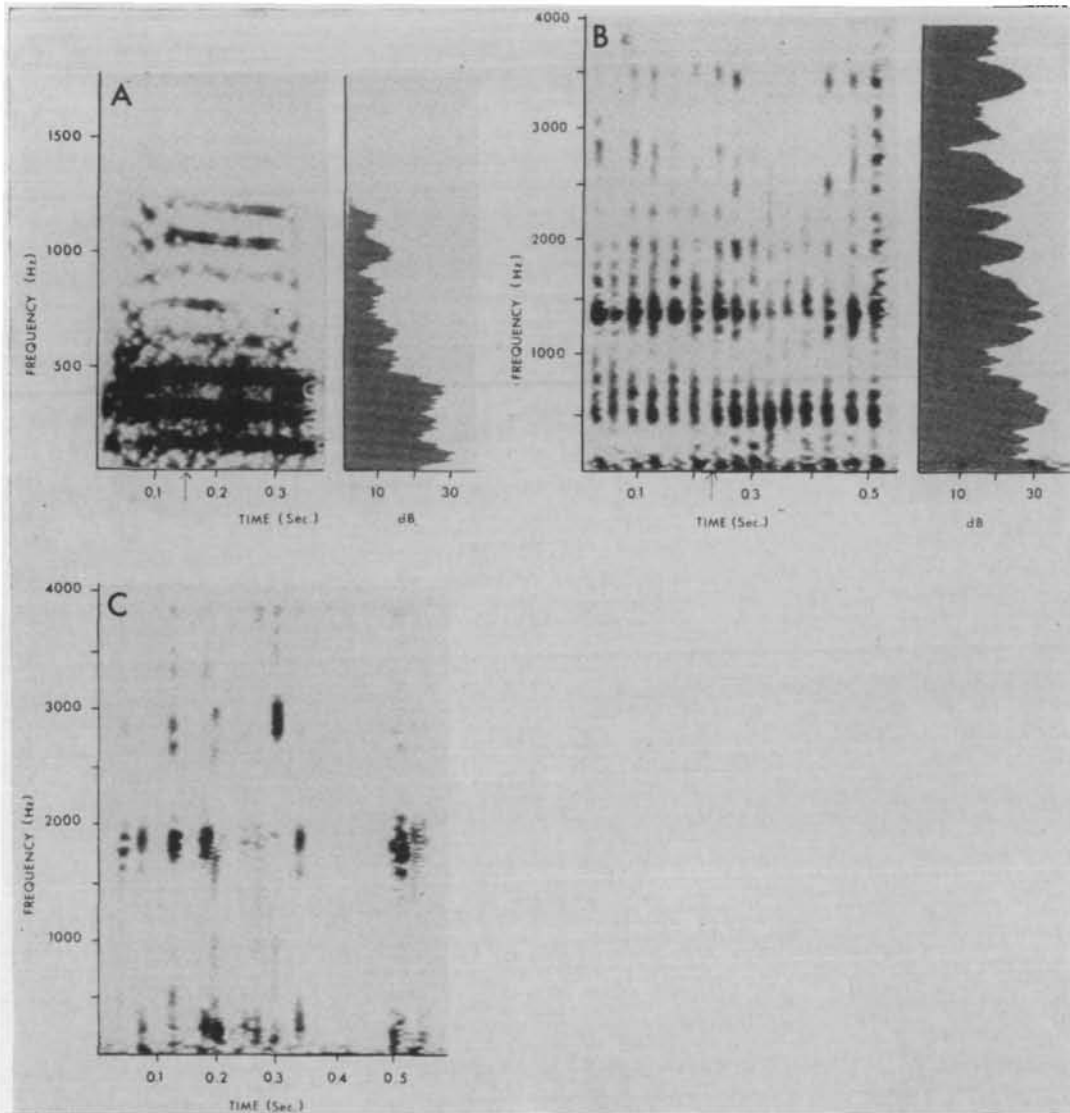
FIG. 1. Spectrograms of sounds of several species of teleosts. *A, Opsanus tau* (toadfish), boatwhistle sound. Arrow indicates point at which intensity section (right) was taken. The section shows relative energy at each frequency in the signal and indicates that the maximum energy is at the fundamental frequency with less energy present at the harmonics. *B, Micropogon undulatus* (Atlantic croaker), sounds produced by extrinsic muscles. *C, Scarus croicensis* (parrotfish), sounds produced by teeth hitting together. Each pulse is produced when the teeth strike. (Sound spectrograms were made from recordings accompanying Fish and Mowbray, 1970.)

of bones or striking of teeth, the sounds contain energy over a wide range of frequencies and appear on the sound spectrogram as pulsed noise (Fig. 1C, teeth striking together in the parrotfish, *Scarus croicensis*).

Investigations of sonic mechanisms in fishes have lagged considerably behind in-vestigations of fish sonic behavior. However, it will be seen that studies of selected species can tell us a great deal about sonic mechanisms in general. Although most of the information to date has been on peripheral mechanisms, it is apparent from work on electrophysiology of sonic mechanisms that the coding for sound production is a

central process (Packard, 1960; Tavolga, 1962; Demski and Gerald, 1972, and others). Data have recently become available on the central nervous system involvement in sound production and a discussion of these mechanisms has been included in this report.

PERIPHERAL MECHANISMS OF SOUND PRODUCTION IN FISHES

Swimming sounds

A number of broad-band sounds are produced by fishes during swimming. Although some workers (Shishkova, 1958) have suggested that these be called hydrodynamic sounds since they are produced by water moving over the body of the fish, Moulton (1960) has indicated that some of the sounds may come from movement of internal body structures and should be called swimming sounds. Moulton (1960) recorded sounds of large schools of *Anchoviella choerostoma* in open water and found that the most intense sound was produced when the fish were veering. Very little sound was produced by schools at rest. Moulton also found that the swimming and veering sounds contained energy up to 2,000 Hz while the bulk of the energy in resting sounds was below 1,000 Hz. Although Moulton did not analyze the precise source of these sounds, it is likely that a considerable number of the sounds were a result of the turbulence produced during swimming (Moulton, 1960; Tavolga, 1964). Investigations of jacks, *Caranx latus* and *C. ruber*, demonstrated that additional swimming sounds were a result of stridulation of the pharyngeal teeth, indicating that internal body sounds can contribute to the swimming sounds in fishes (Moulton, 1960).

Stridulatory mechanisms

Stridulatory sounds generally consist of broad-frequency pulses produced by the striking or scraping of two hard objects against one another. Probably the most

commonly heard sounds in this category are those produced during feeding as the teeth grind together and the food items are crushed (Fig. 1C).

Almost all fish make sounds while feeding. These are usually broad-frequency, non-harmonic crunching sounds. Cummings et al. (1966) describe feeding sounds in the margate, *Haemulon album*, as a burst, which occurs in a series of three to ten rapid pulses with frequencies up to 1,600 Hz, and a pop, which consists of a single pulse of short duration with frequencies up to 700 Hz. The burst sounds are associated with margates feeding on benthic crustaceans. The fish were observed to plunge their heads into the bottom sand to capture their prey and shortly thereafter the burst sounds were heard as sand was expelled from the mouth and opercular openings. The pop sounds were recorded as the margates snapped at plankton in the water column. Crunching sounds associated with feeding have also been observed in sunfish (*Lepomis*), catfish (*Ictalurus*), minnows (*Notropis*), and many others (Gerald, personal observations).

Such sounds are not entirely without biological significance because fish apparently can associate them with food or predation. Moulton (1960) reports observations which suggest that predators such as jacks, *Caranx*, and barracuda, *Sphyraena*, are attracted to the sounds of jacks feeding on schools of anchovy, *Anchoviella*, while the anchovy are repulsed by these sounds. Various freshwater fish (*Notropis, Lepomis*, and others) have been observed to quickly swim toward an individual immediately after it produced the characteristic crunching sounds associated with feeding. This may occur even when there are no obvious feeding movements by the sound-producing individual (Gerald, personal observations).

Another stridulatory mechanism involves snapping the jaws. Pinfish, *Lagodon rhomboides*, produce sharp clicking sounds while vigorously defending their territory against intruders. These sounds are prob-

ably produced by snapping of the well-armed jaws of the territory defender as it chases and presumably nips at the invader. The bulk of the energy in these sounds is low frequency (1-4 kHz), but with harmonics extending beyond 12 kHz. Sound duration is very short, being approximately 0.7 sec (Caldwell and Caldwell, 1967).

A similar situation has been observed in the warmouth sunfish, *Lepomis gulosus,* except that in this instance the aggressive fish snapped at the fleeing fish but did not appear to try to make contact. The aggressive fish changed speeds several times to maintain its distance from the fleeing fish without making contact but snapped vigorously several times (Gerald, personal observations). Another example of this type of sound mechanism is in the redear sunfish, *L. microlophus,* where the males produce popping sounds by jaw snaps near the sides and head of the female during courtship. These sounds have the greatest amplitudes at frequencies under 1 kHz but may exhibit transients with frequency components up to 7 kHz. Sound duration is around 0.7 sec (Gerald, 1971).

Probably the most frequently observed situation in which fish make sounds occurs when they are caught and taken from the water. The best known examples of this type are found in the grunts (Pomadasyidae). Burkenroad (1930) describes the sound of the white grunt, *Haemulon plumieri,* as a loud rasping croak, given when the fish is in difficulty (and possibly at other times as well). These sounds are produced both under water and in air. The swim bladder of these fish acts as a resonator amplifying the sounds of the pharyngeal teeth grating together. If the swim bladder is deflated, the sounds become a dry grating sound rather than the normal loud grunt. Dobrin (1947) reports similar sound mechanisms in the pigfish, *Orthopristis chrysopterus.*

The northern seahorse, *Hippocampus hudsonius,* produces loud clicks similar to the snapping of the finger against the thumb. The frequencies involved extend

up to about 4 kHz with maximum energy under 800 Hz. These sounds are associated with feeding, introduction into new surroundings, courtship and copulation. This stridulatory mechanism involves articulation of the posterior margin of the skull with the anterior margin of the coronet, a star-shaped ossified crest mounted in a socket-like base. When the seahorse's head is extended, the coronet overlaps the other bone and sounds are probably produced when the skull's edge snaps out forcibly. Vibrations thus set up may be transferred to and amplified by the swim bladder (Fish, 1953).

Members of the catfish group make high-pitched squeaks by friction between the joints of the pectoral girdle and the pectoral fins as part of their "fright reaction" which involves locking their strongly serrated pectoral spines in an extended position. This stridulatory sound is caused by the rubbing of a broad tubercle of the spine (friction process) against bony ridges in the joint of the pectoral girdle (Burkenroad, 1931; Tavolga, 1960; Gainer, 1967). The creak sound in the sea catfish, *Galeichthys felis,* is characterized by having a fundamental frequency of 2 kHz, a harmonic at 4 kHz and a duration between 30-50 msec (Tavolga, 1960). The banjo catfish, *Bunocephalus* sp., produces a broad-band sound containing frequencies up to and above 6 kHz with durations of approximately 100 msec (Winn, 1964).

Sculpin (Cottidae) produce sounds that are described as dull growling and sustained groans. These sounds exhibit a fundamental frequency of about 60 Hz and durations up to about 2 sec. The sounds are produced when the fish are handled both in air and underwater. Growls have also been heard during feeding. The sound mechanism involves vibrations of the pectoral girdle by means of the deep cranioclavicular muscles on both sides. The movements of the pectoral girdle set the surrounding medium in motion, thus producing the actual sound vibrations (Barber and Mowbray, 1956).

Some fish apparently produce sounds by blowing bubbles. These sounds may show sonagraphic characteristics similar to stridulatory sounds. The croaking of *Glandulocauda inequalis* is associated with rhythmic air gulping during courtship and consists of pulsed, non-harmonic sounds with significant energy in the higher frequencies (Nelson, 1965). In addition, the American eel, *Anguilla rostrata,* produces clucking sounds by releasing gas bubbles, probably from the pneumatic duct to the swim bladder (Fish and Mowbray, 1970). Details of these sonic mechanisms are not known.

Swim bladder mechanisms

There are two primary mechanisms for sound production involving the swim bladder. In the extrinsic systems the muscles arise in the body musculature, the pectoral girdle or cranium and insert on the swim bladder or on bones closely associated with it. Intrinsic systems involve muscles that are totally on the swim bladder (Figs. 2, 3). In both cases the sounds are produced by muscular contraction which causes changes in the volume of the swim bladder. In some situations, the muscle contraction decreases the volume of the swim bladder (generally in intrinsic systems) and in other cases it increases the swim bladder volume. In either case, the antagonistic system for the muscular contraction is the elastic swim bladder wall which tends to return to the normal position after volume changes. The result of change in swim bladder volume is the matching of impedances between the body of the fish and the water and thus the effective amplification of the produced sound.

One additional mechanism for sound production involving the swim bladder has been reported by Fish (1954). She noted that *A. rostrata* produced sounds by release of a bubble of air through the mouth. The source of the air bubble was probably the swim bladder which is connected to the gut through a duct.

Swim bladder morphology. The teleost swim bladder is a gas-filled thin-walled chamber in the abdominal cavity just ventral to the vertebral column. The shape of the swim bladder varies considerably in different species, but its basic structure is generally cylindrical or ovoid. The swim bladder wall has three layers: an outer tunica externa, a middle layer of connective tissue, and an inner tunica interna. The tunica externa consists of a sheet of highly extensible elastic fibers and short needles of ichthyocol, a form of collagen (Alexander, 1961). The middle layer or submucosa consists of a loose fibrous connective tissue which permits the outer layer to have some limited movement over the middle and inner layers (Chranilov, 1929; Fänge and Wittenberg, 1958). The tunica interna is a thin layer of smooth muscle with some ordinary collagen which does not endow the layer with as high a viscosity as does the ichthyocol in the tunica externa (Alexander, 1961).

The gas in the swim bladder may come from two sources. In some species the swim bladder is connected to the gut through a thin ductus pneumaticus (physostomus swim bladder) which may permit the passage of gas between the swim bladder and gut for filling the swim bladder. In other species with the ductus pneumaticus, and in species without this connection (physoclistic swim bladder), the gas is secreted into the swim bladder by the red gland which is located in the tunica interna. The red gland removes gases from the blood and actively secretes them into the swim bladder (Fänge, 1966). The gas content of the swim bladder varies in different species, but it consists of gases that are dissolved in the water (Fänge, 1966). The pressure of the gas in the swim bladder is generally about ambient except in the Ostariophysi where it is slightly above ambient in order to aid the acoustic function of the Weberian ossicles, a series of bones connecting the swim bladder to the inner ear (Alexander, 1959).

The shape of the swim bladder varies considerably in different species. In some, the swim bladder is a single undivided
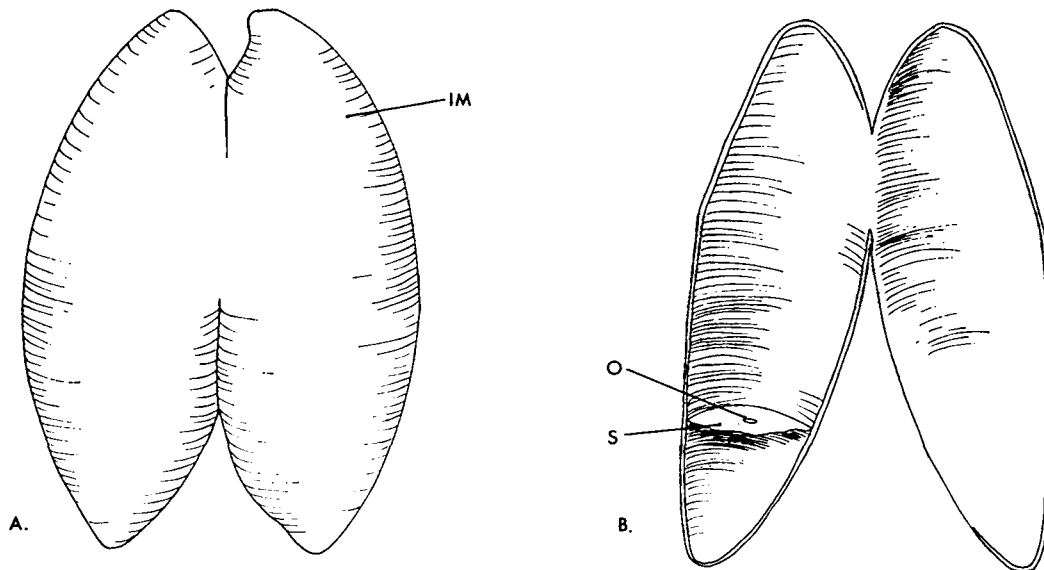
FIG. 2. Swim bladder of *Prionotus carolinus*. *A*, Ventral view. *B*, Longitudinally bisected. Symbols: IM, intrinsic musculature; S., internal septum; O, opening in septum. (Redrawn from Tower, 1908.)

chamber, while in others it is divided into two or more chambers which are connected by a single duct. In other species the swim bladder is divided internally into two or more chambers by septa or diaphragms arising from the tunica interna (Fig. 2*B*, 3*D*). Generally the chambers are open to one another to permit the passage of gases.

In addition to several chambers in the swim bladders, there may be a number of diverticula which increase its volume or length (Fig. 2*B*). For example, in many species of squirrelfishes (Holocentridae), as well as in the herrings (Clupeidae) and elephant-nose fishes (Mormyridae), there are anterior diverticula which bring the swim bladder into close or intimate proximity with the inner ear and may thus increase auditory sensitivity (Nelson, 1955).

Intrinsic mechanisms. Intrinsic sonic mechanisms are found in a diverse group of teleosts including Batrachoididae, Triglidae, Dactylopteridae, Zeidae and Macrouridae.

The sound production mechanisms in two Batrachoids, the toadfish, *O. tau,* and the midshipman, *Porichthys notatus,* have been the most extensively studied of all of the intrinsic mechanisms and may be

typical of the mechanisms in many of the species in these diverse groups. The swim bladder in *Porichthys* is U-shaped with a pair of striated sonic muscles located laterally on each of the two anterior projections (Fig. 2*A*). The muscle fibers run obliquely in a dorsoventral direction (Greene, 1924) and are transverse to the long axis of the muscle (Skoglund, 1961). The swim bladder in *Opsanus* is heart-shaped (Fig. 2*C*) but is otherwise essentially similar to that in *Porichthys*. In both species there is a thin diaphragm located posterior to the anterior diverticula separating the swim bladder into anterior and posterior portions (Fig. 2*D*). A small opening in the diaphragm, surrounded by smooth muscle (Tower, 1908), allows movement of gas between the two chambers. In *Opsanus* the diaphragm has been observed to vary from one-third to one-sixth of the distance from the posterior wall of the swim bladder (Tower, 1908; Fänge and Wittenberg, 1958), suggesting that it may "change position."

The sonic mechanism in *Opsanus* and *Porichthys* is not completely understood but several possibilities have been suggested. Greene (1924) suggested that the
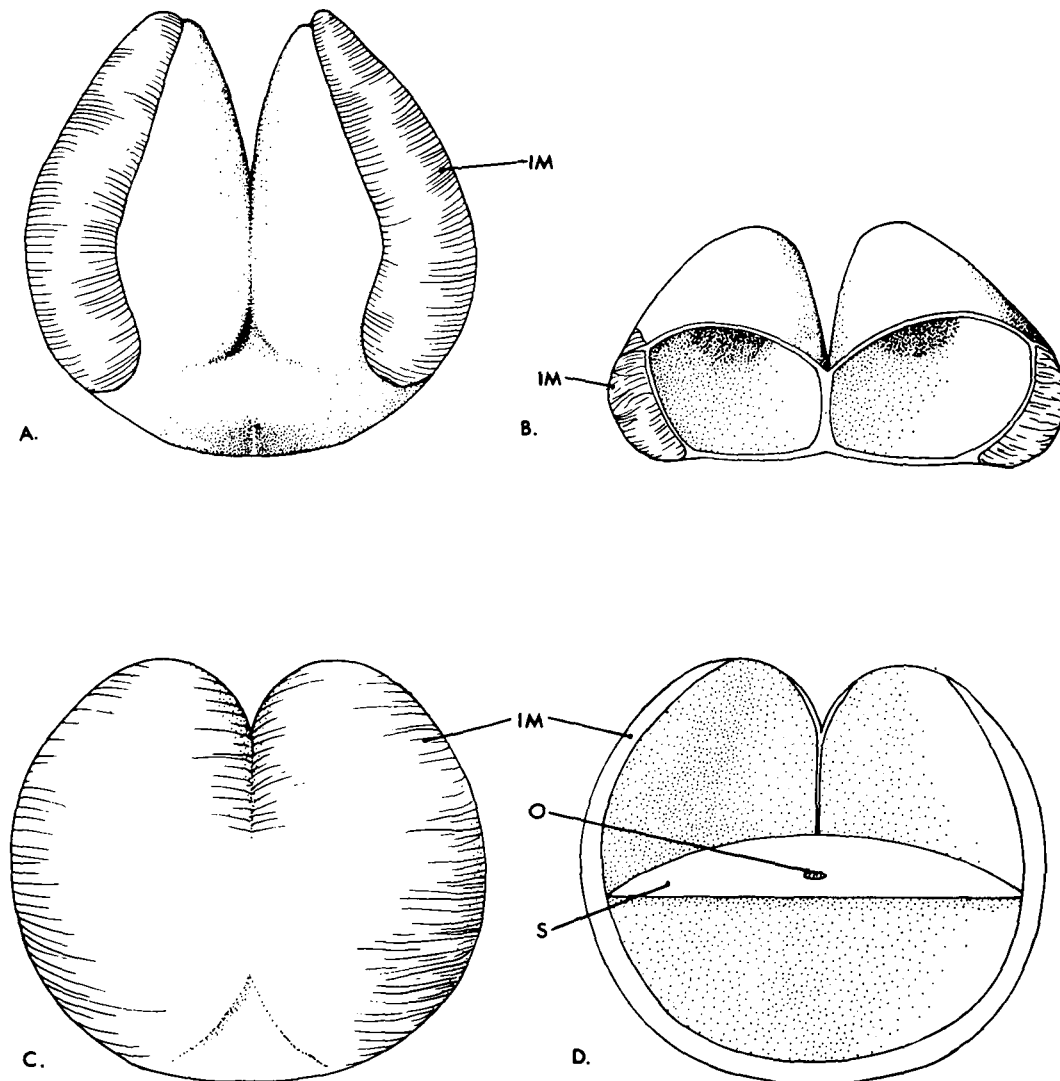
FIG. 3. *A*, Swim bladder of *Porichthys notatus*, ventral view. *B*, Posterodorsal view of a cross section showing the cavities of the anterior horns. *C*, Ventral view of swim bladder of *Opsanus tau.*

D, Horizontally bisected swim bladder of *Opsanus* showing the internal septum. Symbols as in Figure 2. (*A* and *B* redrawn from Greene, 1924; *C* and *D* redrawn from Tower, 1908.)

function of the sonic muscles was to push the air from one chamber of the swim bladder to the other by changing the pressure in the chambers. Movement of air through the small opening in the diaphragm would set the diaphragm vibrating and this would be the source of the sound. More recently, however, Skoglund (1959) deflated the swim bladder in *O. tau* and found that the sound was still audible though at a much lower amplitude than

when the swim bladder was filled with gas. He suggested that the sound is produced directly by the muscles and that the swim bladder is an impedance-matching device between the fish and the water. Muscle contraction could account for the high fundamental frequency found in the sound of the two species since these swim bladder muscles are capable of prolonged contraction at very high rates without tetany (Tavolga, 1964). Further evidence

supporting the significance of the sonic muscles in sound production without the aid of the swim bladder diaphragm comes from experiments by Tower (1908) on a species of Triglidae with an internal diaphragm (*Prionotus evolans*). Tower found that he could block the diaphragm without altering the sound in any way detectable by ear. It is now likely that the role of the internal diaphragm is related to the secretion and absorption of gases (see review by Steen, 1972).

Sound in the Triglidae is produced through contraction of the paired intrinsic muscles which are located laterally on each of the two lobes of the swim bladder (Fig. 3A) (Tower, 1908; Tavolga, 1964). The two lobes are connected near their anterior end, and a single diaphragm is found in the posterior region of the left lobe (Fig. 3C). As mentioned above, Tower (1908) found that blocking the diaphragm did not change the sonic output of the fish.

Although there has not been extensive work on sound production by deep sea fishes, Marshall (1962, 1967) has found muscles in members of the family Macrouridae (rat-tailed fishes) which resemble intrinsic sonic muscles of other species.

Extrinsic mechanisms. The literature on extrinsic sound-producing systems is more extensive than that on intrinsic systems, but in most cases the primary variation is in the origin and insertion in some muscles and not in other aspects of the sonic mechanisms. Rather than discuss each individual study, a few examples will suffice to illustrate different types of systems.

Extrinsic sonic muscles arise away from the swim bladder and insert on or near the swim bladder. In the squirrelfishes (Holocentridae), the sonic muscles arise on the skull just in front of, and dorsal to, the auditory bulla and cross over the dorsal flat areas of the first two ventral ribs to insert by a tendon on the third rib (Winn and Marshall, 1963). Contractions of the bilateral sonic muscles cause grunt-like sounds in *Holocentrus rufus* (Winn and Marshall, 1963) and *H. ascenscionis*

(Tavolga, 1964), with each pulse in the grunts produced by a single synchronous contraction of the sonic muscles (Winn and Marshall, 1963). The fundamental frequency of the sounds in these species is directly related to the contraction rate of the muscles. Similar sonic mechanisms have been reported for the related *Myripristis berndti* (Salmon, 1967) and for the Nassau grouper, *Epinephalus striatus* (Hazlett and Winn, 1962). The sonic muscles in the grouper, however, arise in the body musculature just behind the opercle and insert between the first two central ribs where the muscle is in very close proximity to the swim bladder. The sonic muscles in *Priacanthus cruentatus* (Priacanthidae) and members of the Sciaenidae also arise in lateral body musculature but their insertion is directly onto the swim bladder (Tower, 1908; Salmon and Winn, 1966).

In two species of *Therapon, T. jarbua* and *T. theraps,* the sonic muscles arise on the medial side of the supracleithra and insert on the anteriodorsal portion of the anterior chamber of the two-chambered swim bladder (Schneider, 1964, 1967). In *Therapon* the two chambers are easily distinguished externally since they are interconnected by a thin tube. The swim bladder firmly attaches to the fourth vertebrae just posterior to the insertion of the sonic muscles, and the first few ventral ribs are reduced in size to make room for the large drumming muscle found in these species (Schneider, 1967).

The insertion of the sonic muscles in the sea catfishes, *G. felis* and *Bagre marinus,* is somewhat different than in other species with extrinsic muscles. Tavolga (1962) and others have shown that the sonic muscles, called the protractor muscles, arise on the underside of the optic lamina of the skull and insert on a modified portion of the parapophysis of the fourth vertebra. The anterior ramus of the parapophysis (called the Müllerian ramus) is a thick shelf of bone attached to the anteriodorsal wall of the swim bladder, and it acts as a vibrating element (*Spring-*

federapparat) which strikes the swim bladder. Sound production is accomplished by contraction of the protractor muscle which moves the *Springfederapparat*. The antagonist to the contraction is the spring mechanism of the Müllerian ramus which according to Tavolga (1962) is a highly damped structure. The swim bladders in these catfishes have a large anterior and three smaller posterior chambers which are all contiguous. Tavolga suggests that the division of the swim bladder looks like a series of sound-absorbing baffles in a loudspeaker enclosure and that they may enhance the resonance properties of the swim bladder.

Experiments on sound production in deep sea fishes have not been done, but Marshall (1967) has found that a substantial number of benthopelagic species have mechanisms that would be suitable for sound production using extrinsic systems. Marshall reports that of the 175 species of oviparous Brotulids, males of about 100 species have large drum muscles on the forward swim bladder walls. In these species the swim bladder is suspended from the first three modified ribs which are the insertion points for some or all of the sonic muscles. The origin of the muscles is often on or near the auditory bulla.

Sonic muscles. The muscles associated with sound production in teleosts are among the fastest acting of all known vertebrate muscles (Tavolga, 1964). In addition, high rates of contraction can be maintained for long periods of time without tetany. This high contraction rate is a result of a number of adaptations in the sonic muscles, and these modifications appear to be present in most of the sonic muscles that have been studied. The importance of this high contraction rate has been demonstrated in *O. tau.* Slowing it by cooling the muscles, blocking with curare, or decreasing the strength of nerve stimulation all lead to a considerable decrease in sound amplitude (Skoglund, 1961).

Investigations of contraction of the muscles involved in sound production have shown that contraction rate in *Opsanus* is on the order of 5 msec with a relaxation time of 8 msec (Skoglund, 1959, 1961). In *Holocentrus* the contraction and relaxation times for sonic muscles are 5 msec and 12 msec respectively as compared with a contraction time of 12 msec and a relaxation time of 25 msec for non-sonic muscles (Gainer et al., 1965). Similar high rates for contraction and relaxation have been reported by Packard (1960) for the sonic muscles of the pigfish, *Congiopodus leucopaecilus.*

Measurements of maximum possible stimulation rate indicate that a higher rate of stimulation is possible before onset of mechanical fusion and tetany in sonic as compared with non-sonic muscles. Tavolga (1962) stimulated the sonic protractor muscles in the sea catfish, *G. felis,* up to 300 times per sec before ,tetany occurred. He also noted that for brief periods *Galeichthys* will maintain sounds with a fundamental frequency up to 400 Hz, indicating that the muscles could contract at this rate. Experiments on *H. rufus* have indicated that their sonic muscles will only show mechanical fusion at stimulation rates of about 200 Hz. Non-sonic muscles in the same species show summation at 40 Hz and fusion at 100 Hz (Gainer et al., 1965). Similar experiments with *O. tau* have shown that the sonic muscles can be stimulated up to at least 100 pulses per sec without mechanical fusion (Gainer and Klachner, 1965) and that fusion occurs at about 200 Hz (Skoglund, 1959, 1961). Measurements of the fundamental frequency of sound, while simultaneously recording the sonic muscle action potentials, have shown that a similar high rate of muscle firing occurs in *P. notatus* (Cohen and Winn, 1967). Schneider (1961) measured the muscle response in several species of *Therapon* and found that tetany began at 140 pulses per sec and was complete at 290 pulses per sec. However, he also found that if he continued to stimulate the muscles at these high rates for more than 100 msec, the muscles would fatigue. Sonic

muscles in *Opsanus* and *Prionotus* will respond to stimulation up to 340-380 and 340 pulses per sec, respectively, with tetany occurring by 0.5 sec in both species. *H. ascenscionus* and *Epinephelus guttatus* sonic muscles will respond up to 150-170 per sec (Tavolga, 1964).

Investigations of sonic muscle morphology have shown that their fibers tend to be shorter and of smaller diameter than non-sonic striated muscles in the same species. The fibers in *Opsanus* are on the order of 10 mm long and generally less than 20μ in diameter (Skoglund, 1959, 1961). The fibers in Theraponidae are about 27μ in diameter (Schneider, 1967) and similar small diameter fibers are reported for catfish, squirrelfish, groupers, and Sciaenids (Tavolga, 1964). In comparison the non-sonic muscles in *Therapon* and other species are at least 50μ in diameter (Tavolga, 1964; Schneider, 1967).

Besides having a small diameter, the sonic muscles are highly vascularized as indicated by their red color in most species except the Theraponidae where they are pale (Marshall, 1962; Tavolga, 1964; Schneider, 1967). A high degree of vascularization is consistent with the ability of these muscles to maintain a high contraction rate over long periods. There is also a well-developed sarcoplasmic reticulum and triad system in the sonic muscles of *Opsanus* (Fawcett and Revel, 1961). This specialization has also been associated with high firing rates (Skoglund, 1959, 1961; Gainer and Klancher, 1965).

Contributions of the swim bladder to sound production. The contribution of the swim bladder to the production of sound has been studied for only a few species; however, it is apparent from these studies that the swim bladder acts as an impedance-matching device between the sonic muscles and water (Tavolga, 1962; Harris, 1964; Salmon et al., 1968). Experiments on filling the swim bladder with water or deflation of the swim bladder have shown that there is a considerable loss in sound amplitude as the volume of air in the swim bladder decreases. Skoglund

(1959, 1961) deflated the swim bladder of *O. tau* and found that the sound produced decreased in amplitude and became "dull" as the volume of air was decreased; however, he was able to hear a very low level sound even when the swim bladder was empty, indicating that the muscles, intrinsic to the swim bladder, were responsible for the sound. Winn and Marshall (1963) found that filling the swim bladder of *H. rufus* with water completely eliminated detectable sounds although sound was still evident if there were small amounts of air remaining in the bladder. Muscle contractions could still be felt even when there was no audible sound. Winn and Marshall also removed the swim bladder from its attachment to the first three ribs which are the insertions for the sound producing muscle and found that sound could no longer be detected. In similar experiments, Tavolga (1962) found that damage to the swim bladder in sea catfishes alters signal amplitude and not the harmonic content of the signals.

The swim bladder may not only act as an impedance-matching device effectively amplifying the signals produced, but as suggested, may also specifically amplify portions of the acoustic signal at the resonance or "natural" frequency of the swim bladder (Poggendorf, 1952). The role of the swim bladder in sound production and sound detection has been likened to that of a vibrating bubble of air in water (Harris, 1964; Tavolga, 1964; Alexander, 1966; Weston, 1967). If the swim bladder behaved as an ideal bubble, it would have a typical resonance frequency that would be inversely proportional to its radius. The quality of the signal, or degree of sharpness of amplification at the resonance frequency (Q) would be about 73 (Weston, 1967) and there would be a considerably higher signal at the resonance frequency of the swim bladder than at other frequencies. A Q of 73 is not a likely figure, however, since there is considerable damping of the movements of the swim bladder as a result of the presence of tissue surrounding the bladder (Tavolga, 1964; Alexander, 1966; Weston, 1967). It has been suggested

that as a result of the damping, the Q would be 4 or 5 (Alexander, 1966; Weston, 1967), which would probably result in an increase in signal amplitude of 5 or 6 db at the resonance frequency. Direct experimental observations of the Q of the swim bladder have been limited. Experiments by Poggendorf (1952) suggest that the Q is considerably higher than 4 or 5 but measurements of the response of an excised swim bladder from *O. tau* by Tavolga (1964) showed that a Q of 4 or 5 is a reasonable estimate. More recent experiments by Batzler and Pickwell (1970) using measures of target strength to determine the resonance response of the swim bladder of a goldfish and an anchovy (species not indicated) showed that the Q for a swim bladder in the live fish was from 3.8 to 5.1 (a sample of two animals) and that the Q of the swim bladder removed from the animal was 6.7 and 8.9 (a sample of two animals). Measurements for a single anchovy showed a Q of 4.5 for the swim bladder in the fish and 21.0 for the swim bladder alone. In both species the fish body without the swim bladder did not reflect any significant portions of the sound, substantiating the suggestions of a number of workers that the fish body is "invisible" to sound (Griffin, 1955; van Bergeijk, 1964). As expected, the resonance frequency of the swim bladder decreased with increase in size. Behavioral experiments by Popper (1971) have shown that changes in the Q of the swim bladder do not affect the auditory capabilities of fishes. In addition, measurements of the pressure response of the swim bladder by placing a probe microphone in the intact swim bladder indicated that the loss of sound level from outside the fish to inside the swim bladder (from water to air) was 6 db from 50 to 1,600 Hz with no changes in the phase of the signal (Popper, unpublished). These data suggest that the Q of the swim bladder in small goldfish (4.0 cm) may be less than 3 since there was no perceptible change in response of the swim bladder at different frequencies.

The low Q found for the swim bladder for at least three species of fish (anchovy, goldfish, and *O. tau*) indicates experimentally that the swim bladder is a highly damped structure, which would endow it with several properties that are likely to be important for successful sonic communications. Harris (1967) has pointed out that an important characteristic of a system with a low Q (and therefore a highly damped system) is the ability to respond rapidly to the beginning and termination of stimulation. Therefore, the teleost swim bladder should be able to respond accurately to rapidly pulsed sounds and pass them along to the central auditory system without spreading out the duration of the pulses and making them appear as a single uninterrupted sound. We might similarly consider that the response of the swim bladder in sound production would be significantly altered if the swim bladder were not highly damped. Sounds in many species are rapidly pulsed (Fish, 1954; Tavolga, 1958; Packard, 1960; Schneider, 1967; Fish and Mowbray, 1970, and others). Presumably, in these, the swim bladder is stimulated by the sonic muscles and the vibration of the swim bladder starts and stops quickly. If the swim bladder were poorly damped, the vibrations from a signal pulse would continue even after the stimulation by the muscles has terminated, and this would result in loss of the interpulse silent period if the pulses are close together. In effect, fish would wind up "slurring" pulsed sounds. This is highly unlikely as it has been demonstrated that a significant portion of communication in at least one species of fish, *O. tau*, is dependent upon the pulsed nature of the signal (Winn, 1964, 1967) and that goldfish are sensitive to pulsed signals (Popper, 1972).

Experiments on swim bladder involvement in sound production also indicate that there is at most only a small enhancement of responses at the resonance or natural frequency of the swim bladder. Experiments in which the size of the swim bladder has been altered by deflation or by partially or fully filling it with water (water is the same density as the fish tissue and thus keeps swim bladder internal

pressure the same while decreasing its effective volume) have shown that the major loss is in sound amplitude and not in the spectral characteristics of sounds (Skoglund, 1959, 1961; Tavolga, 1962; Winn and Marshall, 1963; Salmon et al., 1968). However, there are several reports in the literature in which sounds of different sized animals of the same species are indicated to have different frequencies. It has also been reported that larger animals make slightly deeper sounds than smaller animals (Greene, 1924; Fish, 1954; Fish and Mowbray, 1970; Bayoumi, 1970). This is what one would expect if the resonance frequencies of the swim bladders were changing with size. However, it is also possible that the apparent changes (also seen in sound spectrographs) are a result of other factors related to size change such as a decrease in amplitude of the fundamental and a resultant loss in harmonics at higher frequencies or a general decrease in the fundamental due to slowing down of the maximum contraction rate of the sonic muscles due to age. It should also be pointed out that the significance of size of swim bladder on the spectral components of sounds is further minimized, at least on one species of Triglidae where there is little change in spectral content of the sound, although there is considerable intraspecific variation in shape, size, and volume of the swim bladder (Bayoumi, 1970).

CENTRAL MECHANISMS OF SOUND PRODUCTION
IN FISHES

The majority of studies on the neurological control of teleost sound production have been carried out on toadfish of the genus *Opsanus* and therefore the following discussion is based primarily on this group of fishes. The findings discussed in this section are also presented in the form of a model (see Figure 8 and discussion under Summary and Conclusions).

Neuromuscular systems

The sonic muscles in many fishes, in- cluding several marine catfishes, squirrelfish, sea robins, toadfish, and red hinds are innervated by branches of the so-called "occipital nerves." These trunks usually occur in two pairs located between the vagus and the first true spinal nerves (Tavolga, 1962, 1964, 1971). Tavolga (1962, 1971) has stated that the occipital nerves are probably homologous to the hypoglossal or twelfth cranial nerve of tetrapods, and that the sonic muscles in many diverse species may be homologous on the basis of their similar nerve supply. Notable exceptions are found in the croakers and drums (Sciaenidae) in which the sonic muscles are derived from the lateral body wall and are innervated by true spinal nerves (Tavolga, 1971).

Based on histological and physiological studies (Skoglund, 1961), the nerves to the sonic muscles in toadfish have been characterized as containing uniform fibers about 10μ in diameter and having conduction speeds between 25 and 30 m/sec at 21 C. Skoglund (1961) reports that the swim bladder nerve "enters the muscle at its cranial end and runs close to the bladder wall, giving off fine side branches during the first two-thirds of its course, after which the main stem divides in a fan-like way innervating the caudal part of the muscle." This possible difference in nerve fiber length, especially if the fibers are of uniform diameter, is interesting in view of the probable need to synchronize the firing of many muscle fibers in fast-contracting sonic muscles. Bennett (1971) describes several compensatory systems found in the highly synchronous systems that control teleost electroplaque organs. Of particular interest are observations that nerve fibers suppling the most proximal electrocytes have a more tortuous course than those ending on more distal ones. This compensation allows nerve volleys to arrive simultaneously throughout the electroplaque organ. Perhaps an analysis of the total length of fibers in the swim bladder nerve would reveal a similar organization.

Definitive evidence for synchrony in teleost sonic muscle is provided by the
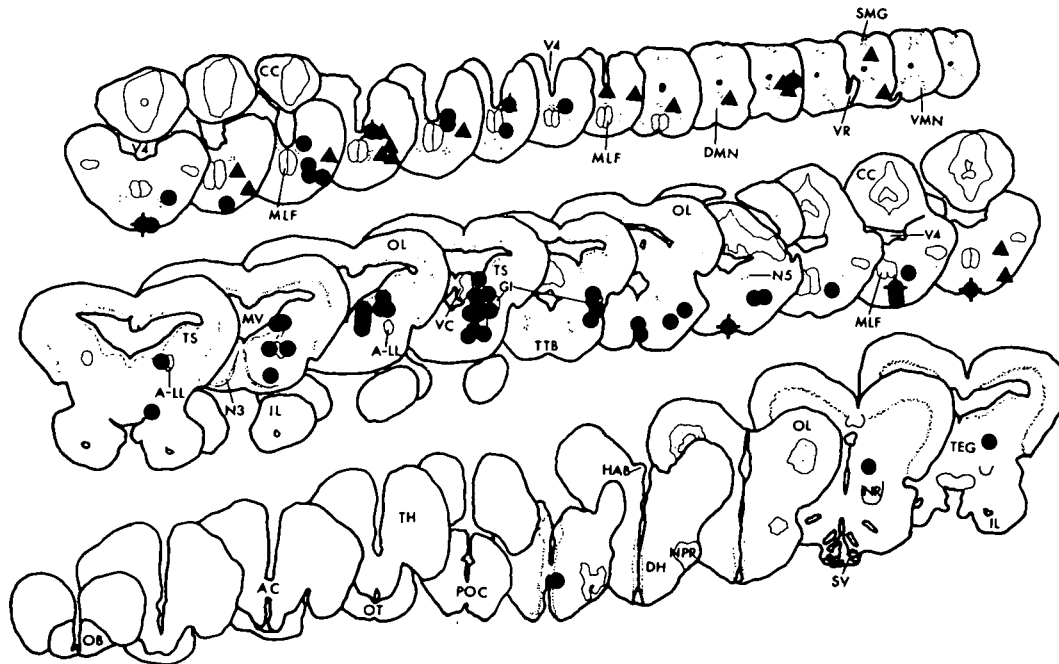
FIG. 4. Distribution of Prussian blue marked stimulation sites from which sounds have been evoked. Points from both sides of the brain have been plotted on the same side on tracings of representative frontal sections taken from the olfactory bulbs (lower left) to the spinal cord (upper right). Symbols: triangles, one-to-one responses; circles, grunts; crosses, boatwhistle-like sounds. Overlapping symbols indicate points from which more than one type of sound was evoked. Elongated symbols represent grunt responses evoked from several contiguous sites along the same tract. Structures were identified according to Ariëns Kappers et al. (1936). Abbreviations: AC, anterior commissure; A-LL, acoustico-lateral lemniscus; CC, corpus cerebelli; DH, dorsal hypothalamus; DMN, dorsal (sonic) motor nucleus; GI, ganglion isthmi; HAB, habenula; IL, inferior lobe of the hypothalamus; MLF, medial longitudinal fasciculus; MV, midbrain ventricle; N3, oculomotor nerve, N5, motor nucleus of the trigeminal nerve; NPR, nucleus prerotundus; NR, nucleus rotundus; OB, olfactory bulb; OL, optic lobe; OT, optic tract; POC, postoptic commissures; SMG, supramedullary ganglion cells; SV, saccus vasculosus; TEG, midbrain tegmentum; TH, telencephalic hemisphere; TS, torus semicircularis; TTB, tractus tecto-bulbaris; V4, fourth ventricle, VC, valvula cerebelli; VMN, ventral motor nucleus; VR, ventral root of spinal nerve. (From Demski and Gerald, 1972.)

finding that up to four or more axons may innervate each muscle fiber in both *Opsanus* and *Holocentrus* (Gainer and Klancher, 1965; Gainer et al., 1965). This polyaxonal innervation was based primarily on decreases in the latency of spikes recorded intracellularly from a sonic muscle fiber during systematic increases in occipital nerve stimulation. Histological identification of motor end plates in close proximity (average separation of 100μ in *Opsanus* and 83μ in *Holocentrus* sonic muscle) is consistent with a polyaxonal innervation (Gainer and Klancher, 1965). As these authors note, the special neuromus-

cular organization found in these sonic muscles provides a means of evoking "simultaneous and distributed action potentials throughout the whole muscle."

Sonic motor systems

The neurons that innervate the swim bladder muscles in toadfish have been described as forming "a spindle-shaped nucleus in the midline of the spinal cord which is just ventral to the central canal at the level of the first spinal segment" (Pappas and Bennett, 1966). This sonic nucleus is readily discernible on Nissl stained

preparations of *Opsanus beta* (Demski, unpublished) where it forms a column extending from the exit of the first spinal nerve to the caudal region of the fourth ventricle (DMN in Fig. 4). Axons from sonic motor cells can be traced in a ventrolateral direction where they exit in large bundles. The cells themselves are characterized by having several large dendrites, dense Nissl substance, large nuclei, prominent nucleoli and soma with an average diameter of 21.4 ± 5.7μ (Demski and Bauer, unpublished).[2]

Electrical stimulation within or immediately adjacent to the sonic nucleus has evoked the same response as stimulation of the nerve; e.g., one sound pulse results from each stimulation pulse at frequencies up to 200 Hz (Demski and Gerald, 1972). These sounds have been termed one-to-one responses (Fig. 5a). The areas of the brain from which they have been evoked are shown in Figure 4.
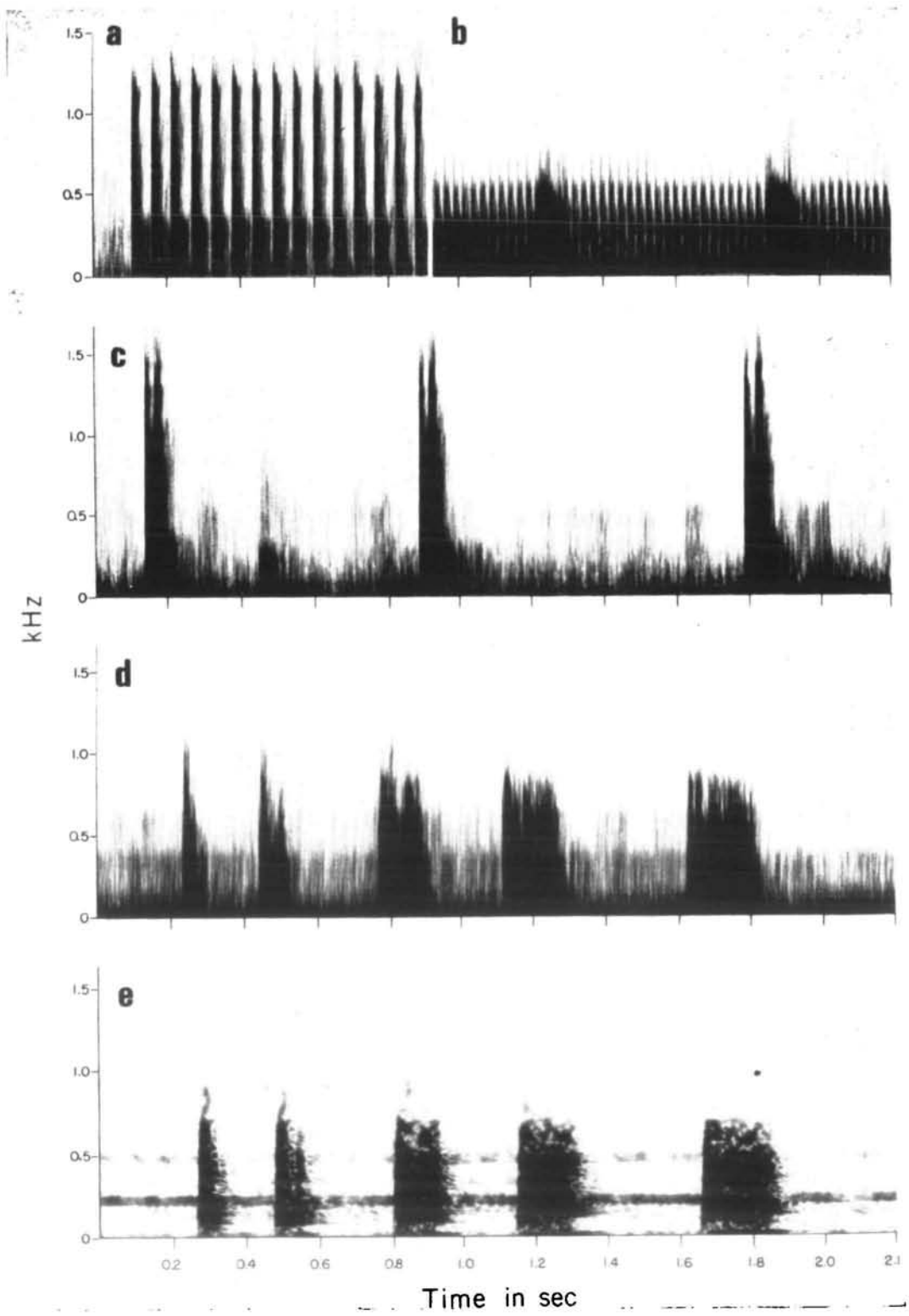
Several observations indicate that the sonic motor neurons are coupled electrotonically. Antidromic activation of the swim bladder nerves at increasing intensities of stimulation has evoked graded depolarizations in the motor cells at latencies similar to that of antidromically activated spikes. Since the dorsal roots were cut, these events could not be brought about by activation of afferents, and the latency of the response was too short to be caused by any known chemically mediated synapse (Pappas and Bennett, 1966). Morphological studies have demonstrated that afferent fibers form junctions on the soma of the swim bladder motor neurons which are suggestive of both chemically and electrically mediated synapses. Dendrosomatic junctions indicative of eletrotonic conduction are also present; however, the electrotonic coupling between

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[2] This mean with standard deviation is based on the measurement of 150 motor cells in five toadfish. Only sections through the nucleolus were used and the smallest diameter of the cell body was measured. The largest diameter of the soma was not determined because of the difficulty in separating the basal portions of the dendrites, usually oriented in this plane, from the cell body itself.

motor neurons appears to be primarily through the afferent fibers (Pappas and Bennett, 1966). A similar system has been previously described for the electroplaque control mechanisms of the catfish, *Malapterurus electricus*, in which Bennett (1971) suggests that the electrotonic coupling between motor cells provides a positive feedback mechanism by which partially depolarized cells tend to depolarize less excited neighboring cells, at the same time becoming less depolarized themselves. The net effect of this mechanism is the synchronous activation of many cells in the nucleus.

The electrotonically coupled afferent fibers have been identified physiologically by recording their firing just before the sonic motor neurons in response to tetanizing stimulation of the spinal cord (orthodromic stimulation) or immediately after the motor cells following antidromic stimulation of the swim bladder nerve (Pappas and Bennett, 1966). As indicated above, a possible chemically mediated synapse also ends on the motor neurons. These terminals are thought to mediate an inhibition or hyperpolarization recorded in the motor cells and electrotonically coupled afferent fibers following tetanic stimulation of the spinal cord (orthodromic stimulation) or strong antidromic activation of the swim bladder nerves. Collaterals of the afferent fiber system are thought to activate this inhibitory mechanism (Pappas and Bennett, 1966). Presumably these collaterals excite interneurons that end on the soma of the motor cells as chemically mediated, inhibitory synapses. That direct collaterals of the motor neurons may trigger this system is less likely since the inhibition occurs only under circumstances that activate the afferent fibers (Pappas and Bennett, 1966). From the above, it is probable that the control of toadfish sonic motor neurons involves both excitatory as well as inhibitory mechanisms.

Sonic motor neurons fire in short bursts (36-65 msec in duration), with a frequency of about 185 per sec in response to tetanic stimulation of the spinal cord or strong

antidromic activation of the swim bladder nerve (Pappas and Bennett, 1966). Longer bursts (up to 1 sec) can be recorded from these cells if the medulla is transected somewhat behind the cerebellum (Bennett, personal communication). This cut presumably removes some type of higher inhibition, possibly mediated by the chemical type synapses reported to end on the motor cells. This system, located somewhere above the lower medulla, may normally function to control the duration of sound pulse trains. The duration and frequency of the short and long bursts suggest that they may be neurophysiological correlates of the grunt and boatwhistle calls respectively (see Demski and Gerald, 1972, for details). The discharge frequency of the motor neurons themselves appears to be set in an area near the obex in the caudal medulla since short duration burst responses can be recorded in the motor neurons when the brain stem is transected above this level but are lost with slightly lower cuts (Bennett, personal communication). The suggested position of this frequency control area would indicate that it may overlap the rostral portion of the sonic motor nucleus, at least in *O. beta* (Demski and Bauer, unpublished). That the frequency control region can be activated by way of the afferent fibers, electrotonically coupled to the motor cells, is indicated by the fact that bursts can be triggered by antidromic stimulation of the swim bladder nerves in preparations with the dorsal roots sectioned. Thus, it seems likely that the reverse is also true, i.e., the frequency control area normally activates the motor neurons via this electrotonically coupled afferent fiber system.

Electrical stimulation in the presumed area (obex) of the frequency control mechanism in lightly anesthetized, partially immobilized toadfish, *O. beta*, has elicited grunt sounds as well as one-to-one responses (Demski and Gerald, 1972). These sounds have been evoked both individually (Figs. 4, 5a, c-e) and simultaneously (Figs. 4, 5b). It can be supposed that for each stimulation pulse, one sound pulse (one-to-one response) results from activation of motor neurons via the electrotonically coupled afferent fibers while grunts are caused by a triggering of the frequency control region. In addition, activation of the inhibitory system may be necessary for grunts to occur. This may require longer periods of stimulation and/or stronger stimulation than needed to drive motor cells on a one-to-one basis. The fact that burst responses recorded in motor cells always begin after an initial hyperpolarization (Pappas and Bennett, 1966) is consistent with this suggestion. Electrical stimulation in slightly higher regions of the medulla, as well as in the spinal cord near the caudal portion of the sonic nucleus, has also elicited simultaneous grunt and one-to-one sounds. In the case of the medullary stimulation, activation of afferent fibers to the frequency control region and/or the inhibitory area is likely to be involved in triggering the evoked sounds. The sounds could then result from the same mechanisms suggested above to account for sounds elicited directly from the frequency control region. In the case of the spinal stimulation, one-to-one responses may have been caused by direct activation of the motor cells or their axons, while the grunts were probably triggered by antidromic activation of the frequency control area through connections to the

FIG. 5. Sonagraphs of sounds evoked by brain stimulation in *Opsanus beta. a,* One-to-one response evoked by stimulation at 20 Hz and 30 μA in the rostral spinal cord. Filter width was 300 Hz. *b,* One-to-one response associated with grunts evoked by stimulation at 40 Hz and 30 μA in the rostral spinal cord. Filter width was 300 Hz. *c,* Grunts evoked as an after-response to stimulation at 45 Hz and 30 μA in the midbrain near the acoustico-lateral lemniscus. Filter width was 300 Hz. *d,* Grunts evoked during stimulation at 50 Hz and 20 μA in the dorsal hypothalamus. The wide filter (300 Hz) emphasizes the time characteristics of the sounds. *e,* The same as *d* but analyzed using a narrow filter (45 Hz) to emphasize the frequency characteristics of the sounds. The continuous horizontal banding is due to background noise. (From Demski and Gerald, 1972.)

FIG. 6. Photograph of a free-swimming, unanesthetized toadfish (*Opsanus beta*), implanted with three monopolar stimulation electrodes. See text for details of implantation and testing techniques. The fish is resting on gravel on the bottom and is facing the front glass of the aquarium, through which this photograph was taken.

fibers that end as electrotonic junctions on the motor neurons. Since the collaterals of these fibers are thought to trigger the inhibitory system (Pappas and Bennett, 1966), it may also be involved in this response. It is obvious that in order to clearly define the neural mechanisms involved in these evoked sonic responses, further studies are needed in which motor neuron activity is recorded intracellularly during stimulation of various areas in the medulla and spinal cord.

Integrative systems

Higher regions of the fish brain (above the lower medulla) involved in sound production have only recently been identified. As will be discussed, these areas may func-

tion by controlling the sonic motor apparatus in relation to various environmental and internal stimuli.

All of the data reported in this section have been derived from electrical stimulation studies in toadfish, *O. beta,* utilizing both lightly anesthetized, partially immobilized (Demski and Gerald, 1972) as well as unanesthetized free-swimming animals (Fig. 6) (Demski, 1972; Demski and Gerald, unpublished). The methods used in these studies have been previously reported in detail (Demski and Knigge, 1971; Demski and Gerald, 1972; Demski and Picker, 1973).

Stimulation in the rostral basal medulla at the level of and slightly caudal to the fifth cranial nerve has elicited both grunt and boatwhistle-like sounds in anesthetized male toadfish (Figs. 4, 7a-c). These evoked boatwhistles usually occurred as several repetitions of a hoot-like portion rather than the normal double hoot pattern reported for *O. beta* calls (Fig. 7e) (Tavolga, 1958, 1960). In a few cases a single hoot was evoked (Fig. 7c) that was more like the normal boatwhistle of *O. tau* (Fig. 7d). *O. beta,* however, has been known to occasionally produce single hoots under natural conditions (Tavolga, 1960). Grunts were always associated with the points from which the boatwhistles were evoked. The position of this region of medulla, situated between the lower sonic motor apparatus and several higher regions related to sound production (described in the next section) suggests that it could contain fibers connecting these latter areas. Alternatively, it could be part of the motor system itself.

Stimulation in the midbrain tegmentum, including the region surrounding the acoustico-lateral lemniscus, the ganglion isthmi, and the medial portions of the torus semicircularis, has also resulted in grunt sounds in lightly anesthetized toadfish. These, as well as grunts evoked from the rostral medulla, occurred during stimulation, as after-responses lasting up to 30 sec following the end of stimulation, and as combined responses, i.e., starting dur-

ing and continuing after stimulation. In this study boatwhistle-like sounds were not evoked from the midbrain. However, in more recent experiments on unanesthetized free-swimming toadfish, *O. beta,* both grunt and boatwhistle-like sounds have been elicited from this area of the brain in both sexes. This finding suggests that the normal appearance of boatwhistles in only males (Tavolga, 1960; Gray and Winn, 1961) may be due to hormonal or other factors rather than primary differences in central sonic mechanisms. The boatwhistle-like sounds evoked in free-swimming fish in some cases have a configuration more like the natural calls of *O. beta* than those in the previous study, i.e., a grunt-like sound followed by a double hoot. As reported above for the basal medulla, some of the boatwhistles evoked from the midbrain were of short duration and formed a series of several repetitions. In addition, in one case a series of evoked rapid grunts merged into a series of short boatwhistles (Demski and Gerald, unpublished). These observations support the idea (see Demski and Gerald, 1972) that the neuroanatomical substrates for both of the sounds are very similar. Further details of the sound analysis will be reported later (Demski and Gerald, unpublished).

As a control in these studies on free-swimming toadfish, several areas of the optic tectum and hypothalamic inferior lobes adjacent to the sonic midbrain region were also stimulated. In none of these cases were sounds evoked. During stimulation of most areas (including the sonic areas of the midbrain) several components of defense behavior and/or locomotor activity (rapid swimming, dorsal fin erection, pushing at the front glass, and circling) were observed. However, there appeared to be no direct correlation between any of these behavior patterns and the evoked sounds. In several cases sound production was accompanied by only slight body jerks.

It seems probable that the toadfish sonic midbrain area is not a center controlling complete or integrated sexual and agonistic responses since this type of activity was not observed during stimulation in this region. It is more likely that it is involved in specific motor patterns such as production of acoustic signals. Visual and auditory stimuli are known to influence subtectal midbrain areas in fishes (Grözinger, 1967; Page, 1970; Page and Sutterlin, 1970) and visual, auditory, and cutaneous stimuli have been reported to influence similar areas in amphibians (Potter, 1965; Ewert and Borches, 1971; Schmidt, 1971). These sensory inputs may represent pathways by which relevant stimuli are able to trigger responses from the sonic midbrain region. That cues in these sensory modalites may be important for sound production in toadfish is suggested by the following examples:

1) *Auditory stimuli.* It is known that male toadfish produce boatwhistles in response to hearing the boatwhistles of other males (Winn, 1964). In addition to triggering sound production, auditory feedback may be important for the normal development of sound production. The fact that the midbrain sound-production areas are adjacent to midbrain acoustic regions may be significant in this regard (Demski and Gerald, 1972). Brown (1969) has made a similar suggestion for avian vocalization systems.

2) *Visual stimuli.* Gray and Winn (1961) have reported that toadfish produce grunts when other toadfish, crabs, and swimmers enter or are placed in their territory. Although other senses may be involved in these responses, vision seems likely to be the most important.

3) *Somatic stimuli.* Toadfish frequently produce grunts in response to being captured, squeezed or prodded (Demski and Gerald, personal observations; Fish and Mowbray, 1970).

Based on the above, we hypothesize that electrical stimulation in the sonic midbrain area is mimicking the effect of various sensory inputs which normally trigger this region and thus result in sound production.

The highest area of the toadfish brain from which sounds have been evoked is
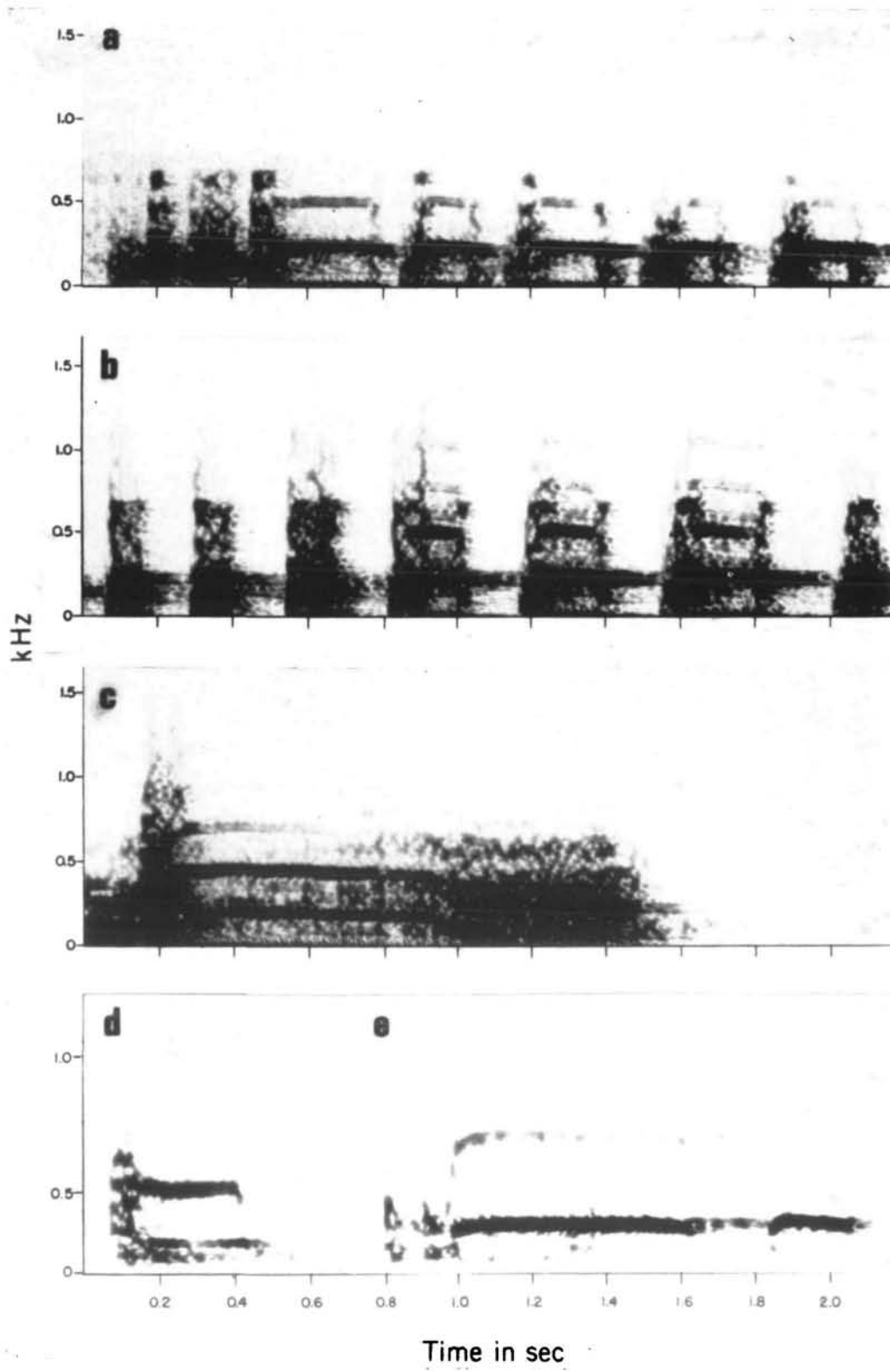
the preoptic region and adjacent hypothalamic areas. In studies using anesthetized toadfish, grunts were repeatedly elicited by stimulation in this area (Figs. 4, 5d) in only one animal (Demski and Gerald, 1972). More recently grunts have been evoked by preoptic stimulation in two unanesthetized, free-swimming male toadfish (Demski and Gerald, unpublished). Further experimentation may determine whether boatwhistles can also be elicited from this region. The apparent absence of overt sexual activity during preoptic stimulation in these toadfish is surprising since courtship, nestbuilding, and sperm release have been evoked from this general region in other teleosts (Demski and Knigge, 1971; Demski et al., 1973); however, a problem exists in a lack of data on the normal reproductive behavior of toadfish, including sound production. Gray and Winn (1961) have suggested that the boatwhistle is a mating call which may attract females to the nest and that grunts may be associated with defense of the nest itself. In this regard, the grunts evoked from the preoptic area may be considered a reproductive response. A similar suggestion has been made for aggressive after-responses associated with evoked courtship in sunfish (Demski and Knigge, 1971). Additional studies on the preoptic area of fishes are needed in order that its functional role in sound production as well as other behavior patterns can be more clearly defined.

Schmidt (1968, 1971) has hypothesized that the preoptic area of amphibians functions as a hormone-sensitive region that triggers lower areas in which the various components of reproductive behavior (including sound production) are organized.

This is based in part on studies (mostly in mammals) which have demonstrated that hormone-sensitive cells are located in the preoptic region (see Michael, 1965; Stumpf, 1970) and that implants of gonadal hormones in this area can restore sexual behavior in castrated or ovariectomized animals (see review by van Tienhoven, 1968). We would like to suggest that the preoptic-anterior hypothalamic area in teleosts may function in a similar manner. Peter (1973) has reported recent studies by Macey, Pickford, and himself in *Fundulus heteroclitus* that support this hypothesis. These workers have demonstrated that preoptic lesions block the spawning reflex in response to administration of neurohypophysial hormones. Presumably these hormones trigger sexual mechanisms through receptors in the preoptic area. We would also like to suggest that olfactory stimuli may play a role in determining the action of this region. This suggestion is based on the findings that olfactory tract stimulation can cause a significant depletion of stainable neurosecretory material in preoptic neurons (Jasinski et al., 1966; Peter and Gorbman, 1968) as well as result in their electrical activation (Kandel, 1964; Hallowitz et al., 1971). Our suggestion is consistent with observations that olfactory stimuli can trigger reproductive responses in a variety of teleosts (Tavolga, 1956; Aronson, 1965; Kleerekoper, 1969; Gerald, 1970). Undoubtedly other systems also influence the fish preoptic area. Some evidence for this comes from studies in which individual sunfish preoptic neurons have been excited as well as inhibited by stimulation of several anatomically distinct forebrain regions (Hallo-

FIG. 7. Sonagraphs of grunt and boatwhistle-like sounds evoked by stimulation in the mediobasal portion of the rostral medulla. a, Two grunts and five boatwhistle sounds evoked at 80 Hz and 40 μA. Filter width was 45 Hz. b, Grunts and boatwhistle-like sounds evoked at 80 Hz and 40 μA. Filter width was 45 Hz. c, A long duration sound similar to the boatwhistle complex. Note that the harmonic portion is initiated by a broad frequency grunt-like sound. A narrow analyzing filter (45 Hz) was used to emphasize the frequency characteristics of the sound. d, Natural boatwhistle sound of *Opsanus tau* recorded by Tavolga. Filter width was 45 Hz. e, Boatwhistle sound of *Opsanus beta* recorded under natural conditions by Tavolga. Analyzing filter width was 45 Hz. (From Demski and Gerald, 1972.)

witz et al., 1971).

SUMMARY AND CONCLUSIONS

Peripheral mechanisms

Swimming sounds are produced by fish moving in water. They may be caused by water flow over the body of the fish and/or movements of internal structures of the fish itself. The exact significance of swimming sounds is not yet known. However, it seems likely that some species such as *A. choerostoma* may use these sounds in maintaining large schools (Moulton, 1960).

There are a wide variety of fish sounds produced by the striking or rubbing together of hard structures. These have been classified as stridulatory sounds and several examples have been given in the text. Many stridulatory sounds are produced during feeding and at least some of these appear to be biologically significant. Other sounds made by jaw movements have been recorded during courtship and aggressive behavior. The pectoral spines and girdle and several cranial bones are also used by various fishes to produce sounds in this category.

The best studied mechanisms of teleost sound production are those which involve volume changes in the swim bladder caused by contraction of sonic muscles. These can be either totally attached to the swim bladder (intrinsic mechanisms) or at least partially attached to some other structure (extrinsic mechanisms).

Although the role of the sonic muscles is being clarified (contraction of muscles dictating a fundamental frequency), there are still many questions as to the contribution of the swim bladder in sound production. It is clear that the swim bladder acts as an impedance-matching device between the sonic muscles and the water (Tavolga, 1962, 1971; Harris, 1964) but other than this, there is still little or no evidence to indicate whether the variation in morphology reported for the swim bladder in soniferous species has any bearing on their

sonic output. Limited data suggest that this is not the case. Experiments on deflation (Skoglund, 1959, 1961; Tavolga, 1964; Salmon et al., 1968, and others) have shown that there are no changes in harmonic content of the signals with changes in volume. Experiments by Bayoumi (1970) have shown that for at least one species there can be considerable variation in size and pattern of the swim bladder without major alteration of the sounds, and Tower (1908) has found that the diaphragm in the swim bladder of *Prionotus* does not seem to play a noticeable role in sound production. The only significant problem with all of these experiments is that they lack the detailed acoustic analyses which might be necessary to reveal sound changes that correlate with variations in the swim bladder structure. Most of the papers have included octave-band analysis or subjective listening to the sounds, and it is possible that changes in sonic output need to be studied with much finer devices which include systems to analyze pulse rates. Of course, we must realize that the sonic output of the animal changes significantly with acoustic environment (Tavolga, 1960, 1962, 1971) and this must be accounted for in any experiments. Beyond this we must question the significance of spectral characteristics of a fish's sound in light of the fact that the sound can change considerably, depending upon the precise habitat of the emitter or producer. For this reason, it is possible that the fishes "ignore" spectral characteristics of the sounds and rely more heavily on the fundamental frequency of the sounds, or, as pointed out by Winn (1964, 1967), fishes may be responding to the pulse rate or other temporal cues in sound rather than frequency components. In this case, the contributions of the swim bladder to sound production would permit considerable variability in shape as long as the swim bladder were highly damped in order to precisely follow rapid rise and decay times.

Central mechanisms

As a means of summarizing the avail-

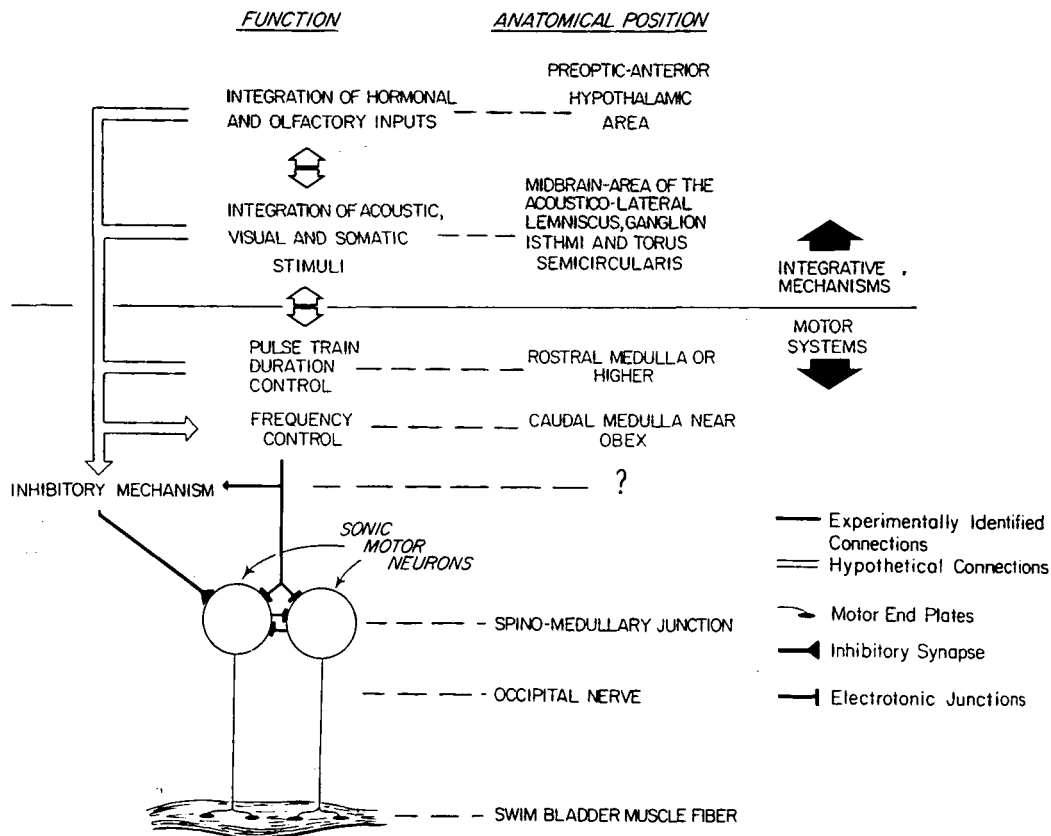HYPOTHETICAL MODEL OF TOADFISH SOUND PRODUCTION MECHANISMS

FIG. 8. A tentative model of sound production mechanisms in toadfish. See text for explanation.

able data in this area, we have constructed the following tentative model of the neural mechanisms controlling sound production in toadfish. We realize that the study of the central mechanisms of fish sound production is only beginning, and any model constructed at this time must indeed be highly speculative. However, parallels can be made to other models such as Schmidt's (1971) for frog vocalization and may justify an attempt at this time to unify some of the findings covered in this review.

The model is illustrated digrammatically in Figure 8. Cell bodies of the sonic motor neurons are located in the spinomedullary junction in a midline nucleus. Their axons form the occipital nerves (Tavolga, 1971) and up to four or more of them may end on each swim bladder mus-

cle fiber (Gainer and Klancher, 1965). This polyaxonal innervation is one of several mechanisms which provide for the synchronous activation of many muscle fibers, and therefore in part the rapid contraction rates possible in toadfish swim bladder muscle. Motor cells are coupled electrotonically by direct interconnections as well as by afferent fibers. This coupling synchronizes the discharge of many cells in the nucleus (Pappas and Bennett, 1966). The frequency of firing of motor neurons is controlled by a mechanism located near the obex in the caudal medulla. Its output is probably by way of the afferent fibers electrotonically coupled to the motor cells and collaterals from these fibers that are thought to trigger an inhibitory mechanism which may influence sonic motor activity by way of chemically mediated syn-

apses. A second control area, located somewhere in or above the rostral medulla, normally limits the duration of activity in the motor nucleus to approximately the duration of the grunt sound. Loss of this area allows longer activity suggestive of boatwhistle calls (Bennett, personal communication; Pappas and Bennett, 1966). Although the mechanism is unknown, areas in the rostral medulla and midbrain near the acoustico-lateral lemniscus, ganglion isthmi, and torus semicircularis can trigger the lower sound production systems (Demski and Gerald, 1972; Demski and Gerald, unpublished). This midbrain region is known to receive acoustic and visual stimuli in fishes (Grözinger, 1967; Page, 1970; Page and Sutterlin, 1970) and acoustic, visual and cutaneous inputs in amphibians (Potter, 1965; Ewert and Borchers, 1971; Schmidt, 1971). On this basis, we suggest that it functions by integrating relevant stimuli in these sensory modes and appropriately triggering the sound-production motor apparatus. This area of the fish brain appears to be at least functionally comparable to the amphibian "afferent vocal center" proposed by Schmidt (1971). The highest region in the toadfish brain known to influence sound production is located in the preoptic area and adjacent anterior hypothalamus (Demski and Gerald, 1972; Demski and Gerald, unpublished). Several studies have demonstrated that similar areas are involved in reproductive activities in fishes (Peter, 1970; Demski and Knigge, 1971; Demski et al., 1973) and amphibians (Aronson and Noble, 1945; Schmidt, 1968, 1969). In addition, it has been suggested that receptors for gonadal and/or neurohyphophysial hormones are located in this area in a variety of vertebrates (Michael, 1965; Stumpf, 1970; Peter, 1973, and others). On this basis, we have suggested that the preoptic region in toadfish may function as a hormone-receptive area which triggers lower regions, including sonic motor systems, involved in reproductive activities. Here again our model is similar to the one proposed by Schmidt (1971). We have also

suggested that the preoptic area in fishes is influenced by olfactory stimuli since the electrical and secretory activity of preoptic neurons can be greatly affected by olfactory tract stimulation (Kandel, 1964; Jasinski et al., 1966; Peter and Gorbman, 1968; Hallowitz et al., 1971).

ADDENDUM

The reader is directed to recent papers by Fish (1972) and Winn (1972) which provide many additional details of toadfish acoustic behavior and to papers by Kelley et al. (1973) and Zigmond et al. (1973) which report identification of testosterone concentrating neurons in the preoptic region of Xenopus laevis and the midbrain sonic area of the chaffinch, respectively. Regarding electrical stimulation of the brain in toadfish, Mr. Michael L. Fine at the Graduate School of Oceanography, University of Rhode Island, has recently been able to evoke one-to-one and grunt sounds from anesthetized Opsanus tau (personal communication). The distribution of his electrode tracts, as plotted on the dorsal surface of the brain, suggests that positive sites were located in the medulla, midbrain and preoptic-anterior hypothalamic area.

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