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DEVELOPMENT OF AN ACOUSTIC TELEMETRY TAG FOR MONITORING ELECTROMYOGRAMS IN FREE-SWIMMING FISH

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Summary

We report the development of an acoustic telemetry tag used to monitor electromyograms (EMGs) remotely from free-swimming marine fish. The device described amplifies and filters the EMG and then converts the electrical waveform into a frequency-modulated acoustic signal that is transmitted through water. The signal is then received, demodulated and recorded by the receiving system. The EMG tag described has been tested on a range of species, including toadfish *Opsanus tau*, spiny dogfish *Squalus acanthias*, yellowfin tuna *Thunnus albacares* and eastern Pacific bonito *Sarda chiliensis*, in different tank environments. In certain tanks the fidelity with which the system replicates the EMG is sufficient to quantify accurately the onset, offset, duration, the integrated area under the absolute value of the signal and the number of signal zero crossings. This EMG tag will expand the scope of questions that can be addressed about the behavior and physiology of free-swimming fish.

Key words: electromyogram (EMG), acoustic telemetry, fish, remote monitoring.

Introduction

Measurements of muscular contraction have been used extensively to address questions that extend from neural pathology in humans (Wu et al., 1995; Valls-Sole et al., 1997) to insect locomotor mechanics (Kutsch et al., 1993). The most common method of identifying muscle contraction is by recording electromyograms (EMGs), the electric potential generated during the initiation of muscle contraction. Measurement of EMGs has been particularly fruitful in studies of fish evolution, ecology, physiology and functional morphology. The activity of the axial musculature has been used to define maximum tail-beat frequencies (Wardle and He, 1988). The timing of contraction of muscle assemblages has been linked with kinetics to examine feeding strategies and their evolution (Gibb, 1997; Motta et al., 1997). Placement of numerous electrode pairs serially along the fish's body has begun to illuminate how the complex muscle fiber orientation and myotomal architecture function in generating thrust (Wardle and Videler, 1993; Rome et al., 1992; Jayne and Lauder, 1994, 1995, 1996). In addition, investigators have quantified the complex character of the EMG signal to examine relative changes in fiber recruitment patterns, muscular efficiency and power output over a range of temperatures and swimming speeds (Rome, 1990; Rome et al., 1992; Jayne and Lauder, 1994, 1995).

Although direct records of muscle activity have been important for studies of fish biology, the equipment and techniques required for measuring EMGs have limited the scope of research. The fish is connected to an amplifier and data-logging system by a pair of electrodes and is usually contained in a small tank or a water tunnel (Rome et al., 1992; Jayne and Lauder, 1994, 1995, 1996). Long-term studies are hampered by the logistical complexity of keeping long, thin electrodes untangled and in place. The range of activities and behaviors that can be examined under laboratory conditions, particularly in large, active fish, is narrow. Studies in the wild are even more challenging.

A number of remote telemetry EMG systems have been developed to monitor muscle activity. Radio telemetry is most commonly used and has been applied to subjects ranging from humans (Peat et al., 1976; Hintermeister et al., 1995; Dyson et al., 1996) to freshwater fish. The primary focus of studies with fish has been to estimate energetic costs or activity levels (Priede and Young, 1977; Ross et al., 1981; Rogers and Weatherley, 1983; Rogers et al., 1984; Armstrong et al., 1989;

Weatherley et al., 1996; Briggs and Post, 1997). One commercial radio tag (Lotek Engineering Inc., Aurora, Ontario, Canada) used in a number of these studies (Weatherley et al., 1996; Briggs and Post, 1997), transmits a radio pulse when a threshold level of cumulative voltage has been generated (the pulse does not necessarily correspond to a tail beat). While these devices have proved useful, no tag has been demonstrated to replicate the complex character of the EMG with the fidelity required for quantitative analysis. Also, radio telemetry cannot be used in a marine environment because the radio signal is rapidly attenuated by sea water.

We report efforts to develop an acoustic system to monitor the full EMG waveform remotely from free-swimming marine fish. The fidelity of EMG replication had to enable quantification of variables indicating the timing and extent of muscle recruitment. The onset, offset, duration, number of zero crossings, the number and mean amplitude of peaks, and the area under the absolute value of the waveform (the rectified waveform) were measured. One or more of these variables are typically used to quantify muscle activity (Loeb and Gans, 1986). We outline our success in developing an EMG transmitter and the challenges of extracting the frequency-modulated signal from the acoustically complex tank environment.

Materials and methods

The objectives of this effort were (1) to fine-tune the tag design and verify its function across a range of species and muscle fiber types and (2) to examine receiver function in different tank environments. Studies were initiated at the Tuna Research and Conservation Center (TRCC) in Monterey, California, USA. Tests were conducted with toadfish *Opsanus tau* L., spiny dogfish *Squalus acanthias* L., eastern Pacific bonito *Sarda chiliensis* Cuvier and yellowfin tuna *Thunnus albacares* (Bonnaterre).

Tag

The EMG tag circuitry had to acquire the EMG signal, amplify and filter it, and then encode the waveform as a frequency-modulated (FM) acoustic signal for transmission through sea water. The EMG signal was obtained using bipolar electrodes consisting of 0.18 mm Teflon-coated stainless-steel wires that were bared 1 mm from their tip. The signal was amplified 2400 times by a differential amplifier. Post-amplification, the signal was passed through a band-pass filter with the low-pass and high-pass poles set at 400 Hz and 10 Hz, respectively. The output of the filter was connected to a voltage-controlled oscillator (VCO). The incoming voltage from the EMG dictated the VCO oscillation frequency producing an FM signal.

The output of the VCO was connected to an acoustic transducer that transmitted the FM signal. The transducer was a 0.95 cm diameter, 0.95 cm long PZT-4 ceramic tube with a hoop-mode resonance frequency of 122 kHz (EDO, Salt Lake City, UT, USA). The acoustic signal fluctuated around 122 kHz by ±5 kHz, depending on the EMG voltage. Tag dimensions were 3.5 cm×2 cm×1 cm (Fig. 1). The tag was powered by two 3 V lithium, coin-cell batteries (Panasonic, BR 2032), providing a 40 h lifetime. A direct connection was made to the band-pass filter output to compare the electrical signal measured from the contracting muscle and the acoustically transmitted EMG. Tags were cast in epoxy resin and four perforated tabs were used to suture the tag to the fish.

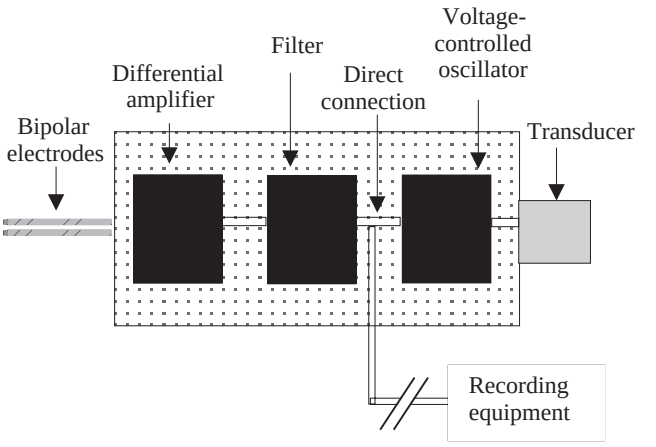

Fig. 1. Schematic diagram of the EMG tag components illustrating the bipolar electrodes (the insulation is removed 1 mm from the end), the differential amplifier, the filter, the voltage-controlled oscillator and the ceramic transducer. Also shown is the direct electrical connection at the output of the filter. A full circuit diagram can be obtained from M. Deffenbaugh.

Receiver

The receiver had to decode the EMG waveform, converting the FM signal back into the EMG voltage. This required continuous measurement of the acoustic signal frequency. Frequency detection in the tank environment is complicated by a phenomenon known as multipath. The signal emitted from the tag has a broad beam-width and there are multiple paths the acoustic signal can follow between the tag and hydrophone, including a direct path as well as paths that reflect one or more times off the tank walls or water surface. Constructive or destructive interference between these paths causes the received signal to fade in and out as the transmitted frequency changes. This fading, along with the variable time delay between the paths, can complicate detection of the transmitted frequency.

Three different receivers were developed. All receivers employed one or two hydrophones equipped with the same transducer as used in the transmitter. Receiver 1, used for the toadfish, digitized and stored the unprocessed acoustic signal. The digitized acoustic signal was later processed in MATLAB to recover the EMG waveform. The average period of the acoustic signal was measured over blocks of 128 cycles, taking the inverse of the period to yield the frequency and converting the frequency back into the EMG voltage based on calibration curves for the tag VCO.

Two additional receivers allowed immediate observation of the received EMG. Receiver 2 (used with spiny dogfish) applied the same decoding algorithm as receiver 1, except the

decoding was accomplished primarily in hardware. The period was averaged over 512 cycles and output in digital form to a laptop computer. The laptop converted the timing results into the EMG waveform, which was displayed. Due to laptop-software limitations, the maximum sampling frequency was 238 Hz. Receiver 2 compared the signal strength from two hydrophones at different locations and rapidly switched between them, selecting at each time the hydrophone with the higher amplitude signal.

Receiver 3 (used with tuna and bonito) used only one hydrophone and was assembled from commercially available equipment. The received acoustic signal was first passed through an 80–260 kHz band-pass filter (AP280–5-SR, AP Circuit Corp.) and then demodulated by an FM receiver (Kenwood TS440) which employed a phase-locked loop for frequency measurement. The phase-locked loop had an internal VCO similar to the VCO of the tag. It applied a varying control voltage to its own VCO in a feedback loop such that its frequency tracked the frequency of the received signal. In the absence of multipath, the control voltage recreates the EMG voltage. The control voltage output was then low-pass filtered (Frequency Devices 901) at 400 Hz. The output was connected to a speaker to provide an audible indication of muscle contraction. The waveform was also recorded to a TEAC XR 7000 tape recorder and later digitized at 6.25 kHz.

Toadfish

Initial tests of the tag were conducted on four toadfish (mass approximately 750 g) obtained from the Marine Biological Supply (Woods Hole, MA, USA). Fish were held in a 1.5 m diameter, 1 m deep fiberglass tank at ambient photoperiod and water temperatures (11–13.5 °C) and fed squid once weekly. Toadfish were anesthetized by immersion using NaH_2CO_3-buffered (2:1) tricaine methanesulfonate (MS222) at 0.1 g l^{-1}. The electrodes (1 m long) were inserted into the fast-twitch axial musculature using a 19-gauge needle and then sutured to the skin. After recovery, the toadfish were placed in a 0.8 m diameter plastic bucket filled with aerated sea water at 13 °C. The uncast tag (circuitry exposed) was secured outside the bucket with the long electrodes leading to the fish. The fish was gently prodded with a glass rod to induce movement. Intermittent recordings were made from the direct connection and the acoustic receiving system for at least 4 h, after which the tag was removed. Receiver 1 was used with the hydrophone suspended in the bucket.

Spiny dogfish

Tests of the tag and receiver 2 were conducted with one spiny dogfish (fork length *FL*=75 cm) at the Marine Biological Laboratory (MBL, Woods Hole, MA, USA). The shark was held in a 4 m diameter, 1 m deep, single-wall fiberglass tank at ambient temperatures (10–12 °C) and photoperiods. For experiments, the specimen was placed in NaH_2CO_3-buffered (2:1) MS222 at 0.1 g l^{-1}. Once anesthetized, the shark was irrigated at 50 % of the initial anesthetic concentration. The electrodes (5 m long) were inserted into the slow-twitch musculature at approximately 75 % of *FL*. The electrodes and the tag (cast in resin) were sutured to the skin. The shark was then returned to its holding tank. To obtain recordings during both burst and sustained activity the shark was gently tapped on the first dorsal fin to induce an escape response. Using receiver 2, the acoustic and direct signals were recorded intermittently over 4 h, after which the shark was recaptured and the tag removed. Both hydrophones were suspended against the inner tank wall, near the surface, approximately 30 cm apart.

Eastern Pacific bonito

Bonito caught off the coast of southern California were transported to the TRCC. The facility contains four long-term holding tanks composed of a single wall of fiberglass. The largest tank is 13.3 m diameter and 3.3 m deep (360,000 l), two are 10 m diameter and 2 m deep (120,000 l) and one is 5.5 m diameter and 1.5 m deep (25,000 l). For short-term holding, an oblong, foam-insulated fiberglass tank was used, dimensions 2 m×1.5 m×0.7 m deep (1230 l). The walls were constructed of three layers; the inner and outer layers consisted of 0.6 cm of fiberglass and the middle layer of 2.54 cm closed cell foam. Tanks are continually supplied with filtered, aerated sea water at 19±1 °C. Bonito were held in the 5.5 m×1.5 m holding tank at ambient photoperiods and fed a mixture of squid and night smelt three times weekly.

Bonito (*N*=2, mass=1.8–1.9 kg, *FL*=54 cm) were captured with a net and placed in a seawater-filled sling containing 1 g l^{-1} buffered MS222. Once anesthetized, the fish were set in a cradle and irrigated at 50 % of the initial anesthetic concentration. The electrodes were inserted with a 19-gauge-needle at 66 % *FL* in the superficial lateral wedge of slow-twitch muscle. The electrodes and tag were sutured to the skin. Tag attachment required less than 7 min.

Following tag attachment, fish were irrigated with sea water until sporadic tail movements occurred. The bonito were then placed in the foam-insulated tank and irrigated until tail beats became regular, at which point they were released. In the small tank, intermittent recordings were made *via* the direct electrical connection and acoustically using receiver 3. The hydrophone was suspended near the water surface against the wall. After at least 1 h, the bonito were moved to the 5.5 m diameter tank where the direct connection was maintained. Following the experiments, lasting approximately 4 h, the tags were removed and the fish returned to their holding tank.

Yellowfin tuna

Yellowfin tuna were caught off southern California and transported to the TRCC. Fish used in experiments (*N*=2, mass=3.5–4 kg, *FL*=60 cm) were held in the 10 m×2 m tanks at ambient photoperiods (19±1 °C) and fed a mixture of squid and night smelt three times weekly. The fish capture and handling, tag attachment and recovery procedures differed from bonito only in that the electrodes were inserted at 50 % *FL*, 2 cm deep into the centralized slow-twitch muscle. After recovery, direct and acoustic recordings were made intermittently in the foam-insulated holding tank using receiver 3. After 1 h, the first tuna

was placed in the 5.5 m tank and the second in the 10 m diameter tank. Only in the 5.5 m tank was the direct electrical connection maintained. Following experiments, lasting 4 and 18 h, respectively, the tags were removed and the fish returned to their holding tank.

Data analysis

For the spiny dogfish, only the tail-beat frequency was determined. Records were not quantified further because of the relatively low sampling frequency (238 Hz) of receiver 2. For tuna and bonito, the onset, offset, duration and the integrated area under the rectified curve were quantified with a MATLAB program. The number of peaks (minimum threshold set at 5 % of the maximum), their mean amplitude (expressed as a percentage of the maximum) and the number of zero crossings were also determined. Given the variation typical between successive EMGs, each individual waveform in the direct signal was compared to the corresponding acoustic waveform. Student's *t*-test was used to compare all signal variables. Values are reported ± S.D. or means ± S.E.M., as appropriate.

Results

The development of the acoustic EMG telemetry system proceeded in a number of stages. The tag circuitry was first tested with the toadfish. Their sedentary nature and small size enabled laboratory tests prior to casting the tag in resin, simplifying initial adjustments to the circuitry. Additional tests were conducted with spiny dogfish. The regular, predictable signal from this continually swimming shark simplified validation of proper tag operation and allowed examination of receiver 2. Ultimately, tests were conducted on tuna and bonito to confirm that the tag worked across species and muscle fiber types, and at the same time, to test receiver 3. We felt it important to demonstrate the tags' application across fiber types and species, given the novelty of the device.

Toadfish

Fig. 2 shows data collected during a toadfish escape response. In Fig. 2A, the signal acquired *via* the direct connection is shown. The arrow indicates when the fish was prodded; the subsequent EMG signal is associated with the contraction of the fast-twitch axial musculature. Fig. 2A shows the simultaneously received acoustic signal before decoding. The acoustic signal shows a variation in amplitude where the transmitted signal (not shown) had constant amplitude. The rapid fading and swelling of the received acoustic signal results from multipath as described above. Fig. 2C shows the decoded EMG waveform. Note that it only approximately resembles the EMG waveform in Fig. 2A. The voltage spikes in the signal are distorted and the burst of activity in the decoded EMG signal continues after it has ended in the directly recorded EMG.

Spiny dogfish

Fig. 3 shows the data obtained during an escape response by the spiny dogfish. Although there is some background noise in the electrical signal (Fig. 3A), an EMG signal corresponding to the escape response is obvious. Note that the electrical signal

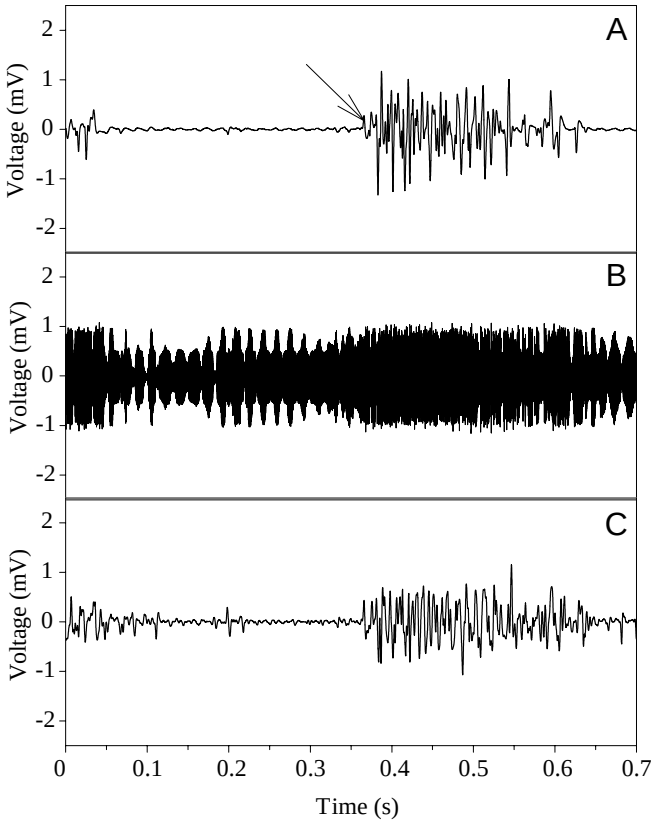

Fig. 2. The direct electrical signal (A), received acoustic signal (B) and decoded acoustic signal (C) from a toadfish *Opsanus tau* held in a 0.8 m diameter plastic bucket. The arrow in A indicates when the fish was prodded with the glass rod. Receiver 1 was used.

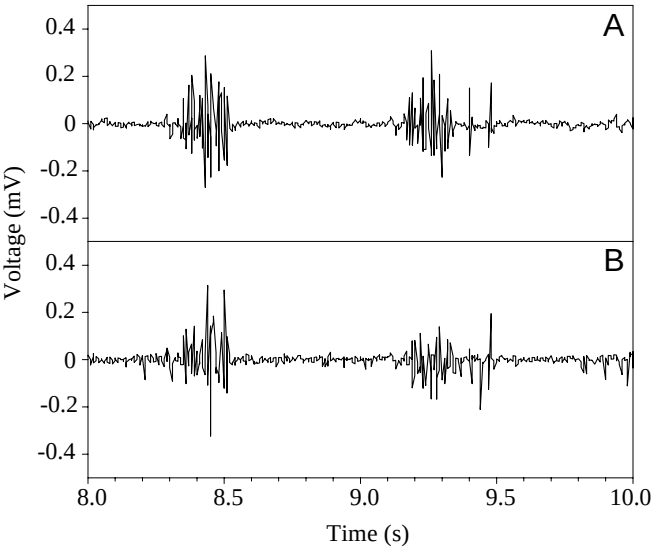

Fig. 3. The direct electrical (A) and the demodulated acoustic signal (B) over 2 s from a spiny dogfish *Squalus acanthias* held in a 4 m diameter, single-walled fiberglass tank. The signals were generated during an escape response by the shark. Receiver 2 was used.

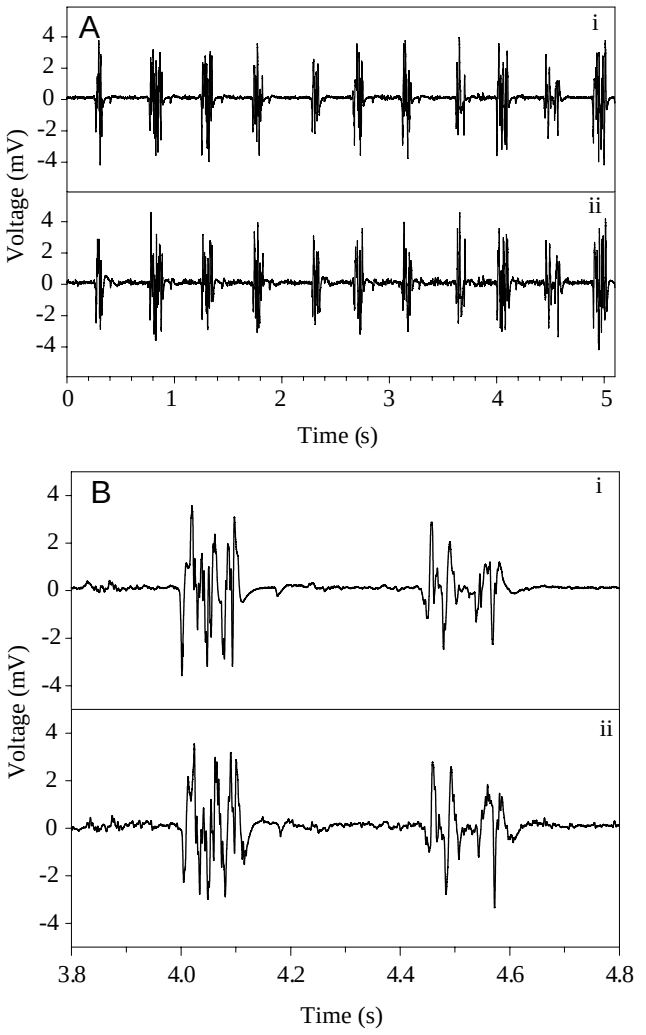

Fig. 4. The direct electrical (i) and the demodulated acoustic signal (ii) from a bonito *Sarda chiliensis* swimming in a small, foam-insulated tank over (A) 5.2 s and (B) 1 s. Receiver 3 was used.

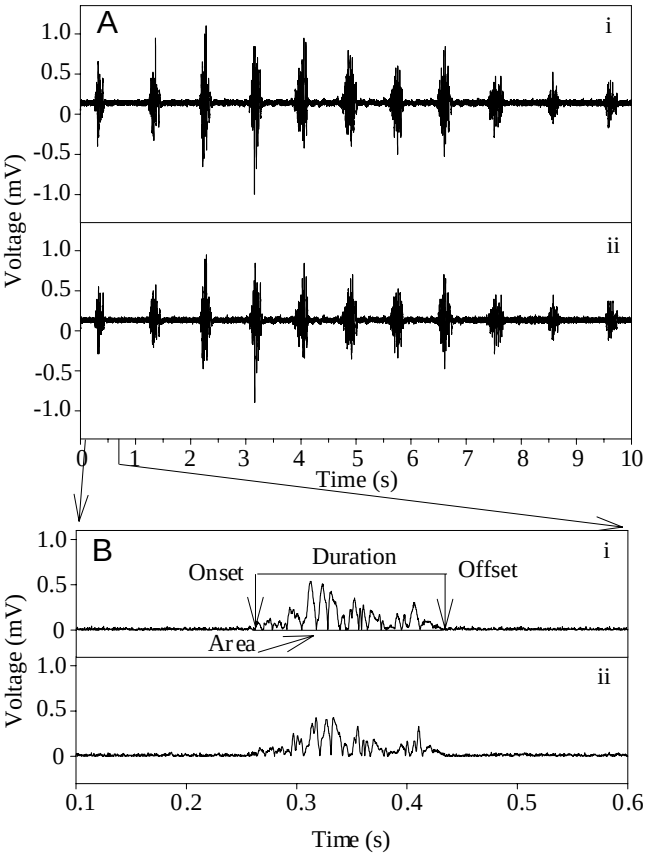

Fig. 5. (A) The direct electrical (i) and the demodulated acoustic signal (ii) from a tuna *Thunnus albacares* swimming in a small, foam-insulated tank over 10 s. (B) The absolute value of the direct (i) and demodulated signal (ii) in A from 0.1 to 0.6 s. The measured variables, onset, offset, duration and area under the absolute value of the curve are shown in Bi.

is matched by a similar acoustic signal in Fig. 3B. Similar patterns were observed during other burst events by this animal as well as during sustained swimming. Some noise spikes are still apparent in the decoded acoustic signal (Fig. 3B), though the overall quality of the telemetry data is improved over that produced by receiver 1 (Fig. 2). The tail-beat frequencies determined from both the electrical and acoustic signals were 1.10±0.20 Hz (mean ± S.D.; N=20) during burst activity and 0.70±0.04 Hz (N=20) during sustained activity.

Eastern Pacific bonito

Fig. 4A shows a representative record of the direct electrical (Fig. 4Ai) and acoustic (Fig. 4Aii) signals obtained for a bonito swimming in the foam-insulated tank. Note how closely matched the two signals are when comparing the rate of the voltage pulses and the general character of the waveform. Closer examination of the same record (Fig. 4B) indicates that the two signals are nearly identical, each inflection of the electric signal (Fig. 4Bi) is paralleled by a similar change in the acoustic signal (Fig. 4Bii). As the data were recorded it was possible to verify audibly and visually that both signals corresponded to the tail beat and thus represent the contraction of the slow-twitch muscle fibers during sustained swimming. The tail-beat frequency is 1.50±0.10 Hz (mean ± S.D.; N=20). Approximately 2 h of data were recorded from two bonito. In the foam-insulated tank both the tag and receiving system appear to function perfectly.

Yellowfin tuna

Results from tests made with yellowfin tuna confirm proper tag function (Fig. 5A) and indicate that the fidelity of EMG waveform replication is sufficient for quantitative analysis. For 70 individual EMG waveforms (representative of steadily swimming tuna in the foam-insulated tank) the time of onset, offset, duration and the integrated area under the rectified waveform were quantified for both acoustic and direct signals (Fig. 5B). The difference in the time of onset (–0.0007±0.0060 s) and offset (–0.0030±0.0050 s) was not significantly different from 0 (mean ± S.D.; P<0.05). There was no difference (P<0.05) in the duration of the waveform

(0.157±0.027 s acoustic: 0.156±0.027 s direct) or in the area under the rectified curve (0.041±0.011 acoustic: 0.041±0.010 direct). 20 signals were analyzed to compare the number and mean amplitude of signal peaks and the number of zero crossings. When comparing individual signals, the difference in number of zero crossings (0.4±1.0) was not significantly different from 0 (P<0.05). Although the acoustic signal had on average 5.3±3.7 more peaks than the direct signal, the mean amplitude was on average 3.0±0.3 % less. The difference in the product of the two (0.4±0.7 %) was not significantly different from 0 (P<0.05). Importantly, the relative change between successive acoustic and direct waveforms was conserved. The tail-beat frequency calculated from both signals was 1.40±0.16 Hz, which again was visually and audibly verified.

Following the transfer to the larger diameter tanks, the intermittent spikes in the acoustic signal (Figs 2C, 3B) reappeared. The spikes occurred throughout the record and in some places distorted the EMG waveform. Despite this, tail-beat frequency was easily calculated from both the direct and acoustic signals and ranged from 2 to 2.6 Hz. Noise was observed in all records from the 5.5 m and 10 m holding tanks for the tuna and bonito. More than 4 h of data was collected from the two tuna.

Discussion

The tests described above indicate that the acoustic EMG tag and receiving system can perform all necessary operations and the full EMG waveform can be obtained from free-swimming marine fish. Results demonstrate that EMGs can be recorded from a range of species and from both slow and fast-twitch muscle fiber types.

Tag

To obtain the variables necessary to quantify the complex character of the EMG from marine fish, the system developed had to (1) be small in size, (2) transmit at a frequency enabling adequate signal propagation in sea water and (3) telemeter the entire waveform.

To minimize potential impact on the fish, the tag was made as small as possible. The general design was simple to reduce component size. The circuitry consisted of only three small integrated circuits, a low-power differential amplifier, a dual-operational amplifier (used for filtering and voltage regulation), and a VCO. The low power requirements of the tag also served to decrease size by reducing battery requirements. The tag electronics required only 1 mW and the transducer 10 mW of power.

The received signal strength in sea water is dependent on the tag's power output, transmission frequency and signal type (e.g. acoustic, electromagnetic). Acoustic signals from 22 to 60 kHz are commonly used for telemetry in the marine environment. The low transmission distance in the tanks resulted in relatively low power requirements and enabled the use of the higher 122 kHz acoustic transmission frequency.

To confirm the ability to transmit the entire EMG waveform acoustically, we must demonstrate that the tag can acquire the EMG signal, amplify and filter it, and then accurately represent the complex waveform in a FM acoustic signal. The direct recordings (Figs 2–5) indicate that the tag circuitry captures, filters and amplifies the electrical signal. The character of these signals is typical of EMGs recorded using standard equipment in other studies (Rayner and Keenan, 1967; Jayne and Lauder, 1994, 1995; Rome, 1990). The tag's ability then to modulate the voltage information and transmit the FM signal is shown by the acoustic trace (Figs 2–5). All electrical signals are matched by a corresponding acoustic signal, allowing, at a minimum, calculation of tail-beat frequency. The results in the small foam-insulated tank (Figs 4 and 5) demonstrate that the EMG waveform is replicated with the accuracy required for complex quantitative analysis. Although the number and intensity of peaks differed slightly between the direct and acoustic signals, the onset, offset duration, number of zero crossings, area under the rectified waveform, and the product of the peak and mean peak intensity were the same. The linear FM regime used to transmit the EMG signal is simple to implement in hardware and is more robust to multipath interference than many other modulation schemes, such as amplitude modulation.

Receiver

The complete process of transmitting an EMG requires a receiver that can detect and decode the acoustic signal frequency to reconstruct the EMG waveform. It is here that we met with the greatest challenge. Receiver 1 was only used in initial tests. Because this receiver did not allow real-time display of the decoded acoustic EMG, examination of tag function was awkward. Also, Fig. 2 indicates problems with multipath. The rapid fading and swelling (Fig. 2B), concurrent with constructive and destructive interference, distorted the decoded EMG signal (Fig. 2C). The time-spreading caused by these reverberations produced distortion within the bursts and the tail at the end of the decoded signal.

To reduce problems with multipath and enable immediate viewing of the decoded EMG, receiver 2 was developed. Receiver 2 employed two hydrophones at different locations in the tank. Fading is uncorrelated between locations that are sufficiently far apart; typically several acoustic wavelengths of separation is adequate. Receiver 2 would lose the received signal only if both hydrophones experienced signal fading simultaneously. From Fig. 3 it is evident that the signal is improved over receiver 1; however, some distortion is still apparent. Receiver 3 was assembled with the hope of reducing problems with multipath. During tests with both tuna and bonito in the foam-insulated tank, the phase-locked loop in the commercial receiver was able to reconstruct the EMG waveform accurately.

A variety of variables will influence the quality of the acoustic transmission. These include the size and shape of the tank, the wall composition, the transmitter and receiver locations and motion, and the receiver design. In this preliminary study, we have not determined the relative importance of these variables. Further work will be necessary

to characterize the acoustic properties of tanks and optimize both the tank and receiver design.

Although work in the open ocean should reduce multipath problems (due to the reduced number of reflective surfaces) we have several reasons for focusing initially on a system for the laboratory. The low-range requirements in the tanks reduced the tag size. The use of captive animals allowed us to verify that the signal corresponded to muscle contraction, simplifying initial development. In the tanks it is possible to maintain a direct connection to the tag for comparisons of the acoustic and electrical EMG waveform. Finally, initial efforts with captive fish, where activity can be monitored and temperature controlled, provide an important foundation for subsequent at-sea research. Our ultimate objective is to develop an inexpensive tag and receiving system for work both in the laboratory and at sea.

Using the acoustic EMG tag and receiver, research can be conducted where standard equipment is impractical. Not only will it be possible to determine when muscle contraction occurs, but also to define indices of relative muscular effort and obtain insight into patterns of muscle recruitment. The onset, offset, duration, area under the rectified waveform, and the number of zero crossings can be accurately determined from the acoustic signal (Fig. 5). Studies over an extended spatial and temporal scale will be possible, expanding the scope of behaviors that can be examined. The records obtained across a range of species and muscle-fiber types indicate the tag's broad application. It should be possible to record from any muscle for which the contraction frequency falls within the range of the band-pass filter (10–400 Hz). The design of the EMG tag can also be applied to other systems where complex analog signals are generated. Remote sensing devices that interface with other sensors such as strain-gauges and flow-probes are conceivable. This new technology will increase the complexity of questions that can be addressed about animals both in captivity and in their natural environment and will expand the use of acoustic telemetry into new fields.

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