ACOUSTICS AND ELECTROPHYSIOLOGY OF SOUND PRODUCTION BY THE NORTHERN SEAROBIN, *PRIONOTUS CAROLINUS*

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Sonic muscles have evolved as a mechanism of sound production in a number of teleost families. These highly specialized, striated, bilateral muscles are found in close association with, or attached to the swimbladder, which amplifies the sounds produced by these muscles (Demski, L.S., Gerald, J.W., Popper, A.N. Amer. Zool. 13:1141-1167, 1973). The fundamental frequency of the acoustic signal is determined by the contraction frequency of the muscle (Skoglund, C.R. J. Biophys. Biochem. Cytol. 10S:187-200, 1961), while acoustic amplitude is determined by the force of contraction. It has been suggested that the sonic muscles of the searobin contract alternately rather than simultaneously (Bass, A., Baker, R. Brain Behav. Evol., 38:240-254, 1991); this would represent a unique mode of function for a teleost sonic muscle.

Simultaneous electromyogram (EMG) and acoustic recordings were made from voluntarily calling male and female searobins. EMG electrodes were placed in one sonic muscle through a small incision in the lateral wall. Audio and EMG recordings were amplified, digitized, and recorded on a personal computer. In separate experiments, fish were anesthetized with MS-222 (Sigma Chemical Co., St. Louis, MO) and the occipital nerve, which innervates the sonic muscle, was exposed and stimulated at frequencies of 50 - 500 Hz. Tetany determinations were made from recordings of single muscle stimulation, while acoustic signal amplitude was compared between single and dual muscle stimulation in the same animal.

Searobin sonic muscles do contract alternately, as indicated by oscillograms and power spectra of simultaneously recorded EMG and acoustic waveforms. Voluntary muscle contraction frequencies of 90.3 to 115.4 Hz were observed from single muscles, while simultaneously recorded sounds expressed fundamental frequencies of 181.5 to 229.4 Hz. In occipital nerve stimulation experiments, maximal acoustic amplitude was observed at a stimulus rate of 121.5 Hz and no sound production was noted at frequencies greater than approximately 200 Hz, however; muscle contraction was evident at stimulus rates as high as 330 Hz. In dual occipital stimulation experiments, the amplitude of sound produced by simultaneously contracting muscles was always greater than that of a single muscle in the same specimen. The sounds produced by searobins were characterized by a median of 14 sound pulses and a multiple-peak power spectrum, with a fundamental frequency of 200 Hz and harmonics at approximately 400 and 600 Hz. A mean delay of 13.15 msec was observed between the initiation of the EMG and that of the acoustic signal, and 1 to 3 damped acoustic waveforms were noted following the final EMG waveform. Measurements of muscle contraction force and pressure change within the swimbladder will be required to determine the cause of the delay and the post-contraction acoustic oscillations, but they may be the result of the elasticity of the swimbladder wall. Little sexual dimorphism was noted in the acoustic signal, though the sonic muscles of males were significantly larger than those of females.

The sonic muscles of the searobin contract alternately, resulting in an acoustic fundamental frequency which is twice the contraction frequency of the individual muscles. A consequence of alternate contraction is a reduction in acoustic amplitude due to the contraction of only half the total sonic muscle mass at any given time. This mode of function represents the evolution of a novel solution to the inherent trade-off between speed and force of contraction noted in many rapidly contracting muscles. In species contracting their sonic muscles simultaneously (at up to 200 Hz), greatly decreased sonic muscle force production (hence acoustic amplitude) has been attributed to the extremely rapid muscle kinetics required for these contraction rates (Rome, L.C., Syme, D.A., Hollingworth, S., Linstedt, S.L., Baylor, S.M. Proc. Nat. Acad. Sci., 93:8095-8100, 1996).

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