It's All a Matter of Timing: Temporal Mechanisms for Production and Encoding of Acoustic Signals

Andrew H. Bass¹,² and Deana Bodnar¹

¹Section of Neurobiology and Behavior, Cornell University, Ithaca, NY 14853; ²UC Bodega Marine Laboratory, Bodega Bay, CA 94923

Abstract: Studies of acoustic communication in teleost fish have identified basic principles underlying both the production and reception of acoustic signals. Male midshipman fish generate long duration mate calls known as "hums" that are multi-harmonic signals with a sinusoidal-like appearance. The rhythmic timing of action potentials is important for both acoustic signalling and reception.

ACOUSTIC COMMUNICATION SIGNALS

Effective acoustic communication is largely dependent on the matching of the sender/receiver characteristics within a species. Investigation of the mechanisms underlying both the sound production and reception of vocal signals can provide insight into the sender/receiver matching process in communication. The plainfin midshipman, Porichthys notatus, is a vocal species of fish that utilizes a repertoire of vocal signals in its social behavior. Large parental males, now known as type I males, excavate den-like nests under rocky shelters in the intertidal and subtidal zones along the western coast of North America. Smaller, type II males do not acoustically court females but rather sneak or satellite spawn while females are in a nest with type I males (4). Type I and II males are also distinguished on the basis of structural characters (review: 1). Midshipman produce at least four classes of acoustic signals which differ primarily in their temporal structure (Fig. 1). (1) "Hums" are long duration (minutes to over 1 hour), multi-harmonic signals with a sinusoidal-like appearance that are only produced by type I males and function as mate calls. (2) "Grunts" are single, brief duration signals that have a fundamental frequency (F0) similar to that of hums, but with wider bandwidths than hums. Single grunts have been recorded from all adult reproductive morphs, although they are of much lower amplitude in type II males and females. "Grunt trains" are only known to be generated by type I males and are defined as a rapid succession of single grunts at intervals of about 400 msec. They function in an agonistic context when a nesting, egg-guarding type I male is challenged by other males. (3) "Growls" are somewhat intermediate in their physical attributes between hums and grunts and are apparently produced only by type I males in agonistic situations. Many growls begin with a large amplitude, short duration burst followed by a relatively constant amplitude. Compared to a hum or a grunt, the F0 of a growl shows far greater variation. (4) Acoustic "beats" result from the temporal overlap of the hums of neighboring type I males. Concurrent hums summate to produce acoustic beats at frequencies equivalent to the difference in fundamental frequencies (dF) between hums. One and two choice playback experiments using underwater loudspeakers and computer-synthesized acoustic signals, conclusively demonstrate the function of hums (5). Only hum-like signals, and not grunts or white noise, can attract gravid females to a speaker. (Some type I and type II males also demonstrate phonotaxis to a single hum, although their responsiveness does not compare to that of a female.) A gravid female will readily choose and directly approach the signal emitted from one speaker when two hum-like tones with difference frequencies (dFs) comparable to natural beats are presented independently through two underwater speakers. Thus, each signal type gives rise to different behavioral responses suggesting that both the production and perception of their characteristic temporal structures plays an important role in behavior. Below is a brief summary of our understanding to date of both the production and reception of the temporal features of midshipman acoustic signals.

TEMPORAL FEATURES OF CALL PRODUCTION

The vocal organ of midshipman consists of a pair of sonic muscles attached to the lateral walls of their swimbladder. One goal of auditory neuroscience has been to identify how neurons determine the physical attributes of communication signals. The vocal motor system of teleost fishes such as midshipman has provided a powerful model for such studies because the fundamental discharge frequency of a vocal neuron circuit directly establishes the fundamental frequency of vocalizations (2). Intracellular recording and staining studies identified a vocal pacemaker-motoneuron circuit in the caudal hindbrain and rostral spinal cord. Pacemaker neurons establish the firing rate of synchronously active motoneurons. Hence, if the sonic pacemaker-motoneuron circuit generates action potentials at a frequency of 100 Hz, then: (1) the motor volley conducted by sonic nerves to the sonic muscles has a periodicity of 100 Hz, (2) both sonic muscles will contract simultaneously at 100 Hz, and (3) a vocalization has a fundamental frequency of 100 Hz.
TEMPORAL CODING OF ACOUSTIC SIGNALS

The principal organ of hearing in midshipman is the sacculus, a division of the inner ear. The sensory epithelium (macula) of the sacculus is innervated by a branch of the eighth nerve. Both primary and secondary octaval nuclei of the medulla project to a midbrain auditory nucleus (nucleus centralis) positioned in the medial torus semicircularis, a homologue of the mammalian inferior colliculus. As defined by spike rate, the majority of midbrain neurons in midshipman have broad tuning properties. However, best frequencies are typically centered near the FOs of vocal signals (3; 5). The results of phonotaxis experiments implied that midshipman must have a neural mechanism that permits them to segregate and discriminate between two signals on the basis of their fundamental frequencies (see above). Studies of the encoding of the separate and combined FOs of two pure tones that form simple beat-like signals have shown temporal coding of beats as defined by vector strength of synchronization, a measure of the degree of phase locking for spikes to a particular phase of an acoustic signal. While afferents exhibit a relatively high degree of synchronization to the individual tones of a beat but a low degree of synchronization to the beat dF, midbrain neurons display relatively low synchronization to the individual beat components and high synchronization to dFs (3; 5). Hence, one explanation for how individual midshipman fish choose one of two concurrent hum-like signals that form an acoustic beat is that they have neurons with temporal coding properties that permit the segregation and discrimination of the fine temporal structure of single and concurrent hums.

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REFERENCES


Fig. 1. Acoustic signals of midshipman fish. The temporal waveform of each signal is shown on two different time scales. Shown are representative examples of a hum (A), concurrent hums (beats; B), grunt train (C) and a growl (D).