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# Central pattern generator for vocalization: is there a vertebrate morphotype?

Andrew H Bass



Animals that generate acoustic signals for social communication are faced with two essential tasks: generate a temporally precise signal and inform the auditory system about the occurrence of one's own sonic signal. Recent studies of sound producing fishes delineate a hindbrain network comprised of anatomically distinct compartments coding equally distinct neurophysiological properties that allow an organism to meet these behavioral demands. A set of neural characters comprising a vocal-sonic central pattern generator (CPG) morphotype is proposed for fishes and tetrapods that shares evolutionary developmental origins with pectoral appendage motor systems.

## Addresses

Department of Neurobiology and Behavior, Mudd Hall, Cornell University, Ithaca, NY, USA

Corresponding author: Bass, Andrew H ([ahb3@cornell.edu](mailto:ahb3@cornell.edu))

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Acoustic communication behaviors are known for the two major radiations of jawed vertebrates (Gnathostomata), the ray-finned and lobe-finned fishes or Actinopterygii and Sarcopterygii (also includes tetrapods), respectively (Figure 1a,b). As reviewed here, these behaviors in fishes rely on temporally precise (i.e., minimal jitter) and synchronous firing of motoneuron populations to drive acoustic modulations at rates that can exceed 100 Hz [1]. Although the challenges of temporal precision on a millisecond timescale and synchronicity across a pool of interconnected neurons may be widely shared among sonic systems, little is known about the underlying neural mechanisms. An added sensory-motor challenge is the need to distinguish one's own acoustic signal from others originating from external sources [2]. With the goal of defining these and related mechanisms, sound-producing fishes are used as model systems. The studies have two, not mutually exclusive, goals. The first is to identify the neural basis for

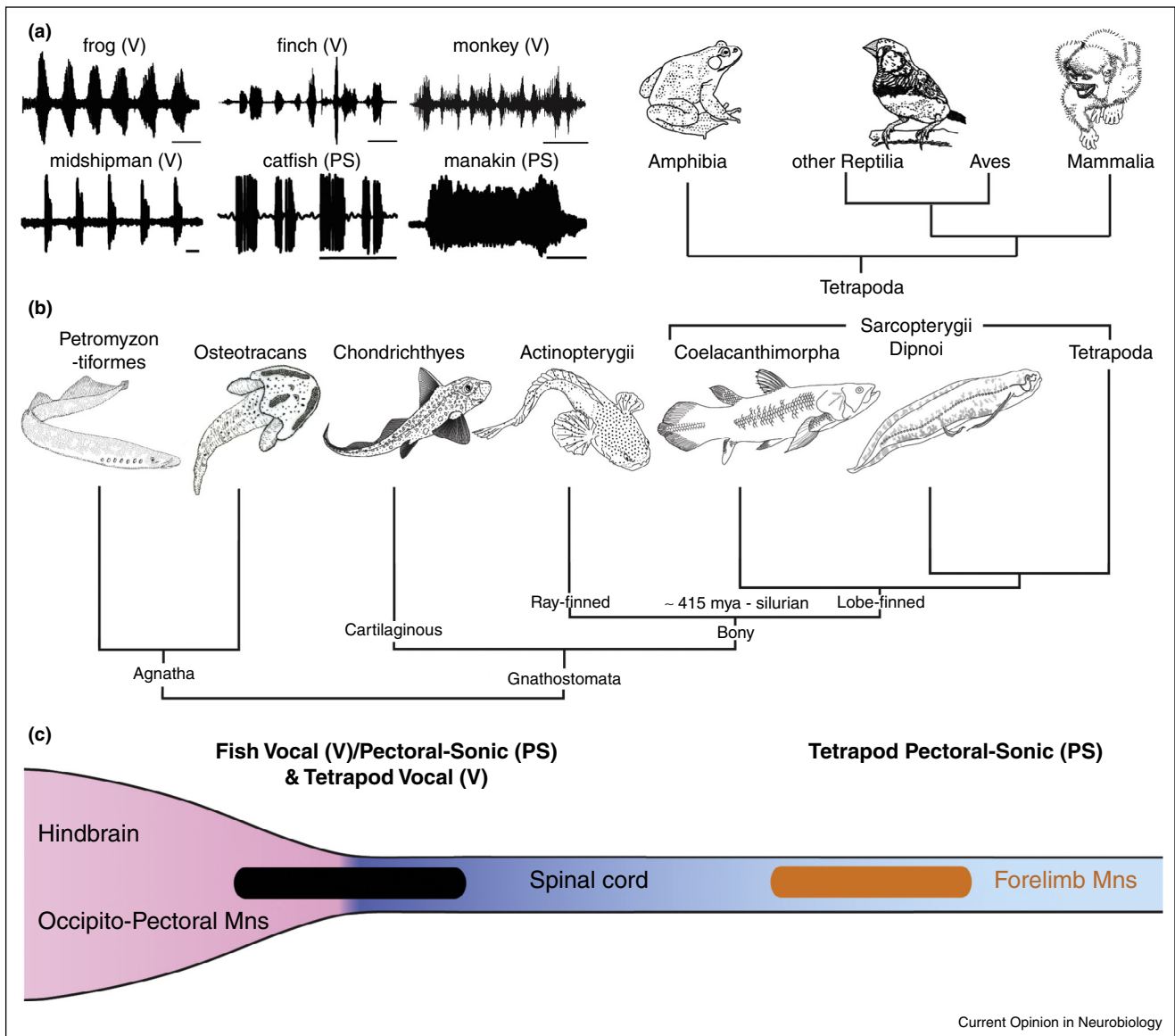
the temporal patterning of acoustic signal modulations on millisecond timescales, complementing ongoing investigations of the sense of hearing [3]. This includes characterization of the intrinsic and network properties of a hindbrain central pattern generator (CPG) for vocalization. A second goal is to identify a vocal-sonic CPG morphotype, 'the characters believed to be present in the common ancestor, based on a determination of shared primitive characters of the stem taxa' [4]. As we speculated earlier [1], can we identify 'the anatomical and neurophysiological properties of sonic-vocal networks in fishes found in the sonic-vocal networks of birds and mammals', in an attempt to 'reconstruct' how the complex vocal phenotypes of birds and mammals were 'built over evolutionary time' [5]?

## Vocal fish as model systems

Sound production among actinopterygian fishes is best known for teleosts, the most species-rich group of vertebrates [6], with reports for more basal actinopterygian groups as well (see [1] for comprehensive review). Among sarcopterygians, sonic species are well documented among all of the major lineages of tetrapods. Sound production in closely related lungfish (Dipnoi) has been noted, but there remains a need for thorough investigations of lungfish and the coelacanth *Latimeria* before we can conclusively state that sonic behavior is a shared primitive character of bony vertebrates (Figure 1b).

We first adopted the term vocal [7] to describe sonic mechanisms in a single order and family of fishes known as toadfishes (Batrachoidiformes, Batrachoididae) that generate sound by rapidly vibrating the swim bladder via the contraction of a single pair of sonic muscles. As noted then, vocal fish share the following characters with sonic tetrapods: (1) social context-dependent acoustic signals, (2) a dedicated sonic organ (swim bladder) analogous to the syrinx and larynx, (3) sonic muscles (syringeal, laryngeal, swim bladder) derived from occipital somites, (4) sonic muscles innervated by occipital nerve roots, homologs of the hypoglossal nerve that innervates syringeal muscles in birds, and (5) consistent with 4, the same central nervous system (CNS) location as the sonic, tracheosyringeal division of the hypoglossal motor nucleus in birds. While acoustic communication may have independently evolved multiple times among teleosts, comparative surveys map the location of vocal premotor and/or motoneurons in distantly related groups to the same region of the caudal hindbrain-rostral spinal cord [8]. Studies of early development show that the vocal premotor-motor circuitry in toadfishes maps to this same

Figure 1



Vertebrate sonic behaviors and phylogeny. **(a)** Representative vocalizations of bullfrog (bar scale represents 1 s), zebra finch (250 ms), squirrel monkey (200 ms), midshipman fish (500 ms), catfish (250 ms) and club-winged manakin (100 ms). Vocal (V) and pectoral-sonic (PS) mechanisms indicated. **(b)** Cladogram showing jawless (Agnatha, e.g., Petromyzontiformes – lamprey) and jawed (Gnathostomata) vertebrate radiations (Osteostracans are an extinct agnathan group with pectoral fins). **(c)** Schematic in longitudinal plane showing location of vocal and pectoral-sonic (PS) motoneurons. Modified from [1].

CNS compartment, overlapping the site of comparable circuitry in tetrapods [9].

The location of sonic motoneurons among vocal vertebrates has been extensively mapped (review in [9]). A wide range of neurophysiological studies, from electromyography to extracellular recordings from the CNS and nerves driving sonic muscles, suggest that the hindbrain can pattern both the fine and gross temporal properties of vocalizations (review in [10]). Whereas a growing literature

continues to show how the cellular and network properties of local brainstem and spinal circuits pattern motor behaviors as divergent as locomotion, eye movement and respiration [11,12\*,13,14], there are few such studies for vocalization (also see Sweeney and Kelley, this issue). For tetrapods, this is due, in part, to strong coupling of vocal with respiratory CPGs that poses significant technical challenges in delineating the neuromuscular patterning of individual syllables and entire calls, and limited surgical accessibility of the hindbrain for recording from vocal

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