

# Shared developmental and evolutionary origins for neural basis of vocal–acoustic and pectoral–gestural signaling

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**Acoustic signaling behaviors are widespread among bony vertebrates, which include the majority of living fishes and tetrapods. Developmental studies in sound-producing fishes and tetrapods indicate that central pattern generating networks dedicated to vocalization originate from the same caudal hindbrain rhombomere (rh) 8-spinal compartment. Together, the evidence suggests that vocalization and its morphophysiological basis, including mechanisms of vocal–respiratory coupling that are widespread among tetrapods, are ancestral characters for bony vertebrates. Premotor–motor circuitry for pectoral appendages that function in locomotion and acoustic signaling develops in the same rh8-spinal compartment. Hence, vocal and pectoral phenotypes in fishes share both developmental origins and roles in acoustic communication. These findings lead to the proposal that the coupling of more highly derived vocal and pectoral mechanisms among tetrapods, including those adapted for nonvocal acoustic and gestural signaling, originated in fishes. Comparative studies further show that rh8 premotor populations have distinct neurophysiological properties coding for equally distinct behavioral attributes such as call duration. We conclude that neural network innovations in the spatio-temporal patterning of vocal and pectoral mechanisms of social communication, including forelimb gestural signaling, have their evolutionary origins in the caudal hindbrain of fishes.**

evolution | vocal communication | pacemaker neurons | speech | language

**E**arly hindbrain development in all major vertebrate lineages exhibits a shared anatomical blueprint of cranial motor nuclei and nerves originating in one or more serially arranged segments or rhombomeres (rhs; e.g., refs. 1, 2). Here, we consider the development and evolution of hindbrain circuitry leading to novel innovations in social signaling, integrating information across behavioral, neurophysiological, and morphological levels of analysis. Two neural networks are the focus: the sonic–vocal basis of acoustic signaling (Fig. 1A) and pectoral control of anterior appendages, fins, and forelimbs (Fig. 1B). For context, we first briefly review vertebrate phylogeny and the ancestral “blueprint” for hindbrain motor phenotypes.

## Vertebrate Phylogeny

Living craniates include jawless vertebrates or agnathans and jawed vertebrates or gnathostomes (Fig. 1B; reviewed in ref. 3). Fossil evidence indicates several lineages of extinct agnathans (e.g., Osteostracans; Fig. 1B; e.g., ref. 4). Chondrichthyes (i.e., cartilaginous fishes) are the most basal group of jawed vertebrates and include two subclasses, Elasmobranchii (i.e., sharks, skates, and rays) and Holocephali or chimaeras. Bony vertebrates, the sister group to Chondrichthyes, include Actinopterygii or ray-finned fishes and the Sarcopterygii or lobe-finned fishes. Sarcopterygians include the coelacanth (*Latimeria*), lungfish (Dipnoi), and tetrapods.

Here, we mainly review recent evidence showing that a caudal hindbrain (rh8)-spinal cord compartment is the developmental origin of premotor–motor circuitry for sonic–vocal and pectoral

behavioral phenotypes. Actinopterygians, which include nearly half of living vertebrate species, were the focus of these studies. By integrating these new findings into a single framework, we aim to achieve a more complete understanding of the evolutionary origins of vocal and pectoral motor systems among vertebrates in general, including the more highly derived pectoral systems of tetrapods that serve a range of functions including nonvocal sonic and forelimb gestural signaling.

## Hindbrain Segmental Blueprint

Vertebrates have two functional series of hindbrain motor nuclei, somatic and branchiomic (1, 2), that were likely present in the earliest, pregathostome vertebrates (5). Somatic nuclei innervate head muscle derived from unsegmented (i.e., prechordal plate) and segmented paraxial mesoderm (i.e., occipital somites); branchiomic nuclei target derivatives of paraxial mesoderm that migrate into the pharyngeal arches (1, 6, 7). Comparative studies delineate a conserved pattern of hindbrain somatic and branchiomic motor nuclei spatially segregated along the rostral–caudal axis across eight rhs (1, 8). Most nuclei originate in one or two rhs with little variation in extent or location across taxa (1). Of particular interest for this review is rh8, which has two to three times the longitudinal extent of more anterior segments and can be subdivided into at least two to three subdivisions in teleost fishes and birds (9–11). Additional evidence for hindbrain segmentation, including a distinct rh8-spinal boundary, comes from rh-specific patterns of gene expression (e.g., refs. 12–14).

## Evolutionary Developmental “Hotspots” for Novel Pattern Generators

Caudal hindbrain rhs are a developmental and evolutionary “hotspot” (*sensu* ref. 15) for innovations in neural networks controlling complex motor function. Bass and Baker (16) hypothesized that the appearance of novel respiratory and cardiovascular pumps during the protochordate–vertebrate transition (17, 18) depended upon the evolution of equally novel, genetically specified pattern generating circuits developing in rhs 7 and 8. Rhombomeres 7 and 8 were also proposed as the source of more recently derived premotor–motor networks unique to jawed vertebrates, such as those controlling sound production, that have

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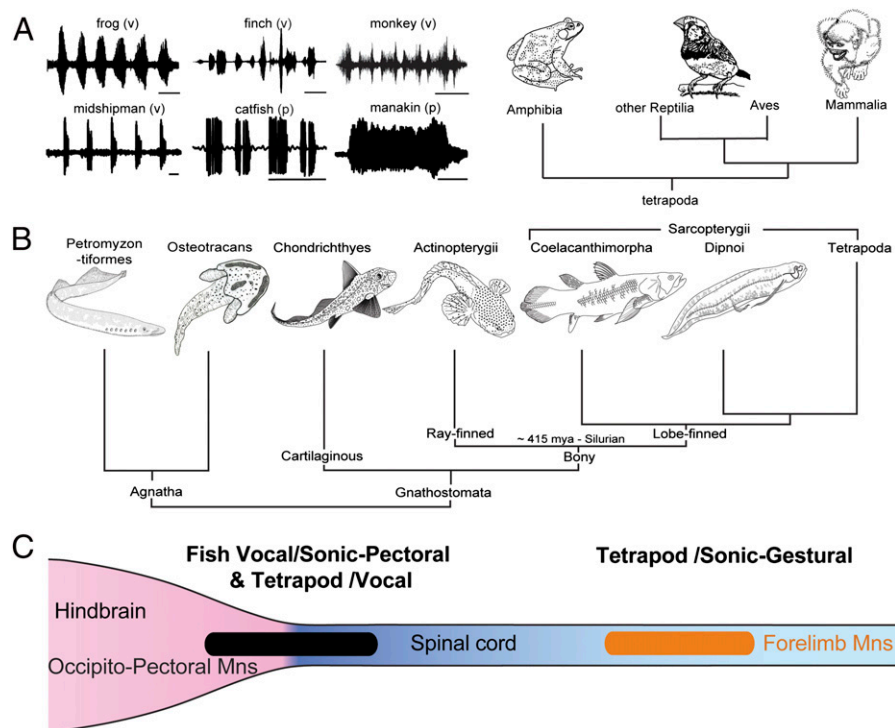
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**Fig. 1.** Evolution of vocal-pectoral motor systems in fishes and tetrapods. (A) Waveforms of representative social vocalizations of bullfrog (time base 1 s), zebra finch (250 ms), squirrel monkey (200 ms), midshipman fish (500 ms), catfish (250 ms), and club-winged manakin (100 ms). Vocal (v) and nonvocal pectoral (p) basis is indicated. (B) Cladogram of vertebrates, including jawless (agnatha) and jawed (gnathostome) radiations (Osteostracans represent an extinct agnathan group with pectoral fins). (C) Summary of location of vocal and sonic motoneurons. Among fishes, the occipitospinal motor column (black) gives rise to motoneurons innervating muscles of vocal organs dedicated to sonic functions (e.g., swim bladder) and pectoral fins that can also serve a sonic function. This same column gives rise to vocal motoneurons in tetrapods. Among tetrapods, forelimb motoneurons (orange) that function in both sonic and gestural signaling are located in the spinal cord. (A adapted from ref. 11; B and C adapted from ref. 13.)

social signaling functions (16). The development of precerebellar climbing fibers from a distinct rh8 nucleus, the inferior olive (10), underscored a preeminent role for caudal hindbrain nuclei in the spatiotemporal patterning of complex motor behaviors such as vocalization and eye movement.

### Sonic-Vocal Pattern Generator

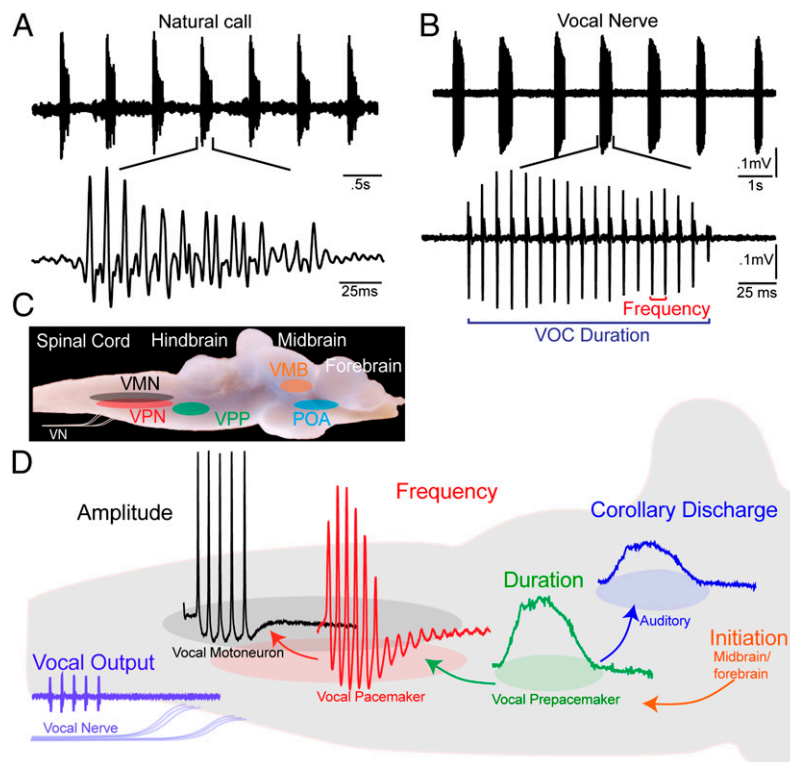
Sonic motor systems in fishes provide excellent models for directly linking neural mechanisms to behavioral outcomes, in part, because the physical attributes of acoustic signals (e.g., interpulse and intercall intervals, duration, amplitude), like its underlying neural activity, are easily quantified (19). Sonic mechanisms vary within and between fish lineages (20–22). Although most species studied so far generate acoustic signals by vibrating the swim bladder, a second well-known set of mechanisms depends on pectoral appendage vibration (23–25). Neuronal patterning of sound production has been most extensively investigated in species using a sonic swim bladder; hence, we first discuss these species. We will then turn our attention to pectoral-dependent mechanisms in the broader context of the motor control of pectoral appendages.

Swim bladder vibration is driven by the contraction of a single pair of muscles attached directly or indirectly to the swim bladder. This biomechanical simplicity has provided a unique opportunity to show how acoustic characters are directly determined by the intrinsic and network properties of a hindbrain central pattern generator controlling one pair of muscles. Toadfishes, a single order and family (Batrachoidiformes, Batrachoididae) of teleost fishes commonly known as toadfish and midshipman fish, have been widely studied as neurobehavioral models for acoustic communication (26–28). Among toadfishes, sonic muscles directly

attached to the swim bladder are innervated by paired occipital nerve roots exiting the caudal hindbrain (20, 22). The temporal properties of occipital nerve motor volleys directly set pulse repetition rate (equivalent to fundamental frequency of harmonic calls for fish), duration, and complex patterns of frequency and amplitude modulation of entire calls (29–32). Individual sound pulses are matched 1:1 with each spike-like, occipital nerve potential (Fig. 2A and B) that results from the synchronous activity of an expansive vocal motor nucleus (VMN) extending from the caudal hindbrain into the rostral spinal cord (Fig. 2C and D) (29). Paired midline VMNs fire in synchrony (29), with bilaterally synchronous occipital spikes leading to simultaneous contraction of both vocal muscles and one sound pulse (33).

A descending vocal motor pathway in toadfishes extends from forebrain preoptic-anterior hypothalamic to midbrain and caudal hindbrain levels (34–36). Premotor vocal pacemaker neurons (VPNs) densely innervate VMNs and receive input from a more rostral, anatomically separate prepacemaker [vocal prepacemaker (VPP)] nucleus (Fig. 2C and D) (29, 34, 37). In an *in vivo* preparation, surgical isolation of the hindbrain-spinal region including the VPP-VPN-VMN network shows this region alone can produce a patterned output matching call temporal properties (30, 31).

Investigations of toadfish known as midshipman, using *in vivo* intracellular recording and staining, show how the VPP-VPN-VMN network determines natural vocal attributes. Chagnaud et al. (37) demonstrate that precise temporal patterning of natural vocalization (Fig. 2A and B) depends on extreme network-wide synchrony and distinct intrinsic properties for each vocal nucleus. Sustained depolarizations in VPP, subthreshold membrane oscillations in VPN, and a combination of differential



**Fig. 2.** Vocal behavior and neural network of plainfin midshipman fish. (A) Oscillogram record of repetitive series of natural calls (“grunt train”) recorded with hydrophone; lower trace shows one call. (B) Spontaneous vocal motor volley recorded from vocal occipital nerve (VOC) with temporal properties like those of natural vocalization; lower trace shows one VOC. VOC duration is time between first and last pulses; frequency is pulse repetition rate. (C) Vocal motor nuclei superimposed on lateral view of intact brain. Indicated are VPN, VPP, and VMN nuclei and vocal nerve (VN). Vocal midbrain (VMB) and forebrain preoptic area (POA) are vocally active sites. (D) Premotor compartmentalization of neurons code for distinct acoustic attributes. Representative intracellular records from vocal nuclei and vocal nerve superimposed on background sagittal image of caudal hindbrain. Descending input from vocal midbrain/forebrain neurons activates vocal hindbrain. Vocal prepacemaker nucleus is source of known corollary discharge informing auditory nuclei about a vocalization’s temporal properties. (Adapted from ref. 37.)

recruitment and low excitability in VMN directly code natural call duration, frequency, and amplitude, respectively (37, 38) (Fig. 2D). In addition to coding duration, prepacemaker neurons are the source of input to a rostral hindbrain nucleus directly innervating the inner ear and lateral line organs that is the anatomical basis for a vocal corollary discharge (Fig. 2D) (39). These new results for fishes, together with nerve recordings and more limited single-neuron recordings in tetrapods, led to the proposal that anatomically separate hindbrain populations code distinct call attributes in fishes and tetrapods (37).

Among tetrapods, the coupling of sound production and respiration leads to airflow-dependent vibration of sonic laryngeal and syringeal membranes (e.g., refs. 19, 40, 41). Despite the close connection between vocal and respiratory pattern generators in tetrapods, evidence for a vocal-respiratory pattern generator in more basal vertebrates like fishes has been missing. Video and sound analysis of advertisement calling (“humming”) by midshipman fish (42) reveals a strong rhythmic correlation between vocal, respiratory and postural (i.e., pectoral) systems (Fig. S1). Vocal-respiratory coupling in this case likely reflects the increased oxygen demands of repetitive muscle contractions during the unusually long duration (from minutes to 1 h) hum vocalizations. Pectoral fin motion may stabilize the body during prolonged calling and/or aid in the increased movement of oxygenated water across the gills during humming (e.g., ref. 43).

We propose that vocal-respiratory coupling originated in fishes and was subsequently adopted by tetrapods. Neurophysiological support for this hypothesis comes from studies of the vocal pattern generator in fully aquatic frogs that produce sound

independent of airflow and yet exhibit vocal-respiratory coupling in the caudal hindbrain (44). In birds and mammals, nuclei integrating vocal (i.e., laryngeal and syringeal) and respiratory activity are also positioned in the caudal hindbrain, adjacent to vocal motoneurons (45–48). Although a vocal-respiratory integration site has yet to be identified in fishes, it will likely be in the caudal hindbrain as in tetrapods.

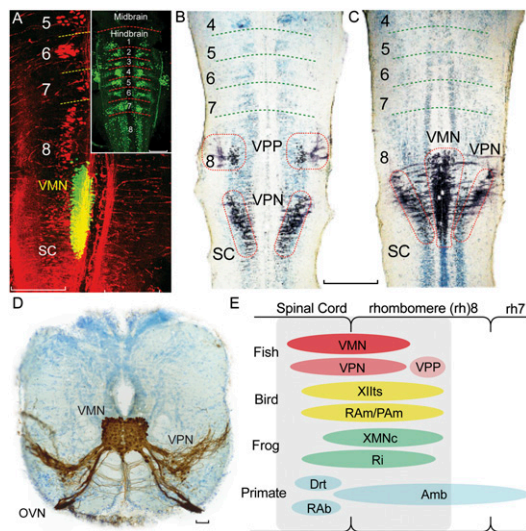
### Evolutionary Development of Sonic-Vocal Pattern Generator

We originally adopted the term “vocal” to describe occipital-innervated sonic systems in fishes, like the toadfishes discussed earlier, because of multiple characters they share with tetrapods (34): (i) production of social context-dependent signals, e.g., agonistic vs. advertisement; (ii) dedication of muscles, like those of the tetrapod syrinx and larynx, to sound production; (iii) shared origins of sonic muscles in fishes and tetrapods from occipital somites; (iv) likely homology of occipital nerve roots innervating fish sonic muscles and hypoglossal nerve roots innervating avian syringeal muscles; and (v) the same location in caudal hindbrain of fish sonic motor nucleus and avian tracheosyringeal division of hypoglossal motor nucleus innervating syringeal muscles (49).

Developmental studies in fishes now support the hypothesis that hindbrain pattern generators for vocalization in the two main clades of bony vertebrates, Actinopterygii and Sarcopterygii (Fig. 1B), share developmental and evolutionary origins. Fluorescent dextran-amine injections into the developing vocal muscle of newly hatched midshipman and toadfish larvae showed a cigar-shaped VMN extending from caudal rh8 into the rostral

spinal cord, a longitudinal extent more than twice that of the more anterior rh8 to 6 (Fig. 3A). Experimental mapping of VMN relative to highly conserved neuronal landmarks in vertebrates showed, for example, rostral VMN coincident with the caudal pole of the vagal motor column and the caudal pole of the precerebellar inferior olive, both of which originate from rh8 in tetrapods (10). Transneuronal neurobiotin labeling in larvae also showed vocal premotor neurons positioned in caudal rh8 immediately lateral and rostral to VMN (Fig. 3B and C), matching the locations of VPN and VPP, respectively, in adults (e.g., Fig. 3D) (11).

Taxonomic analysis, based on developing and adult hindbrain organization, next showed vocal premotor-motor circuitry (including sites of vocal-respiratory coupling, as detailed earlier) in amphibians, birds, and mammals mapping to the same rh8-spinal compartment as the developing VPP-VPN-VMN network of fish (reviewed in ref. 11; also see refs. 44–51; Fig. 3E). Together, the evidence led to the proposal that a rh8-spinal compartment is the developmental and evolutionary origin of hindbrain vocal pattern generating circuitry among all the major lineages of vocal vertebrates.



**Fig. 3.** Map of developing vocal pattern generator in rh8-spinal compartment. (A) Fluorescently labeled neurons in plainfin midshipman fish larvae visualized with laser scanning confocal microscopy (horizontal plane). Simultaneous visualization of reticulospinal neurons labeled via retrograde transport from the spinal cord (Alexa 546 dextran-amine, red) and VMN (Alexa 488 dextran-amine, green) labeled via the developing vocal muscle. Yellow is composite overlap and does not indicate double labeling. *Inset*: Clusters of reticulospinal neurons (Alexa biocytin 488, green) in each rh, from 1 to 8. (Scale bars: 0.2 mm.) (B and C) Mapping in horizontal plane of VPP, VPN, and VMN neurons (black) in Gulf toadfish larvae; labeling via transneuronal transport of neurobiotin from developing vocal muscle. Cresyl violet counterstain reveals segmental, reticulospinal clusters. (Scale bar: 0.2 mm.) (D) Transverse section in caudal hindbrain of toadfish showing transneuronal neurobiotin labeling (brown) of paired midline VMN and adjacent VPNs; VMNs and VPNs have extensive dendritic and axonal branching. VMN axons exit via occipital vocal nerve root (OVN; cresyl violet counterstain). (Scale bar: 100  $\mu$ m.) (E) Sagittal view summarizing relative positions of hindbrain vocal premotor-motor networks in rh8-spinal compartment of fish, birds, frogs, and mammals including primates, based on early-stage and adult phenotypes (see ref. 11 for details). Most laryngeal motor neurons that shape the temporal envelope of mammalian calls originate from caudal nucleus ambiguus (Amb). Drt, dorsal reticular nucleus; PAm, nucleus parambigualis; RAb, nucleus retroambiguus; RAm, nucleus retroambiguus; Ri, inferior reticular formation; Xlits, tracheosyringeal division of hypoglossal motor nucleus; XMNc, caudal XMN. (Adapted from ref. 11.)

### Shared Origins of Sonic-Vocal Musculature and Central Mechanisms

Peripheral sonic mechanisms vary between and even within fish lineages (20–22, 52). For example, sculpin (Scorpaeniformes, Cottidae) lack a swim bladder and instead vibrate a single pair of muscles attached to the pectoral girdle (25). Closely related sea robins (Scorpaeniformes, Triglidae), like distantly related midshipman and other toadfishes, have a pair of vocal muscles that are completely attached to the swim bladder (25). Important to the current discussion is that sound-generating muscles in sculpin and sea robins, like toadfishes and other families of sonic fishes, are innervated by occipital nerve roots (25). This suggests that vocal muscles among fishes share developmental origins from occipital somites (53, 54), irrespective of skeletal mechanics and degree of taxonomic relatedness.

Occipital innervation of vocal muscles originating from a VMN at the same hindbrain (rh8)-spinal level is now documented for nine families of closely and distantly related teleost taxa (20, 25, 55, 56). Piranhas (Characiformes) are an exception to the pattern, with spinal-only innervation and a spinal-positioned VMN (refs. 55, 56; ref. 56 describes other likely examples). However, brain stimulation indicates vocal premotor, pattern-generating circuitry in piranhas in the same caudal hindbrain region as the VPP-VPN circuit in toadfishes (57).

Like the sonic organs of fishes, the nonavian larynx and avian syrinx have lineage-specific skeletal characters (e.g., ref. 19), but share vocal muscle origins from occipital somites (see refs. 7, 58 for tetrapods). Laryngeal and syrinxal premotor-motor networks are also located in the same rh8-spinal compartment as the vocal network in fishes (Fig. 3E). Hence, vocal premotor-motor circuitry, like vocal muscles, shares developmental and evolutionary origins among vertebrates. Studies of frogs further show that laryngeal nerve output resembles occipital nerve activity in fishes. Like the occipital motor volley in vocal fish, the laryngeal motor volley of frogs matches the temporal properties of natural calls (59, 60). These findings, together with those discussed earlier for piranhas, direct our attention to the conserved nature of vocal premotor mechanisms, regardless of motoneuron targets (also see ref. 61).

Among fishes, acoustic communication is widespread and best known for the highly speciose teleosts (e.g., refs. 52, 62–64). There is also well documented behavioral evidence for acoustic signaling in more basal actinopterygians (see ref. 3 for phylogeny) including sturgeon (Acipenseriformes) (65), bichir (Polypteriformes) (66), and bowfin (Amiiformes) (67). Among basal sarcopterygians, sound production (“grunting”) is noted for lungfish (Dipnoi) (68, 69). A critical test of the hypothesis that occipital somite-derived vocal muscle and rh8/occipital-spinal derived vocal networks are ancestral characters for both major clades of bony vertebrates awaits the demonstration of these characters in one of the more basal (i.e., nonteleost) actinopterygians and a basal sarcopterygian (i.e., nontetrapod). If evidence from one of these more basal groups does not support the hypothesis, we would conclude that the observed vocal characters have independently evolved among actinopterygian and sarcopterygian lineages.

### Evolutionary Development of Pectoral Appendage Circuitry

Developmental mapping of the VMN in toadfishes relative to other hindbrain landmarks showed VMN coextensive with the rostral pole of a pectoral motor nucleus (11). This finding led to the suggestion that the rh8-spinal compartment may be the source of neuronal innovations in the central patterning of nonvocal, pectoral-dependent function such as forelimb movement (figure S1 in ref. 11). Since that time, a pectoral motor nucleus in basal and derived groups of bony vertebrates has been shown conclusively to develop in the same rh8-spinal compartment as the vocal

system. By using multiple neuronal markers and alignment of the neuroepithelium with myotomes during the pectoral fin bud stage, Ma et al. (13) precisely mapped the entire extent of the pectoral column along with the cranial-vertebral and rh8-spinal boundaries in representative species from three orders of teleosts used extensively as neurobehavioral models: midshipman (Batrachoidiformes), salmon (Salmoniformes), and zebrafish (Cypriniformes). The results for teleosts were compared with those for paddlefish (Acipenseriformes), a more basal order of actinopterygians (Fig. 4 A–C).

Pectoral muscles were innervated by paired occipital (Oc1, Oc2) and anterior spinal (Sp1, Sp2) nerves (Fig. 4C, *Left*). Pectoral motoneurons, identified following retrograde transport of fluorescent dye from fin buds, were concurrently mapped with other neuronal landmarks including (i) foramina where occipital nerve roots exit the embryonic skull, (ii) genetic markers (hoxb4 expression) for rh8-spinal boundary (70), (iii) nonpectoral motor nuclei including an *islet1*-GFP line labeling cranial motor nuclei (71), and (iv) cerebellar input from the rh8-derived inferior olive nucleus (10). Pectoral motoneurons extended between myotomes 2–3 and 5–6, with axons exiting via paired occipital roots (Oc1, Oc2) through a single foramen rostral to the cranial-vertebral boundary; axons also exited via the first one or two spinal roots (Sp1, Sp2) (13) (Oc1 and Oc2 also innervate vocal muscles; Fig. 4C, *Left*). Given the genetic mapping of cranial-vertebral (Fig. 4A) (72) and hindbrain-spinal (70) (Fig. 4B) boundaries between myotomes 3 and 4, the results demonstrated an rh8/occipital-spinal column innervating pectoral muscles in basal and derived actinopterygian species.

To extend the conclusions more broadly, the actinopterygian innervation pattern was compared with that of more basal cartilaginous fishes (Chondrichthyes, Chimaeriformes/ratfish), and representative fish species in the other major clade of bony vertebrates, Sarcopterygii (Dipnoi, lungfish), that includes tetrapods (Fig. 1B). Together with published accounts for a more basal sarcopterygian, the coelacanth (*Latimeria*) (73, 74) (Fig. 1B), the results showed that occipital and spinal nerve innervation of pectoral muscles was a consistent character across all the investigated lineages of vertebrates.

In sum, precise mapping in pre- and postlarval stages of development showed that the ancestral pattern for pectoral appendage innervation in bony vertebrates is from the rh8/occipital-spinal compartment (Fig. 1C). Pectoral fins, considered

more ancient than pelvic fins (75), were previously assumed to receive innervation only from the spinal cord, like the pectoral forelimbs of tetrapods (reviewed in ref. 13). However, the new results in fishes indicate that spinal-only pectoral innervation is a shared derived character (i.e., synapomorphy), along with decoupling of pectoral appendages from the skull and evolution of a neck (76), only for tetrapod forelimbs (Fig. 1C). Despite the change in motoneuron location, premotor pectoral circuitry may be present in the caudal hindbrain of tetrapods, as it is in fishes (77, 78). Although direct evidence is lacking, brain stimulation suggests that caudal hindbrain circuits configure pectoral/forelimb motoneuron activity in mammals (e.g., ref. 79); single neuron recordings like those in fishes (77, 78) are needed to more rigorously test this hypothesis.

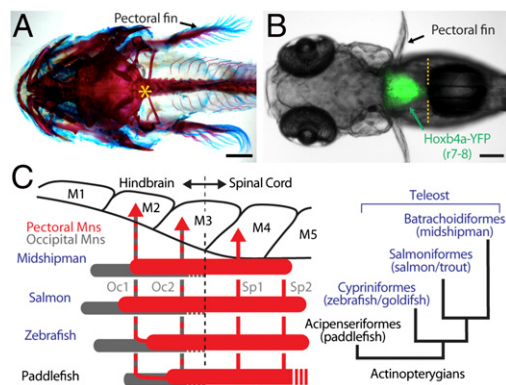
### Shared Origins of Vocal and Pectoral Circuitry

Additional evidence from the studies reviewed here of pectoral motor development suggests that each functional segment of a myotome, e.g., vocal or pectoral, has an rh8/occipitospinal complement. Fluorescent dye labeling of occipital myotomes in midshipman, salmon, and zebrafish embryos showed an occipital motor column, inclusive of pectoral motoneurons, extending approximately one myotome anterior to the rostral pole of the pectoral column with axons exiting via Oc1 and Oc2 (Fig. 4C, *Left*). As vocal muscle develops from myotome 2 (53, 54), this more complete labeling of the developing occipital motor column would also include the vocal motor complement. Vocal motoneurons likely come from a vocal “segment” of the occipitospinal column, separate from a pectoral segment innervating pectoral muscle that is also derived, in part, from myotome 2 (53, 54). Together, the results indicate that vocal and pectoral motor systems in fishes share developmental origins from the rh8/occipitospinal compartment. As discussed later, this would also include pectoral-dependent mechanisms of acoustic signaling.

Sonic mechanisms engaging the pectoral skeleton range from tendon snapping in croaking gouramis (23) to pectoral spine vibration in catfish (Fig. 1A) (24) and pectoral girdle vibration in sculpin that lack a swim bladder (25). Despite these divergent mechanisms, sonic motoneurons are positioned in the same hindbrain-spinal region of the pectoral motor column in sculpin (25, 55), catfish (80, 81), and gouramis (82). Sonic neurons map to the same location in sea robins, close relatives of sculpin that have sonic muscles completely attached to the swim bladder as in distantly related toadfishes (25). Some species of catfish exhibit both swim bladder and pectoral-dependent sonic phenotypes (81). These results highlight the developmental and evolutionary coupling of pectoral motor systems that are multifunctional (locomotion and sound production) with vocal systems that are dedicated to acoustic signaling (e.g., in toadfish and sea robins; Fig. 1C), a character that is observed among tetrapods as well (as detailed later).

### Shared Intrinsic and Network Properties for rh8

Precise temporal patterning of motor output and hence behavior, like that exemplified by vocalization, requires a suite of intrinsic and network properties to synchronize population level activity (e.g., refs. 83–85) including (i) repolarization conductances underlying oscillatory activity of premotor neurons; (ii) electrotonic coupling, within and between premotor and motor populations; (iii) widespread premotor excitatory input to target neurons; (iv) rhythmic firing of premotor and target population; (v) synchronous premotor firing; and (vi) inhibitory input to premotor neurons. Rhombomere 8/occipital premotor populations showing combinations of these characters include the VPP–VPN network (37, 38), pacemaker neurons in electromotor systems (86), area I neurons of the oculomotor system (87), T-reticular neurons (77, 88) driving pectoral motoneurons during the escape response (78), and the inferior olive (e.g., refs. 89, 90) (Table S1).



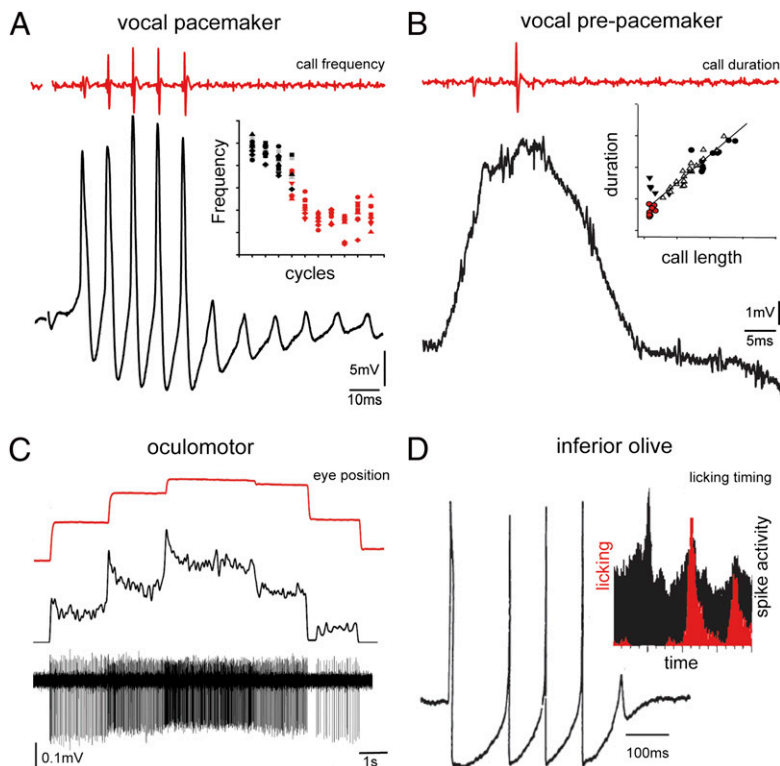
**Fig. 4.** Map of developing pectoral motor nucleus in rh8-spinal compartment of basal and derived groups of actinopterygian fish (A and B, dorsal views). (A) Craniovertebral junction (asterisk) in postlarval, juvenile midshipman fish cleared and stained with alcian blue and alizarin red. (B) Demarcation of rh8-spinal boundary (yellow hatching) in zebrafish *hoxb4a* enhancer trap line. (C) Alignment of myotomes (“M”), occipital (Oc1, Oc2), and spinal (Sp1, Sp2) nerves and pectoral (red) and occipital (gray) motoneurons. Phylogeny of study species is also shown (Right). (Adapted from ref. 13.)

Each rh8 premotor population has a distinct electroresponsive “signature” coding for an equally distinct behavioral attribute. Pacemaker (i.e., VPN) membrane oscillations directly code vocal frequency, whereas VPP-sustained depolarizations code vocal duration (Fig. 5 *A* and *B*) (37). Oscillatory pacemaker neurons in weakly electric fish, a VPN analogue, directly set electric organ discharge frequency (a VPP analogue is likely missing given the constant electric organ discharge) (86). Area I in fish codes for eye position (Fig. 5 *C*) (87, 91, 92). Like the vocal system, inhibitory coupling and synchronous firing, in this case shown by paired recordings, shape area I firing patterns (92, 93). Like VPN, rh8-derived inferior olive neurons (10) tend to fire synchronously in an oscillatory fashion (Fig. 5 *D*) (94, 95). In addition to voltage-dependent conductances underlying this rhythmicity, inferior olive neurons show strong gap junctional coupling that synchronizes functional groups or patches of neurons involved in complex tasks such as tongue licking (Fig. 5 *D*) (89, 96, 97).

Although comparable investigations of intrinsic and network properties are currently lacking for the pectoral motor system, the available neurophysiological data on the neural basis of escape behavior in hatchetfish (Table S1) (78) are consistent with the view that rh8 premotor populations provide a coherent timing signal synchronizing the activity of one or more neuromuscular compartments determining a behavior (*sensu* ref. 97). Recent studies of hindbrain circuitry in zebrafish, including the pectoral network, have begun to identify developmental events establishing the neuronal complement of rh- and neurobehavioral-specific nuclei (77, 98).

### Coupling of Vocal and Pectoral–Gestural Circuitry

There has been much discussion regarding the vocal vs. gestural origins of speech and language (e.g. refs. 99, 100; also see refs. 101, 102). The comparison may, however, be a false dichotomy when we consider the shared developmental origins and social signaling functions of vocal and pectoral systems. Birds and mammals, like fishes (as detailed earlier; also see ref. 103), exhibit vocal and pectoral-dependent mechanisms of acoustic communication. For example, various bird species that use the syrinx to vocalize also use pectoral wings innervated by forelimb spinal motoneurons (Fig. 1 *C*) to generate nonvocal, sonic signals important for communication (e.g., manakin; Fig. 1 *A*) (104–108). Examples of nonvocal, sonic pectoral signaling among mammals that use the larynx to vocalize include drumming by macaque monkeys and gorillas and acoustic gesturing by humans (109, 110). More generally, temporal coupling between vocalization and pectoral forelimb movement in humans has led to the hypothesis that “tasks requiring precisely timed movements of the vocal tract and hands and arms appear to share common brain mechanisms” (ref. 111; also see ref. 100). Vocal–gestural coupling is largely considered to depend on forebrain (e.g., premotor/motor cortex, Broca area) and cerebellar (111, 112) mechanisms, with essentially no consideration of the potential role of hindbrain premotor circuitry. Collectively, the available developmental and behavioral evidence discussed here and in previous sections suggests that the neural basis for vocal and pectoral coupling observed among tetrapods, including nonvocal sonic and gestural signaling, has ancient origins among fishes at the most fundamental level of hindbrain pattern generators (Fig. 1 *C*).



**Fig. 5.** Spatiotemporal coding of behavioral attributes by rh8 premotor nuclei. Shown are single traces of neuronal activity (black) of midshipman fish vocal pacemaker (*A*) and VPP (*B*), goldfish oculomotor (*C*) and guinea pig inferior olive (*D*), and corresponding behavioral readout (red). (*A*) *Inset*: Dependency of membrane oscillations (i.e., cycles) and pulse repetition rate/frequency of vocal output. (*B*) *Inset*: Dependency of duration of membrane-sustained depolarization and call duration (i.e., length). (*D*) *Inset*: Correlation in rats between tongue licking behavior (red) and cerebellar complex spike activity (black) that directly reflects levels of inferior olive activity. [*A* and *B* adapted from ref. 37; *C* reprinted by permission from Macmillan Publishers Ltd: *Nature Neuroscience* (ref. 93), copyright 2001; *D* reproduced with permission from John Wiley & Sons (ref. 95); *D* (*Inset*) reprinted by permission from Macmillan Publishers Ltd: *Nature* (ref. 96), copyright 1995.]

## Concluding Comments

Pattern-generating circuitry underlying the vocal basis for acoustic communication in fishes and tetrapods evolved from an ancestrally shared hindbrain, rh8-spinal compartment. This compartment also gave rise to premotor-motor circuitry for pectoral appendages that serve locomotion and nonvocal, sonic-acoustic signaling functions in fishes. These shared developmental origins suggest that the functional coupling between more highly derived vocal and pectoral mechanisms that have evolved for acoustic and gestural signaling in tetrapods originated in fishes.

More broadly, we propose that, among vertebrates in general, rh8-spinal networks include anatomically separate premotor nuclei, each of which has a distinct suite of intrinsic and network properties determining specific behavioral attributes (Fig. 5). Each network's ensemble of premotor nuclei configures the spatio-temporal activity of one or more neuromuscular systems underlying entire behaviors such as vocalization (also see ref. 97). By

comparing rh8-spinal networks across vertebrate lineages, we can identify ancestral characters contributing to evolutionarily derived networks, e.g., the anatomical and neurophysiological properties of sonic-vocal networks in fishes found in the sonic-vocal networks of birds and mammals. This includes phylogenetically deep homologies, i.e., "molecular and cellular components... contributing to phenotypic novelties" that "enable us to reconstruct how a phenotype was built over evolutionary time" (113).

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