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5. Seismic detection and communication in amphibians

Marcos Gridi-Papp¹ and Peter M. Narins^{1,2}

¹Department of Physiological Science; ²Department of Ecology and Evolutionary Biology
University of California, Los Angeles, CA 90095, USA

Abstract. To date, seismic communication has been demonstrated in a single amphibian, the frog *Leptodactylus albilabris*. Calling males produce both acoustic and seismic signals simultaneously. The inflating vocal sac not only aids in radiating the call into the air, but also strikes the wet substrate generating vertically polarized Rayleigh waves. These animals are highly sensitive to seismic signals (-122 dB rms re gravity) and they alter the timing of their calls in response to playbacks of the seismic component of conspecific calls. Several other frog behaviors have a potential seismic role, including thumping on the ground with the forelimbs and toe-twitching. Acute seismic sensitivities (-90 to -130 dB rms re gravity) have been reported in other amphibians including the frogs: *Lithobates catesbeianus*, *Lithobates pipiens*, and *Rana temporaria*, and the salamanders: *Notophthalmus viridescens*, *Plethodon cinereus* (adults), and *Ambystoma macularum* (larvae). While such sensitivity measurements bypassed the natural coupling of the inner ears to the substrate, amphibians possess an elaborate coupling solution, in which the opercularis muscle connects the

Correspondence/Reprint request: Dr. Marcos Gridi-Papp, Department of Physiological Science, University of California, 621 Charles E. Young Dr. S., Los Angeles, CA 90095, USA. E-mail: mgpapp@ucla.edu

scapula to the oval window. Seismic vibrations that reach the shoulders through the forelimbs are, this way, transmitted directly into the inner ear. The embryos of amphibians are also responsive to seismic vibrations. *Agalychnis callidryas* and five other species of phyllomedusine treefrogs with arboreal egg clutches were shown to hatch immediately in response to seismic vibrations produced by predators. We compare the available data on seismic sensitivity in amphibians with data for other tetrapods, discuss the potential relevance of the substrate from which the animals call for seismic communication and identify questions for future research.

Introduction

The discovery of seismic communication (communication by vibrations transmitted through the substrate) in amphibians is a relatively recent event (1985) and to date only a single example has been studied in detail. Acute seismic sensitivity has been documented in all amphibians studied, however, including two salamanders, five anurans and embryos of five species of anurans with arboreal eggs. In addition, three forms of seismic signal production have been described, with potential uses in sexual communication or in locating prey.

The topics of seismic detection and communication in amphibians have not received much attention during the last decade, with the exception of studies on the Central American red-eyed treefrog, *Agalychnis callidryas* and its close relatives. This species lays its egg clutches on leaves above the water, and the eggs can hatch in a few seconds when stimulated by the vibrations produced by a snake attack on the egg clutch [1-5].

The available evidence for seismic sensitivity in amphibians has been previously summarized in several reviews [6-10]. Considering that the Amphibia represent an entire vertebrate class with more than 6400 species described, and that substrate vibration sensitivity has been measured in only seven species, it seems likely that other cases exist but remain unstudied. We will attempt, therefore, to synthesize the available data emphasizing the most prominent unresolved issues and discuss features of the natural history, acoustics and ecology of several species that might serve as potential subjects of future studies.

Seismic detection

Larvae

The hatching response of *A. callidryas* embryos is subserved by a highly elaborate sense of vibration [1]. Up to 30% of a clutch will hatch early during a snake attack. Rain is another very common source of vibrations on the leafy

vegetation on which the egg clutches are laid, and it produces accelerations within the same range of amplitude produced by snake attacks, but it fails to elicit early hatching [11]. When recorded with an accelerometer placed inside the clutch, rain drop vibrations tend to be short (< 0.1 s), closely spaced (~ 0.2 s) and exhibit a dominant frequency above 60 Hz. Vibrations produced during snake predation events are variable but are on average longer, more widely spaced and of lower dominant frequency. Vibration playback experiments demonstrated that seismic cues by themselves are sufficient to elicit early hatching, and that recorded snake predation events elicited significantly more hatching than recorded rain. Experiments with white noise playbacks that mimicked the duration and interval differences between rain and snake attacks also resulted in significant differences in early hatching. Further experiments tested various combinations of duration and spacing between vibrations, and established the hatching response to be specific to a combination of both stimulus features [2]. Hatching delay from the start of stimulation was correlated to stimulus rate, indicating that embryos balance the risk of incorrectly deciding to hatch or not with the risk of waiting too long to decide and being eaten [3].

Early hatching in response to snake attacks was also found in five other species of phyllomedusine treefrogs with arboreal eggs [4, 5]. It is not yet known if the seismic sensitivity of these arboreal embryos is specialized for predator detection, or if such sensitivity is general to frog embryos, with its effect being more readily observable in species that hatch in response to predator attacks. Sensitivity to seismic vibration in larval salamanders has been shown to be comparable to that of adults [12]. By being immersed in an aquatic medium, embryos and tadpoles do not require middle ears to couple seismic vibrations to the inner ears. Animal tissues, including the head, consist mostly of water, and the impedance of the head should closely match that of the medium [13, 14].

Vibrations that propagate through the water can, therefore, stimulate the inner ears by causing vibrations of the skull. Due to their inertia, mineralized masses suspended in the inner ear (otoconia), vibrate with a phase lag relative to the skull. Such a phase lag between the head and the otoconia stimulates the sensory hair cells, which transduce the mechanical stimuli into receptor potentials [13, 14].

The fact that adult frogs from families other than the Phyllomedusidae are sensitive to seismic vibrations (see next section) does not necessarily imply that their embryos or larvae are also sensitive, because amphibians undergo extensive tissue reorganization during metamorphosis. Hetherington [15] showed that the middle-ear starts developing in later larval stages, with the opercularis system becoming fully formed by the time of metamorphosis,

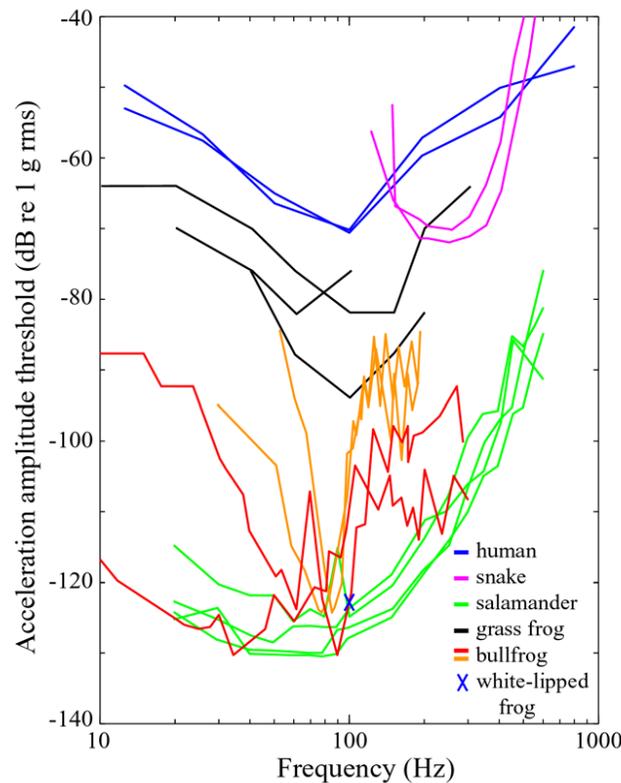


Figure 1. A comparison of the available data on seismic sensitivity thresholds in amphibians and some other tetrapods. Some of the curves are derived from spectral response curves, which were inverted and adjusted to a threshold point, assuming a linear system. Human: the spectrum obtained at constant stimulus amplitude via the vestibulo-ocular reflex was inverted and adjusted to match the threshold obtained at 100 Hz [56]. Snake: midbrain response thresholds for *Crotalus cerastes* (Crotalidae) at 24° C (higher) and 27°C (lower; 52]. Salamander: auditory nerve response thresholds for *Notophthalmus viridescens* (Salamandridae; 20]. Grass frog: three examples of midbrain neuron response thresholds for *Rana temporaria* (Ranidae; 30]. Bullfrog: the frequency responses of four neurons to stimuli with and acceleration amplitude of 0.00063 cm/s² were inverted and adjusted to match the recorded thresholds of 0.0003 cm/s² for saccular axons and 0.0006 cm/s² for axons from the amphibian papilla [24]. White-lipped frog: in the absence of spectral sensitivity curves, we note the threshold reported at the best excitatory frequency with an X [25].

and the tympanum-stapes complex sometimes taking several extra weeks to complete its development. Perhaps more importantly, between larval stages 38 and 41, the neural connections between some auditory nuclei are lost and new connections are formed, leaving the animal effectively deaf for a short period [16]. Developmental changes in seismic sensitivity have not yet been so specifically characterized.

Adults

Herpetologists have long suspected that frogs are sensitive to seismic vibrations (vibrations transmitted through the substrate) as calling frogs frequently cease calling, even on moonless nights, in response to an observer walking at a few meters distance, but not in response to observer-emitted vocalizations. Several early studies on inner ear activity had reported responses to substrate vibrations [17;18]. The first direct measurements of the neural response to seismic vibration were done in salamanders and revealed high sensitivity [19;20;12] (Fig.1). In anurans, seismic sensitivity measurements were first reported in bullfrogs [*Lithobates* (previously *Rana*) *catesbeianus*] and showed high sensitivity [21-24], comparable to that previously reported in salamanders. Subsequent measurements were conducted in the white-lipped frog (*Leptodactylus albilabris*; 25], in the European grass frog (*Rana temporaria*) [26-30] and the North American leopard frog [*Lithobates* (previously *Rana*) *pipiens*] [31].

The inner ear of most amphibians contains eight to nine sensory maculae: three located in the semicircular canals, three in the otolith organs (utricle, saccule and lagena) and three additional sensory epithelia in the amphibian papilla, basilar papilla and papilla neglecta [32-34; Fig. 2). The highest sensitivity to dorso-ventral vibrations of the skull has been found in the saccule, followed by the lagena [18; 22; 25; 27; 29; 35].

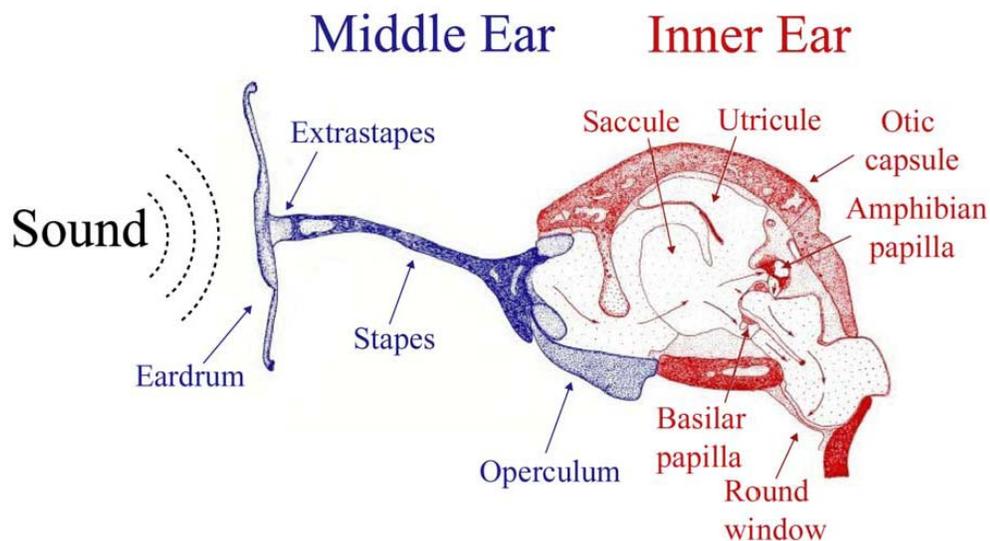


Figure 2. Artistic representation of the main anatomical structures in the ear of the frog *Rana pipiens*. Modified from: Wever, E.G. (1973) The ear and hearing in the frog, *Rana pipiens*. J. Morphol., 141, 461-478.

It should be noted that the vibration sensitivity experiments mentioned above are conducted with the skull of the frog secured to a vibrating platform that provides the seismic stimulus. The results are highly informative about the response of the inner ear organs in relation to vibrations of the head. Such results are less informative, however, about the animal's sensitivity to vibrations of the substrate. In the live frog, the skull seldom makes direct contact with the ground, and substrate vibrations have to traverse the body to reach the head.

Terrestrial vertebrates exhibit several specializations for conducting vibrations of the substrate to the head and inner ear. Behavioral adaptations include dipping the head into the substrate [36-38] and pressing the chin against the substrate [39, 40]. Anatomical adaptations commonly rely on the skeleton, as the rigid structure of bones makes them suitable for faithfully transmitting vibrations with minimal loss. Seismic vibrations can be propagated through the body to the head, and if the skull vibrates with sufficient amplitude, the inertial sensors in the head will detect these vibrations. One such sensor could be the sacculus. It contains loose, mineralized concretions (masses) called otoconia, that vibrate with a phase lag relative to the skull [14]. Another possibility would be the middle ear malleus, which is massive in some species and may also act as an inertial motion sensor [41, 42]. Amphibians have evolved a unique and rather elaborate way of improving the transmission of substrate vibrations to the inner ears: only part of their oval window (the entrance to the inner ear) is occupied by the stapes footplate; the remaining portion is covered by a flat disk of bone, the operculum (Fig. 3). In addition, the dorsal cartilaginous extension of the scapula, called the suprascapula, is positioned only a few millimeters from the otic capsule containing the inner ear. The tonic opercularis muscle connects the shoulders to the inner ear, inserting into the suprascapula in one end, and extensively into the operculum at its other end, where its insertions cover most of the opercular distal surface [43].

The opercularis system transmits vibrations from the pectoral girdle directly to the fluid inside the inner ear. Vibration of the fluid stimulates the inner ear hair cells, dispensing with the mechanism in which whole-head vibrations cause the otoconia to vibrate out of phase with the skull and stimulate the hair cells. This opercularis system provides a gain to the inner ear microphonic responses of bullfrogs to seismic vibrations of 6.5-13.1 dB within the 25-200 Hz range [43-47].

Besides the opercularis system, another less-known mechanism might facilitate detection of vibrations in adult amphibians. Substrate vibrations can potentially be transmitted to the inner ear fluid directly by the skeletal system

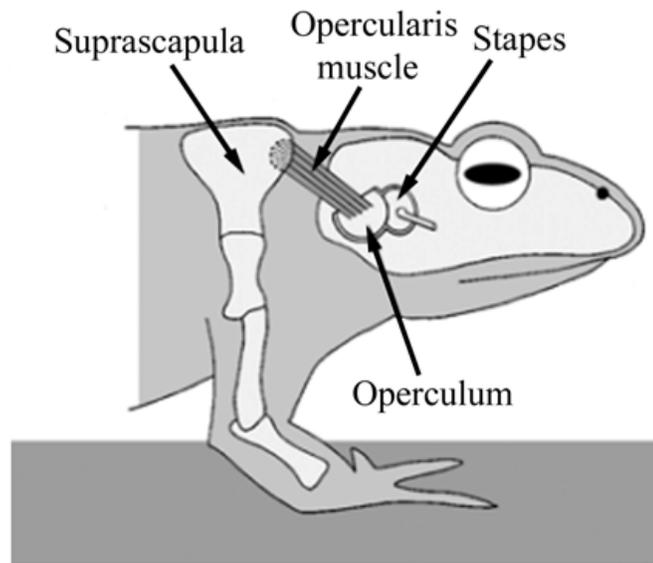


Figure 3. Artistic representation of the anatomical connections in the anuran opercularis system. The tonic opercularis muscle connects the suprascapular cartilage to the operculum bone (which shares the oval window with the stapes footplate), transmitting seismic vibrations from the forelegs to the fluid in the inner ear. From: Mason, M. (2006) Pathways for sound transmission to the inner ear in amphibians. In: Narins, P.M., Feng, A.S., Fay, R.R. and Popper, A.N., (eds). *Hearing and Sound Communication in Amphibians*. New York: Springer-Verlag; 2006. p. 147-183.

along the entire spine. The endolymphatic sac, which contains the inner ear fluid, extends from the head to the coccyx within the spinal cord of anuran amphibians [48]. The degree of extension of the endolymphatic sac varies greatly in other amphibians and in reptiles [49]. The structure also varies in vascularization, but in most cases the sac is filled with aragonite crystals. The endolymphatic sac has been shown to play a role as a calcium reserve, but its potential as a seismic-sensitive organ appears understudied [49-51].

The authors are not aware of any reports of seismic sensitivity involving mechanoreceptors external to the inner ear in amphibians.

Comparison with other vertebrates

Anuran seismic sensitivity thresholds (-90 to -130 dB re gravity) obtained by recording from eighth nerve fibers in frogs at their best excitatory frequencies are the lowest ever recorded for any tetrapod. Most of those measurements were obtained with dorso-ventral stimulation of the skull over 10-500 Hz. Similar measurements from other vertebrates, however, are

scarce. Behavioral audiograms have shown that some fishes such as plaice, cod and dab have similar thresholds (-120 dB re gravity). Snakes in the families Boidae, Colubridae and Crotalidae are sensitive to vibrations as small as 10 Å peak-to-peak displacement amplitude with best excitatory frequencies between 200-400 Hz when measured in the 150 -1000 Hz range [52, 53, Fig.1]. In mammals, vibration thresholds have been measured in squirrel monkeys, guinea pigs and humans. Typically, a shaker is used to deliver a vibration stimulus to the skull, but the point of delivery varies among studies. In one squirrel monkey study, fibers in the vestibular nerve showed highest sensitivity of about -80 dB re gravity at 375 Hz, when tested with vibration frequencies ranging from 50 Hz to 4 kHz [54]. In guinea pigs, only utricular irregular efferent neurons were sensitive to bone-conducted vibration (thresholds near 0.007 g at 500 Hz), but only responses to clicks or tones ranging from 200 Hz to 1500 Hz were tested [55]. In a recent study in humans, vibration stimuli (12.5 – 800 Hz) were applied to the mastoid of the subject while the vestibular response was measured via the vestibulo-ocular reflex [56]. Sensitivities of -70 dB re gravity were found at 100 Hz, 15 dB lower than the hearing threshold of bone-conducted sound for this frequency. It is currently risky to make general conclusions about the vibration sensitivity differences found among classes of vertebrates. The number of species tested is small, various experimental procedures were employed and some examined limited frequency ranges.

Signal production

Two means for generating seismic signals have been described among amphibians: thumping and toe-twitching, both found in terrestrial anurans.

Thumping

This mode of seismic signal production has been described in two species of leptodactylid frogs, *Leptodactylus albilabris* [35], and *L. siphax* [57].

Males of *L. albilabris* call from muddy ground with the posterior half of the body buried. The emission of each advertisement call involves a fast expansion of their large subgular vocal sac, which strikes the substrate producing a surface (vertically-polarized Rayleigh) wave [6].

Thumps are also produced by calling males in *L. siphax* over muddy substrate (57), but there are two important differences between seismic generation in this species and *L. albilabris*: 1) The thump is not produced by the vocal sac, but by beating the forefeet on the ground; and 2) The thump is

produced independently of the vocal output. While neither the spectrum nor the propagation of the putative seismic signals have been characterized, foot thumping is a reasonably vigorous movement that produces an audible “click” with a broad frequency spectrum between ~100 Hz and ~2500 Hz.

Toe-twitching

The behavior of lifting one of the toes repeatedly without moving the foot while perched on the substrate (toe-twitching) is widespread among frogs and has been suggested to have a role in visual luring of prey or intraspecific communication [58-64, 7]. Toe-twitching has been recently shown to work as an effective visual lure in cane toads (*Chaunus marinus*), attracting smaller anurans as prey [59]. While the visual signal produced by toe-twitching can have a luring effect on prey that are themselves visual predators, toe-twitching has also been documented in several frogs that consume mostly herbivorous invertebrates. An alternative explanation for the role of toe-twitching is the production of seismic signals that could play a role in intraspecific communication [60, 7] or stimulate nearby prey to move [61]. Increased prey motion should enhance the ability of anurans to visually detect and locate the prey. This hypothesis can be tested by recording the seismic stimuli produced by toe-twitching and then delivering the vibration stimulus to the substrate (e.g., with a mechanical vibration exciter) in the absence of the frog, to determine if the seismic stimulus by itself increases prey motion or if it has any attractive effect.

Communication

Leptodactylus albilabris is the only amphibian in which both signal production and detection have been demonstrated [25, 31, 35, 65]. The report of foot thumping in *L. siphax* suggests not only that seismic communication should be more common in this genus, but that there are major variations in the mechanism of stimulus production across species [57]. The lack of reports of substrate communication in amphibians may either reflect the paucity of studies in this vertebrate class, or it may indicate that this communication channel is rarely used by frogs.

To date, acute seismic sensitivity has been reported from two anuran families and two salamander families. As noted above, these experiments did not address the coupling of the inner ear to the substrate. Other studies, however, have shown that most anurans and salamanders possess an opercularis system (in which the opercularis muscle connects the shoulders to the oval window), which is highly effective at coupling the inner ear to the

substrate [43-46]. These studies, coupled with abundant anecdotal evidence of behavioral responses of frogs to seismic stimuli in the field, strongly suggest that most amphibians are indeed highly sensitive to seismic vibrations. This raises two questions: 1) Why are amphibians so sensitive to vibration stimuli? and 2) Why is the seismic channel not found more frequently involved in communication?

As mentioned above, the currently available data do not unambiguously confirm or allow a dependable quantification of a sensitivity advantage in amphibians over other tetrapods. It is worth considering, however, which ecological factors could lead anurans to evolve acute seismic sensitivity, since they may generally apply to other vertebrates.

Most anuran species are sit-and-wait predators rather than actively pursuing prey [66-68]. The sit-and-wait strategy allows the predator to establish strong and constant coupling of the body with the substrate, and to remain stationary for extended periods. The low levels of self-generated noise obtained with the lack of body motion and/or optimized coupling might be requirements for the animal to take advantage of a highly sensitive seismic detection system. Such a system could be selected for the detection of predators or prey. While conjectural, this hypothesis can be tested by comparing the seismic sensitivity of predators in a clade that contains both sit-and-wait and active-search specialists, to verify if, in fact, sit-and-wait predators exhibit higher sensitivities. Another test would be to compare vibration measurements of the skull of sit-and-wait predators with: a) those of predators that search actively for prey; and b) the vibrations produced by predators and prey items within attack range.

Seismic communication in *Leptodactylus albilabris* has been suggested to have originated in response to the intense acoustic noise experienced at ponds used for breeding by tropical frogs [7]. Such ponds commonly attract more than a dozen species, with extensive overlap in breeding season and diel calling activity. Under such conditions, differences among species' advertisement call structures and calling sites have been suggested to prevent hybridization [69-71]. The use of seismic communication might be considered another way of avoiding masking by the background acoustic noise, as it would provide *L. albilabris* with a less noisy alternative communication channel. In addition to the reduced noise, detection of the seismic signal could allow the frogs to better estimate the distance to the caller [35]. The signal emitted by the frog propagates at different speeds in air or mud, causing an arrival delay between the acoustic and the seismic components of the call, and this delay is proportional to the distance between caller and receiver.

Avoidance of acoustic noise, by itself, would not explain why seismic signaling would be found in *Leptodactylus* and not in other types of pond-breeding frogs. A non-exclusive, alternative hypothesis is that the composition of the substrate at the calling site and frog density might be the main factors driving the origin of seismic signaling. Seismic signals transmit best in media that are homogeneous, compact and wet [72]. Seismic waves should travel farther in wet soil than in grass, leaf litter or dry soil. Many species of *Leptodactylus* have their calling sites associated with mud nests [73]. This often results in individual males calling with the body in extensive contact with very wet soil, and it can promote a high density of callers, especially when the extent of the muddy area around the pond is reduced. The reproductive biology of *Leptodactylus* might therefore facilitate the use of seismic communication, by promoting conditions in which the signalers are well coupled to a very wet substrate and there is a small separation among individuals. This hypothesis is supported by the observation that male *Leptodactylus albilabris* produce the thump and emit seismic signals only when the ground is wet; otherwise they call without attempting to produce the thump [65]. The current evidence, therefore, indicates that seismic communication might be more easily encountered in species of frogs in which males are well coupled to a wet substrate when calling and are in close proximity to their nearest neighbors.

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