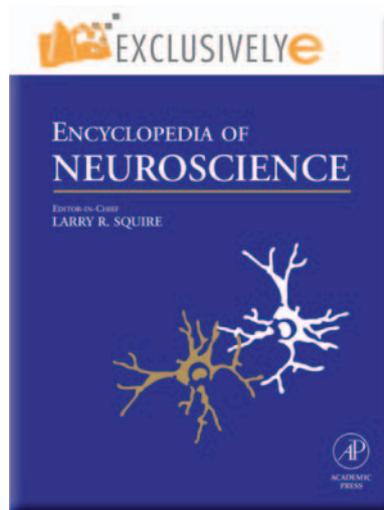


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Narins P M, Losin N and O'Connell-Rodwell C E (2009) Seismic and Vibrational Signals in Animals. In: Squire LR (ed.) *Encyclopedia of Neuroscience*, volume 8, pp. 555-559. Oxford: Academic Press.

Seismic and Vibrational Signals in Animals

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Introduction

Substrate-borne vibrations are a potentially important but largely unexplored signal class for communication in terrestrial animals. The detection of seismic stimuli is a phylogenetically widespread phenomenon, with known examples in every terrestrial vertebrate class. Many of these cases involve animals using seismic cues to evade predators, to locate prey, or to detect environmental changes. Although this is not considered true communication, these cases are worth further investigation since sensitivity to substrate-borne vibrations is often the scaffolding preceding the evolution of intra- or interspecific seismic communication.

The phylogenetic distribution of seismic communication *sensu stricto* is less clear. Well-documented examples of intra- and interspecific seismic communication occur among the mammals, with a few amphibian examples as well. It seems probable, however, that future discoveries will substantially broaden the range of taxa in which seismic communication is known to occur. The two most common methods of creating these signals are percussion and direct coupling of vocalizations with the ground. In the sections below, we will describe recent advances in our understanding of both seismic sensitivity and seismic communication proper in several vertebrate taxa.

Seismic Signal Generation

Percussion can produce both short- and long-distance seismic cues. A spider jumping on a web, foot-drumming in the kangaroo rat and Cape mole rat, head banging in the termite and blind mole rat, and chela drumming of male fiddler crab are examples of close-range percussion-induced signals.

The white-lipped frog (*Leptodactylus albilabris*), a terrestrial amphibian endemic to the neotropics, produces seismic vibrations concomitant with its air borne acoustic signals. During calling, the posterior portion of the frog's body is often buried in the muddy substrate, while the head and forelimbs are above ground. The seismic signal component is created while vocalizing when the frog's rapidly expanding

vocal sac strikes ('thumps') the substrate impulsively. Such substrate-borne vibrations might simply be a natural consequence of the sound production mechanism in this species, but in fact males of *L. albilabris* can detect and respond to these vibrations. The sacculus in the inner ear of *L. albilabris* exhibits the highest sensitivity to substrate-borne vibrations of any terrestrial vertebrate studied. The frequency corresponding to the maximum saccular sensitivity in *L. albilabris* and the frequency spectrum of the seismic component of its vocalization match closely, suggesting that the thumps may be important for communication. Moreover, in response to either audio playback of the conspecific call or seismic playback of the vibrational call components, males of *L. albilabris* reliably modify the timing of their own vocalizations. This is the clearest demonstration of seismic communication in any anuran amphibian.

Seismic detection is not limited to adult anurans. Embryos of the red-eyed tree frog (*Agalychnis callidryas*) respond to particular vegetation-borne vibrations by hatching. The eggs of this species are laid on vegetation overhanging water so that on hatching, tadpoles drop directly into the water below. Aquatic predators may await in abundance, so it pays to delay hatching until the embryos are as mature as possible. Egg mass strikes by oophagous snakes trigger hatching *en masse*, up to 30% earlier than undisturbed clutches; other intense vibrational disturbances, such as rainstorms, do not induce hatching. Vibrations from snake attacks typically exhibit a slower temporal pattern than do rainstorm vibrations; vibration playback experiments have shown that snake recordings induced significantly more hatching than rain recordings. Stimuli that mixed snakelike and rainlike characteristics elicited intermediate levels of hatching. The *A. callidryas* embryos' sophisticated seismic detection and discrimination capabilities, although not an example of true communication, suggest that the use of substrate-borne vibrations in this group may be much more widespread than is currently recognized.

Many mammal species are known to thump their feet against the ground, and in some species these simple thumps may be rapidly repeated in complex 'drumming' sequences. These signals are best known in the Rodentia such as *Dipodomys* and *Georhynchus*, but they are likely more widespread. Many kangaroo species are known to thump their feet; eastern gray kangaroos (*Macropus giganteus*) foot thump when confronted by predators. It is not clear for whom these signals are intended; two possibilities are predators or conspecifics.

Among the rodents, foot drumming is widespread, and these signals are known to propagate seismically between individual burrows. For example, individually distinctive drumming sequences have been found in the banner-tailed kangaroo rat (*Dipodomys spectabilis*). Evidence suggests that the animals may use these signals for individual recognition; drumming sequences are learned early in life and are modified with experience so that they differ from those of close neighbors. When an individual moves to a new territory, it may adjust its drumming sequence to be more recognizable among its new neighbors.

Some species, including kangaroo rats, also drum interspecifically at potential predators, particularly snakes. Snakes are highly sensitive to substrate-borne vibrations, so this antipredator behavior is often an effective signal, causing the snake to retreat. While foot-drumming signals are known to propagate through the soil, it is unknown whether conspecific recipients detect the substrate-borne vibrations directly (via somatosensory or auditory mechanisms) or via air borne vibrations created at the soil–air interface of their burrow walls. In either case, the animals are exploiting properties of seismic transmission, but more work needs to be done to understand the sensory capabilities of these organisms.

Massive terrestrial mammals may generate high-2 amplitude percussive signals; examples include foot thumping in kangaroos, trunk banging in the Asian elephant, and body slamming of male elephant seals. Although the propagation of these particular signals has not been measured through the ground, a man jumping generates a seismic disturbance that is measurable at a distance of 1 km. Locomotion of large mammals also produces ground-borne vibrations; examples include a stampede of bison or an elephant mock charge which ends in foot-stomping behavior. A running herd of zebra or giraffe generates propagated seismic waves which are distinctive at the species level and which could provide information to a predator at a distance.

The coupling of vocalizations with a substrate and the separate propagation of signals along the surface of a particular substrate, be it a plant stem, the forest floor, or open savannah, have the potential for short and long-range transmission. Distance traveled and propagation velocities of the signals depend on signal frequency and energy level as well as the properties of the substrate.

Seismic Signal Propagation

Maximum transmission efficiency of seismic energy occurs in the frequency band between 10 and 40 Hz, precisely the range in which many animals communicate

seismically. In areas with little or no anthropogenic seismic noise, the 20 Hz channel is relatively noise free, save for vibrations associated with thunder or earth tremors, making it a reasonably quiet communication band. In general, for species that generate percussive substrate vibrations or low-frequency vocalizations that couple to the ground, communication signals are produced that often exhibit a spectral peak near 20 Hz and propagate along the surface of the earth as Rayleigh waves. The velocity of these seismic signals depends on the propagation velocity in soil and may be either slower or faster than the velocity of their acoustic signal counterpart. Moreover, depending on physical and environmental limitations, the seismic component may propagate within or potentially beyond the range of the airborne component.

Both airborne and substrate-borne (seismic) waves are subject to interference and alteration due to environmental factors. Variables such as wind and temperature influence airborne sound propagation, whereas the soil type and heterogeneity are among the environmental variables affecting the propagation of a seismic signal. Airborne sound waves spread spherically rather than cylindrically, attenuating more rapidly (losing 6 dB for every doubling of distance) than ground surface waves such as Rayleigh waves (losing 3 dB for every doubling of distance), which all else being equal, favors the long-distance propagation of seismic waves.

Seismic Signal Detection

The signal source intensity and attenuation during transmission, together with the sensitivity and depth of receptors in the receiver and the threshold at which the receptor will be stimulated relative to the frequency and strength of the stimulus define the active space of seismic communication signals. Detection of these signals depends on the expectation, motivation, sensitivity, and decision-making ability of the receiver, as well as the *in situ* condition – for example, the environmental background noise level and the signal trajectory.

There are at least two pathways for detecting seismic signals, either through bone-conducted acoustic detection or through somatosensory reception. Mammals that employ bone-conducted seismic detection have enlarged ossicles, the malleus being particularly hypertrophied, which facilitates independent oscillations of the middle ear bones relative to the skull due to inertia. This is true for species such as the blind mole rat as well as the elephant, but nowhere is this more evident than in members of the family Chrysochloridae (golden moles), which have the

largest malleus relative to body size of any animal. Moreover, recent molecular data place the Proboscidea (elephants) and the golden moles in the same clade – the Afrotheria – which also includes the Sirenia (manatees and dugongs), Hyracoidea (hyraxes), Tubulidentata (aardvarks), and Tenrecomorpha (tenrecs and otter shrews).

In elephants, vibrations travel from the substrate through the feet, up the legs and shoulders, and into the middle ear cavity, or in the case of some marine mammals and small rodents, straight through the skull. Another pathway for seismic signals in small terrestrial mammals is directly from the substrate to the skull. This is facilitated, for example, in the golden mole *Eremitalpa* by head-dipping behavior (in which the animal stops its forward motion and inserts its head in the sand) and in the blind mole rat *Nannospalax* by placing the head against the burrow wall; both behaviors appear to improve substrate–skull coupling.

Vibrations of the middle ear ossicles lag behind the skull motion due to the inertia of the hypertrophied ossicles as well as the displacement of the ossicular center of mass from the rotatory axis, resulting in inner ear stimulation. This appears to be the case for *Eremitalpa* and perhaps *Nannospalax*. In the Cape golden mole (*Chrysochloris asiatica*), there is evidence that the axis of rotation of the middle ear ossicles is frequency dependent. Moreover, low-frequency seismic stimuli result in rotation of the ossicles about the short process of the incus (roughly perpendicular to the long axis of the malleus), whereas high-frequency airborne sound causes a rotation about the long axis of the malleus. A middle ear in which the rotatory axis changes with acoustic modality may provide increased seismic acuity without compromising sensitivity to higher-frequency airborne sounds.

In addition to the enlarged ear bones, the dense fat within the foot pad of the elephant may facilitate a bone-conducted pathway and is similar to the ‘acoustic fat’ found in some marine mammals, particularly in the dolphin melon. This structure functions as an acoustic waveguide for the reception of acoustic communication signals (‘jaw hearing’). An analogous structure, the mandibular fat body, may be used for the detection of vibrational signals by bone conduction in blind mole rats. For reception, the mandibular fat body provides a twofold increase in sound intensity by more efficiently coupling acoustic energy from the vibrating burrow to the bone and thus serving as an impedance-matching mechanism. Likewise, the elephant foot pad may perform an impedance-matching function across the air–ground interface for more-efficient seismic signal detection.

The Manatee’s cartilaginous, fat-filled jaw lacunae and its skull’s aerated sinuses and fatty deposits are thought to play a similar role in coupling sound to the manatee’s ear. Analogously, the elephant’s fatty deposits and aerated skull sinuses may facilitate low-frequency acoustic and seismic detection.

The circumference of the elephant foot just above the toenails increases by as much as 10% when the foot bears weight. The fatty digital cushion is much larger in the front than in the back foot, which may explain why elephants appear to lean forward on their front feet during periods of seismic detection, orienting their feet directly in line with the ear due to the unique graviportal structure of their forelimbs, thus facilitating efficient transmission of vibrations from foot to ear.

Anuran amphibians have in their inner ears two auditory organs sensitive to airborne stimulation: the amphibian papilla (AP), sensitive to low and middle frequencies, and the basilar papilla, sensitive to high frequencies. In addition, the sacculus responds to low-level vibrational stimuli and high-level airborne sounds. Recordings from single fibers in the eighth nerve of *L. albilabris* in response to controlled seismic stimuli revealed the greatest vibration sensitivity of any vertebrate. AP fibers exhibited clear phase-locking to a 130 Hz vibration with a peak acceleration of 0.002 cm s^{-2} . In contrast, using firing rate increase as the threshold criterion, AP thresholds in both northern leopard frogs (*Rana pipiens pipiens*) and white-lipped frogs (*L. albilabris*) reached 0.01 cm s^{-2} .

Seismic communication is not known definitively in any reptile, though chameleons probably possess some form of inter- or intraspecific signaling behavior via vegetation-borne vibrations. Crocodylians generate thoracic vibrations causing a showering of water at the surface prior to their high-amplitude, low-frequency vocalizations and appear to be likely candidates for further investigation of substrate-borne signal communication. In addition, dense pressure receptors located on the body and particularly around the snout of crocodylians are sensitive to water surface vibrations and are thought to be important in prey detection. These same receptors might also facilitate the detection of vibrations generated by conspecifics. Snakes are known to detect both airborne and substrate-borne vibrations through their body surface and can respond behaviorally to both airborne and substrate-borne stimuli. There is, however, no evidence of either airborne or substrate-borne acoustic communication in snakes.

One species of semifossorial snake (the Saharan sand viper, *Cerastes cerastes*) uses substrate-borne vibrations to detect its prey. The snake often strikes prey from a completely submerged position in the

loose sand of the Sahara desert. In the laboratory, *C. cerastes* can strike with accuracy even when its olfactory and vomeronasal organs are denervated. Occluding the eyes reduces striking accuracy somewhat, but the animals are still able to capture live mouse prey. Even with chemosensory-neutral, temperature-neutral targets, these snakes strike with a fair degree of accuracy, providing circumstantial evidence for the importance of vibration sensitivity. Sand vipers, with their sinuous bauplan, are suited to a fossorial lifestyle, and it might be expected that other snake species also utilize vibrational cues in prey location, and perhaps in communication as well. Further work is needed to elucidate the mechanism of seismic detection in snakes.

A second pathway for seismic detection that terrestrial species might employ in addition to or instead of bone conduction is somatosensory reception. Pacinian corpuscles, or pressure receptors, the largest cutaneous mechanoreceptors in mammals (0.5 mm in diameter) are deeply placed whereas Meissner's corpuscles, or touch receptors, are superficially located and smaller (40–60 μm in diameter). Pacinian corpuscles in humans respond over a frequency range of 65–400 Hz, with peak sensitivity at approximately 250 Hz, whereas Meissner's corpuscles exhibit best sensitivity between 10 and 65 Hz.

Many small and large mammals are equipped to detect seismic cues via somatosensory reception. One notable example is the star-nosed mole (*Condylura cristata*), with an elaborate snout surrounded by 22 fleshy, mobile appendages covered with thousands of mechanoreceptive Eimer's organs, which act like a 'tactile eye.' Pacinian corpuscles found in the paws and knees of cats, lamellated corpuscles in the legs of kangaroos, and vibrationally sensitive Herbst corpuscles in the legs of birds are all thought to facilitate prey detection and predator avoidance. Both Pacinian and Meissner's corpuscles can also be found around the tip of the Asian elephant trunk and are as sensitive as the lips of a primate.

Enhancing Signal Detection Range

Temporal summation can be responsible for significant auditory threshold reduction; thus repeated signals can facilitate signal detection. Moreover, longer signals can increase the signal-to-noise ratio, improving signal detection as well. Examples of this can be found in animals communicating in both the acoustic and the seismic realms.

Weddell seals (*Leptonychotes weddelli*) repeat calls to enhance signal detection over long distances and during times of high background noise, as do some whales. Killer whales increase call duration in high background noise from boats. It follows, therefore,

that species that communicate seismically would also employ similar mechanisms to enhance the propagation and detection of signals in noisy environments or over long distances.

To this end, African elephant family groups vocalize within interactive bouts more often than while calling individually. These bouts create an enhanced signal that is effectively three times longer than one produced by a single individual, serving to increase the signal-to-noise ratio and facilitating signal detection and processing at great distances. Furthermore, during departure from a resource, calling bouts are repeated at a greater rate. Elephants listening at a distance might use multiple bouts of longer signals to adjust their physical position to optimize signal resolution. Observations suggest they do just this by freezing for long periods and shifting positions, aligning themselves in the direction of the acoustic or seismic signal source.

Seismic Frequency Discrimination

Elephants can discriminate very subtle frequency differences in the seismic environment. If the pathway for detecting these signals is via bone conduction to the ear, then the seismic frequency discrimination ability should be correlated with the airborne frequency discrimination ability of this species. The acoustic critical bandwidth for the elephant is calculated at 0.75–0.95 Hz across a range of 15–19 Hz, allowing them to detect very small changes in frequency modulation across their low-frequency vocalizations in both the acoustic and the seismic realms.

If the seismic detection pathway is via vibration-sensitive corpuscles, then elephants should still be able to discriminate fine frequency differences, assuming they are at least as sensitive as primates at this task. The tactile frequency discrimination difference limen of adult owl monkeys, for example, is 2 Hz in the region of 20 Hz, which is similar to that of macaques and humans. Since elephants often lay their trunks on the ground during seismic events, they may make use of vibration-sensitive corpuscles described from the trunk, as well as those in their feet, to distinguish frequency modulation between different calls.

Summary

Seismic stimuli are used to navigate within the environment, enhance localization, and detect predators or prey; for intraspecific communication; and possibly as a cue to initiate migration. For percussive signals, large size is often associated with greater source amplitudes, leading to a greater propagation range. Moreover, the use of low-frequency, high-amplitude signals favors more-efficient coupling of airborne

vocalizations to the substrate and increased propagation range.

White-lipped frogs, kangaroo rats, blind mole rats, Cape mole rats, and golden moles appear particularly adept at generating and detecting seismic signals in the face of high levels of background noise. Moreover, they respond to playbacks of seismic signals by changing their signaling behavior or by moving. The seismic components of the foot-drumming signals of the Cape mole rat (*Georychus*) are capable of propagating in the sandy soil between natural burrows of these solitary rodents with little attenuation, whereas their auditory components attenuate into the background noise within a meter of the source. Thus, seismic signaling is strongly implicated in this species as well.

Elephants appear to use long-distance seismic communication by producing low-frequency, high-amplitude vocalizations that efficiently couple to the substrate, where they propagate over long distances and attenuate slowly. Moreover, they are equipped to detect seismic signals. Since of all extant terrestrial animal species, Asian elephants have the largest volume of cerebral cortex available for cognitive processing, we suggest they are likely well-equipped to integrate multimodal signals.

In theory, if a seismic eavesdropper, such as a lion on the African plain, were able to identify a potential prey item such as an antelope or a zebra by its seismic signature, it could be more selective in its hunting forays for preferred food. Likewise, elephant eavesdroppers might learn of the availability of a resource at great distances, which would facilitate intergroup spacing.

The ability to tap into the seismic environment to discriminate biologically relevant information from background noise and to discriminate subtle frequency differences in signals indicates that vertebrates may be using the ground as a communication channel for obtaining much more subtle cues than previously imagined.

See also: Auditory/Somatosensory Interactions; Communication in Frogs and Toads; Communication in Terrestrial Animals; Electrical Perception and Communication; Kinship Signals in Animals; Localizing Signal Sources; Multimodal Signaling in Animals; Signal Identification: Peripheral and Central Mechanisms; Signal Transmission in Natural Environments; Somatosensory Perception.

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