Keeping an “Ear” to the Ground: Seismic Communication in Elephants

This review explores the mechanisms that elephants may use to send and receive seismic signals from a physical, anatomical, behavioral, and physiological perspective. The implications of the use of the vibration sense as a multimodal signal will be discussed in light of the elephant’s overall fitness and survival.

Both African and Asian elephants (*Loxodonta africana, Elephas maximus*) live in social groups where vocal communication is an important aspect of society and, ultimately, survival (25). Elephants produce low-frequency vocalizations at such high amplitudes that they couple with the ground and travel along the surface of the earth with a separate velocity than their airborne counterparts (45, 16). There are physical properties of seismic cues that, if detected on their own or in combination with acoustic cues, could enhance the elephant’s ability to interpret signals (44, 45).

Elephants respond vigilantly to alarm call vocalizations transmitted through the ground, demonstrating that they can detect seismic information from background noise (43). In addition, elephants can also discriminate subtle differences between seismic playbacks of the same call type made by different callers (40). Elephants are well equipped to detect seismic cues through either bone conduction, somatosensory reception, or both (Ref. 6; O’Connell-Rodwell CE, Bouley DM, Hart LA, Arnason B, Hildebrandt T, Ketten D, Hart S, Puria B, unpublished observations). Elephants produce long repeated signals within interactive bouts that serve to improve the signal-to-noise ratio and reduce the noise floor of both seismic and acoustic signals, thus potentially extending their communication range (O’Connell-Rodwell CE, Wyman M, Wood JD, Redfield S, Hart LA, Puria S, unpublished observations). Since elephants have the largest cerebral cortex of all terrestrial animals (18), they are well equipped to process subtle signals from noise and most likely take advantage of the multimodal queues that are available to them.

This review explores what is currently understood about seismic communication in elephants, focusing on both the African and Asian elephant (*Loxodonta africana* and *Elephas maximus*, respectively). The capacity for elephants to send and receive seismic signals will be reviewed from a physical, anatomical, behavioral, and physiological perspective. The implications of the use of the vibration sense as part of a multimodal communication repertoire is discussed in light of the elephant’s cultural and physical survival.

**Background**

Seismic cues are generated through percussion on the earth substrate or acoustical waves that couple with the earth (9). Vibration signal energy depends mostly on the size and available muscular power of the signal producer (30). Percussion can produce both short- and long-distance seismic cues. Direct percussion of the earth can yield a much stronger signal than an airborne vocalization that couples with the ground, as shown in the Cape mole rat (36) and the Asian elephant (45). However, the power that an animal can couple into the ground at low frequencies is related directly to its mass. Animals of low mass cannot generate low-frequency seismic surface waves; thus the mole rat could not produce a seismic signal at 10–20 Hz like the elephant.

The vibration sense is employed by a range of small mammals as a mechanism of prey detection, predator warning and avoidance, habitat sensing, as well as communication. The golden mole uses a head-dipping behavior to detect the vibrations produced by grass mounts in order to position themselves within detection range of the head-banging alarms produced by their termite prey (35). Vibrations made in the context of predator warning or defensive action using foot drumming has been described in kangaroo rats, rabbits, skunks, and other small mammals (51). The foot-thumping behavior of kangaroos (15), body slams of elephant seals (58), and mock charges and trunk banging in elephants (for review, see Ref. 44) indicate that these larger species may also make use of percussive vibrations as a threat. 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 one kilometer (1, 44), demonstrating that these large mammal percussive seismic signals have the potential of propagating long distances.

Locomotion of large mammals also produces ground-borne vibrations (FIGURE 1). A herd of zebra or giraffe propagate seismic waves while running that are distinctive at the species level, which could provide information to a predator in the distance (70), much like a stampede of bison. An elephant running or exhibiting a mock charge, which ends in a foot stomping behavior, also generates a large seismic disturbance detectable at long distances, demonstrating that even relatively small seismic disturbances generated by a large mammal are measurable over great distances (45).

In a few small species, most notably the blind mole rat (37, 50), the cape mole rat (35), and the kangaroo...
rat (52, 53), vibrations are used as a form of communication. There is a growing body of literature to indicate that elephants may also use vibrations to communicate.

**Seismic Signal Generation**

Both African and Asian elephants produce low-frequency vocalizations in the range of 20 Hz at high amplitude (103 dB SPL and 90 dB SPL at 5 m, respectively) (47, 48). The generation of such signals may be facilitated by a large diagram, by a larynx with five rather than the nine bones present in most other mammals (59) and an unusually large nasal cavity. The dolphin melon-like acoustic fat covering the nares in the elephant is layered with a cartilaginous structure also similar to the melon (O’Connell-Rodwell CE, Hildebrandt T, unpublished observations). Since the melon serves to project and focus ultrasound (2), it is worth further investigation to consider whether this structure in the elephant nares might help to project infrasound.

Correlates of both African and Asian low-frequency vocalizations propagate in the ground over long distances, depending on the soil velocity and geological structure of the habitat substrate (16, 44, 45). The coupling of vocalizations with a substrate and the separate propagation of signals along the surface of a particular substrate, whether it be the forest floor or open savannah, has 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 condition of the substrate.

**Signal Propagation**

Seismic energy transmits most efficiently in the frequency range between 10 and 40 Hz (1, 44, 45). In areas with little to no anthropogenic seismic noise, frequencies around 20 Hz are relatively noise-free, other than vibrations associated with thunder or earth tremors, making it a reasonably quiet communication channel. This is the range in which elephants may communicate seismically.

Both airborne and substrate-borne (seismic) waves are subject to interference and alteration due to environmental factors. Factors such as wind and temperature influence airborne sound propagation, whereas the soil type and heterogeneity are among the factors influencing 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 (3 dB loss for every doubling of distance), and thus these ground surface waves maintain integrity longer.

**Seismic Signal Detection**

**Behavior**

Elephants detect (20) and respond to (26, 33) low-frequency acoustic cues (FIGURE 2). In response to seismic playbacks of low-frequency alarm calls, family groups aggregate into significantly denser groups as compared with their spacing before the presentation of the seismic stimulus (43), which is considered a defensive behavior (32) (FIGURE 3). In addition, elephants orient in the direction of the seismic signal.
and spend significantly less time in the area when a seismic alarm is presented (43). Elephants also exhibit more vigilant behaviors as well as those indicative of detecting a distress signal through the ground such as freezing, smelling, scanning, and leaning forward on their front legs (40, 43).

**Bone conduction**

Elephants have two possible pathways for the detection and interpretation of seismic signals, either through bone conduction or through vibration-sensitive mechano-receptors or both (46). Animals that use bone conduction to detect seismic signals have enlarged ossicles, the malleus being particularly hypertrophied, which facilitates independent oscillations of the middle ear bones relative to the skull due to inertia (56). When vibrations transmit through bone, they first couple with the ground via the feet, then travel up through 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 (49).

This pathway for detecting seismic signals is most evident in the golden moles, which have the largest malleus relative to body size of any animal (31). Their freezing and head-dipping behavior may serve to better couple the skull to the substrate (35). Elephants also engage in a freezing behavior when detecting seismic information, such that they lean forward, placing more weight on their larger front feet, which, due to the unique graviportal structure of their forelimbs, are directly in line with the ear (43). The combination of this behavior and the presence of an enlarged malleus would suggest that elephants were employing a bone-conducted pathway for seismic signal detection.

In addition to this freezing behavior, elephants sometimes lift a front foot off the ground, which would facilitate localization through triangulation. They also align themselves not only in the direction of the seismic signal source but perpendicular to it, providing further evidence for the use of a bone-conducted pathway, since this posture positions the elephant’s ears at the greatest distance apart from the source, which would facilitate the localization of these signals (43). With such anatomy and seismic detection behavior in common, it is interesting to note that recent molecular data places the Proboscidia (elephants) and the golden moles in the same clade (1998).

**Bone conduction enhancement**

The role of “acoustic fat” is best known for dolphins, where it is found only in the mandibular channel and the melon (65, 66). For reception, the fat of the mandible causes a twofold increase in intensity of sound, serving as an impedance matching mechanism. The oil-rich lipid in the melon serves as an acoustic lens that efficiently couples acoustic energy to the water (2, 3). Impedance matching would also be a problem at the air-ground interface, and similar mandibular fat is used for the detection of vibrational signals by bone conduction in blind mole rats (49).

The cartilaginous, fat-filled lacunae of the manatee jaw, aerated skull sinuses, and fatty deposits on the manatee skull are thought to play a role in coupling sound to the manatee’s ear (13, 23). The structure of the manatee skull, incorporating unique fat deposits, may function to conduct sounds (39). Fossil data (4, 24) and the morphology of the fetal African elephant ear (10) indicate that Sirenia have common ancestral traits with elephants. Immunological evidence (12) further suggests that elephants and sirenians have a common aquatic ancestor. All head bones of the African elephant’s skull are also aerated by sinuses (64), and except for the solid mandible, the cranium.

**FIGURE 2.** Elephant relatives had ears tuned to higher frequencies, but the modern elephant ear is the lowest frequency ear known to land mammals.
The elephants’ specialized low-frequency ear facilitates detection of both acoustic and seismic signals.
consists of inflated bones compartmentalized to form diploe (59). The fatty deposits and aerated skull sinuses in the elephant may facilitate low-frequency acoustic and seismic detection.

Oils from the dense fat contained in the elephant foot pad are valued by indigenous people (8), and the fatty tissue does not change volume seasonally, even though elephants deplete fat reserves around the kidneys, stomach, and other internal organs during winter (19). This dense fat with cartilaginous nodes appears similar to acoustic fat, which would provide an impedance matching mechanism for more efficient signal propagation and detection of seismic cues (44), or perhaps even serve as a “seismic lens” to improve sensitivity of the elephant to substrate-borne vibrations.

In addition, elephants have a novel sphincter-like skeletal muscle surrounding the external auditory meatus of the ear of both the African and Asian elephant that contracts on tactile stimulation, occluding the opening of the ear canal (O’Connell-Rodwell CE, Bouley DM, Hart LA, Arnason B, Hildebrandt T, Ketten D, Hart S, Puria B, unpublished observations). This occlusion would serve to dampen acoustic signals, facilitating better detection in the seismic environment. In addition, pressure builds up in a sealed air canal creating what is know as a “closed acoustic tube,” which enhances bone conduction (63). This anatomical feature, potentially a remnant of an aquatic ancestry, may facilitate acoustic reception of lower frequencies and/or either potential pathway for seismic detection.

Somatosensory reception

There is a second potential pathway for seismic detection that elephants and other species might employ in addition to or instead of bone conduction. Higher vertebrates have several types of cutaneous sensory organs that are thought to act as mechanoreceptors (57). Pacinian corpuscles, or pressure receptors, are the largest peripheral mechanoreceptors in mammals (62). Pacinian corpuscles are deeply placed, whereas the Meissner corpuscles or touch receptors are superficial. In humans, the peak sensitivity of the Pacinian corpuscles is around 250 Hz with a frequency range of as low as 20 Hz and as high as 1000 Hz (5) and Meissners corpuscles being equally as sensitive between 10 and 65 Hz (29).

Some animals are more equipped to detect seismic stimuli than others, such as the star-nosed mole whose fleshy snout acts like a “tactile eye” (7). Lamellated corpuscles, similar to Pacinian corpuscles, have been found in the legs of kangaroos and are thought to detect ground-borne vibrations (15). Cats have Pacinian corpuscles in their paws and knees (28). The tip of the Asian elephant trunk contains both Pacinian and Meissner corpuscles and is thought to be able to detect movement as subtle as Brownian motion (54). Pacinian corpuscles have also been found in the elephant foot (68), and the distribution of these corpuscles predominantly in the front and back of the dermal layer of the foot reflects their seismic detection posture of leaning forward on their toes or back onto their heels (6) (FIGURE 4).

Detection advantages

Localizing vocalizations centered around 20 Hz with a wavelength of about 17 m, when the inter-ear distance...
is only about 0.5 m, is challenging. Seismic signal localization may be facilitated when soil velocities are slower than air, as is the case in some elephant habitats (210–250 m/s), creating a shorter wavelength of approximately 12.5 m. Thus the distance between an elephant’s feet (2–2.5 m) would provide a greater phase difference to localize these shorter signals (44, 45). Using the vibration-sensitive trunk would provide an additional advantage.

The simultaneous monitoring of both airborne and seismic vocalizations can provide cues about the distance of the vocalizing animal, because seismic signals most often travel at a different velocity than airborne ones, which produces a differential time-of-arrival cue that increases with distance from the source (1, 44, 45). Seismic communication could supplement airborne communication or be especially beneficial when airborne conditions are not ideal for transmission. In addition, since seismically transmitted signals are less susceptible to the environmental influences that limit airborne transmission, and geometric spreading also produces less attenuation for seismic than airborne vocalizations (1/\(r\) for seismic as opposed to 1/\(r\) for acoustic), seismically transmitted vocalizations are potentially detectable at greater distances than airborne vocalizations (1), depending on signal strength and soil velocity (45, 16).

Seismic Discrimination

Elephants not only detect seismic vocalizations (43) but can distinguish subtle differences among seismic components of calls made in the same context (40). Vigilant behaviors increase significantly on detecting seismic playbacks of familiar versus unfamiliar alarm calls (40). Either the familiar alarm is more intense (in terms of frequency modulation), and thus induces a more dramatic response, or it is also possible that alarms made from unfamiliar callers may not be perceived as being a reliable source of information.

Both pathways of detection would facilitate the discrimination of high-resolution frequency differences in seismic signals. If bone conduction to the ear is utilized, then the frequency discrimination ability will be reliant on the elephant’s ability to discriminate acoustic frequencies. And since the elephant’s cochlea shows the sharpest resonance among seven species studied (67), they appear to have a keen ability to discriminate frequency changes within a narrow bandwidth.

The acoustic critical bandwidth in the frequency range of acoustic alarm playback calls is approximately 15–19 Hz. The minimum perceptible frequency change (\(\Delta f\)) is related to the critical bandwidth (CBW) in the following way: \(\text{CBW} = \Delta f \times 20\) (11). Therefore, if this equation holds true for elephants, an estimated \(\Delta f\) of 0.75–0.95 Hz would allow them to detect very small changes in frequency modulation across these calls (40).

If the pathway of detection is via vibration-sensitive corpuscles, then elephants should still be able to discriminate fine frequency differences. The frequency range of the second harmonic of the seismic alarm calls that elephants are able to discriminate varies from about 10 to 19 Hz, which should be within the range of vibrotactile frequency discrimination ability of elephants. Since this measurement has not been made directly in the African elephant, estimates are based on work in other species, using similar sensory structures. The ability of touch receptors to discriminate very small changes in frequency (2 Hz) has been demonstrated in humans and other primates (55). It is likely that elephants have at least the same vibrotactile frequency discrimination abilities as primates, if not better.

The question remains as to how these elephants are able to distinguish between these different calls. But, given that elephant herds can distinguish the contact calls of other herds as being part of their bond group or outside their bond group (32, 33), it seems plausible that the elephants might be capable of doing the same via the seismic environment.

Physiological studies have shown that auditory thresholds are based on temporal summation; thus longer signals should reduce the noise floor, facilitating signal detection (21). In addition, repeated signals appeared to facilitate detection (14, 17). Elephants may benefit from these two physical traits as African elephant family groups vocalize within interactive bouts, which create a signal that is three times longer on average than one produced by a single individual, which would make it easier to detect and process sig-
nals at greater distances (O’Connell-Rodwell CE, Wyman M, Wood JD, Redfield S, Hart LA, Puria S, unpublished observations). This behavior has also been documented among captive bonded individuals (60). Furthermore, during departure from a resource, calling bouts are repeated at a greater rate (O’Connell-Rodwell CE, Wyman M, Wood JD, Redfield S, Hart LA, Puria S, unpublished observations). Elephants also increase their rate of calling during estrus [estrus calls being longer in duration than other calls (27)], thus further adding evidence that elephants may create longer repeated calls to facilitate better detection at greater distances. Since elephant cows have a very narrow window for ovulation (5 days every 4 years) (34), it would be to their advantage to improve the advertising of their hormonal state.

“Elephants are capable of not only detecting these seismic cues but discriminating subtle differences between seismic stimuli.”

Listening elephants at a distance would have an opportunity to optimize their physical position to better resolve multiple bouts of longer signals, which they appear to do by freezing for long periods and shifting positions, aligning themselves in the direction of acoustic or seismic signals. Since the Asian elephant has the largest volume of cerebral cortex available for cognitive processing of all extant terrestrial animal species (18), perhaps they are best equipped to integrate multimodal signals.

Concluding Remarks

The vibration sense is an important tool for survival in many mammal species. Seismic stimuli are used to detect prey, avoid or threaten predators, assess and navigate within the environment, and communicate. Certain conditions need to be satisfied for long-distance propagation of seismic stimuli. For percussive signals, large size is often associated with greater source amplitudes, leading to a greater propagation range. For vocal coupling, the low-frequency and high-amplitude nature of elephant vocalizations are important characteristics for long-distance transmission.

Elephants are capable of not only detecting these seismic cues but discriminating subtle differences between seismic stimuli. This has important ramifications for a herd’s ability to maintain contact with other herds, while minimizing conflict over resources, and also the distance over which a warning of danger can be detected from another herd. Perhaps the more monotonous structure of the Asian elephant vocalization with a strong fundamental frequency and fewer harmonics indicate a selection toward long-distance communication in a forested environment where the higher frequencies and any modulation would be attenuated by the vegetation. The seismic environment may be that much more important to the Asian and forest elephant (Loxodonta cyclotis), where acoustic propagation is severely dampened by vegetation.

Given the ability to detect subtle frequency differences in seismic cues, elephants most probably could also distinguish less subtle infrasonic seismic events, such as an approaching vehicle, helicopters, airplanes, weather (thunder storms), or earthquakes, providing the elephant with a sophisticated ability to exploit the seismic modality for many different purposes. Asian elephants have been reported to respond vigorously to earthquakes (22), or even trumpeting at the approach of an earthquake (38), adding further evidence to the elephant’s ability to detect seismic stimuli, but conflicting reports after the 2004 tsunami in Southeast Asia leaves this possibility in need of additional research (69).

Elephants are capable of detecting seismic information and distinguishing callers and call types seismically, adding a new communication modality that may, in certain circumstances, travel farther than acoustic signals. If elephants detect seismic vocalizations either at short range (2 km) or at longer ranges (16 km) as our previous models predict (16, 45), these seismic cues could either supplement acoustic information, replace acoustic information under poor airborne conditions, or under ideal seismic conditions extend the elephant’s range of communication. The ability to tap into the seismic channel to discriminate biologically relevant information from background noise and to discriminate subtle differences between calls of familiar versus unfamiliar groups indicates that elephants may be using the ground as an additional modality in a complex multimodal communication repertoire.

There are two main challenges that remain in this research area to determine to what extent elephants can use vibrations as a mechanism for long-distance communication. The first challenge is to establish the sensitivity of the elephant’s foot to vibrations produced from elephant vocalizations at a distance. To this end, a captive elephant has been trained to participate in a vibrotactile threshold study, where it touches a target when a vibration is detected within a series of trials that vary in amplitude (decibel level). These studies are ongoing and should result in a better understanding of the elephant’s ability to sense vibrations.

The second challenge is to improve what is understood about how ground-borne waves behave in the far field and in soils of different velocities. Since geophysicists normally collect data on body waves, high-amplitude surface waves produced by earthquakes (and elephant vocalizations) are considered noise and are filtered out of data sets. Once there is a
better understanding of these two remaining aspects of the sender-receiver process, seismic communication could be viewed as adding distance to their already long-distance acoustic communication ability on top of adding an additional sense that the elephant could employ to better communicate and sense their environment.

This work was supported by a grant from the Seaver Institute, a Stanford Bio-X Interdisciplinary Award, and other Stanford internal funding.

References


8. Crader DC. Recent single-caracass bone scatters and the problem of “butchery” sites in the archaeologi


40. O’Connell-Rodwell CE, Wood JD, Kinzley C, Rodwell TC, Poole S, Puria JH. Wild African elephants (Loxodonta africana) discriminate between familiar and unfamiliar conspecific seismic alarm calls. JASA. In press.


44. Rado R, Terkel J, Wollberg Z. Seismic communica
tion signals in the blind mole rat (Spalax ehrenbergi); electrophysiological and behavioral evidence for their use as a communication channel by elephants and other large mammals. Exp Brain Res 206: 1–15, 1999.


49. Reuter T, Nummelta S, Hemilea S. Elephant hear


