Chapter 7
Infrasonic and Seismic Communication in the Vertebrates with Special Emphasis on the Afrotheria: An Update and Future Directions

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Abstract Infrasonic and seismic communication in terrestrial vertebrates is generally poorly known. Moreover, studies of these communication modalities have been restricted to relatively few vertebrate groups. In this chapter we begin with the non-Afrotherian vertebrates and review what is known about their infrasonic (including birds and mammals) and seismic (including amphibians, reptiles, birds, and mammals) communication. We then devote special sections to the Afrotherian vertebrates, concentrating on (1) infrasonic communication in elephants, (2) seismic communication in elephants, and (3) seismic communication in golden moles (Chrysochloridae). Motivated by the lack of detailed knowledge of vibration communication in chrysochlorids, we furnish a blueprint for a set of experiments that would provide novel and interesting data to fill the lacunae in our understanding of seismic signal detection and localization by these enigmatic animals.

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7.1 Introduction to Communication

Terrestrial acoustic communication (TAC) occurs when one organism exhibits a change in its behavior as a direct result of detecting a signal broadcast by a second organism via a channel between the two organisms. Thus, communication involves generation, transmission, and reception of signals. Infrasonic communication refers to TAC for which airborne signals fall in the infrasonic range (<20 Hz), the nominal limit of low-frequency human hearing. Seismic communication refers to TAC for which air is not the intervening channel, but rather signals propagate through a solid substrate such as the ground, a tree branch, or a blade of grass. Several quantitative reports have emerged of terrestrial vertebrates that *either* produce *or* detect infrasonic and/or seismic signals. Although these examples do not strictly qualify as "communication" (sensu the preceding definition), we are including some of them in this chapter because it is likely that further research will reveal infrasonic or seismic communication in these cases.

Infrasonic and seismic communication in terrestrial vertebrates is generally poorly known. Moreover, studies of these communication modalities have been restricted to relatively few vertebrate groups. In fact, the study of vibration communication in the invertebrates has a longer history (for recent reviews see Hill 2008; O'Connell-Rodwell 2010; Cocroft et al. 2014). This chapter attempts to review the current state of knowledge about both infrasonic and seismic communication in terrestrial vertebrates. It is organized in two sections as follows: In Sect. 7.2, a review of the current knowledge of infrasonic and seismic communication in the vertebrates is presented, including amphibians, reptiles, birds, and non-Afrotherian mammals; Sect. 7.3 focuses on these two communication modalities in the Afrotheria, a clade that appears to harbor several seismic specialists.

7.2 Section I

7.2.1 Review of Infrasonic Communication in the Non-Afrotherian Vertebrates

The definition of infrasound is clearly anthropocentric; that is, it is sound below 20 Hz, the nominal lower frequency limit of human hearing. In fact, the human audiogram is not as black and white as the infrasound definition would imply; sounds below 20 Hz may be audible to humans if the intensity is high enough (see human audiogram in Fig. 7.1).
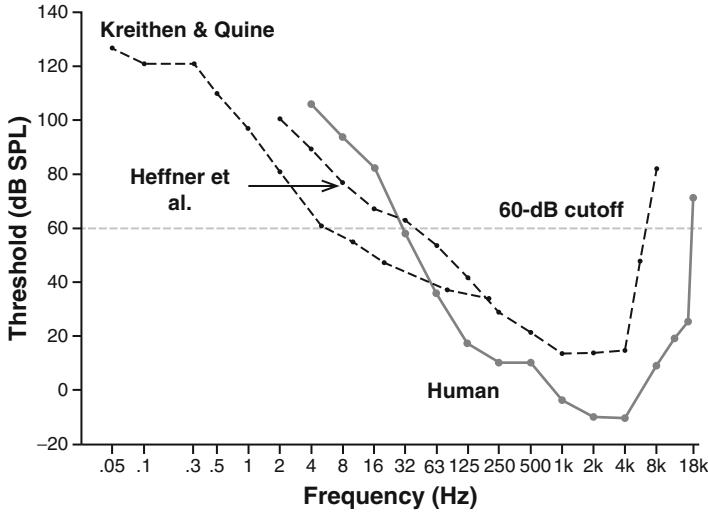
Fig. 7.1 Pigeon and human audiograms. Comparison of human audiogram (from Jackson et al. 1999) to two audiograms from the domestic pigeon, *Columba livia*, obtained from two different studies using two different methods (see text). The pigeon audiograms both indicate better sensitivity to low-frequency hearing than humans (Modified from Heffner et al. 2013)

7.2.1.1 Birds

Several bird species produce infrasound, but only those that either vocalize and/or have been documented as perceiving infrasound will be addressed here. Cassowaries (*Casuarius bennetti*) produce low-frequency vocalizations (Mack and Jones 2003) (ca. 23 Hz) that may extend into the infrasonic range. The sensitivity of chickens (*Gallus gallus domesticus*) to infrasound exceeds that of the homing pigeon (*Columba livia*) (Hill et al. 2014), which are famous for their sensitivity to infrasound, thought to facilitate orientation during migration (Yodlowski et al. 1977).

Rock Dove (Pigeons)

Rock doves (pigeons: *Columba livia*) show remarkable sensitivity to low-frequency sound (below 10 Hz), 50 dB more sensitive than humans; (Kreithen and Quine 1979). Figure 7.1 depicts the results from two different studies in which physiological (Kreithen and Quine 1979) and behavioral (Heffner et al. 2013) data were obtained. Electrophysiological recordings from the pigeon cochlear ganglion reveal sensitivity at frequencies of 1, 2, 5, and 10 Hz presented at 90 dB SPL (Schermuly and Klinke 1990).

Yodlowski et al. proposed that pigeons might detect thunderstorms, weather fronts, magnetic storms, earthquakes, and so forth, and use these low-frequency sounds for orientation, homing, and migration (Yodlowski et al. 1977). Others have

suggested that pigeons might detect summer thermals and approach or avoid them (Schermuly and Klinke 1990). Hagstrum (2000) suggested that atmospheric processes can interfere with infrasonic map cues that cause homing pigeons to veer significantly off-course. Despite these intriguing hypotheses, the mechanisms underlying infrasound detection in pigeons, the best studied of all birds in this context, are still poorly understood.

Guinea Fowl

Using auditory evoked potentials (AEPs) and single-unit data recorded from the auditory midbrain nucleus (MLD) of unanesthetized Guinea fowl (*Numida meleagris*), Theurich et al. (1984) demonstrated that cells in the MLD of these animals exhibited phase-locked responses to extremely low-frequency sinusoids (2–10 Hz) at moderate intensities. The significance of infrasound detection in birds is likely to differ between species. Its use in navigation and homing is reasonable for the pigeon, but it may also be appropriate for the guinea fowl, which lead a primarily terrestrial lifestyle in which selection would presumably be strong for low-frequency acoustic signals that carried for considerable distances (Theurich et al. 1984) or the detection of distant thunderstorms and consequently rain in their natural arid habitat of savannah and grassland (Maier 1982). Follow-up behavioral studies of guinea fowl perception of infrasound are clearly needed.

Indian Peafowl

Freeman and Hare (2015) demonstrated that the male Indian peafowl (*Pavo cristatus*) produce bimodal displays consisting of a conspicuous visual component (tail or "train" erection and movement) and associated infrasonic signal production. In fact, the peacock vocalization (song) is almost completely infrasonic, as are the display components of wing-shaking, shiver train, and others. In acoustic playback experiments, they found that the male's concave train served as a radiator of acoustic signals, and that male wing-shaking displays produce infrasonic signals as much as 20–25 dB above the ambient noise level.

Quantitative morphological analyses of its inner ear confirms that like other galliforms, the Indian peafowl has an area of morphologically similar hair cells at the apical end of the basilar papilla (BP), indicative of a low-frequency specialization with most hair cells and more than half of the BP dedicated to frequencies below 1 kHz (Corfield et al. 2013). Single-unit recordings from the auditory nerve of the peafowl would confirm infrasonic sensitivity in the auditory periphery of these remarkable birds.

7.2.1.2 Mammals

To focus on a treatment of vocalizations made in only the range of 20 Hz and below, we chose to omit reports of "infrasonic" communication in large mammals such as the rhinoceros (*Diceros bicornis* spp.; O'Connell-Rodwell et al. 2001; Budde and Klump 2003), lion (*Panthera leo*; O'Connell-Rodwell et al. 2001), hippopotamus (*Hippopotamus amphibious*; Barklow 2004) and giraffes (*Giraffa camelopardalis* sp.; Baotic et al. 2015) , although these animals produce vocalizations containing low frequencies, published records thus far indicate that they are above 20 Hz.

Mountain Beaver

One of the more remarkable mammals with regard to its hearing range is the mountain beaver or sewellel (*Aplodontia rufa*). It appears to be the most primitive of all living rodents (Nowak 1999) and has a very large and unique cochlear nucleus complex; in fact, the dorsal cochlear nucleus (DCN) is four to seven times larger in volume than in any of 17 other rodent species examined (Merzenich et al. 1973). Single-unit recordings from more than one-third (78) of the 227 neurons studied in the specialized DCN of the mountain beaver responded to infrasonic frequencies below 10 Hz. Moreover, these units were also driven by much slower changes in air pressure. For a few neurons studied with pressure stimulation, the threshold at ca. 1 Hz was estimated to be in the range of 0.1–1.0 μbar. This prompted the suggestion that these DCN units may be specialized for the detection of slow changes in air pressure (Merzenich et al. 1973). The mountain beaver inhabits a large tunnel system in which the ability to detect and respond to pressure changes would be of obvious value. Field studies of this extraordinary animal could provide valuable insights into the function of these infrasonic cells unique within the rodentia.

7.2.2 Review of Seismic Communication in the Non-Afrotherian Vertebrates

7.2.2.1 Amphibians

The available evidence for seismic sensitivity in amphibians has been previously summarized in several reviews (Narins 1990, 2001; Narins et al. 2009; Gridi-Papp and Narins 2010). Some salient examples follow.

Caudate Amphibians: Salamanders

Acute seismic sensitivities (−90 to −130 dB rms re 1 g) have been reported in the salamanders: eastern newt (*Notophthalmus viridescens*), eastern red-backed salamander (*Plethodon cinereus*) (adults), and spotted salamander (*Ambystoma maculatum*) (larvae). Whereas such sensitivity measurements bypassed the natural coupling of the inner ears to the substrate (Ross and Smith 1979, 1980), terrestrial vertebrates exhibit several specializations for conducting vibrations of the substrate to the head and inner ear. Anatomical adaptations commonly rely on the skeleton, as the rigid structure of bones makes them suitable for faithfully transmitting vibrations with minimal loss. Amphibians possess an elaborate coupling solution, in which the opercularis muscle connects the scapula to the oval window (Wever 1973; Mason and Narins 2002). Seismic vibrations that reach the shoulders through the forelimbs are, this way, transmitted directly into the inner ear (Mason 2007a; Gridi-Papp and Narins 2010). This system appears to function quite efficiently, as the seismic sensitivity thresholds in *Notophthalmus viridescens* in the range from 100 to 300 Hz are the most sensitive of any vertebrate tested thus far (Gridi-Papp and Narins 2010). Whether salamanders are able to use low-level substrate vibrations as a source of information about their environment remains an open question (Hill 2009).

Anuran Amphibians: Frogs and Toads

American Bullfrog

Recordings from single axons in the VIIIth cranial nerve of the American bullfrog [*Rana (Lithobates) catesbeiana*] revealed the extraordinary sensitivity of this animal to substrate-borne vibrations (Koyama et al. 1982; Yu et al. 1991). The fibers with the lowest thresholds in this animal (in the frequency range from 15 to 200 Hz) exhibited clear responses to peak accelerations as low as 0.001 cm/s^2, making this the most sensitive quadraped vertebrate to substrate vibrations known at that time. Subsequently, other ranid species have been shown to exhibit remarkable seismic sensitivity: the common frog (*Rana temporaria*; Christensen-Dalsgaard and Jørgensen 1988, 1996; Christensen-Dalsgaard and Walkowiak 1999), and the northern leopard frog (*Rana pipiens*; Christensen-Dalsgaard and Narins 1993; and see "White-Lipped Frog" section).

White-Lipped Frog

The white-lipped frog of Puerto Rico (*Leptodactylus albilabris*) was the first vertebrate for which morphological, neurophysiological, and behavioral evidence has been garnered to support the notion that these animals communicate using seismic signals (Narins and Lewis 1984; Lewis and Narins 1985; Lewis et al. 2001).

   Male white-lipped frogs are nocturnally active in the Puerto Rican rainforests, and often vocalize from cryptic calling sites in the moist substrate to attract females

(Lopez et al. 1988). These calls produce a conspicuous airborne component (peak energy at 2.4 kHz), but males also produce impulsive, low-frequency seismic vibrations ("thumps", peak energy <50 Hz) as their vocal sacs strike wet ground (Lewis and Narins 1985). Bimodal playback experiments reveal that males use these seismic thumps to adjust call timing, ensuring that their calls do not overlap temporally with those of neighboring frogs (Lewis et al. 2001). Although it has been suggested that thump vibrations may subserve the regulation of spacing between signaling males, this has yet to be experimentally demonstrated (Lewis and Narins 1985).

Single-unit recordings from the auditory nerve of males of the white-lipped frog revealed clear stimulus-evoked modulations of their resting discharge rates in response to sinusoidal seismic stimuli with peak accelerations less than 0.001 cm/s^2 (10^{-6} g). Thus, this animal exhibits the greatest sensitivity to substrate-borne vibrations for any known terrestrial vertebrate (Narins and Lewis 1984). Moreover, the vibration-sensitive units in this frog may be grouped into two classes: the first class consists of extremely sensitive fibers with best seismic frequencies (BSFs) between 20 and 160 Hz; the second class is made up of less-sensitive fibers with BSFs between 220 and 300 Hz (Lewis and Narins 1985). It is of note that the peak energy (<50 Hz) in the seismic "thump" signal generated during male calling falls in the low-frequency range of its most sensitive seismic units. This "matched filter" between an animal's seismic signal frequency and its best seismic sensitivity is thought to be one way in which animals improve the likelihood of successful communication in a noisy environment (Capranica and Moffat 1983; Smotherman and Narins 2004; Narins and Clark 2016).

Common Malaysian Treefrog

Frogs in the family Rhacophoridae, the Old World treefrogs, comprise 389 species in 18 genera (http://amphibiaweb.org/). One of these genera, *Polypedates*, contains 26 species found in Japan, eastern China, and throughout tropical southeast Asia (Narins 2001). Acoustic playback studies of the common Malaysian treefrog [*Polypedates leucomystax*; Narins et al. 1998 (non-striped morph raised to species status *P. discantus* sp. nov.; Rujirawan et al. 2013); Christensen-Dalsgaard et al. 2002] revealed that females initiate mating by producing a vibratory signal within the vegetation at night, by tapping their rear toes. The toe-tapping lasts for several minutes, only occasionally accompanied by vocalizations. Nearby males were observed to jump toward the toe-tapping female; amplexus ensued. Tapping may function as a vibrational signal advertising the female's presence to neighboring males, but experimental confirmation of this hypothesis remains lacking.

Red-Eyed Treefrog

In a study of the use of vibrational signals in agonistic interactions, experiments with red-eyed treefrogs (*Agalychnis callidryas*; Caldwell et al. 2010a, b) demonstrated that competing males produce chuckle calls and perform a tremulation display in which one male raises his body off of the substrate, rapidly contracts and extends his hind limbs and shakes his hind end (Fig. 7.2). The resulting vibrations
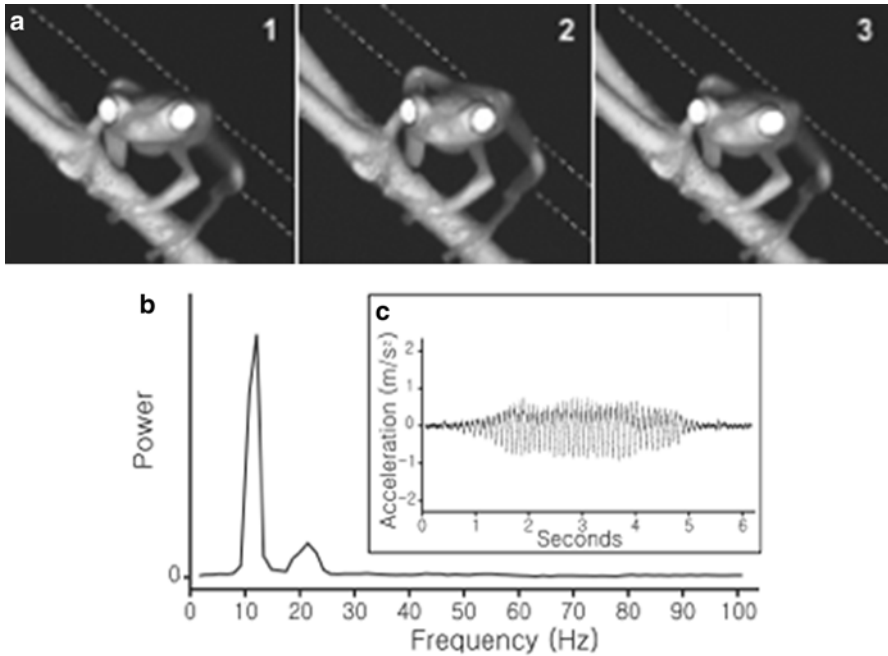
Fig. 7.2 Tremulation display. A1–A3: (**a**) tremulating male *A. callidryas*. (**b**, **c**) Power spectrum and waveform of a typical tremulation vibration, respectively (from Caldwell et al. 2010a)

are transmitted via the animal's legs to the substrate, often a tree branch or a sapling. A second male, often close by and on the same plant, can detect the substrate-borne vibrations from the first male and often responds to them by exhibiting submissive behavior—either fleeing or by remaining motionless. This is one of the few clear vertebrate examples of aggressive interactions mediated by vibrational signals.

In another series of experiments, Warkentin and her colleagues demonstrated that vibrational cues can trigger a predation response in red-eyed treefrog larvae. Tadpoles of red-eyed treefrogs respond to the vibrations produced during a predator (snake) attack by dropping out of their gelatinous egg mass into the stream below (Warkentin 2005; Warkentin et al. 2006, 2007; Warkentin and Caldwell 2009). Moreover, the vibrations caused by falling raindrops on the egg clutches do not have the same effect on the egg clutch. Thus the embryos are capable not only of detecting vibrations, but also of distinguishing between those produced by a benign stimulus (raindrops) and a potentially lethal source (snake).

7.2.2.2 Reptiles

Reptilian seismic communication has been summarized in a prior review of vertebrate vibration communication (Narins 2001). Some key examples from that review are reproduced here, in addition to several additional vertebrates that have been shown to produce and/or detect seismic signals.

Western Rattlesnake

Snakes are extremely sensitive to substrate vibrations: at the most sensitive frequencies (200–400 Hz), a 1 Å peak-to-peak amplitude is suprathreshold (Hartline 1971). Snakes possess two parallel sensory systems that respond to both airborne sound and substrate vibrations: one subserved by the VIIIth cranial nerve and inner ear (auditory), and the other mediated by the spinal cord and cutaneous mechanoreceptors (somatic). Multiunit evoked responses suggested that the auditory system of the western rattlesnake (*Crotalus viridus*) is not especially sensitive to airborne sound, unlike its remarkable sensitivity to substrate vibrations (see earlier in this section). Evoked potential recordings failed to demonstrate that either the somatic or auditory system can distinguish between airborne and substrate-borne vibrations. Although it has been postulated that vibration detection may subserve prey detection in snakes, this function of their remarkable seismic sensitivity has not been confirmed behaviorally in the western rattlesnake.

Sandfish Lizards

The sandfish lizard (*Scincus scincus*) is quite adept at detecting weak vibrations caused by the movements of insects on or below the surface of the sand (Hetherington 1989) at distances up to 15 cm. In addition, the lizard appears to be able to localize these vibrations while remaining submerged in the sand. The mechanism underlying the vibratory source localization in this lizard is unknown (but see "Localization of Seismic Stimuli: A Look Ahead" section for discussion of vibratory source localization in another desert vertebrate).

Veiled Chameleon

Barnett et al. (1999) provided the first example of reptiles using plant-borne vibrations for intraspecific communication. The veiled chameleon (*Chamaeleo calyptratus*) generates body vibrations just anterior to the front legs. Barnett et al. (1999) hypothesized that these vibratory signals served as vegetation-borne vibratory communication signals because they produced no detectable auditory component and they were produced in courtship and disturbance contexts where communication signals would be expected to occur. Nevertheless, conclusive evidence for these signals resulting in a change of behavior of the receiver in this species has not been forthcoming.

Saharan Sand Vipers

Sand vipers in the genus *Cerastes* are specialized semi-fossorial snakes that launch predatory strikes at lizards and rodents while partially buried in the soft sand of the Saharan desert (Young and Morain 2002). Presentation of chemosensory-neutral

targets to the olfactory-denervated, temporarily blinded snakes of the species *Cerastes cerastes* resulted in predatory behaviors similar to those exhibited by intact animals, for both isothermic targets and those heated to mammalian body temperature. Remarkably, every temporarily blinded, anosmic sand viper tested succeeded in capturing free-ranging mice in every trial. These results provide the first experimental evidence for foraging by vibration detection in snakes (Young and Morain 2002).

Pig-Nosed Turtle

Doody et al. (2012), studying synchronous hatching in the nonvocalizing pig-nosed turtle (*Carettochelys insculpta*), demonstrated that this species has evolved rapid hatching in response to hypoxia during nest flooding (Webb et al. 1986). Latency to both hatching and emergence from experimental nests was significantly shorter in groups of eggs than in solitary eggs when subjected to hypoxic conditions, suggesting a group or "sibling effect." Although this study is suggestive of vibration-expedited hatching in the pig-nosed turtle, the recent discovery of underwater vocalizations in two species of fresh water turtles may implicate acoustic communication between embryos in at least some species of Chelonians (Giles et al. 2009; Ferrara et al. 2014).

Royal Python

Vibration and sound-pressure sensitivities were quantified in 11 royal pythons (*Python regius*) by measuring brainstem evoked potentials (Christensen et al. 2012). In this study, the auditory brainstem response to masked and unmasked click stimulations were compared, and forward masking was used to determine the thresholds of vibrational and acoustic sinusoidal stimuli (Berlin et al. 1991; Manley and Kraus 2010; Christensen-Dalsgaard et al. 2011). Their main result is that the pythons are very sensitive to low-frequency vibrations (best sensitivity: −54 dB re 1 m/s^2 at 80–120 Hz) and that the sensitivity to airborne sound is generated by sound-induced head vibrations. This was concluded because, in general, head vibrations induced by threshold-level sound pressure were equal to or greater than those induced by threshold-level vibrations, and therefore sound-pressure sensitivity can be explained by sound-induced head vibration. Thus it was postulated that pythons, and possibly all snakes, lost effective pressure hearing with the complete reduction of a functional outer and middle ear, but have an acute vibration sensitivity that may be used for communication and detection of predators and prey (Christensen et al. 2012).

7.2.2.3 Birds

Vibration communication per se has not been reported in birds. Nevertheless, sensitivity to low-level vibrations has been documented many times. For example, Herbst Corpuscles (HbCs) respond physically to small, uncalibrated displacements

produced by a glass stylus attached to a piezo-electric element (Dorward and McIntyre 1980). HbCs are widely distributed in subcutaneous tissues in close association with the tibia and fibula of the legs of birds as well as close to the follicles of the large flight feathers (McIntyre 1980). Greatest sensitivity to vibration in the pigeon was found in the frequency range of 300–1000 Hz, with thresholds about 0.1 μm; the lowest threshold found was 0.04 μm at 500 Hz (Shen 1983). A subsequent study, also using heart-rate conditioning, determined the vibrational sensitivity of the pigeon wing (Hörster 1990). The highest sensitivity in this study was found at either 800 or 900 Hz, with amplitudes between 0.5 and 0.09 μm. Herbst corpuscles have been suggested to function as a warning device by detecting vibratory disturbances of the ground or other supporting surface (Dorward and McIntyre 1980), or because they respond to rapid oscillatory movements of the flight feathers, they could detect changes from laminar to turbulent air flow and thus act as stall indicators (McIntyre 1980) or as sensors in flight control (Hörster 1990). It appears that behavioral studies of birds' responses to either natural or artificial conspecific vibrations would be timely and would serve to demonstrate avian vibrational communication.

7.2.2.4   Non-Afrotherian Mammals

Mammalian seismic signaling has been the subject of several comprehensive reviews (Francescoli 2000; Mason and Narins 2010; Randall 2010). "Talpid Moles, Marsupial Moles, and Ctenomyid Rodents", "Spalacid Mole-Rats: Example—Blind Mole-Rat (*Nannospalax ehrenbergi*)", "Bathyergid Mole Rats: Example—Cape Mole-Rat", and "Gray Seal" sections review several salient examples that reveal general principles of this communication modality.

Talpid Moles, Marsupial Moles, and Ctenomyid Rodents

Only a subset of subterranean mammals appear to *generate* seismic signals for use in intraspecific communication, but the ability to *detect* substrate-borne vibrations is likely to be universal (Mason and Narins 2010). A striking example is the elaborate snout of the star-nosed mole (*Condylura*) containing about 30,000 Eimer's organs, possibly the most sensitive tactile organ yet discovered for its size (Catania 1995). Although one electrophysiological investigation of Eimer organ afferent sensitivity showed responses of one Pacinian Corpuscle (PC)-like unit to static displacements of 5 μm, the rapidly adapting fibers that responded best at frequencies between 250 and 300 Hz were considerably less sensitive (Marasco and Catania 2007). Perhaps, as these workers imply, it is best to consider that integration of the outputs of several Eimer's organs functions to detect small surface features during brief contact of the star to the surface.

Spalacid Mole-Rats: Example—Blind Mole-Rat (*Nannospalax ehrenbergi*)

There are examples of rodents in both the families Muridae (spalacine mole-rats) and Bathyergidae (bathyergid mole-rats) that have been shown to both generate and detect substrate-borne vibrations (Mason and Narins 2001). Probably the best-studied spalacine mole-rat is the blind mole-rat, a highly solitary fossorial form that rarely encounters conspecifics outside of the mating season (Nevo 1961). The unique morphology of the middle ear of the blind mole-rat and of the articulation between the lower jaw and the skull, coupled with its unusual "jaw-listening" behavior enable substrate-borne vibrations to be transmitted to the inner ear in this animal mainly by bone conduction (Rado et al. 1989). Moreover, it was shown that seismic communication signals are processed primarily by the auditory rather than the somatosensory system (Rado et al. 1998). More recently, evidence for a remarkable finding has emerged that *Nannospalax ehrenbergi* is capable of estimating the location and physical properties of underground obstacles using reflected self-generated seismic waves (seismic "echolocation") (Kimchi et al. 2005). Whether echolocation is considered true communication has been debated for years (Bradbury and Vehrencamp 2011), but regardless, the capacity of this animal to discern underground obstacles in the absence of visual cues certainly deserves further study.

Bathyergid Mole Rats: Example—Cape Mole-Rat

The Cape mole-rat (*Georychus capensis*) is a solitary fossorial animal that communicates with its conspecifics by alternately drumming its hind legs on the burrow floor (Narins et al. 1992). Signal production in this species is sexually dimorphic, and mate attraction is likely mediated primarily by seismic signaling between individuals in neighboring burrows. Foot-drumming signals consist of both auditory and seismic components and the seismic component alone is detectable at distances corresponding to natural interburrow distances (3–4 m); the amplitude of the acoustic component attenuates into the background noise level within 1 m of the source (Narins et al. 1992).

Gray Seal

A recent study of gray seals (*Halichoerus grypus*) showed that males perform body slap threat behaviors, in which a male slams his body onto the ground during male–male conflicts (Bishop et al. 2015), the vibrations of which reliably indicated male size measured more than 125 m from the source. These researchers also demonstrated that substrate-borne vibrations are robust across a range of environmental conditions (Bishop et al. 2015). Future studies will be needed to determine the gray seal's threshold for sensing substrate-borne vibrational cues, but the earlier work on elephant seals (Shipley et al. 1992) indicates that this mode of communication might be more prevalent than previously thought.

7.3 Section II

7.3.1 Infrasonic and Seismic Communication in the Afrotheria

Molecular evidence indicates the likelihood of a common African ancestry for several "odd" groups of mammals (http://www.afrotheria.net/information.php). This ancient radiation of African mammals, the Afrotheria, is a clade of mammals, the members of which belong to groups that are either currently living in Africa or of African origin (Springer et al. 1997; Stanhope et al. 1998). They include seven extant groups with little superficial resemblance to each other: the golden moles, sengis (or elephant-shrews), tenrecs, aardvarks, hyraxes, sea cows (manatees and dugongs), elephants, and the extinct Desmostylia. It is likely that all of the members of this clade have a high probability of communicating using infrasound and/or seismically; nevertheless, to date only two groups of Afrotherians have been studied in this regard. These are the elephants (family Elephantidae, genera *Loxodonta*, *Elephas*) and the golden moles (family Chrysochloridae, genera *Eremitalpa*, *Chrysochloris*). Consequently, the known studies of infrasonic and seismic communication in these two groups will be emphasized. It is hoped that this review will stimulate future work examining low-frequency communication in all Afrotheria.

7.3.1.1 Infrasonic Communication in Elephants

In terms of infrasonic communication, elephants [the African savannah elephant (*Loxodonta africana*), the African forest elephant (*Loxodonta cyclotis*), and the Asian elephant (*Elephas maximus*)] are especially noteworthy because they produce some of the loudest terrestrial animal sounds at frequencies between 10 and 35 Hz (Payne et al. 1986; Poole et al. 1988; de Silva 2010) (Fig. 7.3). These vocalizations with fundamental frequencies in the infrasonic range are commonly termed "rumbles" and can have amplitudes as high as 117 dB SPL at 1 m (Beranek 1988). The rumble is the most common (and also the most studied) vocalization of elephants, whereby most research has been conducted on the African savannah elephant (Langbauer 2000; Soltis 2010).

Rumble vocalizations seem to be multifunctional, being produced in almost all conceivable contexts, from close to long-distance communication within and between groups (Poole 2011). There is evidence that rumbles are used to coordinate the movement and spacing of social groups, helping affiliated individuals find one another as well as triggering defensive or exploratory behavior among those that are unaffiliated (McComb et al. 2000, 2003; Charif et al. 2005; Poole 2011). In addition, coordinated interactive rumble vocalizations generated within groups of bonded individuals result in longer calls that are repeated at a higher frequency than calls emitted in isolation (Fig. 7.4) (O'Connell-Rodwell et al. 2012). Longer repeated calls are more easily detected at long distances (see "Factors Enhancing Signal Propagation" section).
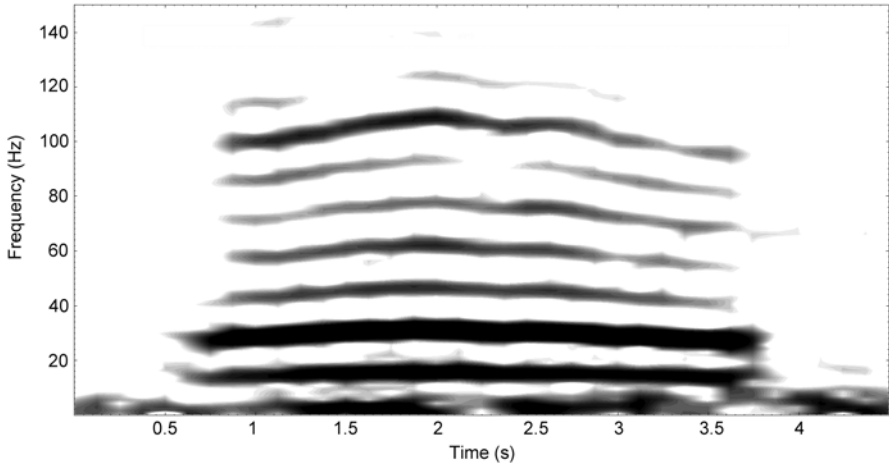
Fig. 7.3 Low-frequency rumble vocalization of a 19-year-old male African elephant (*L. africana*). The fundamental frequency is about 13–14 Hz
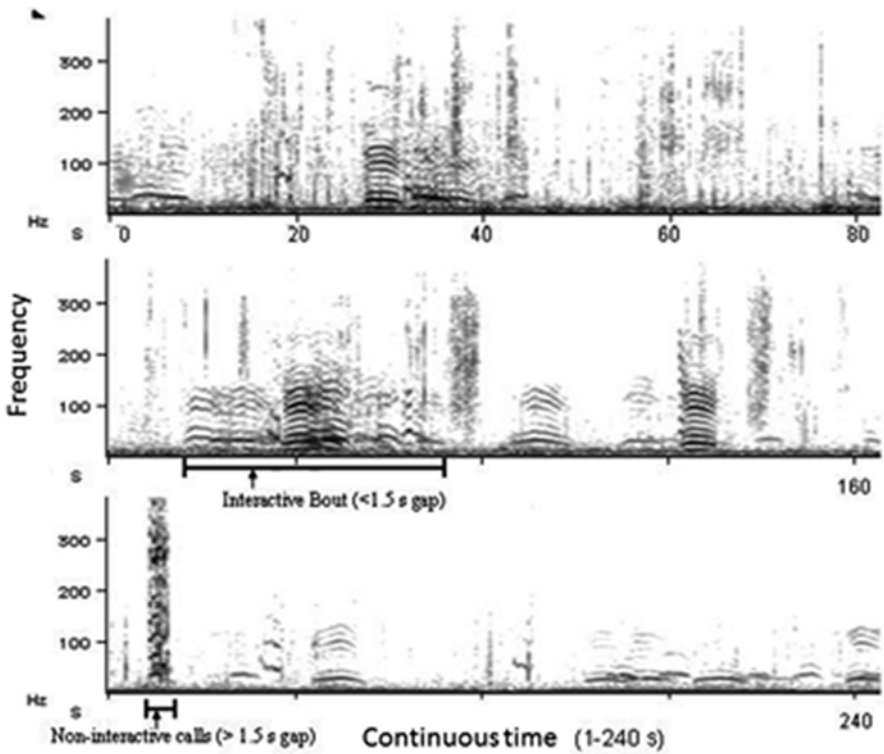

Fig. 7.4 Series of interactive antiphonal bouts of elephant rumble vocalizations (Modified from O'Connell-Rodwell et al. 2012)

One striking feature of the low-frequency rumble is the impressive information content apparently transmitted, where remarkable structural variability reflects all conceivable acoustic parameters including temporal, source, and filter related parameters (vocal tract resonances or formant frequencies). It is not surprisingly, therefore, that rumbles are individually distinctive and recognized as such by elephants (McComb et al. 2003; Soltis et al. 2005; O'Connell-Rodwell et al. 2007). They also differ according to age (Stoeger-Horwath et al. 2007; Stoeger et al. 2014), and structurally varying forms have been linked with reproductive (Poole et al. 1988; Poole 1989) and emotional states (Soltis et al. 2009).

Poole et al. (1988) proposed that rumbles could be used as long-distance mate attraction calls. Playback experiments showed that males respond to female "estrous calls" by orienting and walking 1 km or more toward the sound source (Langbauer et al. 1991). More recent playback experiments indicated that adult males in the hormonal state of musth (Poole and Moss 1981) and subadult males were more likely to respond to these calls than males that were not in musth (O'Connell-Rodwell et al. 2011).

Estrus rumbles are structurally distinct, including lower fundamental frequencies, lower first formant (vocal tract resonance) frequencies, and higher first formant amplitudes (Soltis et al. 2005). In addition, estrus calls are longer and repeated more often than other call types (Leong et al. 2003). These acoustic features are important in long-distance communication as high-amplitude, low-frequency long repeated calls facilitate better propagation.

Although elephant females are generally much more vocal than males, males do produce several distinctive rumble types; the best characterized is the "musth rumble" made in the context of the reproductive condition of musth (Poole et al. 1988), thought to advertise the animal's hormonal state over long distances to females as well as potential rivals (Poole 1989, 1999). Females respond to the rumbles of musth males by vocalizing, so males may indeed identify and locate estrous females over long distances (Poole 1999).

In elephant rumbles, formant variations have proven to be a highly relevant acoustic feature, being important in social context and in referential information coding (McComb et al. 2003; Soltis et al. 2014). Stoeger et al. (2012) demonstrated that African elephants shift between nasal and oral sound emission in rumbling vocalizations depending on social context. Nasal rumbles predominated during long-distance contact calling, whereas oral rumbles were mainly observed during close-distance social bonding. Nasal and oral rumbles varied considerably in their acoustic structure. In particular, the mean frequency spacing of the first two formants predicted the estimated lengths of the two vocal paths (Fig. 7.5). Formant frequency values are determined by the length and shape of the vocal tract, with longer vocal tracts producing lower, more closely spaced formants (Taylor et al., Chap. 9). The observed formant values in Stoeger et al. (2012) corresponded to a vocal tract length of about 2 m for nasal rumbles and about 0.7 m for oral rumbles in the investigated elephants (the study animals were younger than 17 years old and not yet fully grown). Thus, by using the nasal path, an elephant potentially lowers its formants by about threefold.
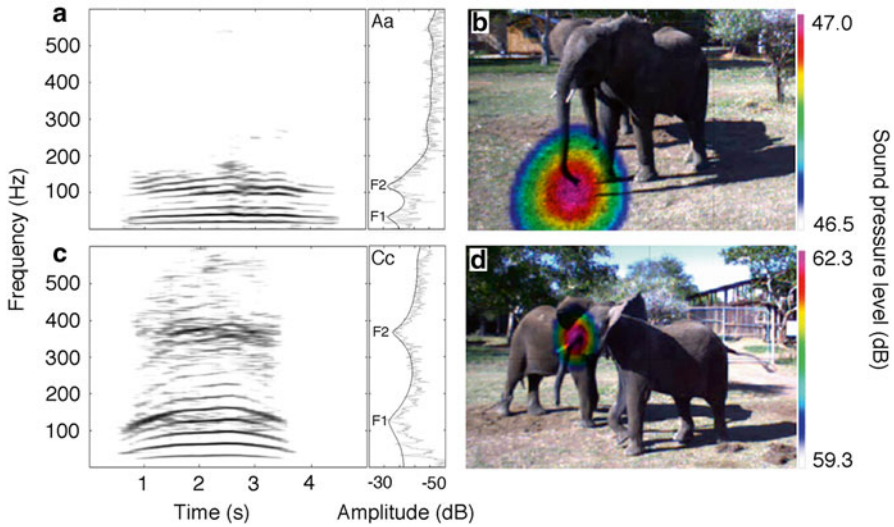
Fig. 7.5 Orally and nasally emitted rumble by a subadult female African elephant. Spectrogram and power spectra of a nasal (**a**) and oral (**c**) rumble revealing the differences in formant structure. (**b**) and (**d**) give the corresponding sound visualizations. *F* formant (Modified from Stoeger et al. 2012 for a nasal and oral rumble)

Formants provide the acoustic basis for discriminating vowels in human speech, transferring important information (Peterson and Barney 1952; Lieberman and Blumstein 1988). Several elephant studies have documented formant variation with context and/or arousal; specifically, an upward shift in the second formant seems to alert other elephants to potential danger (King et al. 2010). Also, females engaged in dominance interactions produce rumbles with lower formant dispersion (spacing) compared to rumbles produced in low-affect contexts (Soltis et al. 2009). Formants in elephants may well play a role in referential calling as elephants can discriminate distinct differences in formant frequencies between alarm rumbles made in response to bees and in response to human voices (Soltis et al. 2014).

In addition, formants are reliable cues to body size in several mammals, reflecting the close relationship between the caller's overall body size, vocal tract lengths, and the frequency spacing of the formants (Reby and McComb 2003; Fitch 2006). Morphological adaptations to elongate the vocal tract to lower formants are present in several species (Taylor et al., Chap. 9). Musth rumbles of male elephants, for example (or rumbles associated with hierarchical interactions), might be under similar selective pressure. Musth rumbles may also function to communicate the size of a musth male to listening males and females, in addition to advertising the hormonal state.

Lowering formants may also promote long-distance call propagation (McComb et al. 2003). The infrasonic fundamental frequency could be a by-product of the large size of the elephant's vocal folds (10.4 cm in an adult female African elephant; Herbst et al. 2012) rather than a specially evolved mechanism for long-distance vocal communication. The amplification of certain frequency regions by using the

nasal vocal tract may have evolved as a result of selection pressures particularly relevant to social and reproductive long-distance communication. McComb et al. (2003) found that harmonics in the range of 115 Hz (which highlighted the second formant) decayed at a lower rate with increasing distance than frequency components below and above them. This finding suggests that harmonics in the second formant area (in nasal rumbles) may experience less interference from wind noise than the fundamental frequency contour itself, but more studies would have to be conducted to determine if this effect is true in the far field.

Low-frequency vocalizations are subject to atmospheric conditions, reducing an elephant's call range by an order of magnitude during the diurnal cycle (Garstang et al. 1995; Larom et al. 1997). Temperature inversions after sunset enhance propagation by channeling sound energy within the surface layer (spreading losses become effectively cylindrical rather than spherical) creating conditions where calls could be heard up to 10 km (Garstang et al. 1995). Elephants might adjust the timing and frequency of their low-frequency calls according to atmospheric conditions. Acoustic and seismic playback studies have been conducted between the hours of 4 P.M. and 2 A.M. because of the increase in family group movements to waterholes and vocalizations during this window (O'Connell-Rodwell et al. 2006, 2007), which supports the atmospheric correlation proposed in the preceding text.

Much less is known about elephant sound perception. To date, the hearing sensitivity of elephants has only been investigated in one 7-year-old female Asian elephant (Heffner and Heffner 1980, 1982) that was more sensitive to low frequencies than any other mammals previously tested. At an intensity of 60 dB SPL, the elephant was able to hear 17 Hz, nearly one octave below the comparable human threshold. Nonetheless, the elephant was still considerably less sensitive to frequencies below 100 Hz than to those between 100 Hz and 5 kHz; however, these measurements may underestimate acuity at the lower frequencies, as the longer waveforms of lower frequency sounds (16 Hz) presented in the Heffner and Heffner (1982) study may have required a longer window of time for detection (O'Connell-Rodwell et al. 2001).

The ability of animals to detect low frequencies is associated with the size of the body, head and distance between the ears, and the size of the anatomical hearing structures (Heffner et al. 1982; Rosowski 1994; Nummela 1995). African elephants have large pinna of about 0.5–1 m (Garstang 2004) and up to 1.8 m (Sikes 1971) which may act as a sound-gathering device and aid in sound localization (Heffner et al. 1982; Pye and Langbauer 1998). Listening elephants freeze, spread their ears, and scan their environment (Poole et al. 1988). In auditory experiments, Heffner and Heffner (1982) noted that their Asian elephant subject extended the ears only during sound localization tests, not during absolute frequency or frequency discrimination tests, locating low-frequency sounds to within an azimuth angle of 1°. Sound localization depends on the difference in waveform phases between the two ears, and such phase changes correspond to the interaural time delays (Hartman 1999). Lower frequencies produce longer interaural time differences. More definitive studies are needed to determine the frequency ranges of best sensitivity and the mechanisms of sound localization in individuals of both genera.

Recent investigations of the neuroanatomical structure of the elephant brain (mainly of the African savannah elephant) (Shoshani et al. 2006; Patzke et al. 2013a; Herculano-Houzel et al. 2014), including infrasonic vocal production and reception (Maseko et al. 2013), will no doubt lead to a better understanding of how elephants perceive low-frequency sound. New research has revealed that at least five regions of the combined vocalization production and auditory/seismic reception system are specialized in elephants (Maseko et al. 2012). Elephants possess a large and distinct nucleus ellipticus, which is otherwise found only in elephant seals and cetaceans (Patzke et al. 2013b). The nucleus ellipticus is a specialization of the periaqueductal gray matter and is suggested to be related to infrasonic vocalization production (Maseko et al. 2012).

In terms of reception and interpretation of infrasonic vocalizations, the enlarged lateral superior olivary nucleus and the unique transverse infrageniculate nucleus appear to be related to air-borne sound waves. The enlarged dorsal column nuclei and the ventral posterior inferior nucleus of the dorsal thalamus, in turn, seem to be related to the seismic aspects of the sound waves (Maseko et al. 2012). The investigations of the elephant diencephalon and the brainstem investigated in the latter study demonstrate that while much of the elephant neuroanatomy is typically mammalian, certain anatomical adaptations related to specialized behavior, including infrasonic and seismic communication, are present and highly instructive in understanding elephant behavior (Maseko et al. 2012).

7.3.1.2 Seismic Communication in Elephants

There have been several reviews on elephant seismic communication, but highlights are summarized in this section (see O'Connell-Rodwell 2007; O'Connell-Rodwell and Wood 2010). As discussed in the previous section, both African and Asian elephants emit (Payne et al. 1986; Poole et al. 1988) and detect (Heffner and Heffner 1982) low-frequency (~20 Hz), high-amplitude rumble vocalizations. These rumbles couple with the ground and propagate along the surface as Rayleigh waves (O'Connell-Rodwell et al. 2000; Gunther et al. 2004). The potential range of seismic rumbles based on average call intensities and different soil types is estimated between 2 and 16 km (O'Connell-Rodwell et al. 2000; Gunther et al. 2004).

Elephant family groups detect and respond to these ground-borne vocalizations by exhibiting defensive "bunching" behavior in response to seismic playbacks of antipredator calls (O'Connell-Rodwell et al. 2006), bunching being an indicator of vigilance (McComb et al. 2000). In addition, elephants exhibit more vigilant behaviors during presentations, orienting in the direction of the seismic signal, and spend significantly less time in the area when a seismic alarm is presented (O'Connell-Rodwell et al. 2006). Elephants are also able to discriminate subtle differences between familiar and unfamiliar callers through the ground (O'Connell-Rodwell et al. 2007). The sophistication with which elephants can detect vibrational cues indicates that the ground is an important medium for elephants in which to send and receive signals.

Seismic Signal Detection

Elephants have two possible pathways for detecting seismic signals, either through bone conduction and/or through vibration-sensitive mechanoreceptors in their feet and trunk (Reuter et al. 1998; O'Connell et al. 1999; Bouley et al. 2007). When vibrations transmit through bone, they first couple with the ground via the feet, then travel up through the legs, shoulders, and into the middle ear cavity (Rado et al. 1998) and detection would then be facilitated by the elephant's hypertrophied mallei (Reuter et al. 1998).

Elephants engage in "seismic listening," which is a freezing behavior that is distinctive from freezing in the context of airborne listening and appears to facilitate the detection of seismic information. Individuals lean forward with ears flat against their bodies, placing more weight on their larger front feet which, because of the unique graviportal structure of their forelimbs, are directly in line with the ear (O'Connell-Rodwell et al. 2006). Sometimes the foot is rolled forward onto the toenail, which would also facilitate bone conduction directly to the toe bones. The combination of this behavior and the presence of an enlarged malleus would suggest that elephants employ a bone-conduction pathway for seismic signal detection. The dense, fatty foot pad of the elephant appears similar to "acoustic fat," which would provide a mechanism for more efficient signal propagation and detection of seismic cues (O'Connell-Rodwell et al. 2001), or perhaps even serve as a "seismic lens" to improve sensitivity of the elephant to substrate-borne vibrations.

The role of "acoustic fat" is best known for dolphins, where it is found only in the mandibular channel and the melon (Varanasi and Malin 1971; Varanasi et al. 1975). 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 (Au 1993).

Elephants sometimes lift a front foot off the ground while freezing, which would facilitate localization through triangulation. This posture would not maximize bone conduction and suggests that there may be some situations where the somatosensory pathway of detection might be preferred to bone conduction. The amount of time an elephant spends with a portion of their trunk lying on the ground while freezing is additional evidence that the somatosensory pathway is important for detecting seismic cues.

Bone Conduction Enhancement

Fossil data (Barnes et al. 1985; Ketten 2000), immunological evidence (Gaeth et al. 1999), and the morphology of the fetal African elephant ear (Fischer 1990) indicate that Sirenia and elephants have a common aquatic ancestor. 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 (Ketten et al. 1992; Gerstein et al. 1999). The structure of the manatee skull,

incorporating unique fat deposits, may function to conduct sounds (Norris 1968). The African elephant's skull is also aerated by sinuses (van der Merwe et al. 1995) and except for the solid mandible, the cranium consists of inflated bones compartmentalized to form diploe (Shoshani 1998). The fatty deposits and aerated skull sinuses in the elephant may facilitate low-frequency seismic detection.

In addition, elephants have muscles surrounding the external auditory meatus that contract, occluding the opening of the ear canal (O'Connell-Rodwell et al. unpublished data), which would dampen acoustic signals and facilitate improved detection in the seismic environment. Pressure builds up in the ear canal upon closure, creating a "closed acoustic tube" that enhances bone conduction (Stenfelt et al. 2003). This anatomical feature, potentially a remnant of an aquatic ancestry, may facilitate acoustic reception of lower frequencies and/or a bone-conducted pathway for seismic detection.

Somatosensory Reception

Elephants have a second pathway for seismic detection through the somatosensory pathway. Pacinian corpuscles, or pressure receptors, are the largest peripheral mechanoreceptors in mammals (Saxod 1996). Pacinian corpuscles are deeply placed whereas the Meissner's 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 (Bolanowski and Zwislocki 1984), Meissner's corpuscles being equally sensitive between 10 and 65 Hz (Makous et al. 1995). The tip of the Asian elephant trunk contains both Pacinian and Meissner's corpuscles in extremely dense concentrations (Rasmussen and Munger 1996). Pacinian corpuscles have also been found in the elephant foot (Weissengruber et al. 2006; Bouley et al. 2007), mostly in the front and back of the dermal layer (Bouley et al. 2007).

Seismic Discrimination

Both pathways of detection would facilitate the discrimination of high-resolution frequency differences in seismic signals. The range of frequency modulation within an elephant acoustic antipredator call is approximately 15–19 Hz (O'Connell-Rodwell et al. 2007). The minimum perceptible frequency change (Δf) is related to the critical bandwidth (CBW) (Greenwood 1961), where CBW $= \Delta f * 20$. An estimated Δf of 0.75–0.95 Hz would allow elephants to detect very small changes in frequency modulation across these calls (O'Connell-Rodwell et al. 2007). If bone conduction to the ear is utilized, then frequency discrimination ability will be reliant on the elephant's ability to discriminate acoustic frequencies. Because the elephant's cochlea shows the sharpest resonance among seven species studied (von Békésy 1944/1960), these animals are capable of discriminating frequency changes within a narrow bandwidth.

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 antipredator calls that were played back to elephants varied from about 10 to 19 Hz, which should be within the range of vibro-tactile frequency discrimination ability of elephants. As 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 (Recanzone et al. 1992). It is likely that elephants have similar vibro-tactile frequency discrimination abilities as primates, if not better given their ability to detect infrasound.

Seismic Signal Propagation

The vibration channel allows signals to propagate farther than acoustic signals owing to the outer limit on airborne signal propagation as defined by Snell's law, where sounds refract back into the atmosphere at 10 km. Airborne sound waves also attenuate more rapidly than Rayleigh waves as they spread spherically rather than cylindrically (losing 6 dB for every doubling of distance vs. 3 dB), and thus ground surface waves maintain integrity longer. Airborne waves are more susceptible to interference and alteration because of environmental factors such as wind and temperature fluctuations, whereas soil type and heterogeneity are factors influencing the propagation of a seismic signal (O'Connell-Rodwell et al. 2000, 2001; Gunther et al. 2004). Wind generates noise in the seismic channel, but that noise does not impart a directional dependent attenuation to the signal. An acoustic signal, however, is affected in a directional manner, the signal heavily attenuated when traveling upwind, while it travels slightly farther downwind.

Certain characteristics are needed 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 (e.g., Bishop et al. 2015). For vocal coupling, the low-frequency, high-amplitude nature of elephant vocalizations are important. The generation of such signals may be facilitated by a large diaphragm, a larynx with five rather than the nine bones present in most other mammals (Shoshani 1998), and an unusually large nasal cavity. Moreover, the weight of an elephant would facilitate the coupling of their vocalizations into the ground.

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. For example, localizing vocalizations centered around 20 Hz, with a wavelength of about 17 m, given an interear distance of approximately 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 (O'Connell-Rodwell et al. 2000, 2001). Using the vibration-sensitive trunk would provide an additional advantage.

Factors Enhancing Signal Propagation

African elephant family groups vocalize within interactive bouts that result in multiple repetitions of a signal that is three or more times longer than one produced by a single individual (O'Connell-Rodwell et al. 2012). As auditory thresholds are based on temporal summation, longer signals would increase the signal-to-noise ratio, facilitating signal detection (Heil and Neubauer 2003). Repeated signals also facilitate detection (Hamilton 1957; Greenwood 1961). If temporal summation and repetition itself increase the detection probability, then it follows that signal detection and processing would be facilitated at greater distances.

Repetitive interactive calling behavior has also been documented among captive bonded individuals (Soltis et al. 2005). Furthermore, during departure from a resource, calling bouts are repeated at a greater rate (O'Connell-Rodwell et al. 2012). Elephants also increase their rate of calling during estrus, emitting calls that are longer in duration than other calls (Leong et al. 2003), adding further evidence that elephants may create longer repeated calls to facilitate their detection at greater distances. Since elephant cows have a very narrow window for ovulation (5 days every 4 years) (Moss 1983), it would be to their advantage to improve the advertising of their reproductive state.

Listening elephants at a distance would have an opportunity to optimize their physical orientation 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. As the Asian elephant has the largest volume of cerebral cortex of all terrestrial mammals (Hart et al. 2001), they are presumably well equipped to integrate multimodal signals.

If a seismic and an acoustic signal are redundant in the near field, the ability to detect the same signal twice in different modalities would improve its chances of detection. Because of the different propagation velocities of the two modalities, the signal will arrive at different times, thus allowing the receiver to be alerted by the first arriving signal to concentrate on the second arriving signal to resolve any signal ambiguity and possibly estimate the distance of the signaler. Signal ambiguity can be mitigated by repeating the signal; however, if dual modalities are utilized, the signal is automatically repeated without any extra effort. Seismic communication could supplement airborne communication or be especially beneficial when airborne conditions are not ideal for transmission (O'Connell-Rodwell et al. 2000, 2001; Arnason et al. 2002). Elephants may also be able to distinguish less subtle seismic events such as an approaching vehicle, helicopters, airplanes, weather (thunder storms), or earthquakes.

Two main challenges remain in this research area. The first challenge is to determine the extent to which seismic correlates of elephant vocalizations propagate in the far field, and second, determining the sensitivity of an elephant's foot to vibrations produced from elephant vocalizations at a distance. Geophysicists normally collect data on body waves, such that high-amplitude surface waves produced by earthquakes (and elephant vocalizations) are considered noise and are filtered out of data sets. More research is needed to determine how ground borne waves behave in

the far field and in soils of different compositions. These two remaining aspects of the sender–receiver process in seismic communication would solidify our understanding of how seismic communication enhances the elephant's already long-distance communication ability.

7.3.1.3 Seismic Communication in Golden Moles

Background and Review of Known Studies

Golden moles are nocturnal, surface-foraging mammals with rudimentary vision. Several species possess massively hypertrophied mallei that presumably confer low-frequency, substrate-vibration sensitivity through inertial bone conduction. The seismic sensitivity of golden moles has been studied anatomically (Mason 2003a, b, 2004, 2007b), behaviorally (Fielden et al. 1990; Narins et al. 1997; Lewis et al. 2006), and physiologically (Willi et al. 2006a, b). What is poorly understood is the mechanism by which these remarkable animals determine the source location of the seismic signals and how they are able to orient and move toward their source.

The quest for features in the golden mole's middle ear that might serve the localization of seismic disturbances is motivated by the known foraging behavior of the Namib Desert golden mole (*Eremitalpa granti namibensis*). In addition to other sand-dwelling invertebrates, the diet of this animal mainly consists of dune termites, *Psammotermes* (Fielden et al. 1990). It has been hypothesized that wind-blown dune grass sets the mounds into resonance, resulting in the emission of concentric Rayleigh (surface) waves, that can, in theory, provide the golden mole a homing vector to the source of this seismic beacon—the sand mounds—and hence to the food cache (Narins et al. 1997). It was demonstrated that in the absence of olfactory cues, golden moles are able to locate the food-containing mounds at a distance, solely using vibrations generated by the wind blowing the dune grass (Lewis et al. 2006).

This golden mole navigates from one grassy tussock to another, punctuating its foraging trail with characteristic sand disturbances in which the animal "head-dips," presumably to obtain a vibrational "fix" on the next mound to be visited. It is thought that head-dipping serves to couple the animal's head to the sandy substrate, so that it can better detect the Rayleigh waves emanating from the mounds.

As the desert golden mole is currently protected under the Convention on International Trade in Endangered Species (CITES), another closely related species, the Cape golden mole (*Chrysochloris asiatica*), was the focus of preliminary studies of vibration localization in golden moles. *C. asiatica* and *Eremitalpa g. namibensis* belong to the same family, golden moles (Chrysochloridae), which inhabit sub-Saharan Africa. *C. asiatica* is not listed as a protected species and as a result is obtainable for study from the Republic of South Africa. The foraging behavior of *E.g. namibiensis* suggests that the animal is able to localize prey by detecting the seismic signals they emit (Fielden et al. 1990; Narins et al. 1997; Lewis et al. 2006). One anatomical feature both species (among others) exhibit, is a

massively hypertrophied malleus (Mason 2003a). Hypertrophied mallei within the family Chrysochloridae have been known for some time (Forster Cooper 1928; von Mayer et al. 1995). Some of the species exhibit the heaviest ossicles relative to body mass of all mammals so far documented (Mason 2003a). Lombard and Hetherington (1993) proposed that the hypertrophied mallei of chrysochlorids are adapted to detect vibrations by means of inertial bone conduction, and Mason (2003b) developed a model, which is based on the middle ear anatomy of a golden mole exhibiting a hypertrophied malleus, and serves the detection of vibrations exploiting inertial bone conduction. Another prominent anatomical feature of some golden moles is the interbullar connection described for three genera of chrysochlorids, *Eremitalpa*, *Chrysochloris*, and *Chlorotalpa* (von Mayer et al. 1995). Its purpose is not known, but functionally it couples the two middle ear cavities. Interaural connections are described in reptiles, amphibians (Henson 1974), birds, and insects, but not in mammals other than moles and golden moles. Experiments in the European mole (*Talpa europaea*), a subterranean mammal that is not related to the golden mole but inhabits a similar environment, have shown that the trabeculated interaural connection enables acoustic coupling between the two ears (Coles et al. 1982). This study suggests that the ear of the European moles may act a pressure-gradient receiver (Mason 2014). The interbullar connection in the three golden mole genera is even more prominent than in the European mole, consisting of a wide and open tube. The perception of interaural time (ITD) and intensity (IID) differences becomes more difficult with smaller interaural distances (the size of the skull). Also, small animals perceive directional cues if the frequency of the source to be localized is high enough, but moles and golden moles inhabit a medium that favors the propagation of low frequencies over high frequencies (Heth et al. 1986). Therefore, some subterranean mammals might have been forced to find means other than detecting ITD and IID to localize a sound source. The interbullar connection might be such an adaptation.

Localization of Seismic Stimuli: A Look Ahead

Procedure for Measuring Directional Hearing in Golden Moles

One of us (P. M. N.), along with Urban Willi, established procedures and designed experiments that allowed us to begin to explore the mechanism of directional hearing in the Cape golden mole, *C. asiatica*. In our setup (Fig. 7.6), a precise and detailed yet preliminary description of the middle ear dynamics involved in the perception of directional cues from seismic and acoustic stimuli was obtained.

In one experiment, the response of one malleus head to vibration stimuli (thumps) presented at different azimuths (–90° to +90°, in 10° increments) at a distance of 20 cm from the animal's head was measured. The inflated epitympanic recess was opened to expose the distal portion of the malleus head of one ear. A thin layer of pure silver powder placed on the malleus head improved the reflection from the ossicle. The cavity was resealed with a piece of a glass cover slip applied with liquid

Fig. 7.6 Setup for measuring malleus velocity in response to seismic signals in the Cape golden mole. *GM* golden mole, *SLDV* scanning laser Doppler vibrometer, *VE* vibration exciter, *ST* sand tank
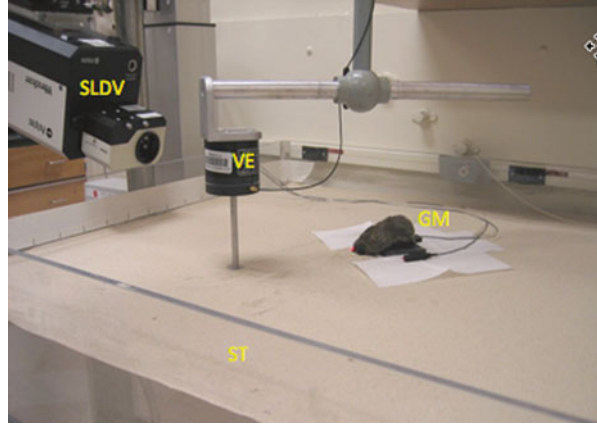
tissue adhesive, which reconstructed the middle ear volume but enabled access for scanning laser Doppler vibrometer (SLDV) measurements. The animal's head was placed exactly in the center of the sand tank. The head was partially buried in the sand in order to bring the long dimension of the malleus parallel with the ground and the head. The direction the animal faced was set as the 0° azimuth. A vibration exciter ("mini-shaker"; Bruel & Kjær, model 4810) was attached to a floor stand allowing us to position the vibration source at an arbitrary angle on a circle centered on the animal's head. Neither the SLDV nor the animal was moved during the measurements. During presentation of the seismic signal at 10° increments in azimuth, the horizontal velocity of the malleus head relative to that of the skull is measured in the time domain with the SLDV. The measurement was triggered by the signal output of the signal generator. Hence, differences in arrival time between seismic waves emanating from two different angles are due only to travel time in the substrate and the response of the malleus to the stimulus.

Although this vibration delivery system provided repeatable seismic stimuli, it was clear that tank reflections would result in secondary waves appearing at the geophone. Although the reflected waves arrived with a delay relative to the direct waves, and although the secondary wave amplitudes were attenuated relative to the direct waves, our stimulus system was nevertheless redesigned to eliminate or reduce secondary waves. Improved procedures have since been devised.

Improved Procedure for Measuring Directional Hearing in Golden Moles

To investigate directional hearing in *Chrysochloris asiatica* in the laboratory, an environment with physical properties similar to the free field needed to be simulated. In contrast to mechanical disturbances in fluids and gases, mechanical disturbances in elastic solids comprise not only compression-waves (P-waves), but also shear-waves (S-waves). Surface waves are a subclass of S-waves, which only exist
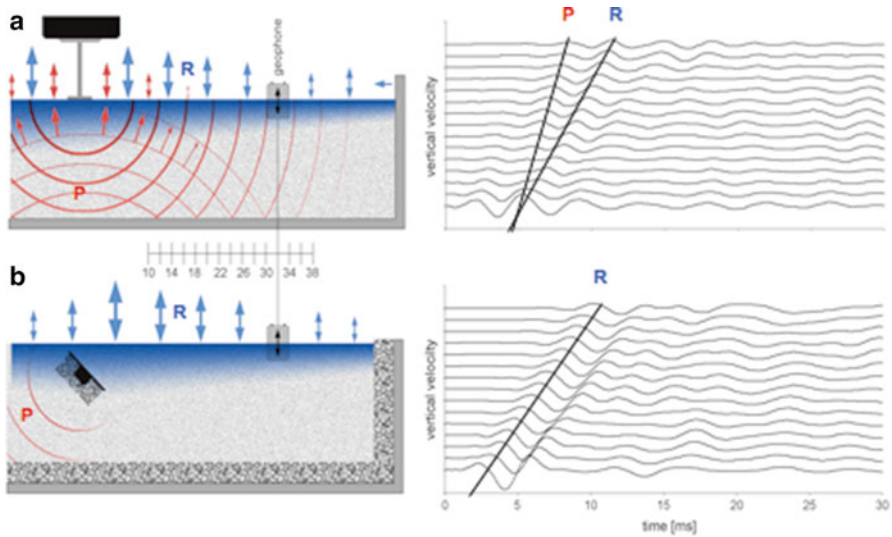
Fig. 7.7 Preliminary and improved setup to investigate directional hearing in the ground. The setup in the sand tank is shown on the *left illustrations*, the vertical velocities measured with a geophone at increasing distance (10–38 cm, 2-cm increments) from the source, is presented in the *right graphs*. (**a**) Interference patterns between the P-wave (P, *red*) and Rayleigh-waves (R, *blue*) are caused by the reflected P-wave in the preliminary setup. (**b**) These interferences were suppressed by reducing the induction of P-waves and reducing their reflection in the improved setup

at boundaries between two media. The two waveforms, P- and S-waves, can be discriminated by their propagation velocity and the orientation of particle motion. P-waves and S-waves in sandy soils travel at about 100 and 40 m/s, respectively (Ishimoto and Idia 1936). P-waves spread spherically into the ground and their attenuation is proportional to $1/r^2$ whereas S-waves propagate only along the surface and, therefore, and are attenuated less ($1/r$) (where 'r' is the distance from the source). In the free field it is relatively easy to separate the two waveforms, due to their difference in propagation velocity. In the lab, however, a medium of much smaller dimensions is a genuine constraint. Instead of the P-wave disappearing into the ground, it is reflected from the shallow tank bottom and interferes with the vertical S-wave (Rayleigh-wave) (Fig. 7.7a, left). The vertical motion measured with a geophone at increasing distance (10–38 cm, 2-cm increments) from the source reveals two components of different propagation speed (Fig. 7.7a, right). To interpret the directional cues reflected by the dynamic response of the moles' middle ear, it is critical to be able to determine the velocity of the stimulus approaching the animal. This was the impetus for instituting the improved properties of the sand tank. First, the entire tank was lined with open cell foam (25 mm thick) reducing the reflection of the P-wave. Second, the source was modified to decrease the generation of the P-wave component. The latter was achieved by using an electromagnetic
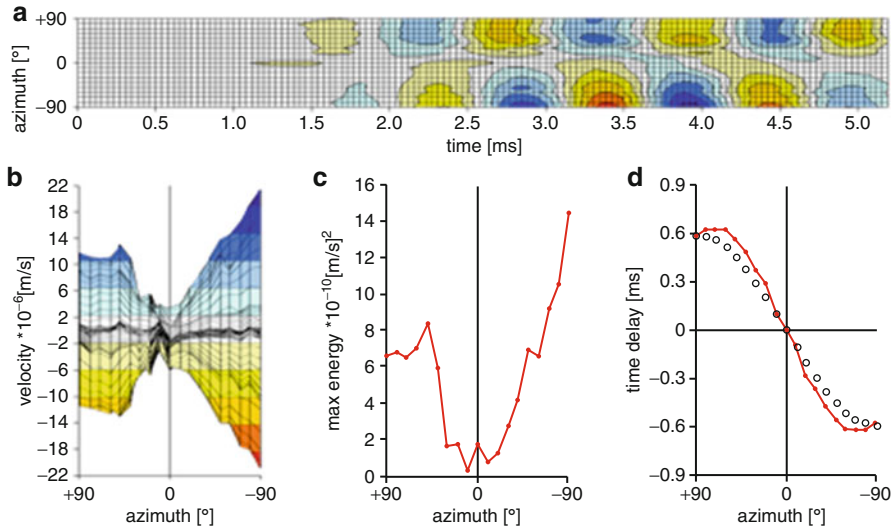
Fig. 7.8 Horizontal motion of the right malleus head as a response to a thump at different azimuths (−90° to +90°, 10° increments). Negative angles represent the ipsilateral side with respect to the right ear. (**a**) Response of the right malleus at all azimuths of the source. (**b**) Maximum response over the time signal shown in graph (**a**). (**c**) Power spectrum peaks at each azimuth over that same time signal. (**d**) *Open black circles*: Time delays calculated assuming a middle ear distance of 12 mm and a wave propagation speed of 40 m/s. *Red solid line*: Time delay calculated by an autocorrelation function, based on the time signals presented in graph (**a**). Hence, the positive and the negative values of the same azimuth were compared

transducer buried about 2–3 cm underneath the sand surface, facing the surface at an angle of 45°. In addition, the back of the transducer was embedded in a layer of open cell foam (25 mm thick). Using these procedures, the interference patterns and reflections disappeared, and the vertical motion generated in this new setup consists of a single slow surface-wave, a Rayleigh-wave (Fig. 7.7b). The peak attenuation over distance falls off as $1/r^{1/2}$ (Narins 1990). This setup allows us to simulate free field situations in the lab. Thus, it is expected that directional cues that might be exploited by the animal to localize seismic sources would be found in the temporal patterns of the malleus motion. Experiments are currently being planned to test these hypotheses.

Vibration Response of Malleus in the Golden Mole: A Look Ahead

In the Cape golden mole, peak horizontal velocities are greatest for ipsilateral stimulation and they gradually decay toward the zero azimuth, revealing a minimal response in front of the animal. In Fig. 7.8a, the time response of the relative malleus motion at each azimuth is shown and the maximal velocities of the same data are shown in Fig. 7.8b.

Contralaterally, the response increases again but does not reach the velocity value seen under ipsilateral stimulation. This phenomenon is most likely due to the anatomy of the ossicular chain: The firmest anchoring of the ossicular chain to the middle ear cavity is given by the ligament at the short process of the incus (LSPI). As the long axis of the malleus is parallel not only to the ground but also to the sagittal plane of the skull, the system is much more susceptible to sideways and vertical motions of the skull than to motion along the anteroposterior axis of the animal. An analogy to this is a pendulum moving relative to its suspension when latter moves sideways but not when it moves along the axis of its suspension (vertically). Figure 7.8c depicts the power spectral peaks at each azimuth and quantitatively confirms the findings in Fig. 7.8b. Figure 7.8d shows the time delay between stimuli reaching the same ear from the same azimuth on the ipsilateral and contralateral sides (e.g., +80°/–80°). The delays (red solid line) were evaluated by cross-correlating the ipsilateral to the contralateral time signal at equal azimuths. The open circles in the same graph represent an estimate of interaural time delay based on an interbullar distance of 12 mm and a measured wave propagation speed of 40 m/s. The estimate and the evaluation of the time delays show a good match, suggesting that the skull motion at each bulla reflects the motion of the ground and that time delays due to the propagation of the wave are accessible to the animal. The values reflect a relative motion of the malleus versus the skull, because the skull motion is already subtracted. Negative azimuth values refer to measurements using ipsilateral stimulation and positive azimuth values refer to measurements using contralateral stimulation. It is remarkable in the time domain that the polarity of the malleus motion switches when the source moves from the ipsilateral to the contralateral side. These data show clear directional cues present in the middle ear in response to the horizontal velocity component of the seismic disturbances and suggest a simple mechanism for localizing seismic cues in the substrate.

However, in this preliminary experiment only the horizontal component of the malleus motion was measured. Future experiments should explore the degree to which the middle ear is susceptible to both the vertical and horizontal motion components and the precise nature of the directional cues provided by them.

7.4   Conclusions

Infrasonic and vibrational forms of communication are still wide open fields of study. Although much is known about invertebrate vibration communication, it is not nearly as well understood in the vertebrates. Although some is known about the bird's ability to sense infrasound and vibrations, how they use this information needs further investigation. There are many cases of the use of vibrations as signals in reptiles and amphibians, and even small rodents, but the extent to which large mammals use vibrational cues either derived from infrasonic vocalizations or percussion still needs further exploration. Elephants can detect and distinguish low frequency acoustic callers and call types seismically. These seismic cues could

supplement acoustic information, replace acoustic information under poor airborne conditions, or, under ideal seismic conditions, extend the elephant's range of communication within a complex multimodal communication repertoire. Remarkably, golden moles, the only member of the Afrotheria other than the elephant in which seismic behavior has been studied extensively, appears to rely on vibrational cues to both detect and localize prey. Examining the mechanisms underlying these fundamental behaviors needs additional study.

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