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8. Seismic sensitivity and communication in subterranean mammals

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Abstract. Many subterranean mammals are reported to generate or respond to seismic vibrations. Potential uses of seismic sensitivity in these animals include intraspecific communication between burrow systems, location of prey, detection of predators and even “seismic echolocation” of distant obstacles. Although the auditory and/or somatosensory systems have been variously implicated, the mechanisms used for the detection of ground vibrations often remain unclear. This chapter will concentrate on three groups of subterranean mammals in which seismic sensitivity and/or communication has been studied in the most detail, the spalacid mole-rats, the bathyergid mole-rats and the golden moles, and will consider how the evolution of seismic sensitivity might have been affected by factors including digging mechanism, food type, sociality and phylogeny.

Introduction

Although many mammals construct burrows, the focus of this chapter is on highly fossorial species, i.e. those with extreme anatomical and physiological

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adaptations to a subterranean environment. These include the talpid moles (order Soricomorpha, family Talpidae), the golden moles (order Afrosoricida, family Chrysochloridae), the marsupial moles (order Notoryctemorphia, family Notoryctidae) and members of several families within the order Rodentia, including the Spalacidae, Bathyergidae, Geomyidae and Ctenomyidae. Except where noted, the taxonomy and nomenclature used throughout this chapter follows Wilson & Reeder [1].

Given the high energetic cost of digging [2], a burrow system represents a valuable resource to a fossorial mammal: a vacant burrow belonging to a member of a solitary species is typically taken over rapidly by a conspecific [3, 4, 5]. However, solitary subterranean mammals are notoriously aggressive to intruders, and the invasion of an occupied burrow system can have fatal consequences [6, 7]. It would clearly be advantageous for these animals to have some way of advertising their territorial presence so as to deter intruders, or in the breeding season to signal their receptive reproductive state.

Scent-marking may help to advertise the occupancy of tunnels [4, 8, 9], but effective transmission of olfactory cues probably requires an animal actually to enter a tunnel system, which could be risky. This problem can be avoided in species with contiguous burrow systems if activity patterns of neighbours are out-of-phase: talpid moles are known to “time share” overlapping areas of territory [10]. Even so, the availability of a communication mechanism allowing a real-time response would offer a number of obvious advantages.

Although vision is of no use underground and is vestigial in many subterranean mammals, most are known to vocalise and social species possess a wide repertoire of calls [11, 12, 13]. Vocalisations tend to be tuned towards the low frequencies which have been found to propagate furthest within tunnel systems, but despite this they may travel only a few metres underground [14]. Behavioural audiograms of subterranean rodents show a restriction of hearing range to low frequencies, but hearing is not unusually sensitive in these animals even at these frequencies, and has been described as “degenerate” or “vestigial” [15, 16, 17]. Although normally solitary species often use vocal cues when in close proximity to conspecifics [18, 19], and selective amplification of particular frequencies might compensate for poor hearing under certain circumstances [20], airborne sound would appear to be of limited use to a subterranean mammal for communicating over long distances underground. Instead, seismic signalling is generally believed to represent a more efficient means of communication between neighbouring burrow systems [21, 22].

Seismic signalling for intraspecific communication is well-documented in solitary fossorial rodents of the families Spalacidae and Bathyergidae,

considered in detail below. Among other subterranean mammals, foot-drumming has been infrequently observed in geomyids [Reichman, pers. comm. in 23], but nothing is known about its behavioural context. Seismic signalling appears not to occur in ctenomyids [19, 24], and has never been documented in talpid or marsupial moles.

While only a subset of subterranean mammals appears to *generate* seismic signals for use in intraspecific communication, the ability to *detect* ground vibrations is probably universal. It is presumably advantageous for any subterranean species to be able to detect vibrations made by approaching predators, for example, and there are numerous reports of animals fleeing on the heavy footfalls of an observer [e.g. 25, 26]. Other uses of seismic sensitivity may relate more specifically to diet. Subterranean rodents were long believed to have no means of locating distant vegetable food sources underground, although evidence now suggests that several species can potentially use odour cues for this purpose [27, 28]. The insectivorous golden mole *Eremitalpa*, however, appears to use vibratory cues to locate its prey: golden moles represent the third subterranean family considered in detail in this chapter.

Seismic communication and echolocation in spalacid mole-rats

The spalacine, myospalacine and tachyoryctine mole-rats are united within the Spalacidae, sister-family to the Muridae within the rodent suborder Myomorpha [29]. Within the Spalacidae, seismic communication appears to be widespread. The East African mole-rat *Tachyoryctes splendens* has been observed to tap the floor or walls of its burrow with its upper incisors, in a sequence of three to ten raps followed by a pause, this being replied to in a similar way by neighbouring conspecifics [30]. There is also evidence for seismic communication by head-thumping in the zokor *Eospalax fontanierii* (= *Myospalax cansus*), from China [31]. However, it is in the spalacine mole-rat *Spalax ehrenbergi* that seismic communication has been most extensively studied. *Spalax ehrenbergi* is considered to represent a superspecies which may be divided into several allospecies distinguished, among other things, by the exact pattern of seismic signals which they produce [3], but the allospecies will here be regarded collectively.

Spalax inhabits a wide range of environments in the eastern Mediterranean countries, but not true desert. Its burrow system is typically based on a main tunnel 20-40 cm below-ground, from which several short secondary tunnels branch off [6]. Like many fossorial mammals, *Spalax* is solitary and very aggressive towards conspecifics outside of the breeding season [32, 33]. Territorial signalling is achieved, at least in part, by means of

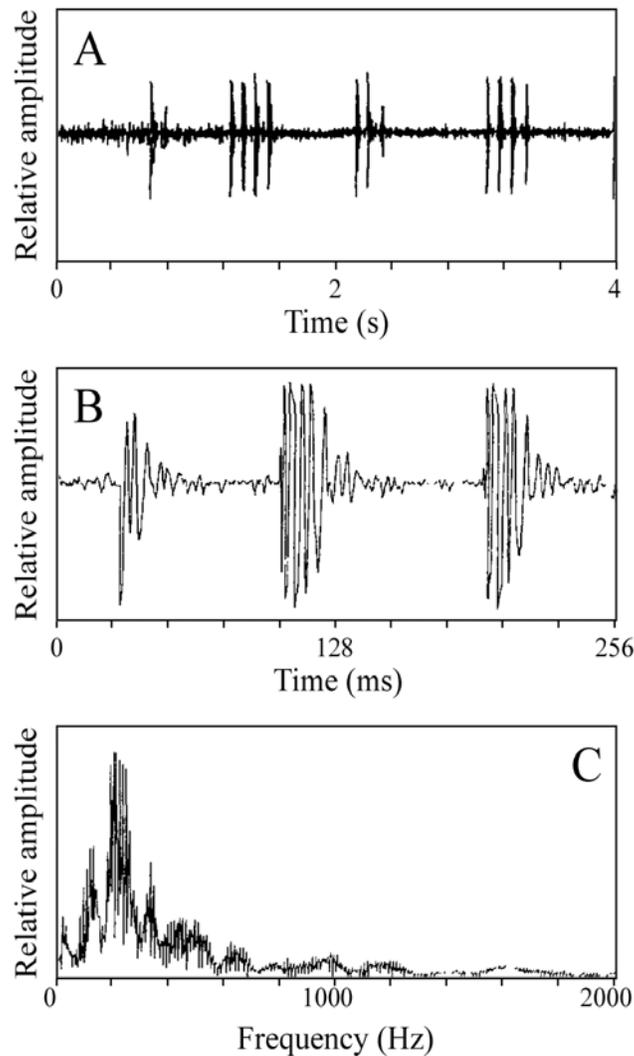


Figure 1. Temporal pattern and frequency content of the head-drumming of the mole-rat *Spalax ehrenbergi*, recorded in its natural habitat using a vertical geophone. A: Oscillogram representing consecutive bursts performed by an individual animal; B: individual head-drums on an expanded time-scale; C: spectral density function of head-drums. Reprinted from *Animal Behaviour*, vol. 35, Rado, R., Levi, N., Hauser, H., Witcher, J., Adler, N., Intrator, N., Wollberg, Z. & Terkel, J., Seismic signalling as a means of communication in a subterranean mammal, pp. 1249-1251, copyright (1987), with permission from Elsevier.

“head-drumming”, whereby the mole-rat repeatedly strikes the roof of its burrow with the anterodorsal surface of its head, in several series of short bursts [3, 34, 35]. Most of the energy in the drumming signal, as recorded in the wild, is between around 100 and 300 Hz [34; Fig. 1]. Experiments with captive specimens in separate Plexiglas tubes showed that only when the

tubes were in contact, allowing vibratory cues to pass between them, was head-drumming initiated, this often leading to head-drumming “duets” [34]. Other, similar experiments on mole-rats in artificial tunnel systems have confirmed that substrate vibrations are much more effective than airborne cues in eliciting behavioural and electrophysiological responses from the animals [21, 36]. Communication switches from vocal to seismic as young *Spalax* mole-rats disperse and inhabit separate tunnel systems from that of their mother [37].

Although most studies have concentrated on seismic signalling for intraspecific communication, it has recently been suggested that *Spalax* might use vibratory signals for a form of “seismic echolocation” [38, 39]. These authors proposed that *Spalax* can use reflected vibrations produced by head-drumming to detect relatively large objects (above around 7 cm diameter) ahead of them in the soil, and perhaps to assess their tunnel depth. Single head-knocks are produced by these animals as they dig bypass tunnels around obstacles, which might be used for orientation if the reflections are detectable within a few milliseconds of production [39].

Audition or somatosensation?

Spalax is effectively blind [see 40 for a review], its vestigial eyes retaining a role only in photoperiodic detection [41]. The cortical somatosensory representation in this species has expanded into the occipital cortex [42], and is the same absolute size as in the much larger laboratory rat [43]. The central auditory system has also taken over typically visual areas [40]. These findings suggest that the somatosensory and auditory systems have both functionally expanded at the expense of sight in *Spalax*, but which of these systems is more important regarding vibratory sensitivity remains a source of controversy.

Nevo *et al.* [21] found that the presence of white noise (120 dB peak equivalent SPL), used to mask airborne auditory cues, made little difference to the evoked potentials recorded from the scalp of a mole-rat in response to tapping on its Perspex tunnel. However, tapping on a tube physically separated from the one that the animal was in, but from the same distance away, resulted in a much smaller evoked response, which was more effectively masked by the white noise. These experiments implicate tunnel wall vibrations rather than airborne sound as the dominant means of signal transmission to the animal. There was no change in scalp-recorded evoked potentials in the animals following surgical destruction of the middle and inner ears, and some continued to respond behaviourally to tapping cues.

Nevo *et al.* argued that the somatosensory system must therefore be the principal mediator of vibrational sensitivity in *Spalax*.

A later study, by Rado *et al.* [36], came to quite the opposite conclusion. These authors found that bilateral deafening of the animals almost eliminated middle-latency responses recorded from the scalp, and over time resulted in a cessation in drumming behaviour. They also found white noise to reduce responses from intact animals, concluding that the auditory system plays the predominant role in the transmission of vibrations, with the somatosensory system relegated to a very minor role. Rado *et al.* proposed that that rate of vibratory stimulation might have affected the results of Nevo *et al.* [21], such that they failed to see the auditory response.

In laboratory conditions, *Spalax* has been observed to hold its cheek and lower jaw against the walls of its tube when a conspecific was head-drumming [44]. These authors suggested that this “jaw-listening” behaviour allows vibratory signals to pass through the lower jaw to the auditory bulla. Vibrations would pass from here to the incus and, bypassing the malleus and tympanic membrane, would then pass via the stapes to the cochlea. Rado *et al.* [36] found that their experimental animals were indeed most sensitive to seismic vibrations when their lower jaws were applied to the vibrating substrate. Aspects of the inner ear of *Spalax* suggest tuning to low frequencies [45, 46], which would be consistent with the hypothesis that low-frequency seismic signals are detected using the auditory system.

Given that the transition from head-drumming to “jaw-listening” would take too long, “jaw-listening” could not be used for transmission of vibrations into the body if *Spalax* uses a form of seismic echolocation [39]. Kimchi *et al.* duly demonstrated that *Spalax* requires only its paws to detect and localise a vibratory source, turning attention once more towards the somatosensory system as the mechanism for detection. The proposed somatosensory and auditory routes for seismic sensitivity in *Spalax* are certainly not mutually exclusive, but their relative importance remains in question.

Somatosensory receptors in *Spalax*

There are several somatosensory structures which might potentially mediate vibration transduction in this species of mole-rat. As well as sensory vibrissae, *Spalax* has a conspicuous white stripe along its muzzle made up of well-innervated hairs [47]. These have a large cortical representation and are presumably of some somatosensory importance [48], but there is nothing to suggest that they are particularly involved in vibratory detection. By contrast, the simple lamellated and Meissner’s corpuscles in the nose pad [47] are the type of receptor that could potentially transduce seismic signals (see

Discussion). Kimchi *et al* [39] identified lamellated corpuscles resembling Pacinian corpuscles in the glabrous skin of the fore- and hind-feet of *Spalax*, which they believe underlie paw-mediated vibratory sensitivity. Finally, the root of the lower incisor tooth in *Spalax* is contained within a hollow, rounded prominence of the mandible which extends lateral to the articular process [49]. It is possible that the “jaw-listening” behaviour observed in *Spalax* [44] involves pressing this protuberance to the substrate, in which case vibration perception might conceivably involve the teeth [50; see later].

Seismic communication in bathyergid mole-rats

The Bathyergidae is a family of mole-rats from sub-Saharan Africa. Classified within the rodent suborder Hystricomorpha, they are only distantly related to the spalacid mole-rats considered previously. Several species of bathyergid have been observed to foot-drum, which might advertise the presence of an occupied burrow to neighbouring animals, or might convey information pertaining to sex and reproductive condition [23].

Among bathyergids, foot-drumming behaviour has been most extensively studied in the Cape mole-rat *Georychus capensis*, both in the laboratory and in the field [22, 23]. *Georychus* constructs complex burrow systems of approximately 130 m length and mean diameter 10 cm [51]; the burrow systems approach within a few meters of each other but are not mutually connected, and the animals thus live alone for most of the year [23]. In captive mole-rats, drumming was found to occur in early June: the male drums with his back legs on the burrow floor for up to two minutes at a frequency of 26 per second, the female responding by drumming for a shorter time and at a lower frequency [23]. Auditory waveforms representing a duet between male and female animals, as recorded by Narins *et al.* [22], are shown in Fig. 2.

In a study designed to determine which component of the foot-drumming signal (auditory or seismic) could be detected by neighbouring animals, Narins *et al.* [22] used a mechanical “thumper” to introduce male and female foot-drumming patterns into a natural *Georychus* burrow in South Africa. The airborne component of the foot-drumming signal was attenuated by its passage through the sandy substrate such that it was indistinguishable from the background noise at distances less than 1 m from the source. In contrast, the seismic component of the foot-drumming signal was at levels significantly above the background noise at five geophone locations above a neighbouring burrow system, which at its closest point was 3.4 m from the burrow system containing the thumper. Moreover, these workers established that the horizontal and vertical components of the surface wave produced by

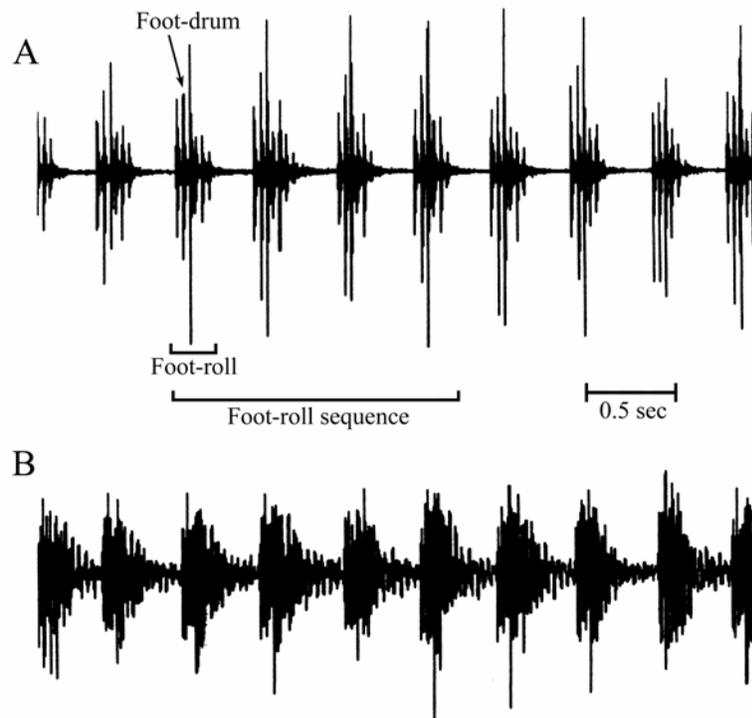


Figure 2. Simultaneously-recorded waveforms of the thumps produced during a foot-drumming duet by (A) female and (B) male Cape mole-rats, *Georychus capensis*. The animals were separated by a transparent divider located in a Plexiglas tunnel system through which they could travel; the recordings were of airborne sound generated by the thumps, and were made using microphones. Note the 1:1 synchrony of the footrolls throughout this interaction. With kind permission from Springer Science + Business Media: *Journal of Comparative Physiology A: Sensory, Neural & Behavioral Physiology*, Seismic signal transmission between burrows of the Cape mole-rat, *Georychus capensis*, vol. 170, 1992, page 15, Narins, P.M., Reichman, O.J., Jarvis, J.U.M. & Lewis, E.R., Fig. 1.

foot-drumming attenuate differentially as they propagate through the soil. By comparing amplitudes of the two surface wave components, a Cape mole-rat could, in principle, determine the distance to a signalling individual.

Considering other bathyergids, foot-drumming occurs in solitary *Bathyergus* species, and in species of the genera *Cryptomys* and *Fukomys*¹ which live in small colonies [23, 53]. In *Cryptomys* and *Fukomys* species, drumming or stamping of the hind-feet against the burrow floor may be performed by sexually-receptive females during encounters with males

¹The generic name *Fukomys* has recently been introduced to replace “*Coetomys*”; *Fukomys* contains some of the species previously referred to as *Cryptomys* [52].

[54, 55, 56], and has also been observed in subordinate animals trying to encourage resting conspecifics to move out of the way of the nesting chamber entrance [57]. If these behaviours do indeed represent seismic signalling, this is clearly operating over much shorter distances in these social species than in *Georychus*. Foot-drumming has not been observed in the solitary *Heliophobius argenteocinereus* [58], nor in *Heterocephalus glaber*, which lives in very large colonies [11, 23]. Within the Bathyergidae, therefore, the presence or absence of drumming behaviour is not clearly associated with social system. It is, however, interesting to note that the eastern African *Heterocephalus* and *Heliophobius* are placed as sister-groups to a monophyletic clade containing the central/southern African *Bathyergus*, *Georychus*, *Cryptomys* and *Fukomys* [see 7, 59]. Since all recorded instances of bathyergid drumming are in species within the central/southern clade, it is tempting to speculate that the behaviour evolved in their common ancestor, perhaps during the hypothesized migration through an “arid corridor” from eastern to southern Africa, and was retained in the descendent lineages for one purpose or another, despite differences in their ecology.

Potential mechanisms for seismic sensitivity in bathyergids

Although facial vibrissae and other sensory hairs are present on the body surface even in the naked mole-rat *Heterocephalus*, which shows clear orienting responses to their tactile stimulation [60, 61], it appears that no specifically vibration-sensitive somatosensory receptors have been described in bathyergids. Nearly a third of the greatly expanded somatosensory cortex of *Heterocephalus* is occupied with representations of the very prominent incisors, which can be excited experimentally by stroking or tapping the teeth [62, 63]. *Heterocephalus* has a flexible mandibular symphysis which allows the lower incisors to be moved independently, and they are known to tap objects with their teeth when investigating their surroundings [62]. Although this particular species does not foot-drum, bathyergids might potentially use their incisors for acoustical vibration reception, as proposed by Poduschka [64].

The malleus and incus are characteristically fused in bathyergids, but their middle ear structures otherwise resemble those of other subterranean rodents [65, 66]. The ossicles are not notably enlarged, and there is nothing obvious to suggest that the middle ear is specialised towards seismic sensitivity. The cochlea of *Fukomys anselli* was found to contain an expanded low-frequency region [67] lacking enhanced mechanical tuning [68], but whether this subserves the detection of vibrations transmitted by some form of bone conduction is unknown.

Seismic prey-detection in golden moles

Golden moles, family Chrysochloridae, are a group of small, insectivorous mammals confined in distribution to sub-Saharan Africa. They are classified with the tenrecs in the order Afrosoricida, which itself forms part of a large group of endemic African mammals known as the Afrotheria. The Chrysochloridae is divided into two subfamilies, the Amblysominae and Chrysochlorinae [69].

When foraging, the Namib Desert golden mole, *Eremitalpa granti namibensis*, moves between small sand mounds or hummocks topped with dune grass (*Stipagrostis sp.*), which contain most of the living biomass in the area. Stomach content analysis has revealed that the diet of *E. g. namibensis* consists principally of termites, with other invertebrates (such as insect larvae), lizards, spiders and root material being of lesser importance [70]. These moles may cover distances of five or more kilometres per night in search of food [71]; they both “sand-swim” within the substrate, leaving no permanent burrow system, and run on the surface of the sand.

Narins *et al.* [72] tested the hypothesis that foraging is random in this animal, such that encounters with food resources (hummocks) are purely stochastic events. Analysis of foraging trail trajectories suggested that rather than stochastically encountering food patches, the animals’ foraging paths appeared to be “sensory guided”: the moles appeared to be able to localize the hummocks at distances up to 20 m. Light winds that normally blow over the Namib Desert cause the dune grass to emit vibrations that are propagated as surface waves across the sand. Geophone recordings revealed that the hummocks generated spectral peaks centred at around 300 Hz, ca. 15 dB greater in amplitude than those from the flats. Above-ground foraging trails of *Eremitalpa* are punctuated with characteristic sand disturbances called “head dips” [70], discrete locations where the animal is thought to obtain a seismic “fix” on the next mound to be visited. In a later field study, Lewis *et al.* [73] provided evidence to suggest that *Eremitalpa* can localise buried vibratory sources emitting seismic signals akin to those produced by the wind-blown dune grass.

Anecdotal reports suggest that *Chrysospalax* and *Chrysochloris* golden moles, which like *Eremitalpa* are chrysochlorines, may also use seismic cues for detecting their prey when foraging on the surface [74]. Surface Rayleigh waves are subject to less attenuation through geometrical spreading than are compressional (*P*) waves travelling in the body of the substrate, while the relatively low conduction velocity of Rayleigh waves in loose sand should facilitate localisation of the source, if based on time-of-arrival cues [75, 76].

Whether or not golden moles are able to make use of seismic time-of-arrival cues is unknown, but surface foraging in sand and other loose substrates might, at least in principle, allow them to take advantage of these favourable seismic transmission properties.

Among the amblysomine golden moles, male *Amblysomus hottentotus* may use foot-stomping as part of a courtship display [77], and there has been one report of this species knocking its head on burrow walls [Duckworth, pers. comm. in 78]. *Amblysomus* constructs permanent burrow systems in a wide range of mesic habitats and is seldom active above ground [78]. However, it remains to be confirmed that *Amblysomus* or any other golden mole uses seismic signals for intraspecific communication.

The role of the middle ear in chrysochlorid seismic sensitivity

The mallei of chrysochlorine golden moles are greatly hypertrophied [79, 80; Fig. 3], those of *Chrysochloris*, *Eremitalpa* and *Chrysochloris* species being the heaviest, relative to body size, of any mammal [66]. The mass of *Eremitalpa* mallei is increased not just through their large dimensions, but also due to the unusually high bone density [81]. This ossicular enlargement has been hypothesized to confer vibratory sensitivity [77, 82], Lombard & Hetherington [83] proposing that ossicular inertial bone conduction might represent the underlying mechanism. This hypothesis was expanded upon by Mason [74, 84]. According to this model, contact with a vibrating substrate results in vibrations of the skull of the golden mole, but owing to their inertia, the ear ossicles do not vibrate with the same amplitude and phase. This results in relative movement between the stapes and inner ear, which is translated into vibrations of the inner ear fluid, the consequent deflections of hair-cell stereocilia being interpreted as sound in the usual way. Ossicular inertial bone conduction requires not just hypertrophy of the ossicular chain, but also a displacement of its centre of mass away from the axis of rotation. Such adaptations are found to a greater or lesser extent in the chrysochlorines, but not in amblysomine golden moles such as *Amblysomus*, which possess middle ear ossicles of more typical size and shape [80, 84, 85, 86; Fig. 3].

Willi *et al.* [87, 88] studied the vibratory behaviour of the hypertrophied malleus of freshly euthanized Cape golden moles, *Chrysochloris asiatica*. Using scanning laser Doppler velocimetry, Willi *et al.* were able to map the motion of the malleus in response to both vertically- and laterally-oriented sinusoidal vibrational stimuli, over a frequency range from 10-600 Hz. Resonant frequencies varied between 71 and 200 Hz between individuals, but did not differ significantly between the two stimulus directions. Below

resonance, the ossicles moved in-phase with the skull, whereas at frequencies above resonance, malleus motion was out-of-phase with the skull, and the distal tip of this ossicle exhibited mean vibratory amplitudes around 6 dB higher for lateral stimulation than for vertical stimulation. The rotatory axis for malleus movement passed through the short process of the incus and was roughly perpendicular to the long axis of the malleus, remaining in this orientation for seismic stimulus frequencies up to 600 Hz. By contrast, for airborne stimulation above ca. 300 Hz the rotatory axis was rotated nearly 90°, now being closely aligned with the long axis of the malleus (Fig. 4).

At low frequencies (up to ca. 200 Hz), the centre of ossicular mass is therefore displaced from the rotatory axis. The ear was interpreted under these circumstances to act as a geophone, highly sensitive to substrate vibrations. However, at airborne frequencies above ca. 300 Hz, the rotatory axis passes close to the centre of ossicular mass, which lowers the angular moment of inertia, presumably improving sensitivity to higher frequencies. The unusual malleus morphology therefore appears to be an elegant solution

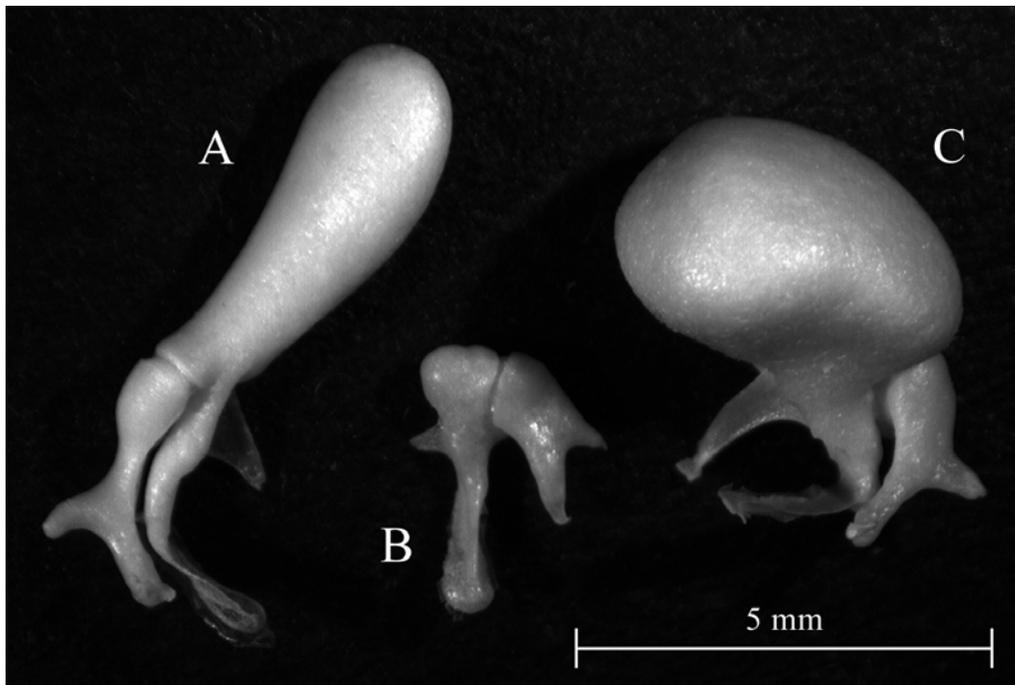


Figure 3. Photomicrograph of the auditory ossicles (malleus and incus) of three golden mole species. A: Left ossicles of *Chrysochloris asiatica* (body mass around 50 g); B: right ossicles of *Amblysomus hottentotus* (body mass around 70 g); C: right ossicles of *Eremitalpa granti namibensis* (body mass around 20 g). In *Amblysomus*, the ossicles are of typical shape and size relative to body mass: note the massively enlarged malleus in the other two species.

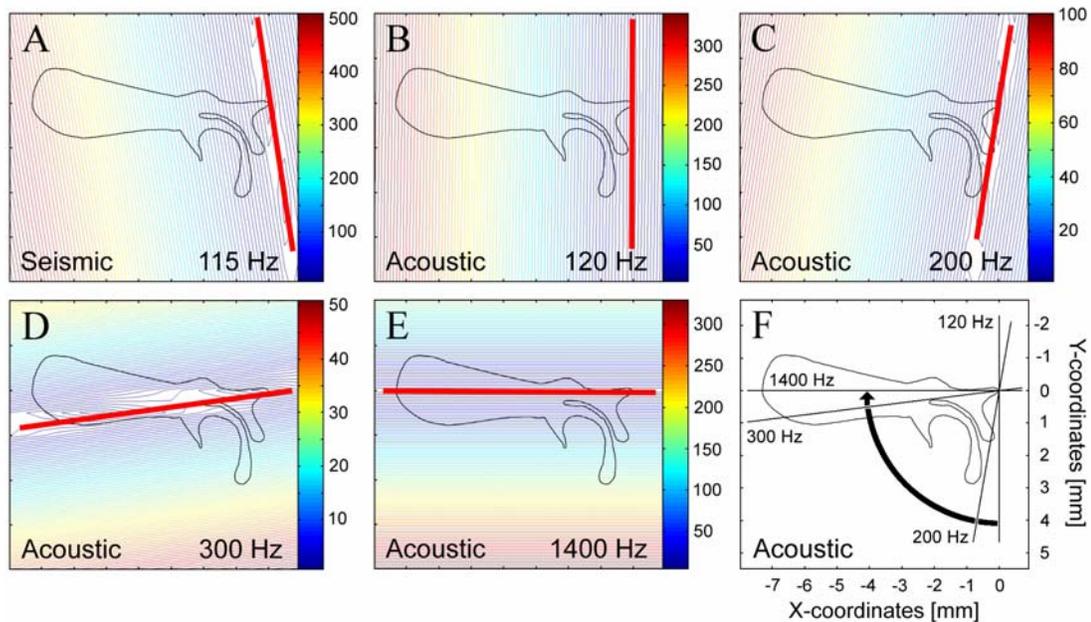


Figure 4. Motion patterns of the ossicular chain in response to (A) seismic and (B-E) acoustic stimulation at different frequencies indicated by iso-velocity lines. The rotatory axis of each mode is defined by the iso-velocity lines of smallest amplitudes, and is indicated with a thick, red bar. Both for low-frequency seismic and airborne stimuli, the rotatory axis is nearly perpendicular to the long axis of the malleus (A-C). The seismic rotatory axis remains constant with increasing seismic frequencies up to ca. 600 Hz (data not shown); for airborne stimulation, it approaches the long axis of the malleus (D, E). The major transition between acoustic modes occurs between 200 and 300 Hz (F). With kind permission from Springer Science + Business Media: *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, Ossicular differentiation of airborne and seismic stimuli in the Cape golden mole (*Chrysochloris asiatica*), vol. 192, 2006, page 273, Willi, U.B., Bronner, G.N. & Narins, P.M., Fig. 8.

to the problem of how a middle ear can exploit an increased ossicular inertia for detecting low-frequency substrate vibrations, at little cost to the animal's airborne sound-detection capability. If this rotatory axis shift were to be reflected in the stapes footplate movement and resulted in differential stimulation of the inner ear fluids, this could form the basis of a novel peripheral mechanism to differentiate airborne and substrate-borne stimuli.

Ossicular hypertrophy in other species

Apart from chrysochlorine golden moles, ossicular hypertrophy has only been documented in two extinct Oligocene palaeoanodonts known only as

fossils [89], and in two Asiatic talpid moles, *Parascaptor leucura* and *Scaptochirus moschatus* [90, 91]. The mallei of these talpids are not as large as in some of the golden moles, and it is not known whether they are used to confer seismic sensitivity. Given the apparent association of ossicular hypertrophy in golden moles with the habit of foraging in sand or on the surface, it is interesting to note that *Parascaptor* constructs runs in loose surface soil [92], whereas *Scaptochirus* has been found in sandy, desert areas [93]. Significant ossicular hypertrophy has not been documented in any fossorial rodent.

Discussion

Several different methods of burrowing are found in subterranean mammals, involving some combination of incisors, forelimbs and/or head [94]. Depending on burrowing mechanism, at least one part of the body of a fossorial mammal is likely to be in intimate contact with the soil on a regular basis, and thus in a position to receive vibratory cues. It therefore seems likely that in the evolution of seismic sensitivity, digging mechanism will have influenced the sensory modality or modalities used [50].

Mammalian glabrous skin contains rapidly-adapting vibration receptors in the form of Meissner and Pacinian corpuscles, of which the former are sensitive to vibrations of up to around 100 Hz with peak sensitivity at 20-50 Hz, and the latter to vibrations up to around 1 kHz, with peak sensitivity at 200-400 Hz [95]. Vibration reception in hairy skin at frequencies up to around 100 Hz may be based largely on responses from hair-follicle afferents, with distant Pacinian corpuscles, located in joints and interosseous membranes between the limb bones, conferring higher-frequency sensitivity [95]. Directionally-sensitive receptor complexes known as Eimer's organs, responsive to vibrations up to a few hundred hertz, are found in the snout of talpid moles [96, 97]. Although such specialised structures have not been described in other fossorial species, the mammalian somatosensory system is clearly pre-adapted to a role in detecting low-frequency vibrations: indeed, even nearby humans can detect the vibrations caused by *Spalax* head-drumming underground, through their feet [6].

Intradental mechanoreceptors and periodontal ligament receptors in cat canine teeth are able to produce entrained responses to vibrations at frequencies up to around 250 Hz and 100 Hz respectively [98], which certainly suggests that the enlarged rodent incisors could also, in principle, be used for low-frequency vibration detection. This intriguing possibility remains to be investigated.

The hearing of all subterranean mammals appears to be tuned to low frequencies, but the transmission of even low-frequency airborne sound through tunnels is limited. For these reasons, the auditory system might readily be exapted into a role emphasizing the detection and localisation of low-frequency seismic vibrations instead, if these vibrations convey useful information over longer distances. Bone conduction of skull vibrations to the inner ear is inevitable in mammals, and might be particularly favoured evolutionarily if the head is used for burrowing, as in *Spalax* and golden moles, during which process it is firmly planted against the soil. Efficient transmission of vibrations to the skull is potentially enhanced by specialised listening behaviours, such as “jaw-listening” in *Spalax* and “head-dipping” in *Eremitalpa*. The central auditory system uses cues from the two ears to localise airborne sound sources very accurately, and it is therefore pre-adapted to do the same with bone-conducted vibrations. In species such as golden moles, where seismic sensitivity appears to be used for the detection of prey, precise localisation of the vibratory source might have favoured the auditory over the somatosensory route if vibrations could excite the two ears differently depending on the direction of the source: ways in which this might occur are discussed by Mason & Narins [99] and Lewis *et al.* [73].

The fact that ossicular hypertrophy has not evolved in fossorial rodents might reflect the vulnerability of an inertial system to blows to the head, as in the head-drumming of *Spalax*, or to skull vibrations caused by gnawing. Whether or not *Spalax* uses an alternative means of bone conduction involving the middle ear, as proposed by Rado *et al.* [44], has not yet been examined experimentally, but other forms of bone conduction exist which do not involve the middle ear ossicles [100]. Experiments suggest that *Spalax* can use its somatosensory system to localise vibratory sources, and it might even use a form of seismic echolocation to determine the presence and shape of distant objects [38, 39]. A comparison of signals from spatially separated receptors, such as those on each paw, might be necessary for this. However, if seismic sensitivity in other fossorial rodents is mainly used for establishing the presence or absence of conspecifics in neighbouring burrow systems, or for assessing their reproductive state, precise localisation of a vibratory source might not be necessary.

This chapter has concentrated on the three families of subterranean mammals in which seismic signalling and/or sensitivity has been best-studied, but what about other subterranean groups, such as talpid moles, marsupial moles, pocket gophers and ctenomyids, about which much less is known? In the case of talpid moles, Eimer’s organs appear to be capable of detecting vibratory cues, but beyond fleeing from heavy footfalls there is little evidence that these animals make use of seismic vibrations in the field.

Further investigation of these less-well-studied groups may demonstrate as-yet unknown physiological and behavioural mechanisms, allowing them too to benefit from this potentially useful communication channel.

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