PII S0361-9230(97)00286-4

The Use of Seismic Signals by Fossorial Southern African Mammals: A Neuroethological Gold Mine

PETER M. NARINS,*[1] EDWIN R. LEWIS,† JENNIFER J. U. M. JARVIS‡ AND JUSTIN O'RIAIN‡

*Department of Physiological Science, UCLA, 405 Hilgard Ave., Los Angeles, CA 90095–1527, USA
† Department of EE & CS, UC Berkeley, Berkeley, CA 94720 USA
‡ Department of Zoology, University of Cape Town, Rondebosch, 7700, South Africa

ABSTRACT: Behavioral adaptations exhibited by two African fossorial mammals for the reception of vibrational signals are discussed. The Namib Desert golden mole (*Eremitalpa granti namibensis*) is a functionally blind, nocturnal insectivore in the family *Chrysochloridae* that surface forages nightly in the Namib desert. Both geophone and microphone recordings in the substrate suggest that the golden mole is able to detect termite colonies and other prey items solely using seismic cues. This animal exhibits a hypertrophied malleus, an adaptation favoring detection of low-frequency signals. In a field study of the Cape mole-rat (*Georychus capensis*), a subterranean rodent in the family *Bathyergidae*, both seismic and auditory signals were tested for their propagation characteristics. This solitary animal is entirely fossorial and apparently communicates with its conspecifics by drumming its hind legs on the burrow floor. Auditory signals attenuate rapidly in the substrate, whereas vibratory signals generated in one burrow are easily detectable in neighboring burrows. The sensitivity to substrate vibrations in two orders of burrowing mammals suggests that this sense is likely to be widespread within this taxon and may serve as a neuroethological model for understanding the evolution of vibrational communication. Neuroethological implications of these findings are discussed. © 1997 Elsevier Science Inc.

KEY WORDS: Vibrational communication, Cape mole-rat, *Georychus*, Golden mole, *Eremitalpa*, Foraging.

INTRODUCTION

Seismic communication is more ubiquitous among the vertebrates than has been previously imagined. We have examined the use of seismic signals in two fossorial mammals from Southern Africa: the Namib Desert golden mole, *Eremitalpa granti namibensis* from the central Namib Desert in Namibia, and the Cape mole-rat, *Georychus capensis* from the Cape region of South Africa. We have reported the principal results of our seismic communication studies of the Cape mole-rat [23], and therefore, only a brief summary will be provided here as a comparison to our more recent results from the investigation of the Namib Desert golden mole.

The various species of golden moles are insectivores in the family *Chrysochloridae*, found in Sub-Saharan Africa, south of a line from Cameroon to Uganda. They are blind [9] and have a massive malleus, which presumably confers low-frequency sensitivity, via the cochlea, to substrate vibrations. Recently, we have investigated the use of seismic signals by the Namib Desert golden mole, illustrated in Fig. 1A. Unlike most other subterranean mam-

mals, *E. g. namibensis* lacks a permanent burrow system and can forage 5 or more kilometers per night [17] for its prey on the dune surface [12]. Foraging animals typically move between miniature sand dunes (hummocks or mounds, Fig. 1B), which are formed by shifting sand accumulating around dune grass (*Stipagrostis*). Foraging trails consist of footprints interspersed with characteristic sand disturbances (Fig. 1C) in which the animal head dips (Fig. 1D), or sometimes sand swims. In the latter case, the animal moves just below the surface, leaving distinctive elongated mounds of sand. As the animal moves forward, the newly made tunnel collapses leaving a distinct track [24]. Head dipping occurs during foraging "when the moles run rapidly along the sand surface, occasionally briefly submerging their head and shoulders, possibly in an attempt to detect the position of the prey from substrate vibrations" [10]. We believe it is likely that head dipping is a means by which the mole may tightly couple its head to the substrate, and that these two energetically costly behaviors are used to sample the animal's seismic environment.

Stomach content analysis has shown that termites are the major dietary item, with other invertebrates (such as insect larvae) and root material being of only minor importance [13]. These workers also demonstrated that biomass of potential prey items was low and food resources were patchily distributed. They concluded that movement patterns of moles are effective in encountering localized areas of high prey concentrations (hummocks) and in minimizing energy expenditure in an energy-sparse environment. In the present study, we tested the hypothesis, first put forward by Fielden et al. [13], that foraging is random in this animal such that encounters with food resources are purely stochastic events, and that the mole's ability to detect prey is effective over short distances only.

MATERIALS AND METHODS

Study Site—Golden Mole Study

Field recordings and characterization of golden moles' foraging trails were conducted during November, 1993, at the Namib Desert Research Station in Gobabeb, Namibia (23° 34' S, 15° 03' E). Foraging trails were located and mapped between 0700 and 1200 h over as long a distance as possible. These animals were found along a narrow perimeter at the base of the slip face of the giant linear dunes in the Namib Desert just south of the Kuiseb River. Trails were marked on a calibrated grid on which all distinguishing land features were noted; e.g., hummock location and size measured by major diameter: (large: >2.0 m; medium: 0.5–2.0 m;
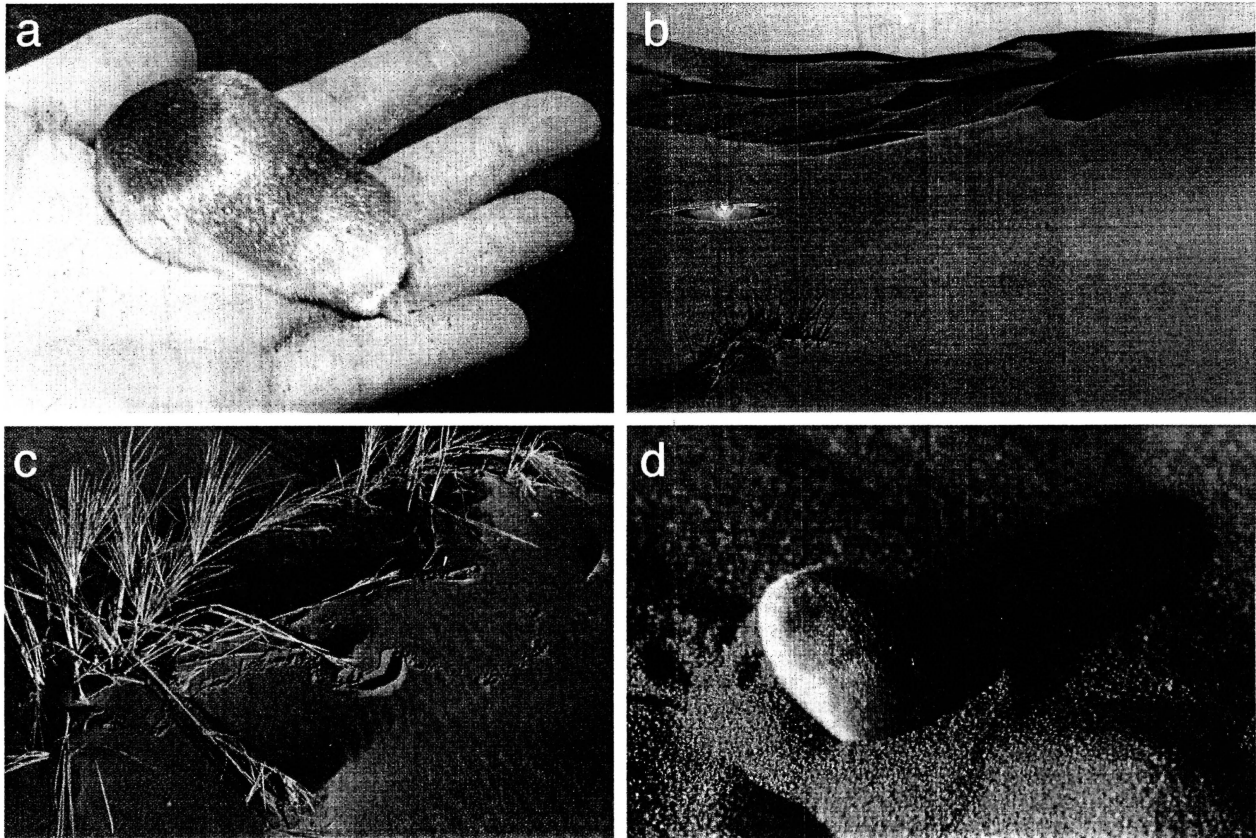
FIG. 1. (A) The Namib Desert golden mole, *Eremitalpa granti namibensis.* (B) View of the Namib Desert at Gobabeb showing linear dunes (background) and hummock (foreground). (C) Foraging trail of a Golden Mole near a hummock. (D) Head-dipping behavior of *Eremitalpa* in which the animal immerses his head and forepaws in the sand while his hindquarters remain exposed. Head-dipping behavior was only observed in captured animals.

small: <0.5 m), presence or absence of dead or live dune grass (*Stipagrostis*) on hummock, dune grass remnants, hummocks visited during foraging, etc. In addition, headdip locations along the foraging trail were noted. Wind velocities were measured to the nearest 0.1 m/s with a hand-held anemometer.

Test of Random Foraging

At night the moles forage over the surface of the sand, traveling from hummock to hummock in search of prey consisting of at least eight orders of insects as well as root material, with the principal dietary item being dune termites, *Psammotermes* [13]. In the early morning, one can readily follow the fresh tracks made by the animal. In late morning when the wind strengthens, the foraging trail is obliterated, creating a *tabula rasa* for the next night.

To determine whether encounters with patches of food resources are indeed random events, we mapped long sections of the foraging trails. For each of six trails, we selected a segment that contained a series of visited hummocks. For each of these hummocks in turn, we fixed one end of a 30-m tape at its center, and walked with the other end in a circle (of radius 30 m) around the visited hummock under test. The angle subtended by each hummock encountered by the 30-m tape during one revolution, whether or not it was visited by the golden mole, was measured with a protractor located at the center of the circle. The total angle, Θ_{ht} subtended by all the hummocks in the circle was then calcu-lated as shown in Fig. 2; Θ_{ht} was then expressed as a percentage of 360°. The figure of 30 m was chosen as the circle radius because it was longer than any interhummock path segment we observed for any mole.

Seismic Signal Measurement and Analysis

Substrate vibrations were measured with both a horizontally polarized and a vertically polarized geophone (AMF Industries 10395; peak response: 10 Hz; sensitivity: 1.0×10^4 mV/m/s). Each geophone was fitted with a leg (7.3 cm) and the whole assembly was completely buried in the sand. This helped achieve a solid mechanical coupling of the geophones to the substrate, and thus minimize measurement error of the local particle velocity. The geophone outputs were separately amplified with battery-powered, calibrated, variable-gain preamplifiers and recorded on separate channels of a two-track portable cassette player (Marantz PMD430). The geophones were placed either in the headdip locations along the foraging trail, on or near the hummocks, or in the sand flats at least 4 m from any hummock.

Seismic signals were analyzed using a calibrated, averaging dynamic signal analyzer (Hewlett–Packard 3561A). Results were plot-ted with velocity as a function of time or as a velocity amplitude spectrum. Each geophone was individually calibrated in the laboratory by producing known accelerations with a vibration exciter (Brüel & Kjaer 4809) driven by a controller (Brüel & Kjaer 1047). Using a
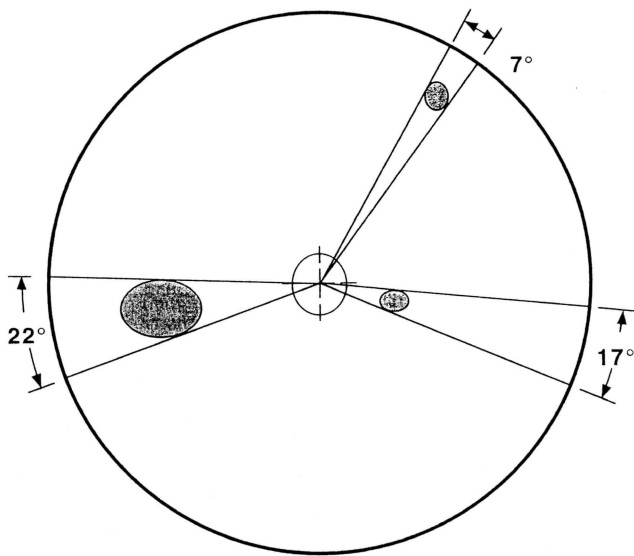
FIG. 2. Method used to calculate total angle subtended by all hummocks within a circle of a 30-m radius (shaded ovals) centered on a visited hummock (unshaded oval). In this example, the total angle subtended by all hummocks within the circle is $22° + 7° + 17° = 46°$. The probability that this mole would encounter any hummock within a 30-m radius of the center hummock by foraging randomly is 46 out of 360 or 0.128.

constant acceleration [measured with a calibrated accelerometer (Brüel & Kjaer 8306)] of 0.2 m/s², the sensitivity of each geophone was determined over the frequency range from 4–500 Hz.

RESULTS

Foraging Trail Analysis

We made detailed maps for a total of 728 m of the foraging paths of six golden moles. A representative section of the foraging trail made by one individual (mole No. 5) is illustrated in Fig. 3. Seven hummocks in this section of trail were visited by the mole. Despite the presence of other mounds near the trail, the animal clearly selected some hummocks while bypassing others (presumably those in which potential prey items were absent). At the selected mounds, evidently those in which it detected termites or other prey, the mole burrowed into the sand, often emerging nearly a meter from the place it entered. Moreover, interhummock path segments appear remarkably straight (see Fig. 3), considering these animals possess only a vestigial eye which is covered with skin and fur [9,24].

Although we cannot be absolutely sure that we did not follow the same mole on a couple of occasions, 1) we sampled several (at least two) runs on a single day, and 2) we sampled in several areas so we are comfortable that we were not looking at the same animals all the time.

We also observed, as have others, that the distance between successive head dips (interhead dip distance, IHD) appeared to shorten as the animal approached a selected hummock. This observation was borne out by our measurements. For each of the eight trail segments analyzed (made by six moles), distances between head dips in the intermound segments (>0.5 m from a hummock) were compared to the distances between head dips in the immediate proximity of a mound (<0.5 m from a hummock). The former were found to be significantly greater ($p < 0.05$, t-test) than the latter in all eight cases. The total number of IHDs analyzed in the intermound segments was 510 (range: 18 to 156,

mean: 64) and the number of IHDs analyzed in the vicinity of a mound was 269 (range: 13 to 76, mean: 34).

The results of a representative test for random foraging are shown in Fig. 4. The pie charts represent the results obtained for each of the hummocks visited successively by mole No. 5 in the section of his foraging trail shown in Fig. 3. The sums of the angles subtended by all hummocks (striped area) and by no hummocks (filled area) inside a 30-m circle centered on each mound are expressed as a percentage of 360°. On average for this mole, hummocks inside a 30-m circle subtended 23.8% of a circle, or the probability that random foraging would result in a hit of any other hummock within 30 m from the last one is 0.238 (the mean probability for four moles analyzed in this way was 0.22). Also shown for mole No. 5 are the cumulative probabilities that random foraging would result in the mole encountering seven consecutive hummocks, given the actual configuration of mounds. For this trail segment, the probability that the mole would arrive at all seven of the hummocks by chance is 0.00004.

Geophone Recordings

Placing one geophone on the top of a hummock (height: 1.5 m) topped by live dune grass and another in the flat sand at a distance of at least 20 m from the hummock under test resulted in a typical
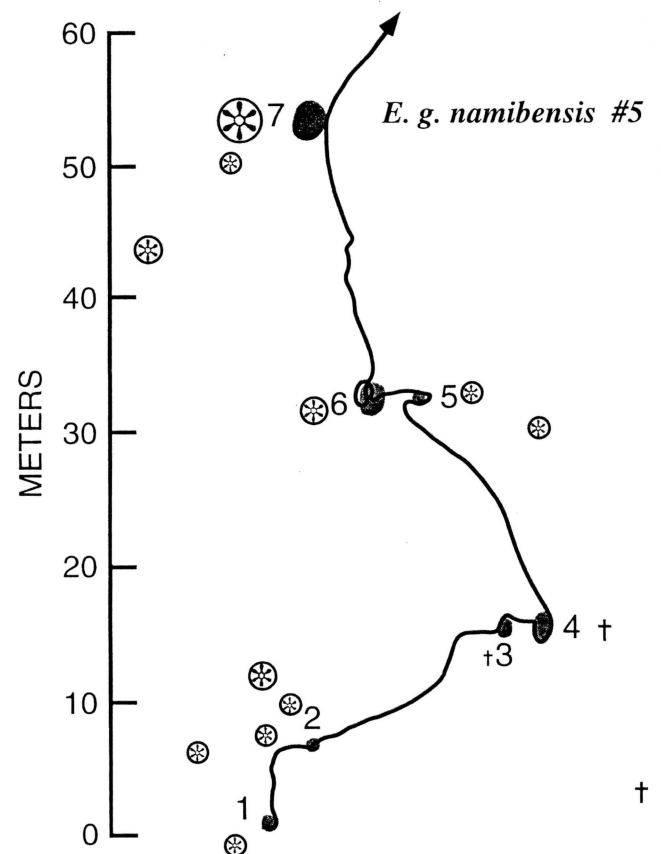

FIG. 3. Representative segment of the foraging trail of golden mole No. 5. The mole visited the seven numbered hummocks (oval shaded areas) following the trajectory indicated. Each visited hummock showed visible signs of burrowing by the mole. Symbols indicate hummock size and state of its dune grass: ✳Large live; ✲Medium live; ✱Small live; †Medium dead; †Small dead.
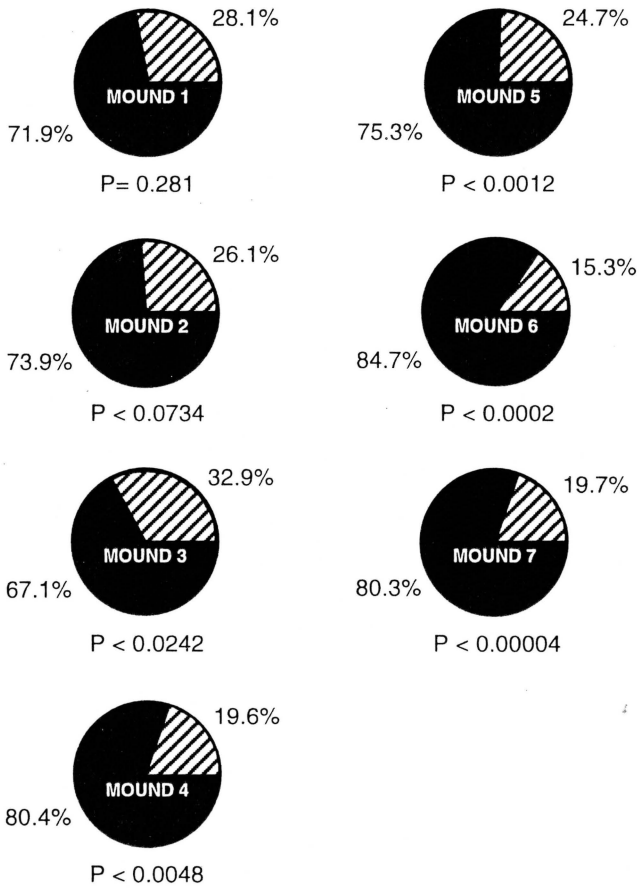
FIG. 4. Pie charts for seven hummocks visited by mole No. 5 during the evening of Nov. 15, 1993. Each chart indicates the percentage of a circle that corresponds to the total angle subtended by all other mounds within a 30-m radius of the visited hummock. The *p*-values for each hummock indicate the cumulative probabilities that random foraging would result in the mole encountering seven consecutive hummocks given the actual hummock configuration.

velocity amplitude spectra shown in Fig. 5A. The spectrum recorded on the flat shows a relatively low-amplitude peak at ca. 120 Hz, whereas the spectral peak recorded from the mound is 17 dB greater in amplitude and centered at 310 Hz. The difference spectrum (Fig. 5B) exhibits a peak frequency at 300 Hz with a relative magnitude above background noise of nearly 30 dB.

Geophone measurements made in the vicinity (<0.5 m) of a visited hummock often produced records that contained clicks, scratches, pops, and other transient waveforms (e.g., Fig. 6A). These were low-amplitude signals, not generally measurable at distances greater than about 1 m from a hummock. Fourier transforms of these transient waveforms revealed, not surprisingly, broad band velocity amplitude spectra, typically exhibiting a single spectral peak at frequencies below 50 Hz (Fig. 6B). On most nights, wind velocities varied from near 0 m/s at ground level to 3.8 m/s at 2 m above the ground during the hours between 2200 and 0100. Typical velocities were 1–3 m/s.

DISCUSSION

The Use of Seismic Signals by the Namib Golden Mole

Preliminary results from this study do not support the premise that golden moles forage randomly and that encounters with food

resources are purely stochastic events. Rather, our data suggest an alternative working hypothesis, namely that the golden mole exhibits sensory-guided foraging behavior. Observations that support this premise are that 1) segments of foraging paths between visited hummocks are remarkably straight (Fig. 3); 2) mounds generate seismic signals that are nearly 30 dB greater in amplitude than those from the desert flats (Fig. 5). We suggest that wind blowing the dune grass on the hummocks could set up vibrations in the hummocks that would result in a relatively strong low-frequency emitted signal. Hummocks would then act as seismic beacons for the golden moles that would be detectable from distances corresponding to typical interhummock distances of 20–25 m. More measurements are needed to confirm or deny this postulate; 3) once the mole is within ca. 1 m of a hummock, prey-generated sounds are detectable as short, click- or pop-like signals; 4) random foraging would result in extremely low encounter rates with individual hummocks, and even lower encounter rates with a succession of hummocks; and 5) the number of headdips increases in the vicinity of a hummock. This may constitute the terminal phase of prey detection by the mole, in which more sampling per unit foraging distance is necessary as the active hummock is approached. Other behavioral observations consistent with this hypothesis are: stomach content analysis of golden moles shows that termites are the principal component of their diet [13]; the mean frequency of occurrence of termite workings was 76% under the plants on the hummocks compared to 9% away from the hummocks [13]; and that we could hear and record distinct popping sounds at distances up to 1 m from some mounds (Fig. 6). The latter observation is consistent with the statement by Fielden et al. [13], that the mole's ability to detect prey is effective over short distances only. These sounds diminished in amplitude as the geophone was moved farther from the mound. It is likely that these are prey-generated sounds. We did not identify their source; but if they were not generated by insects, they still could serve as seismic beacons for mound localization.

In addition, it has long been known that the malleus of the *Chrysochloridae* is hypertrophied [5,8,14,20]. In a study of the middle ear ossicles of Chrysochlorids, von Mayer et al. [20] found that (a) the malleus of *Eremitalpa granti* composed the highest percentage (96.8%) of total ossicular mass of the 10 species
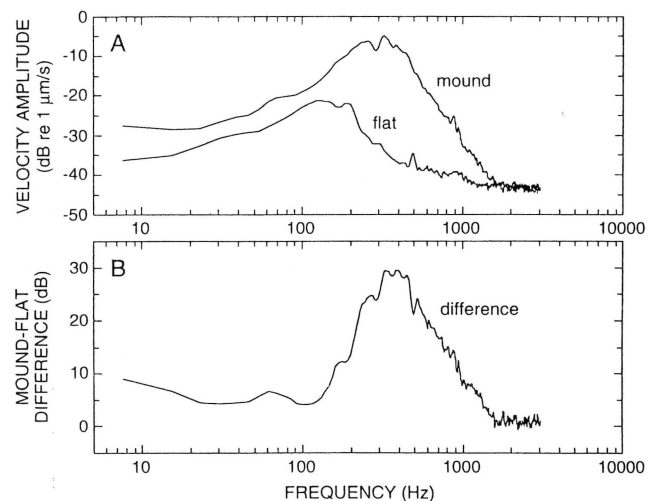

FIG. 5. (A) Typical velocity amplitude spectra for geophone recordings made from the top of a medium-size hummock (see text) and from the flat sand. (B) Difference between the two spectra shown in A.
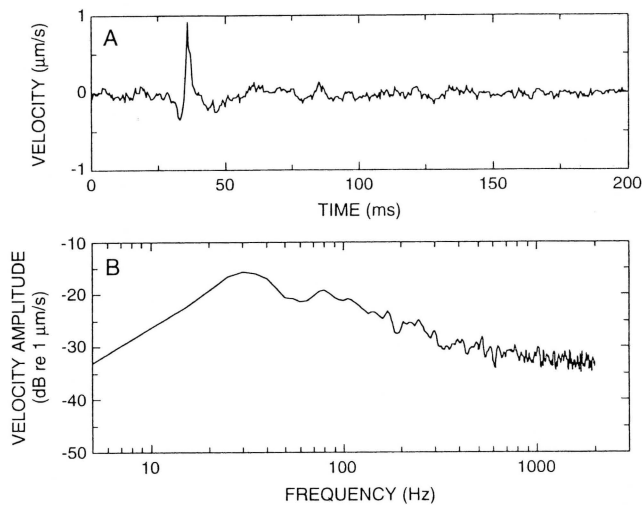
FIG. 6. (A) Velocity waveform recorded in the vicinity of a hummock visited by a golden mole. The click-like signal was most likely produced by termites (*Psammotermes*) inhabiting the hummock. (B) Velocity amplitude spectrum of the waveform in A. The spectrum exhibits peak energy between 30 and 40 Hz.

studied, and (b) the mean mass of the malleus in this species (45.1 mg) is greater than the mean mass of the malleus in *Homo sapiens* (27.5 mg) despite the enormous difference in mean body weight between the two species: 20 g, $n = 16$ [11] vs. 70,000 g! Functionally, the Chrysochlorids appear to be low-frequency specialists; and considering their fossorial nature, it is likely that golden moles hear through substrate conduction [20]. Our data are entirely consistent with this hypothesis.

Comparison with Seismic Communication in the Cape Mole-Rat

Georychus capensis is a subterranean rodent in the family *Bathyergidae* that inhabits underground burrows in sandy clay soils in its natural habitat, the Cape Province of South Africa. They exhibit a mean body weight of 181 g [1] with a maximum of 360 g [28]. Males and females construct complex tunnel systems of approximately 130 m length and mean diameter 10 cm. *Georychus* burrow systems approach within 1 meter of each other and appear to be evenly spaced [1,7], as has been reported for other fossorial rodents [26]. Both seismic and auditory signals were tested for their propagation characteristics in a field study of the Cape mole-rat. This solitary animal is entirely fossorial and apparently communicates with its conspecifics by drumming its hind legs on the burrow floor. Auditory signals attenuate rapidly in the substrate, whereas vibratory signals generated in one burrow are easily detectable in neighboring burrows. That footdrumming of both males and females is detected as a seismic communication signal by these animals is supported by the combination of 1) measurements of propagated soil-borne vibration between *Georychus* burrows that are significantly above the background noise level; 2) vanishingly low levels of propagated air-borne signals that are indistinguishable from background noise measured in an adjacent burrow; 3) saliency of the vertically polarized component of the vibration after transmission in soil over distances approximately corresponding to those between burrows; 4) complexity of the seismic signals that may relay both presence and sex of the individual; and 5) behavioral data indicating females of *Georychus* detect these seismic signals [1,23].

Although these results do not preclude the reception of the airborne component of the signal by *Georychus*, they are consistent with the observation that *Spalax* ignores acoustic portions of the thump signal in the laboratory and responds only to its seismic component [25]. It is likely that the acoustic characteristics of the underground habitat may explain the generally poor sensitivity exhibited by most fossorial forms, while retaining good sensitivity to low frequencies [16].

It is reasonable to assume that *Eremitalpa, Georychus,* and other subterranean forms have evolved specialized adaptations for detection of low-frequency, airborne, and substrate-borne vibrations. That this is the case is known for several species of mole-rats. For example, it has been stated that the Zambian species of *Cryptomys* exhibits an acoustic fovea, in which a disproportionately large fraction of the cochlea is dedicated to the frequency range between 0.6–1.0 kHz [21]. More recent evidence, however, questions the concept of acoustic fovea in *Cryptomys*, because it was shown that the presence of frequency expansion does not necessarily lead to enhanced mechanical tuning in the cochlea [18]. A recent analysis of the vocalizations of a Zambian species of mole-rat (*Cryptomys*) revealed that all sounds occur in a low and middle frequency range that match the hearing range reported from other investigators [6]. But none of these studies directly addresses the issue of sensitivity of mole-rats to substrate-borne vibrations such as has been demonstrated neurophysiologically in several species of nonmammalian vertebrates [2–4,15,19,22,27]. Given that *Eremitalpa* appears to rely on seismic signals for navigation toward prey during foraging, and that *Georychus* depends on vibrational cues for communication between conspecifics, one might predict that these fascinating fossorial mammals would be a veritable neuroethological gold mine for the study of neural and structural adaptations used for detection of substrate-borne vibrations.

REFERENCES

1. Bennett, N. C.; Jarvis, J. U. M. The reproductive biology of the Cape mole-rat, *Georychus capensis* (Rodentia, Bathyergidae). J. Zool. Lond. 214:95–106; 1988.
2. Christensen–Dalsgaard, J.; Jorgensen, M. B. The response characteristics of vibration-sensitive saccular fibers in the grassfrog, *Rana temporaria*. J. Comp. Physiol. 162:633–638; 1988.
3. Christensen–Dalsgaard, J.; Jorgensen, M. B. Sound and vibration sensitivity of VIIIth nerve fibers in the grassfrog, *Rana temporaria*. J. Comp. Physiol. 179:437–445; 1996.
4. Christensen–Dalsgaard, J.; Narins, P. M. Sound and vibration sensitivity of VIIIth nerve fibers in the frogs *Leptodactylus albilabris* and *Rana pipiens pipiens*. J. Comp. Physiol. 172:653–662; 1993.
5. Cooper, F. C. On the ear region of certain of the Chrysochloridae. Philos. Trans. R. Soc. [Biol] 216:265–283; 1928.
6. Credner, S.; Burda, H.; Ludescher, F. Acoustic communication underground: Vocalization characteristics in subterranean social mole-rats (*Cryptomys sp.,* Bathyergidae). J. Comp. Physiol. 180:245–255; 1997.

7. Davies, K. C.; Jarvis, J. U. M. The burrow systems and burrowing dynamics of the mole-rats *Bathyergus suillus* and *Cryptomys hottentotus* in the fynbos of the south-western Cape, South Africa. J. Zool. Lond. 209:125–147; 1986.

8. Doran, A. The mammalian ossicula auditus. Trans. Linn. Soc., Series 11, Zool. 1, part VII; 1878.

9. Dubost, G. Les mammifères souterrains. 1. L'adaptation morphologique à la vie souterraine. Rev. Écol. Biol. Sol. 5:99–133; 1968.

10. Fielden, L. J. Adaptive biology and ecology of the Namib Desert golden mole, *Eremitalpa granti namibensis.* PhD dissertation, University of Natal, Pietermaritzburg, RSA; 1989.

11. Fielden, L. J. Home range and movements of the Namib Desert golden mole, *Eremitalpa granti namibensis* (Chrysochloridae). J. Zool. Lond. 223:675–686; 1991.

12. Fielden, L. J.; Hickman, G. C.; Perrin, M. R. Locomotory activity in the Namib Desert golden mole, *Eremitalpa granti namibensis* (Chrysochloridae). J. Zool. Lond. 226:329–344; 1992.

13. Fielden, L. J.; Perrin, M. R.; Hickman, G. C. Feeding ecology and foraging behaviour of the Namib Desert golden mole, *Eremitalpa granti namibensis* (Chrysochloridae). J. Zool. Lond. 220:367–389; 1990.

14. Findlay, G. H. The development of the auditory ossicles in the elephant shrew, the tenrec and the golden mole. Proc. Zool. Soc. Lond. 114:91–99; 1944.

15. Hartline, P. H. Physiological basis for detection of sound and vibration in snakes. J. Exp. Biol. 54:349–371; 1971.

16. Heffner, R. S.; Heffner, H. E.; Contos, C.; Kearns, D. Hearing in prarie dogs: Transition between surface and subterranean rodents. Hear. Res. 73:185–189; 1994.

17. Holm, E. Contribution to the knowledge of the biology of the Namib Desert golden mole *Eremitalpa granti namibensis* Bauer & Niethammer 1959. Scient. Pap. Namib Desert Res. 41:37–42; 1969.

18. ████ M.; Frank, G.; Burda, H.; Müller, M. Acoustic distortion products from the cochlea of the blind African mole rat, *Cryptomys* spec. J. Comp. Physiol. 178:427–434; 1996.

19. Koyama, H.; Lewis, E. R.; Leverenz, E. L.; Baird, R. A. Acute seismic sensitivity in the bullfrog ear. Brain Res. 250:168–172; 1982.

20. Mayer, A. von; O'Brien, G.; Sarmiento, E. E. Functional and systematic implications of the ear in golden moles (Chrysochloridae). J. Zool. Lond. 236:417–430; 1995.

21. Müller, M.; Laube, B.; Burda, H.; Bruns, V. Structure and function of the cochlea in the African mole rat (*Cryptomys hottentotus*): Evidence for a low frequency acoustic fovea. J. Comp. Physiol. 171:469–476; 1992.

22. Narins, P. M.; Lewis, E. R. The vertebrate ear as an exquisite seismic sensor. J. Acoust. Soc. Am. 76:1384–1387; 1984.

23. Narins, P. M.; Reichman, O. J.; Jarvis, J. U. M.; Lewis, E. R. Seismic signal transmission between burrows of the Cape mole-rat, *Georychus capensis.* J. Comp. Physiol. 170:13–21; 1992.

24. Nolte, H. van der Vyver. The external morphology and functional anatomy of the cranial region in the Namib golden mole *Eremitalpa granti namibensis* Bauer & Niethammer. MSc thesis, University of Pretoria, Pretoria, RSA; 1968.

25. 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. Anim. Behav. 35:1249–1251; 1987.

26. Reichman, O. J.; Whitman, T. G.; Ruffner, G. Adaptive geometry of burrow spacing in two pocket gopher populations. Ecology 63:687–695; 1982.

27. Ross, R. J.; Smith, J. J. B. Detection of substrate vibrations by salamanders: Inner ear sense organ activity. Can. J. Zool. 56:1156–1162; 1978.

28. Smithers, R. H. N. The mammals of the southern African subregion. Pretoria: University of Pretoria; 1983.