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The golden mole middle ear: a sensor for airborne and substrate-borne vibrations

Peter M. Narins, Urban B. Willi

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Abstract

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. When foraging, the Namib Desert golden mole, *Eremitalpa granti namibensis*, typically moves between sand mounds topped with dune grass that contain most of the living biomass in the Namib Desert. Foraging trails are punctuated with characteristic sand disturbances in which the animal “head dips” under the sand, presumably to obtain a vibrational “fix” on the next mound to be visited. Playback experiments with substrate-borne vibrations suggest that in the absence of olfactory cues, golden moles are able to locate the food-containing mounds solely using vibrations generated by the wind blowing the dune grass. Based on middle ear anatomy, the ossicular mass distribution and the anchorage points, we have hypothesized that there are several de-

grees of freedom of the middle ear apparatus of *Chrysochloris asiatica*, a closely-related golden mole. A horizontal vibration, which drives the head laterally will excite the rotational mode ω_y , whereas a vertical vibration excites mode ω_z . We suggest that these two modes play the main role in inertial bone conduction in response to vibrational stimuli, since they depend on both the increased malleal mass and the displacement of its center of mass from the rotational axis. In addition to these two modes, we postulate that there is a third vibrational mode, namely the rotation of the ossicular chain about the long axis of the malleus (ω_x) in response to airborne stimuli. The transition between modes occurs between 200–300 Hz. Laser Doppler vibrometric measurements of the malleus head in response to vibrational stimuli in *Chrysochloris* reveal peak sensitivity to frequencies below 300 Hz. Functionally, golden moles appear to be low-frequency specialists, and it is likely that they detect prey principally through substrate conduction.

1. Introduction

Golden moles (Chrysochloridae), members of the Afrotherian clade, are small (7.6–23.5 cm) fossorial mammals endemic to sub-Saharan Africa. They exhibit a suite of specializations for life underground, are image blind (Fielden 1991) and they are “thought to rely heavily on the sense of smell and hearing” like other fossorial species (Burda et al. 1990; Francescoli 2000). The lack of light and the poor propagation of airborne sound underground limit the importance and reliability of vision and hearing in these species. The presence of conspecifics, prey and most predators is conveyed via substrate vibrations, and long-distance communication via substrate-borne signaling is considered the principal communication modality in subterranean mammals (Nevo et al. 1991).

The proposed means by which substrate vibrations are detected in some golden mole species is inertial bone conduction. This mechanism implies the presence of a mass that impedes ossicular motion while the skull vibrates, and thereby induces relative motion between stapes and skull – an effective stimulus for the inner ear.



Fig. 1 The Cape golden mole, *Chrysochloris asiatica* (Photo: Gary Bronner)

The Cape golden mole (*Chrysochloris asiatica*) is a member of the family Chrysochloridae, within which a variety of middle ear adaptations are found, and is the subject of our middle ear measurements (Fig. 1). Like all mammals, golden moles possess a tympanic membrane that vibrates in response to airborne sounds. Attached to its inner surface is the distalmost of the three auditory ossicles – the malleus, which in the case of the Cape golden mole, is massively hypertrophied. An overview of golden mole middle ear morphology is given by Mason (2003a) and Fig. 2 illustrates five examples from his study.

The most obvious variations in these middle ears are the relative sizes and shapes of the mallei. Among the hypertrophied middle ear types, the malleus head shows two distinct forms: spherical or ball-shaped in *Eremitalpa* and *Chrysospalax* and club-shaped in *Chrysochloris* and *Cryptochloris*. The need for additional mass in order to detect substrate vibrations by means of inertial bone conduction seems straightforward, but what are the functional differences between the two malleus forms?

Hearing in golden moles has not been studied, but a subterranean lifestyle and poor audition are often coupled. One golden mole species that exhibits a spherical hypertrophied malleus is the Namib Desert golden mole (*E.g. namibensis*) and according to observations by Van der Vyver Nolte (1968), it shows “little to no response to sounds”. This animal is sensitive to substrate vibrations and detects and localizes dune grass-topped hummocks containing termites and other arthropods when foraging in the Namib Desert. It presumably uses a two-stage vibrational detection system such that at a distance, the animal detects the vertically-polarized Rayleigh waves emitted by the hummocks themselves in response to wind blowing the dune grass. Then when the golden mole is close to a hummock, it

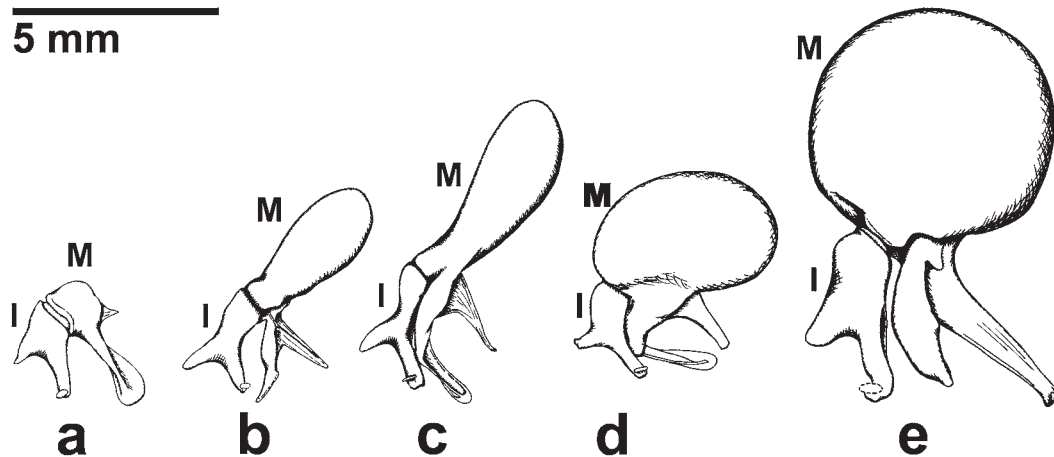


Fig. 2 Middle ear morphologies exhibited by five species of the golden mole family (Chrysochloridae). Only the malleus (M) and the incus (I) of (a) *Amblysomus hottentotus*, (b) *Chrysochloris stuhlmanni*, (c) *Chrysochloris asiatica*, (d) *Erimalpa granti namibensis* and (e) *Chrysospalax villosus* are shown; eardrums and stapes are omitted for clarity. From Mason (2003a and 2007)

can sense the low-level substrate vibrations generated by the prey items as they move through the hummock (Narins et al. 1997). Moreover, these animals are capable of localizing artificial vibrational sources in the absence of olfactory cues (Lewis et al. 2006). The Cape golden mole (*C. asiatica*) exhibits a club-shaped malleus head and, perhaps not coincidentally, clear acoustic interactions between captive *C. asiatica* individuals have been reported (Willi et al. 2006b). Based on observations and on physical considerations, the two distinct morphologies of hypertrophied mallei may reflect differences in the detection abilities of these species to airborne sound.

2. Materials and methods

2.1 Animals

Cape golden moles (*Chrysochloris asiatica*) were caught in the field near Cape Town (RSA) and after at least two weeks of captivity, shipped to the University of California, Los Angeles (UCLA). Animals were housed individually, but they rarely, if ever, vocalized under these conditions. To evoke vocalizations, two animals were placed in the same tank. When they surfaced, a microphone (Brüel & Kjaer, 4134, Naerum, Denmark) placed 0.5 m above the tank recorded acoustic interactions.

2.2 Stimulation with airborne sound and substrate-borne vibrations

After surgical preparation, the caudal portion of the animal's skull was attached to an aluminum block which was fixed to a vibra-

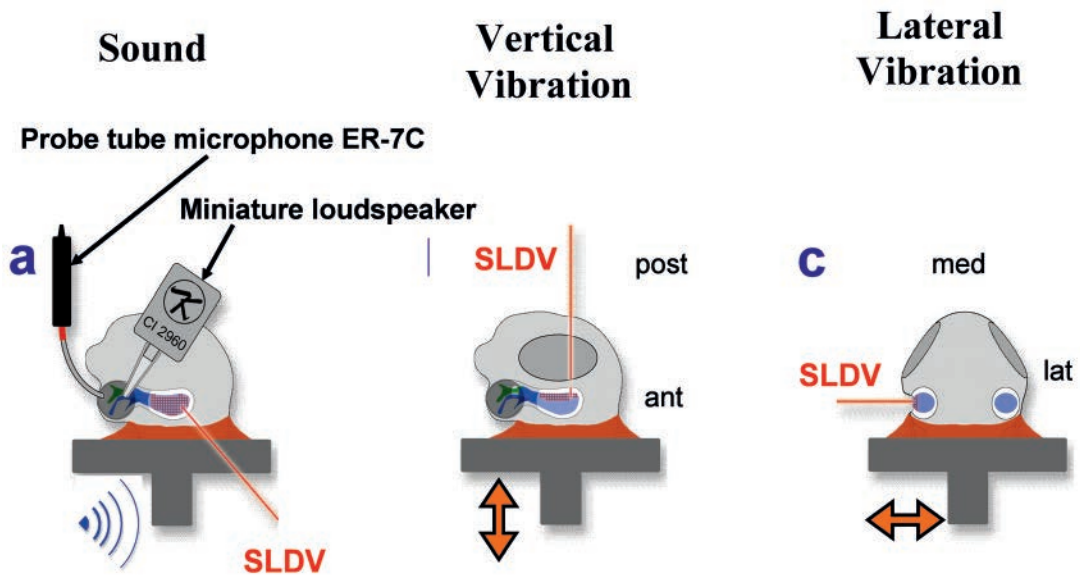


Fig. 3 Caudal portion of the skull of *C. asiatica* mounted on vibration exciter. The middle ear is stimulated acoustically with a miniature loudspeaker and the sound pressure level is recorded with a probe tube microphone close to the tympanic membrane. Vibration exciter stimulating skull in (b) vertical direction, and (c) in horizontal direction. The long axis of the mallei is oriented horizontally, corresponding to that during head dipping

tion exciter (Brüel & Kjaer, 4809, Naerum, Denmark). The middle ear may be stimulated acoustically with a miniature loudspeaker (MS, Knowles, CI-2960) during which the sound pressure level is recorded with a probe tube microphone (PTM, Etymotic Research, ER-7C) close to the tympanic membrane (Fig. 3a). Alternatively, this setup allows for vertical (Fig. 3b) or horizontal (Fig. 3c) vibrational stimulation.

2.3 Velocity measurements

The dynamic response of the malleus was measured by means of Scanning Laser Doppler Vibrometry (SLDV). The system (PSV-300, Polytec, Waldbronn, Germany) allows automated velocity measurements at multiple points (Fig. 4). It includes a built-in video camera (FCB-IX47P, Sony, Minokamo, Japan), which is optically in-line with the la-

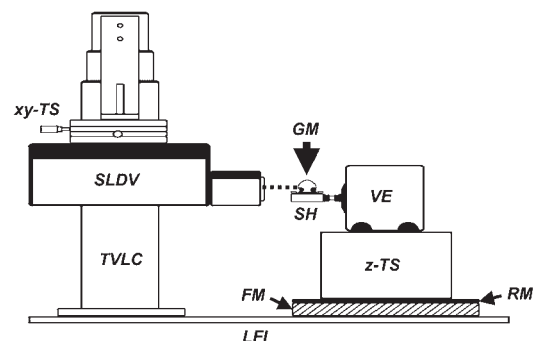


Fig. 4 Airborne/vibrational stimulation apparatus. Golden mole (GM) skull is placed on the sample holder (SH) and the beam from the Scanning Laser Doppler Vibrometer (SLDV) is focused on the head of the malleus. Beam positioning is facilitated by two translation stages (xy-TS and z-TS) and the telescopic vertical lifting column (TVLC). The skull is stimulated by the vibration exciter (VE). RM = rubber mat; FM = open cell foam mat. See text for remaining abbreviations. Modified from Willi et al. (2006b) with permission

ser beam, and displays the selected measurement area on the computer monitor enabling grid selection, positioning and focusing of the laser beam as well as facilitating the positioning of the specimen relative to the SLDV. Such alignment is achieved by the telescopic vertical lifting column (TGC 8AWD3 Magnetic, Liestal, Switzerland) and an XY-translation stage (Newport, Irvine, CA, USA) in two perpendicular directions within the horizontal plane. During velocity measurements in response to both airborne and vibrational stimulation, the laser beam was in line with the medio-lateral axis of the skull, and except for the placement of the microphone and the speaker for acoustic stimulation, the two setups are identical (Fig. 4). The jack that supports the vibration exciter was placed on a rubber mat (6 mm thick) and an open-cell foam mat (25 mm thick) in order to attenuate any vibrations reaching the SLDV during vibrational stimulation. The effect of ambient vibrational disturbances was attenuated further by mounting the entire setup on a high-performance laminar-flow isolator (LFI, Newport, RS-4000, Irvine, CA, USA).

A measurement grid comprising 20–40 measurement points is superimposed on the image of the accessible distal portion of the malleus head and parts of the skull. A scan of these 20–40 points was made. Data acquisition occurred at a frequency resolution of 1 Hz for both acoustic and vibrational stimulation over the corresponding frequency band. Both amplitude and phase of the measured velocities – in case of acoustic stimulation also the amplitude of the sound pressure – were averaged five times for each measurement point.

2.4 Alignment of coordinate system

Following the recording of responses to both the airborne and vibrational stimuli, the specimen holder (aluminum block) with

the skull tightly affixed to it was removed from the vibration exciter. The structures that masked the proximal portion of the ossicular chain containing the short process of the incus (SPI) and the lenticular process of the incus (LPI) during the experiment were carefully removed. All middle ear structures were preserved in order to ensure that the ossicular chain maintained its position relative to the skull. The skull was then repositioned in the measurement setup and aligned to its previous position. The built-in video camera then captured and stored an image of the entire ossicular chain.

During a laser scan, the SLDV-system assigns x- and y-coordinates to each point on the measurement grid. The position and

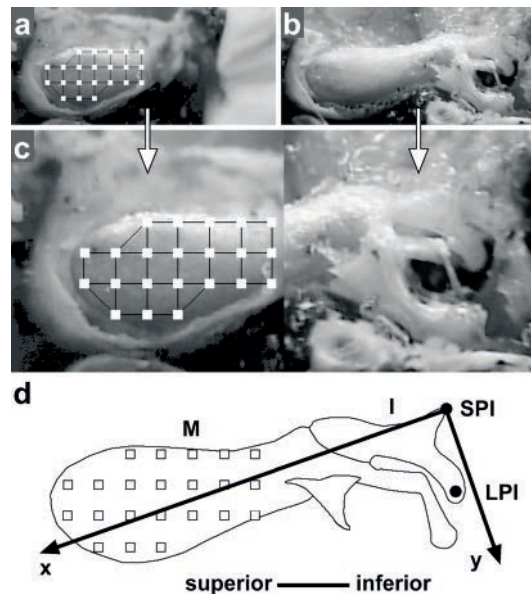


Fig. 5 Superimposition of (a) pre- and (b) post-experimental images. By superimposing the two images all structures of the ossicular chain can be referred to the coordinate system of the measurement grid (c). (d) The coordinate system is aligned to anatomical landmarks e.g., the short process of the incus (SPI), and the coordinates of the lenticular process of the incus (LPI) were determined. Modified from Willi et al. (2006 b) with permission

RM and FM are now explained in the legend, as suggested.

alignment of this coordinate system was scaled and adjusted to anatomical landmarks. The origin of the coordinate system was set at the ligament of the short process of the incus (SPI), whereas the x-axis was coaxial with the long axis of the malleus and the y-axis pointed towards the lenticular process of the incus (LPI). Superimposing the pre- and post-experimental images (Figs. 5a–c) allowed us to refer the coordinates of the measurement grid and the coordinates of the SPI and the LPI to the same coordinate system (Fig. 5d).

3. Results

We found that the long process of the incus or LPI (the attachment point to the stapes) in the golden mole middle ear responded differently to vibrational and airborne stimulation. That is, this structure's resonant frequencies for vibrational stimuli are below 200 Hz, whereas its resonant frequencies for airborne stimuli are in the range of 2 kHz.

3.1 Ossicular response

The medio-lateral motion of the LPI was calculated from the velocity measurements for the same five right ears for vibrational and airborne stimulation. The dataset was reduced to these five ears since the LPI motion was successfully reconstructed for them in response to both modalities. All responses were shifted along the logarithmic frequency axis to align the resonant frequencies at 150 Hz for substrate-borne stimulation and at 2 kHz for airborne acoustic stimulation, respectively.

For vibrational stimulation the resonant frequencies at the LPI were between 71 and

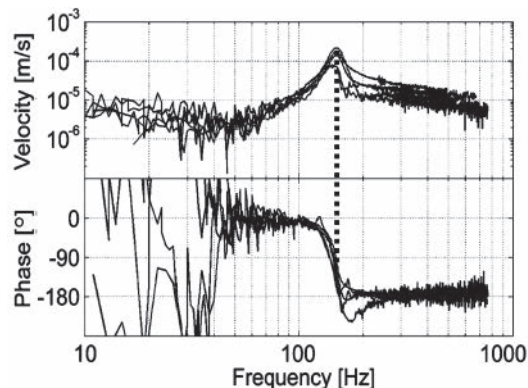


Fig. 6 Ossicular response to medio-lateral vibrational stimulation. All five responses were shifted along the logarithmic frequency scale to align all resonant frequencies at 150 Hz. Note that for frequencies below resonance, the incus and the skull are moving in phase, whereas above resonance these two structures move in antiphase. Modified from Willi et al. (2006b) with permission

200 Hz (mean: 135.7 ± 49 Hz). Below resonance, relative motion between the skull and incus is small and the two structures move in phase; above resonance, they move out of phase by 180° (Fig. 6).

In response to airborne acoustic stimuli the LPI shows a resonance between 1.3 and 2.2 kHz (mean: 1.76 ± 0.43 kHz). At resonance, velocity amplitudes reach $1.4 \pm 0.6 \times 10^{-4}$ m/s. In four out of five specimens, a secondary resonance was observed between 100 and 200 Hz (mean: 145 ± 48 Hz) which coincides well with the resonant frequency in response to the vibrational stimulation (Fig. 7).

In order to visualize the ossicular motion pattern in response to airborne and substrate-borne vibrations, we used the reconstructed iso-velocity amplitude maps generously covering the ossicular chain (Fig. 8). The maps represent the results obtained from the left ear of one animal.

At low frequencies (115 and 120 Hz, respectively) the motion patterns for vibra-

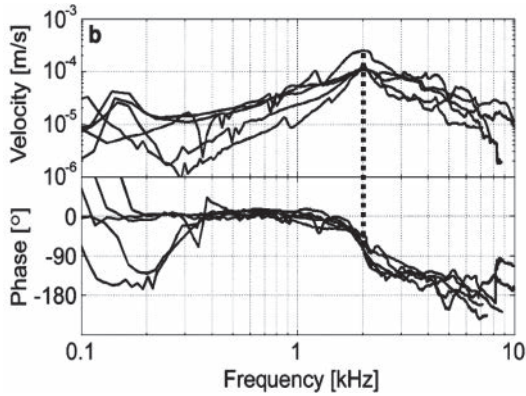


Fig. 7 Ossicular response to acoustic stimulation. All five responses were shifted along the logarithmic frequency scale to align all resonant frequencies at 2 kHz. The phase measurement shows that for frequencies below resonance, the incus and the skull are moving in phase, whereas for high frequencies (>5 kHz), these two structures move in antiphase. Modified from Willi et al. (2006b) with permission

tional and airborne stimulation resemble each other (Fig. 8a, b). The rotatory axis passes through the SPI and is nearly perpendicular to the long axis of the malleus. For vibrational stimulation, this axis is maintained up to 600 Hz. However, with increasing frequency of the acoustic signal, this rotatory axis turns clockwise and at the resonant frequency (1.4 kHz) this axis is in line with the long axis of the malleus (Figs. 8d–e). The orientation of the rotatory axis does not change uniformly with frequency: Between 120 and 200 Hz, it rotates by about 12° , whereas between 200 and 300 Hz the axis performs a clockwise rotation of about 75° . After this rapid change it takes another 1.1 kHz in order to reach the mode at which the ossicular chain rotates precisely through the long axis of the malleus head. This mode is maintained up to about 6 kHz, above which there is a transition to the next higher mode (data not shown).

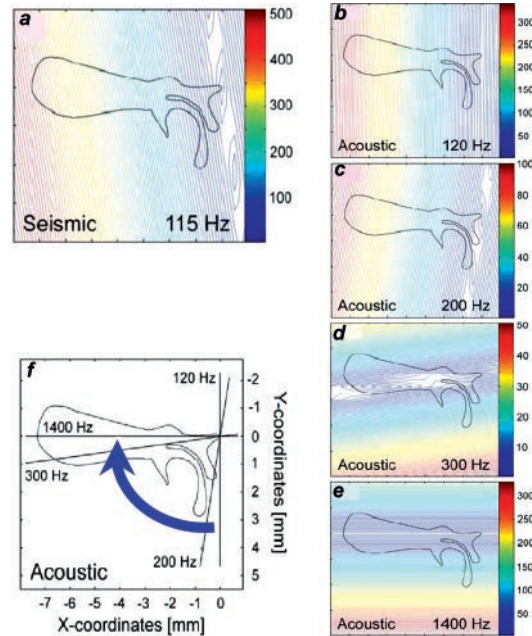


Fig. 8 Motion patterns of the malleus and incus in response to (a) vibrational and (b–e) airborne stimulation at different frequencies indicated by iso-velocity lines. The rotatory axis for each mode is defined by the iso-velocity lines of smallest amplitudes (center of blue lines). At low frequencies the rotatory axis is almost perpendicular to the long axis of the malleus (a–c), whereas with increasing frequency it approaches the long axis of the malleus (d, e). The transition between modes occurs between 200–300 Hz (f). Modified from Willi et al. (2006b) with permission

3.2 Vocalizations

Two distinct types of calls were recorded: chirps and noise bursts. Noise bursts varied in duration between 0.1–0.2 s and covered frequencies from 1–22 kHz containing most energy around 1.5 kHz (fundamental), between 4–5 kHz (third harmonic) and between 10–20 kHz (Fig. 9). The vocalization in Fig. 9 shows a short transition between a chirp (1) and a noise burst (2) but often these two types of calls are separated in time. Chirps appear as short pulses of 0.02 s but

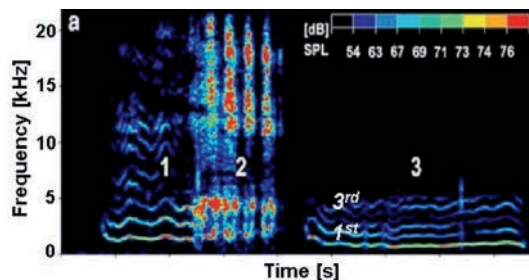


Fig. 9 Spectrogram of calls from *Chrysochloris asiatica*. During handling, the animals emitted two distinct types of sounds: chirps (call component 1 and call 3, and noise bursts (call-component 2). The two vocalizations clearly differ in the frequency band they cover and in their harmonic structure. Modified from Willi et al. (2006b) with permission

also with durations up to 0.5 s. They often contain 3–5 harmonics with most energy contained in the fundamental. High numbers of harmonics (> 10) were only observed when the chirp ended with a noise burst (Willi et al. 2006b).

4. Discussion

That the hypertrophied malleus of the golden mole most likely comprises an adaptation for vibration detection has been discussed by several authors (Henson 1974; Kuyper 1984; Hickman 1990; Lombard and Hetherington 1993; Mason 1999; Mason and Narins 2002; Mason 2003b; Mason and Narins 2010). Moreover, the foraging behavior of the Namib Desert golden mole (*E.g. namibensis*), which also exhibits this middle ear specialization, puts this sensory modality in a meaningful ecological context (Fielden 1990; Narins et al. 1997).

4.1 Modes

The velocity profiles shown in Fig. 8 demonstrate that the ossicular chain of *C. asiatica* exhibits two distinct modes of rotation within the frequency range tested (< 10 kHz). For both vibrational modes, the malleus rotates about an axis that passes through the SPI, and the rotatory axes of the two modes are nearly perpendicular to one another. At low frequencies (~100–200 Hz), be it in response to airborne sound or substrate-borne vibration, the club-shaped malleus head oscillates about the SPI showing maximum amplitudes at its superior end and the rotatory axis is nearly perpendicular to the long axis of the malleus (first mode). In response to higher frequency sounds (~1–6 kHz), the rotatory axis runs parallel to the long axis of the malleus head (second mode). This is not the first report of a middle ear exhibiting such distinct modes. Fleischer (1978) proposed two rotatory axes of the microtype middle ear, one in response to low and one in response to high frequencies, the two axes being perpendicular to one another. Although his ideas were critically discussed by Saunders and Summers (1982) based on velocity measurements on the mouse middle ear, Fleischer's idea and considerations clearly apply to the middle ear of *C. asiatica*.

4.2 Two vibrational modes of the golden mole malleus

The motivation for this study was the question of the functional differences between the two types of hypertrophied mallei, club-shaped and ball-shaped. We showed that the club-shaped malleus in the middle ear of *C. asiatica* responds in two distinct modes: a rotation about an axis perpendicular to the long axis of the malleus (first mode) and a rotation through the long axis of the malleus (second mode). What predictions can we

I don't think vocalizations during handling are necessarily unusual, since they also emitted chirps and noise bursts when left alone. It's just that it was easier to record these vocalization while handling them (they were much more frequent).

I couldn't agree more!

make about the behavior of the ball-shaped malleus of *E. granti* or *C. villosus* (see Fig. 2)?

The hypertrophied mallei have been experimentally shown to respond to vibrational disturbances in *C. asiatica* (Willi et al. 2006a,b; Narins and Willi 2007) and there is good evidence that *E. g. namibensis* relies on the perception of substrate vibrations as well (Fielden 1990; Narins et al. 1997; Mason and Narins 2001, 2002, 2010; Mason 2010;). Therefore both middle ear designs are expected to respond to vibrations. In addition, data suggest that the middle ear of *C. asiatica* is also responsive to airborne sound. What predictions can we make about the middle ear of *E. g. namibensis* with respect to airborne sound detection?

The vibrating skull is the driving force for the middle ear and the displaced center of

mass of the malleus leads to stapes movements through its inertia (Fig. 10). When acoustically stimulated, the skull is not in motion and the force driving the ossicular chain is passed from the tympanic membrane to the manubrium. This results in the first vibrational mode (Fig. 10) of the malleus at low frequencies. With increasing frequency, though, the mass of the malleus increasingly impedes this mode.

In order to partially overcome the impedance of the mass, the middle ear design allows the ossicles to respond in the second mode, which has its rotatory axis passing through the center of mass. This is possible for both middle ear designs, the club-shaped and ball-shaped malleus. However, in the second mode the two designs differ significantly in their angular moment of inertia defined by:

$$I_2 = \frac{1}{2} m r^2 \quad (1)$$

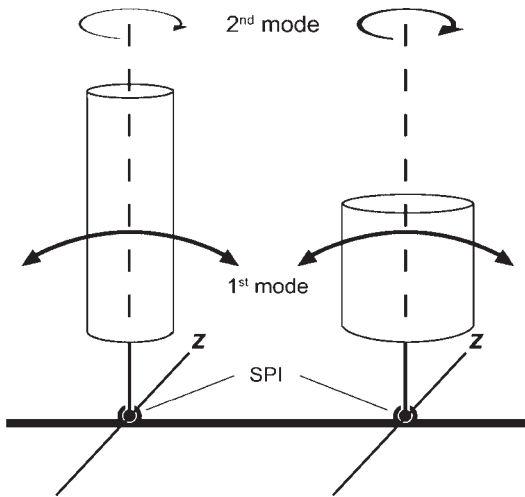


Fig. 10 Simplified schema of the two hypertrophied malleus types represented by cylinders and approximating the club-shaped (left) and ball-shaped (right) malleus for *C. asiatica* and *E. g. namibensis*, respectively. The thickness of the arrows indicates the angular moment of inertia of the ossicular chain in response to low-frequency vibrational stimulation (1st mode) and high-frequency acoustic stimulation (2nd mode). SPI: tip of the short process of the incus. Modified from Willi et al. (2006b) with permission

where I_2 is the angular moment of inertia of the second mode (Fig. 10), m is the mass of the cylinder and r its radius. The thickness of the arrows in Fig. 10 indicates the relative magnitude of the angular moment of inertia. If the angular moment of inertia for the first mode is identical in both designs, then that for the second mode is necessarily different, being larger for the ball-shaped malleus (Fig. 10, right model) compared to the club-shaped malleus (Fig. 10, left model). As a result the responsiveness of the club-shaped malleus would exceed that of the ball-shaped malleus. When the radius is doubled, the angular moment of inertia is quadrupled. An extreme version of a large malleal radius is found in the middle ear of *Chrysospalax villosus* (Fig. 2e) but in *E. g. namibensis* it is also quite large compared to that of *C. asiatica*.

A ball-shaped design is volume efficient, implementing a vibration detector occupying minimal space. In order to allow the

middle ear to respond to higher frequencies with a second mode, the radius of the malleus head is reduced. In *C. asiatica* the radius of the malleus is reduced but it also increases towards the distal end, which shifts the center of mass further away from the anchorage point (SPI). The further away the center of mass is shifted in the club-shaped malleus, the thinner the cylinder may become, while still maintaining the same angular moment of inertia as the ball-shaped design, since the angular moment of inertia for the first mode is determined by:

$$I_1 = \frac{1}{3} m l^2 \quad (2)$$

where I_1 is the angular moment of inertia of the first mode (Fig. 10), m is the mass and l is the distance of the center of mass from the suspension point (highly simplified model).

The unusual malleus morphology in the middle ear of *C. asiatica* has been shown to respond to substrate vibrations and airborne sound. Its design appears to be an elegant solution to the problem of how a middle ear can exploit increased ossicular inertia for the detection of low-frequency substrate vibrations at little cost to the animal's high-frequency airborne sound-detection capability.

Clearly, there are many fascinating questions that remain unanswered: Do the two vibrational modes of the golden mole malleus translate to disparate mechanical input to the inner ear via the stapes? Can the inner ear differentiate between these two separate inputs? How do the viscoelastic and other properties of the malleus confer frequency dependence on the middle ear? How do golden moles localize a vibrational source? This question is especially interesting since in *E.g. namibensis*, the mallei of the two ears are not parallel. This raises the exciting possibility of azimuth-dependent differential malleolar motion, a unique adaptation for vibrational localization in verte-

brates. Experiments are currently planned to test this intriguing hypothesis.

Acknowledgments

Thanks to Gary Bronner for supplying us with Cape golden moles for the middle ear measurements. We also thank the staff of the Division of Laboratory Animal Medicine at UCLA, particularly Dr. Marcelo Couto and Dr. Greg Lawson for their helpful collaboration. This research was supported by NIH grant no. DC00222 to PMN. All animal procedures were approved by the Animal Research Committee at the University of California, Los Angeles, USA.

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**Should be
Willi et al.
2006b. This
was fixed.**

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