Measuring airborne components of seismic body vibrations in a Middle-Asian sanddwelling Insectivora species, the piebald shrew (*Diplomesodon pulchellum*)

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SUMMARY

Self-produced seismic vibrations have been found for some subterranean rodents but have not been reported for any Insectivora species, although seismic sensitivity has been confirmed for blind sand-dwelling chrysochlorid golden moles. Studying the vocal behaviour of captive piebald shrews, *Diplomesodon pulchellum*, we documented vibrations, apparently generated by the whole-body wall muscles, from 11 (5 male, 6 female) of 19 animals, placed singly on a drum membrane. The airborne waves of the vibratory drumming were digitally recorded and then analysed spectrographically. The mean frequency of vibration was 160.5 Hz. This frequency matched the periodicity of the deep sinusoidal frequency modulation (159.4 Hz) found in loud screech calls of the same subjects. The body vibration was not related to thermoregulation, hunger-related depletion of energy resources or fear, as it was produced by well-fed, calm animals, at warm ambient temperatures. We hypothesize that in the solitary, nocturnal, digging desert piebald shrew, body vibrations may be used for seismic exploration of substrate density, to avoid energy-costly digging of packed sand for burrowing and foraging. At the same time, the piercing quality of screech calls due to the deep sinusoidal frequency modulation, matching the periodicity of body vibration, may be important for agonistic communication in this species.

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INTRODUCTION

Self-produced body vibrations have not yet been reported for insectivores (Hill, 2009), although the chrysochlorid golden moles may use seismic waves for detecting their prey (Mason and Narins, 2010). Some features of the golden mole biology, probably related to their somatosensory sensitivity (Mason and Narins, 2010) may also be found in Middle-Asian desert piebald shrews, *Diplomesodon pulchellum* (Lichtenstein 1823). These shrews forage nightly on invertebrates, lizards and spiders, dig out their prey from depths of 2–3 cm, dig their own burrows and cover distances of a few kilometres per night in search of food on the surface of shifting, loose or packed sand (Stalmakova, 1949; Dubrovskij et al., 2011). The piebald shrews are solitary, and most non-sexual contacts between two individuals are indifferent or agonistic (Dubrovskij et al., 2011).

When studying the vocal behaviour of captive piebald shrews, we occasionally noticed that some animals vibrated when held or when lifted up in their plastic pipe shelters. These vibrations resembled the mobile phone vibratory mode and apparently were produced in response to a change in the substrate under their feet. In addition, when examining acoustic recordings from piebald shrews for the presence of ultrasound and audible acoustics, we noticed deep repetitive sinusoid-like frequency modulation in their most intense audible vocalizations, strident screeches. To examine the body vibration and acoustics, we designed an experiment imitating the encounter of a shrew with a new, unknown substrate. This design was inspired by a previous study (Gould et al., 1964), where shrews were tested for exploratory audible or ultrasonic clicks on a disc raised above the ground. The purpose of the present study was to record and analyse spectrographically the airborne waves arising from seismic waves produced by a vibrating piebald shrew placed on a drum membrane, and to inspect the repetitive patterns of their screech calls.

MATERIALS AND METHODS Study site and subjects

Experiments were carried out on 19 (10 male, 9 female) captiveborn piebald shrews (4–6 generations in captivity) at the Scientific Department of Moscow Zoo, Moscow, Russia from 29 July to 20 August 2011. Four male and 5 female adults (2–12 months), and 6 male and 4 female subadults (34–43 days) were used. The animals were kept under a natural light regime at room temperature (24–26°C), singly in plastic cages of $32 \times 50 \times 40$ cm, with a bedding of sand and dry moss, various shelters and running rings, and received small insectivore chow and water *ad libitum*, with a control for obesity.

For all experiments, we adhered to published guidelines (ASAB, 2006). This study was approved by the Committee of Bio-ethics of Lomonosov Moscow State University (research protocol no. 2011-36).

Experimental design

We tested all 19 shrews for vibration, applying one test trial per animal. Additionally, we tested 3 females again 3–8 days after their previous test trials, in order to check whether the animals that produced body vibrations in their previous trial would be able to

2850 The Journal of Experimental Biology 215 (16)



Fig. 1. Vibratory drumming of a piebald shrew: (A) power spectrum and (B) waveform. An airborne sound, generated by a piebald shrew body vibration on the drum membrane, shows peak power at 160 Hz. The waveform reveals the vibration pulses; arrows depict the vibration period.

reproduce this behaviour in the subsequent trials. Thus, all males and 6 females were tested once, 2 females were tested twice and 1 female was tested three times, in a total of 23 test trials with the 19 subject shrews. All shrews were tested between 17:00 h and 19:00 h at temperatures of 24–26°C. A test trial lasted 2–10 min, depending on the behaviour of the animal. An animal was transferred manually from its home cage to the drum membrane (drum height 40 cm, drum membrane diameter 23.5 cm). The drum was standing in a large ($50 \times 70 \times 40$ cm) plastic container. If the animal jumped down before the end of the test trial, it was placed back on the membrane.

For sound recordings, we used a Pettersson D 1000X recorder with a built-in microphone (Pettersson Electronik AB, Uppsala, Sweden) and sampling rates of 192 kHz (14 trials) or 768 kHz (9 trials). The microphone was kept 5 cm from the centre of the drum membrane, which allowed recording of both the vocalizations of the animal under investigation and its body vibrations as amplified by the drum membrane. Each test trial was recorded as a wav-file. Additionally, we video documented some sample tests with a camcorder (Sony DCR-SR300, Sony Corp., Tokyo, Japan). The tested animals were weighed within 2 days following a test trial on an electronic scale (Pesola PPS200, Pesola AG, Baar, Switzerland) with 0.01 g precision. The subadult shrews were weighed in frames from a parallel study of physical development, each second day from birth to 40 days of age. The adult shrews were weighed on the nearest weighing days after the date of their test trials.

Acoustical analysis

Using Avisoft SASLab Pro software (Avisoft Bioacoustics, Berlin, Germany), the acoustic files were inspected for the presence of ultrasound and then downsampled to 11.025 kHz for analysis of the audible airborne waves, arising from seismic waves, produced by a vibrating piebald shrew on the drum membrane. These airborne waves were easily distinguishable from the background noise by ear and by spectrogram (Fig. 1). From each acoustic file, containing the vibration records, we took the mean pulse period for 10 sequential vibration frequency periods (Fig. 1), 4-5 times per file (mean \pm s.d., 4.82 \pm 0.40) with the standard marker cursor in the Avisoft main window. Also, for each subject performing vibrations, we analysed 4-5 (4.82±0.40) screech calls. For each screech call we calculated the mean modulation period for 10 sequential pulses of deep sinusoidal frequency modulation (Fig. 2) using the standard marker cursor in the Avisoft main window, similar to measuring the airborne waves resulting from the vibrations.

Statistics

Statistical analyses were carried out with STATISTICA, v. 6.0 (StatSoft, Tulsa, OK, USA). Means are given \pm s.d. Parametrical tests (repeated measures ANOVA, Student's test and Pearson's

correlation) were used because Kolmogorov–Smirnov tests showed that distributions did not depart from normality (*P*>0.05).

RESULTS

During the tests, we did not record ultrasound from any subject, but 3 adult females produced audible clicks. The airborne components of seismic body vibrations were recorded from 11 (1 adult and 4 subadult males and 2 adult and 4 subadult females) of the 19 tested animals. Of the 8 animals not performing vibrations, 6 were adults (3 males and 3 females) and 2 were subadults (both males). Two of the repeatedly tested adult females failed to vibrate, whereas the third one (subadult) produced vibrations. However, this female failed to vibrate at the third trial, which occurred 8 days after the second trial.

The vibrations were apparently produced from the whole-body wall (supplementary material Movie 1). They were generated in a few bouts during a test trial, but not for the whole duration of the test trial. We could not estimate precisely the duration of the bouts, as the vibration sounds could be recorded at sufficient signal-to-noise ratio only when the focal animal was near the centre of the drum membrane. The mean vibration rate was 160.5 ± 15.0 Hz (range 132-174 Hz, N=11 animals). Analysis controlling for sex and individual identity showed that the vibration rate did not differ significantly from the rate of the deep sinusoidal frequency modulation of loud screech calls (159.4 ± 6.1 Hz, range 148-170 Hz) of the same individuals (repeated measures ANOVA, $F_{1,10}=0.06$, P=0.81).

Body mass of adults (11.7 \pm 2.1 g, *N*=9) was significantly higher than that of subadults (8.8 \pm 1.2 g, *N*=10; Student's test, *t*₁₇=3.79, *P*=0.002). Although only 3 of the 11 vibrating animals were adults, the body mass of the vibrating subjects (9.8 \pm 2.4 g, *N*=11) did not differ from that of the non-vibrating ones (10.8 \pm 1.8 g, *N*=8; *t*₁₇=0.99, *P*=0.33). Body mass did not correlate with the vibration rate (Pearson's correlation, *r*=0.09, *P*=0.79, *N*=11). No correlation was found between the vibration rate and the rate of deep sinusoidal frequency modulation of screech calls of the same animals (*r*=0.15, *P*=0.67). However, a significant negative correlation exists between body mass and the rate of deep sinusoidal frequency modulation of screech calls (*r*=-0.78, *P*=0.005).

DISCUSSION

This is the first study to document self-produced seismic vibrations in a non-blind, surface-dwelling, burrowing shrew species. Nevertheless, this study of piebald shrews has not confirmed the use of ultrasound by piebald shrews, although ultrasonic calls were reported for *Blarina*, *Sorex* and *Crocidura* shrews (Gould et al., 1964; Gould, 1969; Buchler, 1976; Baxter and Meester, 1982; Forsman and Malmquist, 1988). Unlike other small sand-dwelling



Fig. 2. A piebald shrew screech call: (A) spectrogram and (B) waveform. The spectrogram shows pulses of deep sinusoidal frequency modulation of this call. The waveform shows the amplitudes of these pulses; arrows depict the modulation period. Supplementary material Audio 1 contains a natural series of screech calls of an adult female piebald shrew.

mammals that generate seismic vibrations with parts of their body (Randall, 2001; Kimchi et al., 2005), piebald shrews apparently generate vibrations with their body-wall muscles. In the piebald shrews in this study, vibrations occurred in bouts, and the frequency of the airborne component of vibration was about 160 Hz. This vibration rate matched the rate of the deep sinusoidal frequency modulation found in high-amplitude screech calls of the same subjects; however, the reason for such a coincidence is not known. This range of vibration frequencies is similar to the reported frequency ranges of seismic waves used by blind mole rats *Nannospalax ehrenbergi* for social intraspecific long-distance communication (Heth et al., 1987; Rado et al., 1987).

Body vibrations of the piebald shrews were not related to thermoregulatory shivering, as they occurred at rather high ambient temperatures (24–26°C), and did not result from depletion of energy stores, because all animals were well fed at testing. In piebald shrews, feeding strongly affects thermoregulation even at high ambient temperatures. Consuming ≤ 1 g of food per 1 g of body mass per night results in a decrease in body temperature down to as low as ambient temperature, whereas the animals consuming ≥ 1.4 g of food per 1 g of body mass per night keep a constant high body temperature (Kuznetsov, 1972). Also, body vibrations were not fear related, because vibration occurred when the animals were calm (supplementary material Movie 1), whereas the anxious animals tended to escape from the drum membrane.

The piebald shrews are solitary nocturnal animals, and the body vibration is unlikely to have any communicative function, either in the wild or in captivity because it is too soft to propagate even short distances. However, the deep sinusoidal frequency modulation, matching the periodicity of body vibration and strongly affecting the acoustic structure of screech calls, probably does have a communicative function. Besides, piebald shrews have a strong species-specific smell that apparently also has a communicative function.

The piebald shrews are among the few shrews capable of digging (supplementary material Movie 2), and can dig their own burrows in sand with speeds as fast as 1 cm min⁻¹ (Dubrovskij et al., 2011). The longest burrow of 325 cm has been reported for a female piebald shrew with young (Stalmakova, 1949). Before dawn at the end of their night period of activity, the piebald shrews, whose burrows were experimentally buried, were reported digging out simple short burrows of 12–15 cm (Dubrovskij et al., 2011). We propose therefore that body vibration may enable seismic exploration of substrate density, saving energy by avoiding unnecessary, energy-costly digging of densely packed sand. This hypothesis can be tested by releasing an animal into fenced plots with different densities of sand, and observing whether they will produce vibrations, e.g. before digging their short escape burrows.

Our study was carried out indoors in captivity, where the shrews had multiple artificial hides but rather a thin layer of sand as bedding. So, our study shrews did not dig their own burrows in their home enclosures and therefore we could not observe whether the animals would produce vibrations before the start of digging. For the duration of digging (supplementary material Movie 2), vibration movements, even if presented, are masked by active movements of the animal.

For somatosensory detection, piebald shrews may use body parts that are always tightly pressed to the ground, such as their forefeet, bearing ridges of fine hairs (Stalmakova, 1949). It is probable that these hair ridges enable detection of some kind of reflected vibration from the sand below, similar to the seismic exploration reported for mole-rats (Kimchi et al., 2005). For insectivores, the somatosensory detection of ground vibrations *via* the forepaws has also been proposed for star-nosed moles, *Condylura cristata*, as forepaws are hugely represented in the somatosensory cortex, suggesting that the forepaws provide an important sensory surface (Catania and Kaas, 1995).

It is likely that piebald shrews are also capable of detecting substrate-borne vibrations produced by their prey, similar to the golden mole Eremitalpa granti namibensis that forages on insects at night by dipping its head and shoulders into the sand and uses seismic cues for navigation (Narins et al., 1997; Lewis et al., 2006). The organization of the middle ear with a massive malleus, which presumably confers low-frequency sensitivity via the cochlea, together with the behaviour of dipping the head into the sand, would allow these golden moles to locate prey from information carried by Rayleigh waves, created by any motion of the prey (Mason and Narins, 2002; Mason, 2003). Observations in nature suggest that piebald shrews are capable of detecting insects and their larvae under a layer of sand a few centimetres thick, and making up to 30 prey diggings per night (Kuznetsov, 1972; Dubrovskij et al., 2011). Also, piebald shrews are capable of head dips into loose sand for foraging (supplementary material Movie 2). Further research on the auditory system, feet receptors, and vocal and social behaviour is needed to examine the mechanisms and functions of body vibration in the piebald shrew.

Airborne components of seismic vibration have been investigated in some insects (Hill, 2009) and in mole rats (Kimchi et al., 2005). However, the acoustic recording of the vibratory drumming is an innovation of the current study. This method allowed us not only to document substrate-borne vibrations in piebald shrews but also to quantitatively measure the vibration rate. Simple and inexpensive, this method can be applied in other laboratories to obtain comparative data on other captive populations of piebald shrews or other small mammals, for which body vibrations may be revealed.

In our study, we investigated body vibrations in adult and subadult piebald shrews. It would be interesting to track the ontogeny of this

2852 The Journal of Experimental Biology 215 (16)

behaviour since the earliest ontogenetic stages. In some insects, vibrations have been found not only in imago but also for larvae and pupae (Hill, 2009). The ontogeny of vibratory behaviour has not yet been studied for any mammal producing vibrations as adults. In this study, we found matched rates for the deep sinusoidal modulation of screech calls and the body vibrations. Piebald shrews produce screech calls from few days of age. Tracking the rate of the sinusoidal frequency modulation of screech calls through ontogenesis might highlight, though indirectly, the developmental pathway of body vibration in this small insectivore.

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