RESEARCH ARTICLE

Directional vibration sensing in the termite *Macrotermes natalensis*

Felix A. Hager* and Wolfgang H. Kirchner

ABSTRACT

Although several behavioural studies demonstrate the ability of insects to localise the source of vibrations, it is still unclear how insects are able to perceive directional information from vibratory signals on solid substrates, because time-of-arrival and amplitude difference between receptory structures are thought to be too small to be processed by insect nervous systems. The termite Macrotermes natalensis communicates using vibrational drumming signals transmitted along subterranean galleries. When soldiers are attacked by predators, they tend to drum with their heads against the substrate and create a pulsed vibration. Workers respond by a fast retreat into the nest. Soldiers in the vicinity start to drum themselves, leading to an amplification and propagation of the signal. Here we show that *M. natalensis* makes use of a directional vibration sensing in the context of colony defence. In the field, soldiers are recruited towards the source of the signal. In arena experiments on natural nest material, soldiers are able to localise the source of vibration. Using two movable platforms allowing us to vibrate the legs of the left and right sides of the body with a time delay, we show that the difference in time-of-arrival is the directional cue used for orientation. Delays as short as 0.2 ms are sufficient to be detected. Soldiers show a significant positive tropotaxis to the platform stimulated earlier, demonstrating for the first time perception of time-of-arrival delays and vibrotropotaxis on solid substrates in insects.

KEY WORDS: Orientation, Insects, Vibration, *Macrotermes* natalensis

INTRODUCTION

Macrotermes natalensis (Haviland) (Isoptera: Macrotermitinae) builds long subterranean galleries which lead outwards from the nest to their foraging areas. The galleries have physical features that promote vibrational communication and are used as channels for long-distance communication (Hager and Kirchner, 2013). A variety of predators are of potential danger to foraging termites (Longhurst et al., 1978; Huey and Pianka, 1981; Redford, 1984; Kok and Hewitt, 1990). When soldiers are attacked, they tend to drum with their heads against the substrate and create a pulsed vibration. Each pulse arises from a single tap of the termite's head against the ground. The number of pulses per signal varies between five and 22 (Hager and Kirchner, 2013). Nestmates are extremely sensitive to these vibrations. The vibration sense organ of the termites is the subgenual organ, a chordotonal organ in the legs. The organ lies in the dorsal blood-space of the tibia. When the leg is vibrated, the cuticle transfers the vibration to the subgenual organ (Howse, 1964).

Ruhr University Bochum, Faculty of Biology and Biotechnology, D-44780 Bochum, Germany.

*Author for correspondence (Felix.Hager@rub.de)

Received 28 January 2014; Accepted 7 April 2014

In response to drumming nestmates, soldiers also start to drum themselves, thereby amplifying the intensity of the signal, leading to a social long-distance communication through chains of signalreamplifying termites (Röhrig et al., 1999; Hager and Kirchner, 2013). If a termite somewhere in the vast gallery system detects alarm signals, it has to make a decision to walk either in one direction or the other. In this context it would be advantageous for the termites to extract information about the direction of the source of vibration out of the vibrational signals.

To date, more than 40 behavioural studies have demonstrated the ability of insects to localise the source of vibration, but there is little information about the underlying mechanisms (for reviews, see Virant-Doberlet et al., 2006; Hill, 2009). The only arthropods in which it has been clearly demonstrated that the direction of a source of vibrations can be perceived through simultaneous comparisons of the signals arriving at the legs are the wandering spider Cupiennius salei (Hergenröder and Barth, 1983), which can detect time delays of 4 ms, and the sand scorpion *Paruroctonus mesaensis*, detecting time delays as short as 0.2 ms (Brownell and Farley, 1979). In insects there are vibration receptors in all six legs, which would be suitable for a directional vibration sensing and vibrotropotactic orientation, if time and/or amplitude differences are large enough to be processed in their central nervous system (Cokl et al., 2006; Virant-Doberlet et al., 2006). Here we demonstrate that M. natalensis soldiers solve the task as well as sand scorpions.

The first aim of this study was to investigate the response of workers and soldiers of *M. natalensis* to substrate-borne alarm signals. With their strong head capsule and mandibles, soldiers are morphologically well protected. In contrast, workers are much more vulnerable. Therefore, we assumed that workers and soldiers would show different behavioural strategies in response to vibrational alarm signals. The second objective was to investigate whether substrate-borne alarm signals provide a directional cue used for orientation. Because of the low propagation velocity of surface waves in the termite nest (Hager and Kirchner, 2013), the third objective was to investigate whether time delays of the arriving substrate-borne waves between the legs are used as a cue for orientation.

RESULTS

Directional response of termite workers and soldiers to substrate-borne alarm signals at the termite mound

To ensure that directly observable termites were located at the nest surface, predator attacks were simulated by drilling holes into the conical base of termite mounds. Specialised predators, such as aardvarks and pangolins, with their powerful front legs, can open nests. This is associated with both a flow of air into the gallery system and vibrations of the nest material (Connétable et al., 1999; Röhrig et al., 1999; Hertel et al., 2011). Both stimuli elicit drumming behaviour in *M. natalensis* within 1 s (Hager and Kirchner, 2013). After some time, termites appear at the nest surface and start to close





Fig. 1. Preference index of workers (grey bars) and major soldiers (white bars) of *Macrotermes natalensis* at the nest surface in experiments with a vibrational alarm stimulus and control experiments without playback of a vibrational signal. Playback of drumming signals leads to a significant decrease in the number of workers (n=45 experiments) and to a significant increase in the number of soldiers (n=45 experiments) at the nest surface. In control experiments there is no significant difference in the number of workers (n=25 experiments) and soldiers (n=25 experiments). Boxes show first and third quartiles; bold lines indicate medians; whiskers are truncated (1.5 times interquartile range). Asterisks indicate significant changes in the number of termites at the nest surface (**P<0.01).

the hole in the nest wall. This results in the presence of observable termites at the nest surface used in the subsequent experiment. In response to artificial vibrational stimuli at the surface of the termite mound, termite workers fled towards the nest, whereas soldiers were recruited towards the source of signal at the nest surface. Playback of substrate-borne drumming signals led to a significant decrease in the number of workers (Wilcoxon signed-rank test, P<0.001, n=45) and to a significant increase in the number of soldiers (P<0.005, n=45) at the nest surface (Fig. 1). In control experiments without vibrational stimuli, no effects were found (workers: P=0.569, n=25; soldiers: P=0.132, n=25).



Fig. 2. Preference index of individual soldiers of *M. natalensis* in an arena. If vibrational alarm signals are presented (grey bar), termites stay significantly longer at the arena side facing the source of vibration than on the other side (n=134 termites). In control experiments without playback of vibrational signals (white bar), termites do not show side preferences (n=30 termites). Boxes show first and third quartiles; bold lines indicate medians; whiskers indicate minima and maxima. Asterisks indicate a significant side preference (**P<0.01).



Fig. 3. Preference index of *M. natalensis* in relation to the time delay of vibrational stimuli generated with two movable platforms. For all tested time delays, soldiers tend to turn to the platform vibrated earlier. When the platforms are vibrated with a small time delay of 0.09 ms (n=26) or 0.16 ms (n=49), orientation towards the platform vibrating first was not significant. When the platforms vibrated with time delays of 0.20 ms (n=86) or 0.29 ms (n=26) termites turn significantly more often to the platform vibrated first. Asterisks indicate significant side preferences (*P<0.05; **P<0.01).

Individual directional response of soldiers to substrateborne alarm signals

Single major soldiers were tested in arena experiments in the laboratory on natural nest material for their ability to localise the source of vibrational pulses. Termite soldiers oriented towards and stayed significantly longer at the arena side facing the source of a vibrational stimulus (Wilcoxon signed-rank test, P<0.005, n=134; Fig. 2). In control experiments without a vibrational stimulus, termites did not show a side preference (P=0.588, n=30).

Directional response of soldiers based on time-of-arrival differences

Termites standing with the legs of one body side on a vibrating platform and with the legs of the other body side on a platform vibrating a short moment later turned towards the platform that vibrates first. We tested four different time delays. For all tested time delays, termites showed a tendency to turn to the platform vibrated first (Fig. 3). In experiments with small time differences of 0.09 ms (χ^2 =0.61, *P*<0.43, *n*=26) and 0.16 ms (χ^2 =0.18, *P*<0.67, *n*=49), the effect could not be supported statistically. However, the effect was significant with time delays of 0.2 ms (two-tailed χ^2 =7.86, *P*<0.005, *n*=86) and 0.29 ms (χ^2 =3.846, *P*<0.05, *n*=26). Time differences as short as 0.2 ms were sufficient to be detected and to provide information about the direction of the source of vibration.

DISCUSSION

Here we report that time-of-arrival delays of the vibrational signals are used for tropotactic orientation by an insect. The only arthropods for which it has been directly shown that time of arrival is the cue used for orientation are the arachnids *Paruroctonus mesaensis* (Brownell and Farley, 1979) and *Cupiennius salei* (Hergenröder and Barth, 1983). Similar experiments using two movable platforms that vibrate legs with different amplitudes or time delays have so far not been conducted with insects (Virant-Doberlet et al., 2006). The time delays detected by the termites are as small as the time delays detected by the scorpion *P. mesaensis* and 20 times smaller than those detected by *C. salei*.

The temporal resolution of the system seems to be sufficient to solve the task of directional orientation for termite soldiers: in the nests of *M. natalensis*, vibrational alarm signals are propagated with

a velocity of approximately 130 m s^{-1} (Hager and Kirchner, 2013). The distance between the front leg of one body side and the hind leg of the other body side is approximately 16 mm, leading to time lags of approximately 0.12 ms between legs. Our experiments using two movable platforms showed a tendency of soldiers to turn towards the platform vibrated earlier, even with time lags of 0.09 ms, and time differences as short as 0.2 ms were sufficient to generate a significant directional orientation in arena experiments. This is in the same order of magnitude as the time lag of 0.12 ms calculated above. Under more natural conditions the resolution might even be better.

This is the first behavioural study demonstrating that time-ofarrival differences of vibrational signals on solid substrates can be detected by insects. Our results confirm indirect evidence from behavioural studies in various insects (Cocroft et al., 2000; Virant-Doberlet et al., 2006; Hill, 2009). They also demonstrate that the body size of most insects is sufficient for a vibrotropotactic orientation based on the analysis of time-of-arrival delays.

On a physiological level, the temporal resolution of vibrational direction sensing has been studied by Čokl et al. (Čokl et al., 1985). They showed in *Locusta migratoria* that the response pattern of ventral cord neurons depends on the direction and the time delay of the presented vibrational stimulus. Directional processing occurs at the ventral cord level by integrating the inputs from the vibratory receptors from several legs. Because of the locust's relatively large size, receptors in different legs are at a distance of approximately 5 cm, leading to a time delay between 0.4 and 4 ms (Čokl et al., 1985).

A task that is in some respects comparable to directional vibration sensing on solid surfaces is solved by the backswimmer *Notonecta glauca*, which can detect the direction of waves on the water surface. At the low frequencies of water surface waves, backswimmers are able to detect phase differences between their legs (Wiese, 1974).

Vibration sensing is at one end of a continuum in the insectan mechanoreceptor-based communication system for detecting signal sources. This continuum also includes tympanal hearing (Hoy and Robert, 1996). Several mechanisms have been identified by which acoustic parameters may be represented in receptor responses, including temporal coding for directional information. Directional sound sources generate intensity differences at the two ears, so that interaural differences in response rate or latency, or both, could encode directional information (Mason and Faure, 2004). With the exception of the fly *Ormia ochracea* (the eardrums are mechanically coupled), pressure difference reception has become the standard explanation for directionality in small animals (Michelsen and Larsen, 2008).

Insect auditory systems have to deal with time delays that are even smaller than those detected by our termites. In locusts, the interaural time differences are in the range of 0.01 ms (Mörchen et al., 1978), and they are even less in smaller insects such as the tiny fly O. ochracea. As this fly's eardrums are less than 0.5 mm apart, interaural time delays are approximately 50 ns (Mason et al., 2001). However, insect auditory organs solve the problem either mechanically in the periphery by translating time delays in amplitude differences, or neuronally through binaural interactions inducing latency differences in the manageable range of some hundred microseconds to a few milliseconds (Schöneich and Hedwig, 2010; Mason et al., 2001). The approach used in the present study to show directly and unequivocally that time-of-arrival differences between the legs are used to localise sources of vibrational signals has previously exclusively been used to study the temporal resolution of vibrotropotactic reactions in the sand scorpion. Now that we know that at least one insect species solves the task as well as the sand scorpion, it will be interesting to use this experimental approach for comparative studies with other insect taxa in which directional responses to vibrations have been reported.

MATERIALS AND METHODS

Termites

All experiments were performed with termites of the species *M. natalensis*. The experiments were carried out at the Lajuma Research Centre in the Soutpansberg Mountain range, Limpopo Province, South Africa ($23^{\circ}02'S$, $29^{\circ}26'E$), and at the Pullen Farm field station of the University of the Witwatersrand in Mpumalanga, South Africa ($25^{\circ}34'S$, $31^{\circ}10'E$), using a total of six colonies of *M. natalensis* with a mound height between 1 and 1.5 m. Termite mounds were opened at their conical base to collect major soldiers for the laboratory experiments. Soldiers were maintained in plastic containers until used in experiments. All experiments were conducted on the day of collection.

Artificial drumming signals

When soldiers of *M. natalensis* are disturbed, they drum with their heads against the substrate and thereby create a vibrational alarm signal. We synthesised and analysed vibrational stimuli using the software SoundRuler (Gridi-Papp, 2007) and RavenPro (Bioacoustic Research Program, 2011). The artificial drumming signals used in all three experiments were square pulses with a pulse repetition rate of 11 Hz. Bursts of 10 pulses with 1 s silence between bursts were repeated three times. Artificial drumming signals were generated by a notebook computer connected to an external sound card (Tascam US-144) and a vibration exciter (Brüel & Kjaer 4810, Naerum, Denmark).

Directional response of termite workers and soldiers to substrate-borne alarm signals at the termite mound

Predator attacks at the termite mound were simulated by drilling holes (diameter=8 cm) into the conical base of termite mounds. The experiments started 10 min after the first termite appeared at the surface. Artificial drumming signals were generated by a vibration exciter mechanically coupled to the nest 0.1 m from the edge of the drilled hole. The vibrational peak amplitude of the nest material was calibrated to 0.5 m s^{-2} peak to peak using an accelerometer (B&K 4381) and a charge amplifier (B&K 2635) connected to the computer. This amplitude is in the natural range of vibrational alarm signals produced by M. natalensis (Hager and Kirchner, 2013). The accelerometer was mounted with wet nest material on the nest surface 0.05 m from the coupling point of the vibration exciter. Wet nest material dries within minutes, ensuring a very tight coupling. Soldiers and workers were counted separately before the drumming stimulus was given (t_1) and 1 min after the treatment (t_2) . Control experiments without playback of drumming signals were also conducted. The vibration exciter was also attached to the termite mound, but no vibrational stimuli were offered. Soldiers and workers were counted separately before the fake stimulus was given (t_1) and 1 min after the control treatment (t_2) . For visualisation preference, indices (x_i) were calculated separately for major soldiers and workers by: $x_i = t_2 - t_1/t_2 + t_1$. Wilcoxon signed-rank test was used for statistical analysis. The two related groups are 'number of workers/soldiers before' and 'after' the vibrational stimulus. Forty-five experiments and 25 control experiments were conducted at four different termite mounds. Each termite colony was tested in 10 to 12 experiments and in six to seven randomly selected control experiments. Subsequent experiments/control experiments at the same termite mound were carried out at least 2 days later.

Reaction of soldiers to artificial drumming signals on a piece of nest material

Single major soldiers were tested in the laboratory for their ability to localise the source of vibrational pulses. We used a piece of natural nest material as substrate $(0.4 \times 0.28 \times 0.18 \text{ m})$. A lid of a Petri dish (diameter=5.5 cm) kept at a distance of 1 mm above the substrate to exclude mechanical coupling was used to restrict the termites' locomotory activity. At 10 cm to the left and to the right of the arena, vibration exciters (B&K 4810) were attached via two



Fig. 4. Experimental aperture for the behavioural measurement of vibrational directional sensing. (A) Diagram of two movable platforms with a group of five termite soldiers under a Petri dish. The platforms are mounted on an accelerometer (B&K 4381) and a vibration exciter (B&K 2635). (B) The vibrational stimulus was triggered by an observer when the termite straddled the experimental setup, with the legs of one body side on one platform and the legs of the other body side on the other platform. To determine the termite's position on the platform accurately, experiments were recorded on video.

PVC rods (150 mm long, 10 mm diameter) to the substrate. Artificial termite drumming signals were generated as described before. The vibrational peak amplitude of the nest material was calibrated (0.5 m s^{-2} peak to peak) using two accelerometers (B&K 4381) and two charge amplifiers (B&K 2635) connected to the computer 0.01 m from the coupling points of the vibration exciters. The accelerometers were mounted with wet nest material on the nest surface. Vibrational alarm stimuli were given either on the left or on the right side of the arena. The experiment was started when the termite entered the arena through a tube. The termite's locomotory activity was observed for 30 s. The Petri dish was marked with a line in the middle so that we could measure the time the termite spent in the right- or the left-hand part of the arena. Termites from four mounds were used in this experiment. Termites were tested only once. For visualisation preference, indices were calculated as described before with t_1 =time (s) on the vibration far arena side and t_2 =time (s) on the vibration facing arena side. For statistical analysis, the Wilcoxon signed-rank test was used. The two related groups are 'time (s) on the vibration facing arena side' and 'time (s) on the vibration far side'.

Soldiers on two movable platforms

We measured vibratory directionality using walking responses of major soldiers of M. natalensis. The detection of time delays was studied in the laboratory using artificial drumming signals as described above, induced by a personal computer and two vibration exciters (B&K 4810) mechanically coupled to the bottom of two square PVC platforms (15×15×0.5 cm). A gap of 1 mm width ensured mechanical isolation between the platforms. To prevent termites from leaving the platforms, a Petri dish lid (diameter=5.5 cm) was mounted upside-down 1 mm above the two platforms (Fig. 4). Five major soldiers were placed in the arena under the Petri dish. To prevent termites from slipping, the bottoms of the platforms were coated with filter paper (diameter=7 cm). The filter paper was cut into two pieces to ensure mechanical isolation. To ensure a better adhesion of the filter papers on the platforms, the two pieces of filter paper were moistened with 0.5 ml water each. The amplitudes of the stimuli were determined using two accelerometers (B&K 4381), two charge amplifiers (B&K 2635) and a computer. The amplitude of the drumming signal was 0.5 m s⁻² peak to peak measured at the bottom of the platforms; both platforms were calibrated and vibrated in exactly the same way, except for a short time delay (Fig. 5). The platform that vibrated first was chosen randomly. The experimenter was not aware which platform vibrated first. The vibrational stimuli were triggered by an experimenter watching termites in real time; data were analysed from video recordings and only cases where all legs were appropriately positioned were selected.

The termite's reaction was video recorded using a camcorder (Panasonic HDC-SD20). The video recording was synchronised with the vibrational stimuli via the audio channel of the camcorder. During video analysis, the experimenter was not aware which platform side vibrated first. For data analyses, the video was stopped one frame (video recording at



Fig. 5. Artificial drumming signals. (A) Oscillogram of 10 pulses measured beneath one of the movable platforms. The pulse repetition rate is 11 Hz. The amplitude of the vibrational pulses is 0.5 m s^{-2} peak to peak. (B) Frequency spectrogram of the pulse group shown in A (band-pass filter 10 Hz to 3 kHz). (C) Oscillogram of signals recorded simultaneously on the platform vibrating first (a) and on the platform vibrating a short moment later (b). Red bars indicate the time delay of 0.29 ms between the vibrational stimuli.

25 frames s⁻¹) before the vibrational signal was given. The frozen image was used to select the tests in which the three tarsi of the termite's one body side were in contact with one platform and the tarsi of the other body side were in contact with the other platform. It was regarded as a reaction to one of the platforms when the termite entered the particular platform within 1 s of the start of the drumming stimulus. It was regarded as a reaction towards the source of vibration when the termite turned to the platform that vibrated first. Termites from two different termite mounds were tested. The termites were not individually marked; as in previous studies of termite responses to vibrational stimuli (Kirchner et al., 1994; Röhrig et al., 1999; Hager and Kirchner, 2013), no attempts were made to estimate the inter-individual within-colony variance of the response. To avoid habituation effects, stimuli were offered at intervals of at least 2 min. The termite groups were tested in up to 20 trials, and then five new soldiers were placed under the Petri dish. Overall, 32 termite groups were tested. For visualisation preference indices were calculated as described before with t_1 =termite turns to the platform vibrating later and t_2 =termite turns to the platform vibrating first. Chi-square analysis was used to test for deviation from expected values.

Acknowledgements

We thank Rheta and Ian Gaigher for their hospitality and the opportunity to conduct research at the Lajuma Research Centre, and the School of Animal, Plant and Environmental Science, University of the Witwatersrand, Johannesburg, for allowing us to use the field station Pullen Farm for our projects.

Competing interests

The authors declare no competing financial interests.

Author contributions

This study is part of the PhD thesis of F.A.H. Both authors conceived and designed the study. F.A.H. carried out the experiments, analysed the data and wrote the manuscript. W.H.K. supervised experiments and data analysis.

Funding

This study was supported by grants of the German Academic Exchange Service (DAAD).

References

Bioacoustic Research Program (2011). Raven Pro: Interactive Sound Analysis Software (Version 1.4). Ithaca, NY: The Cornell Lab of Ornithology.

- Brownell, P. and Farley, R. D. (1979). Orientation to vibrations in sand by the nocturnal scorpion, *Paruroctonus mesaensis*: mechanisms of target localization. J. Comp. Physiol. A 131, 31-38.
- Cocroft, R. B., Tieu, T. D., Hoy, R. R. and Miles, R. N. (2000). Directionality in the mechanical response to substrate vibration in a treehopper (Hemiptera: Membracidae: Umbonia crassicornis). J. Comp. Physiol. A 186, 695-705.
- Čokl, A., Otto, C. and Kalmring, K. (1985). The processing of directional vibratory signals in the ventral nerve cord of *Locusta migratoria*. J. Comp. Physiol. A 156, 45-52.
- Čokl, A., Virant-Doberlet, M. and Zorović, M. (2006). Sense organs involved in the vibratory communication of bugs. In *Insect Sounds and Communication* (ed. S. Drosopoulos and M. F. Claridge), pp. 71-80. London: Taylor & Francis.
- Connétable, S., Robert, A., Bouffault, F. and Bordereau, C. (1999). Vibratory alarm signals in two sympatric higher termite species: *Pseudacanthotermes spiniger* and *P. militaris* (Termitidae, Macrotermitinae). J. Insect Behav. **12**, 329-342.
- Gridi-Papp, M. (2007). SoundRuler: Acoustic Analysis for Research and Teaching. Available at: http://soundruler.sourceforge.net.
- Hager, F. A. and Kirchner, W. H. (2013). Vibrational long-distance communication in the termites *Macrotermes natalensis* and *Odontotermes* sp. J. Exp. Biol. 216, 3249-3256.
- Hergenröder, R. and Barth, F. G. (1983). Vibratory signals and spider behavior: how do the sensory inputs from the eight legs interact in orientation? J. Comp. Physiol. A 152, 361-371.
- Hertel, H., Hanspach, A. and Plarre, R. (2011). Differences in alarm responses in drywood and subterranean termites (Isoptera: Kalotermitidae and Rhinotermitidae) to physical stimuli. J. Insect Behav. 24, 106-115.
- Hill, P. S. M. (2009). How do animals use substrate-borne vibrations as an information source? *Naturwissenschaften* 96, 1355-1371.
- Howse, P. E. (1964). An investigation into the mode of action of the subgenual organ in the termite, *Zootermopsis angusticollis* Emerson, and in the cockroach, *Periplaneta americana* L. J. Insect Physiol. **10**, 409-424.

- Hoy, R. R. and Robert, D. (1996). Tympanal hearing in insects. Annu. Rev. Entomol. 41, 433-450.
- Huey, R. and Pianka, E. R. (1981). Ecological consequences of foraging mode. Ecology 62, 991-999.
- Kirchner, W. H., Broecker, I. and Tautz, J. (1994). Vibrational alarm communication in the damp-wood termite Zootermopsis nevadensis. Physiol. Entomol. 19. 187-190.
- Kok, O. B. and Hewitt, P. H. (1990). Bird and mammal predators of the harvester termite *Hodotermes mossambicus* (Hagen) in semi-arid regions of South Africa. S. Afr. J. Sci. 86, 34-37.
- Longhurst, C., Johnson, R. A. and Wood, T. G. (1978). Predation by *Megaponera foetens* (Fabr.) (Hymenoptera: Formicidae) on termites in the Nigerian Southern Guinea savanna. *Oecologia* 32, 101-107.
- Mason, A. C. and Faure, P. A. (2004). The physiology of insect auditory afferents. *Microsc. Res. Tech.* 63, 338-350.
- Mason, A. C., Oshinsky, M. L. and Hoy, R. R. (2001). Hyperacute directional hearing in a microscale auditory system. *Nature* **410**, 686-690.
- Michelsen, A. and Larsen, O. N. (2008). Pressure difference receiving ears. *Bioinspir. Biomim.* 3, 011001.
- Mörchen, A., Rheinlaender, J. and Schwartzkopff, J. (1978). Latency shift in insects auditory nerve fibers. *Naturwissenschaften* 65, 656-657.
- Redford, K. H. (1984). Mammalian predation on termites: tests with the burrowing mouse (Oxymycterus roberti) and its prey. Oecologia 65, 145-152.
- Röhrig, A., Kirchner, W. H. and Leuthold, R. H. (1999). Vibrational alarm communication in the African fungus-growing termite genus *Macrotermes* (Isoptera, Termitidae). *Insectes Soc.* 46, 71-77.
- Schöneich, S. and Hedwig, B. (2010). Hyperacute directional hearing and phonotactic steering in the cricket (Gryllus bimaculatus deGeer). PLoS ONE 5, e15141.
- Virant-Doberlet, M., Čokl, A. and Zorović, M. (2006). Use of substrate vibrations for orientation: from behaviour to physiology. In *Insect Sounds and Communication* (ed. S. Drosopoulos and M. F. Claridge), pp. 81-97. London: Taylor & Francis.
- Wiese, K. (1974). The mechanoreceptive system of prey localization in Notonecta. J. Comp. Physiol. 92, 317-325.