Chapter 12
Directionality in Insect Vibration Sensing: Behavioral Studies of Vibrational Orientation

Felix A. Hager and Wolfgang H. Kirchner

Abstract Insects need to orient to various environmental stimuli. Many behavioral studies suggest orientation based on vibrational cues and signals, but they rarely exclude other potential stimuli such as chemical, visual, or airborne sound signals. Here, we review the behavioral evidence for directional vibrational orientation in insects. First, we discuss the potential of vibrational cues and signals for orientation and briefly state the importance of the material properties of the substrate. We then review what is known about vibrotaxis in some particularly well-studied species. Our selection aims to show the different experimental approaches that have been used and, as far as known, which kind of taxis and which kind of vibrational cue are used by the insects to orientate. We show that a growing body of current behavioral studies reveal the remarkable ability of insects to orientate via vibrational cues and signals in various contexts.

12.1 Introduction

Insects need to orient to various environmental stimuli to find mates, food, or to escape predators. In the context of mate location, there should be a high selection pressure on the evolution of mechanisms allowing accurate localization of a potential mate. The same applies in the context of predation, since the survival of predators depends on their ability to catch prey. In the like manner, prey would benefit if predators could be detected, localized, and thereby avoided. In these contexts, different sensory channels such as the visual, olfactory, or mechanical can be employed. Whereas directional hearing, i.e., localization of mechanical signals in air or water, has been studied in vertebrates as well as in arthropods in great detail, localization of sources of surface waves is much less well studied (Cocroft et al. 2014). Solid media are much more variable in parameters affecting signal

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transmission (Elias and Mason 2014). Amplitude differences, time-of-arrival delays or phase angle differences perceived at two or more sensors highly depend on the characteristics of the substrate. In the context of vibrational orientation, the physical properties of the substrate are therefore of fundamental importance. The rich diversity of substrate properties was recently reviewed by Elias and Mason (2014), Michelsen (2014), and Mortimer (2017). Although several behavioral studies demonstrate the ability of insects to localize the source of vibrations (Virant-Doberlet et al. 2006), it is still not well understood how insects can perceive directional information from vibratory signals on solid substrates. Some species seem to solve this task without making any use of directional cues; others, however, localize sources of vibrations using either a klinotactic directional orientation (i.e., temporal comparison of signal parameters) or tropotactic directional orientation (i.e., simultaneous comparison of signals arriving at two sense organs). In this chapter, we review behavioral studies demonstrating the ability of insects to localize the source of vibration and focus particularly on vibrational orientation, i.e., klinotactic and tropotactic orientation.

12.2 Directional Cues for Vibrational Orientation

Insects producing vibrational signals, such as drumming, tremulation, and stridulation, or vibrational cues by walking and feeding induce different vibrations of the substrate with different frequencies and amplitudes (for review, see Hill 2008, 2014). The material's characteristics, like impedance, density, mass, and internal damping, as well as its geometry and boundary condition (Inta et al. 2007; Mortimer 2017) lead to vibrational waves travelling with very different characteristics. This leads to a certain velocity, attenuation, and dispersion of the wave travelling through the substrate. After the vibrational waves have travelled some distance through the substrate a receiver might detect them. Several sense organs are involved in substrate vibration detection in insects: subgenual organs, chordotonal organs and campaniform sensilla (Lakes-Harlan and Strauß 2014). The receiver could use different behavioral strategies to encode directional information. One strategy is to compare measurements over time (klinotaxis). The other behavioral strategy in the context of vibrational orientation is the comparison of the inputs of at least two receptors (tropotaxis). The insect's size is crucial because the distance between the legs, i.e., the receptors, directly influences the magnitude of the differences. For a given insect's size, i.e., two receptors in a given distance to each other, the magnitude of the differences is a function of the substrate's characteristics. Theoretically a vibrational wave should arrive at each receptor at different times and with different intensities. The most obvious directional cues are therefore differences in time of arrival (Δt) and amplitude (Δd) (Virant-Doberlet et al. 2006).

On a physiological level, the temporal resolution of vibrational direction sensing has been studied by 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 5 cm, leading to a time delay between 0.4 and 4 ms (Čokl et al. 1985).

Between different receptors, the insect could compare the first onset of the vibrational wave, the onset of certain frequency components, or other characteristics like the peak amplitude to obtain directional information. For a long time, it has been thought that time-of-arrival differences (Δt) might be too small to be detected on natural substrates because of the high propagation velocity of vibrational waves (Virant-Doberlet et al. 2006). The first arthropods for which it could be clearly demonstrated that time-of-arrival differences are used for tropotactic orientation on solid substrates are the sand scorpion *Paruroctonus mesaensis* and the wandering spider *Cupiennius salei.* The scorpion can detect time delays as small as 0.2 ms (Brownell and Farley 1979) and the spider can detect time delays of 4 ms (Hergenröder and Barth 1983). Recently it was shown for three different insect taxa that time-of-arrival delays are used for vibrotaxis by termites (Hager and Kirchner 2014), hemipterans (Hager et al. 2016; Kirchner et al. 2017) and ants (Hager et al. 2017). The time delays used by insects on solid substrates are in the same range as the time delays detected by scorpions.

Differences in amplitudes expressed as velocity, acceleration, or displacement could be compared between receptors that are spatially arranged on the substrate (tropotaxis), or if the insect moves and probes at different locations (klinotaxis). Vibrational orientation using amplitude gradients has been demonstrated in locusts. Directionality coding of some neurons is improved if, in addition to the time-delayed stimulation, a signal attenuation is simulated. Perception of signal amplitudes and its neuronal comparison leads to directionality-dependent response patterns in ascending neurons (Čokl et al. 1985). Behavioral experiments show that in stinkbugs amplitude differences are sufficient for vibrational orientation (Hager et al. 2016; Kirchner et al. 2017). Whether amplitude differences in the relevant range reliably occur on host plants needs further observation. Recently it was shown for a stinkbug's host plant (*Phaseolus vulgaris*) that only a time delay between the arrival of vibrational waves was a reliable directional cue, since the signal amplitude at the branching point was often higher on the stalk away from the female (Prešern et al. 2018).

Due to frequency-dependent filtering characteristics of some substrates the relative amplitude of different frequency components changes while travelling through the substrate. Assuming the insects' receptors are frequency sensitive in the relevant range, they could compare amplitude ratios between receptors. Moreover, different frequencies travel with different velocities, thus the temporal structure of the substrate vibration changes with distance. For example, a frequency sweep that begins with a high frequency and ends at a low frequency will increase its duration when it travels, but a sweep with increasing frequencies will decrease in duration (Michelsen 2014). Insects on solid substrates may also use phase differences between receptors to solve the orientation task, as it was shown for the backswimmer *Notonecta glauca* (see Sect. 12.6.6; Wiese 1974). Directional information could also be available in mechanical response of the insect body to substrate vibrations, as it was proposed for treehoppers (Cocroft et al. 2000).

12.3 Substrates

The physics of mechanical waves in solids and along media interfaces is quite complicated. Depending on the mechanical properties of the media and on the size and shape of the materials involved, a considerable number of different wave types with quite diverse physical characteristics can occur (Markl 1983). In the following, we summarize briefly what is known about the physical characteristics of solids and the water surface relevant to the context of vibrational orientation. We will focus on the types of waves occurring in the substrates and their propagation velocity, attenuation, and dispersion characteristics. We primarily focus on characteristics that are important to elucidate time-of-arrival and amplitude differences that have the potential to be biologically meaningful. For comprehensive reviews, see Cremer et al. (2005), Markl (1983), Michelsen (2014), and Mortimer (2017).

12.3.1 Plant Stems

In plant stems, vibrations travel as bending waves with a relatively low group propagation velocity. In some plant species, the group propagation velocity is only 36–95 ms^{-1} at low frequencies of 200 Hz and 120–220 ms^{-1} at higher frequencies of 2 kHz (Michelsen et al. 1982). These velocities would lead to time-of-arrival delays between receptors positioned at a 1-cm distance to each other in the range of 0.05–0.27 ms. The energy loss of bending waves in plant stems by friction at frequencies below some kHz is relatively low. Communication is therefore possible over distances of some meters (Michelsen et al. 1982). For some plant species, it was shown that the amplitude of vibrations does not decrease monotonically with distance from the vibration source (Michelsen et al. 1982). Therefore, amplitude gradients are thought to be unreliable cues. However, if measurements are either taken at points with a certain distance between them (by performing klinotaxis), or if measurements are made at special positions on the stem or at the two sites of a node or between the stem and the adjacent petiole of leaves, amplitude differences could be reliable cues (Stritih et al. 2000).

The 2D motion of plant stems changes with distance from the source. Close to the vibration source the motion perpendicular to the stem is ellipsoidal, while further away the motion is circular. An insect standing on a plant stem positions its legs in a three-dimensional array around the stem and could use these differences for orientation (Virant-Doberlet et al. 2006). If vibration perception is influenced by motion along more than one axis, then describing stem motion within a 2D coordinate plane may be important for understanding how vibrations are transmitted and perceived. Sensitivity to orthogonal axes of motion in a vibrational stimulus is important in vibration localization in some scorpions (e.g., Brownell and Farley 1979) and spiders (Barth and Geethabali 1982). To our knowledge, there is only one comprehensive study linking the insect's movement decisions and the complex motion of plant stems (Gibson and Cocroft 2018).

Gibson and Cocroft (2018) studied mate searching in thornbug treehoppers on living plants and mapped search paths of male treehoppers. At each of the males' sampling locations, two-dimensional laser vibrometry was used to measure stem motion produced by female vibrational signals. Thereby, properties of the vibrational signals could be related to the males' movement direction, intersample distance, and accuracy. Males experienced gradients in signal amplitude and in the whirling motion of the plant stem, and these gradients were influenced to varying degrees by source distance and local stem properties. Males changed their sampling behavior during the search, making longer intersample movements farther from the source where uncertainty is higher.

The primary directional cue used by searching males was the direction of wave propagation, and males made more accurate decisions when signal amplitude was higher, when time delays were longer between front and back legs, and when female responses were short in duration (Gibson and Cocroft 2018).

12.3.2 Sand and Soil

Mechanical impacts on a sandy substrate release different types of waves with different properties (Brownell 1977; Aicher and Tautz 1990). In the context of vibrational orientation, Rayleigh surface waves are thought to be particularly interesting. Loose sand conducts Rayleigh surface waves at relatively low velocities of 40–50 ms^{-1} (Brownell 1977). The sand's particle size and frequency of vibrational waves both influence the propagation properties. The damping coefficient at a frequency of 300 Hz varies from 0.26 to 2.61 $\mathrm{dB\ cm}^{-1}$ and is inversely proportional to the size of the sand particle (Devetak et al. 2007). Due to these characteristics, time-of-arrival and amplitude differences occur that have the potential to be biologically meaningful. Generalizations of the soil's physical properties are difficult to make because particle size, degree of heterogeneity, and overall complexity can vary (Hill 2008). Moreover, soils are no static substrates and propagation properties can change from day to day with temperature and moisture content (Hill and Shadley 2001).

12.3.3 Water Surface

Surface waves on the water have quite special physical properties and propagate with relatively low velocity (Markl 1983). Local disturbances of the water surface generate waves that consist of concentric movements of the water particles at the surface. Waves with amplitudes that are much smaller than the water depth are radiated with dispersion. The damping of the waves, which highly depends on frequency, especially causes a loss of high-frequency components during signal propagation (Lang 1980; Bleckmann 1985). Phase velocity reaches its minimum at about 13 Hz, while the minimum of the group velocity is situated at about 6 Hz. At 13 Hz, phase and group velocities are equal and only 0.23 ms^{-1} (Lang 1980). Due to these special physical properties, relatively large time-of-arrival and amplitude differences occur.

12.4 Experimental Methods

Many behavioral studies of insects suggest orientation based on vibrational cues and signals, but they rarely exclude other potential stimuli such as chemical, visual, or airborne sound signals (Virant-Doberlet et al. 2006). In the context of directional vibration sensing, two different experimental designs can be distinguished that allow different conclusions on the insect's orientation abilities. In closed-loop conditions the insect can successively update directional information as it changes its position or orientation relative to the vibration source. In nature and in most arena experiments, insects move freely from a releasing point toward the vibration source and could thereby obtain some kind of amplitude gradient or other characteristics of the vibrational waves that change while travelling through the substrate. In closed-loop conditions, a clear distinction between klinotaxis and tropotaxis is not possible (Gerhardt and Huber 2002). In open-loop conditions, the insect must make decisions without receiving any feedback. Open-loop experiments, therefore, allow observers to discriminate clearly between klinotactic and tropotactic orientation. A very elegant experimental design was first applied by Rupprecht (1968) who glued metal filings to the legs of stoneflies, which allowed him to vibrate single legs independently by means of an electromagnet. By vibrating one leg only he could show that stoneflies turn in the direction of the vibrated leg (Fig. 12.5). This strongly suggests that directional information can be extracted by the stonefly, but does not allow one to draw conclusions about the directional cue that is employed. Wiese (1974) improved this method by vibrating the four legs of the backswimmer that contact the water surface with four electromagnets independently (see Sect. 12.6.6).

12.5 Behavioral Evidence for Vibrational Orientation in Insects

There are several studies indicating that insects can localize the source of vibration. Virant-Doberlet et al. (2006) carefully reviewed behavioral evidence that supports the idea that insects can accurately localize the source of vibration. To localize the source of vibration does not require the insect necessarily to exhibit directional reactions. It could just by chance arrive at the source and then detect it. For example, the drywood termite *Cryptotermes secundus* prefers, in dual choice experiments, wood, i.e., food pieces, that were vibrated over not vibrated pieces (Evans et al. 2007). Clearly the termites detect the vibrations and may show some kind of kinesis, but whether they orientate to the source of vibration, i.e., display a vibrotaxis, remains open. Studies suggest that host-associated vibrations are exploited by parasitic wasps (for review, see Meyhöfer and Casas 1999). *Pimpla turionellae*, for example, employs self-produced vibrations to detect its hosts (Wäckers et al. 1998). However, no study shows vibrotaxis in parasitic wasps.

There are a great number of studies demonstrating that insects arrive at the source of vibration under closed-loop conditions (Virant-Doberlet et al. 2006). As it is often difficult to differentiate whether insects show kinesis or taxis, and closed-loop experiments do not allow one to differentiate between klinotaxis and tropotaxis, we focus on open-loop experiments, which are suitable for distinguishing between klinotaxis and tropotaxis. Table 12.1 provides a summary of the studies demonstrating vibrotropotactic orientation in insects. The studies are compared concerning the species, substrate, behavioral context, and experimental design. So far as it is known, the vibrational cues (Δt and Δd) used for orientation are given.

12.6 Case Studies

In the following, we review what is known about vibrotaxis in some particularly well-studied species. Our selection aims to show the different experimental approaches that have been used and, as far as known, which kind of taxis and which kind of vibrational cue are used by the insects to orientate. Therefore, we first describe the behavioral context and very briefly what is known about the substrate's characteristics relevant to vibrational orientation.

12.6.1 Stinkbugs

The ability of insects to localize the source of vibrations is particularly well studied in the context of mate location behavior in stink bugs. In *Nezara viridula*, the female produces rhythmic calling songs. A male located on the same plant, answers and

Table 12.1 Studies Demonstrating Vibrotropotactic Orientation in Insects

Species	Context	Design	Cue	References
Plant stems				
Atta cephalotes	RC	PB, Y branching	na	Roces et al. (1993)
Atta sexdens	RC	PB, two platforms	$\Delta t = 0.1$ ms	Hager et al. (2017)
Conocephalus nigropleurum	ML	PB, T maze	na	De Luca and Morris (1999)
Euschistus heros	ML	PB, two platforms	$\Delta t = 0.2$ ms $\Delta d = 1$ dB	Kirchner et al. (2017)
Nezara viridula	ML	PB, two platformsLC, branching	$\Delta t = 0.1$ ms $\Delta d = 3$ dB$\Delta t = 0.3$ ms	Hager et al. (2016) Prešern et al. (2018)
Perla marginata	ML	MF, 2D	na	Rupprecht (1968)
Telenomus podisi	HL	PB, Y maze	na	Laumann et al. (2007)
Tettigonia cantans	ML	PB, Y branching	na	Latimer and Schatral (1983)
Soil and sand				
Euroleon nostras	PL	PB, 2D	na	Fertin and Casas (2007), Mencinger-Vračko and Devetak (2008)
Gryllus bimaculatus	ML	PB, Y maze	na	Weidemann and Keuper (1987)
Macrotermes natalensis	AC	PB, two platforms	$\Delta t = 0.2$ ms	Hager and Kirchner (2014)
Water surface				
Gerris remigis	PL	PB, 2D	na	Murphey (1971)
Notonecta glauca	PL	MF, 2D	phase $\Delta t = 8$–16 ms	Wiese (1974)
Notonecta undulata	PL	PB, 2D	na	Murphey (1973)

AC alarm communication, *ML* mate location, *HL* host location, *RC* recruitment communication, *PL* prey location, *PB* playback, *LC* live couple, *MF* magnetic field, Δt time-of-arrival difference, Δd amplitude difference, *na* not available

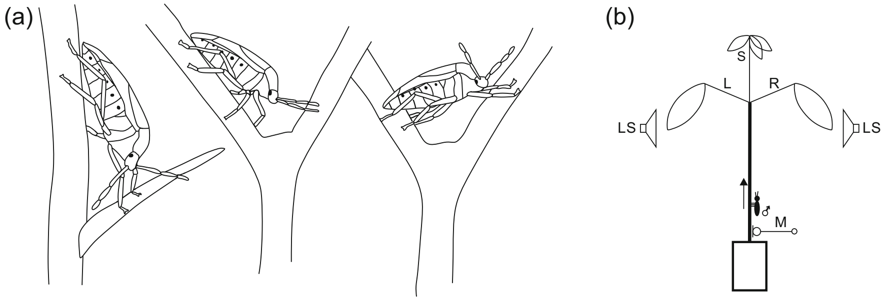


Fig. 12.1 (**a**) Behavior of male *Nezara viridula* at a petiole—the male straddles the forelegs across the fork, places its antennae on the opposite stem, or straddles its legs on the opposite stem (modified from Ota Ota and Čokl 1991). (**b**) Experimental setup used during directionality tests on a bean plant. L: left branch; R: right branch; M: microphone for monitoring the bug's responses; S: middle stem; LS: loudspeaker (modified from Čokl et al. 1999)

searches for the female. When encountering branching points, the male stops and straddles its legs across the fork to compare the vibrations in the two branches (Fig. 12.1) (Ota and Čokl 1991; Čokl et al. 1999). Measurements of vibrational signals on plant stems show significantly different amplitudes and arrival times between the two different branches (Virant-Doberlet and Čokl 2004). It has been shown that differences in amplitude and frequency cause different neuronal responses (Čokl 1983), and Čokl et al. (1999) proposed that time-of-arrival and amplitude differences are used as directional cues. On the host bean plants, the propagation velocities of the bending waves are between 40 ms^{-1} and 80 ms^{-1} (Michelsen et al. 1982; Čokl and Virant-Doberlet 2003). With a leg span of 1 cm this creates a time-of-arrival difference between 0.12 ms and 0.25 ms. As the males straddle their legs across the fork to compare the vibrations while searching for the female, the distance between the legs can reach up to 2 cm. This would increase the time-of-arrival delay to up to 0.5 ms (Čokl and Virant-Doberlet 2003; Virant-Doberlet et al. 2006).

Experiments on natural plants, however, do not allow the examination of whether male *N. viridula* use amplitude or time-of-arrival differences to find the female. This question can be answered by vibrating the legs independently and thereby creating time-of-arrival or amplitude differences between receptors. This method enables us to examine both parameters independently. Stink bugs, standing with the legs of one side of the body on a vibrating bridge and with the legs of the other side of the body on a bridge vibrating a short moment later, turn toward the bridge that vibrates first (Hager et al. 2016). Time delays of 0.1 ms are detected and used for tropotactic orientation (Fig. 12.2a). This clearly shows that the stinkbug's temporal resolution matches with the time delays occurring in natural substrates. In experiments with amplitude differences, stinkbugs turn to the side vibrating more. Amplitude differences of 3 dB are sufficient for tropotactic orientation (Fig. 12.2b). Whether such an amplitude difference reliably occurs on plants is under discussion (Mazzoni et al. 2014; see Sect. 12.4). Furthermore, contrary

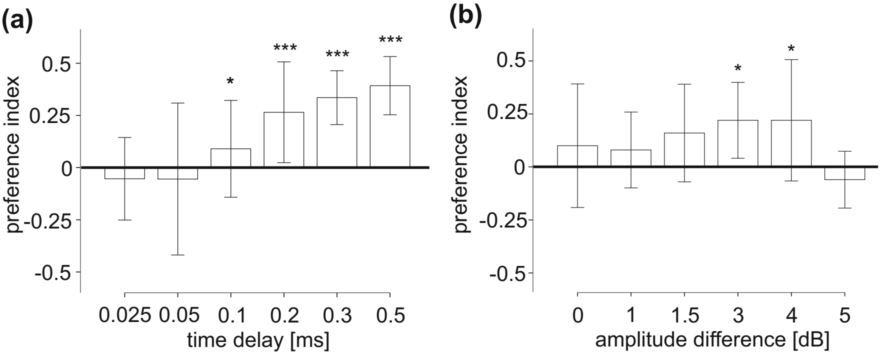


Fig. 12.2 (**a**) Behavioral response of male *Nezara viridula* standing on two bridges that were vibrated independently. Preference indices in relation to the time delay of vibrational stimuli generated with the two bridges. (**b**) Preference indices of *N. viridula* in relation to amplitude differences (Hager et al. 2016)

combinations of a time-of-arrival and amplitude differences were tested. It was possible to counterbalance time-of-arrival differences with amplitude differences (Hager et al. 2016). This could be explained by decreasing latency of the vibratory interneurons with increasing stimulus intensity, as it was found in a cave cricket (Stritih 2009).

Recently a very comprehensive study revealed that on bean plants (*Phaseolus vulgaris*) only time delays are reliable cues (Prešern et al. 2018). At the junction between the main stem and the leaf stalks, the male placed his legs on different sides of the branching and orientation at the branching point was not random. Measurements with laser vibrometers clearly show that only a time delay between the arrival of vibrational wave to receptors located in the legs stretched across the branching was a reliable directional cue underlying orientation, since the signal amplitude at the branching point was often higher on the stalk away from the female (Prešern et al. 2018).

12.6.2 Antlions

Antlions are sit-and-wait predators that dig a funnel-shaped pit into loose sand. They sit on the ground within the trap and wait motionless for their prey to approach. The remarkable ability of directional vibration sensing in antlions was recently reviewed by Devetak (2014). As soon as an antlion detects prey, the head and forelegs are moved to collect sand. Subsequently, the sand is tossed with a violent jerk of the head and prothorax in the direction of the prey; thereby a sand avalanche, which eventually pulls the prey in the trap, is caused (Devetak 1985; Mencinger 1998; Fertin and Casas 2007; Mencinger-Vračko and Devetak 2008).

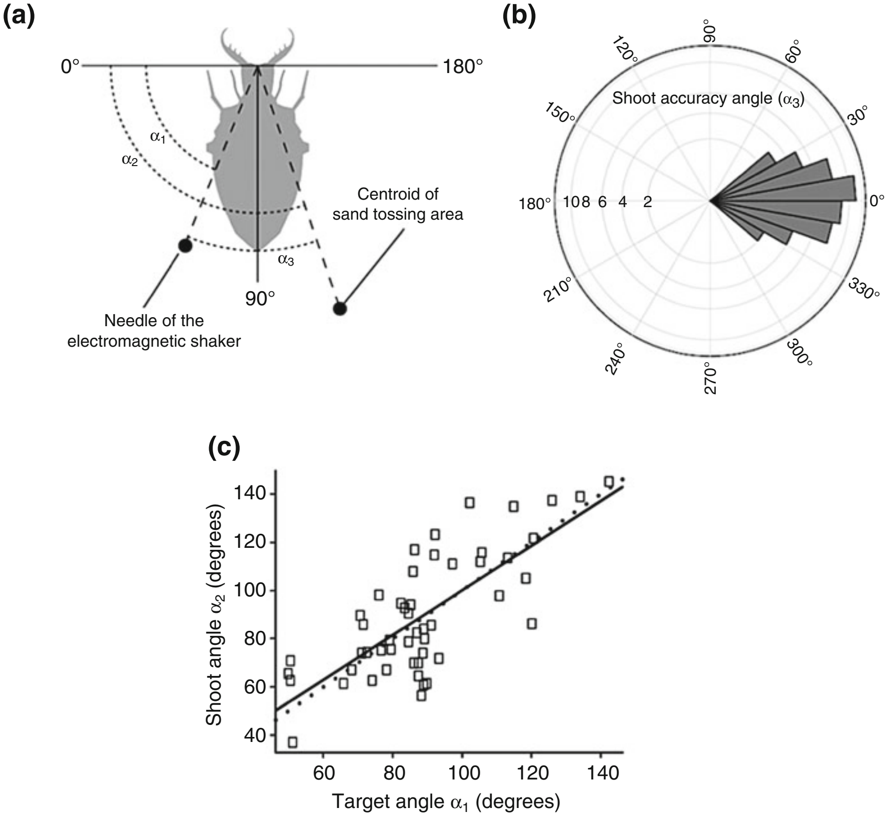


Fig. 12.3 Vibrotropotactic orientation in *Euroleon nostras*. (**a**) Reference frame and angle definition. $\alpha 1$, angle to the tip of the electromagnetic shaker; $\alpha 2$, angle to sand tossing area; $\alpha 3$, angle between tip location and sand tossing area, reflecting the precision of sand tossing. (**b**) Circular distribution of the precision angle of sand tossing ($\alpha 3$). The area of each sector is proportional to its frequency. The scale is indicated on the left half of the circle. (**c**) Angle of sand tossing ($\alpha 2$) as function of the angle of the tip ($\alpha 1$). This response is linear (solid line) and close to the perfect response (dotted line) (Fertin and Casas 2007)

In open-loop experiments, substrate-borne vibrations induced by walking ants were played back with electromagnetic shakers. The angle of sand tossing is a linear function of the angle of the electromagnetic shaker tip with near-perfect correlation—the antlion *Euroleon nostras* throws sand in the direction of the vibration source (Fig. 12.3) (Fertin and Casas 2007). Covering the larval photoreceptors does not affect the antlion's localization ability, thus vision as a directional cue can be excluded (Mencinger-Vračko and Devetak 2008). Antlions usually occupy fine sands or sands with medium particle size (Devetak and Arnett 2015). In those substrates, attenuation with distance is moderate (Devetak et al. 2007). Amplitude differences between receptors might therefore be too small to be detected. Surface

Rayleigh waves in dry loose sand travel with velocities of about 25–35 ms^{-1}, corresponding to time-of-arrival differences in the range of 0.2–0.5 ms, which are most likely in a detectable range (Mencinger-Vračko and Devetak 2008; Devetak 2014). Since it is not possible to investigate the role of amplitude and time-of-arrival differences independently in natural substrates, it remains open which one is the directional cue.

12.6.3 Termites

The termite *Macrotermes natalensis* communicates using vibrational drumming signals transmitted along subterranean galleries (see Chap. 16). 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 (Hager and Kirchner 2013). Soldiers make use of directional vibration sensing in the context of colony defense. Under closed-loop conditions at the nest surface, soldiers are recruited toward the source of the signal. In arena experiments on natural nest material, soldiers can localize the source of vibration. Experiments under open-loop conditions with two movable platforms allowing one to vibrate the legs of the left and right sides of the body with a time delay show that the difference in time of arrival is a directional cue used for tropotactic orientation (Fig. 12.4). Delays as short as 0.2 ms are sufficient to be detected. Soldiers show positive tropotaxis to the platform vibrating earlier (Hager and Kirchner 2014). The

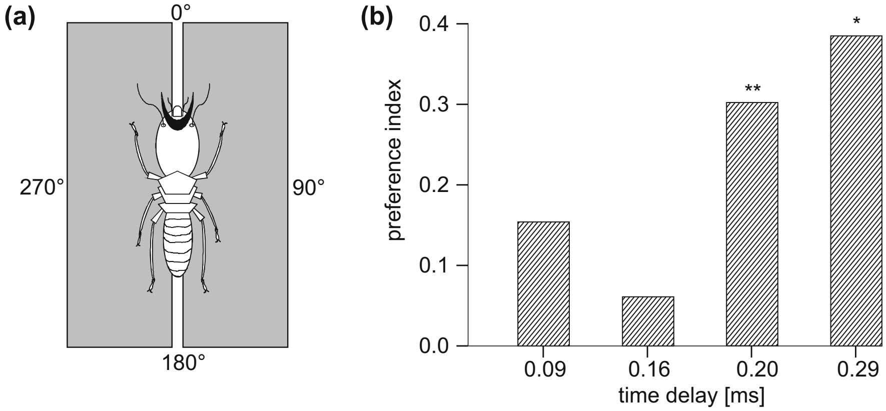


Fig. 12.4 (**a**) Experimental setup for the behavioral test of vibrotropotaxis in *Macrotermes natalensis*. The vibrational stimulus was triggered by an observer when the termite straddled the experimental setup, with the legs of one body side on one platform and the legs of the other body side on the other platform. (**b**) Preference indices of *M. natalensis* in relation to the time delay of vibrational stimuli generated with two movable platforms (Hager and Kirchner 2014)

propagation velocity of the vibrational signal in the termites' nest is approximately 130 ms^{-1}, and with distance between the leg of 16 mm, time-of-arrival delays of 0.12 ms are created (Hager and Kirchner 2013). This is in the same range as the time delays detected by the termites. Whether amplitude differences are used, additionally, for vibrotaxis remains open.

12.6.4 Stoneflies

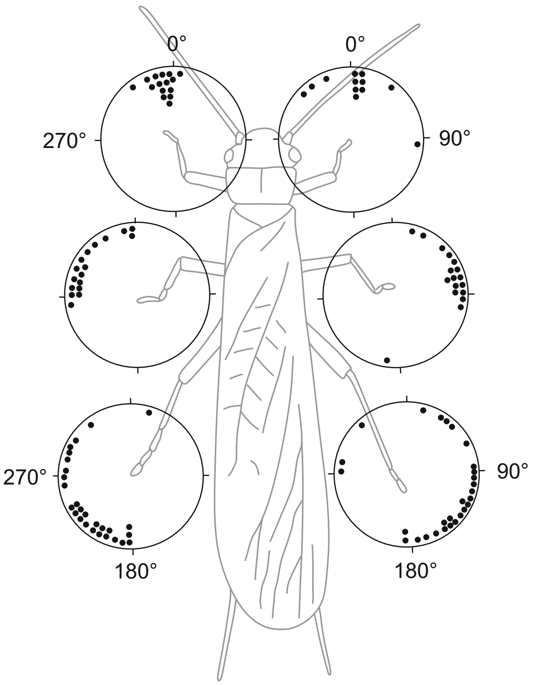
Stoneflies (Plecoptera) of the suborder Arctoperlaria have developed a very diverse and complex system of vibrational communication (Stewart and Sandberg 2006). Vibrational signals are produced by drumming, stridulation, and tremulation with either the unmodified or specialized distal ventral portion of the abdomen. In the context of mate location, a species-specific duet is established: the male call is answered by the female, and in some species the male then replies (Rupprecht 1968, 1969; Stewart and Sandberg 2006). In most species, males search for the stationary females. The transmission range of vibrational signals through dead plants in the medium-sized stonefly *Perlinella drymo* is up to 8 m (Stewart and Zeigler 1984). Several studies demonstrate that once a duet is established males find the female faster, compared to trials in which the females do not reply (Rupprecht 1968; Abbott and Stewart 1993).

In a pioneering study, Rupprecht (1968) carefully described the production, temporal pattern, and behavioral context of drumming signals in European stoneflies (Plecoptera). He could show that drumming signals travel through the substrate and are perceived by the subgenual organ in the legs. Moreover, he demonstrated in *Perla marginata* that substrate vibrations are used for orientation by gluing small iron filings to the tarsi and vibrating single legs with an electromagnet. The stoneflies turn in the direction of the stimulated leg (Fig. 12.5). If one of the front legs is stimulated, the stoneflies move ahead; if one of the hind legs is stimulated, the stoneflies turn around and move backward (Fig. 12.5). By stimulating a middle leg, the stoneflies move in circles (Rupprecht 1968). This is the typical behavior one can observe if one of two receptors is eliminated in insects normally performing tropotactic orientation. This study would probably have gained much more attention, if it had been published in English rather than in German.

12.6.5 Leafcutter Ants

Leafcutter ants communicate with the substrate-borne component of the vibratory emission produced by stridulation. They stridulate by raising and lowering their gaster, so that a cuticular file located on the first gastric tergite is rubbed against a scraper situated on the preceding third abdominal segment (Roces et al. 1993). *Atta sexdens* and *A. cephalotes* workers stridulate when they cut an attractive leaf.

Fig. 12.5 Vibrotropotactic orientation of the stonefly *Perla marginata* after the respective single legs were vibrated independently by gluing metal filings to the legs and vibrating with an electromagnet (modified from Rupprecht 1968)



The vibrations migrate along the body of the leafcutter ant and are transmitted from the ant's head to the substrate. Nearby workers respond to the vibrations transmitted through the plant material by orienting toward the source of the vibration and subsequently join in leafcutting (Roces et al. 1993; Roces and Hölldobler 1996). Workers also stridulate when they are buried by a cave-in of the nest and thereby attract other workers, which subsequently start to dig and rescue the buried ant (Markl 1967). Workers of *Atta vollenweideri* stridulate while engaged in nest digging and attract nestmates to join excavation activity at the same location, thus contribute to the spatial organization of collective nest building (Pielström and Roces 2012).

Open-loop experiments with two movable bridges reveal that time-of-arrival delays of the vibrational signals are used for tropotactic orientation in *A. sexdens* (Fig. 12.6). Ants, standing with the legs of one body side on a vibrating bridge and with the legs of the other body side on a bridge vibrating a short moment later, turn toward the side that vibrates first. With time delays down to 0.1 ms, ants turn more often to the side vibrating first (Hager et al. 2017). It is perfectly possible that time delays in this range can be found in natural substrates; although, leafcutter ants routinely move through different environments while foraging and are found on diverse surfaces such as the nest substrate, the surrounding soil, plant stems, and leaves. The transmission properties may dramatically differ from substrate to substrate. In this context, it would be interesting to analyze the vibrations produced

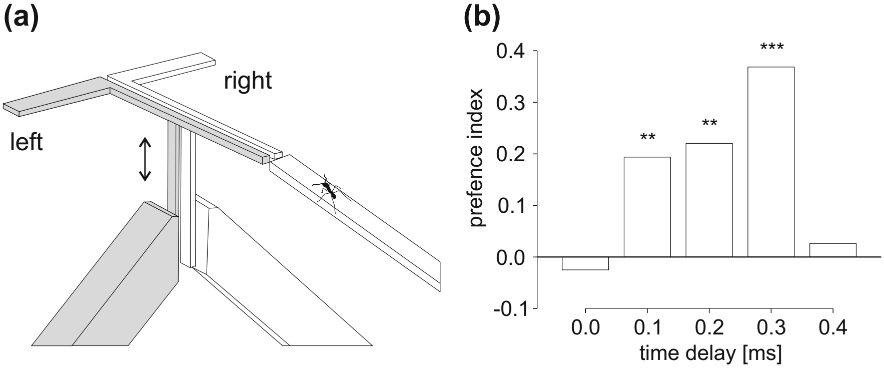


Fig. 12.6 (**a**) Experimental setup to test vibrotropotaxis in ants. Foraging *Atta sexdens* walked over a bridge to enter the experimental setup. Two L-bridges were vibrated independently with short time delays when an ant walked with three legs on one side and with the three other legs on the other side. (**b**) Preference indices of *A. sexdens* in relation to the time delay of the vibrational stimuli generated with the two movable bridges (Hager et al. 2017)

by signaling ants and to answer the question whether leafcutter ants pursue a generalist strategy by producing signals that are effective across the range of substrates they encounter.

12.6.6 Backswimmer

The well-studied backswimmer *Notonecta glauca* makes use of vibrational waves travelling on the surface of water to detect its prey. It swims upside-down and touches the water surface with the legs of the pro- and mesothorax and the tip of its abdomen. The two hind legs are specialized for strong swimming strokes that are directed toward prey that falls in the water. The struggling prey causes concentric boundary waves at the interface between air and water. The waves propagate across the two-dimensional plane and its velocity depends on surface tension, water density, gravity, wavelength, and water depth (Markl 1983). The attenuation of the wave's amplitude depends on its frequency, with high attenuation above some 10 Hz. For an attenuation of 6 dB, a 5-Hz wave may travel 6 cm, while a 140-Hz wave is already diminished by the same amount over only 0.7 cm distance (Lang 1980). Struggling prey insects on the water surface induce the strongest waves in the frequency range of 10–100 Hz (Wiese 1972). *N. glauca* is sensitive to surface vibrations of 5–300 Hz and the threshold is lowest at around 100 Hz, expressed as displacement, or between 5 and 20 Hz, expressed as acceleration (Markl and Wiese 1969). The dispersive characteristics of water surface waves, the vibrational cues emitted by the prey, and the perception threshold of the predator perfectly match at around 20 Hz.

The backswimmer's orientation toward prey, i.e., the source of vibration, is very precise. If the prey is in front of the backswimmer, it turns instantaneously with about 2° accuracy toward the prey. A source of vibration located behind the backswimmer induces responses with a slightly decreased accuracy of 18° (Markl et al. 1973). Wiese (1972) proposed that time-of-arrival and amplitude differences between receptors are used for tropotactic orientation. Electrophysiological experiments showed that sinusoidal waves in the frequency range of 0.5–150 Hz elicit one response of the phasic receptors per sine cycle. Having in mind that the backswimmer touches the water surface with four receptors in the legs and maybe one in the abdomen, it appears likely that time delays between responses of different receptors are transduced into the adequate turning angle.

Amplitude differences, however, appear unlikely to be compared accurately. This is mainly because the amplitude attenuation of the surface wave over a distance of 10 mm, this corresponds with the distance between the leg positions on the water surface, is much smaller than the perceptual threshold in the relevant frequency range (Wiese 1972). Wiese (1974) conducted an elegant experiment by gluing iron filings to the backswimmer's claws. Four electromagnets were allowed to vibrate the four legs independently (Fig. 12.7a). According to the distance between the insects' legs, i.e., vibration receptors, time delays, i.e., phase shifts of a traveling 20 Hz surface wave, were simulated (Fig. 12.7b). Simulation of surface waves evoked turning reactions well matching the expectations (Fig. 12.7c, d). This experiment clearly shows that time differences caused by phase shifts are used for tropotactic orientation. The time delays are in the range of 8–16 ms (Wiese 1974). Moreover, prey-induced vibrations show characteristic temporal structures and frequencies and the backswimmer makes use of these surface waves to discriminate prey from nonprey (Lang 1980).

12.7 Conclusion

Vibration sensing is at one end of a continuum in the mechanoreceptor-based 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 occurring on many substrates used for vibrational orientation. 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

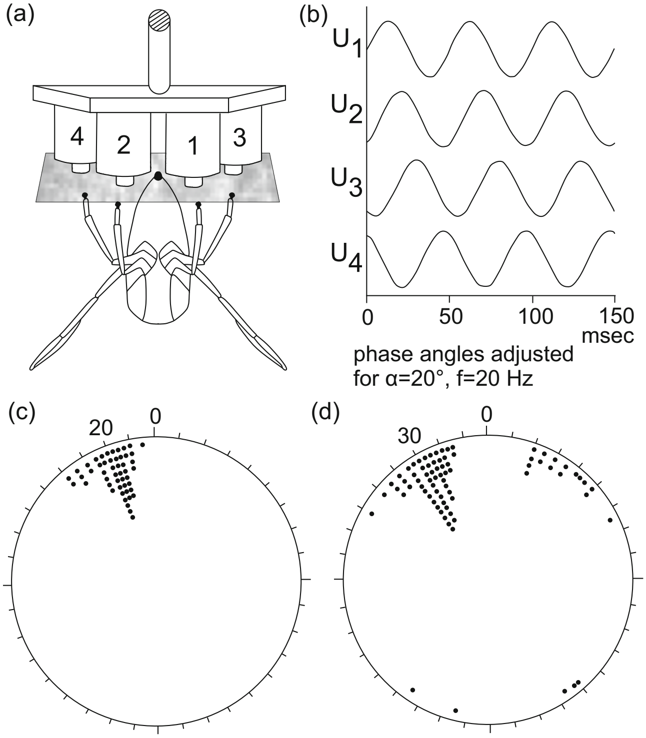


Fig. 12.7 Vibrotropotactic orientation in *Notonecta glauca*. (**a**) Experimental setup to simulate water wave stimuli. Iron filings were glued to the claws and vibrated independently by local alternating magnetic fields. (**b**) The shifting of phase angle corresponds to the travel times of the wave front between the four receptors under stimulation. (**c**) Reactions of *Notonecta* to simulated wave signals for $\alpha = 20°$ (**d**) and for $\alpha = 30°$ (modified from Wiese 1974)

apart, interaural time delays used for orientation are approximately 50 ns (Mason et al. 2001). 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 (Mason et al. 2001; Schöneich and Hedwig 2010). The latency of insects' neuronal responses is inversely related to the intensity of the stimuli (Gerhardt and Huber 2002). In the nonhearing cave cricket *Troglophilus neglectus* latency of the vibratory interneurons decreased with increasing stimulus intensity (Stritih 2009). At the integration level, such intensity-dependent time delays could enhance the time delay of arrival of the signal at different legs (Virant-Doberlet et al. 2006). On a physiological level, auditory perception is much better studied than vibrational perception. Since the vibratory mode is ancient, it would not surprise if similarly sophisticated mechanisms have evolved for directional vibration sensing. We can look forward to exciting findings in this field.

As shown here, behavioral studies reveal the remarkable ability of insects to orientate via vibrational cues and signals in various contexts. Future studies should combine behavioral, physiological, and physical aspects to gain a comprehensive understanding of directional vibration sensing. An interesting hypothesis could be tested by vibrating all six legs of free-moving insects, independently with electromagnets, as it was done by Rupprecht (1968). We may be surprised that such a clever method has not been applied with current technical achievements.

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