

Spatial orientation in the bushcricket *Leptophyes punctatissima* (Phaneropterinae; Orthoptera): I. Phonotaxis to elevated and depressed sound sources

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Received: 8 August 2006 / Revised: 11 October 2006 / Accepted: 15 October 2006
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Abstract Many species of acoustically interacting insects live in a complex, arboreal or semi-arboreal habitat. Thus mate finding by phonotaxis requires sound localization in the horizontal and vertical plane. Here we investigated the ability of the duetting bushcricket *Leptophyes punctatissima* to orient to one of three speakers, positioned at different levels in an artificial grid system, where each point in space could be reached by the male with almost equal probability. The system was designed analogous to a spherical calotte model of bismuth, where, once the male arrived at any nodal point had to decide between only three directions: either up or down and/or left and right. This design does not favour any phonotactic path of the males. All 12 males tested reached the three speaker positions (one in the horizontal plane, one elevated by 45°, one depressed by 45° relative to the starting position) with only little deviation from the shortest possible path. There was no significant difference with respect to the whole phonotactic time needed, the number of segments passed, or the number of stimuli received for the different speaker positions. This remarkable spatial orientation is achieved although the insects have no specialized external ear structures such as mammals, or some owls.

Keywords Bushcricket · Spatial orientation · Sound localization · Phonotaxis

Abbreviations

IID Interaural intensity difference
SPL Sound pressure level

Introduction

Sound localization in insects has been studied at various levels: behaviour, the physical cues available for the ear, the directionality of the ears, or the peripheral and central processing by receptors and interneurons (review Lewis 1983; Michelsen 1998; Pollack 2000). So far, almost all studies have been restricted to the perception of sound in the horizontal plane. One exception is a study on crickets which demonstrated—by using a habituation–dishabituation test—that flying crickets were able to discriminate between ultrasound sources separated in elevation (Wytenbach and Hoy 1997), confirming an observation by May et al. (1988) that flying crickets respond differently to ultrasound from above and below. The second exception is a behavioural study on the parasitoid fly *Ormia ochracea*, which exhibit a remarkable phonotactic accuracy in 3D space, so that after a flight distance of about 4 m the flies approach and land on a loudspeaker within close proximity (Müller and Robert 2001). However, since the one investigation deals with spatial acuity of ultrasound hearing in the context of nocturnal predation by bats, and the other with the acuity of a parasitoid to locate its host, nothing is known about spatial orientation of insects in the context of intraspecific communication.

The perception of source height, i.e., elevation and depression, is certainly significant for many crickets and bushcrickets, and probably some grasshoppers as

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well. The microhabitat used by many bushcrickets and crickets are trees and bushes, where the vertical position of signallers and receivers can differ by many meters, and thus spatial hearing is essential. Furthermore, many tropical Phaneropterine bushcrickets live in the rainforest at canopy or mid-canopy levels, and biologically important sounds may arise from positions above and below the receiver, as well as from different locations in azimuth.

Several reasons may contribute to our lack of knowledge with respect to spatial hearing in insects: one may be historical, because the first profound studies on the proximate mechanisms of hearing and acoustic communication in insects have been dominated by work on field crickets (review Huber et al. 1989; Gerhardt and Huber 2002), which were supposed to live and orient acoustically near the ground. Thus, sound localisation in the azimuth was supposed to be the only relevant task. Later researchers also discovered positive and negative phonotaxis of crickets in flight, where spatial hearing might become more relevant than for crickets walking on the ground (Popov and Shuvalov 1977; Moiseff et al. 1978; Huber et al. 1989). Furthermore, experimental paradigms for studying directional hearing have been applied either to flat arenas, to Kramer treadmills or to walking belts, all of which unsuited to study directional hearing in the vertical plane. And finally, the only valid hypothesis to explain spatial hearing derived from biophysical and behavioural work on mammals and birds like owls, with strong evidence that the detection of the elevation of a sound source depends either on pinnae in mammals or on ear asymmetries in owls (review in Knudsen and Konishi 1979; Heffner and Heffner 1992; Brown 1994). In mammals, the particular shape of the external pinna provides important information for the vertical orientation of a sound source because pinnae act as spatially dependent filters for sound (Butler and Belendiuk 1977; Blauert 1983; Fuzessery 1996; Wotton and Simmons 2000). As a result of this filtering spectral cues are created that humans and other mammals appear to use in localizing the elevation of a source.

However, Gerhardt and Rheinlaender (1982) were the first to demonstrate that the existence of such structures may not be essential for spatial hearing. They showed that green tree frogs *Hyla cinerea*, which lack pinnae or similar anatomical structures; readily localize an elevated sound source. Tree frogs and bushcrickets thus face a similar problem: both live in a complex, arboreal or semi-arboreal habitat and need to obtain cues about both azimuth and elevation of sound sources without having specialized ear structures.

In the present paper, we used a bushcricket species, which offers several advantages to investigate spatial hearing. *Leptophyes punctatissima* is a Phaneropterine bushcricket, which uses an elaborate communication system between male and female. Pair formation is achieved by duetting, where the male song elicits an acoustic reply in the female, to which the male then responds by phonotaxis with very high probability (Hartley and Robinson 1976; Robinson 1980; Robinson et al. 1986; Zimmermann et al. 1989; Bailey 2003). The male call is both a prerequisite for phonotaxis and a reliable indicator for the motivation of the male to orient to a female. Further, each following localization process can easily be recognized by the experimenter. Because the male with its short wings is unable to fly, phonotaxis occurs during walking, which facilitates video-monitoring and quantification. The vertical distribution of male and female *Leptophyes* can vary considerably during pair formation in the natural habitat, ranging from a position close to the ground to a height of up to 5–10 m in a tree (Rheinlaender and Robinson, unpublished observations). Thus, a male in nature must distinguish source positions in the azimuth and elevation to perform the phonotactic approach towards a female successfully.

We combined these advantages in a behavioural paradigm and present for the first time data on spatial hearing in the context of pair formation of an invertebrate.

Methods

Male and female *L. punctatissima* were collected as larvae during the early summer period of 2004 from wild stock locations in the vicinity of Nordkirchen (Germany). Both sexes were kept physically and acoustically isolated from each other in wooden cages (90 × 50 × 40 cm), supplied with their favoured plant food (*Urtica dioica*, *Heracleum spondylium*, *Cirsium vulgare*) and water ad libitum. Pair formation takes place about 1 week after the final moult of females. Only males 1–6 weeks after the final moult were used for behavioural experiments.

Phonotaxis was studied in an artificial grid system, in which each point in space could be reached by the male with equal probability. For this purpose we constructed the most simple model, analogous to a spherical calotte model of bismuth (Fig. 1a). The advantage of such a 3D-grid is that the male, when arriving at any nodal point has to decide between only three directions: either up or down and/or left and right (Fig. 1b). This is in contrast to a cubic model, where there are five possi-

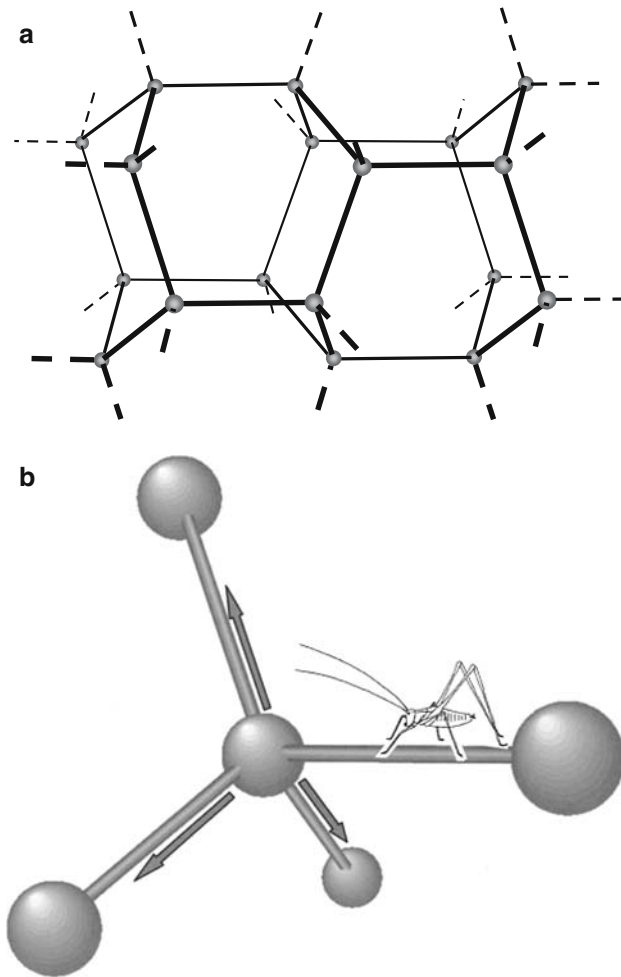


Fig. 1 **a** Section of the artificial grid system, based on a spherical calotte model of bismuth. **b** A male arriving at any nodal point has to decide between only three directions: either up or down and/or left and right. Note that neither the size of the insect relative to the grid system nor the size of rods and spheres is at scale. For further explanations see text

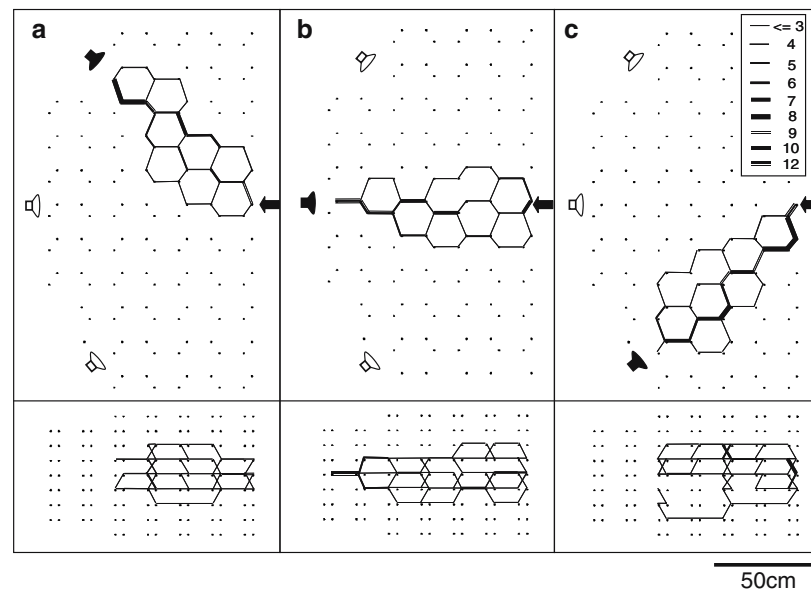
ble decisions for any nodal point and, more importantly, some directions would be biased due to a straight path relative to others. This is true only when the horizontal and vertical axis of the grid are oriented along the axis of the starting point to speaker, and the insect orients towards the source. With respect to the complexity of right–left and up–down decisions the design of the grid does not favour any phonotactic paths of the male, be it to horizontal or elevated/depressed speaker positions.

The grid model had dimensions of 169 cm in height (9 calottes), 62 cm in width (4 calottes), and 106 cm in length (6 calottes). The aim was that while orienting to one of the speakers a male should never reach the border of the grid, which would have caused a bias in the orientation. Three identical piezo tweeters (Motorola, bullet-type KSN1005) were miniaturized by removing

the horn, so that they had a diameter of 40 mm and a depth of 16 mm. They were suspended at the edges of the model, one in a horizontal direction from the starting point, and two others at 45° elevated or depressed positions relative to the starting point. Speakers were isolated by about 15 cm from the target sphere (see Fig. 2). They had no direct contact with the grid to prevent vibrational transmission of the signal from the active speaker. Furthermore it was guaranteed that also in the final phase phonotaxis took place only in the far field of the active speaker (Beranek 1954). The distance between starting point and each speaker was 105 cm. The whole grid was suspended 50 cm above ground level with two ropes attached to a solid bar, so that any vibration of the soil due to movement of the experimenter did not reach the grid.

The model was composed of wooden rods and spheres as nodal points; the distance between two nodal points was 13 cm. This dimension was adapted to the song rate and the walking speed of males, so that a male was expected to produce at least one song ahead of each decision point (but often more than one; see Results). Much care was taken to adapt the dimensions of the grid to the general orientation behaviour of the males. The diameter of the rods was 8 mm, similar to the size of the insect (body length 10–14 mm; diameter 3–4 mm). The size of the rods provided a regular walking pattern of the insect, with its body always above the rods, except for vertically oriented ones. The males could also turn their longitudinal body axis slightly to the right and left side, and in particular showed tilting movements, when on a horizontal rod (see below). In a grid system with a reduced size of the rods males abandoned this orientation behaviour, as has been shown in control experiments. Moreover, males often jumped, rather than walked continuously, in a grid with smaller rods; a behaviour which is quite unusual in normal phonotaxis. Jumping would also render the quantitative analysis of phonotaxis more difficult. The diameter of the spheres was 30 mm; each sphere was marked with a number/letter code for identification in the phonotaxis protocol (see below). This size generally induced a slight reduction in the speed of locomotion, so that the insects realized the sphere as a point of decision between different branching rods. Thus, the dimensions of rods and spheres represents a compromise between the need for providing a substrate for normal phonotactic movement, and a grid system which does not produce too strong scattering of sound with a signal of 40 kHz (wavelength 8.5 mm). Despite the fact that the rods and spheres must have caused some scattering of sound (e.g., when the speaker was in the depressed position and the insect walking on top of

Fig. 2 Superimposed phonotactic tracks of 12 males to elevated (a), horizontal (b) and depressed (c) sound sources. The top panels show the lateral view of the grid system, the lower panel the top view. Segments used by the males are indicated by lines, the thickness of lines represents the number of males which used a given segment during phonotaxis. The arrow indicates the starting position; the filled speaker symbol represents the active speaker broadcasting the female reply



a rod), the result would rather indicate that it did not affect the precision of orientation into this direction more than in any other direction (see Results).

Twelve males were tested successfully in phonotactic trials, each male once for the horizontal, elevated and depressed position of the speaker, respectively. All trials had the same starting position (see Fig. 2). The phonotactic path of a male was monitored via voice protocol by indicating the directional decision a male had made at each nodal point. Each song and the location where it was produced was also recorded via voice protocol. With these data the total song rate per phonotactic trial, its duration, and the number of songs per segment could be quantified. The succession of trials to horizontal, elevated and depressed speaker positions was randomised for each male. Because the speakers were not physically attached to the grid, males could not reach the speakers directly by walking. We therefore defined a phonotactic trial successful when a male reached the sphere in closest proximity to the target speaker.

Phonotaxis by male *L. punctatissima* can be elicited very reliably if a minimum set of parameters are fulfilled. Providing that a calling male receives a reply from a female at a frequency of 40 kHz, of short duration (1 ms) and within a given time window of 25–55 ms after its own song he will perform phonotaxis (Robinson et al. 1986; Zimmermann et al. 1989). If a male calls and there is no reply by the female, he does not perform any kind of phonotaxis, although he is highly motivated (evident in his song activity). In our experiments, the part of the female in the duet was mimicked electronically. The call of the orienting male

was recorded by a bat detector (QMC Instruments Ltd) placed above the grid. The frequency filter of the detector was set at 40 kHz (mean frequency of the male call), and its sensitivity adjusted so that the song could be recorded at each position of a male within the grid. The output of the bat detector triggered the generation of a synthetic female reply with a delay of 30 ms. This female reply was a click of 1 ms duration with a SPL of 80 dB (peak reading) at a distance of 20 cm to the speaker, corresponding to the SPL of a female reply at the same distance. The SPL of this signal at the starting point in the grid was about 60 dB. The male song also triggered a storage oscilloscope to monitor both the male song and the generation of the female reply.

Experiments were performed in open air above a lawn and at night, starting shortly after sunset. Ambient temperature varied between nights from 19 to 22°C. To exclude possible effects of moon- or starlight, an opaque curtain was positioned above the grid. Four red light bulbs were positioned at half the distance between release point and speakers, two above and below the grid, respectively. The intensity was controlled by a dimmer to provide just enough light for the experimenter to see both the male and its position in the grid by the letter/number code at the decision points.

We also performed control experiments with each of the 12 males to demonstrate the general locomotory behaviour without acoustic feedback. For this purpose the males were positioned in the centre of the grid. All males were highly motivated, as evident from their song rate, but since there was no acoustic reply, they

would not orient. Over a period of 10 min the calling and walking behaviour of males was monitored. If there would exist any non-acoustic orientational bias in the grid system, it should be evident in this experimental paradigm.

Results

When male *L. punctatissima* call they indicate a high motivation for communication with females. This was the case for all 12 males tested. As soon as the call elicited a female reply they performed phonotaxis and reliably reached the sound source, irrespective of its spatial location. The phonotactic tracks are documented in Fig. 2, and described quantitatively in Table 1. The figure shows the superimposed tracks from a lateral and top view of the grid. With the active speaker oriented in the horizontal plane, all males deviated in their path towards the speaker by no more than one calotte element from the ideal path, both in the horizontal and vertical plane. Also, with the active speaker either elevated or depressed by 45° relative to the starting position all males reached the target with a similar amount of deviation (see in particular the top views in Fig. 2).

In the control experiments, the same highly motivated males were placed in the centre of the grid without providing them with the artificial female reply. Their subsequent locomotory pattern over the next 10 min varied strongly between males (Fig. 3). Three males actually remained at the release site while still singing or moved over only a few segments, whereas the remaining males moved into various directions, mostly upwards and rarely downwards. Two males reached the border of the grid after some minutes, and were immediately replaced to the starting position. Although there was some tendency for males moving upwards, no male oriented either to one of the silent speakers or to any of the light bulbs, so that visual orientation to one of these targets can be excluded. Furthermore, when males received no female reply their

song interval was more than doubled (mean 6.8 s; compare with values in Table 1).

Each phonotactic path is composed of a given number of segments between two spheres. The number of segments a male used for the approach is a measure of the precision of the phonotactic path. This is of course true only when males walk rather than jump; in none of the trials males jumped. This lack of jumping is confirmed in earlier orientation experiments in the horizontal plane (Hardt 1988; Zimmermann et al. 1989) and was also confirmed in the field (Rheinlaender and Robinson, unpublished). The mean value of segments in a phonotactic trial ranges from 11.9 to 12.9, and thus only one to two segments more than the shortest possible path. More importantly, with the three speaker positions there is no difference in the shortest possible path towards the target (Kruskal–Wallis One Way ANOVA on ranks, $P > 0.05$).

We also measured the time needed by each male for its phonotactic approach, which exhibited some inter-individual variation, but again there was no difference for different target positions (Table 1; horizontal 112 ± 19.6 s; elevated 116.6 ± 21.7 s; depressed 115.4 ± 18.1 s; One Way ANOVA, $P > 0.05$). Although all males demonstrated a high motivation for pair formation in general, males varied in the total number of songs produced for a given approach (horizontal 35.5 ± 7.0 ; elevated 37.4 ± 7.7 ; depressed 38.5 ± 7.8). However, there was no statistical difference for approaches to different speaker positions (One Way ANOVA, $P > 0.05$). The same was true for the song intervals (horizontal 3.2 ± 0.6 ; elevated 3.2 ± 0.6 ; depressed 3.1 ± 0.5). The number of songs produced by males per segment is summarized in Fig. 4 for all speaker positions. There is a high probability for the production of at least one song during the passage of one segment. In only three of a total of 503 segments passed by the 12 males there was no song produced. Thus only in these few cases a male did not receive new information regarding the spatial location of the target through the female reply.

Table 1 Summary of quantitative values for the spatial orientation of the 12 males to horizontal, elevated and depressed speaker positions

Speaker position	Duration of phonotaxis [s] (mean \pm SD)	No. of song cycles (mean \pm SD)	No. segments passed (mean \pm SD)	Call interval [s]
Horizontal	112 ± 19.6	35.5 ± 7.0	12.9 ± 1.0	3.2 ± 0.6
Elevated	116 ± 21.8	37.4 ± 7.7	12.9 ± 0.9	3.2 ± 0.6
Depressed	115.4 ± 18.1	38.5 ± 7.9	11.9 ± 0.8	3.1 ± 0.5

For further explanations see text

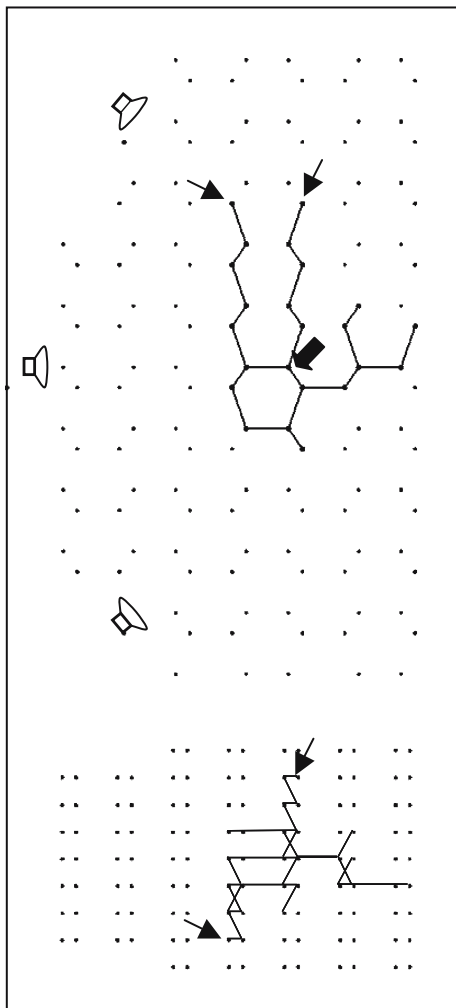


Fig. 3 Result of the control experiments with the movement pattern of the same 12 males observed over 10 min. Males were singing but they received no female reply. The *large arrow* indicates the starting position, *small arrows* indicate the position where males reached the lateral borders of the grid system. Note the random movement with respect to speaker positions. For further explanations see text

Discussion

Leptophyes punctatissima appears to be an ideal experimental subject to study spatial orientation: the duetting mode of communication provides the male with a self-triggered female reply and thus a reliable information about her position. The high rate of male song and female reply on the one hand, and the subsequent locomotory orienting response on the other, guarantees a step-by-step phonotactic approach over considerable distances. Each of these steps can be distinguished and analysed quantitatively by appropriate methods. The

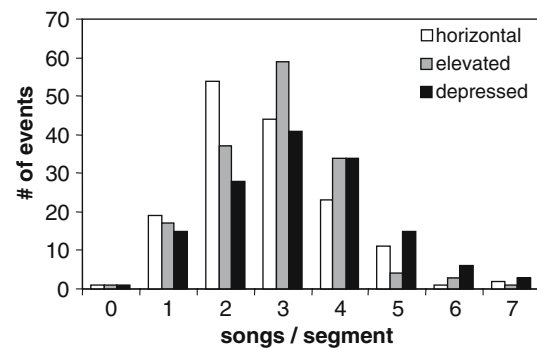


Fig. 4 Number of songs produced per segment for horizontal, elevated and depressed speaker positions (12 males). Note that in only 3 of 506 cases a male produced no song, and thus received no directional information, on a segment. The mean number of songs per segment does not differ for the speaker positions

male song lasts for about 15 ms, the latest female reply eliciting a male motor response is at about 55 ms, and the onset of the male turning response occurs at about 150–200 ms after receiving the reply (Hardt 1988; Zimmermann et al. 1989). Therefore all phonotactic responses principally occur under open loop conditions. This contrasts with many other insect acoustic communication systems, where the male calls either more continuously or with longer duration, to which then the receptive female responds by phonotaxis. Consequently, the single orienting event is hard to define for the observer, and necessarily it takes place under closed loop conditions. Despite these differences between insect taxa one common feature is the repetitive mode of their orienting behaviour. This is different to the spatial orientation of birds and mammals, where single acoustic events have been shown to be sufficient for eliciting often very precise orientation movements (Popper and Fay 2005).

Although directional hearing has been studied extensively in insects at the level of behaviour, biophysics and neurophysiology, almost nothing is known about spatial orientation in the context of pair formation (Gerhardt and Huber 2002). *L. punctatissima* lives in habitats of tall grass, bushes and even trees, so that males and females are commonly separated in the horizontal and vertical plane. Therefore spatial hearing is a prerequisite for pair formation. The results clearly demonstrate that male *L. punctatissima* easily localized and approached both horizontal and elevated/depressed sound sources.

The artificial grid system used in the experiments was an appropriate paradigm to study this behaviour. First, the construction based on spheres and intersphere segments provided no bias for any of the speaker positions, which would have been the case e.g., with a cubic grid system. The dimensions of the rods

were similar to those of twigs and leaves in a natural habitat and the speed of movements was comparable to that observed in the field (own observations), and on a walking compensator (Hardt 1988; Ofner et al. 2005). Importantly, the analysis of the male calling rate during phonotaxis demonstrated, that during the passage of each rod the male called at least once with high probability and thus received the directional information from the synthetic female (Table 1). This information could be used at the next sphere for a right–left and/or up–down decision. Obviously, males used this information sequentially because the actual path taken by males was quite close to the ideal, shortest possible path in the grid (see Table 1, number of segments/approach). We can therefore define each sphere as a decision point, although we do not know whether the actual decision was made precisely at the sphere or immediately at the time when receiving the female reply.

How does *L. punctatissima* achieve such a spatial resolution? *Leptophyes* has a typical Phaneropterine bushcricket ear, where the sensory organ is located in the tibia of the foreleg. Both anterior and posterior tympanal membranes are exposed, with no tympanal cavities or slits developed. Furthermore, a typical anatomical feature of the ear is a spiracular opening in the side walls of the prothorax, which is supposed to conduct the sound via the large leg trachea to the inside of the ear. There are of course no other anatomical structures such as external ear asymmetries, like in owls, or pinnae, like in mammals, which could be used for azimuthal sound localization (for a review on external ear structures in bushcrickets see Bailey 1990). So far, the directionality of the ear is only known in the horizontal plane, which results from direction-dependent sound diffraction around the thorax at the opening of the spiracle (Michelsen et al. 1994). The maximal interaural intensity difference (IID) thus achieved has been measured both behaviourally and neurophysiologically in unilaterally deafened male *L. punctatissima*, and varied between 13 and 19 dB (Rheinlaender et al. 1986). Based on these findings, and on preliminary neurophysiological data on spatial hearing in *Leptophyes* (Kostarakos et al. 2005), Fig. 5 shows a model for the changes in IIDs associated with an elevated sound source. With the sound source in the horizontal plane or 30° elevated, large IIDs are established when the insect turns left or right and thus the sound incidence is at more lateral positions. With increasing elevation of the sound source, the resulting IIDs decrease for any azimuthal angle, as shown schematically for elevations of 60° and 75° in Fig. 5. Based on this principal pattern of changes in IIDs we suggest the following mechanism

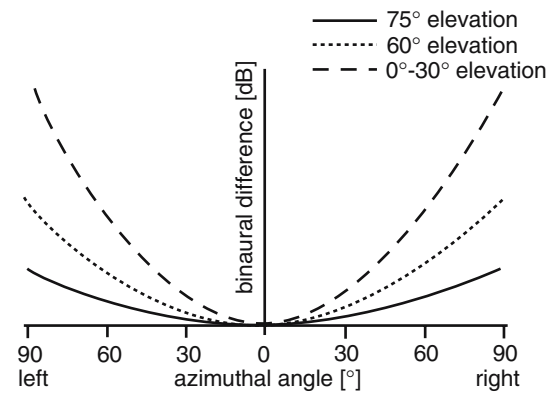


Fig. 5 Hypothetical proximate mechanism for the behavioural performance of male *L. punctatissima* during phonotaxis towards elevated or depressed sound sources. The model assumes, that when the insect performs a turning in the azimuth, the magnitude of changes in interaural intensity differences is larger than if the sound source is at more elevated positions. By comparing the magnitude of these changes, the insect would get an indirect measure of the amount of source elevation. This mechanism requires a sequential comparison of binaural cues with successive localisation events

for spatial orientation in *L. punctatissima*. Bushcrickets typically approach a sound source in a meandering pattern and with successive orientation movements (Römer and Rheinlaender 1989). If the sound source is in the horizontal plane, the magnitude of changes in IIDs is independent of its distance to the speaker and does not change during the course of the phonotactic approach. However, if the insect approaches an elevated sound source from a distance and stays in the horizontal plane, the model predicts a systematic decrease of IIDs, because the source would virtually move to a more elevated position. Thus, successive sound localization provides the insect indirectly with reliable information regarding the elevation of the sound source. An important point for this mechanism is that it requires a sequential comparison of binaural cues with successive localisation events.

Such a model for the proximate mechanism of spatial orientation is supported by a special behaviour of male *L. punctatissima*, which most often occurred in the initial phase of an approach: males tilt their head and thorax in a downward direction by up to about 90 degrees relative to the horizontal plane. This movement is often associated with a shift of the longitudinal body axis by up to 30° to either side, and also with bending the dorso-ventral axis to left and right. Such behaviour occurs while the male is stationary and still singing. It has never been observed in males not motivated for mate finding, as indicated by their singing activity. This kind of tilting behaviour, given the speaker is in the horizontal plane, produces a virtual

shift of the source into the elevated position. As a result, the IIDs decrease without an approach. By contrast, if the source would be in a depressed position, the same tilting behaviour would produce a virtual shift of the source into the horizontal plane, resulting in an increase in IIDs. We suggest that this tilting behaviour is second kind of sequential spatial analysis.

The core of our model for spatial orientation in this bushcricket is the suggestion, that this orientation requires a sequential analysis of binaural cues, thus involving memory. Ongoing behavioural experiments are devoted to this question.

Acknowledgments Funding was provided by the Austrian Science Foundation (FWF), Project P14257-BIO to HR.

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