

Mechanisms underlying phonotactic steering in the cricket *Gryllus bimaculatus* revealed with a fast trackball system

B. Hedwig* and J. F. A. Poulet

University of Cambridge, Department of Zoology, Downing Street, Cambridge CB2 3EJ, UK

*Author for correspondence (e-mail: bh202@cam.ac.uk)

Accepted 13 December 2004

Summary

Phonotactic steering behaviour of the cricket *G. bimaculatus* was analysed with a new highly sensitive trackball system providing a spatial and temporal resolution of 127 μm and 0.3 ms, respectively. Orientation to artificial calling songs started at 45 dB SPL, it increased up to 75 dB SPL and then saturated. When exposed to two identical patterns of different intensity, crickets significantly steered towards the louder sound pattern, whenever the intensity difference was greater than 1 dB. Bilateral latency differences in sound presentation did not always cause clear orientation towards the leading side. The overall walking direction depended on the number of sound pulses perceived from the left or right side with the animals turning towards the side providing the larger number of pulses. The recordings demonstrated rapid changes in walking direction performed even during a chirp. These rapid steering responses occurred with a

latency of 55–60 ms, well before the central nervous system had time to evaluate the temporal structure of a whole chirp. When every other sound pulse was presented from opposite directions, the crickets followed the temporal pattern of sound presentation and rapidly steered towards the left and right side. Steering towards individual sound pulses does not agree with the proposal that crickets analyse the quality of sound patterns and then steer towards the better pattern. Rather, these experiments suggest that fast steering to single sound pulses determines the lateral deviation of the animals and that complex auditory orientation emerges from this simple mechanism of auditory steering.

Key words: cricket phonotaxis, track ball system, sound localisation, steering, pattern recognition.

Introduction

The primary physical cues animals can exploit to analyse the direction of a sound source are interaural amplitude differences and interaural time differences of a sound wave approaching each ear. Once processed by the biomechanics of the hearing system, mechanosensory transduction and coding by the auditory afferents provides the animal's central nervous system with information to calculate the direction of a sound source (Lewis, 1983; Michelsen, 1998; Hennig et al., 2004). Female crickets are attracted by the males' calling song (Regen, 1913). From treadmill experiments with intact and single eared crickets (*Gryllus campestris*) the general rule 'turn to the louder side' was proposed as the most simple rule to stabilize the direction during phonotactic walking (Huber et al., 1984; Schildberger, 1994). Any deviation from the direction of the sound source would initiate counter turnings and, thus, stabilize the animal's path. This most parsimonious rule for auditory orientation, however, does not consider the significance of pattern recognition for orientation. The use of acoustic signals for intraspecific communication and mate attraction requires not only the localization of the sound source but also the recognition of the species-specific signal. Thus, the animal's auditory

orientation may additionally depend on the quality of the perceived pattern.

The existence of two bilaterally paired recognisers that allow crickets to choose between two sound patterns was first proposed by Pollack (1986). In two-stimulus situations crickets (*Teleogryllus oceanicus*) preferred the conspecific pattern to a heterospecific song, which was seen as the result of two interacting recognisers. Stabel et al. (1989) and Wendler (1990) exposed walking crickets to two sounds simultaneously and demonstrated that the animals walk towards the side where the sound pattern is better represented in the activity of ascending auditory neurons. They concluded that the recognition process is based on the temporal pattern of the neuronal activity and postulated that recognition and localization are performed sequentially with two central nervous recognisers, one on each side of the body, whose output is compared either in the brain or at the thoracic motor networks. The selective response of identified auditory brain neurons to temporal patterns indicated that corresponding pattern recognition networks might be located in the protocerebrum (Schildberger, 1984, 1994). This model has become an accepted view on pattern recognition and

localization in the crickets *G. bimaculatus* and *G. campestris* (Horseman and Huber, 1994; Helversen and Helversen, 1995; Pollack, 1998, 2000; Stumpner and Helversen, 2001; Hennig et al., 2004). Consequently, when simultaneously exposed to two sound sources crickets are expected not just to turn to the louder side but to the better pattern (Helversen and Helversen 1995; Helversen 1997).

The cricket's ability of pattern recognition is always deduced from the animals' steering or orientation behaviour in flight (Ulagarai and Walker, 1973; Nolen and Hoy, 1986; Pollack and Hoy, 1979) or walking (Murphey and Zaretsky, 1972; Popov and Shuvalov, 1977). Major experiments in walking crickets were based on female phonotaxis performed on treadmills that provided the mean walking velocity and the overall path of the walking cricket, but due to low resolution could not reveal information about the rapid dynamics of the underlying steering behaviour (Weber et al., 1981; Schmitz et al., 1982; Doherty and Pires, 1987; Doherty 1991). We recently developed a highly sensitive trackball system, which allowed us to measure cricket walking behaviour at the level of the animals stepping cycle (Hedwig and Poulet, 2004), an accuracy not achieved in previous experiments. With this system we analysed the fast dynamics of cricket auditory steering and investigated the impact of intensity differences, time differences and split-song paradigms on cricket auditory orientation and the implication for pattern recognition.

Materials and methods

Animals

Female crickets (*Gryllus bimaculatus* de Geer) were taken as last instars from a crowded colony of the Department of Zoology. They were isolated from any singing males and raised individually to enhance phonotactic responsiveness (Cade, 1979). The animals had unlimited access to water and dried pet food. About 5–10 day after the final moult a metal pin (weight 32 mg, cricket weight: 1200–1300 mg) was waxed vertically to the abdominal tergites, close to the animal's centre of gravity. The cerci were covered with wax, to prevent the animals responding to air currents. The crickets were tethered by a needle holder and were positioned in natural walking posture on the top of a trackball (Fig. 1A). Experiments were performed under open loop conditions. While the animals rotated the trackball with their legs, their body position and orientation remained stationary. All experiments were performed in the dark at a temperature of 24–28°C.

Trackball system

A trackball, with a diameter of 56.5 mm and a weight of 3.0 g, was manufactured out of Rohacell 31 (Röhm KG, Darmstadt, Germany). The surface of the ball was speckled with black ink to enhance its optical contrast. The ball fitted into a transparent acrylic half-sphere, which contained 24 holes and was mounted on top of a small cylinder. The cylinder was connected to a constant air supply and the air pressure was adjusted so that the trackball was gently lifted and was free to

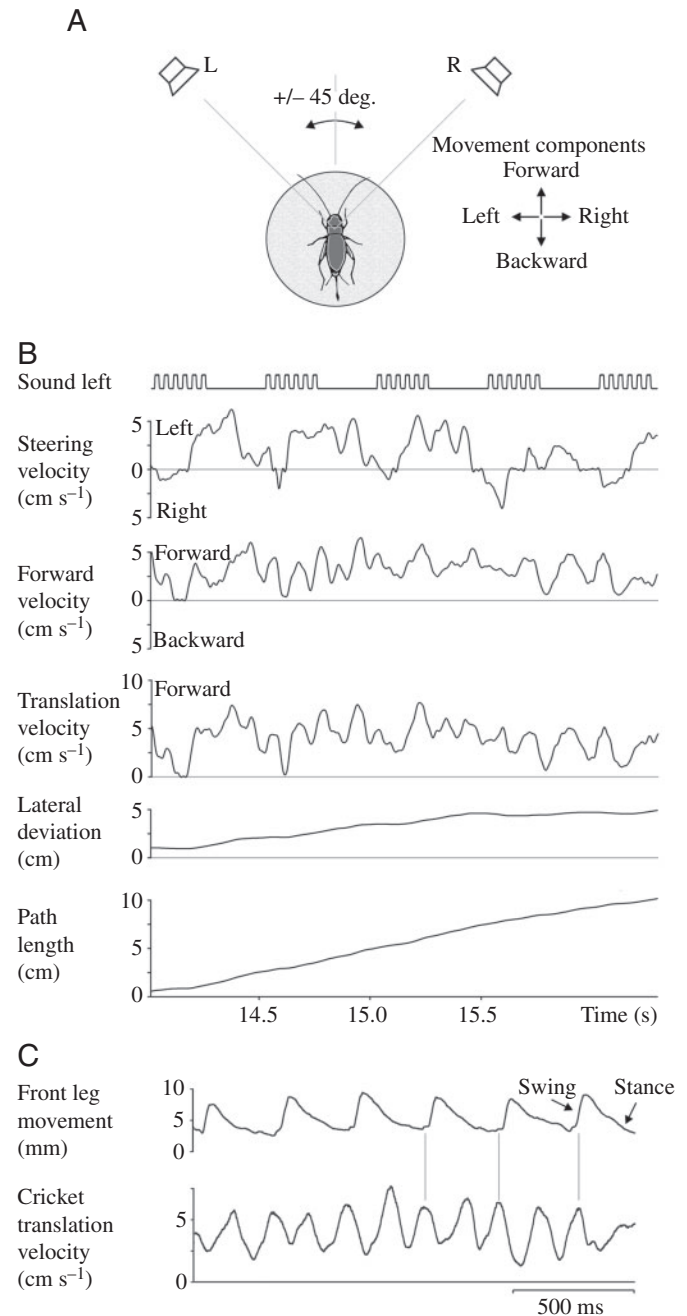


Fig. 1. (A) Experimental arrangement for measuring cricket phonotaxis. The animal was fixed on top of a trackball and during walking rotated the trackball with its legs. An optical sensor aligned below the trackball (not shown) monitored the forward-backward and left-right trackball movements. Speakers at a distance of 87 cm were arranged at 45 deg off the animal's length axis. (B) Simultaneous recording of the forward-backward and left-right movement component of a walking cricket, as picked up from the rotating trackball. From these two components, the translational velocity of the animal was calculated as well as the lateral deviation of the path and the total path length. (C) The step cycle of a foreleg recorded with an optoelectronic camera (Hedwig, 2000) and the translation velocity of a walking cricket. Due to the insect tripod gait the movement of the foreleg was in phase with every other peak in the velocity signal.

rotate with minimal friction. An optical sensor (ADNS-2051, 2D Optical Mouse Sensor; Agilent, Farnell Electronics, Oberhaching, Germany) was aligned opposite the south pole of the trackball. The LED of the sensor illuminated the lower area of the trackball through the acrylic sphere. The optical pattern reflected from the surface of the trackball allowed the sensor to monitor any trackball movements in the forward–backward and left–right direction simultaneously. The output of the sensor chip was processed on-line with a quadrature to pulse converter, which generated two data channels and produced for every movement increment of 127 μm in the forward–backward and left–right direction a coding pulse of 150 μs duration and 1.5 V amplitude, respectively. Positive coding pulses indicated forward or left increments, and negative pulses indicated movements to the back or right.

Data evaluation

The coding pulses of the two movement components and the envelope of the sound stimuli were sampled online at 10 kHz per channel using an A/D board (PCI-Mio 16-E-4; National Instruments, Newbury, UK) controlled by software programmed in LabView 5.01. Data were stored on the hard disk of a PC for later off-line analysis with custom-made software. From the repetition rate of the coding pulses the velocity of both movement components was derived. The forward–backward and left–right velocities were then used to calculate the translation velocity of the animal and were 250 Hz low-pass filtered. Velocity signals were integrated to reveal the overall lateral deviation and the path length covered by the walking cricket (Fig. 1B). Measurements of overall lateral deviation and path length were exported to Excel for pooling and statistical analysis. We refrained from any binning of the coding pulses to maintain maximum temporal and spatial sensitivity of the measurements. With an A/D sampling rate of 10 kHz, the maximum rate of coding pulses (150 μs) that could be resolved was about 300 Hz. With the given specification of the sensor chip the system should perform linearly up to trackball speeds of 38 cm s^{-1} in either direction.

Sound stimulation

The speakers and trackball system were located inside a sound proofed chamber (L150 cm, W100 cm, H70 cm) lined with Illsonic tiles (Sonex 65/125; Illbruck, Bodenwöhr, Germany). The noise level inside the chamber measured at the top of the trackball was 38 dB SPL rel. 10^{-5} N m^2 (band pass filter 200–200,000 Hz) when the air supply for the trackball was turned on. The standard sound pattern had a frequency of 4.8 kHz, syllable duration of 21 ms (including 2 ms rise and fall times), a syllable period of 42 ms, chirp duration of 250 ms and a chirp period of 500 ms, and corresponded to an syllable repetition interval pattern (SRI 42) that Thorson et al. (1982) used in previous phonotactic experiments. Sound stimuli were digitally generated at 22.05 kHz sampling rate (Cool Edit 2000; Syntrillium, Phoenix, USA) and were presented by PC audio boards *via* 2 active speakers (SRS A57; Sony, Tokyo,

Japan). These were positioned at a distance of 87 cm frontal to the cricket each at an angle of 45° to the animal's length axis (Fig. 1A). Sound intensities were calibrated with an accuracy of 0.5 dB at the position of the cricket using a Bruel and Kjaer (Nærum, Denmark) free field microphone (Type 4191) and measuring amplifier (Type 2610). To analyse phonotactic walking, sound patterns were generally presented from the left and/or right speaker for durations of 30 s. An electronic circuit produced the envelope of the sound pattern with a RMS chip (Type 637; Analog Devices, Walton-on-Thames, UK) set to a time constant of 0.5 ms.

Results

Trackball recordings and cricket movements

With crickets walking on top of the trackball (Fig. 1A) the optical sensor recorded the left–right and forward–backward rotations of the trackball while the animals were exposed to a sound pattern. From the coding pulses of the sensor we calculated the left–right velocity and the forward–backward velocity of the animal's intended movements (Fig. 1B, top). We will refer to the left–right velocity component as the animal's steering velocity. The actual translation velocity of the animal, reflecting the velocity in the direction of the animal's length axis, was calculated from the forward–backward and left–right velocity components (Fig. 1B, middle). The translation velocity generally showed changes in amplitude between 2–9 cm s^{-1} within a few milliseconds indicating that the crickets had a very good control of the trackball. Finally, we revealed the overall lateral deviation of the animal's path from a straight line and the overall path length walked within a test interval by integrating the left–right velocity and the translation velocity, respectively (Fig. 1B, bottom).

In one set of experiments we measured with an optoelectronic camera (Hedwig, 2000) the stepping cycle of one front leg simultaneously with the trackball rotations of the walking animal. These recordings revealed that the translation velocity was modulated in phase with the animal's stepping (Fig. 1C). Due to the tripod gait of insects, which moves a set of three legs at any time, the recording showed regular oscillations in the amplitude of the translation velocity with twice the frequency of the front leg movements. Thus, the track ball system actually resolved the cricket walking velocity components at the level of the stepping cycle.

Intensity function of phonotactic steering

During the experiments, sound was played from a left or right speaker each positioned frontally at 45° from the animal's length axis. Since the crickets could not alter their orientation towards the speakers the acoustic stimulus conditions remained constant. The sound pattern used to test the animals had been effective at eliciting phonotaxis in previous experiments (Thorson et al., 1982). It had a syllable duration of 21 ms and a syllable interval of 21 ms. Six syllables were grouped into a chirp and were repeated every 500 ms. Sound intensity was

increased from 45 dB SPL in steps of 5 dB to 85 dB SPL. Each pattern was presented for 30 s from the left and right side, respectively.

When tethered on top of the trackball most crickets started walking spontaneously. Without acoustic stimulation the animals walked and randomly deviated towards the left or right side. When the sound pattern was presented the crickets started steering towards the active speaker (Fig. 2A) and upon each change in the side of sound presentation the animals changed their walking direction correspondingly. We calculated the lateral deviation from a straight path as a measure of the animal's steering towards a sound source and the animal's translation velocity within the test time interval of 60 s (Fig. 2B). With increasing sound intensity the lateral deviation towards the sound source and the walking velocity increased. For 17 crickets we quantified the behaviour for all sound intensities tested. Phonotactic steering significantly started at 45 dB SPL with a mean deviation of 8.4 cm min^{-1} and increased linearly with sound intensity to 51.0 cm min^{-1} at 75 dB SPL. Further increase in sound intensity led to a saturation of auditory steering and at 85 dB SPL the mean

lateral deviation (52.0 cm min^{-1}) was not significantly different from the value at 75 dB SPL. By comparison, the overall path length increased from $161.8 \text{ cm min}^{-1}$ at 45 dB to $280.8 \text{ cm min}^{-1}$ at 85 dB SPL. Between 45 and 75 dB the overall lateral deviation increased 6.1-fold whereas the path length increased only by a factor of 1.7. From these experiments we conclude that the animals performed phonotactic behaviour when walking on the trackball. The low auditory threshold and the reliable steering manoeuvres after changes in sound direction indicated that the behaviour was not impeded by the experimental situation.

We took advantage of the high temporal and amplitude resolution, and analysed the dynamics of phonotactic steering for responses towards the 75 dB sound patterns. The lateral steering velocity demonstrated that the animals do not steer with constant amplitude, but produced steering transients triggered by the sound pattern (Fig. 3A). Consequently each chirp shifted the animal's path to the left by about 4–5 mm. Compared with the steering velocity, the forward-backward velocity component was only weakly modulated by the acoustic stimulus. Averaging the velocity components (Fig. 3B) demonstrated that the lateral steering velocity started to increase after the second sound pulse of a chirp. It reached 2.6 cm s^{-1} after the end of the chirp and then decreased again. The average forward velocity remained at a high constant level and exhibited a transient minimum at the beginning of each steering response. These averaged profiles of the forward velocity components were different in individual crickets. In some steering animals the forward velocity component was modulated only to a very small degree. This could indicate separate mechanisms for the control of lateral steering and forward speed. Animals that showed a good phonotactic performance were used for further experiments.

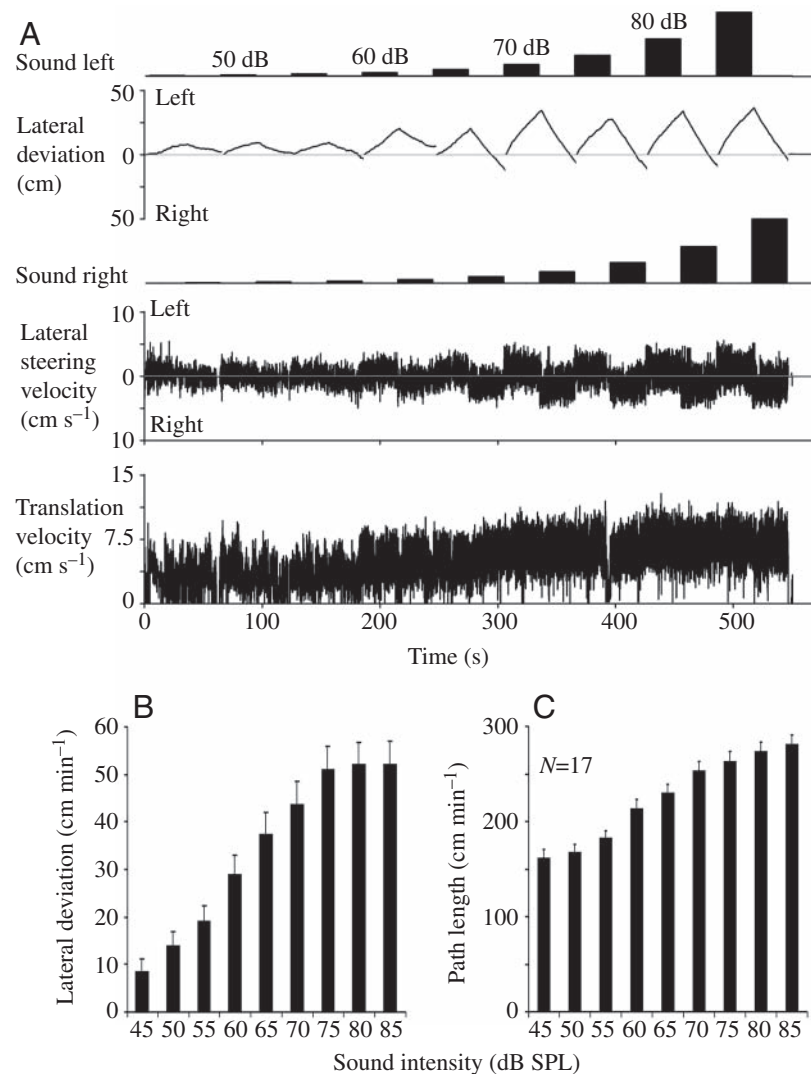


Fig. 2. Intensity function of phonotactic behaviour. (A) Phonotactic orientation of a cricket towards an optimal sound pattern presented from the left and right for 30 s at increasing intensities from 45 to 85 dB SPL. For each sound intensity the lateral deviation (top) is plotted over time. At the start of each trial the lateral deviation is reset to zero. The lateral steering velocity (middle) oscillated around zero at low sound intensities. At high sound intensities oscillations in the velocity signal were still evident, but the signal was shifted towards the side of acoustic stimulation. The translation velocity (lower trace) exhibited a broad variation in amplitude due to the temporal resolution of individual velocity peaks underlying walking. (B) Intensity dependence of the behaviour. With sound intensity increasing from 45 to 75 dB SPL the overall lateral deviation from a straight line increased 6.1-fold. The overall path length walked increased 1.7-fold with increasing sound intensity as calculated for the 60 s trial.

Steering towards bilateral intensity differences

For auditory orientation animals can exploit interaural intensity differences and/or interaural latency differences. A basic rule for cricket phonotactic walking was 'turn towards the louder side' (Huber et al., 1984; Schildberger, 1994). This parsimonious explanation of cricket orientation has never been analysed with a trackball system and there is no information, to what degree crickets are able to exploit left–right intensity differences for phonotactic steering. We presented identical sound patterns simultaneously from both speakers at an intensity of 60 dB SPL. During the test the intensity of one speaker was consecutively increased by 1, 2, 3, 4, 5, 10 and 15 dB. Each intensity difference was presented for 30 s from the left and right side, respectively. For 12 crickets the overall lateral deviation was calculated and is given relative to the phonotactic response of the animals to a 75 dB SPL stimulus used as a 100% reference response (Fig. 4).

When exposed to the test paradigm without any intensity differences (Fig. 4A) the animals steered to the left and right side with the same intensity and consequently walked straight ahead. At intensity differences of just 1–2 dB, the animals started orientated behaviour and steered towards the louder

speaker. With increasing intensity difference the deviation towards the louder side gradually increased (Fig. 4A). However, even at 10 and 15 dB intensity differences the lateral deviation was not as straight as during the threshold tests (compare with Fig. 2) and lateral deviation appeared less precise. Quantitative analysis demonstrated that at 1 dB intensity difference the deviation from the midline was 12.0% of the lateral deviation to a 75 dB unilateral sound and was just significant at 97% level. Averaging the steering response towards the 1 dB louder speaker (Fig. 4C, top) demonstrated that the mean steering velocity was slightly shifted towards the louder speaker. At higher intensity differences the animals' performance increased. At 2 dB intensity difference it reached 24.0% of the standard response (Fig. 4B) and the averaged steering velocity exhibited a clear response towards the louder speaker (Fig. 4C, middle). At 10 dB difference the orientation towards the louder sound corresponded to 74.4% of the reference value (Fig. 4B) and caused a clear turning reaction as revealed by the averaged steering signal (Fig. 4C, bottom). Finally at 15 dB difference, with one speaker at 65 dB SPL and the other at 80 dB SPL, the orientation towards the louder speaker reached 98.0% of the standard response.

Calculating the overall path length walked during this test (Fig. 4D) demonstrated that all animals walked about 205 cm min^{-1} and that the results are not biased by preferences towards particular combinations of intensities. We therefore conclude that crickets are sensitive to bilateral intensity differences of at least 2 dB and that they are able to exploit these minute acoustic cues for auditory steering. The steering amplitude, however, is intensity dependent with larger differences in sound intensity leading to larger steering responses.

Steering towards bilateral time differences

The exploitation of interaural time differences for auditory orientation may be challenging for the cricket *G. bimaculatus*. The distance between the bilateral spiracle openings is about 5 mm and the distance between the ears in the front legs is about 9 mm. Thus, the interaural time difference for impinging sound waves corresponds to about 15–30 μs and insect ears are limited to exploit these interaural time differences for directional processing (Lewis, 1983; Michelsen, 1998). We experimentally introduced a time difference in the range of 2–12 ms between the sound patterns

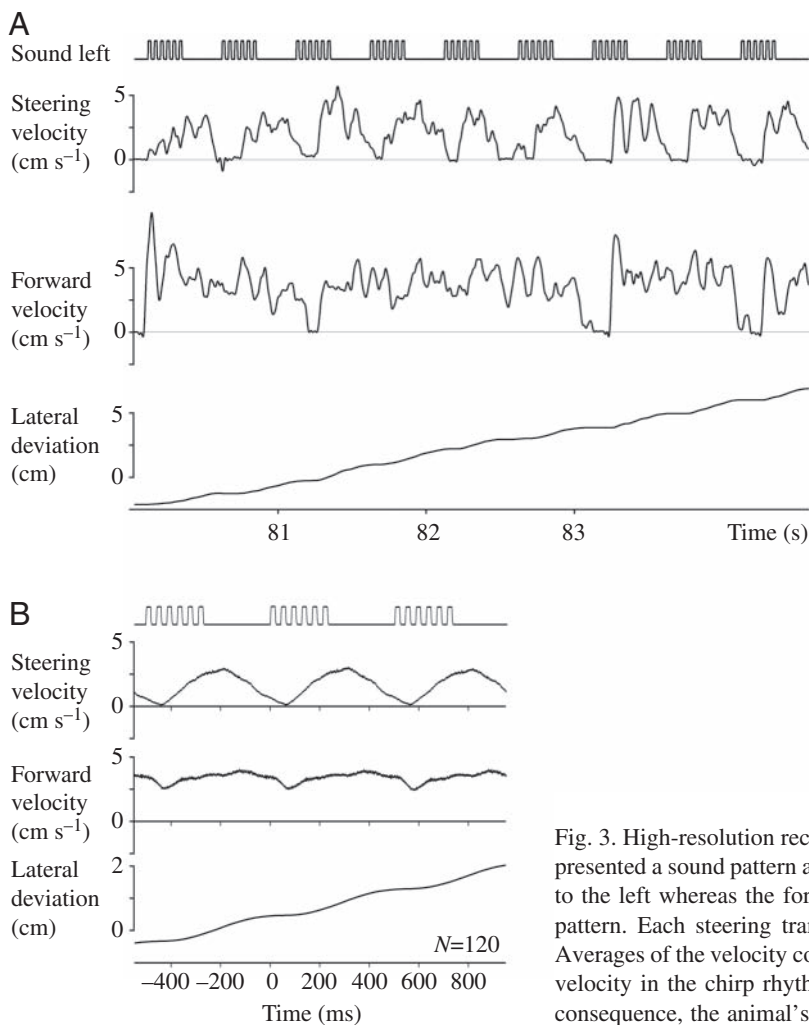


Fig. 3. High-resolution recording of an animal steering towards the left speaker, which presented a sound pattern at 75 dB. (A) Each chirp released a steering velocity transient to the left whereas the forward velocity was only weakly modulated by the stimulus pattern. Each steering transient caused a shift of the animal's path to the left. (B) Averages of the velocity components demonstrate the strong modulation of the steering velocity in the chirp rhythm and the weak modulation of the forward velocity. As a consequence, the animal's deviation to the left was modulated by the sound pattern.

presented from the left and right side. Due to the stimulus amplitude of 75 dB in these experiments the leading sound pulse will also activate the afferents at the contralateral side before the delayed sound pulse starts. Such a situation may

arise when a female is exposed to the songs of many males singing with slightly different chirp or syllable rates. We analysed to what degree females may exploit these time differences for auditory orientation and exposed 11 females to

identical sound patterns of 75 dB SPL in amplitude with one pattern consecutively leading the acoustic stimulation by 2, 4, 6, 8, 10 and 12 ms. Each time difference was presented for 30 s from each side of the animals and phonotactic steering was plotted and evaluated (Fig. 5).

The walking paths encountered when the animals were exposed to time differences were strikingly different to those in response to intensity differences. Although one might expect a clear orientation towards the leading sound pattern, a typical example of the phonotactic performance of a cricket (Fig. 5A) demonstrated that the females hardly steered towards leading pattern. Only at time differences of 4 and 8 ms the animals preferred the leading sound pattern. When we pooled the responses of all females tested, this weak reaction towards the leading sound pattern became statistically evident.

At a time difference of 2 ms the crickets actually orientated towards the delayed sound pattern by 7.1% of the standard response, i.e. the turned away from the leading pattern. The orientation towards the leading pattern at differences of 6 ms and 12 ms corresponded just to 5.7% and 1.7% and was not significantly different from walking straight ahead. The animals demonstrated a weak, but significant, steering towards the leading sound pattern only at differences of 4 ms (26.3%), 8 ms (15.2%) and 10 ms (14.8%). However, even at these delays averaging the steering velocity did not reveal a clear phasic turning response towards the leading pattern (Fig. 5C). Instead, there was only a weak general shift towards the direction of the leading speaker, similar to responses we observed for intensity differences of about 2 dB (compare with Fig. 4C). Although the experimentally induced time differences are well within the physiological range of synaptic processing and should easily be resolved in the CNS, the experimental data indicate that crickets may not or only weakly exploit time differences for auditory localization.

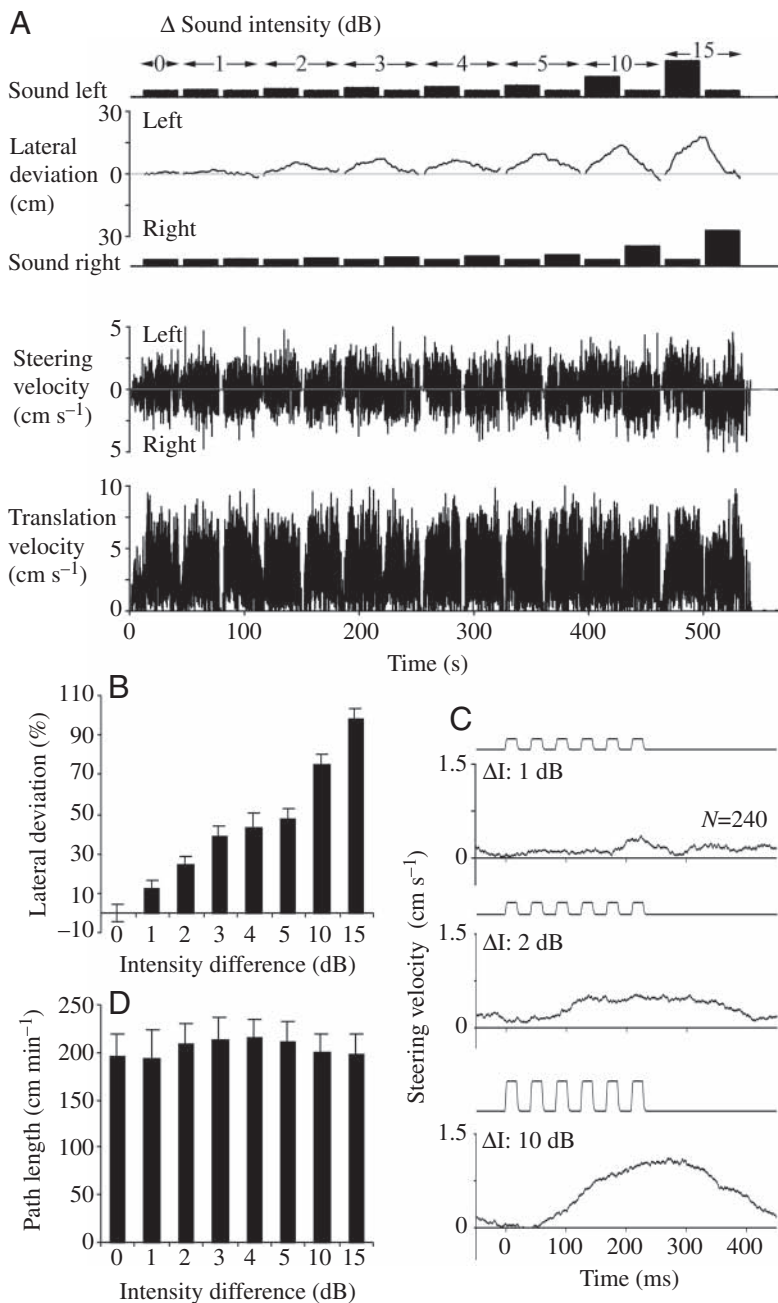
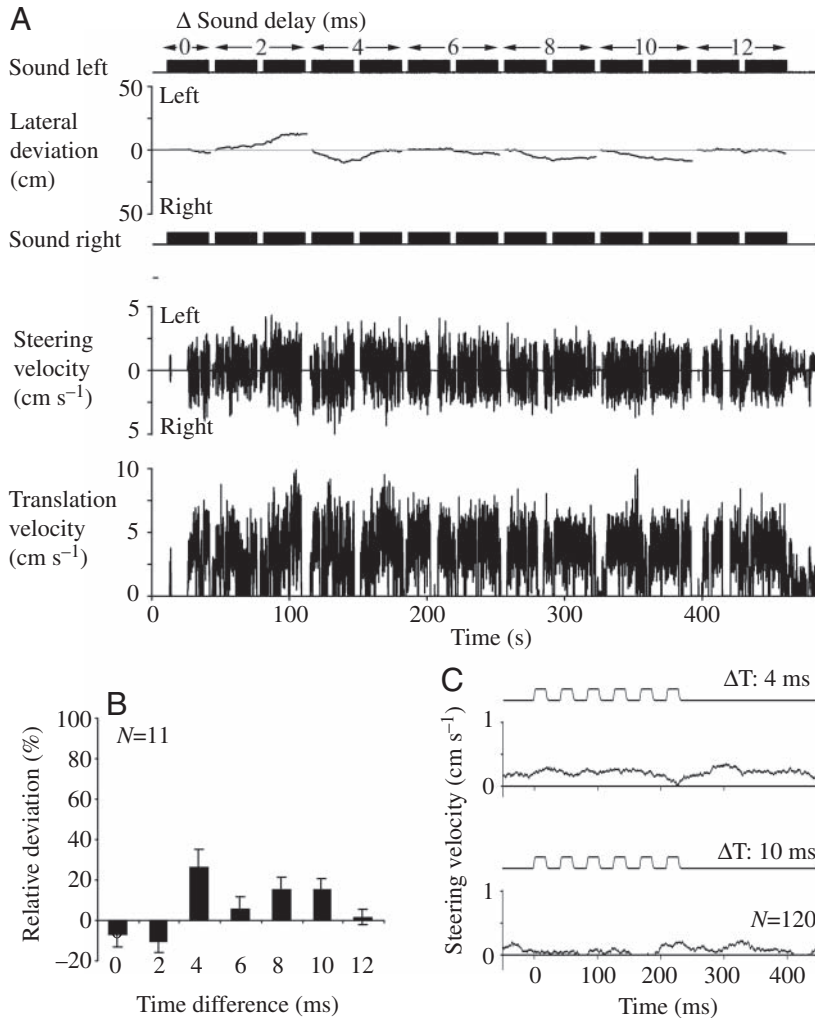


Fig. 4. Intensity differences and steering responses. (A) A reference sound pattern of 60 dB SPL was presented simultaneously with a test pattern of equal or higher amplitude. Intensity differences are indicated above the top trace. Lateral deviation towards the louder sound pattern was minute at 1 dB and increased with increasing intensity difference. Oscillations in the lateral steering velocity occurred during each test together with oscillations in the translational velocity. (B) Lateral deviation as a function of the intensity difference is presented. The lateral deviation is expressed as a percentage of the steering towards a 75 dB reference pattern presented from one side only. (C) Average steering response of a cricket when exposed to intensity differences of 1, 2 and 10 dB. (D) Overall path length walked during the different tests.

The impact of bilateral syllable numbers on phonotactic steering

Neurobiological experiments by Nabatiyan et al. (2003) on discharge rate coding by auditory interneurons pointed towards the importance of single sound pulses for phonotaxis. With split-song paradigms (Weber and Thorson, 1988) we tested to what degree single syllables have an impact on phonotactic steering and generated sound patterns with a systematic variation in the number of sound



pulses presented from the left and right side. We started with the standard six syllable chirp and we gradually reduced the number of syllables played from one side from 6 to 0 and at the same time gradually increased the number of syllables presented at the other side from 0 to 6 (Fig. 6A,B). For each combination it was always the last syllable of a chirp that was altered and each paradigm was played for 30 s from each side of the animal (see Fig. 7 for details of the sound pattern). Between the tests was a silent period of 10 s.

Like all other crickets, the animal in Fig. 6A steered best when all six sound pulses were presented from one side (6:0 and 0:6). However, when we played the last sound pulse of the chirps from the contralateral side (5:1), a considerable reduction of the steering response towards the five-syllable chirp occurred. This effect increased with the increasing number of syllables presented from the contralateral side. When the first three and last three pulses of the chirps were presented from opposite sides, the overall deviation to any side became small, but still the animals generally orientated stronger towards the leading syllables. Also the pattern 2:4 elicited orientation towards the left side where only two pulses of a chirp were presented. In this case, even after the consecutive switch, when four syllables from the right

Fig. 5. Latency differences and steering responses. (A) Two identical sound patterns of 75 dB SPL were presented with increasing delay. Latency differences are indicated above the top trace. Lateral deviation towards the leading sound pattern was negative at 0 and 2 ms. It was significant at 4 ms and weak thereafter. Oscillations in the lateral steering velocity during each trial and oscillations in the translation velocity are given below. (B) Lateral deviation in dependence of the latency difference presented. The maximum response occurred at 4 ms difference. The lateral deviation is expressed as percentage of the steering towards a 75 dB reference pattern presented from one side only. (C) Average lateral steering response of a cricket when exposed to latency differences of 4 and 10 ms did not indicate an obvious response towards the leading sound pattern.

preceded two syllables from the left, the animal kept walking to the left. When the pattern 1:5 was given the overall response was dominated by orienting towards the five syllables. We quantified the response for 12 crickets and found a close correlation between the number of syllables presented from each side and orientation (Fig. 6B). With the decreasing ratio of pulses presented from the left and right side the orientation of the animals towards the left side gradually decreased from 89.5% at 6:0 to 73.9% at 5:1, then to 53.2% at 4:2 and finally 26.4% at a syllable ratio of 3:3. Orientation then changed towards the right with -26.0% at 2:4, -82.4% at 1:5 and -91.6% at 0:6. Although there was always a slight bias towards the side presenting the start

of a chirp, each change in the ratio of pulses presented, caused a stepwise change in the lateral deviation. The overall phonotactic performance was good in all animals tested (Fig. 6C). The path length was at a maximum when the animals were exposed to the 3:3 pattern. The gradually reduced lateral orientation could be interpreted in a way that the attractiveness of the sound pattern was affected by changing the number of syllables presented from both sides and that, therefore, the animals turned less when exposed to this pattern. However, as another possibility the animals might steer towards individual sound pulses and in fact might have turned to the pulses presented from both sides in the same way. In both cases the dynamics of the underlying steering responses would be fundamentally different. To distinguish between both possibilities, i.e. reduced attractiveness or steering towards individual sound pulses we analysed the dynamics of the animals steering behaviour.

Temporal dynamics of lateral steering

The trackball system used demonstrated that phonotactically walking crickets do not steer with a constant lateral velocity. Moreover, they consecutively produce lateral steering movements with considerable amplitudes of 2–7 cm s^{-1}

although their overall lateral deviation indicates a directed walking path when analysed at low spatial resolution (Fig. 2A top, 6A top). To demonstrate the dynamics underlying the auditory steering responses we averaged the lateral steering velocity evoked by the acoustic test patterns presenting different syllable numbers (Fig. 7).

When all six sound pulses were presented from the left (Fig. 7A), the animals started steering towards the left at 55–60 ms after chirp onset, i.e. just before the end of the second sound pulse. Steering reached a mean maximum amplitude of 2.2 cm s^{-1} , it lasted for the duration of the chirp and then gradually decayed to 0.5 cm s^{-1} (compare with Fig. 3B). The time course of this response already indicates,

that the animals did not evaluate the temporal pattern of the whole chirp until steering started. Instead steering was already initiated, while the second sound pulse was still playing. When we presented the stimulus pattern 5:1 (Fig. 7B) steering to the left started again during the second sound pulse. However, due to the single pulse presented from the right, steering to the right commenced earlier, faster and to an average steering velocity of 0.0 cm s^{-1} between the chirps. Note: as a reference, the response to six pulses presented from the left is always indicated in blue. Turning towards the right side gradually increased with the number of sound pulses presented from the right (Fig. 7C). When the last three pulses were presented from the right (Fig. 7D) the animals started to turn right during the chirp, i.e. after the 2nd pulse from the right. The overall steering response towards the right sound pulses compensated the initial steering towards the leading left pulses. It brought the mean steering velocity to zero but it was not strong enough to actually turn the animal to the right. As a consequence, the cricket still orientated to the side of the leading pattern (see Fig. 6A at 3:3). The steering response to the initial sound pulses actually has to be overcome by a stronger response to the following pulses. In this case, even at 2:4 (Fig. 7E), the animal clearly responded to the four sound pulses presented from the right. However, this response was not strong enough to overcome the initial response to the two pulses from the left. Consequently the orientation of the cricket was still to the left (see Fig. 6A at 2:4). The initial response towards the single pulse presented from the left was only overcome by consecutive steering towards the five pulses from the right in the 1:5 trial (Fig. 7E) and the orientation of the animal was to the right. These averages of the steering velocity clearly indicate that the animals steer towards individual sound pulses and that steering changes even during ongoing chirps. Therefore, orientation cannot be based on an evaluation of the chirp pattern. It also indicates that by evaluating a cricket's walking path or its direction with low temporal and spatial resolution only, the underlying steering and auditory processing mechanisms cannot be revealed.

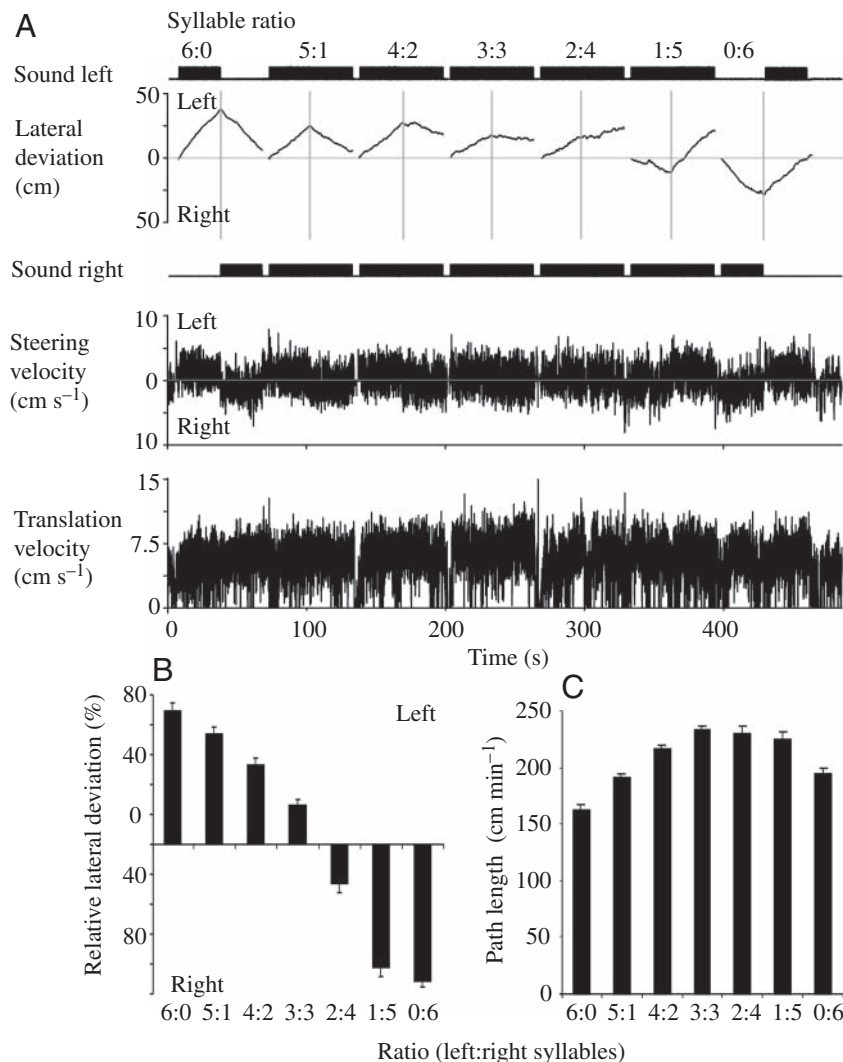


Fig. 6. Bilateral pulse numbers and steering. (A) Patterns with different numbers of sound pulses were presented from the left and right side. The numbers of pulses presented from the first and second speaker varied from 6:0 to 3:3 to 0:6. Lateral deviation depended on the number of sound pulses presented from each side. When the same number of pulses was presented from both sides, the animals almost walked straight ahead. (B) Lateral deviation in dependence of ratio of sound pulses presented from the left and right speaker. The lateral deviation depended on the pulse numbers perceived at each side. (C) Overall path length walked during the trials. Translation velocity increased with the amount of steering.

pattern, i.e. there is a serial processing of pattern recognition and localization. Our previous experiments demonstrated that crickets even steer towards individual sound pulses and start steering after 55–60 ms. These rapid steering responses question whether steering is based on a comparison of the quality of auditory patterns perceived at the left and right side. To analyse this matter more closely we took the split-song paradigm to the extreme (Hedwig and Poulet, 2004) and presented every other sound pulse of the chirp pattern from the opposite side (Fig. 8).

When exposed to these split sound patterns, the crickets perceived the same number of sound pulses from the left and right side. Correspondingly, they generally walked straight ahead (Fig. 8A), or could show a slight bias towards the side presenting the first pulse. This may be interpreted as if the animals kept a course between both speakers where the perceived pattern was optimal. The lateral steering velocity

signal demonstrated, however, that the animals permanently produced steering transients to the left and the right side. These transients in the lateral steering velocity were linked to the individual sound pulses (Fig. 8B). Superimposing the steering velocity signal (Fig. 8C) revealed that the animals rapidly and reliably steered towards the left and right side and altered their turning direction corresponding to the split-song pattern. We averaged the lateral steering velocity signal for the duration of a split-song chirp and revealed the time course of these steering transients (Fig. 8D). This demonstrated that the crickets alternatingly steered to the sound pulses presented from the left and right side, corresponding to the presentation of the split-song sound pulses. Even under these extreme circumstances the animals steered towards the individual sound pulses. Steering again occurred with a latency of 55–60 ms. During this rapid steering behaviour, responses to the left (i.e. the first) pulses were at least compensated by responses to the right (i.e.

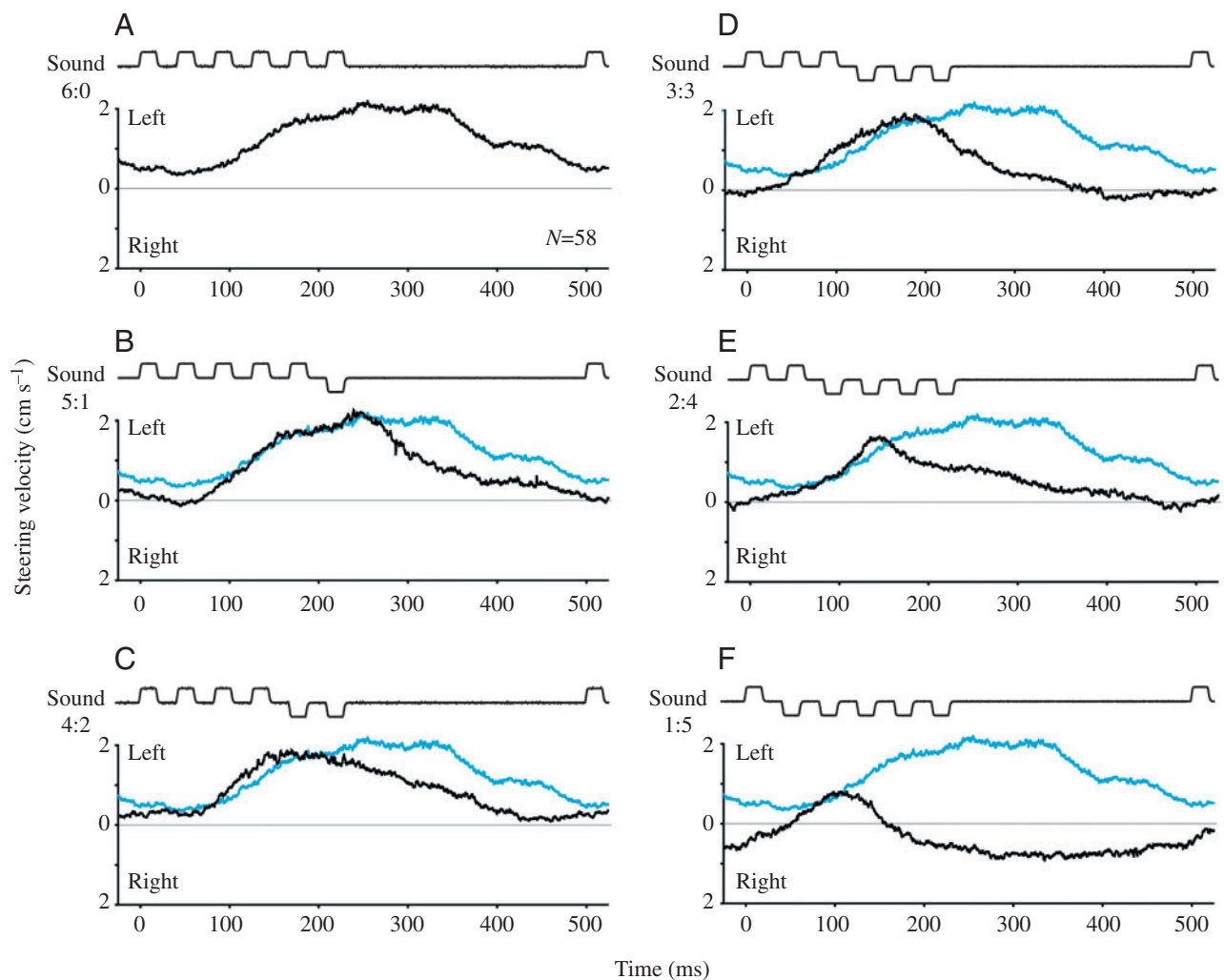


Fig. 7. Averages of lateral steering velocity in response to different numbers of sound pulses presented by the leading and following speaker. (A) With six pulses presented from the left side, steering occurred towards the side of sound stimulation. (B) When the last pulse was presented from the right side, the animal started to turn towards the right side in response to the single sound pulse. (C–E) With increasing numbers of sound pulses presented from the right side, the animals steered stronger to the right side. (E) The cricket started to steer towards the single pulse presented from the left side and then turned towards the right side presenting five pulses. For all tests the steering response to six pulses from the left is given as a reference (in blue). Number of trails 60.

the following) pulses and at the end of a chirp the responses to the last pulse dominated the steering response. As a consequence, cricket orientation was straight ahead or slightly biased towards the side with the leading pulses. These

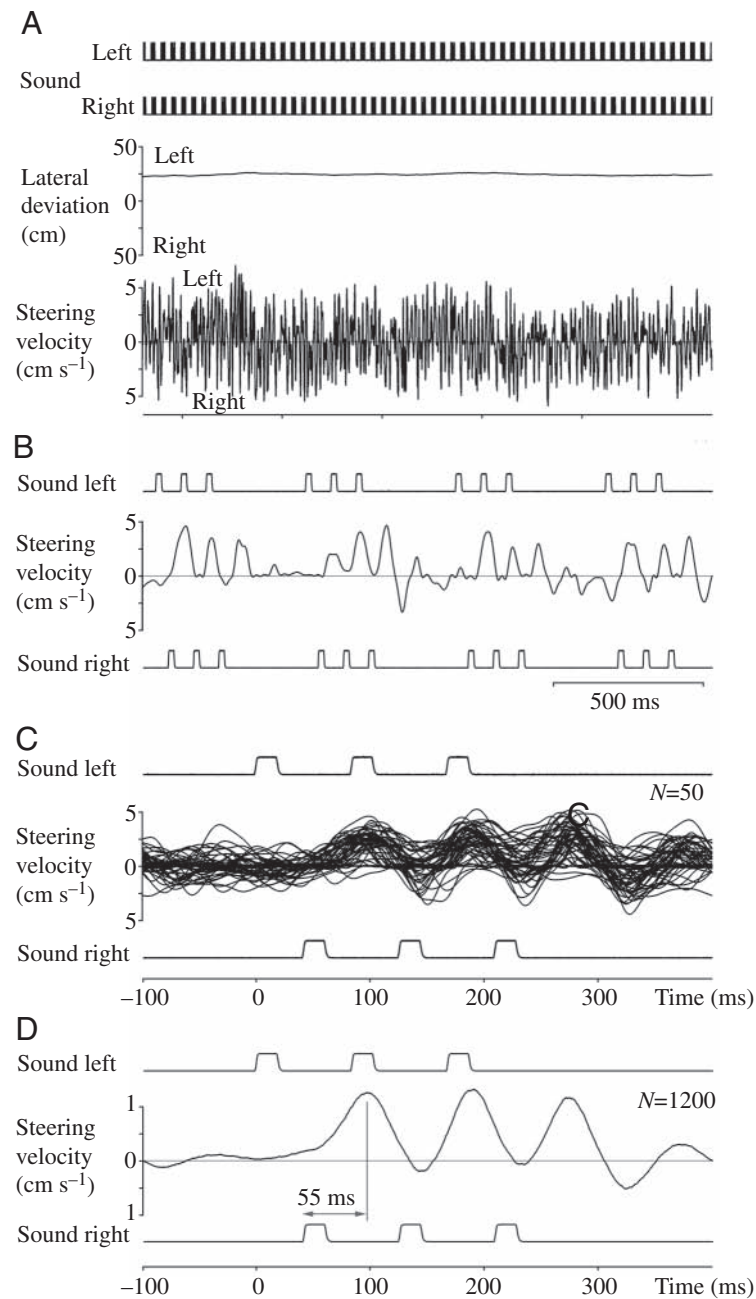


Fig. 8. Steering response to extreme split-song pattern. (A) The crickets were exposed to a split-song paradigm with every other sound pulse presented from opposite sides. The animals walked straight ahead or slightly deviated towards the leading pattern. The steering velocity oscillated around zero. (B) A plot at high temporal resolution demonstrates, that each sound pulse elicited a rapid steering response directed towards the corresponding speaker. (C) Superposition of consecutive steering responses during split-song chirps. (D) Average of the steering velocity when the crickets were exposed to the split-song paradigm. The steering responses towards single sound pulses occurred with a latency of about 55–60 ms and were initiated just at the end of the consecutive sound pulse.

experiments finally demonstrated that crickets rapidly steer towards individual sound pulses. The intensity of the steering responses could vary in the course of a walking sequence and from animal to animal. Since these auditory steering responses occurred with a rate of 24 Hz it appears that leg movements underlying walking behaviour were modulated in a reflex-like way.

Discussion

In our experiments we used a high-speed trackball system to analyse the dependence of cricket auditory steering on sound intensity, latency differences and on the temporal organisation of split-song paradigms. We were especially interested to characterise the temporal dynamics of the auditory steering responses. This determines the cricket's walking path and orientation, and especially allows conclusions about the interaction of pattern recognition and localization.

Technical considerations of the trackball systems

The design of the trackball system allowed a single 2D sensor chip to monitor the cricket's walking path. The sensor detected any forward–backward and left–right movements of the trackball with a spatial resolution of just 127 μm and should work linearly to velocities of 38 cm s⁻¹. Since the sensor data were processed without any temporal averaging, the data resolved single steps of the walking pattern and fine temporal details of the steering behaviour. The temporal and spatial resolution of our system is superior to previous open loop (Doherty and Pires, 1987; Schildberger and Hörner, 1988; Stabel et al., 1989) and closed loop systems (Weber et al., 1981; Schmitz et al., 1982) used to analyse cricket phonotactic walking. The closed loop Kramer treadmill system was adjusted to compensate the mean speed of the walking cricket. Its dynamic performance was not sufficient to capture the velocity modulation corresponding to the animal's tripod gait or rapid changes in the velocity components during steering or at the start and end of walking bouts (see Weber et al., 1981, their fig. 4). For data analysis the velocity signal generally was binned and calculated only during certain time windows or path length, e.g. every 500 ms by Schmitz et al. (1982) or over 1 s by Doherty and Pires (1987). Based on our presented data we conclude that temporal and spatial details of the crickets steering behaviour could not be resolved with such methods. Our track ball system generated low background noise (38 dB SPL) as compared with 58 dB SPL of the compensated walking sphere (Schmitz et al., 1982). Phonotactic steering therefore could be elicited even at 45 dB SPL, it increased up to 75 dB and, as in *G. campestris* (Schmitz et al., 1982), saturated at higher intensities.

During turning movements, tethered animals are

expected to have problems controlling the inertia of the trackball if the trackball is larger than 1.5 times of the animal's mass (Weber et al., 1981). A female cricket weighted about 1200–1300 mg. The effective mass the crickets had to control when rotating the trackball was 1200 mg (2/5 of the total sphere mass) and, thus, closely corresponded to the animal's body mass.

Open loop trackball systems may be regarded as restrictive to the animal's behaviour. However, the low threshold for the release of phonotaxis and the dynamic of the steering behaviour observed indicate that in our system walking was not impeded. The considerable advantage of our open loop system is that the animal's turning responses do not alter the conditions of acoustic stimulation. Since the crickets remained at a constant position relative to the speakers their steering responses could be measured and quantified, with high temporal and spatial resolution.

The effect of bilateral intensity differences on phonotactic steering

A major rule for cricket phonotaxis has been 'turn towards the louder side' (Huber et al., 1984; Schildberger, 1994). A direct analysis of the crickets' actual ability to exploit bilateral intensity differences, however, had not been obtained. When we exposed phonotactically walking crickets to bilateral sound patterns of different intensity, the animals significantly steered towards the side of the louder sound source as soon as the intensity difference was greater than 1 dB SPL. However, during bilateral stimulation even at intensity differences of 15 dB their steering behaviour appeared to be noisier and the lateral deviation less accurate as during unilateral stimulation. A sensitivity of crickets towards binaural intensity differences of at least 2 dB had been inferred from auditory lateralization experiments by Rheinlaender and Blätgen (1982). Our measured sensitivity supports this conclusion. The crickets' sensitivity is thus similar to the performance of the grasshopper *Chorthippus biguttulus* (Helvesen and Rheinlaender, 1988) and the bush cricket *Gampsocleis* (H. Römer, personal communication). In these species turning behaviour towards the louder of two stimuli is reliably correct as soon as the interaural intensity differences are 1–2 dB.

The effect of bilateral latency differences on phonotactic steering

When both ears of walking crickets were exposed to identical sound patterns shifted in time, the animals only weakly steered towards the leading sound pattern. Even the best response at 4 ms was comparably poor and was similar to a response to bilateral intensity differences of just 2 dB. This was unexpected since in flying crickets a delay of 4–75 ms between ultrasound pulses causes a clear precedence effect with the animals steering away from the leading sound pulse. Only between 0–2 ms is the direction of the turn arbitrary relative to the sound pulse (Wytttenbach and Hoy, 1993). Rheinlaender and Mörchen (1979) demonstrated that during

binaural stimulation of a locust directionally sensitive auditory interneurone, a time difference of just 4 ms is sufficient for the leading stimulus to completely suppress the response towards the sound following from the contralateral side. In behavioural experiments, grasshoppers reliably orientate towards the leading of two identical sound patterns, as soon as the delay between the patterns reaches 1 ms (Helvesen and Rheinlaender, 1988). A network for bilateral auditory contrast enhancement operates in the auditory pathway of crickets. The mutual inhibitory network of the Omega neurons seems to be designed for the processing of directional information (see Hennig et al., 2004, for review). We therefore had expected a clearer orientation of the crickets towards the leading sound. One possibility for the poor directional responses could be a direct unilateral effect of the auditory input onto the ipsilateral motor networks. Under these circumstances, the motor effects evoked at both sides would cancel. However, the averages of the steering responses should have revealed an initial phasic steering response towards the side of the leading sound pattern. Such a response was not evident in the averages. We therefore also consider that superimposing two effective patterns may have reduced the effectiveness of the resulting pattern, either within the peripheral auditory system due to detrimental phase shifts of the sound waves [which may have led to a loss of directionality (Michelsen and Löhe, 1995)], or due to deteriorating the overall temporal structure of the song for the recognition process. However, our data are in agreement with auditory steering in flying crickets, which also depends on intensity differences of auditory afferent activation rather than latency differences (Pollack, 2003).

Rapid steering to single sound pulses, and concepts of pattern recognition and orientation

After a change of sound direction, previous studies have reported that crickets change their walking direction within 1500 ms (Schmitz et al., 1982) or after 500–1000 ms (Schildberger and Hörner, 1988). These values may indicate that the crickets turning response is based on the evaluation of the chirp pattern but rather may be due to the low temporal resolution of the treadmills. Our highly sensitive trackball system revealed latencies for turning 20 times faster. In our split song paradigms, crickets changed their walking direction even within a chirp and steered towards single sound pulses with a latency of just 55–60 ms. These rapid steering responses have important consequences for the currently proposed concepts of pattern recognition and orientation.

Auditory steering within 55 ms poses the question about whether such responses can be mediated with the participation of temporal filtering circuits in the brain. The band-pass circuits in the brain seem to be tuned towards the species-specific syllable rate and are regarded as central elements for pattern recognition (Schildberger, 1984). A simple calculation provides the processing time for the proposed type of pattern recognition required. At 70 dB SPL, the cephalic arborisations of the ascending interneurone AN1 responds after about 20 ms. The band-pass neurons BNC2, which are assumed to be central

to pattern recognition, are activated with a latency of about 45 ms (Schildberger, 1984). A band pass network has to process at least two syllables to evaluate the syllable rate and to activate the proposed band-pass recognition process. With the SRI42 sound pattern used here this corresponds to 63 ms. After activation of BNC2 another 5 ms will be needed to transmit any resulting steering command towards the thoracic system and we may assume an additional 30 ms to generate the motor activity. Thus, a steering command that is based on the output of the proposed band-pass filter in the brain will need about 143 ms to evoke a motor response. The rapid turning behaviour towards individual syllables (55–60 ms) therefore leaves no time for the band-pass pattern recognition process to be involved in the encountered rapid phonotactic steering. Conversely, Schildberger and Hörner (1988) describe changes in walking direction upon modulating the activity of ascending auditory neurons but unfortunately do not give the latency of these responses. Some descending brain neurons respond to sound and appear to be involved in the control of walking (Böhm and Schildberger, 1992). They respond to high intensity sound after a latency of 25–40 ms (Staudacher, 2001). The auditory response of these descending brain neurons was not very regular and the neurons were activated by other sensory modalities as well. The auditory response latency of some of these neurons may just be short enough so that they could be directly involved in the control of rapid turning responses, however the pathways by which they are activated are not yet known.

A generally accepted concept for cricket phonotaxis suggests a serial organisation of pattern recognition and localization. It is proposed that two bilateral recognisers in the cricket CNS first filter the ascending information and that the output of these two recognisers is then compared to allow the animal to steer towards the 'better' of two patterns (Pollack, 1986; Stabel et al., 1989; Wendler, 1990; Helversen and Helversen, 1995). The rapid steering responses towards single sound pulses, however, demonstrate that the overall temporal structure of the sound pattern is not evaluated for steering. Our behavioural data therefore refute the proposed serial organisation of the recognition and localization process. During phonotactic walking each sound pulse presented from one side of the cricket generated a steering response towards that side. There was a clear dependence between the number of syllables presented from one side and the overall lateral deviation of the animals. The relation between the number and the intensity of sound pulses perceived at each ear determined the overall direction of walking. As a consequence cricket auditory orientation emerges from singular steering events and not from the calculation of a steering direction. The cricket *G. bimaculatus* solves the complex task of auditory orientation with a most simple algorithm by turning towards individual sound pulses (Hedwig and Poulet, 2004). Female *G. campestris*, when exposed to sound patterns interleaved from a left and right speaker, walked in a direction between the speakers (Weber and Thorson, 1988). This may be due to an optimum zone for recognition and tracking, but may also be

the consequence of symmetrical steering responses to both speakers, which led to an intermediate walking path involving steering responses that were not resolved by the treadmill system.

Is there a thoracic pathway for steering?

The rapid auditory steering responses may be controlled by the brain and/or they may be mediated directly to the walking motor network at the thoracic level. Considering the evolutionary history of the cricket auditory organ may support the second assumption. In insects, hearing organs have evolved from chordotonal organs providing proprioceptive feedback to the CNS. In crickets and bushcrickets, in particular, the chordotonal organ in the front leg has evolved to a hearing organ (Fullard and Yack, 1993). In acridid Orthoptera, the homologous chordotonal organ in the forelegs is involved in mediating fast proprioceptive feedback to motor networks controlling leg position and walking (Burrows, 1996). Although in the cricket a postsynaptic thoracic pathway has evolved for the processing of sound, at least part of the 'old' proprioceptive network linked to motor control may have been conserved (Dumont and Robertson, 1986) and may still provide a fast and effective auditory-to-motor interface. Thus, a direct reflex-like link may allow integrating rapid responses to sound pulses into the walking motor pattern. Evidence for these still speculative thoughts may be gained from further analysis of the auditory steering responses.

Future analysis: interaction of pattern recognition and steering

If phonotaxis is strictly based on responses to individual sound pulses, then *G. bimaculatus* should indiscriminately steer towards any auditory pattern with an appropriate carrier frequency. Phonotactic walking, however, depends on the temporal structure of the sound (Weber et al., 1981). Thus, pattern recognition is necessary for phonotaxis to occur. However, the functional relationship between the recognition and localization process may be dynamic and both may even have different selectivity for temporal patterns. Steering towards non-attractive patterns occurred temporarily after crickets were exposed to attractive songs (Weber et al., 1981), and steering could even be elicited when non-attractive patterns were combined with an attractive pattern resembling the species-specific songs (Doherty, 1991). These experiments indicate that a recognition process may control and activate a separate localization process. However, to understand further the organisation of cricket phonotaxis we propose that a thorough re-evaluation of pattern recognition and its impact on localization is required.

The BBSRC (Ref.: 8/S17898) and the Royal Society supported the project. We are most grateful to M. Knepper for continuous development of our data evaluation software and to P. Williams for software and hardware developments. We thank D. Roosen of the Röhm KG, who generously provided a sample of Rohacell.

References

- Böhm, H. and Schildberger, K.** (1992). Brain neurons involved in the control of walking in the cricket *Gryllus bimaculatus*. *J. Exp. Biol.* **166**, 113-130.
- Burrows, M.** (1996). Walking movements. In *The Neurobiology of an Insect Brain*, ch. 8.10 (ed. M. Burrows), pp. 326-405. Oxford: Oxford University Press.
- Cade, W. H.** (1979). Effect of male deprivation on female phonotaxis in field crickets (Orthoptera: Gryllidae; *Gryllus*). *Can. Ent.* **111**, 741-744.
- Doherty, J. A.** (1991). Song recognition and localization in the phonotaxis behaviour of the field cricket, *Gryllus bimaculatus* (Orthoptera: Gryllidae). *J. Comp. Physiol. A* **168**, 213-222.
- Doherty, J. A. and Pires, A.** (1987). A new microcomputer based method for measuring walking phonotaxis in the field crickets (Gryllidae). *J. Exp. Biol.* **130**, 425-432.
- Dumont, J. P. C. and Robertson, R. M.** (1986). Neuronal circuits: an evolutionary perspective. *Science* **233**, 849-853.
- Fullard, H. F. and Yack, J. Y.** (1993). The evolutionary biology of insect hearing. *Trends Ecol. Evol.* **8**, 248-252.
- Hedwig, B.** (2000). A highly sensitive opto-electronic system for the measurement of movements. *J. Neurosci. Meth.* **100**, 165-171.
- Hedwig, B. and Poulet, J. F. A.** (2004). Complex auditory behaviour emerges from simple reactive steering. *Nature* **430**, 781-785.
- von Helversen, D.** (1997). Acoustic communication and orientation in grasshoppers. In *Orientation and Communication in Arthropods* (ed. M. Lehrer), pp. 301-341. Basel: Birkhäuser Verlag.
- von Helversen, D. and von Helversen, O.** (1995). Acoustic pattern recognition and orientation in orthopteran insects: parallel or serial processing? *J. Comp. Physiol. A* **177**, 767-774.
- von Helversen, D. and Rheinlaender, J.** (1988). Interaural intensity and time discrimination in an unrestrained grasshopper. A tentative behavioural approach. *J. Comp. Physiol. A* **162**, 333-340.
- Hennig, R. M., Franz, A. and Stumpner, A.** (2004). Processing of auditory information in insects. *Micros. Res. Tech.* **63**, 351-374.
- Horseman, G. and Huber, F.** (1994). Sound localization in cricket. II. Modelling the role of a simple neural network in the prothoracic ganglion. *J. Comp. Physiol. A* **175**, 399-413.
- Huber, F., Kleindienst, H. U., Weber, T. and Thorson J.** (1984). Auditory behaviour of the cricket: 3. Tracking of male calling song by surgically and developmentally one-eared females, and the curious role of the anterior tympanum. *J. Comp. Physiol. A* **155**, 725-738.
- Laurent, G. and Richard, D.** (1986). The organization and role during locomotion of the proximal musculature of the cricket foreleg. II. Electromyographic activity during stepping patterns. *J. Exp. Biol.* **123**, 285-306.
- Lewis, B.** (1983). Directional cues for auditory localization. In *Bioacoustics, A Comparative Approach* (ed. B. Lewis), pp. 233-257. London Academic Press.
- Michelsen, A.** (1998). Biophysics of sound localisation in insects. In *Comparative Hearing: Insects* (ed. R. R. Hoy, A. N. Popper and R. R. Fay), pp. 118-162. New York: Springer.
- Michelsen, A. and Löhle, G.** (1995). Tuned directionality in cricket ears. *Nature* **375**, 639.
- Murphey, R. K. and Zaretsky, M. D.** (1972). Orientation to calling song by female crickets, *Scapsipedus margiatus* (Gryllidae). *J. Exp. Biol.* **56**, 335-352.
- Nabatiyan, A., Poulet, J. F. A., de Polavieja, G. G. and Hedwig, B.** (2003). Temporal pattern recognition based on instantaneous spike rate coding in a simple auditory system. *J. Neurophysiol.* **90**, 2484-2493.
- Nolen, T. G. and Hoy, R. R.** (1986). Phonotaxis in flying crickets. I. Attraction of calling song and avoidance of bat like ultrasound are discrete behaviours. *J. Comp. Physiol. A* **159**, 423-439.
- Pollack, G. S.** (1986). Discrimination of calling song models by the cricket, *Teleogryllus oceanicus*: the influence of sound direction on neural encoding of the stimulus temporal pattern and on phonotactic behaviour. *J. Comp. Physiol. A* **158**, 549-561.
- Pollack, G. S.** (1998). Neural processing of acoustic signals. In *Comparative Hearing: Insects* (ed. R. R. Hoy, A. N. Popper and R. R. Fay), pp. 139-196. New York: Springer.
- Pollack, G. S.** (2000). Who, what, where? Recognition and localization of acoustic signals by insects. *Curr. Opin. Neurobiol.* **10**, 763-767.
- Pollack, G. S.** (2003). Sensory cues for sound localization in the cricket *Teleogryllus oceanicus*: interaural difference in response strength versus interaural latency response. *J. Comp. Physiol. A* **189**, 143-151.
- Pollack, G. S. and Hoy, R. R.** (1979). Temporal pattern as a cue for species-specific calling song recognition in crickets. *Science* **204**, 429-432.
- Popov, A. and Shuvalov, V. F.** (1977). Phonotactic behaviour of crickets. *J. Comp. Physiol. A* **119**, 111-126.
- Rheinlaender, J. and Blätgen, G.** (1982). The precision of auditory lateralization in the cricket, *Gryllus bimaculatus*. *Physiol. Entomol.* **7**, 209-218.
- Rheinlaender, J. and Möhrchen, A.** (1979). 'Time-intensity trading' in a locust auditory interneuron. *Nature* **281**, 672-674.
- Regen, J.** (1913). Über die Anlockung des Weibchens von *Gryllus campestris* durch telefonische Übertragung der Stridulation des Männchens. *Pflügers Arch. Eur. J. Physiol.* **155**, 193-200.
- Schildberger, K.** (1984). Temporal selectivity of identified auditory neurons in the cricket brain. *J. Comp. Physiol. A* **155**, 171-185.
- Schildberger, K.** (1994). The auditory pathway of crickets: adaptations for intraspecific acoustic communication. *Fortschritte der Zoologie* **39**, 209-225.
- Schildberger, K. and Hörner, M.** (1988). The function of auditory neurons in cricket phonotaxis. I. Influence of hyperpolarization of identified neurons on sound localisation. *J. Comp. Physiol. A* **163**, 621-631.
- Schmitz, B., Scharstein, H. and Wendler, G.** (1982). Phonotaxis in *Gryllus campestris* L. (Orthoptera, Gryllidae). I. Mechanism of acoustic orientation in intact female crickets. *J. Comp. Physiol. A* **148**, 431-444.
- Stabel, J., Wendler, G. and Scharstein H.** (1989). Cricket phonotaxis: localization depends on recognition of the calling song. *J. Comp. Physiol. A* **165**, 165-177.
- Staudacher, E. M.** (2001). Sensory responses of descending brain neurons in the walking cricket, *Gryllus bimaculatus*. *J. Comp. Physiol. A* **187**, 1-17.
- Stumpner, A. and von Helversen, D.** (2001). Evolution and function of auditory systems in insects. *Naturwissenschaften* **88**, 159-170.
- Thorson, J., Weber, T. and Huber, F.** (1982). Auditory behaviour of the cricket. II. Simplicity of calling-song recognition in *Gryllus*, and anomalous phonotaxis at abnormal carrier frequencies. *J. Comp. Physiol. A* **146**, 361-378.
- Ulagaraj, S. M. and Walker, T. J.** (1973). Phonotaxis of crickets in flight: attraction of male and female to male calling songs. *Science* **182**, 1278-1279.
- Weber, T., Thorson, J. and Huber, F.** (1981). Auditory behaviour of the cricket I. Dynamics of compensated walking and discrimination on the Kramer treadmill. *J. Comp. Physiol. A* **141**, 215-232.
- Weber, T. and Thorson, J.** (1988). Auditory behaviour of the cricket. IV. Interaction of direction of tracking with perceived split-song paradigms. *J. Comp. Physiol. A* **163**, 13-22.
- Wendler, G.** (1990). Pattern recognition and localization in cricket phonotaxis. In *Sensory Systems and Communication in Arthropods. Advances in Life Sciences*, pp. 387-394. Basel: Birkhäuser Verlag.
- Wytenbach, R. A. and Hoy, R. R.** (1993). Demonstration of the precedence effect in an insect. *J. Acoust. Soc. Am.* **94**, 777-784.