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Sensory basis for sound intensity discrimination in the bushcricket *Requena verticalis* (Tettigoniidae, Orthoptera)

Abstract The ability of the female bushcricket, *Requena verticalis*, to discriminate between two conspecific sound signals that differed in sound pressure level (SPL) was tested in a two-choice paradigm. Significant discrimination was achieved with a 2-dB difference. The property of each pair of receptors to establish binaural discharge differences was investigated in electrophysiological experiments. The threshold to the conspecific signal varies for each fibre from about 40 to 90 dB SPL, allowing for a range fractionation of the hearing organ. Each pair of receptors establishes significant binaural discharge differences only within a restricted intensity range about 10 dB above threshold. Based on a model of the intensity response function of a receptor the total discharge of the 22 receptors in both ears was calculated with monaural and binaural stimulation. The profile of receptors exhibiting significant discharge differences changes with increasing SPL, from the most sensitive fibres with a characteristic frequency between 12 kHz and 35 kHz at low SPLs to the least sensitive fibres at very low and high characteristic frequencies at medium to high SPLs. The discharge difference with an intensity difference of 2 dB is rather small (4% of the total receptor activity) and limited only to a few pairs of receptors.

Key words Behaviour · Sensory coding · Sound intensity difference · Insect · Bushcricket

Abbreviations *CF* characteristic frequency · *HF* high frequency · *ILD* interaural level difference · *IR* intensity response · *LF* low frequency · *PSTH* peristimulus-time histogram · *RMS* root mean square · *SPL* sound pressure level

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Introduction

Many male Orthoptera use acoustic signals for the attraction of mates as well as for competition with other conspecific males (Alexander 1975; Otte 1977; Bailey 1991). The most significant feature of the signal for species recognition is its amplitude modulation, allowing both males and females to identify and to respond to other conspecifics within the population. Other sound parameters, such as the carrier frequency, intensity, and call duration also convey information, which may relate to the distance of the sender, its quality, size or mating status (Thiele and Bailey 1980; Hedrick 1986; Römer and Bailey 1986; Searcy 1986; Simmons 1988). Of these parameters, intensity has been shown to be of greatest significance, both in regard to the outcome of male–male interactions (Dadour and Bailey 1985; Latimer and Schatral 1986) and to the preferences exhibited by females in a two-choice situation (Gwynne 1982; Bailey 1985; Doherty 1985; Latimer and Sippel 1987; Bailey et al. 1990).

Two problems are associated with processing information on the intensity of a signal. The first is determining the direction of a single sound source, and the second concerns the discrimination of sound pressure levels (SPLs) of two or more sound sources from different directions. Both problems are, however, concerned with separating the afferent discharges from receptors in both ears. If one takes the simplest case of a binaural system receiving sound from one side of the insect's body, the directionality of the auditory system will create differences in SPLs at the two ears (interaural level differences; ILDs); these vary according to the direction of sound incidence. If the ILD is large enough it will result in significant differences in the afferent discharge of the receptors, which may be used by the insect for a phonotactic approach by following the simple rule: turn to the side on which the stimulation is strongest (Schildberger 1989; Rheinlaender and Römer 1991).

When acoustic stimulation is precisely controlled in experiments using dichotic ear stimulation techniques, both grasshoppers and bushcrickets appear able to detect ILDs as small as 0.5–1 dB that reliably elicit a turn to the louder side (von Helversen and Rheinlaender 1988; J. Rheinlaender, H. Römer, J. Shen, unpublished observations). It is remarkable that certain vertebrates, including man, with their vastly greater number of receptors in their ears do not perform better (Wakeford and Robinson 1974; Wegener 1974; Houben and Gourevitch 1979). Similar stimulation techniques with large cross-talk barriers, used in electrophysiological experiments, further demonstrate that interneurones of the auditory pathway are capable of responding to similarly small ILDs (Rheinlaender and Mörchen 1979; Römer and Rheinlaender 1983). Importantly, the difference in the amount of binaural discharges in the sensory afferents is completely unknown for these small ILDs.

Dissecting the behavioural and neurophysiological effects of small ILDs in a sound-controlled laboratory may be of little relevance to the natural situation with a receiver in a population of several signallers, in which the monaural stimulation paradigm probably rarely occurs. In the field the insect may receive two or more signals from different directions, and of different intensities at the same time, thus complicating the task of discriminating between these signals on the basis of intensity differences. Yet despite these difficulties, when insects are given a choice between two conspecific signals of different intensity, they inevitably approach the louder signal (Popov and Shuvalov 1977; Thorson et al. 1982; Forrest 1983; Latimer and Sippel 1987; Partridge et al. 1987; Bailey and Yeoh 1988; Bailey et al. 1990; Schatral and Bailey 1991; review in Ryan and Keddy-Hector 1992). In some of these experiments the intensity difference at the orienting female's decision point was in the range 1–3 dB. Again, the binaural difference in the afferent discharge established in such situations is unknown, as is the number of afferent fibres which may contribute to these differences.

In the present paper we examine the discharge of the whole population of auditory receptors in the ear of the bushcricket, *Requena verticalis*, using a monaural and binaural stimulation paradigm. We quantify the binaural discharge differences under both paradigms by experiment and by modelling the receptor responses. We compare the electrophysiological results with those of the insect's behaviour where we use similar stimulus conditions. We estimate the minimum binaural discharge difference in the auditory system necessary to elicit reliable intensity discrimination by an orienting female.

Materials and methods

Behaviour

Requena verticalis is a small listrocelinid bushcricket (pronotum length 7.6 ± 0.066 mm; length of hind tibia 14.2 ± 0.151 mm; diameter of thorax 6.5 ± 0.181 mm; means ± SD for females;

$n = 41$) abundant in the reticulated gardens of the University of Western Australia, Perth. Females were collected as penultimate instars early in the season and reared to adulthood in the laboratory. Over 90 females were used for behavioural experiments. In order to maintain independence within trials each female was used only once.

The arena used for two-choice trials was made of fibreglass flywire mesh, suspended free from the ground and the loudspeakers, so avoiding the transmission of substrate vibration. Two speakers were mounted with their axes directed to the centre of the arena with an angular separation of 150°. Females were released at the centre of the flat arena from a small plastic vial. The insect was allowed to settle for 2 min, after which the sound stimulus was switched on. If the insect had not moved from the vial or the centre of the arena within 5 min the trial was aborted. Similarly, if the female had not reached the perimeter of the arena within 10 min of the time the sound was switched on the trial was aborted. The track of each female was recorded on a map of the arena (see Bailey and Yeoh 1988), indicating a direct path from the release point to the speaker. The chosen speaker was scored when the insect crossed a "line" set at 60 cm from the centre of the arena and within an arc of 45° to each speaker. In all cases where a female crossed this line on its way to a speaker, the "decision" to track either speaker had been taken within 10 cm of the release point, where the difference in SPL between the two speakers was as indicated. By scoring only females crossing this arbitrary 60-cm line we were able to exclude data from animals exiting the arena without showing phonotaxis to either speaker.

The stimulus used in all experiments was derived from a calling song of an isolated male, which was recorded in an anechoic room using a 1/4″ microphone (Bruel & Kjær, type 4163), preamplified through a sound-level meter (Bruel & Kjær, type 2209). The signal was digitized on a custom-made AD/DA converter (12 bit, sampling rate of 125 kHz). A sequence of three chirps (total duration 1030 ms; see Fig. 1A) was used as a standardized stimulus and then re-recorded onto two channels of a tape recorder (Racal store 4D). In order to achieve a random temporal relationship between the sequence of the two stimuli on each of the two channels the interval between the chirps differed with one at 1330 ms and the other at 1270 ms. Stimuli were broadcast through wide-band amplifiers (Realistic 80 W) and speakers (Technics EAS-10 TH400A). The intensity of the signals was controlled by two attenuators separately. Sound intensities were measured at the release site of the females and are given as root mean square (RMS fast reading) SPLs re: 20 µPa. A standard intensity of 70 dB SPL was provided at the centre of the arena which is close to the intensity of the natural call at a distance of 1 m (Bailey and Yeoh 1988).

Intensity differences were established by attenuating one song in steps of 1, 2, 5 and 10 dB. Speakers were randomized with respect to side and signal. Song spectra (Fig. 1) are provided as the output of the speakers at the release site of the arena.

Morphology of the crista acustica

A total of 14 tympanal organs was analysed with respect to the number of receptors in each ear. A foreleg was mounted under a dissecting microscope with the tympanal slits pointing upward. The cuticle covering the leg trachea above the ear was carefully removed by a razor blade and the preparation covered for 10 min in a saturated solution of janus green or neutral red. After washing in Ringer the cap cells in particular show up clearly and their number was established for each ear.

Neurophysiology

Fifty-four adult males and females were used for electrophysiological experiments. Only medium-sized to large insects were used for experiments, since body size in *Requena* is correlated with the size of the spiracular opening, which in turn correlates with hearing sensitivity (W.J. Bailey, unpublished results). Therefore, interindi-
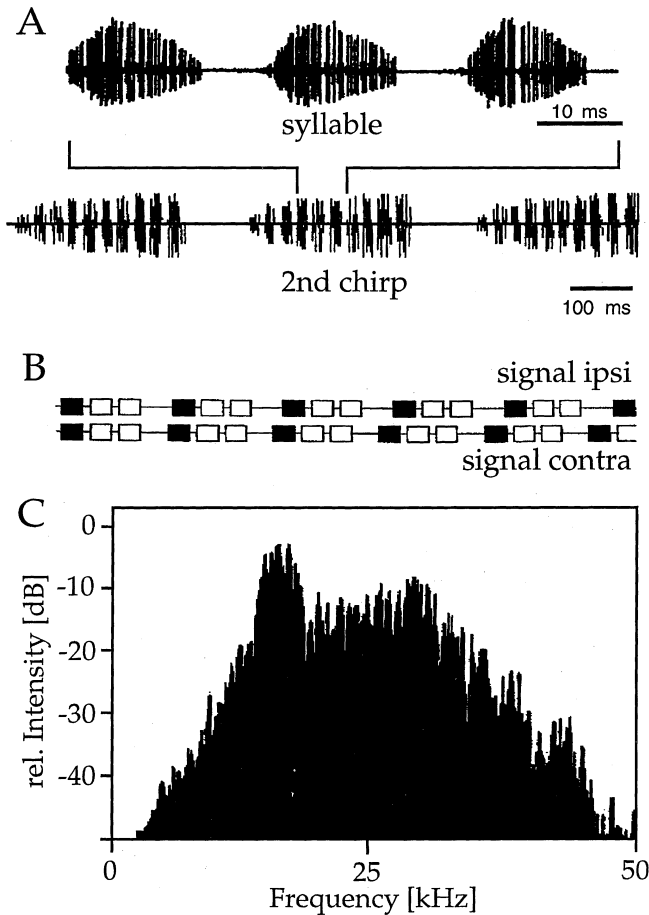
Fig. 1 Oscillogram (**A**) and spectrum (**C**) of the signal used in behavioural and electrophysiological experiments. The stimulus was a series of three identical chirps, each with ten syllables of about 15 ms duration. The intersyllable interval was 8–12 ms; the interchirp interval 120 ms. In order to achieve a random temporal relationship between the ipsi- and contralateral signal (see schematic diagram in **B**, first chirp in the series black), the interval between the series of three chirps was 1330 ms for the signal on one side and 1270 ms for the other

The preparation was placed in the centre of an anechoic chamber at a distance of 50 cm from two speakers (Type Technics EAS-10 TH400A), each oriented 90° off the longitudinal body axis of the preparation. One of the speakers could be rotated in steps of 15° or 30° in the horizontal plane around the animal. The experimental protocol was as follows: after tuning of the fibre was completed the monaural IR function was established with both ipsi- and contralateral stimulation. Depending on the absolute threshold in response to the calling song, the fibre was then stimulated binaurally, with the SPL of both stimuli adjusted to either 50, 60, 70 or 80 dB. Next, the SPL of the contralateral stimulus was attenuated in steps of 2, 5 and 10 dB, while the ipsilateral signal was kept constant. Finally, the corresponding attenuation was performed with the ipsilateral stimulus, and the contralateral signal was kept constant. Each stimulus configuration was repeated ten times. Assuming that a receptor fibre identical to the one recorded exists in the opposite ear, the described stimulation paradigm allows to calculate the discharge difference between a given pair of receptors in the right and left hearing organ for each kind of stimulation.

Action potentials were recorded on a tape recorder (TEAC A-3440) in parallel with the trigger for the ipsi- and contralateral stimuli. The discharges were later analysed either as peri-stimulus time histograms (PSTHs) or the total number of spikes/stimulus.

Results

Behaviour

In the first series of trials, when the signal at one speaker was attenuated relative to the other, females were able to distinguish between speakers when the intensity difference was 2 dB (Table 1; experiment 1). In a second series, the high-frequency (HF) part of the spectrum was digitally attenuated relative to the low-frequency (LF) part. The choice was between the original signal and a progressively decreasing intensity of the HF part, while the absolute intensity of both signals was maintained equal. Females were able to distinguish between speakers when the intensity of the HF part of the signal differed by 2 dB (Table 1; experiment 2). There was no

vidual variation in absolute sensitivity of identified receptor fibres was kept low by choosing individuals of similar size. Extra- and/or intracellular recordings were made from a total of 392 tympanal fibres in the prothoracic ganglion, close to the area where the fibres branch into the auditory neuropile (Römer et al. 1988). Animals were anaesthetized with CO_2 and mounted ventral side up on a small, thin metal sheet with the forelegs oriented perpendicular to the long axis of the body. A small flap of cuticle covering the prothoracic ganglion was removed. The action potential activity of receptor fibres was recorded using glass microelectrodes filled with 3 mol·l^{-1} KCl (resistance 10–50 MΩ). In ten preparations individual fibres were also stained at the end of the physiological experiment with lucifer yellow using conventional staining protocols. Stainings were later analysed both as wholemounts and sectioned material. Physiologically, receptors were characterized on the basis of their tuning and their monaural intensity-response (IR) function with ipsi- and contralateral stimulation. Sound pulses with different pure-tone carriers (2–80 kHz, standard duration 30 ms; repetition rate 1/s) were generated to study the tuning of individual fibres. Sound stimuli were amplified and attenuated in 10-dB or 1-dB steps (Akustischer Stimulator II, Burchard). The threshold of a fibre was determined according to a procedure described in detail by Rheinlaender and Römer (1980).

Table 1 Number of females moving to a male call broadcast in a two-speaker choice trial. Experiment 1: high- and low-frequency components of the signal were maintained at the same level (see Fig. 1) while the absolute sound pressure level (SPL) of the signal at one speaker was progressively attenuated in steps of 1 dB. Once Δ2 dB was distinguished there was no value in proceeding to higher intensity differences. Experiment 2: only the power in the high-frequency (*HF*) part of the signal (frequencies > 20 kHz) was attenuated by 10, 5 and 2 dB, while the absolute SPL of both signals was maintained at 70 dB SPL (two-tailed binomial test; *P* < 0.005). *NS* Not significant

	HF attenuation	Preference	Significance
Experiment 1			
70 dB–69 dB	0 dB	6:9	NS
70 dB–68 dB	0 dB	8:0	*
Experiment 2			
70 dB–70 dB	10 dB	8:0	*
70 dB–70 dB	5 dB	9:1	*
70 dB–70 dB	2 dB	9:1	*
70 dB–70 dB	0 dB	7:8	NS

significant difference in female preference between speakers in the 99 successful trials (54 to speaker 1; 45 to speaker 2).

Number of tympanal receptors

It is generally assumed that sensory performance increases with the number of receptors in the sense organ or nerve cells in the associated sensory pathways. The number of tympanal receptors in the ear of tettigoniids varies between 16 and 39 (Schumacher 1973; Lakes and Schikorski 1990; Bailey and Römer 1991). In 14 preparations of the crista acustica of *R. verticalis* the number of cap cells (and thus of receptor cells) varied between 19 and 22. The size of the cap cells decreases at the distal end of the crista, which in some preparations made a separation of individual cells more difficult. It is therefore reasonable to assume that fewer than 22 receptors per ear reflects methodological limitations rather than real variability between ears. We thus suggest that the behavioural intensity discrimination performance described above should be based on a comparison of the afferent activity of 22 receptors in each ear.

Physiology

The frequency sensitivity of the tympanal organ covers a range of frequencies between about 3 kHz and 80 kHz. Within this range each of the 22 receptors is tuned to a different characteristic frequency (CF). Figure 2 shows tuning curves from a selection of these receptors recorded in one insect over a frequency range of 3–58 kHz. A consistent observation was that some receptors have identical CFs but differ by up to 25 dB in their absolute threshold. Direct evidence for the existence of both high- and low-threshold receptors with t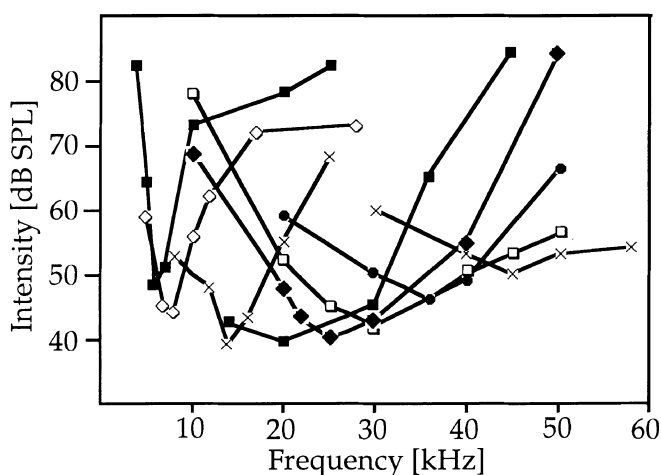he same CF was obtained in experiments in which up to 15 different fibres have been recorded in one animal and characterized by their tuning and IR function. In contrast, when the identical receptor fibre was recorded from the right and left hearing organ their tuning and absolute thresholds usually differed very little.

All receptor fibres exhibit a sigmoid IR function in response to the conspecific calling song with a dynamic range of about 20–25 dB and a similar saturation level of 120–130 spikes/stimulus (Fig. 3). Within this dynamic range the response level changes by 6 spikes/dB; with a 2-dB change the response level is significantly different. Moreover, as a result of their different tuning there is a large variation between auditory receptors with respect to the threshold of the IR function (Fig. 3). Receptors with CFs between 16 kHz and 30 kHz are more sensitive to the calling song than LF or HF receptors because of the different overlap of their tuning curve with the power spectrum of the song. The less sensitive receptors, however, increase the dynamic range of a hearing organ up to about 100 dB SPL.

Binaural differences with monaural stimulation

For each receptor we tested the dynamic range of the IR function with ipsi- and contralateral stimulation. The difference in the response level of these IR functions can be taken as the discharge difference between a pair of receptors with monaural stimulation at a given SPL, provided there exists a bilateral symmetry of these receptors in the two ears. Figure 4A shows the ipsi- and contralateral IR function of a LF and HF receptor, tuned to 8 kHz and 35 kHz, respectively. Despite their different tuning the threshold of the IR function with ipsilateral stimulation is almost identical, since their
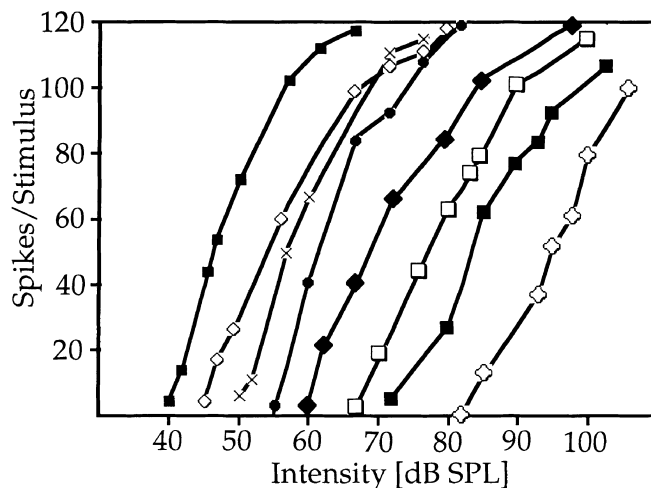

Fig. 2 Tuning curves of eight different tympanal fibres recorded in one animal

Fig. 3 Intensity response (IR) functions of eight different receptor fibres in response to conspecific song recorded in one animal. Note that the dynamic range of each receptor is limited to about 20 dB, and the range fractionation of the organ with a total dynamic range of about 40–100 dB SPL. Fibres are not identical to those shown in Fig. 2
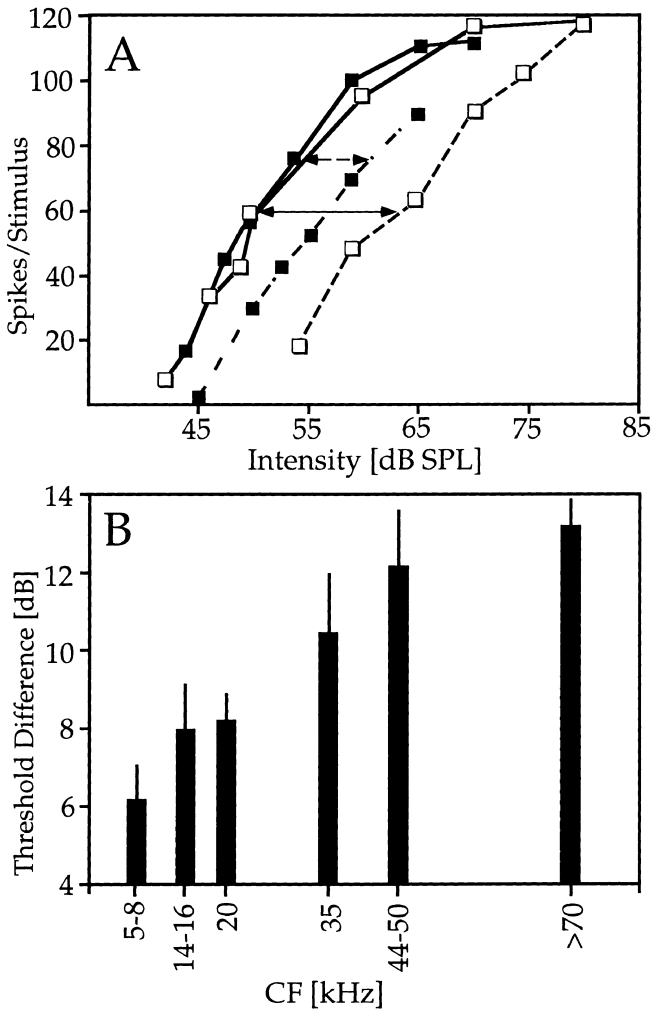
and asymptotes to approximately 13 dB for HF receptors tuned to frequencies of 50 kHz or more.

Binaural differences with binaural stimulation

It is evident from the findings presented in Figs. 3 and 4 that three variables determine the activity of a receptor with binaural stimulation: (1) its threshold to the ipsilateral stimulus, (2) its threshold to the contralateral stimulus, and (3) the absolute intensity of both stimuli. This is demonstrated in Fig. 5 with the PSTHs of the responses of a receptor (CF 14 kHz) with ipsilateral stimulation at 60 dB SPL and varying intensities of the contralateral stimulus. Given an ipsilateral threshold of 44 dB SPL, the fibre is activated 16 dB above threshold at 60 dB SPL with ipsilateral stimulation, whereas a contralateral stimulus of 50 dB SPL does not activate the fibre at all due to the direction-dependent loss of 8 dB (Fig. 5A). However, when both stimuli are presented at 60 dB SPL (Fig. 5B) the fibre is activated by both stimuli since the contralateral signal is also well above threshold. As a consequence of the fact that the two stimuli are not phase locked the temporal pattern of the spike response is obscured, the more the contralateral stimulus contributes to the response (see dot display and PSTH at 70 dB SPL for the left signal in Fig. 5C).
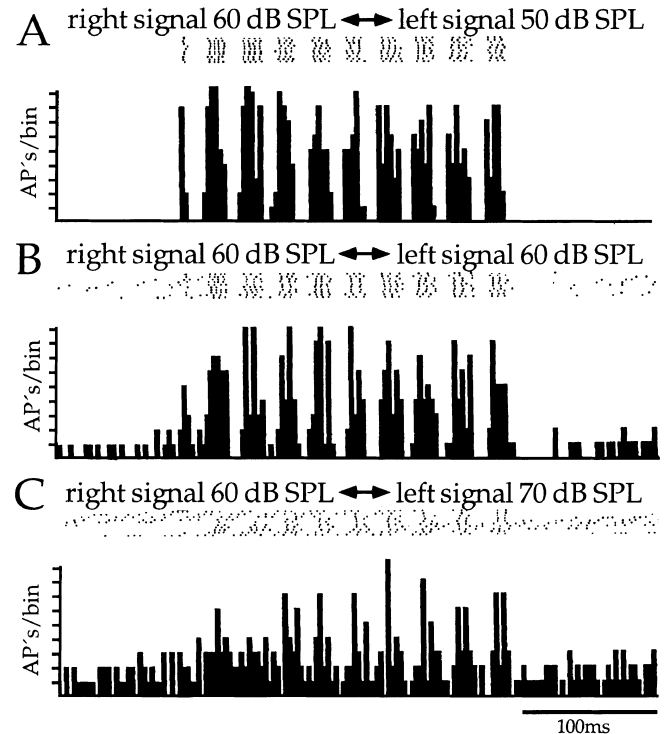
Fig. 4 A IR function of two receptor fibres tuned to 8 kHz (*filled squares*) and 35 kHz (*open squares*), respectively, in response to ipsi- and contralateral stimulation with conspecific song. Note the almost identical IR function of the fibres with ipsilateral stimulation despite their different tuning, but the 6-dB shift of the contralateral IR function (*broken lines*) for the low-frequency (*LF*) fibre, and about 12 dB for the high-frequency (*HF*) fibre. **B** Correlation of the characteristic frequency (*CF*) of receptor fibres and their dB shift with contralateral stimulation (mean ± SD; $n = 115$). Fibres have been grouped according to their CF, as indicated in the figure

tuning is shifted to either the LF or HF end of the main energy peak of the calling song. Stimulation from the opposite side resulted in a shift of the IR function of both receptors to higher intensities. However, this shift is only 6 dB for the receptor tuned to 8 kHz, but 12 dB for the receptor tuned to HFs. Given this difference in directionality the pair of HF receptors exhibits large binaural differences (for example about 60 spikes/stimulus at 65 dB SPL) compared to only 20 spikes/stimulus for the pair of LF receptors.

Figure 4B summarizes the correlation between the CF of auditory receptors and their directionality (i.e. the shift of their IR function with contralateral stimulation). With increasing CF the threshold shift increases from a minimum of 6 dB for receptors tuned to about 5 kHz

Fig. 5 Peri-stimulus time histograms (PSTHs) and dot-displays of the activity of a fibre in response to binaural stimulation, with the intensity of the ipsilateral signal maintained at 60 dB SPL, and the contralateral signal at 50 (**A**), 60 (**B**) and 70 dB SPL (**C**). The threshold of the fibre to ipsilateral stimulation is 44 dB SPL; the PSTH was triggered with the ipsilateral signal

We can predict from these results that discharge differences between a given pair of receptors will be most prominent if the intensity of one signal remains subthreshold for the mirror-image receptor fibre in the other ear. Experimental proof is given by the example in Fig. 6 with a receptor stimulated binaurally at 50 dB and 70 dB SPL. The direction-dependent decrease in sound intensity of the contralateral signal was 10 dB for this fibre; as a result of a threshold of 42 dB SPL the contralateral signal remained just at threshold. Binaural stimulation at 50 dB SPL therefore elicits the same activity in the fibre as does monaural stimulation. Furthermore, binaural stimulation with intensity differences of 2, 5 or 10 dB (i.e. a SPL of 48, 45 or 40 dB at the contralateral side) does not change the activity of the receptor of the more strongly stimulated side, whereas the mirror-image receptor changes its activity according to the monaural IR function. The discharge differences between the pair of receptors can amount to 60 spikes/ stimulus with intensity differences of 10 dB. Significant differences (10 spikes/stimulus) were found with an ILD of 2 dB.

When the same pair of receptors was stimulated at 70 dB SPL, which corresponds to about 30 dB above the ipsilateral threshold, ILDs of 2 dB or 5 dB did not result in significant discharge differences between the two receptors. Even large binaural differences of 10 dB create only small, just significant differences in the responses of these receptors. This is a direct consequence of the saturated IR function at 30 dB above threshold, and the fact that each receptor is driven by both signals well above threshold.

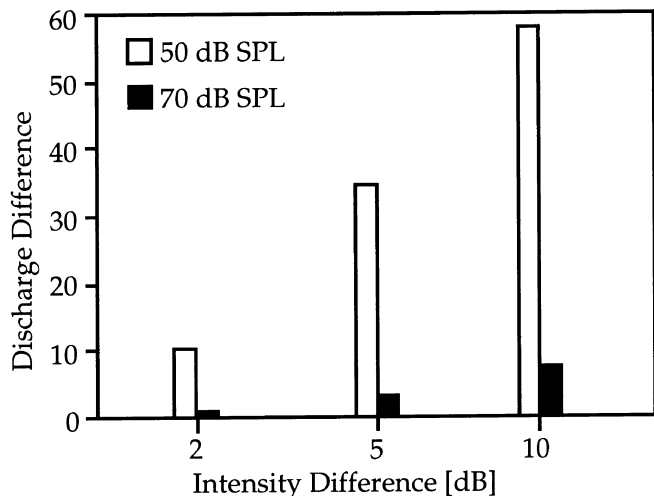The example shown in Fig. 6 demonstrates that a single pair of receptors can establish large discharge differences from small ILDs only within a restricted intensity range. This intensity range is characterized by the threshold of the fibre to the calling song and by its directionality, i.e. the shift of the IR function with contralateral stimulation. Therefore the contribution of each pair of receptors for the total discharge difference between the two ears is different, as exemplified for three receptors in one ear at an absolute intensity of 60 dB SPL (Fig. 7). The pair of receptors tuned to a CF of 35 kHz (ipsilateral threshold 42 dB SPL) established significant discharge differences only with an ILD of 10 dB, in contrast to the less sensitive pair of receptors which provide large interaural discharge differences even when the ILD is only 2 dB. Again, the total discharge difference for the pair of HF receptors is larger than for the LF receptor since its directionality is much larger (12 dB compared to 6 dB).
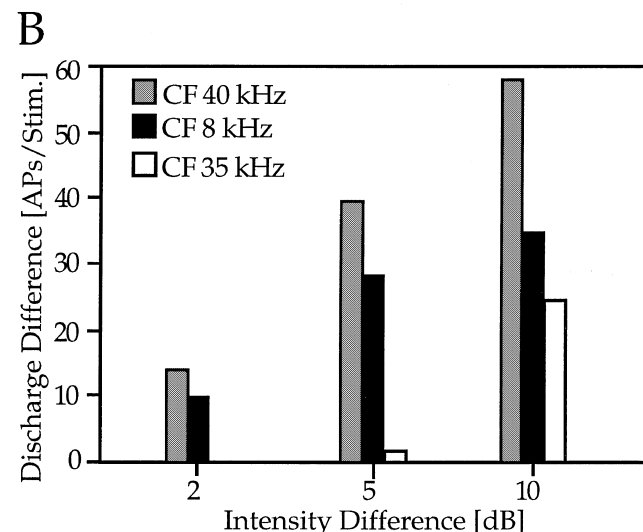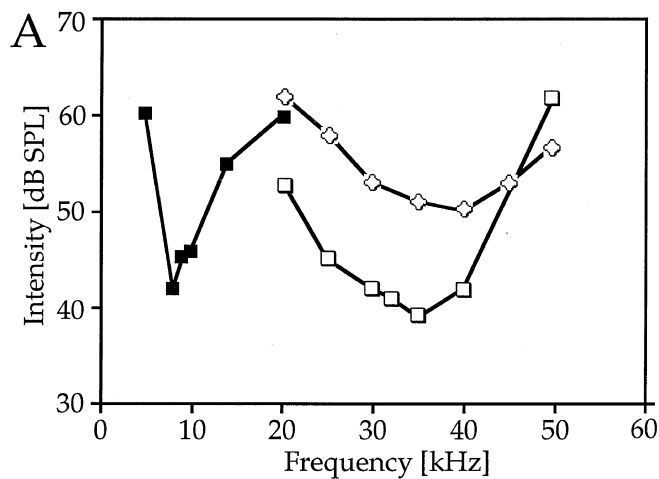
Fig. 6 Binaural discharge differences of a pair of receptors (CF 25 kHz), when the right stimulus is at 70 dB SPL or 50 dB SPL, and the left stimulus is attenuated relative to the right one by 2, 5, or 10 dB. Discharge differences are large and significant with an intensity difference of 2 dB at 50 dB SPL, but not at 70 dB SPL. For further explanation see text

Fig. 7A, B Binaural discharge differences of three pairs of receptors recorded in one animal, when the right stimulus is maintained at 60 dB SPL, and the left stimulus is attenuated relative to the right one by 2, 5 or 10 dB. The tuning of the three receptors is shown in **A**. Note that the discharge difference for the most sensitive pair of receptors is only significant with interaural level differences (ILDs) of 10 dB

Modelling the activity of auditory receptors

We have shown for each of the 22 pairs of receptors in the tympanal organ that significant binaural discharge differences are established only within a restricted range of intensities, defined by the threshold to the signal and the directionality of the receptor. However, we obtained experimental proof only for some absolute SPLs and intensity differences. In order to quantify the sensory basis for auditory intensity discrimination at any absolute intensity level and any intensity difference we used a model of an auditory receptor, based on a mathematical description of the sigmoid IR function of a receptor,

$$F(\mathbf{x}) = F_\infty \frac{e^{\alpha(x-x_{\mathrm{m}})}}{1 + e^{\alpha(x-x_{\mathrm{m}})}},$$

where the maximum discharge is given by F_∞, the steepness of the linear part of the IR function by the rate constant α. The threshold can be defined by the point of inflection x_{m} of the function.

The calculation of the activity of a receptor in response to binaural stimulation was based on the sum of the corresponding values of the ipsi- and contralateral IR functions. However, as shown by experiment with binaural stimulation, the total activity of a receptor is not linearly related to the sum of the responses with ipsi- and contralateral stimulation. If a receptor is activated well above threshold (at saturation level or close to it) in response to one signal, an additional contralateral signal will only slightly increase the activity, in particular during the silent periods of the ipsilateral signal (compare with Fig. 5). We considered this non-linearity in the

model with binaural stimulation by adding a weighting factor for values of the ipsilateral IR function which is proportional to the saturation level of the receptor response. As shown in Fig. 8, the theoretical IR function,

$$F(\mathbf{x}) = 120 \frac{e^{0.2(x-x_{\mathrm{m}})}}{1 + e^{0.2(x-x_{\mathrm{m}})}},$$

(with x_{m} = threshold + 8 dB) fits the empirically determined IR function of a receptor quite well. The model allows calculation of any binaural intensity difference the resulting discharge difference over the whole physiological intensity range. These calculated values are shown, in comparison with experimental data, in Fig. 9A for a pair of receptors with an ipsilateral threshold of 40 dB SPL and a directionality of 12 dB, for three binaural intensity differences of 2, 5 and 10 dB. Starting at the threshold of 40 dB SPL the discharge difference increases up to 52 dB SPL, since the receptor is only activated by one signal and the discharge differ-
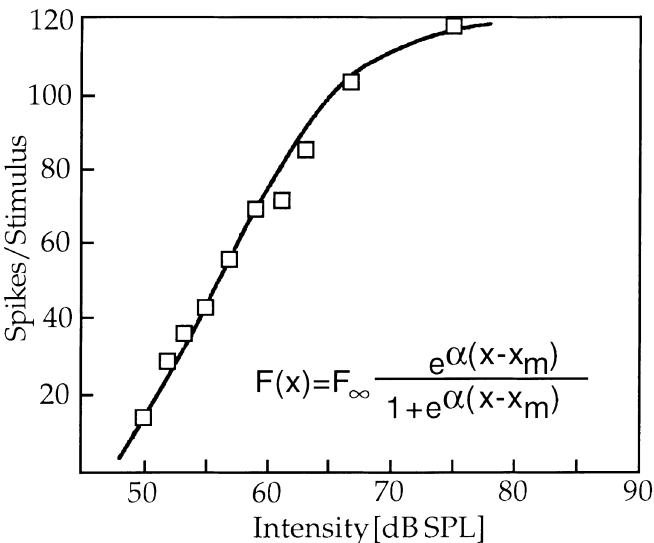

Fig. 8 Model IR function of an auditory receptor, based on a mathematical description as indicated, where the maximum discharge is given by F_∞, the steepness of the linear part of the IR function by the rate constant α. The threshold can be defined by the point of inflection x_{m}. The theoretical IR function with x_{m} = threshold + 8 dB, $F_\infty = 120$, $\alpha = 0.2$ fits the empirically determined IR function of a receptor quite well
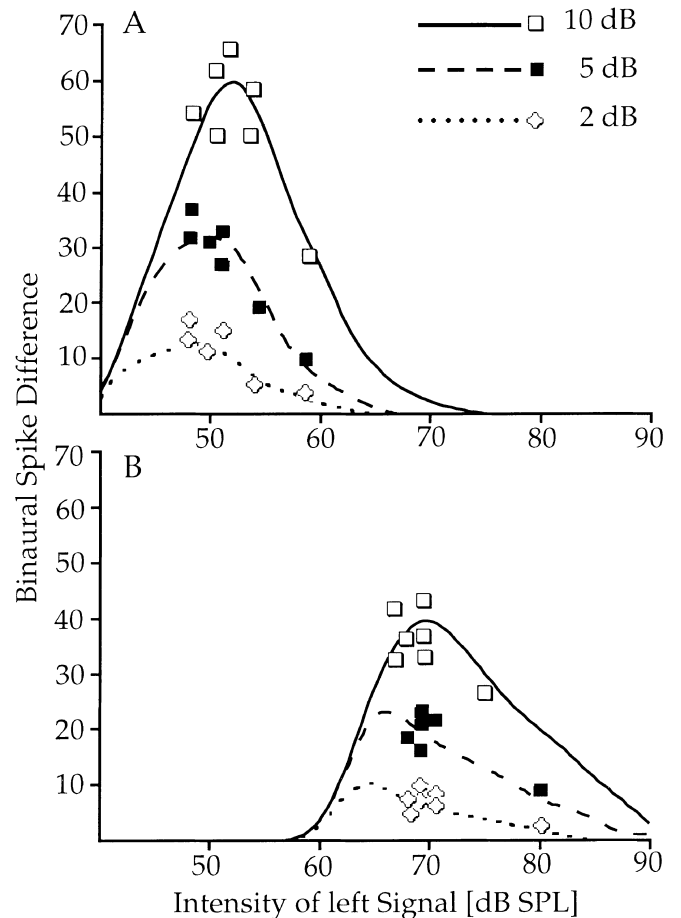

Fig. 9 Calculated binaural discharge differences for a pair of HF receptors (**A**) and LF receptors (**B**) at ILDs of 2, 5 and 10 dB, at intensities between 40 and 90 dB SPL. For comparison, experimental values of receptors with corresponding thresholds are superimposed the calculated curve. Note that the pair of LF receptors exhibits reliable binaural discharge differences at intensities, where the corresponding differences of the pair of HF receptors are almost zero

ence can maximally amount to the activity according to the monaural IR function. Maximal values are 62 spikes at 10 dB, 34 spikes at 5 dB and 12 spikes at an ILD of 2 dB. With increasing absolute intensity of the signal, however, the discharge difference decreases as a result of increasing activation of the opposite receptor. At 70 dB SPL (30 dB above ipsilateral threshold) the discharge difference is almost zero even with an ILD of 10 dB. A comparison between calculated values and those obtained by experiment (compare curves and data points in Fig. 9) further shows that the model reliably predicts the activity and discharge differences of receptors in the monaural and binaural stimulation paradigm.

Figure 9A indicates that this pair of receptors does not contribute significant discharge differences at 70 dB SPL, even when the ILD is as large as 10 dB. Figure 9B presents the discharge differences for a pair of LF receptors, which are about 20 dB less sensitive in response to the conspecific calling song (ipsilateral threshold 60 dB SPL). This pair of receptors provides significant discharge differences at much higher absolute intensities between 60 dB and 80 dB SPL, though the total spike differences are smaller compared to a HF receptor due to the reduced directionality of only 6 dB. Again, the calculated and measured discharge differences deviate little and confirm that calculations based on our model are reliable.

Discharge differences of all 22 tympanal receptors with binaural stimulation

Based on a total of 392 recordings of individual receptor fibres we summarized the physiological characteristics of the 22 receptors in each hearing organ with respect to their tuning and threshold at the CF, the threshold in response to the calling song, and the directionality (dB shift with contralateral stimulation). The summary reveals a broad range of CFs from 5 kHz to 70 kHz, where about half of the receptors match the spectrum of the calling song with their CF. As a result the thresholds to the calling song are not evenly distributed; at 50 dB SPL about half of the receptors are activated suprathreshold, whereas at higher intensities range fractionation is only based on a few receptors.

Based on these physiological properties of all receptors we calculated the discharge differences at a given binaural intensity difference for the whole population of receptors. As an example, Fig. 10 shows the result of such a calculation for ILDs of 2, 5 and 10 dB, at four absolute SPLs (80, 70, 60 and 50 dB; A–D). At 50 dB SPL (Fig. 10D) 12 of 22 receptors remain subthreshold; only those tuned to frequencies between 14 kHz and 32 kHz are activated above threshold and develop large discharge differences. At 60 dB SPL (Fig. 10C) the number of activated receptors increases, but at the same time the discharge differences decrease for the most sensitive receptors. Largest discharge differences are now established by receptors which are activated just above
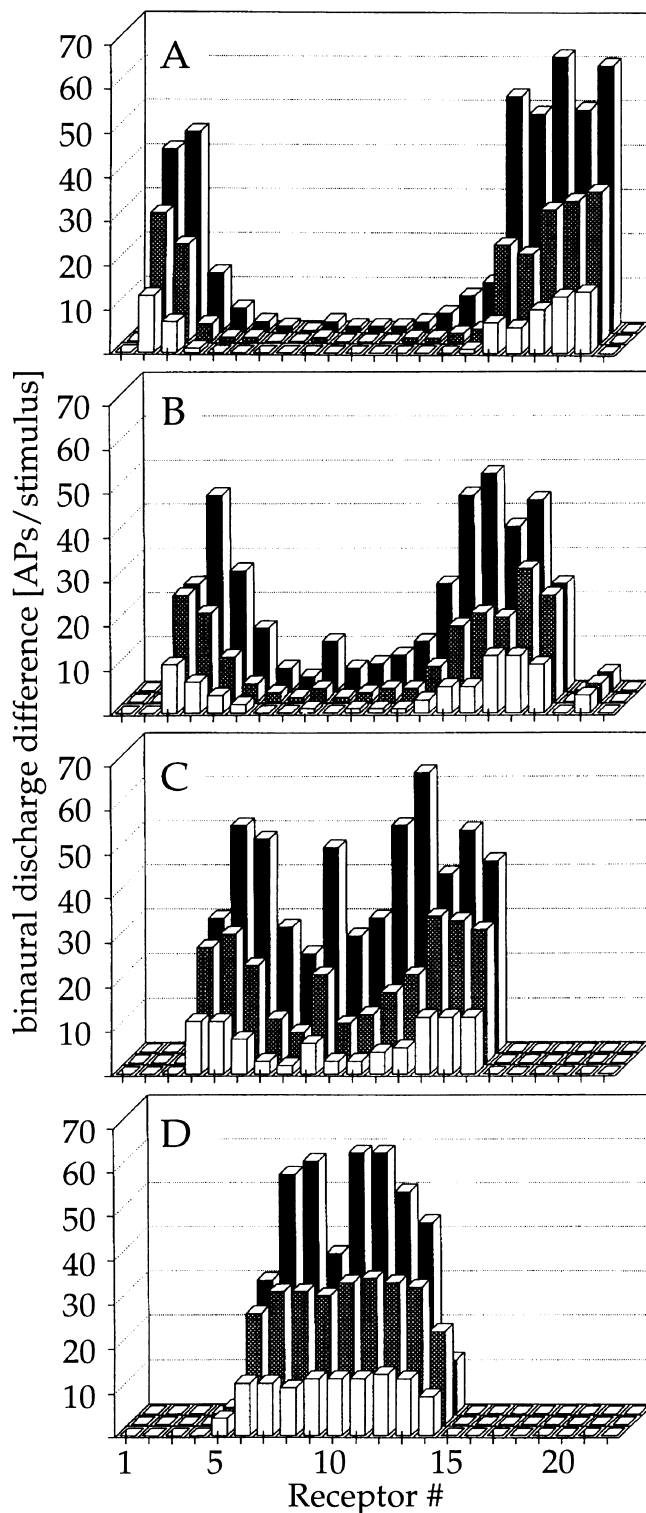

Fig. 10 Calculated binaural discharge differences of all 22 receptors in the crista acustica of *R. verticalis* at four absolute intensity levels of 80, 70, 60 and 50 dB SPL (**A–D**) and at ILDs of 2, 5 and 10 dB (*white, hatched* and *black bars*, respectively). Note that the profil of receptors with significant discharge differences changes with absolute SPL

threshold, due to their lower or higher CFs. The same tendency can be seen at 70 dB and 80 dB SPL (Fig. 9A, B); significant discharge differences are limited to a few

receptors which are not tuned to the calling song frequencies. By contrast, the most sensitive receptors are activated maximally, but their discharge difference is almost zero (compare with Fig. 9). Larger ILDs are encoded by the population of receptors in a similar way, but the discharge differences are much larger and can amount to 65 APs/stimulus with a binaural difference of 10 dB.

Discussion

Females faced with a two-choice situation predictably headed for the louder of the two signals, when the intensity of the whole signal differed by 2 dB, or when only the HF part was attenuated by the same amount. This discriminatory ability of R. verticalis is well within the range of other acoustic insects that have been examined in both the field and laboratory. One decibel has been reported for Gryllus campestris (Weber et al. 1981), 3 dB in the molecricket Scapteriscus acletus (Forrest 1983) and 2 dB in the undescribed zaprochiline tettigoniid (Gwynne and Bailey 1988). Experiments with a dichotic ear stimulation in both a grasshopper and a bushcricket reveal ILDs of 0.5–1 dB that reliably elicit a turn to the louder side (von Helversen and Rheinlaender 1988; J. Rheinlaender, H. Römer, J. Shen, unpublished observations).

Twenty-two receptors per ear in R. verticalis is somewhat intermediate between the "primitive" ear of some moths (1–4 auditory receptors) and the more elaborate ears of bushcrickets and grasshoppers (up to 40 or 100, respectively) or cicadas (up to 1500 receptors) (Schwabe 1906; Vogel 1923; Roeder and Treat 1957; Gray 1960; Schumacher 1973; Young and Hill 1977; Surlykke and Miller 1982; Surlykke 1984; Spangler 1988). It has been discussed whether fibres responding to LF airborne sound may originate from either the intermediate organ or the subgenual organ, rather than the crista acoustica (Rheinlaender 1975; Zhantiev and Korsunovskaja 1978; Kalmring et al. 1978, 1993. However, only recently Stumpner (1996) unequivocally demonstrated cells originating either in the subgenual organ or in the intermediate organ which responded to frequencies between 3 kHz and 8 kHz with thresholds of about 65 dB SPL, in addition to similar LF receptors of the crista acoustica. If this is also true in R. verticalis, such LF receptors of the intermediate and the subgenual organ would also contribute to the coding of binaural differences, primarily at SPLs of 70 dB or higher because of the mismatch of their tuning with the calling song spectrum.

Many auditory receptors in other species of bushcricket have been examined with respect to their tuning, intensity coding, tonotopicity or central branching pattern, but here we have shown for the first time how the whole population of sensory afferents encodes a physical ILD between two conspecific signals into a physiological discharge difference. Based on a large number of ex-

perimental data a model of the IR function of a receptor allows us to predict any afferent activity as a result of monaural or binaural stimulation.

Binaural discharge differences with monaural stimulation

The usual experimental paradigm for studying phonotactic behaviour in Orthoptera is to present a single stimulus from different angles of sound incidence, and then to measure stimulus and turn angles in the freely running insect, or the responses of receptors or associated interneurons in the restrained animal. One neurophysiological result was that changing sound direction from ipsi- to contralateral leads to a relative decrease of stimulus intensity at the ipsilateral ear, thus providing a shift of the IR function of a receptor to higher intensities with contralateral stimulation. The finding that receptors with high CFs exhibit a much larger ipsi-contralateral shift than LF receptors (Fig. 4) corroborates earlier results with bushcricket auditory interneurones (Rheinlaender 1975; Rheinlaender and Römer 1980; Hardt 1988). This difference is due to the fact that HF receptors are activated by the HF energy within the broadband signal and the directionality of the bushcricket auditory system provides greater ILDs for HFs rather than for LFs.

With monaural stimulation the discharge differences between any pair of receptors can easily be calculated from the difference of the corresponding ipsi- and contralateral IR functions (Fig. 4). The differences are constant where the IR functions run parallel; as a consequence, a pair of receptors codes ILDs into large spike differences within an intensity range of about 15–20 dB (Fig. 11). Studies on the phonotactic behaviour of various orthopteroid insects have shown that stimulus an-
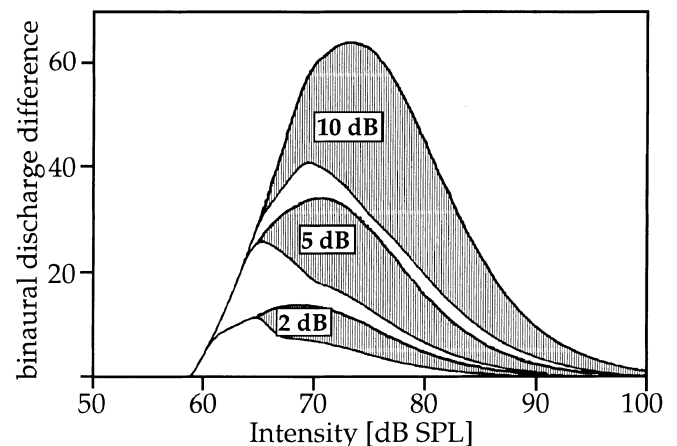

Fig. 11 Comparison of calculated binaural discharge differences for a pair of LF receptors with monaural stimulation, assuming threshold differences of 2, 5 and 10 dB between the right and left receptor (*upper curves*); and binaural stimulation with ILDs of 2, 5 and 10 dB (*lower curves*). The difference between the monaural and binaural stimulation is indicated by the *shaded area*. For further explanation see text

gles of 5–30° in the frontal zone of the animal are sufficient to elicit a reliable turn to the ipsilateral side (Rheinlaender 1984, review). In *R. verticalis* a stimulus angle of 30° in the frontal zone of the animal result in ILDs of only 4 dB (H. Römer, unpublished results). Using our data on all 22 receptors, we calculated that all receptors provide an absolute discharge difference of 95 action potentials, given a monaural stimulation with the conspecific song at 70 dB SPL and a frontal stimulus angle of 15°. This difference is at a total level of afferent activity of 1584 action potentials in the ipsilateral and 1489 in the contralateral ear; the difference corresponds to 6% of the total activity.

The above calculation assumes that a central "integrator" exists somewhere in the afferent auditory pathway which compares the afferent activity of all 22 receptors from both ears. However, in addition to broad-band central integrating interneurons, anatomical and physiological work has also demonstrated the existence of segmental and ascending auditory interneurons in the CNS of bushcrickets which receive afferent activity from only a small subpopulation of fibres, for example HF receptors (Römer 1987; Hardt 1988; Römer et al. 1988). Assuming that the behavioural acuity would be based on the comparison of such a subpopulation (e.g. receptors 15–22), the above calculation reveals a more significant figure of a total activity of 321 spikes in the ipsilateral and 268 spikes in the contralateral tympanal fibres (a discharge difference of 17%) for a stimulus angle of ±7.5°. Thus, the probability for a correct turn to the ipsilateral side would be increased by comparing the discharge of only a few pairs of receptors.

Binaural discharge differences with binaural stimulation

In contrast to the monaural stimulation paradigm each element of a pair of receptors will be activated by the ipsi- and contralateral signal, once the absolute intensity exceeds a value given by the ipsilateral threshold plus the dB shift of the receptor with contralateral stimulation. As a result binaural discharge differences with binaural stimulation are smaller, and limited to a smaller intensity range, when compared with monaural stimulation (Fig. 11). When dichotic ear stimulation techniques have been applied to grasshoppers and bushcrickets in behavioural experiments, intensity differences of as little as 0.5–1 dB could be discriminated (von Helversen and Rheinlaender 1988; J. Rheinlaender, H. Römer, J. Shen, unpublished observations). Similarly, in electrophysiological experiments an ILD of 1 dB was sufficient to create significant discharge differences between mirror-image pairs of afferent auditory interneurons (Rheinlaender and Mörchen 1979; Römer and Rheinlaender 1983). In some of these experiments cross-talk barriers of 50 dB or more could be achieved with independent ear stimulation. As a consequence minor changes in stimulus intensity on one side influence only the receptors on the corresponding side, according to their ipsi-

lateral IR functions. It is therefore reasonable to assume that the small cross-talk barrier between the ears with free-field stimulation is the reason for the somewhat less accurate intensity discrimination behaviour, since it produces less binaural discharge differences (Fig. 11).

A further consequence of the cross-talk in the free-field situation can be depicted from the summary in Fig. 10. At medium to high intensities (60–80 dB SPL) there is only a small fraction of fibres which provides a significant binaural discharge difference. For example, at 80 dB SPL only four pairs of receptors exhibit discharge differences of more than 5 spikes/stimulus. Another pair is still below threshold, whereas the majority is fully activated, but their discharge difference is small to zero. Therefore it can be concluded that the reliable intensity discrimination of 2 dB in the behavioural paradigm must be based on the discharge differences of only few pairs of receptors. The absolute discharge difference is quite small at such a binaural difference of 2 dB: 1697 compared to 1627 action potentials in all fibres, which corresponds to a total difference of only 4.1%. Again, if we assume a more selective comparison, for example between the pairs of HF receptors in both ears (compare with monaural stimulation), this difference would increase significantly up to 16%.

Signal structure, information content
and intensity discrimination

To evaluate the amount of binaural discharge differences from binaural intensity differences both the temporal structure of the individual signal and the temporal relationship of the two signals are important variables. Within the diverse taxon of tettigoniids natural and/or sexual selection has created a large variety of acoustic signals and signal interactions (Bailey 1991). At the one extreme are the shortest possible acoustic signals of some phaneropterines lasting no longer than 0.2–0.5 ms (Robinson et al. 1986; Hardt 1988; Zimmermann et al. 1989). Each auditory receptor, once activated above threshold, fires only one spike in response to such a click-like signal, so that any intensity difference can be encoded only in the number of activated fibres per ear, but not by the steepness of the IR function of the individual fibre (Hardt 1988). Since the number of tympanal fibres is similarly small in these bushcrickets, the capacity for intensity discrimination of such a system is drastically reduced and it is very unlikely that these insects rely very much on intensity differences for intraspecific communication (Zimmermann et al. 1989).

At the other extreme are the almost continuous calling songs of some tettigoniids, with a highly redundant repetition of chirps. This is of great advantage for encoding intensity or intensity differences, since the number of excitatory levels that can be discriminated by a receptor can be calculated by $n = F \cdot t + 1$ (F = max. discharge frequency; t = time of analysis; Grüsser 1972). Thus, signals of longer duration increase the po-

tential for intensity discrimination. In this paper we assumed a time of analysis of only 1 s, with a signal of three successive chirps, which is within the range of variation of calling in *R. verticalis* males (Schatral and Bailey 1991). If males produced longer sequences of chirps this would further increase discriminatory abilities in a receiver. An increase in ambient temperature has a similar effect, since it also increases the discharge frequency of receptor fibres. In our control experiments at 15 °C and 25 °C the discharge frequency was doubled at the higher temperature. Comparative effects have been observed with auditory receptors in grasshoppers (Abrams and Pearson 1982; Ronacher and Römer 1985).

Another variable determining the number of intensity levels that can be discriminated by a sensory system is given by the amount of noise in the system. The "internal noise" of tympanal receptors is extremely small in the acoustically controlled condition in the anechoic room. As a result the system provides significant discharge differences with a binaural difference of only 2 dB. However, the conditions for discrimination of acoustic signals in the field are usually quite different from those examined in the laboratory. Due to the specific transmission properties of the habitat a broadcast signal will vary in its amplitude, the degree of amplitude modulation, and its spectrum (Wiley and Richards 1978; Römer and Bailey 1986, 1990; Römer and Lewald 1992). In addition, there may be considerable SPLs as a result of acoustic communication of other species (Römer et al. 1989). This "external noise" will create a high degree of variance in the discharge of receptors and thus reduce their capacity for intensity discrimination. In *R. verticalis* and a number of other bushcrickets a high redundancy by repetition of the stereotyped calling song may counterbalance this effect of the transmission channel, since it enables the insect to integrate the signals over longer periods of time. Though there is currently little physiological proof for the degree of temporal integration in the auditory system of insects, evidence from behavioural observations in the field indicates that Orthoptera may be able to integrate sensory information for periods of hours before making a decision (Rost and Honegger 1987). Future experiments under controlled noisy conditions may reveal the necessity for longer signalling and signal processing times for better intensity discrimination in higher levels of noise.

Implications for intensity discrimination in the field

Female insects (and frogs) can discriminate under choice conditions with a threshold of about 2 dB, and males base their spacing on absolute SPL with similarly refined thresholds (Shuvalov and Popov 1973; Bailey 1985; Latimer and Sippel 1987; Bailey and Yeoh 1988; Bailey et al. 1990; Forrest and Green 1991; Gerhardt 1994). When a female moves phonotactically towards a group of calling males, the absolute SPL of the call(s) increases with decreasing distance from the source(s). One question therefore is whether the intensity discrimination of females also changes when approaching a male. Forrest (1994) listed the few instances in which intensity discrimination by insects and frogs was tested in two-choice experiments at low and high SPLs. Weber's law predicts that the minimum detectable intensity difference between two sounds is a constant proportion of their absolute level (the so-called Weber fraction). The behavioural data suggest that Weber's law does not hold for frogs and insects, since discrimination is poorer at higher intensities. For example, at low SPLs 70% of female *A. domesticus* chose the more intense of two songs differing by 5 dB, but at high SPLs only 12% did so (Stout and McGhee 1988). Similarly, in frogs 100% of female *Hyla cinerea* chose the 3 dB louder sound at low SPLs, but only 50% of females did so at high SPLs (Gerhardt 1987). This is consistent with the data summarized in Fig. 10, since the discharge differences between the pair of hearing organs are larger at low to medium, rather than high SPLs. By contrast, in birds and mammals the deviation from Weber's law is in the opposite direction; intensity discrimination is better at higher levels. With decreasing distance to the source(s) the absolute level of excitation in all receptors increases (e.g. from 471 APs/stimulus at 50 dB SPL to 1697 APs at 70 dB SPL), which is the most parsimonious explanation for the higher attractiveness of more intense signals.

Greenfield (1990) described acoustic interactions in aggregations of singing bushcrickets as either: (1) synchrony, (2) alternation, or (3) crude overlap of singing activity without finer temporal correlation of song elements. The stimulus paradigm used in the present paper is the one used by *R. verticalis* males and corresponds to the third type, where song elements randomly overlap at the position of a receiver listening to this interaction. As evident from the data presented here the binaural discharge difference between a pair of receptors is negatively correlated with the degree of temporal overlap of the signals at the two ears. Thus, with perfectly alternating signals the binaural differences will be greater and can maximally amount to values achieved with monaural stimulation. On the other hand, in perfect synchrony of the two signals we would expect binaural differences less than those calculated here with randomly presented signals, since both signals almost always effect the opposite ear at the same time. Laboratory and/or field experiments with alternating and synchronizing species are needed to solve the interesting question of whether intensity discrimination is better, or plays a major role, in species where males alternate their songs.

References

Abrams TW, Pearson KG (1982) Effects of temperature on identified central neurons that control jumping in the grasshopper. J Neurosci 2: 1538–1553

Alexander RD (1975) Natural selection and specialized chorusing behaviour in acoustical insects. In: Pimental D (ed) Insects, science and society. Academic Press, New York, pp 35–77

Bailey WJ (1985) Acoustic cues for female choice in bushcrickets (Tettigoniidae). In: Kalmring K, Elsner N (eds) Acoustic and vibrational communication in insects. Parey, Berlin, Hamburg, pp 107–111

Bailey WJ (1991) Mate-finding: selection on sensory cues. In: Bailey WJ, Ridsdill-Smith J (eds) Reproductive behaviour of insects: individuals and populations. Chapman and Hall, London, pp 42–74

Bailey WJ, Römer H (1991) Sexual differences in auditory sensitivity: mismatch of hearing threshold and call frequency in a tettigoniid (Orthoptera, Tettigoniidae: Zaprochilinae). J Comp Physiol 169: 349–353

Bailey WJ, Yeoh PB (1988) Female phonotaxis and frequency discrimination in the bushcricket Requena verticalis. Physiol Entomol 13: 363–372

Bailey WJ, Cunningham RC, Lebel L (1990) Song power, spectral distribution and female phonotaxis in the bushcricket Requena verticalis (Tettigoniidae, Orthoptera): active female choice or passive attraction? Anim Behav 40: 33–42

Dadour IR, Bailey WJ (1985) Male agonistic behaviour of the bushcricket Mygalopsis marki Bailey in response to conspecific song (Orthoptera: Tettigoniidae). Z Tierpsychol 70: 320–330

Doherty JA (1985) Trade off phenomena in calling song recognition and phonotaxis in the cricket Gryllus bimaculatus (Orthoptera, Gryllidae). J Comp Physiol 156: 787–801

Forrest TG (1983) Phonotaxis and calling in Puerto Rican mole crickets (Orthoptera: Gryllotalpidae). Ann Entomol Soc Am 76: 797–799

Forrest TG (1994) From sender to receiver: propagation and environmental effects on acoustic signals. Am Zool 34: 644–654

Forrest TG, Green DM (1991) Sexual selection and female choice in mole crickets (Scapteriscus: Gryllotalpidae): modelling the effects of intensity and male spacing. Bioacoustics 3: 93–109

Gerhardt HC (1987) Evolutionary and neurobiological implications of selective phonotaxis in the green treefrog, Hyla cinerea. Anim Behav 35: 1479–1489

Gerhardt HC (1994) Selective responsiveness to long-range acoustic signals in insects and anurans. Am Zool 34: 706–714

Gray EG (1960) The fine structure of the insect ear. Philos Trans R Soc Lond B 243: 75–94

Greenfield MD (1990) Evolution of acoustic communication in the genus Neoconocephalus: discontinuous songs, synchrony, and interspecific interactions. In: Bailey WJ, Rentz DCF (eds) The Tettigoniidae: biology, systematics and evolution. Crawford House Press, Bathurst, pp 71–97

Grüsser OJ (1972) Informationstheorie und die Signalverarbeitung in den Sinnesorganen und im Nervensystem. Naturwissenschaften 59: 436–447

Gwynne DT (1982) Mate selection by female katydids (Orthoptera: Tettigoniidae, Conocephalus nigropleurum). Anim Behav 30: 734–738

Gwynne DT, Bailey WJ (1988) Mating system, mate choice and ultrasonic calling in a zaprochiline katydid (Orthoptera: Tettigoniidae). Behaviour 105: 202–223

Hardt M (1988) Zur Phonotaxis von Laubheuschrecken: Eine vergleichende verhaltenphsiologische und neurophysiologisch/neuroanatomische Untersuchung. PhD thesis, Ruhr University, Bochum

Hedrick AV (1986) Female preferences for calling bout duration in a field cricket. Behav Ecol Sociobiol 19: 73–77

Helversen D von, Rheinlaender J (1988) Interaural intensity and time discrimination in an unrestraint grasshopper: a tentative behavioural approach. J Comp Physiol 162: 333–340

Houben D, Gourevitch G (1979) Auditory lateralization in monkeys: an examination of two cues serving directional hearing. J Acoust Soc Am 66: 1057–1063

Kalmring K, Lewis B, Eichendorf A (1978) The physiological characteristics of primary sensory neurons of the complex tibial organ of Decticus verrucivorus L. (Orthoptera, Tettigoniidae). J Comp Physiol 127: 109–121

Kalmring K, Rössler W, Ebendt R, Ahi J, Lakes R (1993) The auditory receptor organs in the forelegs of bushcrickets: physiology, receptor cell arrangement, and morphology of the tympanal and intermediate organs of three closely related species. Zool Jahrb Physiol 97: 75–94

Lakes R, Schikorski T (1990) Neuroanatomy of Tettigoniids. In: Bailey WJB, Rentz DCF (eds) The Tettigoniidae: biology, systematics and evolution. Crawford House Press, Bathurst, pp 166–190

Latimer W, Schatral A (1986) Information cues used in male competition by Tettigonia cantans (Orthoptera: Tettigoniidae). Anim Behav 34: 162–168

Latimer W, Sippel M (1987) Acoustic cues for female choice and male competition in Tettigonia cantans. Anim Behav 35: 887–910

Otte D (1977) Communication in Orthoptera. In: Sebeock T (ed) How animals communicate. Indiana, Bloomington, pp 334–361

Partridge L, Hoffmann A, Jones JS (1987) Male size and mating success in Drosophila melanogaster and D. pseudoobscura under field conditions. Anim Behav 35: 468–476

Popov AV, Shuvalov VF (1977) Phontactic behaviour of crickets. J Comp Physiol 119: 111–126

Rheinlaender J (1975) Transmission of acoustic information at three neuronal levels in the auditory system of Decticus verrucivorus (Tettigoniidae, Orthoptera). J Comp Physiol 97: 1–53

Rheinlaender J (1984) Das akustische Orientierungsverhalten von Heuschrecken, Grillen und Fröschen: Eine vergleichende neuro- und verhaltensphysiologische Untersuchung. Habilitation thesis, Ruhr University, Bochum

Rheinlaender J, Mörchen A (1979) "Time-intensity trading" in locust auditory interneurons. Nature (Lond) 281: 672–674

Rheinlaender J, Römer H (1980) Bilateral coding of sound direction in the CNS of the bushcricket Tettigonia viridissima L. (Orthoptera, Tettigoniidae). J Comp Physiol 140: 101–111

Rheinlaender J, Römer H (1991) Hearing in insects and its adaptation to environmental constraints. In: Lüttgau HC, Necker R (eds) Biological signal processing. VCH, Weinheim, pp 146–162

Robinson D, Rheinlaender J, Hartley JC (1986) Temporal parameters of male-female sound communication in Leptophyes punctatissima. Physiol Entomol 11: 317–323

Roeder KD, Treat AE (1957) Ultrasonic reception by the tympanic organ of noctuid moths. J Exp Zool 134: 127–157

Römer H (1987) Representation of auditory distance within a central neuropil of the bushcricket Mygalopsis marki. J Comp Physiol 161: 33–42

Römer H, Bailey WJ (1986) Insect hearing in the field. II. Male spacing behaviour and correlated acoustic cues in the bushcricket Mygalopsis marki. J Comp Physiol 159: 627–638

Römer H, Bailey WJ (1990) Insect hearing in the field. Comp Biochem Physiol 97A: 443–447

Römer H, Lewald J (1992) High-frequency sound transmission in natural habitats: implications for the evolution of insect acoustic communication. Behav Ecol Sociobiol 29: 437–444

Römer H, Rheinlaender J (1983) Electrical stimulation of the tympanal nerve as a tool for analysing the response of the auditory interneurons in the locust. J Comp Physiol 152: 289–296

Römer H, Marquart V, Hardt M (1988) The organization of a sensory neuropil in the auditory pathway of grasshoppers and bushcrickets. J Comp Neurol 275: 201–215

Römer H, Bailey WJ, Dadour I (1989) Insect hearing in the field. III. Masking by noise. J Comp Physiol A 164: 609–620

Ronacher B, Römer H (1985) Spike synchronization of tympanic receptor fibres in a grasshopper (Chorthippus biguttulus L., Acrididae). J Comp Physiol 157: 631–642

Rost R, Honegger HW (1987) The timing of premating and mating behavior in a field population of the cricket *Gryllus campestris* L. Behav Ecol Sociobiol 21: 279–289

Ryan MJ, Keddy-Hector A (1992) Directional patterns of female mate choice and the role of sensory biases. Am Nat 139: 4–35

Schatral A, Bailey WJ (1991) Song variability and the response to conspecific song and to song models of different frequency contents in males of the bushcricket *Requena verticalis* (Orthoptera: Tettigoniidae) Behaviour 116: 163–179

Schildberger K (1989) Acoustic communication in crickets: neural mechanisms of song pattern recognition and sound localization. In: Erber J, Menzel R, Pflüger HJ, Todt D (eds) Neural mechanisms of behavior. Thieme, Stuttgart, pp 84–89

Schumacher R (1973) Morphologische Untersuchung der tibialen Tympanalorgane von neun einheimischen Laubheuschrecken-Arten (Orthoptera, Tettigonioidea). Z Morphol Tiere 75: 267–282

Schwabe J (1906) Beiträge zur Morphologie und Histologie der tympanalen Sinnesapperate der Orthopteren. Zoologica 20: 1–154

Searcy WA (1986) Sexual selection and the evolution of song. Annu Rev Ecol Syst 17: 507–533

Shuvaluv VF, Popov AV (1973) Significance of some of the parameters of the calling songs of male crickets *Gryllus bimaculatus* for phonotaxis of females (in Russian). J Evol Biochem Physiol (USSR) 9: 177–182

Simmons LW (1988) The calling song of the field cricket, *Gryllus bimaculatus* (DeGeer): constraints on transmission and its role in intermale competition and female choice. Anim Behav 36: 380–394

Spangler HG (1988) Moth hearing, defense, and communication. Annu Rev Entomol 33: 59–81

Stout JF, McGhee R (1988) Attractiveness of the male *Acheta domesticus* calling song to females. II. The relative importance of syllable period, intensity, and chirp rate. J Comp Physiol A 164: 277–287

Stumpner A (1996) Tonotopic organization of the hearing organ in a bushcricket. Physiological characterization and complete staining of auditory receptor cells. Naturwissenschaften 83: 81–84

Surlykke A (1984) Hearing in notodontid moths: a tympanic organ with a single auditory neurone. J Exp Biol 113: 323–335

Surlykke A, Miller LA (1982) Central branching of three sensory axons from the moth ear (*Agrotis segetum*, Noctuidae). J Insect Physiol 28: 357–364

Thiele DR, Bailey WJ (1980) The function of sound in male spacing behaviour in bushcrickets (Tettigoniidae: Orthoptera). Aust J Ecol 5: 275–286

Thorson J, Weber T, 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 141: 215–232

Vogel R (1923) Über ein tympanales Sinnesorgan, das mutmassliche Hörorgan der Singzikaden. Z Anat Entwicklungsgesch 67: 190–231

Wakeford OS, Robinson DE (1974) Lateralization of tonal stimuli by the cat. J Acoust Soc Am 55: 649–652

Weber T, Thorson J, Huber F (1981) Auditory behavior of the cricket. I. Dynamics of compensated walking and discrimination paradigms on the Kramer treadmill. J Comp Physiol 141: 215–232

Wegener JG (1974) Interaural intensity and phase angle discrimination by Rhesus monkeys. J Speech Hear Res 17: 638–655

Wiley RH, Richards DB (1978) Physical constraints on acoustic communication in the atmosphere: implications for the evolution of animal vocalizations. Behav Ecol Sociobiol 3: 69–94

Young D, Hill KG (1977) Structure and function of the auditory system of the cicada, *Cystosoma saundersii*. J Comp Physiol A 117: 23–45

Zhantiev R, Korsunovskaja O (1978) Morpho-functional organization of the tympanal organs in *Tettigonia cantans* (Orthoptera, Tettigoniidea) (in Russian) Zool J LVII 7: 1012–1016

Zimmermann U, Rheinlaender J, Robinson D (1989) Cues for male phonotaxis in the duetting bushcricket *Leptophyes punctatissima*. J Comp Physiol A 164: 621–628