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ORIGINAL PAPER

Listening for males and bats: spectral processing in the hearing organ of *Neoconocephalus bivocatus* (Orthoptera: Tettigoniidae)

Gerlinde Höbel · Johannes Schul

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Abstract Tettigoniids use hearing for mate finding and the avoidance of predators (mainly bats). Using intracellular recordings, we studied the response properties of auditory receptor cells of *Neoconocephalus bivocatus* to different sound frequencies, with a special focus on the frequency ranges representative of male calls and bat cries. We found several response properties that may represent adaptations for hearing in both contexts. Receptor cells with characteristic frequencies close to the dominant frequency of the communication signal were more broadly tuned, thus extending their range of high sensitivity. This increases the number of cells responding to the dominant frequency of the male call at low signal amplitudes, which should improve long distance call localization. Many cells tuned to audio frequencies had intermediate thresholds for ultrasound. As a consequence, a large number of receptors should be recruited at intermediate amplitudes of bat cries. This collective response of many receptors may function to emphasize predator information in the sensory system, and correlates with the amplitude range at which ultrasound elicits evasive behavior in tettigoniids. We compare our results with spectral processing in crickets, and discuss that both groups evolved different adaptations for the perceptual tasks of mate and predator detection.

G. Höbel
Department of Biological Sciences,
University of Wisconsin-Milwaukee,
P.O. Box 413, Milwaukee, WI 53201, USA

J. Schul (✉)
Division of Biological Sciences,
University of Missouri-Columbia,
207 Tucker Hall, Columbia, MO 65211, USA
e-mail: schulj@missouri.edu

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Abbreviations
CF characteristic frequency

Introduction

In crickets (Grylloidea) and katydids (Tettigonioidea), hearing functions in two behavioral contexts: reproductive communication and predator (bat) avoidance (review in Gerhardt and Huber 2002). In crickets, adaptations of the hearing system for the processing of the spectral ranges of both signal types (i.e., low frequency calls and ultrasonic bat cries) have been described (Imaizumi and Pollack 2001; Pollack 1994). Because the frequency ranges of cricket calls (main energy below 10 kHz) and the ultrasonic echolocation cries of aerially hunting bats (20–100 kHz; Miller and Surlykke 2001) show little if any overlap, the functional interpretation of spectral processing is straightforward. By contrast, the calls of most tettigoniids have broadband spectra which extend well into the ultrasonic range (above 50 kHz; Heller 1988). Due to this spectral overlap it is difficult to detect specific adaptations for intraspecific communication or bat avoidance in the hearing system of most tettigoniids.

In the tettigoniid genus *Neoconocephalus*, however, male calls have most energy focused in a narrow low-frequency band and ultrasonic components have much reduced amplitude (Greenfield 1990; Libersat and Hoy 1991; Schul and Patterson 2003). For example, the calls of male *Neoconocephalus bivocatus* have most energy concentrated around 10 kHz ($Q_{3dB} = 5.5 \pm 1.1$) and the ultrasound component is 20 dB lower in amplitude than the

low-frequency band (Fig. 1). Because *Neoconocephalus* calls have their main energy in a much lower frequency band than bat echolocation cries, this genus is well suited to study adaptations of the katydid hearing organ that contribute to the processing of each of these two signal types. For example, intensity response functions derived from whole nerve recordings were linear for male call frequencies, but showed distinct non-linearities for ultrasound, which were interpreted as adaptations for bat-detection (Schul and Patterson 2003).

Here we study spectral processing in the hearing organ of *N. bivocatus* to detect differences in the representation of the frequency ranges of male calls and bat cries. We describe the spectral sensitivity of individual auditory receptor cells and use these results to estimate the response of the whole receptor population to different signal types. We show that the tuning properties of receptor cells differ as a function of their characteristic frequency (CF), resulting in different patterns of receptor cell recruitment when responding to male calls or bat echolocation cries.

Materials and methods

Animals

Adult *N. bivocatus* Walker, Whitesell and Alexander were collected from grasslands surrounding Columbia, MO, USA. We collected data from 32 animals (5 males and 27 females), and could not detect differences between the data collected in males and females.

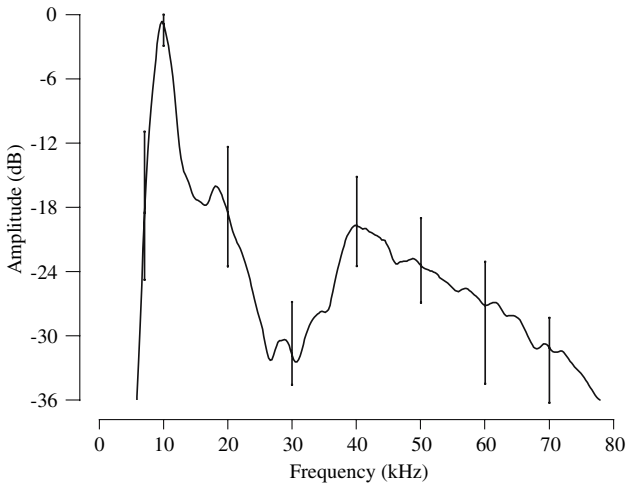

Fig. 1 Average spectrum ($n = 8$) of the call of *N. bivocatus* (adapted from Schul and Patterson 2003). The *error bars* indicate the range of the individual spectra

Morphology

To determine the number of receptor cells in the hearing organ (crista acustica), forelegs were removed and mounted on glass microscopy slides, with the tympanal slits pointing upward. The cuticle covering the leg trachea above the ear was carefully removed with a razor blade and the preparation was covered for 10 min in a saturated solution of Janus green (Yack 1993). After rinsing with saline the cap cells were counted under 400 × magnification using a transmitting light compound microscope.

Electrophysiology

The animals were anesthetized with CO_2 and mounted ventral side up on a freestanding metal holder with a wax/resin mixture. The front legs were fixed on a wire holder perpendicular to the body axis, middle and hind legs were fixed along the body wall. The prothoracic ganglion was exposed by removing a small piece of cuticle and covered with saline (modified after Fielden 1960). The ganglion was stabilized by a NiCr-spoon, which also served as an indifferent electrode.

Experiments took place in an anechoic Faraday cage (1.2 m × 1.2 m × 0.7 m) at 26–28°C. Intracellular or quasi-intracellular recordings were made with thick walled borosilicate glass microelectrodes filled with 0.5-mol l^{-1} LiCl (resistance 20–40 MΩ). Recordings of the receptor fibers were made at the entrance of the leg nerve into the prothoracic ganglion. The recorded signals were amplified (Warner Instr. Corp. IE-210), low-pass filtered at 4 kHz (Krohn-Hite 3384) and stored on DAT (TEAC RD-180T). A trigger signal was recorded on a separate track for off line synchronization of stimulus and response.

Acoustic stimulation

The stimuli were delivered via a loudspeaker (Technics 10TH400C) located 50 cm from the preparation, perpendicular to the insect's body axis and ipsilateral to the recording site. Stimuli were generated using a custom built 16-bit DA-converter system (sampling rate: 250 kHz), amplified, and their amplitude manipulated by a computer-controlled attenuator. Signal amplitudes were calibrated at the position of the insect using a 1/4" free field microphone (G.R.A.S. 40BF, Vedbaek, Denmark), and a B&K 2231 sound level meter (Bruel and Kjaer, Naerum, Denmark). Signal amplitudes are given in dB peak SPL (re: 20 μPa). Due to the necessary obstacles in the sound field (micro-manipulator, probe) slight influences of echoes were inevitable; these did not change sound amplitudes by more than 2 dB.

Thresholds were determined for sinusoids in the range of 4–80 kHz (1 kHz steps from 4 to 10 kHz; 2 kHz steps from

10 to 20 kHz; 5 kHz steps from 20 to 50 kHz and 10 kHz steps from 50 to 80 kHz). Stimuli had a trapezoid-shaped envelope with a rise and fall time of 1 ms and a 20 ms plateau time. Each frequency was played back at seven different amplitude attenuations in steps of 12 dB from 18–90 dB SPL. The stimulus protocol included the playback of "no stimulus" (i.e., a digital stimulus consisting only of 0s) at the same attenuation settings as the other stimuli. These stimuli were used to determine the spontaneous activity of the recorded cells and to control for noise generated by the playback setup. The sequence of frequency/amplitude combinations, including the "no stimulus" was presented three times. In each sequence, every frequency was presented from low to high amplitudes, and the frequencies were sorted from low to high. A pause of 350 ms was kept between different amplitudes of the same frequency; between frequencies a pause of 500 ms was kept.

Data analysis

Recordings from the receptor fibers were digitized (10 kHz sampling rate, 16-bit resolution, InstruNet 100B, Omega Engineering, Inc., New York) and evaluated with custom designed computer programs. Spikes were counted in a 50 ms-window after stimulus onset. The threshold of each frequency was determined by interpolating the steepest part of the intensity response curve to a response of one spike above the spontaneous activity of a given receptor cell (see Stölting and Stumpner 1998).

For each recorded receptor cell, we constructed a threshold curve and determined its CF, bandwidth, and roll-off rates above and below the CF. The CF of a receptor cell was determined as the geometric mean of the two frequencies with thresholds 6 dB higher than the cell's most sensitive threshold (i.e., the square-root of the product of the two frequencies); the geometric mean is the mid-point between the two frequencies on a logarithmic frequency axis. This approach grouped similar threshold curves consistently together and was not significantly influenced by slight inaccuracies caused by the method of threshold determination or the imperfect sound field. For five (out of 146) receptor cells the threshold curve did not rise 6 dB above the most sensitive threshold either above or below the CF. Here, we used the frequency with highest sensitivity as CF.

Bandwidths were measured 10 dB above the most sensitive threshold and are given in octaves. For four receptor cells with CF below 6 kHz and 15 receptor cells with CF above 55 kHz bandwidth could not be determined because the threshold curve did not rise 10 dB above the most sensitive threshold both above and below the CF.

The roll-off rate (in dB/octave) of both the low- and high-frequency flanks was determined between 6 and 18 dB above the most sensitive threshold.

Model of the recruitment of the receptor cell population

To summarize the individual receptor cell thresholds for the dominant frequencies of male and bat signals (Greenfield 1990; Miller and Surlykke 2001), we constructed threshold profiles of the receptor population for 10 and 40 kHz stimuli. The threshold profiles describe how thresholds for 10 and 40 kHz for the receptor cell population recorded here changed with the tuning of individual receptor cells along the crista acustica.

To obtain a threshold profile, we first extracted the threshold of all receptor cells for the given stimulus frequency, and plotted them as a function of each cell's CF (Fig. 6). Then we divided the hearing range (lowest to highest CF measured) into 18 equidistant bins on a logarithmic frequency scale and calculated the median threshold value for each bin (3–16 cells/bin). The curve formed by these 18 mean values was then smoothed by calculating the gliding average over three bins to generate the final threshold profile (lines in Fig. 6).

Based on these threshold profiles, we estimated the receptor cell recruitment in the hearing organ of *N. bivocatus* during stimulation with 10 and 40 kHz of increasing stimulus amplitude. In katydids, the receptor cells are tonotopically organized in the crista acustica, with CF of receptor cells increasing from proximal to distal (Oldfield 1982; Stölting and Stumpner 1998). We modeled a hypothetical hearing organ with 35 receptor cells (see Sect. "Results"), assuming that the frequency tuning (i.e., the CF) of these cells is evenly distributed on a logarithmic frequency axis from 6 to 60 kHz. Whole nerve recordings of the tympanic nerve suggested that in *N. bivocatus* the distribution of the CF of the receptors cells does not grossly deviate from this assumption (Schul and Patterson 2003). The thresholds for 10 and 40 kHz of the 35 model receptors were read from the threshold profiles at their hypothetical CF. We then counted how many receptor cells would be stimulated above threshold for stimulus amplitudes between 20 and 90 dB SPL in 1 dB steps (Fig. 7).

Results

Number of receptor cells in the crista acustica

We were able to unequivocally count the cap cells in five preparations. In three preparations we counted 35 cells; 34 and 33 cells were each counted in the other two preparations. We used the number of 35 receptor cells for our model calculations.

Response properties of individual receptor cells

We collected electrophysiological data from 146 receptor cells in 32 animals (1–12 cells/preparation); characteristic

examples of tuning curves of individual receptor cells are given in Fig. 2b. The CF from our sample ranged from 5 to 70 kHz; sensitivity at the CF ranged from 16 to 42 dB SPL (Fig. 2a), with cells tuned to the frequency range of 8–20 kHz being most sensitive. Sensitivity at the CF in our sample largely resembled the frequency tuning of the hearing organ as determined through whole nerve recordings (Schul and Patterson 2003, Fig. 2a), however our data indicated a 10–15 dB higher sensitivity. We also found a small number ($n = 5$) of cells with CF of around 10 kHz with significantly higher thresholds (50–55 dB SPL; crosses in Fig. 2a; curve VII in Fig. 2b). Because of the small sample size, we excluded these five receptor cells from further analyses. They likely originate in the intermediate organ (Stölting and Stumpner 1998) and may play a role at higher stimulus amplitudes.

The dynamic range of the responses of individual receptors was 20–30 dB. The shape of intensity-response functions was uniform across different receptor cells and independent of stimulus frequency (Fig. 3a, b). Response latencies (20 dB above threshold) were between 8 and 10 ms for all cells (data not shown). These response properties of the *N. bivocatus* receptor cells were comparable to those in other tettigoniids (Kalmring et al. 1990, 1993; Römer et al. 1998).

The bandwidth of the tuning of individual receptor cells varied distinctly with their CF. The tuning of receptor cells with a CF between 11 and 16 kHz and above 26 kHz (Fig. 2a, curves III and V) was considerably broader than that of both receptor cells with intermediate and lower CF (curves II, IV). This is quantified in Fig. 4, where the bandwidth is plotted as a function of CF. Receptor cells with a CF between 11 and 16 kHz and above 26 kHz had median bandwidths of 1.34 and 1.51 octaves, respectively; receptor cells with a CF between 6 and 10 kHz and between 17 and 25 kHz had median bandwidths of less than 1 octave. These differences were statistically significant (Fig. 4b).

We did not find any significant correlation between bandwidth and steepness of roll-off (data not shown). Thus, differences in bandwidth were due to the width of the range of highest sensitivity, rather than to the steepness of the roll-off of the tuning curves (compare curves II and III in Fig. 2b). In the range of 6–18 dB above the most sensitive threshold, the tuning curves showed steep, linear roll-offs. Roll-off rates were 33 ± 9 dB/octave [mean ± SD] toward the low frequencies and 38 ± 22 dB/octave toward the high frequencies.

The spectral selectivity of most receptor cells with intermediate CF showed another noteworthy feature: Their tuning curves did not maintain their initially steep roll-off toward higher frequencies, but instead leveled off

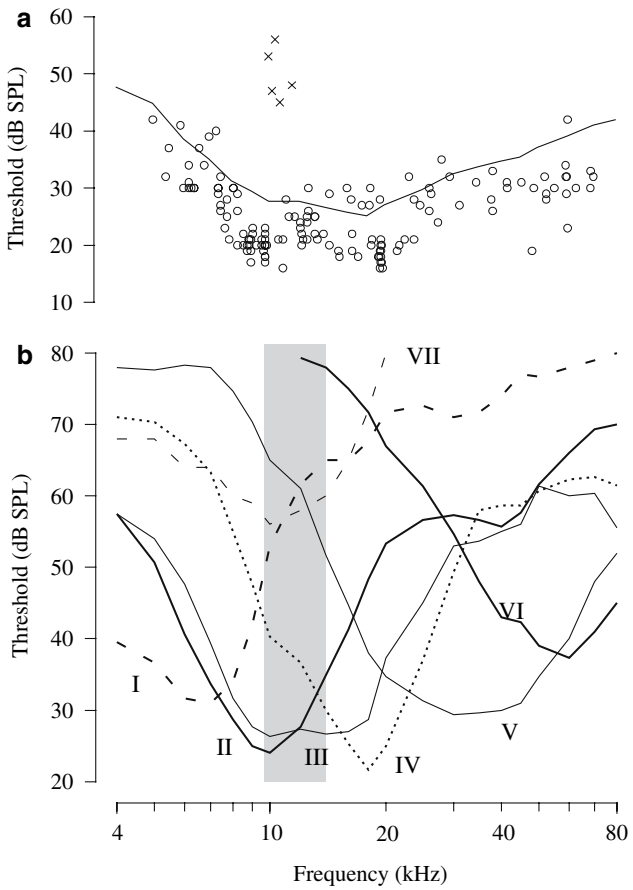

Fig. 2 **a** Thresholds of receptor cells at their CF. The distribution of the CF (*symbols*) largely resembled the tuning curve determined from whole nerve recordings (*line*, adapted from Schul and Patterson 2003). The *circles* indicate cells likely originating from the crista acustica, the *crosses* indicate cells likely originating from the intermediate organ (see text). **b** Sample of tuning curves of individual *N. bivocatus* receptor cells. The *curves* were obtained by calculating the gliding average over three consecutive data points for each curve. The *shaded area* indicates the frequency range emphasized in the male call. Note that the tuning of cells with CF between 11 and 16 kHz (*curve III*) and above 26 kHz (*curve V*) is considerably broader than that of both cells with intermediate (*curve IV*) and lower CF (*curve II*)

at 30–40 dB above highest sensitivity (Fig. 2b, curves II–IV). As a consequence, 40 kHz thresholds for most receptor cells with a CF between 8 and 20 kHz were 50–60 dB SPL (see below). Figure 5 shows the iso-intensity response functions of one receptor cell typical for such cells. The effective frequency range expands symmetrically around the CF with increasing stimulus amplitude, up to 54 dB SPL. At 66 dB SPL and above, however, the effective frequency range doubles, mainly by adding the range between 15 and 40 kHz. Iso-intensity curves always broadened without clear secondary peaks; sharply defined secondary sensitivity peaks, as described in crickets (Imaizumi and Pollack 1999), never occurred in our sample.

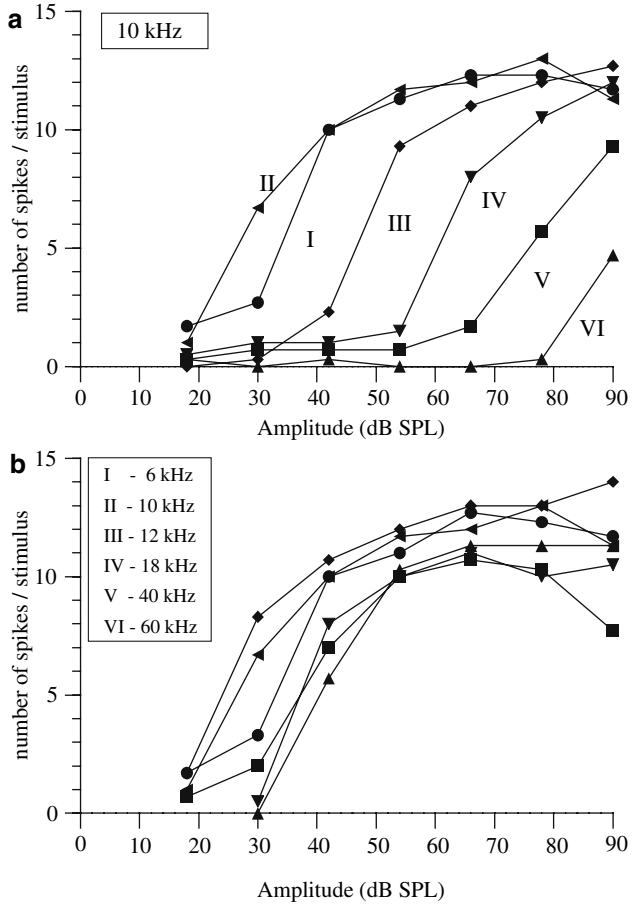

Fig. 3 **a** Intensity-response characteristics of six cells (corresponding to curves *I–VI* from Fig. 2b) in response to 10 kHz, the dominant frequency of the male call. **b** Intensity-response characteristics of the same cells in response to the frequency corresponding to their CF. *Symbols* correspond to the cells in **a**

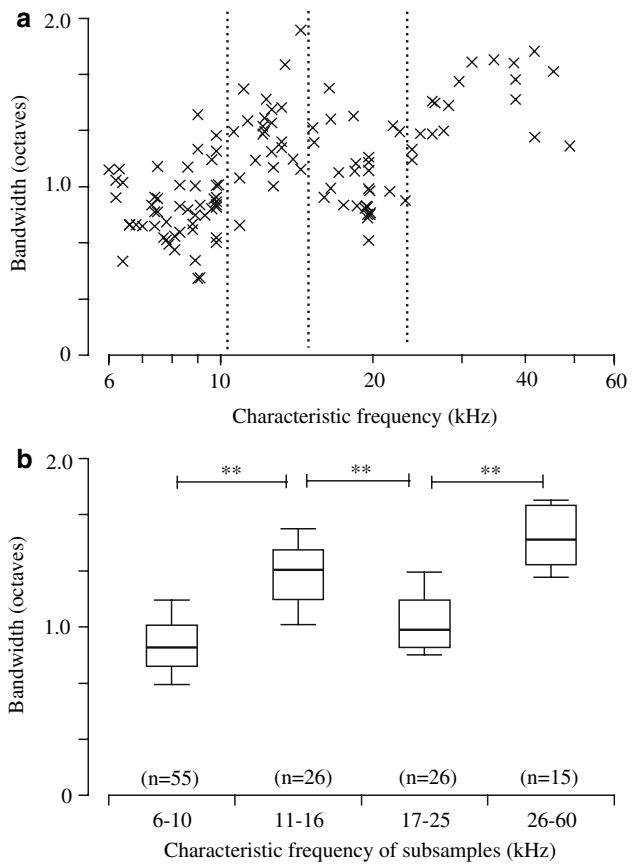

Fig. 4 **a** Bandwidth of receptor cells as a function of CF. The *dashed vertical lines* denote the grouping of cells used for the *box plots* in **b** and statistical analysis. **b** *Box-and-whisker plots* of the data shown in **a**; the *box* indicates 25th and 75th percentile, whiskers 10th and 90th; *bold line* gives the median. The bandwidth of cells with CF of 11–16 kHz was significantly broader than the bandwidth of cells with CF of 6–10 kHz (Mann–Whitney's *U*: $U = 103$, $N = 26$, $M = 55$, $P < 0.0001$) and 17–25 kHz ($U = 455$, $N = 26$, $M = 26$, $P < 0.01$). Cells with CF of 26–60 kHz had significantly broader bandwidth than cells with CF of 17–25 kHz ($U = 376$, $N = 26$, $M = 15$, $P < 0.001$). For 19 of the 141 tympanal receptor cells shown in Fig. 1b the bandwidth could not be determined (see Sect. "Methods")

Threshold profiles

Figure 6 plots the thresholds of each receptor cell for 10 kHz (circles) and 40 kHz (crosses) as a function of each cell's CF. From these data, we calculated the threshold profiles of the hearing organ for both frequencies (lines in Fig. 6; see Sect. "Methods"). For 10 kHz (Fig. 6, solid line) receptor cells with a CF close to 10 kHz were most sensitive. Thresholds for 10 kHz increased for receptors cells with CFs higher or lower than 10 kHz. Receptor cells with a CF above 40 kHz had thresholds for 10 kHz close to 80 dB SPL, resulting in a flat threshold profile for the hearing organ in this frequency range.

The threshold profile for 40 kHz (Fig. 6, dashed line) had only a weakly pronounced sensitivity peak for cells with a CF above 30 kHz; this reflects the rather broad tuning of receptors with a CF in this frequency range. For cells with a CF from 30 kHz down to 20 kHz, thresholds for 40 kHz increased steeply. Below 20 kHz however, the threshold profile leveled out as thresholds for 40 kHz of receptor cells tuned to this frequency range increased only slightly with decreasing CF. This leveling of the threshold profile at 40 kHz reflects the "plateaus" in the high-frequency roll-offs of the threshold curves of these receptors (Fig. 2).

Recruitment of the receptor cell population

Based on the threshold profiles, we modeled how the 35 receptor cells in each ear would be recruited during stimulation with increasing amplitudes of 10 and 40 kHz (see Sect. "Methods"). For 10 kHz (Fig. 7, solid line), the number of "responding" receptor cells (i.e., cells with thresholds lower than the stimulus amplitude) would increase steadily

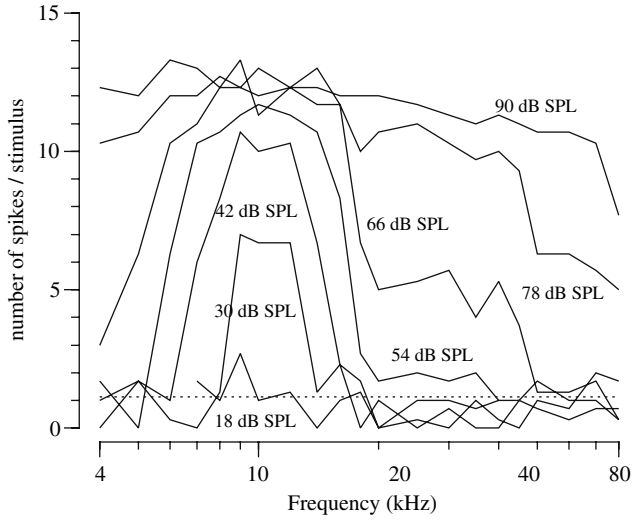

Fig. 5 Iso-intensity curve of a receptor cell with a CF of 10 kHz (*curve II* from Fig. 2b) for stimulation with sinusoids from 4 to 80 kHz and stimulus amplitudes of 18–90 dB SPL. *Dashed lined* denotes level of spontaneous activity

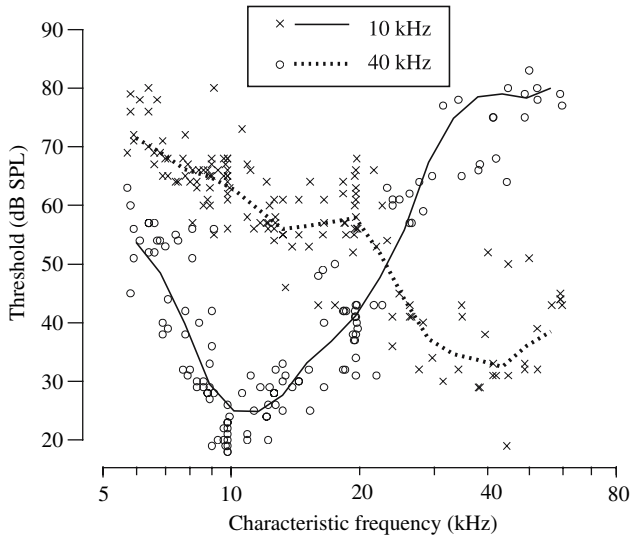

Fig. 6 Threshold profiles for stimulation with 10 kHz (*solid line*) and 40 kHz (*dashed line*). *Symbols* indicate thresholds of individual cells for 10 kHz (*circles*) and 40 kHz (*crosses*) that were used to calculate the threshold profiles. See Sect. "Methods" for details

from 21 dB SPL to 48 dB SPL. For higher amplitudes (up to 75 dB SPL), the rate of recruitment would decrease somewhat until the neurons least sensitive to 10 kHz start responding abruptly between 75 and 80 dB SPL.

For 40 kHz (Fig. 7, dashed line), our calculations indicated that recruitment would take place in two distinct steps. The first step occurred when 11 of the model's receptor cells started responding at stimulus amplitudes between 31 and 39 dB SPL and the second step consisted of 18 model receptor cells that started responding between 55 and 67 dB SPL. The latter group comprised cells with CF

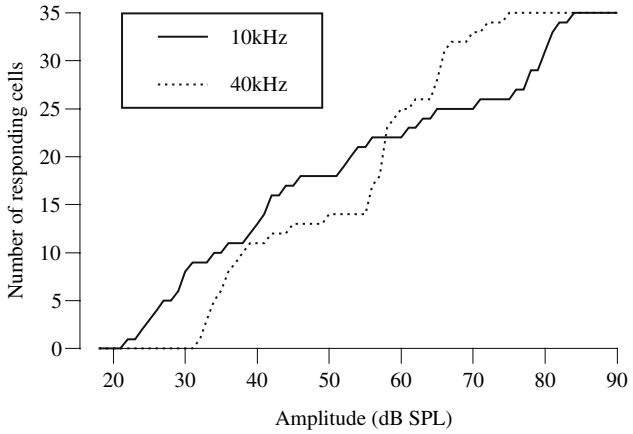

Fig. 7 Modeled receptor cell recruitment in the hearing organ of *N. bivocatus*. Shown is the cumulative number of cells responding to 10 kHz (*solid line*) and 40 kHz (*dashed line*) with increasing signal amplitude. See Sect. "Methods" for details

between 7 and 22 kHz, i.e., the cells that showed the plateau in the high-frequency roll-off of their tuning curves (Fig. 2b). At 75 dB SPL, all 35 model receptor cells responded to 40 kHz; thus at this frequency recruitment of the whole model hearing organ occurred in a smaller amplitude range (42 dB) compared to 10 kHz (61 dB).

Discussion

Most response properties of auditory receptors of *N. bivocatus* (threshold curves, intensity response functions, latency) were comparable to those described in numerous tettigoniid species (Kalmring et al. 1978, 1990, 1993; Lin et al. 1993; Oldfield 1982, 1983, 1985; Römer 1983; Römer et al. 1998, Stölting and Stumpner 1998). However, we detected two properties in the *N. bivocatus* receptor cell population which have not been described in other tettigoniid species. First, the receptor cell bandwidths varied distinctly with their CF, in that cells with a CF of 11–16 kHz had significantly broader tuning than cells with higher and lower CF (Fig. 4). Second, threshold curves of low- to mid-frequency receptor cells showed distinct plateaus in the high-frequency roll-off, which resulted in considerable sensitivity of these cells for ultrasound (Figs. 2, 6). Below, we discuss these two properties as adaptations for the processing of male and bat signals, respectively.

Variation of bandwidth may facilitate call localization

Female phonotaxis requires the effective localization of the male call. Directional hearing in tettigoniids utilizes the interaural amplitude difference (Römer et al. 1998). In *N. bivocatus*, reliable phonotaxis occurred at call amplitudes

as low as 40 dB SPL (Deily and Schul 2006), but females also encounter call amplitudes of 100 dB SPL at close distances to calling males (Schul and Patterson 2003). Therefore, the hearing system of *N. bivocatus* should reliably encode call amplitudes over such a wide range to allow accurate call localization.

In the hearing organs of most tettigoniids, the CF of the individual receptor cells are more or less evenly distributed over the range of sensitivity and the tuning curves of the individual receptor cells have approximately equal bandwidths (e.g., Kalmring et al. 1990; Römer 1983, 1987; but see Schul 1999; Stölting and Stumpner 1998). Broadband calls, typical for many tettigoniids (Heller 1988), will activate a considerable number of receptors at amplitudes only few dB above hearing threshold. For example, in *Requena verticalis* almost half of the receptor cells responded when a conspecific call was presented at 10 dB above hearing threshold (Römer et al. 1998). This activation of a large proportion of the receptor cell population allows reliable encoding close to hearing threshold and results in effective localization at low call amplitudes. Due to their V-shaped threshold curves, additional receptor cells will be recruited with increasing call amplitude, while the responses of more sensitive receptors saturate (Römer et al. 1998).

Due to their narrow spectral content, calls of *N. bivocatus* should stimulate a considerably smaller proportion of receptor cells compared to a broadband call. This reduced number of active receptor cells should, especially at low amplitudes, lead to less accurate encoding of the call amplitude, and thus result in less accurate call localization. However, in *N. bivocatus* the number of receptor cells responding to 10 kHz at low amplitudes is increased due to the large bandwidth of receptor cells with a CF between 11 and 16 kHz (Fig. 4). In our model eight out of 35 model receptor cells were activated at 10 dB above threshold (= 31 dB SPL; Fig. 7).

To demonstrate the effect of the increased bandwidth of the 11–16 kHz receptors on receptor cell recruitment, we replaced them in our recruitment model with receptor cells tuned to the same CF but with the average bandwidths, of receptor cells with 10 kHz CF. Figure 8 contrasts this modified "equal bandwidth" model to the original model based on our tuning data for 10 kHz. Between stimulus amplitudes of 25 and 50 dB SPL the original model (Fig. 8; bold line) shows a higher number of responding receptors than the equal bandwidth model (Fig. 8; thin line). This effect is especially significant at very low amplitudes where the number of active receptors is twice as high (e.g., 8 vs. 4, at 31 dB SPL; Fig. 8; arrow). Therefore, we interpret the increased bandwidth of receptor cells with a CF between 11 and 16 kHz as an adaptation for localization of the narrow-band *N. bivocatus* call, especially at long distances.

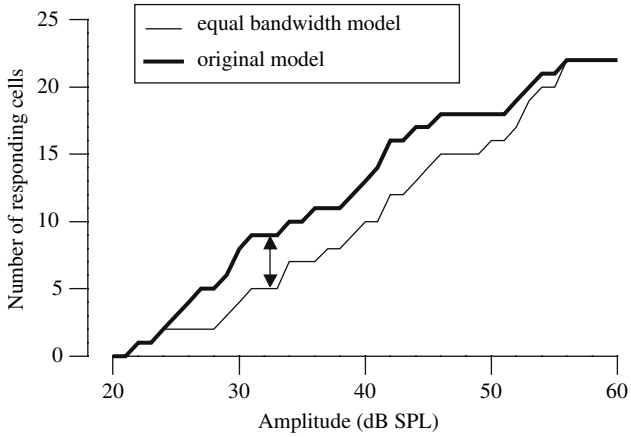

Fig. 8 Receptor cell recruitment during 10 kHz stimulation as modeled by an "equal bandwidth" model (*thin line*) and the original model (*bold line*) shown in Fig. 7. In the "equal bandwidth" model the broadly tuned receptor cells with CF of 11–16 kHz were replaced with units of the same CF, but with the narrower average tuning curve of receptors with CF of 10 kHz. See text for further explanations. The *x*-axis scaling differs from Fig. 7

Our recruitment model further shows that the hearing organ should reliably encode call amplitudes as high as 100 dB SPL: the number of receptor cells responding to 10 kHz increases up to 85 dB SPL (Fig. 7), and the dynamic range of individual receptor cells adds another 15–20 dB to the total dynamic range of the hearing organ. Phonotactic behavior reflected the recruitment over such a wide amplitude range: localization acuity in *N. bivocatus* was high for call amplitudes between 40 dB SPL and 100+ dB SPL (Deily and Schul 2006; J. Schul, unpublished).

Do low- and mid-frequency receptors contribute to bat detection?

The second function of the tettigoniid hearing system is to detect and encode the ultrasonic echolocation cries of aerially hunting bats. Tettigoniids show a variety of bat evasive behaviors (Faure and Hoy 2000a; Libersat and Hoy 1991; Schulze and Schul 2001; B.B. Barrus and J. Schul, in preparation). Thresholds of such bat-evasive behaviors were between 55 and 80 dB SPL (equivalent to distances between bat and insect of approximately 10 to 3 m; Schulze and Schul 2001). The detection range of bats for large insects such as tettigoniids was estimated between 8 and 3 m (Schulze and Schul 2001; Holderied and Helversen 2003); thus bat avoidance behaviors occur at about the distance where the bat first detects the insect. Tettigoniids most likely hear bats at much lower amplitudes (and longer distances) as evidenced by the generally high sensitivity of TN-1 in the frequency range of bat cries (e.g., Schul 1997; Faure and Hoy 2000b; J. Schul, unpublished in *N. bivocatus*) and direct measurements in one species (Schul et al. 2000).

Whole nerve recording revealed that in *N. bivocatus* two groups of receptor cells responded to ultrasound, which differed in their threshold by approximately 30 dB (Schul and Patterson 2003); this phenomenon occurred in all five *Neoconocephalus* species tested, including the species in which bat avoidance was described (*N. ensiger* Libersat and Hoy 1991). Our single receptor cell recordings show that the first, more sensitive group comprises cells tuned to ultrasound, while the second, less sensitive group comprises cells with a CF between 8 and 20 kHz which have intermediate thresholds for 40 kHz (Figs. 2 curves II–IV, 6). This grouping is reflected in their recruitment occurring in two distinct steps between 31–39 dB SPL and 55–70 dB SPL, as indicated by our model calculations (Fig. 7). The recruitment of the second, less sensitive group is remarkable since the 55–70 dB range coincides with the behavioral thresholds for bat evasive behavior in *Neoconocephalus* (Libersat and Hoy 1991; B.B. Barrus and J. Schul, in preparation) and other tettigoniids (Schulze and Schul 2001). Due to this step-wise recruitment pattern (compared to the gradual recruitment occurring at 10 kHz), the amplitude of ultrasound signals is not as finely encoded as the amplitude of low frequency signals (Fig. 7). However, the large number of receptor cells which start to respond to bat echolocation cries between 55 and 70 dB SPL should ensure that these signals, upon reaching this critical amplitude range, are prominently represented in the central nervous system. Therefore, it is reasonable to interpret the ultrasound plateaus in the tuning curves of low- and mid-CF receptors as an adaptation for the detection of bat cries.

That bat evasive behavior might be driven by receptor cells tuned to the male call, appears counterintuitive. However, the large auditory interneuron (TN-1) that is probably responsible for transferring information about bat echolocation cries to the brain in tettigoniids receives input not only from ultrasound receptors, but also from receptors tuned to frequencies as low as 10 kHz (Faure and Hoy 2000b; Schul 1997; in *N. bivocatus*: J. Schul, unpublished). Thus, low- and mid-CF receptor cells are connected to pertinent parts of the ultrasound circuitry in the nervous system of tettigoniids, and their responses may contribute evoking ultrasound avoidance behavior. The segregation of bat signals and communication signals by TN-1 seems to be based on temporal rather than spectral signal parameters (Schul and Sheridan 2006).

Similar to the situation in *Neoconocephalus*, the acoustic world of crickets is largely split into two functional frequency ranges: male communication signals (below 15 kHz) and bat echolocation cries (above 15 kHz) (Wyttenbach et al. 1996). Both crickets and *Neoconocephalus* show bat evasive behaviors during flight, but, different mechanisms are implemented to emphasize the representation of bat signals in the sensory system. In *N. bivocatus*, a large number of receptor cells respond to ultrasound of the critical amplitude range. Crickets, on the other hand, have only few receptors that are tuned to, or respond to ultrasound (Imaizumi and Pollack 1999). Yet, the synaptic weighting of these few receptors on auditory interneurons is much stronger than that of low- and mid-frequency receptor cells, which increases the "conspicuousness" of ultrasound for central circuitry (Pollack 1994). Thus, in crickets, the few receptor cells responding to ultrasound "speak more loudly" (Pollack and Imaizumi 1999), while in *N. bivocatus* a "larger choir" represents this frequency range.

The two main functions of the tettigoniid hearing system—phonotaxis toward calling males and bat avoidance—have different and partly incompatible demands on the receptor organ. Phonotaxis requires the faithful encoding of call amplitude in a *wide amplitude range*, to allow accurate localization of the calling male. In contrast, bat avoidance behavior requires reliable detection of bat cries in the *limited amplitude range* when, or just before, bats first detect the insect. More sophisticated amplitude encoding is not necessary, as most behavioral responses are non-directional (Libersat and Hoy 1991; Schulze and Schul 2001). In *N. bivocatus*, two response properties of auditory receptor cells, which are unusual for Tettigoniids, appear to be adaptations for these two diverging/opposing demands. These adaptations likely were possible because the two signal classes are spectrally separated, while in most tettigoniids there is a wide overlap between the frequency ranges of male calls and bat cries.

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