Matched Filters in Insect Audition: Tuning Curves and Beyond

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Heiner Römer

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H. Römer (✉)
Institute of Zoology, Karl-Franzens University Graz, Universitätsplatz 2, Graz 8010, Austria
e-mail: heinrich.roemer@uni-graz.at

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Abstract

The sense of hearing evolved in insects many times independently, and different groups use sound for intraspecific communication, predator detection, and host finding. Although it can be generally assumed that ears and associated auditory pathways are matched to the relevant properties of acoustic signals and cues, the behavioral contexts, environmental conditions, and selection pressures for hearing may differ strongly between insects. Given the diversity in ear structure, active range of hearing, and the behavioral and ecological context under which hearing evolved, it is probably not surprising to find cases of sensory systems apparently mismatched to relevant parameters of the physical world. Indeed, such cases may be equally instructive for the principle of matching as the perfectly matched ones, since they may tell us something about the conflicting selection pressures and trade-offs associated with a given solution. The examples I have chosen cover the most traditional aspect of matching in the acoustic domain, namely, how the carrier frequency of the relevant sound is matched to the tuning of receivers and how central nervous processing allows species-specific responses to the temporal parameters of song. However, economical filtering also occurs in the intensity domain, starting as early as in the receptors and continuing at the first synapse of central processing. All examples serve to illustrate the similarities and differences between the sensory systems; both may help to define the conditions under which matching operates and may have evolved.

Abbreviations

BF	Best frequency
CF	Carrier frequency
HF	High frequency
IID	Interaural intensity difference
IPI	Inter-pulse interval
ITD	Interaural time difference
SPL	Sound pressure level

4.1 Introduction

This book makes a case for one of the most common principles governing sensory processing in functionally and phylogenetically diverse systems: the matching of sensory cells or whole sensory organs with properties of a signal. The selectivity of sensory systems is the result of selective forces to concentrate on only some aspects of the physical world while ignoring the rest. It is almost trivial to say that this selectivity is for biologically relevant aspects of the physical world, i.e., those which are important for survival and reproduction. If we take a closer look at such matching, however, it is not at all trivial how exactly such a match is realized or why it is not perfect for a given task.

Both the taxon and the sensory modality of the current chapter offer a rich source of new discoveries concerning sensory matching. One reason is the multiple and independent evolutionary origin of insect ears, perhaps 19 times in 7 insect orders, and they can be found on almost any body part in different insect groups (Yack and Fullard 1993; Hoy and Robert 1996). Another reason may be the different context under which hearing has originally evolved: predator detection (such as in moths, mantises, lacewings, and grasshoppers), intraspecific communication (katydids, crickets, cicadas), or the detection and localization of hosts (parasitoid flies). Furthermore, insect hearing is mediated by two different kinds of sound receivers: one type responds to the particle velocity component of the sound field, such as the filiform hairs on the body wall or the cerci (Gnatzy and Tautz 1980) or the antennae of mosquitoes (Johnson 1855). The other type are tympanal ears, responding to the pressure component (for various aspects of the anatomy, neurobiology, or sensory ecology of insects hearing, find reviews in Hoy et al. 1998; Römer 1998; Yager 1999; Yack 2004; Hennig et al. 2004; Hedwig and Pollack 2008). Given the diversity in ear structure, active range of hearing, and the behavioral and ecological context under which hearing evolved, it is probably not surprising to find cases of sensory systems apparently mismatched to relevant parameters of the physical world. Indeed, such cases may be equally instructive for the principle of matching as the perfectly matched ones, since they may tell us something about the conflicting selection pressures and trade-offs associated with a given solution. The examples I have chosen serve to illustrate the similarities and differences between the sensory systems; both may help to define the conditions under which matching operates and may have evolved.

4.2 Matched Filters for “Good” and “Bad”: The Cricket Case

The communication system of crickets probably comes closest to what we imagine immediately in the context of matched filtering. Males produce an almost pure-tone calling song with modified forewings (tegmina), and an area of the tegmina (harp) is set into vibration at its resonant frequency when the plectrum of the left tegmen acts against the file of the right one (Elliott and Koch 1985; Bennet-Clark 1989; Montealegre-Z et al. 2011). As a result of environmental selection on the acoustic communication channel, one would expect to find a correlation between the sound spectrum produced by the sender and the tuning properties of receivers (Endler 1992; Ryan and Keddy-Hector 1992; Meyer and Elsner 1996). Not surprisingly, most auditory receptors in the ears are tuned to the carrier frequency of the song. A subset of receptors is sensitive to frequencies up to 100 kHz (Imaizumi and Pollack 1999); the hearing of these ultrasonic frequencies indicates the second major function in cricket audition, namely, predator detection and avoidance (Moiseff et al. 1978; Hoy 1992; Fullard 1998). Behavioral experiments with tethered flying crickets (*Teleogryllus oceanicus*) indicate that they perform initial frequency discrimination, by dividing the entire range of frequencies into only two categories of low and high frequencies, with a sharp border in between at about 15 kHz (Wyttenbach et al. 1996). Such categorical perception allows matching the huge range of frequencies in the outside world into just two categories of sound important for reproduction and survival: “good”=cricket-like and “bad”=bat-like. There is no evidence of further frequency discrimination ability within the high-frequency range (Ehret et al. 1982; Wyttenbach and Farris 2004). These two categories of frequency are represented in two behaviorally relevant interneurons in the afferent auditory pathway: auditory responses to the male song are forwarded toward the brain via a single ascending interneuron AN1 (Schildberger and Hörner 1988; Schildberger et al. 1989; Kostarakos and Hedwig 2014), whereas AN2 is tuned to ultrasonic frequencies, and its activity has been shown to be necessary and sufficient for eliciting steering away from ultrasound in flight (Nolen and Hoy 1984: Pollack and Hoy 1989; Pollack 2014).

In a world with several species of bats echolocating at various ultrasonic frequencies, and only one (conspecific) species of cricket with a calling song below 15 kHz, the detection and identification of the cricket signal would be no problem, since it could be simply based on a separation of these two frequency ranges. In real worlds, however, background noise by other species competing for the same transmission channel is a selection pressure demanding for more sophisticated solutions (Römer 2014). One obvious sensory adaptation is the tuning of the ear around the species-specific CF. Thus, any sound outside the sensitivity range of the filter will play a reduced role in masking of the signals. In this way, the peripheral filter frees the central nervous system from the complicated task to distinguish between afferent activity resulting from background noise and relevant signals. This is the core of the matched filter hypothesis (Capranica and Moffat 1983; Wehner 1987).

We would expect that such filters are shaped by natural selection in their selectivity, with more sharply tuned receivers evolving when the potential for call frequency overlaps and masking interference is higher. This has been studied in a comparison of a rainforest cricket, suffering from strong competition for call frequencies with other crickets, and two species of European field crickets, where such competition does not exist (Schmidt et al. 2011). As predicted, the rainforest species exhibited a more selective tuning compared with the European counterparts. The filter reduced background nocturnal noise levels by 26 dB, compared with only 16 and 10 dB in the two European species. As a result, the representation of the species-specific amplitude modulation of the male calling song in the afferent auditory pathway was provided even in high-background noise levels.

In a choice between two males, one calling at the BF of the female receiver and the other at a higher or lower CF, a female should consistently prefer the first one, since the signal provides a stimulation which is more intense relative to the alternative. Kostarakos et al. (2008) followed this prediction from the “matched filter hypothesis” by studying the tuning of AN1 in a field cricket, known for its function in phonotaxis, and correlating this with the preference of the same individuals in two-choice trials. Females vary in their neuronal frequency tuning, which strongly predicted their preference in a choice situation between two songs differing in CF. Thus, the tuning of a female receiver is not only important for reducing the amount of irrelevant information but has also direct consequences for mate choice. These findings are different from those in the inferior colliculus in mice where the tuning curves of neurons were not good predictors of the actual neural responses to the vocalizations (Portfors and Roberts 2014).

4.2.1 Variable CFs and Matched Filters?

The frequency filter outlined above represents a reliable solution for receivers in noisy worlds reducing the representation of biologically irrelevant sound (heterospecific songs) outside the filter frequencies. But what if the CF of the signal does vary with environmental conditions and receivers are tuned to a fixed best frequency? This is the case in tree crickets, where the CF of the calling songs changes with temperature (Metrani and Balakrishnan 2005). A sender–receiver match under these conditions would be possible if either the receiver shifts its tuning according to the changing signal (temperature coupling; Gerhardt and Huber 2002) or the tuning of receivers is less selective, allowing equal perception of the entire variation in the CF of the signal (with the trade-off of increased signal masking).

The tree cricket *Oecanthus henryi* is acoustically active from 18 to 28 °C; within this temperature range, its CF changes from 2.4 to 3.3 kHz. Mhatre et al. (2011) investigated the behavioral response of females to songs with different CFs and the mechanical frequency response of their tympanum. They found that songs with a CF from 2.5 to 4.5 kHz were equally attractive across all temperatures. Remarkably, and different from field crickets, the displacement transfer function of the anterior tympanum in the ear showed very little change in amplitude in response to a wide range of frequencies from 1.75 to about 12 kHz. Thus, *O. henryi* females appear to solve the problem of sender–receiver matching in the spectral domain by being broadly tuned both mechanically and behaviorally, consistent with results on other *Oecanthus* species (Walker 1957; Brown et al. 1996). However, as discussed by Mhatre et al. (2011), choice experiments would probably provide better answers on the preferences for particular CFs by females without any tympanal tuning. The discriminatory potential of receivers from preference functions obtained in no-choice trials is potentially misleading, since females will track a male calling song for a large range of CF, given that the sound pressure level is well above the behavioral threshold for phonotaxis (Kostarakos et al. 2008), whereas in a choice situation, the relative intensities of the two signals become highly relevant, if the neuronal elements responsible for the behavior are tuned.

4.2.2 The Problem of Matching Two "Matched Filters"

In addition to the task of detecting and identifying a male signal, female crickets also need to localize the sound source. In order to exploit interaural intensity differences (IIDs), they cannot rely on diffractive mechanisms due to the unfavorable ratio l:λ (body size to the wavelength of sound). Instead, the necessary IIDs result from a pressure difference receiver with a functional three-input system for the sound, provided by a complicated anatomical arrangement of connecting trachea between the ears in the forelegs (Fig. 4.1), and a phase delay mechanism

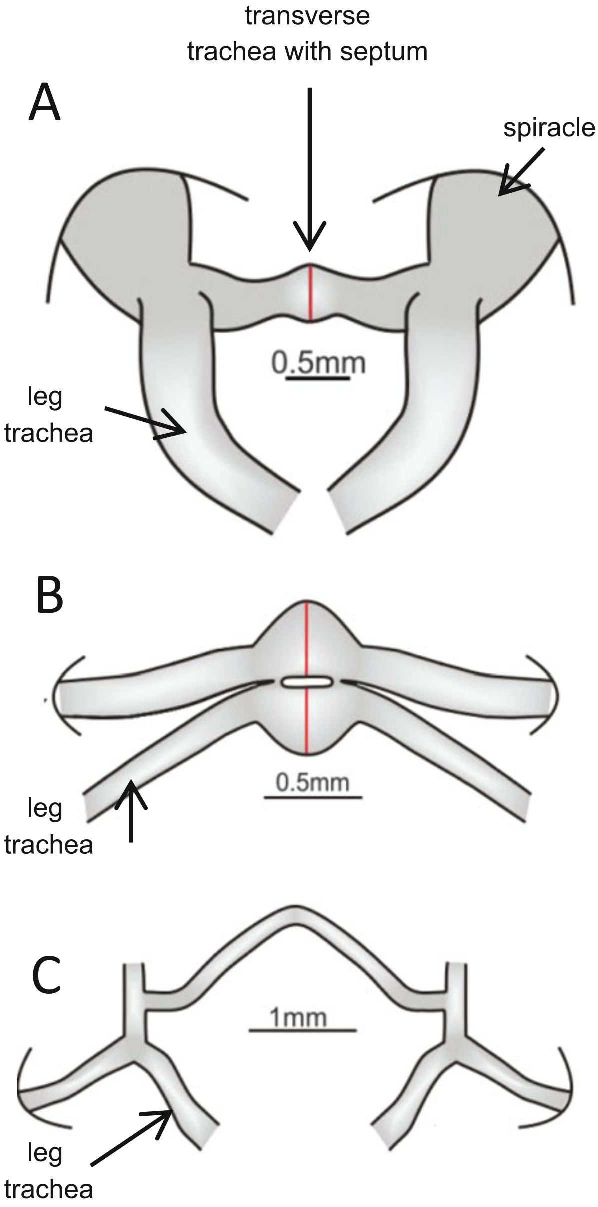

Fig. 4.1 The morphological basis for the pressure difference receiver in cricket ears. Shown are three types of acoustic tracheal systems: (**A**) *Gryllus bimaculatus* (Gryllidae: Gryllinae), (**B**) *Paroecanthus podagrosus* (Gryllidae: Eneopterinae), and (**C**) a member of the subfamily Gryllacridinae (Gryllacrididae) considered as primarily non-hearing, with an unspecialized connecting trachea without a septum, which appears to be the most basic form. One of the most conspicuous features concerns modifications of the transverse acoustic trachea providing the anatomical basis for the contralateral input to the ear. Within the Gryllidae, the simplest structural modification in the midline of the transverse trachea is a single, small-sized vesicle as in *G. bimaculatus*, whereas in other cricket species, the acoustic vesicle can be enlarged or structurally modified into a double acoustic vesicle as in *P. podagrosus* (Modified from Schmidt and Römer 2013)

(Hill and Boyan 1976; Wendler and Löhe 1993; Michelsen 1998; Michelsen and Löhe 1995; Robert 2005). However, the directionality of the ear is strongly frequency dependent, so that reasonable IIDs are only provided for a narrow range of frequencies. Thus, there exists a second "matched filter" for directional hearing in the receiver, depending on sound frequency as well.

In an ideal receiver, the sensitivity filter and the directionality filter should both be tuned to the same frequency, so that the CF of a male call can be perceived with highest sensitivity *and* localized with maximal IIDs. However, by examining both "matched filters" in the same individuals, Kostarakos et al. (2008) could show that the frequency providing strongest stimulation for the auditory system may provide only poor directional cues and vice versa. For *Gryllus bimaculatus*, they reported on average a discrepancy of 400 Hz between the two frequency optima. A comparison with three further species of field crickets (*G. campestris*, *Teleogryllus oceanicus*, and *T. commodus*) confirmed such mismatch (with the exception of *T. commodus)*, which can amount to 1.2 kHz (Kostarakos et al. 2009). In *G. campestris* and *T. oceanicus*, the tuned directionality may even peak at frequencies outside the range of carrier frequencies of males. These results show that a mismatch between the sensitivity and directionality tuning is not uncommon in crickets.

Sensory tuning may impose stabilizing sexual selection on the male signal (Brooks et al. 2005; Bentsen et al. 2006; Ryan and Keddy-Hector 1992). In *G. bimaculatus*, the afferent sensitivity is tuned on average at 4.9 kHz, whereas the directional tuning is best at 4.5 kHz. Thus, there are two different preference peaks, which may exert selection on male signals. The fact that the average CF of male calls in a population is close to 4.7 kHz, and thus right between both receiver optima, would indicate that sexual selection is stabilizing, with both filters probably contributing to the evolution of the CF in the male signal (Kostarakos et al. 2008).

4.3 Mismatched Filters or Result of Complex Sensory Drive?

As we have seen in the above examples, for most animals that use sound to communicate between the sexes, there is a match between the carrier frequency of the signal and the hearing sensitivity of the receiver. It has been argued that stimulus filtering, i.e., the ability of sense organs and associated neural networks to ignore vast amounts of information in the outside physical world, is highly adaptive to focus on biologically relevant information. There are, however, a number of exceptions to this general rule among the insects which might tell us more about adaptive filtering. On the one hand, we find obvious cases of mismatch between the social signal and tuning of the ear, as in the primitive ensiferan insect *Cyphoderris monstrosa* (Mason 1991; Mason et al. 1999). The frequency spectrum of the calling song is narrowly centered at 12 kHz, whereas best hearing is at 2 kHz, resulting in reduced sensitivity to 12 kHz by 30 dB. No plausible explanation for this discrepancy could be offered by the authors, except for the possibility that the auditory system appears to be adapted to a function different from intraspecific communication. A number of cases of sender–receiver mismatch have also been reported for cicadas (Popov 1981; Huber et al. 1990). In two species of 17-year cicadas, a perfect match between call frequency at 1.4 kHz and auditory nerve responses exists only in *Magicicada septendecim*, whereas in *M. cassini*, a sender–receiver mismatch was found (Huber et al. 1990). During the short period of emergence and reproductive activity, they overlap in their daily singing time and may chorus together. Due to the mismatch, the ear in *M. cassini* responds better to calls of the heterospecific cicada compared to the conspecific one. How the species solves this problem is currently unknown. In another cicada species (*Cicadetta sinuatipennis*), auditory nerve responses are completely mismatched to the spectrum of the tymbal sound usual for cicadas but match quite well with sound produced by wing flicking (Popov 1981). Notably, a mismatch can also occur between the hearing sensitivity of parasitoid flies and their host (Lakes-Harlan et al. 1999), although in all other reported cases of parasitoid/host interactions, the flies' hearing is well matched to the host calls (Robert et al. 1992; Lehmann 2003; for review on such interactions, see Lakes-Harlan and Lehmann 2014).

The example of the atympanate bladder grasshopper *Bullacris membracioides* with no less than six pairs of ears demonstrates that responses to biologically significant sound may not depend on sender–receiver matching, given that some conditions are met (van Staaden and Römer 1998; van Staaden et al. 2003). These insects possess six pairs of ears: one in abdominal segment 1, homologous to the single pair of tympanate ears found in "modern" grasshoppers, and in addition, five posterior pairs of ears in abdominal segments 2–6, resembling pleural chordotonal organs (plCOs) in other grasshoppers. All six pairs of plCOs respond to acoustic stimulation within a biologically meaningful intensity and frequency range, although only the organs in the posterior segments matched with their tuning to the male call at 1.7 kHz. By contrast, the organ in the first abdominal segment is tuned to 4 kHz, but since it is extremely sensitive (absolute threshold 13 dB SPL), the active range of the signal achieved with this "mismatched organ" is much higher than the corresponding value of the matched pairs of ears (van Staaden et al. 2003).

We can assume that sensory matching has been arrived at by selection on both signalers and receivers (Endler 1992), with four major sources of selection: (i) mate choice (Andersson 1994), (ii) predator detection and avoidance (Endler 1992), (iii) prey detection by acoustically orienting predators (Cade 1975), (iv) and the transmission channel for sound (Römer 1998). Thus, call frequency and the tuning of the ear may be under selection from potentially conflicting forces, and Endler (1992) refers to the complex evolutionary processes that shape the sensory systems as "sensory drive." I argue here that such processes may have shaped the following example of mismatch and probably more yet undiscovered ones.

The CF at 5 kHz in the call of the Australian katydid *Sciarasaga quadrata* is unusually low for tettigoniids (Römer and Bailey 1998). The hearing system is most sensitive to frequencies of 15–20 kHz, an effective mismatch resulting in a reduced sensitivity of approximately 15−20 dB for the conspecific signal (Fig. 4.2A). One likely source of selection for shifting the call CF away from best hearing is the parasitoid fly *Homotrixa alleni*, which detects and orients toward the male host

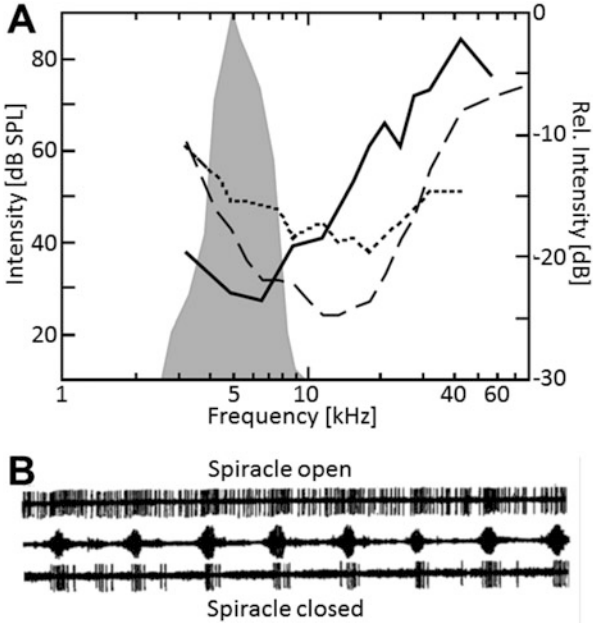

Fig. 4.2 (**A**) Hearing sensitivity of *Sciarasaga quadrata* in the open (*dashed line*) and partially blocked (*solid line*) spiracle condition compared with the sensitivity of the ear of its most common predator, the parasitoid fly *Homotrixa allenii* (*dotted line*; after Lakes-Harlan et al. 1995). Note the selective advantage to *S. quadrata* of hearing conspecifics by shifting the carrier frequency of the call to 5 kHz relative to the ability of the fly to detect its prey at this low frequency. The shaded area represents the spectrum of the calling song of *S. quadrata*. (**B**) Activity of the omega neuron in response to sound recordings with a conspecific male and a number of heterospecifics calling in the background. The amplitude of the heterospecific calls was approximately 20 dB lower than that of the conspecific. Note that in the open spiracle condition (upper recording), the neuronal response to the species-specific call is strongly masked by the less intense background whereas in the blocked condition (lower recording), there is a clearly detectable response pattern to the species-specific call (From Römer and Bailey 1998)

using the host call. The flies' hearing system is most sensitive between 10 and 20 kHz (Stumpner et al. 2007); thus, shifting the call CF toward low frequencies results in a partial sensory escape from the parasitoid. Nevertheless, since the shift also reduces the sensitivity to the own call, these katydids have evolved an intriguing flexible mechanism to change the tuning of the ear: by partial occlusion of the acoustic spiracle in the foreleg, they reduce the high-frequency input to the inner tympanum. Under these conditions, the ear is tuned to the call at 5 kHz (solid line in Fig. 4.2A). At the same time, they avoid the strong masking due to the singing activity of other species at frequencies higher than 10 kHz (Fig. 4.2B). Finally, the low-frequency call is well transmitted in the habitat of the katydid, almost without excess attenuation. Thus, this insect may show all components of sensory drive: sexual selection and natural selection acting on the male signal and female receiver, including selection through properties of the transmission channel for sound. The outcome may be a matched or mismatched system depending on the ability of species to flexibly modify components in the hearing system.

4.4 Passive and Active Frequency Filters in Insect Ears

Insects ears have evolved many times independently, they can be located on almost any part of the body, and the external anatomy of the sound receiving structures varies strongly between antennal and tympanal receivers (Hoy and Robert 1996; Yager 1999; Göpfert and Robert 2008). Despite this anatomical diversity, the cellular basis of all these ears is rather uniform, comprising single or grouped chordotonal sensilla (scolopidia; Field and Matheson 1998; Yack 2004). For decades, the observation that mechanosensory organs are more or less finely tuned to signals of biological relevance has been attributed to the structural biomechanics and material architecture of the respective sound receivers, although vertebrate ears were known to employ positive mechanical feedback to actively amplify their sensitivity to sound, a process known as the cochlear amplifier (Ashmore and Gale 2004; Hudspeth 1997, 2008 for review). First experimental evidence for active mechanical processes in insects ears has been the discovery of distortion product otoacoustic emissions in tympanal ears (Kössl and Boyan 1998), whereas such active processes have been more thoroughly studied in antennal ears of mosquitoes and flies.

Ignoring the chronological sequence of discoveries on active hearing processes in insects, I start with a case study on a tympanal ear of a moth, before turning to the best studied cases of antennal hearing in mosquitoes and drosophilid flies. More detailed information on all aspects of active mechanisms, including its molecular basis, can be found in Göpfert and Robert (2008), Göpfert (2008), Kavlie et al. (2014), and a recent review by Mhatre (2014).

4.4.1 The “Simple” Ear of a Moth and Its Adaptive Shift in Tuning

Insectivorous bats constitute a strong selection pressure on their prey, which favored the evolution of sensory mechanisms to detect them (Fullard 1998; ter Hofstede et al. 2013). The effect of this selection pressure has been demonstrated for many nocturnal insects in different taxa, including moths, where most species developed simple ears with the sole purpose of detecting bats (Roeder and Treat 1957). Although there is an association between the tuning of moth ears and the cues provided by sympatric bat predators (ter Hofstede et al. 2013). Windmill et al. 2006 were puzzled by the finding that in these moth, the ears are most sensitive between 20 and 40 kHz and thus somewhat mistuned to the higher echolocation calls shortly before prey capture. When they analyzed the vibrational response of the moth’s tympanum, they found a conspicuous nonlinearity and a strong shift in the resonant frequency with stimulus intensity: at low SPL, the resonant peak was at

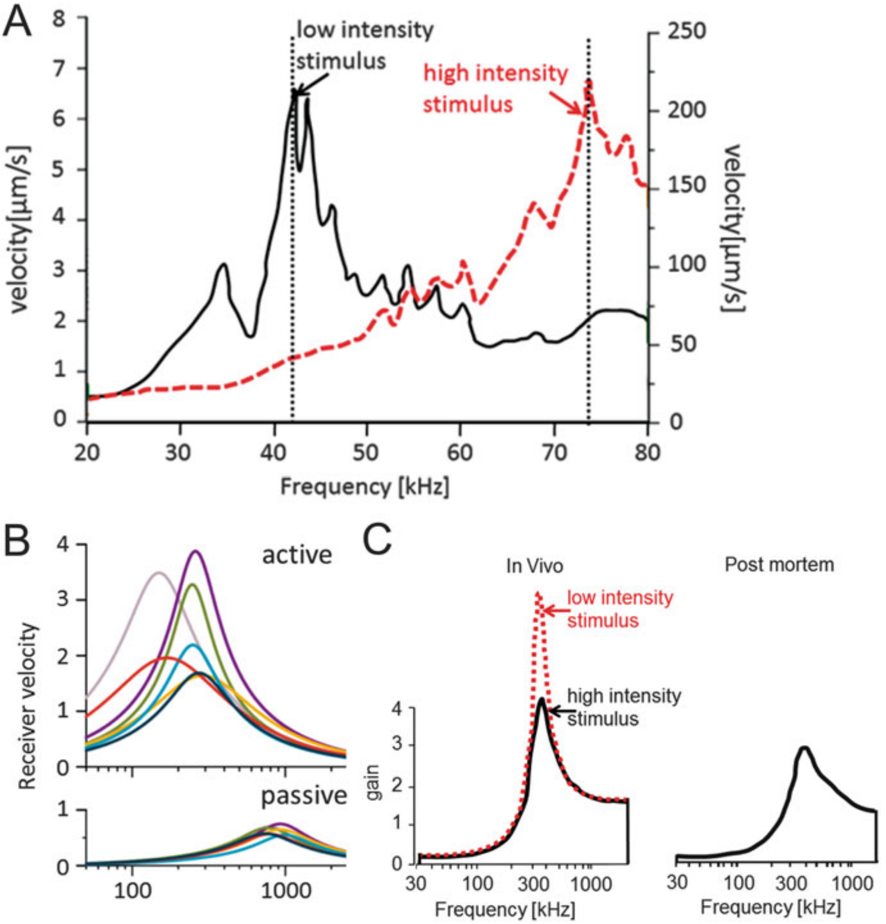

Fig. 4.3 (**A**) Frequency spectrum of the mechanical response of the tympanum in the moth *Noctua pronuba*. The *black* continuous curve depicts the response to stimulation at low stimulus intensity (left ordinate), and the *red* stippled curve depicts the response at high stimulus intensity (+35 dB; right ordinate) (Modified from Windmill et al. 2006). (**B**) Species-specific frequency tuning of antennal ears in seven species of Drosophila. The free mechanical fluctuations of the antennae are well described by a simple harmonic oscillator model both in the active receivers of awake (*top*) and in the passive receivers of CO_2-anesthetized (*bottom*) flies. Note the shift in frequency tuning with active hearing (From Riabinia et al. 2011). (**C**) Mechanical sensitivity of the mosquito antenna in response to sound. The dimensionless quantity df/dp represents the gain of the response, with df the antennal vibration velocity (the mechanical output) and dp the acoustic particle velocity (the acoustical input). The mechanical response is nonlinear at resonance frequency: gain increases as stimulus intensity decreases (Modified from Robert and Göpfert 2002)

42 kHz, and at higher SPL, the peak shifted to 74 kHz (Fig. 4.3A). In dead animals and those under CO_2 hypoxia, the shift never occurred, which is one of several indications that active processes cause this shift. Further experiments revealed that

at an SPL of 87 dB, equivalent to a bat about 3 m away, the moth ear tuned up to the higher frequency within 0.75 s, but the return to the low-frequency state may take several minutes, i.e., the tuning is hysteretic. This is highly adaptive, keeping the ear tuned up for a possible return of the bat.

Such findings are remarkable, since they demonstrate that the most peripheral filter in an auditory system is variable and strongly dependent on the active state of the sensory cells. In the case of the studied moth, there are only two sensory cells and another one (the B cell) of unknown function. Earlier work on tympanal ears of locusts and other moths had already provided evidence for active hearing mechanics (Kössl and Boyan 1998; Coro and Kössl 1998, 2001). The distortion product otoacoustic emissions (DPOAEs) recorded with two-tone stimulation showed characteristics quite similar to those from vertebrate ears, including physiological lability.

4.4.2 Antennal Ears of Mosquitoes and Flies: Mechanical Feedback Amplification and Tuning

Although the above studies had demonstrated that the mechanics of insect tympana are nonlinearly improved by physiological processes, the remarkable antennal receivers of both mosquitoes and drosophilid flies provided more in-depth results on various aspects of the active processes. The antennal ear of *Drosophila* consists of the funiculus and arista, which together act as the sound receiver, and the pedicellus, harboring the Johnston's organ with about 150–200 chordotonal sensilla (with two to three sensory neurons each; Caldwell and Eberl 2002). In response to near-field sound, the entire third segment twists around its longitudinal axis, which is the adequate stimulus for the Johnston's organ in the pedicellus (Göpfert and Robert 2001b). This antennal receiver demonstrates strong nonlinearity and frequency-specific amplification: in dead animals and those under anesthesia, the mechanical response is linear and tuned to around 800 Hz similar to a moderately damped harmonic oscillator. The same is true in live animals at high stimulus intensities, but with decreasing intensity, the tuning is shifted toward lower frequencies around 200 Hz and the sensitivity at resonance is increased (Göpfert and Robert 2002). The shift to lower frequencies is one of two highly adaptive processes mediated by active hearing, since it matches the receiver frequency rather precisely with the spectral composition of Drosophila courtship song pulses. This has been demonstrated in a comparative study on seven members of the *D. melanogaster* species group by Riabinia et al. (2011). The authors used CO_2 anesthesia as a tool to distinguish between active and passive tuning mechanisms, since it reversibly eliminates the active feedback from sensory neurons (Göpfert and Robert 2003). They found a species-specific tuning with best frequencies ranging between about 150 and 300 Hz, whereas in CO_2-sedated flies, the passive tuning shifted strongly in all fly species toward 800–1000 Hz (Fig. 4.3B).

The second adaptive process mediated by active hearing plays a role in the intimate link between acoustic communication and flight in Diptera and in the dual role the antennae have as sensors in the courtship behavior and for flight control (Budick et al. 2007). For the seven members of the *D. melanogaster* species group, Riabinia et al. (2011) also measured the wing beat frequencies and the peak-to-peak antennal displacement amplitudes during tethered flight. The wing beat frequencies ranged between 145 and 213 Hz and thus close to the range of CFs of the sine songs. However, the displacement amplitudes were several orders of magnitude higher than those resulting in mechanical feedback amplification. As a result, the authors found high displacement gains ($\text{displacement}_{\text{active}}/\text{displacement}_{\text{passive}}$) of about 8 for deflections <300 nm, but a gain of only 1 for deflections >10 µm, so that these deflections drive the antenna into the passive regime during flight, tuned at about 800 Hz. Taken together, the mechanical feedback amplification and its level dependency is an excellent mechanism to enable the detection of the subtle stimuli to which the antenna is exposed during courtship, whereas the much larger stimuli during the animals own flight become negligible.

Combined laser Doppler vibrometry and electrophysiological recordings revealed the extraordinary sensitivity of the chordotonal sensilla in the Johnston's organ of mosquitoes (Göpfert and Robert 2001a). The organ in the second segment of the antenna contains about 15,000 sensilla in the male, which connect to the third segment, a long flagellum representing the sound receiver proper (Göpfert et al. 1999). At the threshold of hearing, the flagellum is deflected by only 0.1 millidegree, and at the location of the sensory neurons in the Johnston's organ, displacement amplitudes as small as 0.3 nm can be calculated. This extraordinary sensitivity is again the result of active auditory mechanics with an intensity-dependent nonlinearity (Göpfert and Robert 2001a). The antenna shows a moderately damped resonance at 430 Hz in dead males, and in live animals, the tuning was similar when the stimulus intensity was high (Fig. 4.3C). At low intensities, however, the response increased and sharpened at the resonant frequency. The gain in sensitivity at resonance was between 1.5 and 2. This boost in sensitivity allows male mosquitoes to hear the faint sound of their females as a result of the wing strokes. Thus, unlike the antennal receiver in drosophilid flies, the nonlinear active process in mosquitoes operates to amplify rather than to tune the receiver.

4.5 The Tuned Frequency-Filter Paradox in Katydids

The ears of many insect species are capable of at least some basic peripheral spectral analysis (crickets: Imaizumi and Pollack 1999; grasshoppers: Michelsen 1968; Römer 1976; Jacobs et al. 1999; cicadas: Fonseca et al. 2000). For the best studied ears of katydids, two recent studies (Palghat Udayashankar et al. 2012; Montealegre-Z et al. 2012) have shown that impedance conversion and dispersive wave propagation underlie the tonotopic representation of frequencies previously reported in the crista acustica (the linear arrangement of receptors) in the ear (Oldfield 1982; Stumpner 1996; Stölting and Stumpner 1998). The tonotopic arrangement in the periphery is also reflected in their central projections within the auditory neuropile (Römer 1983; Römer et al. 1988; Stölting and Stumpner 1998), and the frequency tuning of the first-order interneurons can be predicted from their dendritic branching pattern within the neuropile (Römer 1985; Römer et al. 1988). Surprisingly, however, most of the detailed frequency representation of the periphery is lost centrally due to strong neuronal convergence (for rare exceptions, see Stumpner 1998). So we may ask what the tonotopic arrangement of the periphery is good for (Hildebrandt 2014). Here, I suggest four cases of auditory processing in ecologically important contexts, where spectral information through the series of frequency filters in the ear can be used: (1) estimation of distance to signalers, (2) intensity discrimination, (3) novelty detection, and (4) improvement of SNR for temporal processing (see also Pollack and Imaizumi 1999; Hennig et al. 2004; Hildebrandt et al. 2014).

4.5.1 Distance Estimation: *Odotopic* Rather Than *Tonotopic* Maps?

When female katydids make phonotactic decisions between several potential mates based on long-distance acoustic cues, it should be highly adaptive to estimate the distance to the sound sources. The same holds for males spacing out in a population, where they maintain a mean acoustic distance to each other (Thiele and Bailey 1980; Römer and Bailey 1986). For this task, they could use spectral information provided by the series of frequency analyzers in the crista acustica. As sound propagates through the environment, the broad spectrum of a male katydid calling song suffers frequency-dependent excess attenuation over distance (Keuper and Kühne 1983; Römer and Lewald 1992). Individual receptors have different tuning and absolute sensitivity; in combination with the frequency filtering effect of the transmission channel, each receptor differs in the distance at which it starts to respond (threshold distance). In this way, spectral information can be used for a range fractionation in the coding of distance to a signaler (Römer 1987). Moreover, the tonotopic arrangement of axonal endings of these receptors and their range fractionation results in a specific spatial distribution of afferent activity which can also be interpreted as an *odotopic map* (Pollack and Imaizumi 1999): a systematic relationship between distance to the sound source and spatial distribution of activity in the auditory neuropile.

4.5.2 Intensity Discrimination

The series of frequency analyzers in the crista acustica of katydids provides a frequency hearing range from about 1 kHz up to 100 kHz; yet, the species-specific calling song is often restricted to a mid-frequency range. Thus, receptors outside the frequency range of the calling song appear to be mismatched to the song. The consequences for intensity discrimination have been studied in the katydid *Requena verticalis*, with only 22 receptors in each ear (Römer et al. 1998; see also Stumpner and Nowotny 2014). However, as a result of such mismatch, the threshold to the conspecific signal varies from about 40 dB SPL for those afferents tuned to the song spectrum up to 90 dB SPL for the mismatched ones, allowing for a range fractionation within the hearing organ. Thus, an important function of these mismatched afferents is the extension of a detailed intensity coding over the complete intensity range, since the intensity-response function of each single afferent is sigmoid and saturates after only about 15–20 dB above threshold, providing a rather limited range for detailed intensity coding. For *R. verticalis*, it has been shown that at low stimulus intensities (50 dB SPL), only the mid-frequency afferents (the matched ones) provide large and reliable discharge differences with IIDs, whereas the mismatched ones remain subthreshold. By contrast, at high sound pressure levels (80 dB SPL), the mid-frequency afferents are completely saturated, so that only a few very low- and high-frequency tuned receptors provide the necessary information about IIDs (Römer et al. 1998). Hardt (1988) pointed to the importance of such range fractionation for those species with extremely short communication signals, as in the Phaneropterine katydid *Leptophyes punctatissima*, where the female response to the male call is less than 1 ms in duration. In response to this signal, a single receptor response shows no dependence to the SPL and is activated with only one action potential at suprathreshold intensities. Hence, the only information about intensity is provided by the increased recruitment of differently tuned receptors in each ear.

Future work on this topic may concentrate on those species of katydid where the frequency spectrum of the song is narrowly tuned, often at high sonic or ultrasonic frequencies (Morris et al. 1994; Montealegre-Z and Morris 1999; Montealegre-Z et al. 2006). If these species have a similar representation of frequencies in the crista acustica of the ear as outlined above, most of these receptors would be really mismatched and could not be recruited by the conspecific signal even at high SPLs. It is quite possible that we may find an interesting adaptive modification of the frequency representation, analogous to an “acoustic fovea,” in that several receptors are concentrated at the point along the crista where the relevant frequency in the traveling wave is represented (Montealegre-Z et al. 2012). Strauss et al. (2012) have provided some morphological evidence that receptors in the crista acustica are not always arranged linearly.

4.5.3 Noise Filtering Through Novelty Detection

Acoustic insects often communicate in choruses of many conspecific and heterospecific signalers, which produce a more or less constant acoustic background, so that the detection of relevant signals is problematic. In this context, a series of frequency analyzers in the ear can be advantageous, as shown by Schul et al. (2012). They described the selective coding of a biologically important sound (the echolocation pulse of a bat) by an auditory interneuron, under the simultaneous playback of a highly repetitive series of conspecific call pulses.

Responses to the bat pulses in this interneuron occurred only when its carrier frequency was sufficiently different from the standard pulses, both when the bat pulses had a higher or lower carrier frequency than the standard. They called the phenomenon “novelty detection” because it relies on the detection of a sudden change in the acoustic scene, indicated by a frequency difference between the signal and background. The ability to detect such changes is also of relevance for the detection of conspecific stimuli. Siegert et al. (2013) examined acoustic masking in a chirping katydid species of the *Mecopoda elongata* complex due to interference with a sympatric species where males produce continuous trills at high amplitudes. Strong masking of chirps under the continuous trill could be expected, since the frequency spectra of both songs range from 1 to 80 kHz and strongly overlap. However, the chirper species has some more energy in a narrow frequency band at 2 kHz. Behaviorally, chirper males detect conspecific chirps under masking conditions at signal-to-noise ratios (SNRs) of −8 dB, but when the 2 kHz band in the chirp had been equalized to the level in the masking trill, detection was only possible at an SNR of +7 dB. Apparently, this species uses its potential for frequency analysis in the ear to detect the small spectral difference between the conspecific and a heterospecific signal to avoid strong masking. Intracellular recordings of identified interneurons revealed two mechanisms providing response selectivity to the chirp (Kostarakos and Römer 2015). Several identified interneurons exhibit remarkably selective responses to the chirps, even at signal-to-noise ratios of –21 dB, since they are sharply tuned to 2 kHz. Another group of interneurons is broadly tuned and thus responds strongly to the masker. However, because of strong stimulus-specific adaptation to the masker spectrum and “novelty detection” to the 2 kHz band present only in the conspecific signal, these interneurons respond selectively to the chirp shortly after the onset of the continuous masker. Both mechanisms rely on the selective tuning of receptors to the 2 kHz component in the signal; they provide the sensory basis for hearing at unfavorable signal-to-noise ratios.

4.5.4 Improving the Signal-to-Noise Ratio for Temporal Processing

A series of frequency analyzers in the ear may also be advantageous for the coding of the temporal song pattern. In their outdoor approach, Römer and Lewald (1992) modified the spectral content of a stimulus from a pure tone (CF 20 kHz) to a broadband signal and studied the response of an auditory neuron at some distance from the source. They reported a decreasing variability of responses with increasing bandwidth of the signal, i.e., the temporal pattern was more reliably encoded in the afferent activity. With increasing bandwidth, more and more independent frequency channels in the ear are being activated, which increases the reliability of coding more efficiently as compared to a system where all elements are equally tuned (Klump 1996).

4.6 Filters in the Time Domain

4.6.1 Filter for Species-Specific Temporal Call Pattern

A distinctive feature of insect sound signals is their pattern of amplitude modulation (the sound envelope), varying from simple repetitions of single sound pulses to more complex grouping of pulses into chirps (Alexander 1962; Hennig et al. 2004). The amplitude modulation provides the most crucial cue for song recognition and allows crickets and grasshoppers to respond adaptively only to signals of their own species. “Innate releasing mechanism” was the term created by the early ethologists to describe an unknown filter in the brain of receivers to explain these selective behavioral responses. In the following section, I shortly describe two recent approaches to identify this temporal filter in the brain of insects.

4.6.1.1 A Modeling Approach for Grasshoppers and Crickets

One approach was to describe behavioral preference functions of females in response to male signals using a modeling framework (Clemens and Ronacher 2013; Clemens and Hennig 2013; review in Ronacher et al. 2014). The model consists of three processing steps: (1) feature extraction with a bank of “**LN** models,” each with a **L**inear filter followed by a **N**onlinearity, (2) temporal integration, and (3) linear combination. The specific properties of the filters and nonlinearities were determined using a genetic learning algorithm trained on a large dataset of song features and the corresponding behavioral response scores. The model showed an excellent prediction of the behavioral responses to the song models tested. Surprisingly, the genetic algorithm found Gabor-like functions as the optimal filter shapes for both crickets and grasshoppers, although these two taxa differ considerably in the organization of their auditory pathways and in the complexity of their songs.

These findings shed new light on the black box “innate releasing mechanism” in the brain of female receivers, but since insects provide the advantage to analyze auditory processing at the level of identified neurons, we would also like to know how the neuronal network tuned to the species-specific temporal pattern of song looks like. Cross-correlation (Hennig 2003), internal template matching (Hoy 1978), or oscillatory responses of individual neurons (Bush and Schul 2006) have been proposed to explain the neural basis of temporal selectivity, and Schildberger (1984) provided evidence for sequential processing in low-pass and high-pass filter neurons shaping the band-pass response properties of brain neurons.

4.6.1.2 The Neuronal Network in Crickets

Kostarakos and Hedwig (2012, 2014) and Schöneich et al. (2015) characterized the temporal filtering of auditory neurons in the cricket brain and compared it with the phonotactic responses of females. They described an area in the anterior protocerebrum where the neurites of four newly identified local brain neurons overlap with the axonal arborizations of an ascending interneuron (TH1-AC1, formerly known as AN1) which forward the information about the calling song to the brain.

Whereas the spike activity of TH1-AC1 and one local interneuron copy different auditory patterns regardless of their temporal structure, two other neurons match the temporal selectivity as seen in behavior, but they also responded to some non-attractive temporal patterns. One local brain neuron (B-LI4), however, exhibits band-pass response properties; its different auditory response functions match the behavioral tuning almost perfectly. The selectivity of this neuron is based on fast interactions of inhibitory and excitatory synaptic inputs. The authors also demonstrated that selective processing requires only one specific pulse interval to elicit an enhanced response to the next sound pulse, a property which is very different from band-pass filtering by low-pass and high-pass neurons as suggested by Schildberger (1984).

4.6.1.3 The Neuronal Network for Pulse Song Intervals in Drosophila

The courtship song in Drosophila is composed of the sine song and pulse song, with a distinct temporal pulse pattern in the latter. In *D. melanogaster*, this part of song is a series of pulses with inter-pulse intervals (IPI) of about 35 ms (Shorey 1962); other species differ in their mean IPI and other aspects of courtship song. Although the importance of IPI for reproductive isolation between sympatric species is known for a long time, the neuronal pathways necessary for processing and discriminating conspecific song were unknown until recently. Vaughan et al. (2014) identified the circuitry underlying courtship song responses in males and females. They distinguished seven major classes of auditory projection neurons (aPNs) and five classes of auditory local neurons, with arborizations in the antennal mechanosensory and motor center and projections to a variety of downstream regions. The authors tested each class of interneuron for its role in courtship hearing, using shibire^{TS}-mediated silencing and dTrpA1-mediated hyperactivation. Surprisingly, only one class of projection neurons and one class of local interneurons are necessary for behavioral responses to song in either sex. Direct recordings of this specific class of projection neurons revealed an intracellular band-pass filter favoring IPIs of conspecific song.

4.6.2 Time Windows: A Most Efficient and Economical Filter in the Temporal Domain

The signaling of most acoustic insects is rather “speculative” (Zimmermann et al. 1989), since males producing a calling song do not know the effectiveness of their signaling until the moment of arrival of a female. This is not the case for some short-horned grasshoppers and katydids, where pair formation is achieved by duetting: the male song elicits an acoustic reply from the female, so that the male (in most species) then responds phonotactically (von Helversen 1972; Heller and von Helversen 1986; review in Bailey 2003). Remarkably, however, the female reply is extremely short in the order of a few milliseconds: in *Leptophyes punctatissima*, a click of less than 0.5 ms in duration. This creates a problem for signal recognition since such a short click does not provide the species-specific amplitude modulation usually necessary to distinguish between songs of species (see Sect. 4.6.1).

The solution is a female response which occurs after a very short delay time (28 ms in *L. punctatissima*; Robinson et al. 1986), and the female reply has to occur within a time window after onset of the male song in order to elicit phonotaxis in the male. The delay time of the female is a very precise and species-specific characteristic, varying between species from less than 20 ms up to 450 ms and could be used by the male as a temporal feature for species recognition (Heller and von Helversen 1986). The combination of extremely brief signals, a narrow time window of the male, and the corresponding delay time of the female may be particularly advantageous under noisy field conditions. Indeed, by listening for and only accepting a signal in a narrow time window of about 50 ms, while completely ignoring the rest of the time, may reduce many false alarms. It would be even more economic than the more or less selective filters for CF as outlined in Sect. 4.2. This has, however, never been tested under realistic outdoor conditions and awaits further experimental proof. We also do not know yet how these time windows are implemented in the nervous system of an insect.

4.7 Filters for Sound Amplitude

4.7.1 Gain Control Is an Effective Filter Matched for Eliminating Low-Intensity Sound

The more or less sharply tuned frequency filter outlined for crickets (see Sect. 4.2) works sufficiently well in species with tonal carrier frequencies, to free the CNS from computational processing for separating relevant from irrelevant sound. However, many insects communicate acoustically in aggregations, where a receiver is within earshot of several conspecific signalers (Römer and Bailey 1986; Greenfield 1994). The temporal overlap of several conspecific signals arriving from different directions and distances may result in a severe masking of the temporal song pattern at the position of the receiver, which is so important both for species identification and female choice (see Sect. 4.6.1). Pollack (1988) for crickets and Römer and Krusch (2000) for katydids discovered a neuronal gain control mechanism in first-order interneurons that could selectively code the more intense of two simultaneously presented sound signals, analogous to the "cocktail party phenomenon" familiar to humans (Cherry 1953). For example, a low-intensity signal at 45 dB SPL was quite effective when presented alone but completely suppressed when given simultaneously with another signal at 60 dB SPL. In rainforest crickets, the same membrane characteristic is also efficient to suppress activity resulting from background noise at various SNRs, thereby increasing the contrast between the relevant signal and background (Schmidt and Römer 2011). In this way, an effective intensity filter is established, again at a rather early point of the auditory pathway, so that the central nervous temporal filter in the brain can deal with clear representations of the temporal pattern.

4.7.2 Reduced Sensitivity as a Matched Filter for Irrelevant Sound?

If we agree with the gain control mechanism as an efficient filter for some irrelevant sound, we should further develop the argument and consider that a reduced peripheral hearing sensitivity may represent such a filter as well, following the notion made by Wehner (1987; see also Wehner, this volume) that ". . .. perceiving the world through such a 'matched filter' severely limits the amount of information the brain can pick up from the outside world, but it frees the brain from the need to perform more intricate computations to extract the information finally needed for fulfilling a particular task." In the context of detection of acoustic predator cues, this argument seems to be intuitively wrong, because it is generally accepted that in the sensory arms race between predator and prey, the detection distance is of crucial importance for both (Surlykke and Filskov 1999; see Schul et al. 2000 for an experimental approach). Hence, by reducing the hearing sensitivity of a nocturnal flying insect to the ultrasonic calls of a bat, it would reduce the distance over which the insect gets aware of the predator and can initiate appropriate escape responses. However, for the insect, it is not relevant to achieve the *maximal possible* detection distance through high sensitivity, but a detection distance *just sufficient* for escape. Even more important, there is a trade-off between increased sensitivity of a sensory system and the potential for confounding high-frequency calls from other sources in the background (e.g., katydid calls) with bat predators, thus producing "false alarms." In an environment with a high incidence of misleading sound, it would likely be adaptive that the threshold for eliciting either an escape behavior or neuronal responses is rather high. This is indeed a property of the HF channel which holds for insect taxa as diverse as crickets, praying mantis, lacewings, tiger beetles, butterflies, and moth (Yager and Hoy 1989; Yager et al. 2000; Yack and Fullard 2000). With the exception of arctiid moths with reported thresholds close to 40 dB SPL, those of the other insect groups are considerably higher and range between 50 and 80 dB SPL. Corresponding thresholds of many rainforest cricket species are consistently between 70 and 80 dB SPL (M. H. Brunnhofer, 2015, personal communication). Since background noise levels between 60 and 70 dB SPL have been reported in the same environment (Lang et al. 2005), the reduced sensitivity in the HF channel may release the central nervous system from the difficult task to distinguish between irrelevant HF events and those indicating real danger.

Thus, with respect to filters for the intensity domain, we find the interesting situation that in some cases, exquisite active mechanisms have evolved to boost up the sensitivity in response to very faint sound, and at the same time reducing the effect of higher amplitudes. It is probably not by chance that this is found in particular in the context of flies hearing near-field sound, where relevant stimulus amplitudes can be minute. On the other hand, gain control mechanisms and reduced general sensitivities filter stimulus levels in the opposite direction, favoring larger stimulus levels. In any case, it is obvious that these different solutions are highly adaptive in the particular ecological context.

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