Chapter 3
Masking by Noise in Acoustic Insects: Problems and Solutions

Heiner Römer

Abstract In most environments, acoustic signals of insects are a source of high background noise levels for many birds and mammals, but at the same time, their own communication channel is noisy due to conspecific and heterospecific signalers as well. In this chapter, I first demonstrate how this situation influences communication and the evolution of related traits at the population level. Solutions for communicating under noise differ between insect taxa, because their hearing system evolved independently many times, and the signals vary strongly in the time and frequency domain. After describing some solutions from the senders' point of view the focus of the chapter is on properties of the sensory and central nervous system, and how these properties enable receivers to detect relevant acoustic events from irrelevant noise, and to discriminate between signal variants.

3.1 Introduction

This book is mainly on the impact of background noise on intraspecific communication. However, a chapter about noise and hearing in insects should consider the fact that in some taxa (Lepidoptera, Neuroptera, Dictyoptera, and Coleoptera), ears appear to have evolved primarily for the function to escape attacks of insectivorous bats, through the ability to detect their echolocation calls in flight (e.g., Roeder 1967; Miller and Olesen 1979). By contrast, in two groups of Orthoptera, the katydids and crickets, hearing evolved in the context of intraspecific communication, most likely long before the appearance of bats in the Miocene (Alexander 1962; review in Hoy 1992). The fact that many katydids and crickets adopted a nocturnal lifestyle made them potential prey for insectivorous bats,

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

H. Brumm (ed.), *Animal Communication and Noise*,
Animal Signals and Communication 2, DOI: 10.1007/978-3-642-41494-7_3,

when on the wing, which most likely has been the selection pressure for the evolution of bat avoidance as a secondary function of their hearing system (Popov and Shuvalov 1977; Moiseff et al. 1978; Libersat and Hoy 1991; Yager 1999; Faure and Hoy 2000). In any case, hearing in insects includes the two behavioral contexts of identification and localization of mates or rivals (intraspecific communication), and the detection and localization of predators (or, in the case of parasitoids, the detection and localization of hosts). Given the dramatic consequences of not detecting a predator acoustically under masking conditions compared to those missing a mate, I will include some aspects of predator detection under noise as well.

3.2 The Problem

The information needed by an organism for shaping its behavior and for decision making is transmitted via afferent nerves and encoded in trains of action potentials. Sensory systems and the brain have to make adaptive assumptions about what had happened in the physical world, by decoding this information. In all sensory systems investigated, receptor cells or sensory interneurons always reveal short episodes of high-frequency firing of action potentials (bursts) in addition to single, spontaneous APs (Eggermont and Smith 1996; Metzner et al. 1998; Krahe and Gabbiani 2004). These bursts convey information about important stimulus features (Metzner et al. 1998; Marsat and Pollack 2006). In the past, behavioral ecologists had a tendency to study communication systems by looking at signal design and signaling behavior, but ignoring the sensory and brain mechanisms that enable receivers to make sense of signals in a noisy world. They simply assumed that natural or sexual selection would have provided individuals with the sensory and neuronal machinery to perform a given task sufficiently well (i.e., to increase their fitness). However, in recent years claims were made by more and more scientists that a comprehensive understanding of communication systems and sexual selection by female choice greatly benefits from considering the cognitive mechanisms underlying decisions where signal processing is involved (e.g., Guilford and Dawkins 1991; Römer 1992; Bateson and Healy 2005; Ryan et al. 2007; Castellano 2009; Miller and Bee 2012). Such a brain-based point of view is illustrated in Fig. 3.1.

Here, the action potential activity of a first-order sensory interneuron of a katydid was recorded at night in the insects' habitat, a tropical rainforest. A crucial task of the auditory pathway is the recognition and classification of acoustic objects important for survival and reproduction. If the brain has to rely on the bursting activity of the cell, how does the insect form object classes based on bursting activity? For example, how does the brain distinguish the calling activity of a conspecific male (burst marked by asterisk) from irrelevant events caused by heterospecific signalers (noise)? Another important acoustic object class would be represented by bursts induced by a predator (echolocating bat; repetitive bursts

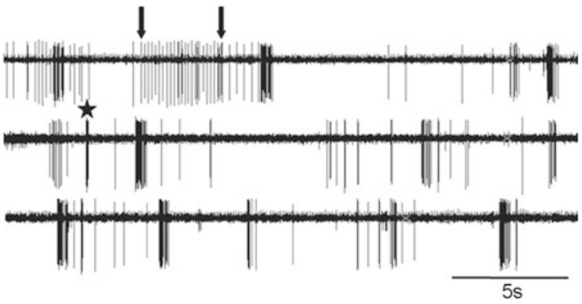

Fig. 3.1 Outdoor recording of the activity of an auditory interneuron (omega neuron) of a katydid at about 2 h after sunset in the tropical rainforest of Panama. Note the different bursting activity of the cell in response to sound events in the background. The task of the CNS of the receiver is to identify and classify acoustic objects based solely on this information. The short burst marked by the *asterisk* was elicited by a conspecific signal, the repetitive bursts between *arrows* by an echolocating bat. For further explanation see text

between arrows). How does the brain form one common "predator" object class from such repetitive bursts when different bat species vary in the rate of calls in their search phase? Moreover, and even more demanding: how to distinguish variations within one object class which carry important information (e.g., quality of a signaler or its distance to the receiver) from variations caused by the noisiness of the transmission channel or sensory processing? In the example given in Fig. 3.1, does variation in duration and spike count of the longer bursts carry information about distance of the same signaler, or differences in the signal structure of different signalers varying in quality? Ronacher et al. (2004) summarized the causes and consequences of spike train variability for processing temporal acoustic patterns in insects, and the interested reader is strongly referred to this comprehensive review. The authors list a number of factors contributing to this variability, including external noise caused by signal degradation on the transmission channel and masking signals from conspecific and heterospecific signalers, as well as intrinsic noise induced at various levels from signal transduction, spike generation, and synaptic transmission in the sensory system.

As a result of the unavoidable noisiness of spike trains in neurons of sensory pathways one should expect that mechanisms evolved which reduce the mistakes, that a nervous system falsely classifies noisy events as signals. On the other hand, minute variations in spike trains may well reflect differences between objects or object classes which are important for the receiver, such as small differences in the size of a sender, or the loudness or frequency composition in the sound signal of a mate. Such small differences, in contrast to those caused by noise, should be preserved during sensory processing, since they represent the neuronal basis for discrimination between mates or other decisions of importance for the fitness of receivers (Ronacher et al. 2004).

Signal detection theory represents a conceptual framework with the objective to assess the efficiency by which a given receptor/detector system can detect a single signal or a group of specified signals against a specified background noise, or to distinguish between signal variants. Signal detection theory can handle both behavioral and neuronal data and is therefore useful for many chapters in this book. Thus, for a more general consideration of SDT the reader is referred to Chap. 2 by H. Wiley, this volume.

3.2.1 Ecological Evidence for Masking: Acoustic Niche Partitioning

Some of the best evidence for the important role acoustic masking can have for the fitness of individuals would be to demonstrate spectral, temporal, and/or spatial niche partitioning as a result of calling activity of other species (see also Chap. 5 by Schwartz and Bee, and Chap. 7 by Brumm and Zollinger this volume). Of course, the role of competition for limited resources in natural selection has been known for a long time, and ecologists recognized that competition for resources may be an important factor affecting the abundance and the distribution of species. The competition for a communication channel has however, only rarely been considered in this context (but see Greenfield 1983; Greenfield and Karandinos 1979 for chemical communication, and Chap. 13), although it should be evident that as the number of species in an ecosystem using the same channel increases, the chances of successful communication will decrease.

Competition for a communication channel is particularly evident for the air-borne-sound channel, since for every additional species that vocalizes at the same time and location, the background noise level increases, the signal-to-noise level decreases and signal detection and/or discrimination is severely impaired. Impressive examples are known for insects (e.g., Gogala and Riede 1995). In particular, tropical rainforests are among the habitats with highest species diversity, and acoustic noise measurements in a Neotropical rainforest of Panama at night have demonstrated sound pressure levels as high as 70 dB (Lang et al. 2005). Spectral analysis revealed that a great proportion is due to the signaling activity of insects (Diwakar and Balakrishnan 2006; Ellinger and Hödl 2003; Lang et al. 2005; see sonogram of a recording in Fig. 3.2). Of these, the calling activity of crickets constitutes the main frequency band between about 2 and 9 kHz where most acoustic energy is concentrated. However, the frequency channel in the high audio and ultrasonic range is also occupied, mainly by the calling activity of katydids (Fig. 3.3), and of course the echolocation activity of bats. The potential for masking at these higher frequencies is often underestimated, because such recordings are usually made from the ground, and many of these signaling katydids broadcast from canopy or mid-canopy regions, and as a result their high frequency or ultrasonic-signals suffer from stronger excess attenuation compared to frequencies used by crickets below 10 kHz (Römer and Lewald 1992). Thus, the situation in a nocturnal tropical rainforest looks terribly complicated for any

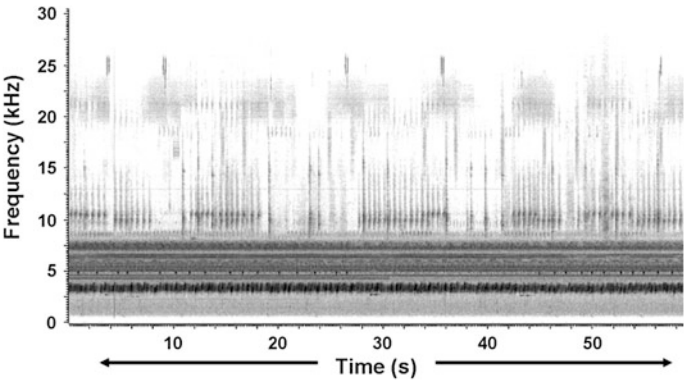

Fig. 3.2 Sonogram of a sound recording of 1 min in the tropical rainforest of Panama (Barro Colorado Island) at about 2 h after sunset. Note the strong audio component between 3 and 9 kHz mainly due to calling of crickets and frogs, and the various song patterns in the high sonic and ultrasonic frequency range (mainly katydid calls)

involved taxon. The fact, however, that so many species still communicate under these conditions means that they can deal with these environmental conditions to an extent that the use of acoustic signals in fitness-related tasks is still a likely evolutionary outcome of natural selection (Brumm and Slabberkoorn 2005).

3.2.2 Different Solutions for Different Taxa

Depending on the kind of signals used by the different taxa of acoustic insects, one would expect that niche partitioning in the acoustic communication channel should be different. Male crickets produce calling songs which usually have a pure-tone character limited to frequencies from 2 to 9 kHz (Bennett-Clark 1998; for few exceptions of ultrasonic signaling in crickets see Robillard et al. 2007). Most grasshoppers and katydids, however, produce broadband signals with a frequency spectrum that may extend far into the ultrasonic range; some include only ultrasonic frequencies, in some cases of tropical species up to more than 100 kHz (Heller 1988; Morris et al. 1994). Again, exceptions have been reported for a group of nine tettigoniid species, the calls of four were narrow band and in the audible range similar to those of gryllids (Diwakar and Balakrishnan 2006). Thus, theoretically, crickets could solve the problem by partitioning their signals in the frequency domain, simply by using a narrow, but different carrier frequency within the available range from 2 to 9 kHz. By contrast, grasshoppers and katydids would suffer from strong frequency overlap in heterospecific interactions, and should rely on partitioning in time and space. We can further predict that in such interactions the species with the higher duty cycle will gain an advantage over the other species, since the detection/recognition of a high duty cycle signal will be favored under these conditions (but see other solutions below).

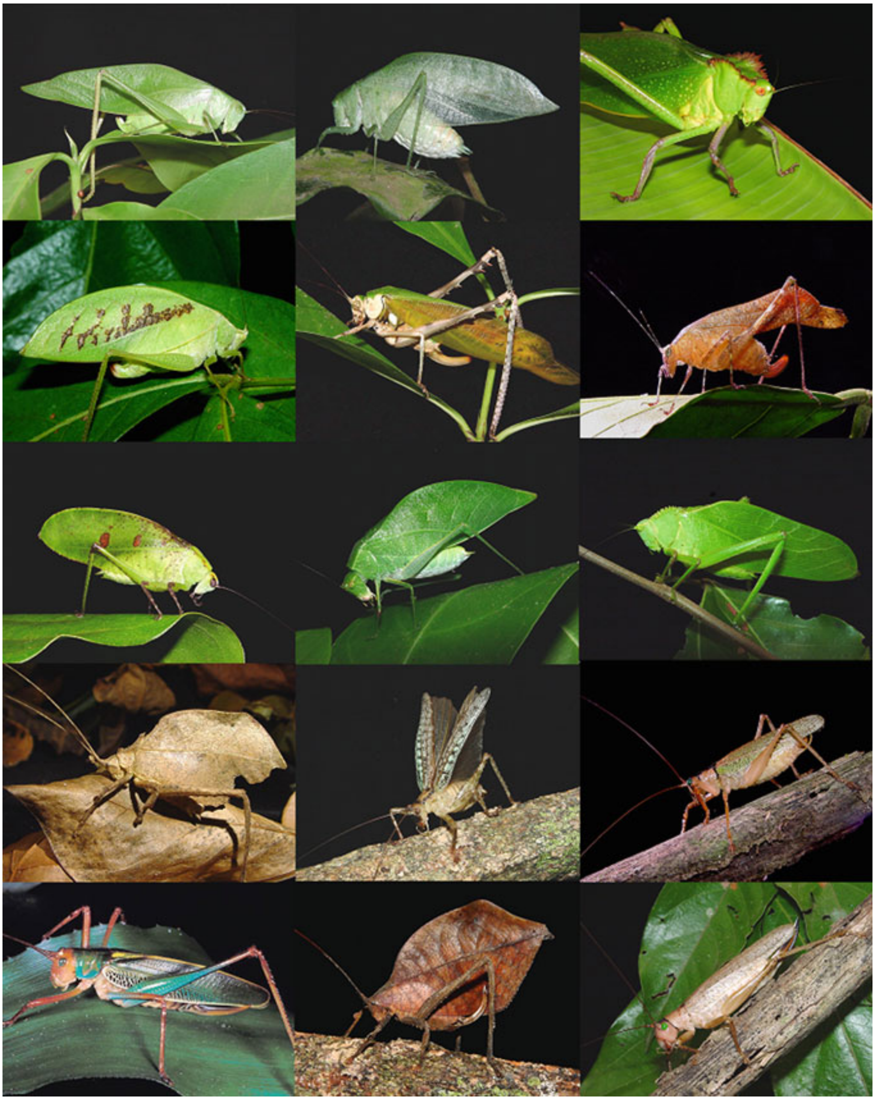

Fig. 3.3 Fifteen of about 70 species of katydid in the rainforest of Panama which cause most of the high-frequency or ultrasonic noise at night, as seen in the sonogram of Fig. 3.2. More than 50 species of cricket add to the sonic background noise with their calling songs between 2 and 10 kHz. The *upper* nine species are Phaneropterine katydids, the six *below* are Pseudophyllines. Photographs by Alexander Lang

Evidence for the latter hypothesis comes from two ecological studies on katydids (Greenfield 1988; Römer et al. 1989) which demonstrate that when only two species use a spectrally similar signal, this can result in complete suppression of calling activity of one species by the other, or a shift in the diurnal calling activity of one species. In one study, the katydid *Hemisaga denticulata* (a species with a low duty cycle call) was acoustically active over the afternoon, but showed a strong decline of signaling after sunset, when another katydid *Mygalopsis marki* started singing, which increased the noise level from 48 dB SPL to 60 dB SPL (Römer et al. 1989). Experimental manipulation of song interference by removal of all singing *M. marki* males resulted in a recovery of singing activity of *Hemisaga* males after only 15 min. Furthermore, in another habitat without the interfering species and an overall noise level of only 40–45 dB SPL the number of singing *H. denticulata* remained constant even after sunset. A similar removal experiment was performed by Greenfield (1988) with two species of Neoconocephalus (*N. spiza* and *N. nebrascensis*). The species with the low duty cycle song shifted its singing activity to the day as a result of the masking sound of the other species, but after removal of the competing species became nocturnally active again (see also Sect. 4.5 for a further argument why in these interactions the signal with a low duty cycle is at a disadvantage). Of course, the argument of strong song interference does also hold for narrow-band acoustic signals such as in crickets. For two species of rainforest crickets (*Paroecanthus podagrosus* and *Diatrypa spec*.) with their carrier frequency of calling songs at 3.9 and 4.0 kHz, we found in more than 100 h of sound recordings not a single case where both species were calling at the same time and space (Schmidt and Römer unpublished). This is true even though both species have more selective frequency filters compared to European field crickets (see below). Finally, frequency overlap can result in heterospecific interference between insect and vertebrate taxa, as has been suggested by Ryan and Brenowitz (1985). Cicada choruses have been shown to inhibit the evoked territorial calling of male frogs, because the call frequencies of both species overlap between 3 and 7 kHz (Paez et al. 1993).

Although the majority of behavioral and neurophysiological studies agree with the hypothesis of a strong advantage of signals with a high duty cycle over low ones, other solutions have been discovered as well, based on the habituation/dishabituation properties of nerve cells. If a highly repetitive signal of one species results in strong habituation of a sensory neuron, but the less redundant signal evokes dishabituation in the same neuron due to some novel property in its signal, then the less redundant signal could still be detected in the noise of the competing species. Schul and Sheridan (2006) provided an example for such a "novelty detector," where the "noise" constitutes the conspecific signal with pulse repetition rates of 140 Hz, under which the echolocation pulses of bats have to be detected. Given that carrier frequencies between these two signals are different (e.g., 15 kHz vs. 40 kHz), the dishabituation described above resulted in almost 100 % response probability to the bat signal. Future behavioral studies need to demonstrate, however, that such physiological properties of identified nerve cells are also found in the behavioral ability to respond to the less redundant signal.

In addition to the frequency domain, the above examples indicate the second possibility of niche partitioning in the time domain. Another example comes from a Bornean mixed dipterocarp forest, where the "dusk community" consists of a well-defined ensemble of cicada, cricket, and frog species, in which the first half-hour is dominated by cicadas and the second half-hour by crickets and frogs. Furthermore, the signaling activity of a given cicada species exhibits a surprisingly narrow temporal segregation in the range of minutes (Gogala and Riede 1995). Furthermore, two studies on cicadas (Sueur 2002) and crickets and katydids (Diwakar and Balakrishnan 2007) included other parameters for acoustic niche partitioning in their analysis. Sueur (2002) found a set of properties that facilitated niche partitioning among a cicada community, which also included (apart from call frequency) calling height and timing, as well as behavioral categories such as the tendency to aggregate, and the calling strategy (‘call-fly’ vs. ‘call-stay’). In the rainforest study by Diwakar and Balakrishnan (2007) calling heights of both gryllid and katydid species ranged from the ground to the canopy, with more gryllid than katydid species occupying the ground and herb layer. Their study revealed vertical stratification of calling heights, with three main layers corresponding to the canopy, understorey, and the ground layer. Importantly, these clusters emerged from the raw data of calling heights of individuals of each species without a priori distinction of layers.

Although this chapter is on acoustic insects where communication happens in the acoustic far field, it should be evident that acoustic masking may also happen in the acoustic near field (i.e., the range close to a sound source where the energy component due to particle displacement is greater than the sound pressure component). Samarra et al. (2009) reported the masking of courtship song in *Drosophila montana* by background noise at frequencies overlapping with those in the song, based on female behavioral responses. This happened at a signal-to-noise-ratio of −6 dB, and it is highly unlikely that natural habitat noise levels can account for the observed masking in the acoustic near field. The authors therefore speculate that when a female is courted by several males it might create the relevant biotic noise. This remains to be tested in future experiments, in which the near-field acoustic environment of females is determined with appropriate microphones.

3.2.3 Background Noise and Signal Synchrony or Alternation

Some of the most impressive interactions occur in insect and anuran choruses when the signaling of individuals is influenced by the precise timing of signaling of other individuals (see also Chap. 5 by Schwartz and Bee). If individuals are able to signal in silent gaps of masking noise (Zelick and Narins 1985) this may be a solution to the problem of masking interference. Extreme forms of fine-scale signal timing occur when neighboring individuals either synchronize or alternate their signals with those of neighbors, i.e., when the phase angles approximate either 0° or 180°, respectively (Walker 1969; Sismondo 1990; Greenfield 1994; Greenfield and Roizen 1993; Hartbauer et al. 2005). Although the models explaining synchrony and alternation at the proximate level differ to some extent, it is obvious that the phase response curve of the underlying song oscillator should be sensitive to background noise, because of two possible reasons: On the one hand, the signal of the neighbor could simply be masked by the background and thus cannot influence the oscillator any more. On the other hand, noisy events in the background could reset the oscillator if they occur within a certain phase of the phase response curve.

Figure 3.4 shows one result of the breakdown of synchrony due to background noise (Hartbauer et al. 2012). In the undisturbed situation, a male katydid (*Mecopoda elongata*) was entrained to conspecific chirps and established a very regular synchronous interaction, with his signal being delayed relative to the broadcast one (follower role; upper trace). Under masking noise conditions, the fixed temporal relationship broke down at a SNR of −1 dB (lower trace). It remains to be examined whether the breakdown is a simple masking effect and/or due to noise resetting the oscillator.

3.3 Solutions by the Sender

In the following section, I discuss some solutions to the problem of communicating under noise from the senders' point of view, which are by no means restricted to insects. We would expect that rather different taxa dealing with the same problem might have evolved similar, though not identical, solutions. Thus,

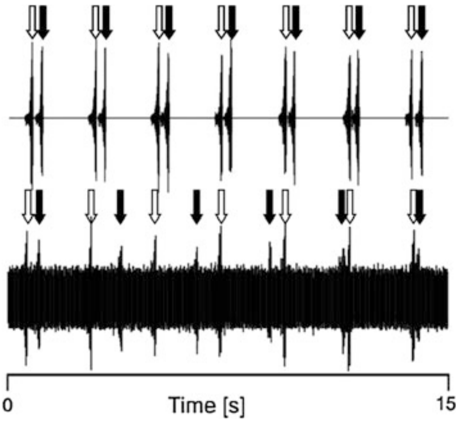

Fig. 3.4 Breakdown of call synchrony under background noise. In the upper panel, a male *Mecopoda elongata* (*filled arrow*) synchronized his chirp with a regularly repeated conspecific stimulus (*open arrow*) and establishes a constant follower relationship with the stimulus. Under background noise at a SNR of −1 dB synchrony breaks down and the males' chirp is produced at different phases of the stimulus period. For further explanation see text (modified from Hartbauer et al. 2012)

Chap. 5 by Schwarz and Bee on frogs and Chap. 7 by Brumm and Zollinger on birds deal with the same issues discussed in this section.

3.3.1 No Lombard Effect, But Strong Selection for Increased Loudness

The Lombard effect describes one of the most obvious mechanisms to overcome masking noise problems, namely an increase in the amplitude of the signal under noise. The effect appears to be very common in birds and mammals, and Chaps. 7 and 9 describe in detail findings related to the Lombard effect, and for a failure of a demonstration of the effect in anurans see Chap. 5. Similarly, there is no such report for insects. This is somewhat surprising given the fact that the decrease in SPL of a male calling song at higher distances is rather flat, so that a small increase in loudness (or efficiency in transmission) of only a few decibels may result in a better SNR, and thus a relatively large increase in the active range of the signal. In fact, the greatest advantage one would expect for those species where the signal suffers little or no excess attenuation, so that the decrease in loudness over distance follows the 6 dB per doubling of distance rule. In these cases, the decrease is exponential and thus rather flat at greater distances. The bladder grasshopper *Bullacris membracioides* (Pneumoridae; Orthoptera) is a striking case for this phenomenon, and achieves hearing distances between 1.5 and 2 km (van Staaden and Römer 1997), due to the use of a resonator for sound production and favorable atmospheric conditions for sound transmission after sunset. Theoretically, the active range of the male signal being just at the masked threshold for a receiver at, e.g., 500 m would increase with a small increase in loudness of 5 dB to 800 m, with a corresponding impressive effect for the broadcast area (from 0.78 to 2.01 km^2).

Differential attraction of females to louder calling songs is known for insects (see Forrest and Green 1991 for a field study); comparable results have been obtained in many laboratory-based choice experiments, where 2–3 dB have been sufficient for females choosing the more intense song. Fruitflies, mole crickets, crickets, and katydids preferentially approach the louder of two conspecific signals of different intensity, and selection has favored the use of resonators, amplifying burrows, and baffles to achieve an increased sound output (review in Römer 1998). However, although many acoustic insects suffer from masking by conspecific and heterospecific signalers, in order to argue for a Lombard-like effect in this taxon it has to be demonstrated that either (i) populations differing in the amount of masking also differ in their sound output, or (ii) individuals regulate their sound output depending on the SPL of background noise. So far, no empirical evidence has been reported which would support these ideas.

Importantly, the lack of empirical evidence for a Lombard effect in insects does not mean that there is no plasticity in modifying the SPL depending on ecological conditions. This can, curiously enough, best be demonstrated in cases where insects *down-regulate* their sound output. Again males of the bladder grasshopper *B. membracioides* represent one example: they produce their 100 dB SPL call until they receive an acoustic female reply, which is a low intensity call at 60 dB SPL. The female response then induces a duet and male phonotaxis, until she is finally contacted. Interestingly, observations in the field indicate that the SPL of the male call is not always at the maximum close to 100 dB, in particular when the male has established reliable duetting with the female (which means that both are within the active range of the signals of the opposite sex). In these cases males often down-regulate the SPL of their call. The most likely explanation for this behavior is competition by “unintended receivers” from conspecific males, particularly alternate male morphs, which cannot call and fly at all, but intercept the acoustic duet of calling males with the female (Alexander and van Staaden 1989; Donelson and van Staaden 2005).

3.3.2 Use of Multimodal or Alternative Signals Under Masking Noise Conditions

In recent years it has become evident that many animal displays may be rather complex, including more than one signal component in different sensory modalities. Several hypotheses have been proposed why such complexity exists, in particular in mating signals (reviewed by Candolin 2003). Of these, the back-up signal (or redundant signal) hypothesis proposes that multiple signals allow a better assessment of mate quality as each signal reflects the same quality with some error (Møller and Pominakowski 1993; Johnstone 1997). Under masking noise conditions, where errors in the detection of differences among mates will increase, mate choice would become more reliable with multiple back-up cues. In Acridid grasshoppers, for example, the act of sound production (stridulation) involves the strong up-and-down movement of the hindlegs rubbing against a stridulatory file on the hindwings. In some species the hind legs or joints between femur and tibia are brightly colored, so that at close range the acoustic display also includes a striking visual display (Riede 1986). Some Acridid families have given up acoustic signaling altogether (Leptysminae, Rhytidochrotinae, Ommatolampinae, Melanoplinae, Proctolabinae, and Bactrophorinae), but show conspicuous movements of hindlegs (“knee-waving”) and antennae (Riede 1987). Katydids with their elytral stridulation broadcast airborne-sound signals, but the same act of stridulation produces vibrations on the substrate where signaling takes place (Keuper and Kühne 1983). The additional information via the vibrational channel improves the localization of singing males by females (Latimer and Schatral 1983).

Neither in grasshoppers nor katydids is there conclusive evidence that the use of such additional modalities is correlated with the amount of background noise in the airborne-sound channel. However, in a neotropical katydid which uses airborne sound for long distance communication, but also an alternative form of private signaling through substrate vibration, the various trade-offs when communicating in these two modalities have been studied in more detail (Römer et al. 2010). As demonstrated earlier, the background noise level for the airborne-sound channel can be quite high in the nocturnal rainforest, whereas it is low in the vibration channel in the low frequency range of the vibration signal (carrier frequency 13 Hz) and in the plant in the understory where the insect lives (but see Cocroft and Rodriguez 2005 for arguments for a noisy vibratory channel). Indeed, in a comparison of signal perception using neurophysiological methods under outdoor conditions, the detection of the signal in the vibratory channel was more reliable than the detection of the short, airborne-sound signal, in particular with respect to the false alarm rate. One should keep in mind, that the benefit of using such an alternative signaling modality is reduced or offset due to a reduced active space of the vibration signal.

3.3.3 Signal Duration and Redundancy to Counteract Masking by Noise

The difference in the duration and/or rate of acoustic signals in different insect species is striking: from single clicks lasting less than a millisecond (see Sect. 4.4) to stereotyped repetition of single song elements for many minutes and hours (Gerhardt and Huber 2002). It appears evident that stereotyped repetitions could support both the detection and recognition by receivers when amplitude fluctuations, reverberations, or masking noise in the transmission channel are superimposed on the signal at some distance from the source (see also Chap. 7 for experimental evidence in birds). Indeed, when the effect of amplitude fluctuations and reverberations on the perception of conspecific song patterns was studied in a katydid outdoors, the temporal song pattern was represented in the central nervous system of a receiver with remarkable accuracy at distances well beyond the nearest neighbor distance (Rheinlaender and Römer 1986; Römer and Lewald 1992).

However, in a series of behavioral studies on the grasshopper *Chorthippus biguttulus* the stereotyped repetition of song elements did not improve the ability to detect and recognize the conspecific signal substantially (Ronacher and Krahe 1998; Ronacher et al. 2000; Ronacher and Hoffmann 2003). In this species, the song of females to which the male performs phonotaxis is composed of a series of identical subunits each characterized by their species-specific amplitude modulation. Although the natural female song lasts for more than one second, males responded behaviorally to a shortened song containing only three subunits (corresponding to 250 ms duration). Ronacher et al. (2000) conducted similar experiments under unmodulated noise, which decreases the depth of the AM-pattern. The expectation in these experiments was that with female songs containing more subunits higher noise levels would be tolerated. Surprisingly, however, even under high noise levels the results indicated an upper limit for temporal integration in the order of 450 ms, since the performance of males did not improve with more than five subunits. When these experiments were conducted under amplitude-modulated noise, modulation frequencies >15 Hz were the most efficient in masking the AM-pattern of the song. Thus, their results indicate that a chorus-like, temporally structured noise does more efficiently mask the signal than unmodulated noise with the same carrier frequency spectrum as the signal.

Altogether, the authors concluded that in the case of *Ch. biguttulus* the insect does not seem to rely very much on the serial redundancy of the signal for recognition under masking noise conditions. They point out however, that such redundancy, or longer duration signals may be most relevant in the context of sexual selection, via both female choice and male–male competition (see also Römer 1998). And as outlined in Sect. 4.5, the gain control mechanism observed in katydid and cricket receivers is most effective with intense and long duration signals, so that signalers with these signal properties may better be able to outcompete other signalers from being represented in the sensory system of receivers.

At the other end of the continuum of signal duration and redundancy in insect signals are those species with extremely short signals, repeated at a very low rate. Acoustically orienting predators may represent one selection pressure for their evolution (Zuk and Kolluru 1998). Except for duetting Phaneropterine katydids with their use of temporal windows we are lacking empirical data on the behavioral performance of receivers concerning detection/recognition of these signals. We might predict that species lacking redundant signals have to maintain smaller interindividual distances to achieve better SNRs. Based on an informal survey of the genus *Neoconocephalus* and other katydids Greenfield (1990) concluded that indeed discontinuously (less redundant) singing species experience high-density populations more frequently than do continuously singing species. Using unsupervised clustering as a tool to analyze the bursting activity of an auditory interneuron recorded under noisy conditions of the rainforest, Pfeiffer et al. (2012) demonstrated that small modifications of a stimulus (e.g., a double syllable compared to a single syllable) strongly enhanced the ability of the algorithm to separate bursts resulting from a stimulus from those resulting from noise.

3.4 Solutions by the Receiver

Similar to Chap. 4, I will now discuss solutions to the problem of communicating under noise from the receivers' point of view, which are again not restricted to insects. The section is particularly connected with Chaps. 6 and 8 on the same topics in frogs and birds, respectively.

3.4.1 Frequency Tuning: Increasing the Selectivity of Filters

In contrast to katydids with their broad range of frequencies in the calling songs another solution does only work for taxa such as crickets, where the sender concentrates acoustic energy within a small frequency range. One of the potential solutions to cope with a complex noisy acoustic environment is an improvement (mostly sharpening) in stimulus filtering by the peripheral or central nervous systems, which is found in other taxa as well (see Chaps. 6, 8, 10, and 12). Thus, any sound outside the sensitivity range of the filter would play a reduced role in masking of the signals, depending on the sharpness of the tuning (the matched filter hypothesis, Capranica and Moffat 1983; Wehner 1989).

Schmidt et al. (2011) studied the frequency tuning of an auditory neuron (AN1-neuron) mediating phonotaxis in a rainforest cricket (*P. podagrosus*; carrier frequency of calling song at 3.7 kHz) which suffers from strong acoustic competition, in comparison with the same, homologous neuron in European field crickets where such competition does not exist. As predicted, the neuron in the rainforest species exhibited a more selective tuning compared to the one in its European counterparts (Fig. 3.5). Remarkably, a comparison of the filters indicates that the increased filter performance of the *Paroecanthus* AN1 (best frequency at 3.9 kHz) is mainly due to the increased steepness of the slope toward higher frequencies. If the filter has been shaped by natural selection to avoid masking interference, this is exactly what we would expect to happen, because in the crickets' habitat there is more masking potential in the noise spectrum at higher compared to lower frequencies (see sonogram in Fig. 3.2). A rather similar situation has been reported for the two sympatric cricket species *Teleogryllus oceanicus* and *T. commodus* with calling song frequencies of 4.8 and 4.0 kHz, respectively, where the AN1 filter of

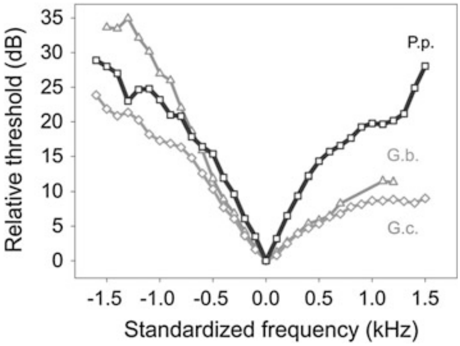

Fig. 3.5 Comparison of the standardized average sensitivity tuning of the AN1-neuron in *P. podagrosus* (P.p.), a rainforest cricket under strong acoustic competition from other crickets, with the tuning of the same homologous neuron in two species of field crickets *G. bimaculatus* (G.b.) and *G. campestris* (G.c.) where acoustic competition in neighboring frequency bands does not exist. Data for the *Gryllus* species are taken from Kostarakos et al. (2009) (modified from Schmidt et al. 2011)

T. commodus exhibits a steeper slope toward higher frequencies compared to other field crickets, which could aid in separating the frequency of its own calling song from that of the sympatric species (Kostarakos et al. 2009).

The performance of the filter of the rainforest cricket has been quantified by Schmidt and colleagues in two ways: first, by examining the representation of the species-specific amplitude modulation of the male calling song in the sound signal, when embedded in background noise. The filter of the rainforest cricket performed significantly better in representing this important signal parameter (Fig. 3.6). Second, the neuronal representation of the song pattern within receivers was maintained for a wide range of signal-to-noise ratios, up to −6 to −9 dB.

Although the above study appears to be conclusive concerning the hypothesis of environmental selection on a frequency filter to avoid masking, it cannot exclude

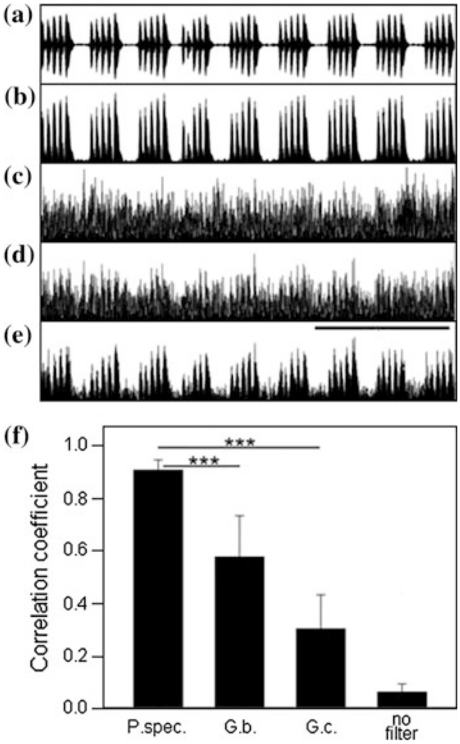

Fig. 3.6 The effect of the different filter functions in detecting the specific amplitude modulation (AM) of the *Paroecanthus* calling song embedded in background noise. **a** Oscillogram and **b** AM of *Paroecanthus* calling song. **c** AM of *Paroecanthus* calling song embedded in background noise without any filtering, **d** with the filter of *G. campestris*, and **e** with the filter of *P. podagrosus*. Note the increase in the quality of representation of the AM of conspecific song by using the more selective filter. Time bar 120 ms. **f** Correlation of the AM of *Paroecanthus* calling song with the AM of the same calling song embedded in background noise ($N = 9$) under the filter regimes of the three cricket species, and without any filter (Schmidt et al. 2011)

the possibility that the differences in filter characteristics between the European and rainforest cricket species are the outcome of phylogenetic constraints rather than adaptations to environmental conditions. Future studies on more species (of different subfamilies) would be helpful, or a comparison of different populations of a single species communicating under different noise levels and/or noise spectra (e.g., Amézquita et al. 2005, 2006). Such studies could also give us additional information about the possible impact such changes in receivers might have for signalers. More selectively, tuned receivers could impose strong selection on signalers to call exactly at the carrier frequency where they are tuned, because otherwise males would be unable to stimulate the females' hearing system adequately. Given this bias in female selectivity, we would expect to find in future studies a reduction in the variance of the male carrier frequency compared to those species where the selectivity in tuning is reduced. Interestingly, a reduced variance in this important song trait for female preference would in turn reduce the potential for female preference for the trait, pointing to the close interrelationship between signals, environmental conditions and the sensory and central nervous system of receivers (the "sensory drive hypothesis"; Endler 1992, 1993).

3.4.2 Frequency Tuning: Changing the Best Frequency of Filters

A fundamental assumption for the solution presented in the above section is a match between the carrier frequency of the signal and the hearing sensitivity of the receiver (Ryan and Keddy-Hector 1992). Although there are a number of exceptions to this general rule among the insects (e.g., cicadas: Huber et al. 1990; katydids: Bailey and Römer 1991; for a sex-specific mismatch see Dobler et al. 1994; haglids: Mason et al. 1999), it can be assumed that such matching has been arrived at by co-evolution between signalers and receivers (Endler 1992). The case of mismatch between the CF of the male call at 5 kHz and the best hearing sensitivity between 10 and 20 kHz in the katydid *Sciarasaga quadrata* (Austrosaginae: Tettigoniidae) is therefore surprising, given the fact that masking calls of up to 16 sympatric katydid species are in this frequency range of hearing. The solution to the problem is a mechanism that allows peripheral control of a sound guide to the ear, thereby shifting the sensitivity of the ear to 5 kHz, i.e., the CF of the call (Römer and Bailey 1998). The advantage of signaling at a lower frequency is in fact threefold: (1) to escape the masking noise conditions of heterospecific katydid species, (2) to achieve a better transmission of the conspecific call, which is close to the 6 dB/doubling of distance (geometric spreading) for the 5 kHz signal in the insect's habitat, and (3) finally, as *S. quadrata* is heavily parasitized by an acoustically orienting parasitoid fly, *Homotrixa alleni,* the call of the katydid may be under strong selection to be outside the best frequency range of the flies hearing system, which is most sensitive to frequencies >10 kHz (Stumpner et al. 2007).

Thus, as this example shows, it may be difficult to disentangle unequivocally the specific impact of one particular selection pressure (background noise or escape from parasitoids) for the evolution of a specific trait.

3.4.3 Noisy Conspecifics and Solutions to Cocktail Party-Like Problems

Although masking noise is most often associated with the sound production of heterospecific signalers, insects may also communicate in dense populations of conspecific individuals. If more than one signaler is within hearing range of a receiver, the temporal overlap of several songs arriving from different directions may result in a severe masking of the individual species-specific temporal song pattern at the position of the receiver. Insect choruses are therefore noisy social environments for acoustic communication, a situation quite common among humans (known as the cocktail party problem) and nonhuman animals (see Chap. 6, this volume). Bee and Micheyl (2008) therefore strongly argued for studies of the cocktail party problem in the context of animal acoustic communication because many of the sensory solutions to the human cocktail party problem may also represent potentially important mechanisms underlying acoustic communication in nonhuman animals.

3.4.3.1 Spatial Release from Masking

One of the mechanisms discussed by Bee and Micheyl is spatial release from masking, which refers to the improved detection of a sound signal when the masker is spatially separated to some degree from the signal (Klump 1996). However, surprisingly little is known for insects on this mechanism. Ronacher and Hoffmann (2003) investigated the influence of amplitude-modulated noise on the recognition of species-specific communication signals in a grasshopper behaviorally, and found little evidence for spatial release from masking. They explained their negative finding with the particular mode of processing signals for pattern recognition in grasshoppers (summation of signals from both auditory sides; von Helversen 1984). However, this is not the case in crickets and katydids (Pollack 1988; von Helversen and von Helversen 1995; Schul et al. 1998; Römer and Krusch 2000), and although spatial release from masking was not addressed directly in these studies, they nevertheless suggest that the mechanism works effectively in these taxa. In particular, katydids, with their known high peripheral directionality and contrast enhancement through lateral inhibition along the longitudinal body axis appear to possess the proximate basis for spatial release from masking (review in Gerhardt and Huber 2002; Hedwig and Pollack 2008).

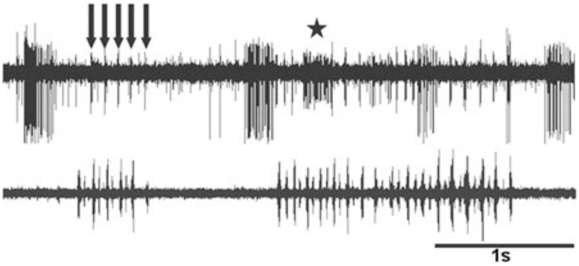

Fig. 3.7 An extreme case of spatial release from masking in a katydid. Simultaneous AP-recording of both omega cells (large spikes contralateral, small spikes ipsilateral cell, *upper line*) and the output of a bat detector, recording HF-sound ipsilaterally (*lower line*). Note that both auditory sides represent completely different "acoustic worlds" in their spike discharge: the ipsilateral cell responds to a bat (*arrows*) and to some other HF-background, not detected by the bat detector (*asterisk*), whereas the contralateral cell does not respond to these events at all. One would expect similar effects in crickets and other acoustic insects, depending on their degree of directional hearing

In one study designed to simulate the complex chorus situation in the katydid *Tettigonia viridissima*, Römer and Krusch (2000) investigated the representation of up to three acoustic signals, presented without a fixed temporal relationship, in the responses of a pair of local interneurons (omega cells), while varying the intensity and direction of these signals. The results suggest that the auditory world of the katydid is rather sharply divided into two azimuthal hemispheres, with signals arriving from any direction within one hemisphere being predominantly represented in the discharge of neurons of this side of the auditory pathway (see also for an extreme case of spatial release from masking in Fig. 3.7). Similar results were reported for crickets (Pollack 1986) where the homologous omega neuron did respond selectively to an ipsilateral stimulus when an equally intense stimulus was presented from the opposite side.

3.4.3.2 Do Results of Conventional Masking Experiments Tell us the Truth About Real-World Situations?

Spatial release from masking is usually tested in behavioral and neurophysiological experiments by presenting the signal and masker (the noise) both from the ipsilateral side, examining the masked threshold, and then by moving the masker spatially away from the location of the signal to test the threshold again. If we do this experiment with the rainforest cricket *P. podogrosus* introduced earlier, using the ambient nocturnal noise as masker (at realistic real-world SPLs between 55 and 60 dB), the signal-to-noise-ratio at the masked threshold is between −6 and −9 dB with masker and signal on the same, ipsilateral side, owing to the excellent filter performance (Schmidt et al. 2011; see Fig. 3.5). Shifting the masker to contralateral improves this value on average by further 8 dB, due to the directionality of the system. However, if we then place the same preparation directly in the rainforest with a background noise level between 56 and 58 dB SPL and repeat the threshold measurement, we never measured masked thresholds as high as those measured in the laboratory. Rather, masked thresholds were close to the *unmasked* threshold in the lab (range 32–35 dB SPL; Schmidt and Römer 2011). Thus, under natural conditions where the masking noise acts on the receiver from all directions, the signal-to-noise-ratio at threshold can amount to −23 dB. Such findings are consistent with the warning by Bee and Micheyl (2008) that “an approach using one or a limited number of masking noise sources in highly controlled laboratory studies of spatial unmasking does not wholly reflect the real-world listening conditions that many animals face.” Furthermore, as pointed out by Brumm and Slabberkoorn (2005) in most studies the critical bandwidth of the signal for a perceptually relevant ratio is not known at all, because we only rarely know the filter properties of receivers (either from behavior or from physiological approaches), and in these cases overall SPL measurements of the noise do not tell us very much about the limits of hearing outdoors. Of course, signal-to-noise-ratio measures using “spectrally shaped” noise that has the spectrum of naturalistic acoustic scenes are more useful.

3.4.3.3 No Evidence for Comodulation Masking Release in Insects

Comodulation masking release describes the finding of improved detection of signals in masking noise as a result of coherent patterns of amplitude modulations in the noise across different frequency channels (Klump 1996; Buus 1998). Ronacher and Hoffmann (2003), and Ronacher et al. (2004) discuss in detail their results on signal detection in the grasshopper *Ch. biguttulus* with respect to comodulation masking release. Since the ear of a grasshopper does not provide the basis for much frequency resolution (Römer 1976; Jacobs et al. 1999), and the spectrum of the noise and the signal was rather similar in their experiments, comodulation masking release was not likely to happen in these grasshoppers.

3.4.4 Listening for a Signal in a Short Time Window

As illustrated in Fig. 3.1, the masking problem for a receiver in most communication systems is mainly due to the fact that he does not know exactly, when the signaler(s) produced a signal, so that the afferent activity has to be evaluated continuously for relevant information. If, however, the receiver would know the timing of the signal, noisy events before and after this time could be completely ignored, which would make the task of signal detection/identification much easier. Such a system exists in most phaneropterine katydids, where both sexes produce sound, and pair formation is achieved by duetting (Zhantiev and Dubrovin 1977; Heller and von Helversen 1986; Robinson et al. 1986; Bailey 2003). Here, the male calling song elicits an acoustic reply in the female and the male then responds by phonotaxis. In order to elicit phonotaxis by the male, the time delay of the female response must occur within a rather narrow time window, which is species-specific and matches the species-specific female delay time (Heller and von Helversen 1986; Robinson et al. 1986). In the katydid *Leptophyes punctatissima*, for example, the actual width of the time window for accepting the reply is only 30 ms. Because the female reply is only 0.3 ms in duration and therefore unable to transmit information about species identity via its amplitude modulation, the temporal window could be used by the male as a feature for recognition. However, the extremely short female reply carries the problem that it will induce only a short, unspecific burst in afferent neurons of the male (Kostarakos et al. 2007), which might be confused with bursts of action potentials caused by noisy events in the transmission channel and create false alarms (and thus misdirected phonotaxis) in the male. Can the small time window for listening for females reduce or eliminate such a detrimental effect of noise?

In a neurophysiological study in the insect's habitat we recorded bursts of action potentials in an afferent interneuron in response to female replies and background noise (Ofner and Römer, unpublished). Based on responses of the neuron to the female signal in the undisturbed situation we could determine the amount of hits and false alarms using a given bursting criterion of the cell. With a call rate of the male of 1/3 s, and assuming that the male will listen to an acoustic reply of the female for the next 3 s, we measured an average of 1.5 false alarms over this time. If the male would only listen to the female reply within the species-specific time window of 30 ms, however, the rate of false alarms would be reduced 100 times to 0.015. Thus, temporal windows in these duetting species may not only solve the problem of species recognition with a signal that otherwise offers little chance of identification, but may at the same time reduce the effect of masking noise considerably.

3.4.5 Noise Reduction Due to Automatic Gain Control in the Afferent Auditory Pathway of Receivers

In the natural chorus situation of acoustic insects outlined above, the mechanism of spatial release from masking would be quite helpful to separate signalers on opposite sides of the receiver. However, the distribution of signaling males in populations of crickets and katydids (Thiele and Bailey 1980; Forrest and Green 1991; Arak and Eiriksson 1992) would suggest that the acoustic situation for receivers in such populations may be far more complex, since more than one signaler can broadcast from one auditory side, and the intensity between signalers at the position of the receiver (distances to receiver), and their differences, can vary strongly.

For crickets (Pollack 1988, 2000) and katydids (Römer and Krusch 2000) a neuronal mechanism has been described that can cope with these chorus situations. Although each auditory pathway is selectively listening to, and encodes the temporal pattern of predominantly ipsilateral sounds (see above), each pathway also selects for the most intense of several alternative sounds. The underlying synaptic mechanism, first described for crickets by Pollack (1988), is based on a dual mode of synaptic activity. In addition to a fast excitatory depolarization, a signal also causes an inhibition which can be seen as a hyperpolarization with a slow build-up and decay time. The latter component is most likely a calcium-activated potassium current (Sobel and Tank 1994; Baden and Hedwig 2007). The inhibition prevents suprathreshold depolarization of the membrane in response to softer signals, thus representing a gain control effectively filtering out the less intense of several competing signals. The information transmitted to the brain is thus not confounded in its amplitude modulation (Fig. 3.8).

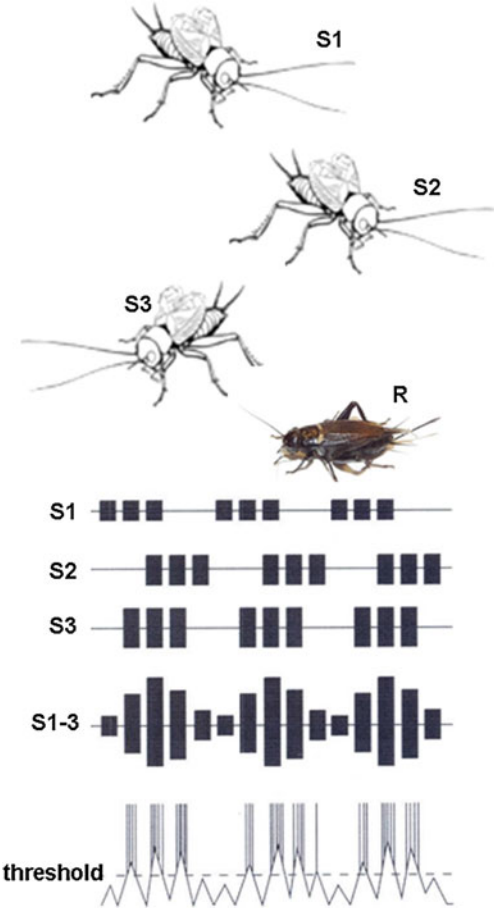

Fig. 3.8 Schematic illustration, of how the gain control mechanism in an auditory neuron can create a selective response to only one signal in a chorus. A female receiver (R) is confronted with calling songs of three males (S1–3) from different distances. The SPL of their signal at the receiver differs due to distance, and a microphone at the receiver's position would record the combined, masked signal S1–3. Due to the long lasting inhibition, the EPSPs elicited by the more distant songs remain subthreshold, and the spike response of the neuron represents the temporal pattern of only one signaler (modified from Pollack 2000)

Both, the strong directionality and the proximate mechanism of gain control in crickets and katydids constitute properties of what Guilford and Dawkins (1991) called the receiver's psychology, and in sensory drive models of sexual selection (Endler and Basolo 1998) such characteristics (most likely their bias type 3 and 4) will bias the direction of evolution by affecting which new courtship signals will be most successful. For example, the properties of the gain control mechanism described above should result in selection acting on males to produce more intense signals because the active range of these signals is greater, and they inhibit the representation of competitive signals if the difference in amplitude is 2–5 dB. Indeed, this view is supported by virtually all studies on acoustic insects (reviews by Ryan and Keddy-Hector 1992; Forrest 1994; Römer 1998).

The second property of the gain control mechanism, i.e., the unusually long time-constant of the membrane hyperpolarization, may have a similarly strong impact for the evolution of acoustic signals and for intra- and heterospecific interactions in these two taxa. Short duration signals, or singing bouts of low duty cycle, would have little or no effect in eliciting the suppression of competitive signals in the receiver. In a population of males competing for phonotactically responding females, long duration signals or singing bouts would therefore be favored over short ones, since only the former would be able to reliably initiate the inhibitory effect. The choice of females for signals with longer duration, such as in female crickets (Hedrick 1986), may thus be explained at the proximate level by passive attraction only (Parker 1983) where females merely move to the male producing a signal that activates its sensory pathway most strongly.

The gain control mechanism could also play an important role for the structuring of mixed species choruses. If the mechanism is common to all crickets and katydids and represents an evolutionary conservative feature in their auditory system, this would result in a disadvantage for species with lower duty cycles/short duration signals: in the case of sympatry with higher duty cycle species the representation of their own song in conspecific receivers would be suppressed, due to the properties of the underlying membrane hyperpolarization. In fact, the behavioral observation in two sympatric pairs of katydid species discussed in Sect. 2.1 (Greenfield 1988; Römer et al. 1989), where noise produced by one species inhibited the calling activity of the other species would represent exactly such cases, because the species with the low duty cycle song was the one being suppressed in both studies. The examination of these and other sensory biases represents an extremely interesting field for future research for the study of acoustic communication, since we can expect that basic properties of the sensory and/or central nervous system will be modified by selection if the disadvantage is too high. The possibility of addressing this issue in insects using comparative studies of single, identified neurons presents many advantages over similar studies in vertebrates.

3.5 Acoustic Predator Detection and Decision Making for Evasive Responses in Noise

It is intuitively clear that the fitness loss of a receiver falsely interpreting the quality in the courtship signals of two males are quite moderate compared to a receiver missing the information about a nearby predator. Natural selection should thus favor appropriate solutions for predator detection and discrimination from noise. In this review I therefore include some information about what is currently known about the effect of noise in an acoustic predator-related detection system, using the now classical bat echolocation—insect prey as an example. Almost any nocturnally active insect on the wings will be under the risk of predation by insectivorous bats. The difficult task of the afferent auditory system of potential prey is therefore to provide reliable information about the presence and vicinity of the predator, so that higher brain centers are enabled to perform a decision regarding the type of behavioral response, as well as the best timing and direction (Altes and Anderson 1980). The task is difficult because the prey has to distinguish the echolocation calls of a bat from high frequency acoustic noise within the environment, from potential acoustic noise generated by its own movements (Waters and Jones 1994; Poulet and Hedwig 2002) and intrinsic noise within its own auditory system (Fullard 1987; Waters 1996). The solution to the task is also quite different in the three major taxa where this problem has been investigated, namely noctuid moth, crickets, and katydids.

For example, the evolution of bat-evasive behavior in crickets and katydids is shaped by different constraints. Cricket ears are most sensitive to the carrier of their calling songs but also to frequencies far into the ultrasonic range up to 100 kHz (review in Pollack 1998), the latter indicating the second major function in cricket audition, namely predator detection and avoidance (Fullard 1998; Hoy 1992). Behaviorally, Wyttenbach et al. (1996) demonstrated categorical perception of frequency, i.e., based on sound frequency crickets discriminate "good = mate" (<15 kHz) from "bad = bat" (>15 kHz). The extremely broad tuning of the HF - channel bears some cost, however, such as the susceptibility to any high-frequency noise produced by other insects, which could elicit unnecessary bat avoidance behavior.

Katydids cannot discriminate conspecific signals from bats simply based on spectral information, because their own calling songs are usually broadband signals with a frequency spectrum that extends far into the ultrasonic range (Heller 1988; Morris et al. 1994), also used by most aerial-hawking bats (Fenton et al. 1998). Thus the only reliable information for discrimination between "good" and "bad" should be based on temporal cues (Schul et al. 2000; but see Schul and Sheridan 2006 and Sect. 2.1).

3.5.1 *External Noise and Predator Detection by the Repetitive Nature of Bat Search Calls*

Katydid receivers face the problem of detecting cues from echolocating bats in the time domain, but afferent spike trains can be very noisy if katydids are active in the nocturnal rainforest (see Fig. 3.1). Hartbauer et al. (2010) recorded AP activity of the omega neuron first in the laboratory when stimulated with sequences of bat calls at different repetition rates typical for the guild of insectivorous bats, in the presence of background noise. The spike activity typical for responses to bat echolocation contrasts with responses to background noise, producing different distributions of inter-spike intervals. These interval distributions allowed the development of a 'neuronal bat detector' algorithm, optimized to detect responses to bats in afferent spike trains. Application of the algorithm to more than 24 h of outdoor recordings of the same cell demonstrated a remarkably reliable detection rate: in 95 % of cases, the algorithm detected a bat reliably, even under high background noise, and correctly rejected responses due to background noise when an electronic bat detector showed no response.

3.5.2 *Internal Noise, Coding Inaccuracy, and Predator Detection*

When a noctuid moth in flight has to make a decision about the presence of an echolocating bat, it has to rely on information from only two sensory cells in each ear, the A1 and A2 cell, the latter being about 20 dB less sensitive (Roeder 1964). Waters (1996) investigated two kinds of noise in the A1 cell for its ability to encode information about a nearby bat: the first was spontaneous discharge, which may produce an incorrect decision that a bat is present. Spontaneous APs are the main problem in distinguishing bat from non-bat at low intensity levels; they occur at a median rate of 7.4 Hz. Depending on the recognition criterion (number of APs within a given time period) the author could calculate that false alarms (i.e., the moth mistakenly identifies a bat as being present on the basis of spontaneous APs) would occur every few seconds. Ecological data based on bat—moth encounters by Roeder and Treat (1962) demonstrate that the selective advantage of reacting over nonreacting moths in encounters with bats is 44 % per encounter, indicating that the costs of a missed detection (the moth mistakenly deciding a bat is not present) are high. Ironically, the high directionality of the moth hearing system (interaural intensity differences of about 20–30 dB; Payne et al. 1966; Madsen and Miller 1987) does prevent an easy solution to the problem: simultaneous APs in A1 cells of both ears would represent a reliable information of a real source, but due to the high directionality of the system this does not happen.

Can the afferent information be processed in a way to increase information transfer to decision-making centers in the brain? Boyan and Fullard (1988) described an interneurone (IN 501) which they suggested represents a “noise filter”, because it shows a 1:1 spiking relationship with the A1 afferent only at very high A1 discharge rates. However, Waters (1996) calculated that with such decision criteria the moth would strongly reduce its sensitivity and maximum detection range. The second kind of intrinsic noise is inaccurate encoding of stimulus intensity due to response variability, in particular to the short duration calls of bats. Altogether, these results led Waters suggest that, for bats using short duration calls, the moth would only be able to recognize an approaching bat from the repetitive nature of the incoming signal. This is consistent with results on katydid receivers and detection of bat-like sound described above.

3.6 Conclusions

Compared with vertebrates, insects explore a wide range of signal carrier frequencies, from below 1 kHz to more than 100 kHz, with strong differences in the amount of excess attenuation, and thus the range of communication. Because many insect species communicate in choruses of both conspecific and heterospecific signalers, the problem of masking interference is severe. Despite the broad range of possible frequency channels insects are often forced into certain frequency ranges due to phylogenetic or biophysical constraints, and clearly suffer from cocktail party-like hearing problems similar to vertebrates. They solve some of the problems by exploiting microhabitats with favorable communication conditions, via the evolution of novel traits in signaling and/or hearing, or via individual plasticity in signaling behavior.

In my review, I emphasized the particular advantage that insects offer compared to vertebrates for an organismic approach to acoustic communication systems, in which behavioral and environmental approaches are combined with neurophysiological approaches on the receiver side under laboratory and field conditions. In this way the role of the often ignored “receiver psychology” for insect signaling and hearing can be examined and placed in the context of the possible selection pressures that may have shaped the character of the signals and the sensory systems necessary for signal detection, discrimination and final decision making. Results achieved with this approach are promising for future research on the sensory ecology of hearing, which is still in its infancy.

Acknowledgments I acknowledge the comments of Mark Bee, Henrik Brumm and an anonymous reviewer, which greatly improved the chapter. My own research on the sensory ecology of acoustic communication in insects was strongly influenced by collaboration with Jürgen Rheinlaender and Win Bailey, who focused my interest on field work and evolutionary aspects of acoustic signaling and hearing. I also thank M. van Staaden, G.K. Morris, I. Dadour, and D. Gwynne for numerous discussions during our field work. Own research for this article was supported by grants from the Austrian Science Foundation FWF, projects P09523-BIO and P20882-B09.

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