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Insect acoustic communication: The role of transmission channel and the sensory system and brain of receivers

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Abstract

1. For decades, acoustic insects have been used as model organisms for behavioural neurobiologists to understand mate choice or predator avoidance, because behaviour can easily and reliably be elicited in the laboratory, and behaviourally relevant, identified nerve cells be studied under these conditions. However, signalling often takes place in complex environments, in which the signal perceived by the receiver may differ greatly from the one broadcast due to the biotic and abiotic properties of the sound transmission channel. Thus, the key challenge is to transfer the insights of these laboratory-oriented experiments to more natural settings.
2. Signal detection, identification and discrimination, as well as localization, are complicated by the transmission channel in several ways. Here, I review the empirical evidence from outdoor studies, demonstrating how excess attenuation reduces the active space and the information of a signal at some distance from the sender. At the same time, these frequency-dependent processes allow to maintain acoustic distances to neighbours in a population.
3. Insects often communicate within choruses of signallers of the same and different species, giving rise to high levels of acoustic masking interference. I discuss the evidence found for temporal or spatial partitioning of species in multispecies assemblages, and I show that solutions to the masking problem are based on a combination of adaptations in the behaviour of signallers and in the sensory system of receivers.
4. Whether or not the perceived signal elicits a behaviour in receivers will depend on the design of the sensory system and the brain. I give examples for active mechanical processes in insect sensory receptors that influence the responses to external stimuli. In addition, neuronal filters in the frequency, intensity or time domain, and even the memory of individual receivers, provide the basis for adaptive receiver decision-making in mate choice scenarios.
5. Finally, I describe the advantages of having access to the relatively simple nervous systems of insects and how this access, combined with the use of a variety of behavioural tests, allows new insights into acoustic communication and its evolution.

KEYWORDS
acoustic insects, background noise, decision-making, mate choice, signal perception, sound localization, transmission of sound

1 | INTRODUCTION

A communication system usually involves four components: (a) the production of a signal by the sender, (b) the transmission of the signal through the environment, (c) the detection of the signal by the sensory system of the receiver and (d) a decision by the receiver about what to do next as a result of the detection and discrimination of this signal from other signals or noise (Endler, 1993). Traditionally, studies of such communication systems have been dominated by the identification of the signal properties that are preferred by receivers and the correlation of these properties with the underlying qualities of the sender (Andersson, 1994). It has been generally assumed that natural or sexual selection has provided individuals with the necessary neuronal machinery to perform a given task sufficiently well. As argued by Rosenthal (2013), "…we continue to be more interested in the train of the peacock than the mind of the peahen." Over the past 30 years, however, an increasing number of scientists have pointed out the benefits of gaining a comprehensive understanding of communication systems by considering the sensory and cognitive mechanisms that underlie important behavioural decisions (Bateson & Healy, 2005; Castellano, 2009; Chittka, 1997; Chittka & Menzel, 1992; Dukas, 1998; Endler, 1993; Guilford & Dawkins, 1991; Miller & Bee, 2012; Nityananda, 2016; Ryan, Akre, & Kirkpatrick, 2007; Wehner, 1987).

Except with respect to acoustic communication systems that work at close range where the properties of the transmission channel can be ignored (such as cases in which signals use near-field sound and the corresponding particle velocity receivers), the signal produced by the sender is usually not the one perceived by receivers. A potentially informative character such as the specific amplitude modulation of a sound signal may be degraded by reflection or echoes from structures. Frequency-dependent attenuation may result in strong filtering of a spectrally complex signal over a distance, so that frequency components that contain important information about the quality or distance of a sender are not available to receivers (Römer, 1998). These conditions suggest that a signal that functions efficiently in one environment may not be ideal in another. Therefore, populations inhabiting different habitats may diverge in terms of the most important properties of their mating signals (see Endler, 1992 for visual signals). For this reason, I place a focus on the properties of the transmission channel with respect to the evolution of acoustic signals or insect signalling behaviour in this review. I additionally highlight some recent advances in our understanding of the "receiver psychology" (Guilford & Dawkins, 1991), with a particular emphasis on sensory and brain mechanisms that solve problems associated with the acoustic ecology of insects.

2 | THE TRANSMISSION CHANNEL FOR THE SIGNAL

In most ecological situations, a sound signal must be detected, identified as conspecific, discriminated from those of other conspecifics and localized. These processes take place either when the insect interacts with a predator or conspecific mates or rivals. The transmission channel for sound complicates these tasks in several ways. Three seminal papers by Morton (1975) and Wiley and Richards (1978, 1982) represented a framework of empirical and theoretical studies on the importance of the transmission channel for acoustic communication. These studies on the birdsong system also stimulated similar ecological studies on insect sound communication, given that acoustically communicating insects face problems such as the frequency-dependent sound transmission and signal degradation, as does any other terrestrial animal that uses a sound communication system (Bradbury & Vehrencamp, 2011; Dusenbery, 1992; Gerhardt & Huber, 2002).

3 | SIGNAL ATTENUATION AND ACTIVE SPACE

When a sound wave propagates away from a source, its pressure inevitably decreases with increasing distance as a result of the geometry of the air space occupied by the sound energy. Such geometric spreading causes a 6-dB decrease for each doubling of distance (6 dB/dd). In most environments, however, acoustic signals suffer from attenuation in excess of geometric spreading due to the effects of absorption, scattering by vegetation and turbulence, or sound interference encountered in stratified environments (see Römer, 1998 for a review of these effects on insect sound communication). Most of these effects are strongly frequency-dependent, increasing in the high sonic or ultrasonic frequency ranges. Since the calling song spectra of insects often include such high frequencies (Greenfield, 2014; Montealegre-Z, Morris, & Mason, 2006), attenuation in excess to geometric spreading is a general rule rather than an exception. For katydids living in dense vegetation, excess attenuation of 30 dB due to scattering has been measured over a distance of only 10 m for a carrier of 40 kHz, compared to <6 dB for a carrier of 5 kHz (Römer & Lewald, 1992). Thus, the transmission channel essentially acts as a low-pass filter. Strong excess attenuation reduces the active space of the signal (Brenowitz, 1982), defined as the area within which the signal amplitude is above the detection threshold of potential receivers. Selection would act on the signaller, favouring individuals that can reach as many intended receivers as possible, by choosing calling sites with less excess attenuation. Crickets and katydids can strongly increase the active space of their signals by calling from elevated positions (Arak & Eiriksson, 1992; Paul & Walker, 1979; Römer & Bailey, 1986; but see Sueur & Aubin, 2003 for two species of cicadas). In habitats with strong vertical stratification such as tropical rainforests, the foliage density (and, thus, the effects of frequency-dependent attenuation and signal distortion in the time domain) differs between the layers. However, Diwakar & Balakrishnan (2007) and Jain and Balakrishnan (2012) did not find support for the hypothesis that the observed vertical stratification of calling insect species represents an acoustic adaptation to the habitat acoustics. We should keep in mind that factors other than optimal signal transmission may influence where acoustic insects live and communicate in particular microhabitats (protection from predators, finding food, etc.).

Signal degradation in the time domain due to reverberations and amplitude fluctuations induced by wind or atmospheric turbulence (Wiley & Richards, 1978) may have important consequences for insects, because information about species identity or the attractiveness of males is primarily encoded in the temporal structure of the signal (Hennig, 2009; von Helversen & von Helversen, 1998). Thus, when reverberations and amplitude fluctuations are superimposed on the amplitude-modulated insect signals, receivers face increased difficulties to identify the signal. Weather conditions, time of day or the size of objects in the channel can produce echoes, influencing such changes in the time domain (Richards & Wiley, 1980). One outdoor study on the neuronal coding of pulse patterns in a katydid (Römer & Lewald, 1992) found that signal degradation increased with distance, and the effects observed were much larger with pure tones compared to broadband signals. Nevertheless, the overall temporal pattern of the conspecific signal was well-preserved over distances of up to 30 m in the afferent neuronal activity, depending on the height of the receiver. In addition to distortions in the time domain, frequency-dependent excess attenuation may cause substantial variability in the attractiveness of male signals for a receiver, if the transmission channel differs in terms of vegetation density and structure for different males (for effects of frequency-dependent excess attenuation on sound localization, see below).

Apart from these detrimental effects for acoustic communication, the ranging hypothesis states that frequency-dependent excess attenuation (or degradation of acoustic signals in the time domain) can be used as sensory cues to estimate the distance to a signaller (Naguib & Wiley 2001). For a katydid with two song modes at high sonic and ultrasonic frequencies, it was shown that it could use differential spectral attenuation to space themselves with conspecific rivals (Morris, Hall, & Römer, 2018). Each of these two song modes is differently affected by excess attenuation in the field, and the reported mean inter-male distances roughly approximated the distance at which the switch in the amplitudes of both modes occurred.

The acoustic adaptation hypothesis (Morton, 1975) suggests that the signal design evolved in such a way as to reduce the detrimental effects of the specific habitats in which a species communicates. Whereas some evidence for this hypothesis in vertebrates has been presented (Ey & Fischer, 2009), only one rigorous test has been conducted in acoustic insects. Couldridge and van Staaden (2004) compared the transmission of calls of seven species of bladder grasshoppers in four habitats. Their results provided mixed evidence for the acoustic adaptation hypothesis: the calling songs of species that communicated in two of the investigated habitats were less attenuated and distorted in the time domain in their native habitats, whereas the signals of the other species could be transmitted even more effectively in non-native habitats. Jain and Balakrishnan (2012) also found no evidence that vertical stratification in a rainforest is driven by acoustic adaptation.

We may, however, not find many cases for two reasons: (a) the combined effects of selection pressures other than those for optimal signal transmission could be much stronger, resulting in a choice of a habitat that is not optimized for signal transmission, and (b) the signalling behaviour, such as the selection of calling sites and/or times, appears to be flexible enough to compensate for the potential detrimental effects of the transmission channel.

4 | BACKGROUND NOISE AND MASKING IS A CHARACTERISTIC OF THE TRANSMISSION CHANNEL

In addition to the abiotic constraints imposed by the transmission channel for sound, insects often communicate within choruses of signallers of the same and different species, which gives rise to high levels of acoustic masking interference. In a nocturnal neotropical rainforest, for example, the background noise level produced by crickets and katydids can reach an average 65–70 dB sound pressure level (SPL). The background noise due to insect signalling is strong enough to interfere even with vocalizations of birds during their dawn chorus (Stanley, Walter, Venkatraman, & Wilkinson, 2016).

We can refer to the ecological niche concept (Pianka, 1973; Schoener, 1974) when studying strategies that deal with masking interference, since the transmission channel for sound signals can be regarded as an ecological resource. With an increasing number of species, the probability of masking interference increases, as do problems related to signal detection and discrimination. In terms of behavioural adaptations, insects that could partition signalling in time and/or space could avoid (or reduce) the masking problem. Different to the situation with resource partitioning of sonar frequency bands in bats (Heller & von Helversen, 1989) in communities with many species of insects, little evidence has been found for temporal or spatial partitioning (reviews in Balakrishnan, 2016; Römer, 2014; Schmidt & Balakrishnan, 2015). Although cicada species are largely diurnal and thus temporally separated from most other singing members of Orthoptera, a study conducted on a cicada community revealed extensive overlaps in calling activity at dawn and dusk (Sueur, 2002). However, evidence for both temporal and spatial displacement due to song interference between two species of katydids has been found in the field (Greenfield, 1988; Römer, Bailey, & Dadour, 1989), and temporal separation of calling time within a dusk community of a tropical rainforest was reported for cicadas by Gogala and Riede (1995).

Signallers of different species could avoid acoustic interference by spacing themselves apart from individuals of other species, just as individual signallers space themselves out within a population of conspecifics. For two rainforest communities of Orthoptera in Panama and India, no support for spatial partitioning at the community level has been found (Jain, Diwakar, Bahuleyan, Deb, & Balakrishnan, 2014; Schmidt, Römer, & Riede, 2013). Furthermore, although the vertical stratification of signallers has been examined in both studies, it is still unclear whether it reduces acoustic interference.

Acoustic insects use an enormously broad range of carrier frequencies in their calling songs so that, theoretically, partitioning in the spectral domain of sound would be possible. Some insect taxa (grasshoppers, most katydids and cicadas) do not have this option since the bandwidths of their calling songs are usually rather broad, covering tens of kilohertz, which results in varying amounts of spectral overlap. In contrast, crickets use almost pure-tone calling songs with bandwidths that fall within the relative narrow frequency range of 2–10 kHz. If different species would use a distinct frequency within this range, they could separate their signals in the frequency domain. After Riede (1993) provided some support for the frequency partitioning hypothesis, three more quantitative approaches were taken with assemblages of acoustic insects in the tropical rainforests of Barro Colorado Island (Panama; Schmidt et al., 2013), Kudremukh National Park (India; Jain et al., 2014) and Borneo (Grant, 2014). Very little overlap within the cricket, or cricket and katydid, assemblages was found. The spectral overlap of the cricket assemblage was significantly smaller than would be expected by chance when compared to a null model (Schmidt et al., 2013).

However, the consideration of the acoustic niche concept is largely incomplete unless the receivers´ sensory systems are considered. If the carrier frequency of the signal matched the frequency of best auditory sensitivity of the receiver, the signal-to-noise ratio for perception would improve (the matched filter hypothesis; Capranica & Moffat, 1983; Wehner, 1987). In addition, since receivers that have more sharply tuned filters can more effectively reduce non-relevant, noisy information, species that must communicate under conditions of high levels of background noise would be expected to exhibit more selective frequency tuning. This hypothesis was supported in a study in which a nocturnal tropical rainforest cricket was compared with two temperate species that communicate under much less noisy conditions. The authors demonstrated that the rainforest cricket exhibited increased sharpness of the tuning and increased signal-to-noise ratios by 10–16 dB for signal perception (Schmidt, Riede, & Römer, 2011).

The "Lombard effect" (Lombard, 1911) describes a voluntary increase in the amplitude of the signal under noise, which would be one of the most obvious mechanisms to overcome masking noise problems. Although the effect is well documented in birds and mammals, there is no empirical evidence showing that insects regulate the SPL of their signal depending on the amount of background noise. However, selection has favoured the use of resonators, amplifying burrows and baffles to achieve an increased sound output (review in Römer, 1998), and a recent study demonstrates that a cricket species can even enhance the amplitude of its calls by using novel, anthropogenic environments as singing sites (Erregger & Schmidt, 2018).

The advantage of an increased active space for attracting mates is obvious, but the same signal may also attract "unintended receivers" such as predators, parasitoids or male rivals. For example, neotropical rainforest katydids in Panama often produce short duration calls at an exceptionally low rate (Symes, Page, & ter Hofstede, 2016), so that it is currently unknown how the intended (female) receivers are able to detect the conspecific signal in the nocturnal background noise. Belwood and Morris (1987) suggested such calls are an evolutionary adaptation to the selection pressure by bats passively listening to their prey calls. A low-redundant call would be more difficult for the bat to detect or locate their prey. Another group of unintended receivers for acoustic insects are parasitoid flies. To find their host to deposit eggs or larvae, female flies localize calling males and have evolved a very sensitive ear only for this purpose (Lakes-Harlan & Lehmann, 2015). In a comparison between two host katydid species differing in their number of acoustic pulses, the species with the higher number was parasitized at higher levels (Lehmann & Heller, 1998). This indicates a strong trade-off between the advantage of mate attraction and the likelihood of parasitization.

5 | EFFECTS OF THE TRANSMISSION CHANNEL FOR SOUND LOCALIZATION

Receivers need to be able to detect a signal, identify the signal as conspecific, discriminate it from other conspecifics and localize the signal in order to move either towards or away from the sound source. Under precisely controlled laboratory conditions and using different devices to quantify the accuracy of localization, an acuity of localization with a spatial resolution of 1–2° has been documented (parasitoid flies: Mason, Oshinsky, & Hoy, 2001; field crickets: Schöneich & Hedwig, 2010). The available interaural intensity and time differences are as small as 0.5–1 dB and 0.5–1 ms, respectively. Ultimately, however, it has yet to be demonstrated how such excellent spatial acuity works under natural field conditions, because it is not clear how well the relevant binaural cues are preserved for a receiver after signal transmission outdoors. Two reasons may account for a reduction in directional cue outdoors. First, the sound field around the receiver may have a reduced directionality due to the effects of multiple reflections and scattering within vegetation. Second, for insect ears that rely on the diffraction mechanism of sound around their body to establish interaural intensity differences, these differences are higher at high carrier frequencies. However, these frequencies are also more likely to be filtered by the surrounding vegetation (see above). A neurophysiological study conducted in a natural habitat with a katydid indeed showed that the directional cues in a sound signal can be completely lost at certain positions in vegetation, although the insect could still hear the signal (Rheinlaender & Römer, 1986). A similar result was found in an outdoor study on field crickets, where males broadcast their song parallel to the ground (Kostarakos & Römer, 2010). For small grasshoppers, it was shown that binaural directional cues are strongly affected by the presence of dense vegetation but not gravel or sparse vegetation (Gilbert & Elsner, 2000). Altogether, such outdoor studies reveal that directionality is not only an inherent property of the auditory system, but is also dependent on the transmission channel for sound.

Given these distorted directional cues, how can the phonotactic behaviour of insects cope with these conditions? Only three studies have quantified phonotactic tracks of acoustic insects towards a sound source in no-choice or choice trials outdoors, two for field crickets (Hirtenlehner & Römer, 2014; Mhatre & Balakrishnan, 2008) and one for a parasitoid fly approaching the target in flight (Tron & Lakes-Harlan, 2017). The significant findings were as follows: in no-choice trials, all female crickets approached the target, but the distance covered was significantly larger compared to similar laboratory trials. In two-choice trials or more complex stimulus settings, the difference in loudness necessary for a preference was 5 or 6 dB in both studies, again significantly higher than in arena trials (3 dB) or on trackball systems (1–2 dB). Thus, it appears that variation in the signal imposed by the properties of the transmission channel reduced the ability of the receivers to reliably assess variation among signallers, and larger signal differences are necessary for mate choice decisions based on these differences.

6 | THE RECEIVER PSYCHOLOGY

6.1 | A brain-based viewpoint of acoustic communication

The central nervous system of the receiver is at the mercy of the sensory system that provides access to information from the outside world, and this information is only available in the spike trains of afferent neurons. The problem faced by the receiver's brain is illustrated in Figure 1, which shows the action potential activity of an interneuron in the afferent auditory pathway of a katydid recorded in the nocturnal rainforest (H. Römer, unpublished result). Whereas the bat detector placed next to the insect preparation provided the researcher with the information that the repetitive bursting pattern of the neuron was in response to echolocation calls of a bat passing by (upper panel in Figure 1), this information was not available for the insect brain. Moreover, the insect's brain also needs to interpret the remaining bursting activity of the cell in order to decide which bursts were due to a conspecific signal (asterisk) and which were due to predators or background noise. Taking a strictly brain-based point of view and using such recordings under the habitat conditions where insects communicate (Rheinlaender & Römer, 1986), we can examine the information that is represented in the spike trains of afferent neurons. Such a method is particularly informative when working with insects, since interneurons can be studied in this way, which are behaviourally relevant, such as the AN1 of crickets for positive phonotaxis (Schildberger & Hörner, 1988) or AN2 for bat avoidance in flight (Nolen & Hoy, 1984). For example, Hartbauer, Radspieler, and Römer (2010) reported the reliable detection of predator cues (bat echolocation pulses) in insect spike trains despite the presence of high levels of background noise. Stimulus reconstruction is another method that allows researchers to estimate the informational content of spike trains and analyse what kind of information about parameters in the stimulus is lost (Rieke, Warland, de Ruyter van Steveninck, & Bialek, 1997).

6.2 | Nonlinear, active processes in auditory receptors

The first step in signal perception is the transduction process of the sound stimulus in auditory receptors. Insect ears show a tremendous amount of diversity in terms of their location and the external anatomy of the sound-receiving structures (Göpfert & Robert, 2008; Hoy & Robert, 1996; Yager, 1999), whereas their cellular make-up is rather uniform and consists of single or grouped chordotonal sensilla (Field & Matheson, 1998; Yack, 2004). How these ears are tuned to receive stimuli of biological relevance has long since been explained through analyses of the structural biomechanics of the sound receivers. However, research conducted on locusts, crickets, moths, mosquitoes and fruit flies over the past 20 years has supported the existence, and allowed the description, of active mechanical processes in insect ears that influence the responses to external stimuli (reviews in Göpfert & Robert, 2008, Mhatre, 2014). In the ear of a moth, which has only two sensory cells, Windmill, Jackson, Tuck, and Robert (2006) found a strong degree of nonlinearity and a shift of the resonant frequency in the vibrational response of the moth's tympanum that correlated with stimulus intensity: at low SPL, the

FIGURE 1 Action potential activity of an auditory interneuron of a katydid (lower panel) recorded in the nocturnal rainforest, and a bat detector (upper panel) placed next to the preparation. The asterisk indicated a burst of APs in response to a conspecific sound pulse, and the arrows mark a response to a bat echolocation not seen in the bat detector

resonance was at 42 kHz, whereas at higher SPL, the peak shifted to 74 kHz. This active shift guarantees that the ears are not insensitive to the higher frequency of the echolocation calls shortly before prey capture. The tuning also shows hysteresis because, at 87 dB SPL, the up-tuning occurred within 750 ms, but the return to the low-frequency state took up to several minutes. Again, this property is highly adaptive because the ear remains up-tuned to detect the possible return of the bat.

Johnston's organ in the pedicellus of the antennae of fruit flies receives the near-field sound produced by the male during courtship (Göpfert & Robert, 2001). This receiver also demonstrates a strong degree of nonlinearity and frequency-specific amplification. The mechanical response of the antenna in dead animals is tuned to around 800 Hz and, in live animals, to high stimulus intensities. However, with decreasing intensity, the tuning is shifted towards 200 Hz and the sensitivity of the resonance increases (Göpfert & Robert, 2002). This shift matches the receiver's best frequency with that of the carrier frequency of the courtship song pulses (Riabinia, Dai, Duke, & Albert, 2011).

The situation is even more complicated because, for instance, the antennae in *Drosophila* play roles both as receivers during acoustic communication and as sensors for flight control (Budick, Reiser, & Dickinson, 2007). The wing beat frequencies during tethered flight for seven members of the *Drosophila melanogaster* species group were close to the range of the carrier frequency of the sine songs during courtship (Riabinia et al., 2011). However, the displacement amplitudes of the antenna during flight were several orders of magnitude higher than those that resulted in mechanical feedback amplification. As a result, high displacement gains of about eight were found for deflections <300 nm, in contrast to a gain of only one for deflections >10 μm, so that these deflections drive the antenna into the passive regime during flight, which is tuned at about 800 Hz. Thus, the mechanical feedback amplification and its level dependency enable the insect to detect the subtle stimuli to which the antennae are exposed during courtship, whereas the much larger stimuli received during the insect's own flight are rendered negligible. The presence of active amplification and adaptive tuning has also been demonstrated in the tympanal ear of a tree cricket (Mhatre & Robert 2013), enabling high auditory sensitivity and tuning to conspecific songs. Altogether, these findings on active processes in acoustic receivers are remarkable since they demonstrate that the most peripheral filter in an auditory system is variable and strongly dependent on the active state of sensory cells.

6.3 | Salience filters and attention-like processes

The perceptual tasks faced by animals when they communicate in large aggregations are rather similar to the difficulties faced by humans when they attempt to understand speech in noisy social settings (Cherry, 1953; reviewed in Bee & Micheyl, 2008). In these large and noisy groups, the detection, identification and discrimination of sound signals are common problems. Even without considering signallers of other species and their contributions to background noise (see above), field measurements in katydid populations have revealed that receivers might have to discriminate among the individual calls of more than ten conspecific males within hearing range, some of which are quite similar in amplitude (Römer & Krusch, 2000). The auditory system, thus, needs to segregate many irrelevant sound sources from a few biologically important ones (i.e. signals from conspecifics and sound cues from predators). Humans and other primates have evolved the ability to reduce the vast amount of information present in the various stimuli and only pay attention to the ones of interest (Knudsen, 2007). In an attempt to compare this ability in primates with attention-like processes in insects, Nityananda (2016; see also Skorupski, Spaethe, & Chittka, 2006) argued that both salience filters and selective attentional processes have been documented in insects that enable them to select one stimulus or a subset of stimuli and segregate them from several other non-relevant stimuli. Selective attention could be defined as a process that specifically leads to a preference for certain stimuli over others that are, nonetheless, perceived equally well when presented alone.

Neural tuning of auditory receptors and interneurons represents a classical way in which the receiver can become biased towards a subset of signals. Not surprisingly, most auditory receptors in the ears of cricket receivers are tuned to the carrier frequency of the male song. However, a subset of receptors is sensitive to frequencies of up to 100 kHz (Imaizumi & Pollack, 1999), indicating that predator detection and avoidance is a second major function of cricket audition (Fullard, 1998; Hoy, 1992; Moiseff, Pollack, & Hoy, 1978). In tethered flight, crickets demonstrate categorical perception abilities by turning towards stimuli with lower frequencies and away from those with high sonic and ultrasonic frequencies. A sharp border exists in between at about 15 kHz (Wyttenbach, May, & Hoy, 1996). In this way, the insect can sort the huge range of frequencies to which its ear is sensitive into just two categories of sound that are important for reproduction and survival, namely “cricket-like” and “bat-like.” At the neuronal level, Schul and Sheridan (2006) described the properties of an auditory interneuron (TN1) that segregates bat-like calls from cricket-like calls based on frequency.

In the chorus situation outlined above, a male or female receiver can reduce the number of irrelevant signals by using more selective filters, but what if these signals are of potential interest (e.g. from different males) but the receiver can only respond to one of them? In this case, the possession of selective attention mechanisms would enable the representation of relevant signals in the receiver in a competitive situation with irrelevant signals, although they would also be easily perceived when presented alone. Evidence from both behavioural (Greenfield & Snedden, 2003; Nityananda, Stradner, Balakrishnan, & Römer, 2007; Snedden, Greenfield, & Jang, 1998) and neurophysiological studies (Pollack, 1988; Römer & Krusch, 2000) has indicated that such selective attention mechanisms are at work in a chorus situation. A low-intensity signal at a 45-dB sound pressure level quite effectively influences the activity of individual interneurons of crickets and katydids when presented alone, but this activity is completely suppressed when it is received simultaneously with another signal at 60 dB SPL. The differences in intensity between the signals that compete for representation in receivers can be quite small (in the order of 2–5 dB), and the differences in the duration of signals are also relevant in that signals with lower duration are filtered out in favour of those of with higher duration (Römer & Krusch, 2000). Crickets and katydids make use of a low-level gain-dependent mechanism that enables them to restrict their behavioural responses to specific signals of interest while simultaneously ignoring other perceivable alternatives. Notably, the mechanism was described in first-order interneurons of the auditory pathway, without involving brain circuits. Nityananda (2016) suggested that insect sensory systems evolved such simple solutions in response to tasks and environments that required selective attention, irrespective of the sensory modality involved.

6.4 | Receiver psychology and sensory biases

The sensory bias model of sexual selection suggests that a bias in the sensory and central nervous system of receivers may predispose them to prefer certain signals over others in various fitness-relevant contexts (Endler & Basolo, 1998; Ryan & Keddy-Hector, 1992). A striking case of sensory bias was described in moths by Nakano, Takanashi, Skals, Surlykke, and Ishikawa (2010). Moths evolved ears in response to the strong selection pressure of insectivorous bats in order to detect bat echolocation calls and organize adaptive escape behaviours (Greenfield, 2014; Roeder, 1962). Being equipped with ears, some moths subsequently evolved intraspecific acoustic communication and/or defensive responses against predators (Conner, 1999; Greenfield, 2014). In several species of noctuid and pyraloid moths, the males produce a very soft call during courtship which the female is unable to distinguish from a generic bat echolocation signal (Nakano, Takanashi, Skals, Surlykke, & Ishikawa, 2008). Moths freeze in response to echolocation calls of bats, which is an adaptive behavioural response that increases the likelihood of their survival (Greenfield & Weber, 2000; Roeder, 1962). However, the quiet calls of male moths elicit the same freezing response in the female as the bat calls (Nakano et al., 2008), with the result that the female may remain in a receptive posture for a longer duration, increasing the likelihood that the male can approach and mate with her. This is consistent with the idea that the male signal in the studied moth evolved via a sensory bias mechanism, exploiting a female response that originally evolved in a nonsexual context.

Ter Hofstede, Schöneich, Robillard, and Hedwig (2015) also describe a case of sensory exploitation of an aversive cue, albeit one that can evolve into a classic communication system with benefits for both senders and receivers. In one group of crickets (Eneopterinae: Lebinthini), Robillard, Grandcolas, and Desutter-Grandcolas (2007) found that males produce calling songs with unusually high carrier frequencies that overlapped with the lower range of bat echolocation calls. This was surprising for a mate attraction signal given that such high frequencies had been shown to elicit avoidance behaviour in all other described crickets (Wyttenbach et al., 1996). Female lebinthines do not perform phonotaxis towards the high-frequency male call but instead produce vibrational responses, which the male then uses to track the female. Field cricket species closely related to the Lebinthini produce an acoustic startle response to high-frequency sounds that generates substrate vibrations similar to those produced by female lebinthine crickets. The authors concluded that the startle response could have served as the evolutionary basis for the female lebinthine vibrational signal. In contrast to the moth example presented above, male lebinthine crickets also seemed to have exploited a pre-existing bias (the startle response) in the female but, in their case, was adapted into a new communication signal.

6.5 | Cognitive rules for decision-making

One of the main functions of acoustic communication in insects is to find and select mates. Consider, for example, a cricket or katydid female in a chorus of several males that are advertising their quality to female receivers. Leaving aside the problem that mate choice is often multimodal (Candolin, 2003; Higham & Hebets, 2013), acoustic signals of males differ in a number of attributes such as the temporal pattern, intensity, duration or spectral content. Females have the ability to perceive these cues, discriminate between signals and localize individual males (Hedwig & Pollack, 2008; Hildebrandt, Benda, & Hennig, 2015; Ronacher, 2016). How do they use this information to make their final mating decisions? What are the decision heuristics? How well-adapted are they to the demands of communication in the natural settings?

Decision-making is no easy task because the signals can provide information about different underlying qualities, and the choice is made more complicated by the fact that the signalled qualities may not necessarily be positively correlated: an attractive song pattern may be perceived at a low intensity, indicating that a long distance must be covered to reach the signaller, as compared to a less attractive song of another male close-by. Thus, females must weigh the conflicting attributes of the males. Bateson and Healy (2005) suggested that trade-offs between the efficiency of the decision-making and the accuracy of resulting choices are likely to have resulted in the evolution of receiver mechanisms that are based on a comparison of the available alternative signals, rather than absolute standards. To differentiate between absolute and relative decision-making rules, they proposed the inclusion of rigorous tests for rationale decision-making which are known from human studies, such as tests for transitivity and independence from irrelevant alternatives. Transitivity is a property that applies to a series of binary choices. Independence from irrelevant alternatives implies that the preference between two options should be independent of the presence of additional, inferior alternatives. Violations of both transitivity and independence from irrelevant alternatives are regarded as strong evidence for the existence of comparative, rather than absolute, choice mechanisms (Tversky & Simonson, 1993).

Tests conducted on field crickets have shown strong evidence for comparative decision-making. In one study, Gabel, Vural, Mariot, and Hennig (2016) systematically varied the pattern attractiveness and intensity of two competing signals in a choice situation. To examine the relative contribution of both cues to the female's choice, an equivalence function for both was derived that indicated at which levels both cues compensated for one another. The psychometric data and equivalence function revealed a strong impact of even small intensity differences for patterns of high attractiveness, whereas large intensity differences for patterns with low attractiveness were required to influence female decisions. Thus, the integration of both cues is facilitated by a gain control mechanism that reflects the nonlinear weighting of intensity differences by pattern attractiveness. Under natural field conditions where the female is confronted with several calling songs that differ in attractiveness and intensity, this processing scheme would result in a preference for a softer (more distant), but more attractive pattern due to the gain control mechanism. However, when the attractive signal is too far away (i.e. intensity differences are greater than 12 dB in favour of the less attractive signal), the trade-off would result in a choice of the less attractive signal. Rather than the result of complex cognitive mechanisms, such decisions may probably also be explained by physiological properties of sound processing in the auditory pathway (Mhatre & Balakrishnan, 2008). These authors tested field cricket acoustic orientation in complex acoustic conditions in the field and successfully predicted female orientation using a simulation model based on auditory physiology.

Hirtenlehner (2014) tested the assumption of independence from irrelevant alternatives in arena trials using female field crickets. When presented with a choice between two equally attractive calling song patterns that differed by 3 dB in intensity, females showed a significant preference for the louder signal. However, when a third signal, which was also 3 dB quieter than the attractive signal, was broadcast from the direction of the other less attractive signal, the significant preference for the more intense signal disappeared. This is referred to as a violation of regularity, and it is regarded as strong evidence for the existence of comparative evaluation mechanisms (Tversky & Simonson, 1993). It suggests that male crickets could maximize their success in mate attraction by using two different signalling strategies. On the one hand, they could modify the dynamic properties of their acoustic signals to produce, for example, songs at higher chirp rates, which has, however, higher costs due to the higher energy investment. A more intriguing prediction based on the comparative mate evaluation mechanism is that males could manipulate their attractiveness simply by signalling next to a competitor that produced an inferior calling song. This is a testable hypothesis that could be studied in the future either by analysing neighbouring males in a population or by examining the singing positions chosen by male crickets (i.e. next to males that produce inferior or superior calling songs).

The calling songs of male grasshopper *Chorthippus biguttulus* consist of repeated syllables separated by pauses. The whole sequence of amplitude modulation is species-specific and may last for about 3 s. Clemens, Krämer, and Ronacher (2014) used mixed sequences of song subunits with either attractive, species-specific features or non-attractive subunits and determined how females integrated this information over the duration of the song. They found that information of attractive and non-attractive song features was weighted asymmetrically: females weighted information associated with non-attractive features strongly, whereas attractive features added little to the decision-making process. Accordingly, non-attractive song features effectively vetoed female decisions. The authors argued that asymmetrical weighting of negative and positive information may reflect the fitness costs associated with mating with a non-attractive over an attractive singer, which are also highly asymmetrical.

6.6 | Memory and social experience can alter receiver psychology

An additional consequence of the comparative evaluation of male signals by females is the variation in the outcome of the choice with respect to the sensory or social context. In a chorus of males, the acoustic microenvironment in which each female receives signals—in terms of both space and time—differs from that of other females.

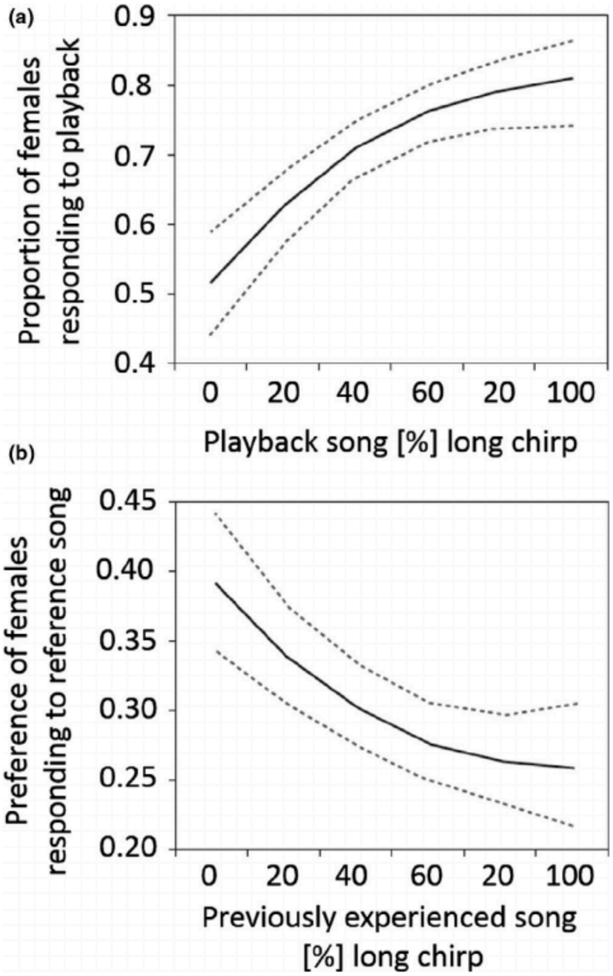

FIGURE 2 (a) Preference function of female cricket *Teleogryllus oceanicus* for song models differing in the proportion of long chirps. (b) The female's preference to a reference song playback (mean of the male population) depends on the attractiveness of the song she heard previously. Dashed lines represent 1 standard error. Redrawn from Bailey and Zuk (2009)

As argued by Bateson and Healy (2005), this could be a solution to the lek paradox, since the variation in the chosen males could be maintained as a result of the varying social/sensory conditions under which female receivers must operate, rather than a result of errors in female choice (Neff, 2000).

Nevertheless, in addition to the variation in the *actual* differences in perceived male signals for each female in a chorus of males, females will also differ in terms of the acoustic information they *remember* (i.e. they have received prior to making their choice). Bailey and Zuk (2009) tested the influence of such a social experience by exposing female crickets for 5 min to male song models that differed in attractiveness. After an intervening period of 30 s of silence, they exposed females to a standard male song that represented the mean of the male population. The preference behaviour of these females was then compared with that of naive females (i.e. without prior acoustic experience). The preference of the latter was open-ended (Figure 2a); these naïve females favoured more attractive male songs, whereas the short acoustic experience prior to the test dramatically reversed the other females' preferences (Figure 2b). Females that had been exposed to highly attractive song models displayed lower levels of attraction to the reference playback, and females that were exposed to less attractive songs showed greater relative levels of attraction to the reference playback.

These results demonstrated that females not only compared the ongoing sensory information received from several alternative signals and used these in comparative decision-making, but also remembered signals that they had previously received and compared that information with currently received signals to make final mating decisions. The results of these experiments demonstrate the extremely high flexibility displayed by female insects while making mate choice decisions. These findings, taken together with those of Hebets (2003), who reported that even pre-adult experiences could influence female mating preferences and ultimately the evolution of male traits in arthropods, clearly indicate that the influence of learning and memory on adult mate choice in acoustic insects could be an important avenue of future research.

7 | CONCLUSIONS

For decades, crickets and some other acoustic insects have been used as model organisms for behavioural neurobiologists to understand mate choice or predator avoidance, for two reasons: behaviour can easily and reliably be elicited in the laboratory, and behaviourally relevant, identified nerve cells be studied under these conditions. However, the natural habitat in which insects communicate can have significant effects on their signals and acoustic behaviour, since the physical structure of the environment may modify the signal, and the presence of predators or rivals as unintended receivers may result in trade-offs concerning the attractiveness of a signal. Clearly more outdoor studies are needed, in particular for insects with larger active spaces of the signal, since the detrimental effects of the transmission channel will accumulate over distance. Although this poses some methodological problems when recording the movement of insects and conducting the analyses, studying phonotaxis in vegetation with a more complex structure would allow researchers to understand how a receiver can compensate behaviourally for the complete loss of a signal or the directional information at some locations. Combining this with approaches that take into account the sensory framework in the brain of receivers, effects of attention and short- or long-term memory on decision-making will complete our understanding of fitness-relevant behaviours under natural settings.

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All data used in this manuscript have already been published or archived elsewhere.

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