Animal Behaviour 103 (2015) 125–135

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Effects of noise on sound localization in male grasshoppers, *Chorthippus biguttulus*

Michael S. Reichert[*]

Insitut für Biologie, Abteilung Verhaltensphysiologie, Humboldt University, Berlin, Germany

ARTICLE INFO

Article history:
Received 14 December 2014
Initial acceptance 15 January 2015
Final acceptance 16 February 2015
Published online
MS. number: 14-01016R

Keywords:
lateralization
noise
Orthoptera
phonotaxis
sound localization

The localization of acoustic signals is an important component of mating behaviour in many species. However, in natural environments sound localization may be hindered by background noise that masks acoustic cues that enable the determination of sound direction by the auditory system. I studied the effects of noise on the sound localization abilities of male grasshoppers, *Chorthippus biguttulus*, in response to female songs. Males respond to female songs with a stereotyped lateralization behaviour in which they turn towards the perceived sound direction; repetition of this behaviour allows them to approach females. Under quiet conditions, males are highly sensitive to small differences in the timing or amplitude of signals that arrive at each ear. I tested whether noise affected male lateralization accuracy by presenting males with female songs that differed in time or amplitude cues of sound direction, under different levels of masking noise. Noise sharply reduced the responsiveness of males to female songs. However, when males did lateralize the female song, they were surprisingly accurate, even at the highest noise levels. These results suggest that noise only weakly impairs males' directional hearing abilities, but strongly affects their abilities to detect and respond to female songs. Noise therefore probably increases mating costs, because both males and females must expend additional time and energy in mate attraction.

Acoustic signalling is a characteristic component of mating behaviour in many species (Bradbury & Vehrencamp, 1998). In addition to playing a major role in the mate evaluation process, acoustic signals are an important means by which potential mates localize one another. Particularly in acoustically communicating insects and anurans, mate selection is characterized by a process of phonotaxis, in which an individual moves towards the signals of a potential mate until they encounter one another (Gerhardt & Huber, 2002). The abilities of animals to localize relevant sounds in nature is complicated by the presence of often high levels of background noise that potentially mask or interfere with the signal characteristics that convey directional cues to receivers (Brumm, 2013; Brumm & Slabbekoorn, 2005; Römer, 2015). Impaired signal localization abilities in a mate choice context can be costly to both partners: signallers must spend more time producing signals that are potentially energetically costly (Mowles, 2014; Prestwich, 1994) and conspicuous to predators (Zuk & Kolluru, 1998), and receivers may take a more circuitous path to the signaller, again increasing time, energy and predation costs (e.g. Gwynne, 1987; Heller, 1992). Although much recent research focuses on the effects of noise on acoustic communication (Brumm, 2013), most of these studies deal with processes related to signal detection and discrimination and relatively little is known about the effects of noise on animals' directional hearing abilities (Feng & Schul, 2007).

Insects are particularly interesting systems for the study of directional hearing in noise because physical constraints on sound reception in these species have led to a remarkable series of adaptations to enable accurate sound localization (Robert, 2005). In large animals with tympanal hearing organs, sound direction can in principle be determined from differences in the time of arrival or intensity of sounds at each of the two ears (Yost & Gourevitch, 1987). However, these physical cues are generally reduced for insects due to their small body size (Michelsen, 1979; Robert, 2005). None the less, many insects are capable of very precise sound localization, which is achieved by anatomical features such as pressure difference receivers, in which the sound arrives at each tympanum via both external and internal pathways (Michelsen & Rohrseitz, 1995), and neurophysiological amplification of directional cues (reviewed by Hedwig & Pollack, 2008; Hennig, Franz, & Stumpner, 2004; Pollack, 2000). Noise is a serious challenge for

---

[*] Correspondence: M. S. Reichert, Humboldt-Universität zu Berlin, Institut für Biologie, Abteilung Verhaltensphysiologie, Invalidenstraße 43, 10115 Berlin, Germany.

E-mail address: michael.s.reichert@hu-berlin.de.

http://dx.doi.org/10.1016/j.anbehav.2015.02.020

many insect species that signal to attract mates in dense aggregations of competing conspecific and heterospecific signallers (Römer, 2013; Schmidt & Balakrishnan, 2015). In addition to these natural noise sources, insects are clearly impacted by rising levels of anthropogenic noise (Lampe, Schmoll, Franzke, & Reinhold, 2012; Schmidt, Morrison, & Kunc, 2014). However, some of the solutions utilized by other taxa for effective hearing in noise are either unlikely to be utilized in insects (comodulation masking release; Ronacher & Hoffmann, 2003) or are plausible but have thus far received limited empirical support (spatial release from masking; Schmidt & Römer, 2011). Noise is likely to reduce the abilities of insects to detect relevant signals, and thus reduce their overall responsiveness to sounds. Even when insects respond to signals, the accuracy with which signals are localized may be reduced by interference from noise. Even in ideal conditions, insects require complex mechanisms to extract directional cues from acoustic signals (Robert, 2005). Noisy conditions create additional challenges for directional hearing and are likely to have exerted a significant selection pressure on the evolution of acoustic signalling systems (Wiley, 2013). Thus, understanding the effects of noise on insect sound localization abilities is likely to lead to new insights into the ways in which sensory systems deal with environmental complexity.

I investigated the effects of noise on directional hearing in the grasshopper *Chorthippus biguttulus*. This species is an especially good insect model for studies of directional hearing in noise because its sound localization behaviour is stereotyped and easily quantified. Furthermore, noise is a relevant factor in communication in this species because acoustic signalling interactions during mate localization occur in crowded and noisy gatherings of singing conspecifics and heterospecifics (Kriegbaum, 1989; Kriegbaum & von Helversen, 1992). Male *C. biguttulus* produce calling songs to attract females. A receptive female will respond to a male calling song by producing a song of her own. The male then performs phonotaxis, using acoustic cues in the female's response song to localize her and begin close-range courtship (Von Helversen, 1997; Von Helversen & von Helversen, 1994). In response to female songs, male *C. biguttulus* perform a stereotyped lateralization behaviour in which they turn rapidly towards the side of sound incidence (Von Helversen & von Helversen, 1983). Males appear to be unable to determine the exact angle of the sound source relative to the body axis: their response is usually a 90°–120° turn to the left or right, largely independent of the stimulation angle. Then males take a few steps forwards and resume singing (Von Helversen, 1997). In this fashion, males take a zigzag path towards singing females in which turns, which are usually too wide, are corrected on the following lateralization response.

Thus, male mating success in *C. biguttulus* depends on their ability to localize females acoustically. However, because of their small body size, external time or intensity difference cues indicating sound direction are generally insufficient for this task. Sound localization in this species relies on a pressure difference hearing mechanism that magnifies the available directional cues from an incoming sound (Michelsen & Rohrseitz, 1995). The phase difference between the sound impinging on both sides of the tympanum results in pressure differences between the ears which then are translated into spike count and latency differences between the left and right auditory pathways (Krahe & Ronacher, 1993; Rheinlaender & Mörchen, 1979; Ronacher & Krahe, 2000). The resolution of the auditory system for directional cues can be studied at the behavioural level by placing males equidistant between two speakers and simulating directional cues by playing the stimuli from one speaker slightly louder or slightly earlier in time than from the other. With this paradigm, previous studies showed that although males have poor angular resolution abilities, their ability to lateralize stimuli to one side or the other is extremely sensitive (Von Helversen & Rheinlaender, 1988). Males lateralized, with essentially no errors, stimuli that differed by as little as 1 ms or 1–2 dB (Von Helversen & Rheinlaender, 1988); these differences are on the order of those capable of being resolved by the hearing systems of large vertebrates, including humans (Stumpner & Ronacher, 1994). However, these previous studies were performed in quiet laboratory conditions and it is unknown whether noise affects males' sensitivities to directional cues. If noise reduces males' directional sensitivities, this raises challenges for mate localization in naturally noisy field conditions.

In this study, I examined the effects of noise on male response to female songs in *C. biguttulus*. I utilized the stereotyped lateralization response of males as an assay for directional hearing and responsiveness to female song stimuli. I varied the directional cues available to males by presenting female songs through speakers located on either side of the male, and varying the time delay or amplitude of the song broadcast from one speaker relative to the other. I tested two primary hypotheses in this study. The first was that noise affects the responsiveness of males, that is, their likelihood of lateralizing the sound at all. The second hypothesis was that noise affects the accuracy of the male lateralization response, that is, whether their lateralizations were directed towards the correct location of the simulated sound source. The extent to which noise affects these two variables determines the expected consequences of noise on mate localization in naturally noisy environments and gives insights into how the auditory system's ability to detect signals and resolve directional cues is affected by noise.

METHODS

Adult male *C. biguttulus* used in these experiments were obtained from the field (July–September 2013, 2014) from populations in the vicinity of Berlin and Göttingen, Germany and Kühtai, Austria or were laboratory-reared from eggs collected from the Göttingen and Kühtai populations in 2012 and 2013. Preliminary analyses indicated no differences in responsiveness between populations or between field-caught and laboratory-reared individuals. Males were group-housed separately from females and were kept at temperatures of 22–28 °C and given fresh grass ad libitum. I selected males for testing that sang vigorously in the group cage and showed lateralization in response to playback of a female song stimulus (see below). Tests were performed with wild males from July to October 2013–2014 and with laboratory-reared males from May to November 2013 and January to May 2014. This research adhered to the ASAB/ABS Guidelines for the Use of Animals in Research and the current laws for animal care in Germany.

Playback Stimuli

I measured the effects of noise on male responses to playbacks of female songs that varied in directionality cues. All playback stimuli consisted of a digitally synthesized female *C. biguttulus* response song. The song's duration was 1.2 s and it consisted of 12 syllables, each of which contained six pulses that were designed to mimic the temporal and spectral characteristics of natural female songs (Fig. 1a). Unless otherwise noted, each speaker broadcast the female song stimulus at 60 dB sound pressure level (SPL) at the position of the male; this was confirmed using a sound pressure level meter (Brüel and Kjaer 2231 with no. 4133 microphone; Naerum, Denmark). The input to the sound pressure level meter was passed through a bandpass filter (high pass 3 kHz, low pass 10 kHz) to calibrate the SPL of the female song playback at the relevant frequencies for male detection of female signals (Von Helversen & von Helversen, 1997).