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ORIGINAL PAPER

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Auditory behaviour of a parasitoid fly (*Emblemasoma auditrix*, Sarcophagidae, Diptera)

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Abstract Females of the parasitoid fly *Emblemasoma auditrix* find their host cicada (*Okanagana rimosa*) by its acoustic signals. In laboratory experiments, fly phonotaxis had a mean threshold of about 66 dB SPL when tested with the cicada calling song. Flies exhibited a frequency dependent phonotaxis when testing to song models with different carrier frequencies (pulses of 6 ms duration and a repetition rate of 80 pulses s^{-1}). However, the phonotactic threshold was rather broadly tuned in the range from 5 kHz to 11 kHz. Phonotaxis was also dependent on the temporal parameters of the song models: repetition rates of 60 pulses s^{-1} and 80 pulses s^{-1} and pulse durations of 5–7 ms resulted in the highest percentages of phonotaxis performing animals coupled with the lowest threshold values. Thus, parasitoid phonotaxis is adapted especially to the temporal parameters of the calling song of the host. Choice experiments revealed a preference of a song model with 9 kHz carrier frequency (peak energy of the host song) compared with 5 kHz carrier frequency (electrophysiologically determined best hearing frequency). However, this preference changed with the relative sound pressure level of both signals. When presented simultaneously, *E. auditrix* preferred 5-kHz signals, if they were 5 dB SPL louder than the 9-kHz signal.

Keywords Phonotaxis · Carrier frequency · Temporal pattern · Insect

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Introduction

Fly parasitoids locate their insect host by various cues. A few species in two genera (Tachinidae and Sarcophagidae) are known to use acoustic cues from singing hosts for localisation (Leonide 1969; Cade 1975; Soper et al. 1976; Barraclough and Allen 1996). In recent years, the auditory receptors responsible for acoustic localisation have been identified and the first studies on the auditory neuronal network have been performed (Lakes-Harlan and Heller 1992; Robert et al. 1992, 1994, 1996; Lakes-Harlan et al. 1995, 1999; Stumpner and Lakes-Harlan 1996). The phonotactic behaviour of *Ormia ochracea* (Tachinidae) in the field has been studied for several years (Walker 1993). Its auditory behaviour appears to be tuned to the frequency and temporal patterns of the calling songs of its host (Walker 1993; Ramsauer and Robert 2000). Hearing species of the Sarcophagidae are much less investigated. The ear of the sarcophagid fly *Emblemasoma auditrix* is homologous to that of the Tachinidae and represents a case of a convergent evolution within the Diptera (Lakes-Harlan et al. 1999; Robert et al. 1999). *E. auditrix* mainly parasitizes the calling males of the non-periodical cicada *Okanagana rimosa* (Soper et al. 1976). The host's calling song is a monotone buzz of several seconds. It consists of chirps produced at a repetition rate of about 83 pulses s^{-1} (pps) with a total chirp duration of 4–7 ms. It contains the main energy at 7–10 kHz (peak 9 kHz; Lakes-Harlan et al. 1999). Initial electrophysiological investigations of the sensory system of the parasitoid did not reveal any specific adaptations to the host. Extracellular recordings from ascending interneurons showed that the auditory system of *E. auditrix* is most sensitive around 5 kHz (Lakes-Harlan et al. 1999). Thus, the parasitoid seems not to be specifically adapted to the frequency content of the host's calling song. However, it could be shown that in the field flies responded best to song models resembling the calling song of the host (Lakes-Harlan et al. 1998). The attraction success depended on the carrier frequencies as well as temporal parameters, such as repetition rate and pulse duration. However, these field experiments were influenced by a number of variables, from the unknown size of the fly population to abiotic weather conditions. Because of this, we attempted to investigate the auditory behaviour of the sarcophagid fly in a much more controlled environment. We especially wanted to determine the threshold for phonotaxis, which is important in estimations of the natural hearing range in the field.

Furthermore, parasitoid-host systems may provide greater insight into insect auditory behaviour in general. Intraspecific acoustic communication is often tuned to conspecific sounds where the temporal patterns seem to be more important than frequency contents (Pollack 1998). Detailed studies on *E. auditrix* should reveal if interspecific phonotactic behaviour also depends on the temporal pattern or on the frequency content of the host's calling song.

Materials and methods

Investigations were performed at the Biological Station of the University of Michigan, Pellston. Female *E. auditrix* were attracted to broadcasted calling songs of the host cicada *O. rimosa* in habitats near the station (Soper et al. 1976; Lakes-Harlan et al. 2000), captured and then transferred to the laboratory. Animals were individually marked with dots of paint on the pronotum and had their wings clipped off to prevent escape. They were kept in small cages, with sugar and water ad libitum. Flies were tested up to 7 days after their capture.

The test arena (50 cm × 70 cm) was weakly illuminated from above (300–430 lx). The arena was covered with cloth to minimise optical cues. For most tests one piezo loudspeaker (HT-Horn; Conrad Electronic) was placed in the centre of one front side. In choice experiments two loudspeakers were placed 40 cm apart from each other. In between choice experiments the test signals were randomly switched between loudspeakers. Flies were released 50 cm in front of the loudspeaker or at the same distance in between the two loudspeakers used in choice experiments.

As a control, the auditory behaviour in response to the calling song of the host was tested with intact flies in the field. These experiments revealed similar percentages of phonotactically active flies at the different intensities (55–70 dB SPL) compared to the laboratory where flies had their wings clipped. In a second control experiment 12 flies were tested in the laboratory for their movement patterns in the absence of sound. None of these flies moved towards the loudspeaker.

Signals

The calling song of the known host cicada, *O. rimosa,* was digitised (from a mastertape belonging to T. Moore, Ann Arbor, USA) and stored on a compact disc (44.1 kHz sampling rate). The signal largely consisted of chirps with 8–10 kHz peak frequency, ca. 6 ms duration and a repetition rate of 83 pps (Fig. 1a). A variety of artificial signals were created using CoolEdit (Syntrillium). These signals were also recorded onto compact disc at a sampling rate of 44.1 kHz. Examples of the artificial signals (rectangular pulses with smooth edges) are depicted in Fig. 1b. Signals were varied in carrier frequency (4–12 kHz), repetition rate (20–120 pps), pulse duration (2–10 ms) and in sound pressure level (55–80 dB SPL). Signals, in which the temporal structure was modulated all had a 9-kHz carrier frequency. The signals were played back with a Discman (Sony D-131) connected to a custom build amplifier and attenuator in order to adjust sound pressure level (SPL) at the release point of the flies. SPL was measured using a sound level meter (Bruel and Kjael 2203) equipped with a 1/2″ microphone (B and K 4165) and is expressed in dB SPL relative to $P_0 = 2 \times 10^{-5}$ N m^{-2}. In order to verify the quality of the signals at the release point of the flies, they were recorded with the Bruel and Kjael microphone onto DAT recorder (Sony 5DJ A). They were subsequently analysed with Fast-Fourier Transformation using a HP Spectral analyser (HP 5327). All signals had their main energy peak at the respective frequency and peaks of harmonics were at least 25 dB lower (5-kHz example in Fig. 1d). The SPL was usually varied in steps of 5 dB between 60 dB and 75 dB SPL with additional tested intensities in selected experiments.

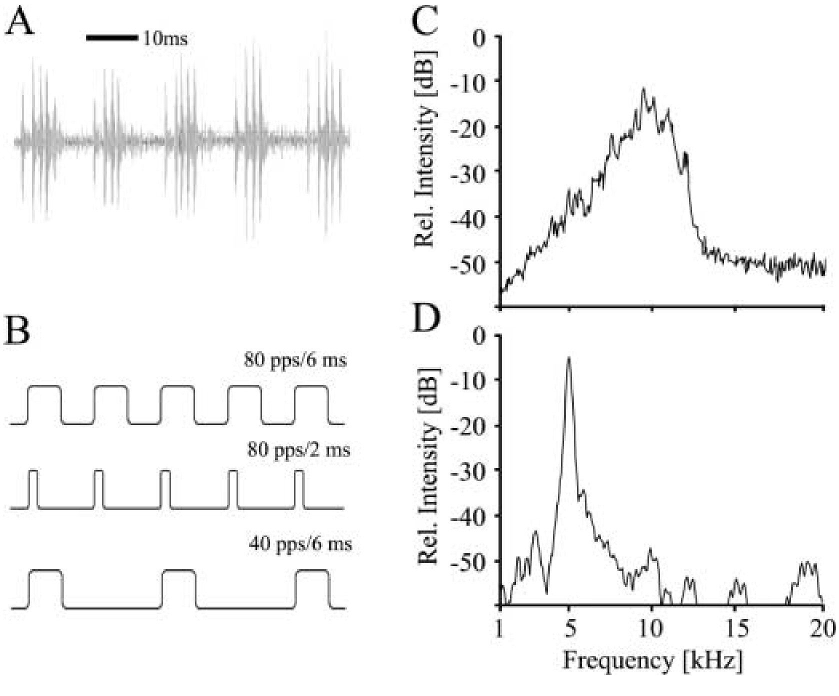

Fig. 1a–d Examples of signals used in the experiments. **a** Temporal structure of the calling song of *Okanagana rimosa*. **b** Examples of artificial song models used to test fly phonotaxis. *Upper trace*: song model for testing different carrier frequencies with 6 ms pulse duration at 80 pps (pulses per second) repetition rate. *Middle trace*: model signal with 2 ms pulse duration at the same repetition rate. *Lower trace*: model signal at 40 pps with 6 ms pulse duration. **c** Spectrum of the calling song. **d** Spectrum of the 5-kHz song model (6 ms pulse duration; 80 pps repetition rate) as recorded at the release point of the flies in the laboratory arena

Positive phonotaxis was defined as reaching the cloth in front of the loudspeaker. Threshold was defined as the lowest SPL at which phonotaxis was observed. Each fly was tested only once in a set of experiments. Statistical analysis included contingency table tests and ANOVA generated using Prism software (GraphPad).

Results

SPL-dependent phonotaxis

All flies were captured in the field by their phonotactic response towards the calling song of the host. However, a varying percentage of them showed phonotactic behaviour in the laboratory. Therefore, all flies were tested daily with a calling song at 75 dB SPL and only those flies exhibiting phonotaxis were used for further experimentation.

Using calling song, a SPL-dependent reaction towards the loudspeaker was observed (Fig. 2). No response was seen at 55 dB SPL, but at 60 dB SPL, 33% of the flies ($n=15$) showed positive phonotaxis. At 70 dB and 75 dB SPL all flies walked directly towards the loudspeaker. In some cases they reached the loudspeaker within 4–5 s (50 cm distance). From the marked individuals a mean threshold value of 65.6 dB SPL ($n=12$) was calculated.

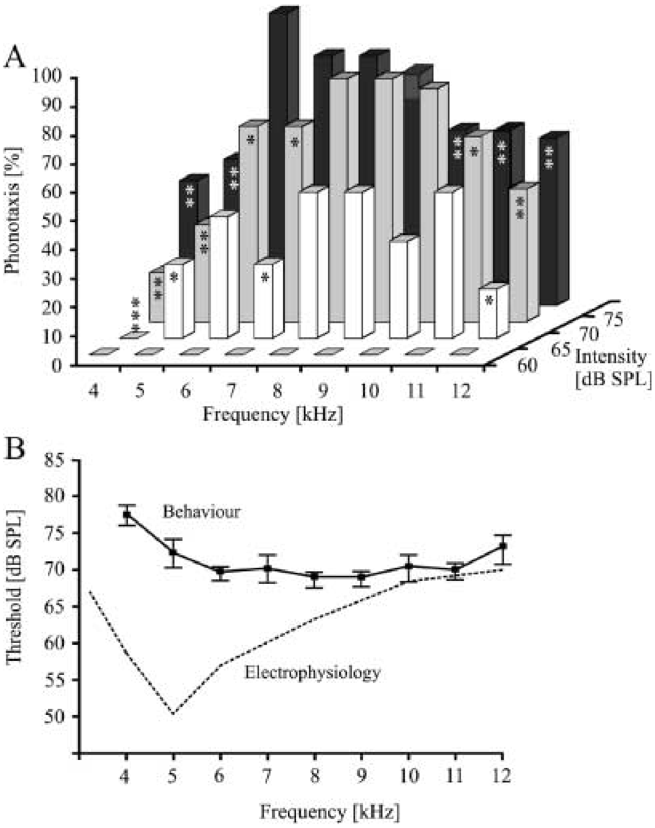

Fig. 3a, b Phonotaxis of *E. auditrix* towards song models (80 pps repetition rate; 6 ms pulse duration) with different carrier frequencies. **a** The percentage of reacting flies generally increased with increasing SPL. Furthermore, most flies walk towards the loudspeaker in the frequency range from 6 kHz to 11 kHz. Statistically significant lower percentages than to the calling song with the respective SPL are indicated with *asterisks* (*$P<0.05$; **$P<0.01$; ***$P<0.001$; ANOVA; $n=8$–15 per data point). **b** Frequency-dependent threshold curve of the flies. The behavioural thresholds are means of 8–12 animals per frequency (± SEM). The electrophysiological threshold has been determined by extracellular recordings from the neck connective (modified after Lakes-Harlan et al. 1999)

Frequency-dependent phonotaxis

When artificial signals with different carrier frequencies were used, a frequency-dependent phonotaxis was observed at intensities of 65–75 dB SPL (Fig. 3a, b). Pulses (6 ms duration, 80 pps) composed of different carrier frequencies at a SPL of 60 dB SPL did not evoke any phonotactic response (Fig. 3a). Starting at 65 dB SPL, the number of reacting females generally increased with increasing SPL. At 70 dB SPL a bell-shaped curve of reacting animals was observed with 80–83% of the flies performing phonotaxis at a carrier frequency of 7–9 kHz. At low frequencies (4–5 kHz) and high frequencies (11–12 kHz), a significantly lower percentage of flies performed phonotaxis than compared to the natural calling song at the same intensities (ANOVA; Fig. 3a). Only calling-song models at 8 kHz and 9 kHz had the same percentages of phonotactically reacting flies at all intensities (compared to the calling song).

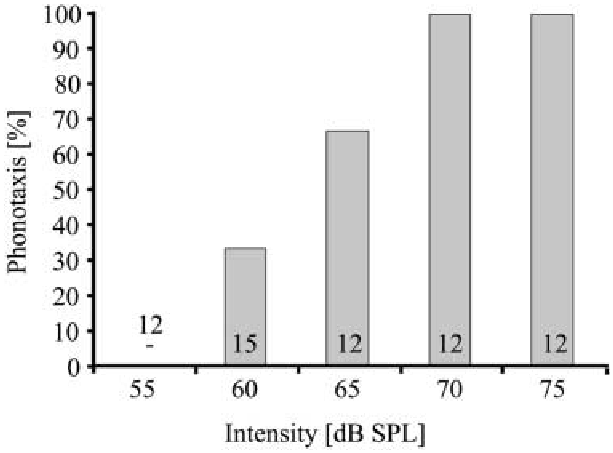

Fig. 2 Sound pressure level (SPL)-dependent phonotaxis of female *E. auditrix* towards the calling song of the host in the laboratory. All tested flies showed phonotactic response at intensities above 65 dB SPL. The number of tested females is given in the columns

Plotting the means of the individual threshold values showed a broad frequency tuning (Fig. 3b). The thresholds are around 68–70 dB SPL (means of 8–12 animals) for frequencies from 6 kHz to 11 kHz. Thus the behavioural threshold differs especially in low-frequency range from that determined by extracellular recordings (Fig. 3b; electrophysiological data from Lakes-Harlan et al. 1999). The observed behaviour was also frequency dependent, although this was not quantified: At

7–10 kHz the animals behaved in a similar manner as was seen during phonotaxis towards the calling song. However, at lower and higher frequencies, the flies often did not walk in a straight line towards the loudspeaker. They took a curved pathway and needed more time to reach the loudspeaker. They often began grooming before walking or in between walking sequences.

Temporal pattern-dependent phonotaxis

For investigations of the relevance of the temporal pattern for phonotaxis, artificial signals with a carrier frequency of 9 kHz were used. When the repetition rate was held constant at 80 pps but the pulse duration varied, flies were observed to be most responsive to pulses with 6 ms and 7 ms duration. With increasing SPL flies responded also to pulses of other durations. The calculated means of the threshold revealed the lowest values (66–68 dB SPL) at 5–7 ms pulse duration (Fig. 4a). When the pulse duration was held constant at 6 ms, variations of the pulse repetition rate showed that flies react best to rates of 60 pps and 80 pps (Fig. 4b). The number of reacting flies increased with increasing SPL, so that in the range from 65 dB to 75 dB SPL most flies reacted at 60 pps and 80 pps. The calculated means of threshold also revealed that the lowest thresholds (70–71 dB SPL) were the same at both repetition rates (Fig. 4b). In both experiments the lowest thresholds are within the range of the variation of the calling song structure and of the behavioural threshold to the calling song (Fig. 4a, b, shaded area; data from H. Stölting et al., unpublished observations).

Choice experiments

Experiments with single frequencies had shown that more flies were attracted to a 9-kHz (near the peak of the calling song spectrum) than to a 5-kHz signal (best hearing frequency). To examine this difference further we performed choice experiments with 5-kHz and 9-kHz signals broadcasted simultaneously at a SPL of 70 dB SPL, both with 6 ms duration and 80 pps repetition rate. As expected the flies preferred the 9-kHz signal (Fig. 5, left columns; $n = 12$). However, this frequency preference was not exclusive. When the SPL of the 5-kHz signal was increased to 75 dB SPL, then all flies responded to the louder signal (Fig. 5, right columns; $n = 12$).

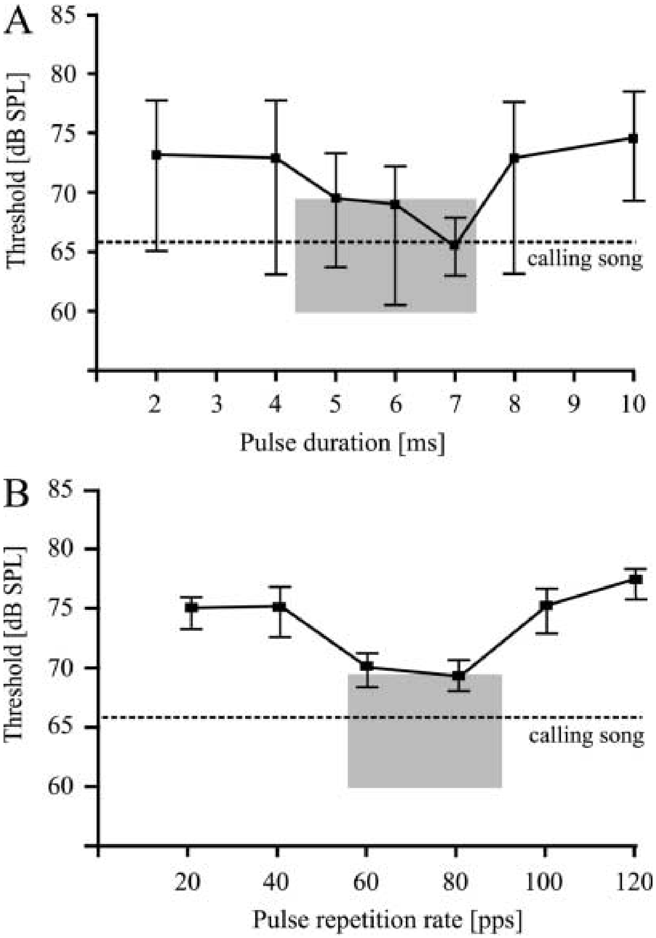

Fig. 4a, b Phonotaxis of *E. auditrix* towards song models with different temporal structures. **a** Pulse duration-dependent threshold curve of flies. Means of 5–7 animals per pulse duration (± SEM). The signal had a repetition rate of 80 pps and 9 kHz carrier frequency. **b** Repetition rate-dependent threshold curve of the flies. Means of 9–12 animals per rate (± SEM). The signal had a pulse duration of 6 ms and 9 kHz carrier frequency. In both diagrams the mean phonotaxis threshold to the natural calling song is indicated by the *dotted line*. The *shaded area* marks the range of the variation of the parameter in the calling song (after H. Stölting et al., unpublished data) and the SEM of the calling song threshold in a vertical direction

Discussion

The laboratory investigations of phonotaxis in females of the sarcophagid parasitoid *E. auditrix* revealed that the behavioural responsiveness depended on the frequency content and temporal patterns of the host calling song. A comparison of experiments done in the laboratory with experiments done in the field showed that similar percentages of flies reacted to the calling song at the different sound intensities. The experimental necessity of clipping the wings to prevent escape seemed to have no adverse effects on fly phonotaxis. Flies tested immediately following wing clipping showed normal phonotactic responsiveness and lived just as long as flies with wings (up to 14 days in the laboratory; Schniederkötter and Lakes-Harlan, unpublished observations). Furthermore, in field experiments walking has been observed as normal behaviour for approaching the host (Lakes-Harlan et al. 2000).

Threshold of phonotactic behaviour

The mean threshold was 65.6 dB SPL for the calling song of the host cicada *O. rimosa*, whereby some indi-

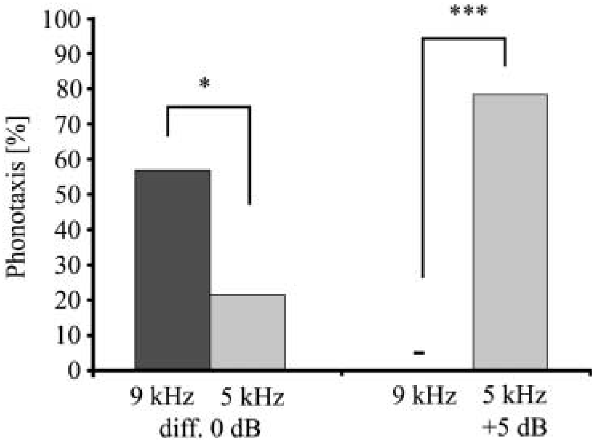

Fig. 5 Two-tone choice experiment. On the *left side of the diagram* both frequencies (5 kHz and 9 kHz) had the same SPL of 70 dB SPL. Female flies preferred the 9-kHz tone ($n = 12$; contingency table analyses with chi-square test: $P = 0.0265$). Increasing the SPL of 5 kHz to 75 dB SPL (*right side*; + 5 dB) results in preference of the louder tone ($n = 12$; contingency table analyses with chi-square test: $P < 0.0001$)

viduals reacted even at 60 dB SPL (Fig. 2). These data are important for an estimation of the hearing range and have consequences for the search strategy of host finding. The host emits the calling song with a SPL of about 90 dB SPL at 10 cm distance (H. Stölting et al., unpublished observations). With the phonotaxis threshold of about 66 dB SPL, one can calculate a maximal phonotaxis distance of the fly of about 1.6 m for locating a host (at best 3.2 m with 60 dB SPL threshold). Given that the sound is absorbed and diffracted within the habitat the hearing range might be even smaller. However, first experiments with transmitted calling song in the habitat did not reveal an excess attenuation at frequencies from 6–12 kHz (H. Stölting et al., unpublished observations). As a consequence of the rather small range for phonotaxis, flies would have to actively search for a host, especially in years where cicadas occur in low numbers and their spatial distances are much larger than 3 m. Correspondingly, a high mobility of flies was observed in the field (Schniederkötter and Lakes-Harlan, unpublished observations). Random search flights might be an important part of the host finding behaviour. Flies are able to perform phonotaxis during flight, whereby the resulting movement might reduce the hearing sensitivity even further, similar to the effects of movements in grasshoppers (Hedwig and Meyer 1994).

Species of tachinid flies can have much larger hearing ranges due to generally more sensitive hearing thresholds (as determined in similar electrophysiological experiments as in *E. auditrix*) and due to higher sound intensities of the host species, e.g. the hearing threshold (about 45 dB SPL) of *Therobia leonidei* may enable it to hear its host over a distance of 200 m under ideal conditions (Stumpner and Lakes-Harlan 1996). Females of the tachinid *Ormia ochracea* have even a lower threshold of about 20 dB SPL at the carrier frequency of the host (Robert et al. 1992) with a behavioural threshold of about 40 dB SPL (Ramsauer and Robert 2000).

Frequency dependence of phonotactic behaviour

Fly phonotaxis seemed to be broadly tuned within 5–10 kHz (Fig. 3). Thus, the peak frequency of the host's calling song (9 kHz) is not especially represented in the behavioural threshold. These results contrast with the finding, that in the field *E. auditrix* is almost exclusively attracted to 9-kHz signals when compared to 5-kHz signals (non-choice experiments; Lakes-Harlan et al. 1998, 2000). In the present experiments signals with 9 kHz and 5 kHz carrier frequency differed in their "attractiveness". This is seen in the low percentages of flies reacting to 5-kHz signals and in the choice experiments. In the latter experiments flies discriminated different frequencies and preferred 9 kHz over 5 kHz at an equal SPL (70 dB SPL; Fig. 5). However, SPL seems to play an important role, perhaps together with the motivational state or "arousal" of the females. In our laboratory experiments we used females with a motivational state as uniform as possible (all had been caught by phonotaxis; all were tested for phonotaxis prior to an experiment). A motivational influence might also be indicated by the observation, that flies that were attracted to the calling song in the field also orientated towards many other sounds (e.g. hissing), if the loudspeaker was turned off (R. Lakes-Harlan, unpublished observations). The influence of motivation and "arousal" will be investigated to more detail in future experiments.

The broad tuning of the phonotaxis threshold does not reflect the shape of the extracellularly determined hearing threshold with a minimum at 5 kHz. This finding might either be discussed in the context of adaptations to the host (see below) or seen as a lack of information on the neurophysiology of the auditory system. It is possible that interneurons sensitive to higher frequencies were not recorded with the summed recording from the neck connective. Comparable conditions have been described for cicadas, in which single interneurons are tuned to frequencies which are not reflected in extracellular recordings of the tympanal nerve (Fonseca et al. 2000). Summed recording of the tympanal nerve of *E. auditrix* also showed a rather broad tuning (H. Stölting, personal communication). Intracellular studies of interneurons and afferents of *E. auditrix* will disclose the auditory tuning in greater detail.

Temporal pattern dependence of phonotactic behaviour

Frequency might be an important factor for host recognition, but the temporal pattern is necessary as well. By varying different parameters (repetition rate, pulse duration) of the chirps, we showed that the phonotactic behaviour of *E. auditrix* seems to be tuned to parameters of the host's calling song. Lowest thresholds or best responses were observed at 60–80 pps and 6–7 ms pulse duration (Fig. 4), both prominent temporal parameters of the host's calling song. These temporal parameters might also be important for discrimination of different species of cicadas. Probably it is a combination of parameters which, when coupled with the motivational status of the gravid female leads to a positive phonotactic response. This is also indicated by the fact that the lowest phonotactic threshold was seen in experiments with natural calling song compared to those with artificial song models.

Adaptation to the host's calling song

How well is *E. auditrix* adapted to the calling song of the host? The rather high threshold and the rather broad tuning of phonotaxis seem not to be specific adaptations. On the other hand, *E. auditrix* responded best to song models with temporal parameters of the host's calling song. Considering potential host species for the parasitoid, only ten species of cicadas are found in Michigan (Ciszek et al. 1996). An important species with overlapping seasonal and geographic distributions is the partly sympatric species *Okanagana canadensis*. The calling song of *O. canadensis* has a similar spectral content, but a pulse repetition rate of 28–40 pps (H. Stölting et al., unpublished observations). Thus, the temporal tuning of *E. auditrix* might be sufficient to discriminate between the two species. *E. auditrix* could not be attracted to the loudspeaker in experiments with calling song of *O. canadensis* (Lakes-Harlan et al. 2000). In the field, *E. auditrix* larvae have not yet been observed in *O. canadensis* and generally no other host species of *E. auditrix* are known.

However, despite the broad tuning of the phonotaxis threshold curve flies are able to discriminate between frequencies. In the field, they probably use the spectral information together with the temporal information for phonotaxis. In general, insect phonotaxis depends on frequency as well as on temporal patterns, whereby the latter is thought to be more important (Pollack 1998). Crickets discriminate only between rather broad frequency bands (Wyttenbach et al. 1996) and also in grasshoppers broad frequency bands are important for sex recognition (von Helversen and von Helversen 1997). Therefore a broad frequency tuning of *E. auditrix* is not surprising, although a frequency-dependent phonotaxis has been described in tachinids, *O. ochracea* (Walker 1993). Temporal pattern, on the other hand, is very important in crickets and grasshoppers, not only for species discrimination, but also for sex discrimination (Thorson et al. 1982; von Helversen and von Helversen 1997; Pollack 1998). Thus, the auditory system of *E. auditrix* which is adapted to detect sounds of a different species, the host species, displays the same basic characteristics as other insects adapted for intraspecific communication.

The broad tuning and the relatively low sensitivity can also be seen as an early stage in the evolution of the auditory sense organ of the parasitoid. If compared to the homologous ear of the tachinid flies, that of the sarcophagid flies seem much less elaborated (Lakes-Harlan et al. 1999). However, although the auditory signal seems to be the major cue for host finding of *E. auditrix*, other sensory cues are additionally used (Schniederkötter and Lakes-Harlan, unpublished observations). These visual cues are hardly usable by the nocturnal tachinids and it can be speculated that a lack of other sensory cues was a selective factor for the evolution of a sensitive ear.

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References

Barraclough DA, Allen GR (1996) Two species of *Homotrixa* Villeneuve (Diptera: Tachinidae: Ormiini) from southwestern Australia, with data on biology and ecology. Aust J Entomol 35:135–145

Cade W (1975) Acoustically orienting parasitoids: fly phonotaxis to cricket song. Science 190:1312–1313

Ciszek D, Cooley JR, Alexander RD, Moore TE (1996) New records of Michigan Cicadidae (Homoptera), with notes on the use of songs to monitor range changes. Great Lakes Entomol 29:165–169

Fonseca PJ, Münch D, Hennig RM (2000) How cicadas interpret acoustic signals. Nature (Lond) 405:297–298

Hedwig B, Meyer J (1994) Auditory information processing in stridulating grasshoppers: tympanic membrane vibrations and neurophysiology. J Comp Physiol A 174:121–131

Helversen D von, Helversen O von (1997) Recognition of sex in the acoustic communication of the grasshopper *Chorthippus biguttulus* (Orthoptera, Acrididae). J Comp Physiol A 180: 373–386

Lakes-Harlan R, Heller K-G (1992) Ultrasound-sensitive ears in a parasitoid fly. Naturwissenschaften 79:224–226

Lakes-Harlan R, Stumpner A, Allen G (1995) Functional adaptations of the auditory system of two parasitoid fly species, *Therobia leonidei* and *Homotrixa spec*. In: Burrows M, Matheson T, Newland P, Schuppe H (eds) Nervous systems and behaviour. Thieme, Stuttgart, p 358

Lakes-Harlan R, Stölting H, Stumpner A (1998) Phonotaxis of the parasitoid fly *Colcondamyia auditrix* (Sarcophagidae, Diptera). In: Elsner N, Wehner R (eds) Göttingen Neurobiology Report 1998. Thieme, Stuttgart, p 285

Lakes-Harlan R, Stölting H, Stumpner A (1999) Convergent evolution of insect hearing organs from a preadaptive structure. Proc R Soc Lond Ser B 266:1161–1167

Lakes-Harlan R, Stölting H, Moore TE (2000) Phonotactic behavior of a parasitoid (*Emblemasoma auditrix*, Sarcophagidae, Diptera) in response to the calling song of the host (*Okanagana rimosa*, Cicada, Homoptera). Zoology 103:31–39

Leonide JC (1969) Recherches sur la biologie de divers Diptères endoparasites d'Orthopteres. Mem Mus Nat Hist Nature A (fasc unique), 246 p

Pollack GS (1998) Neural processing of acoustic signals. In: Hoy RR, Popper AN, Fay RR (eds) Comparative hearing in insects. Springer, Berlin Heidelberg New York, pp 139–196

Ramsauer N, Robert D (2000) Free-flight phonotaxis in a parasitoid fly: behavioural thresholds, relative attraction and susceptibility to noise. Naturwissenschaften 87:315–319

Robert D, Amoroso J, Hoy RR (1992) The evolutionary convergence of hearing in a parasitoid fly and its cricket host. Science 258:1135–1137

Robert D, Read MP, Hoy RR (1994) The tympanal hearing organ of the parasitoid fly *Ormia ochracea* (Diptera, Tachinidae, Ormiini). Cell Tissue Res 275:63–78

Robert D, Miles RN, Hoy RR (1996) Directional hearing by mechanical coupling in the parasitoid fly *Ormia ochracea*. J Comp Physiol A 179:29–44

Robert D, Miles RN, Hoy RR (1999) Tympanal hearing in the sarcophagid parasitoid fly *Emblemasoma* sp.: the biomechanics of directional hearing. J Exp Biol 202:1865–1876

Soper RS, Shewell GE, Tyrrell D (1976) *Colcondamyia auditrix* nov. sp. (Diptera: Sarcophagidae), a parasite which is attracted by the mating song of its host, *Okanagana rimosa* (Homoptera: Cicardidae). Can Entomol 108:61–68

Stumpner A, Lakes-Harlan R (1996) Auditory interneurons in a hearing fly (*Therobia leonidei*, Ormiini, Tachinidae, Diptera). J Comp Physiol A 178:227–233

Thorson J, Weber T, Huber F (1982) Auditory behaviour of the cricket. II. Simplicity of calling-song recognition in *Gryllus* and anomalous phonotaxis at abnormal frequencies. J Comp Physiol A 146:361–378

Walker TJ (1993) Phonotaxis in female *Ormia ochracea* (Diptera: Tachinidae), a parasitoid of field crickets. J Insect Behav 6:389–410

Wyttenbach RA, May ML, Hoy RR (1996) Categorial perception of sound frequency by crickets. Science 273:1542–1544