COMPARING CRICKET EARS

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1. INTRODUCTION

Cricket calls are cheerfully musical in contrast to broad-band sounds made by many other insects. This musicality is due to their ubiquitous use of single-frequency carrier pulses to form the male calling song,broadcast to attract a female mate. Most crickets worldwide -- >3000 described spp. (Otte & Naskrecki 1997) -- call at a carrier near 4 kHz (Otte 1992), the wavelength of which is about 7 cm -- far longer than any cricket's body dimensions. Thus a distant cricket female, localizing a male's call to guide her approach, has a body too small to create useful side-to-side amplitude differences by body diffraction. Yet substantial binaural differences in response activity between right and left tympana (located on the forelegs) do occur (Michelsen et al. 1994) and females are well able to localize singing males. The mechanism apparently relies upon binaural differences in phase (Michelsen et al. 1994).

1.1 *Gryllus* cricket ear anatomy

Tracheae are branching, interconnected tubes reinforced by spiralled exoskeleton (taenidia). They conduct respiratory gases throughout the insect body and as such are preadapted to also conduct sound. From behind each eardrum in *Gryllus* spp. a trachea runs bodyward along the leg to the prothoracic segment (Fig. 1). Here, near the body wall of its side, it joins the anterior face a of larger-diameter transverse trachea. This transverse trachea connects right and left prothoracic spiracles. This cross-body trachea, together with the two leg tracheae, comprise an acoustic waveguide system with four entry points for sound: the two spiracles (capable of being closed or open) and the two eardrums.

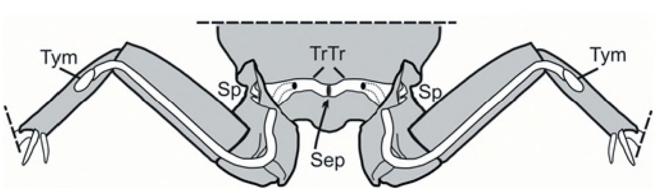

Fig. 1. There are four sound inputs to the internal sound system of *Gryllus*. A leg trachea runs from behind each tibial tympanum (Tym) and enters the large transverse trachea (TrTr) anteriorly (see right and left solid-black [small] ovals); the transverse trachea crosses the body between right and left prothoracic spiracles (Sp), with the phase-shifting septum (Sep) at the body midline. The upper portion of the cricket's body and leg tarsi are removed.

1.2 *Gryllus* ear function

Consider a field cricket facing forward (0º) and a sound source aimed directly at its right ear, at 60º to the cricket's longitudinal axis (Fig. 1). External incidental sound interacts with that entering via two other ports:1) contralateral spiracle, and 2) ipsilateral spiracle [input via the contralateral ear is feeble and can be disregarded (Michelsen et al. 1994)]. The sum of these two internal sounds as vectors (taking into account transmission gain in the tracheae, and phase at the rear of the eardrum) will interact with the incident sound to determine a resultant pressure change moving the ipsilateral ear. At the same time as the ipsilateral ear is very active in tracking the sound of the speaker at 60º, the contralateral eardrum at 300º is made comparatively inactive by the interaction of the same mirror-image vectors. Phase difference effected by cross-body transmission from the contralateral spiracle thus creates what body diffraction cannot: substantial binural differences in perceived sound that vary with changes in the orientation of the cricket toward the source. The greatest difference in left-right eardrum response occurs when the source faces the ipsilateral tympanum at either 30 or 330 degrees.

1.3 Mechanical phase shifter

This localization mechanism relies on an internal phase shift of no less than 313º at the 4.5-kHz carrier of the cricket *Gryllus bimaculatus*. And the carrier wavelength is an important aspect of the adaptiveness of this shift, i.e., only at the carrier wavelength is the shift of appropriate dynamic range for creating usable binaural differences. But path length differences to the rear of the right and left ears for an eccentric species-specific carrier source, cannot alone account for the phase change. Somehow a mid-body septum in the transverse trachea adds a phase delay of as much as 259º. When this septum is perforated, the phase delay is lost (Michelsen & Löhe 1995).

2. Acoustic tracheae in a nemobiine

Allonemobius fasciatus, the striped ground cricket, is a member of the subfamily Nemobiinae and is distributed across temperate North America. (For more information about this cricket see Singing Insects of North America [http://buzz.ifas.ufl.edu/]). The calling carrier of *A. fasciatus* is about 7.2 kHz, nearly 3 kHz higher than that of a field cricket. It is a relatively small species with a body length near 10 mm, about half the body length of *Gryllus* spp.

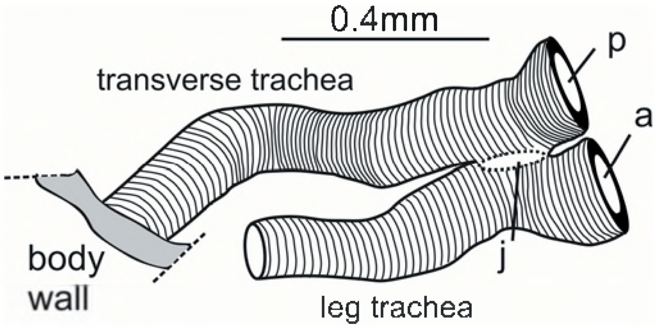

Fig. 2. Dorsal view of left half of prothoracic acoustic tracheal system of *A. fasciatus*. The left leg trachea connects to the transverse trachea via the junction j close to the midline and joins also to the leg trachea of the right side via a second midline septum anteriorly (a).

Situated low in the prothorax, just above the prothoracic ganglion, the transverse trachea of *A. fasciatus* (Fig. 2) traverses the body from left to right between the prothoracic spiracles. As with *Gryllus* there is a midline septum (**p**, Fig. 2). The leg trachea of the left side (shown truncate in Fig. 2) runs from behind the left tympanum inside the foreleg and joins with the left half of the transverse trachea at a location (**j**, Fig. 2) very close to the midline. But in contrast to *Gryllus* spp. the left leg trachea of the nemobiine links with its right-side equivalent at a second septum (**a**, Fig. 2).

The two septa are circular and, at a gross level, appear identical. In a newly killed insect, dissected under Ringers, there is a central circular region, opaquely white, surrounded by a narrow periphery that is semitransparent. (The solid black of Fig. 2 indicates the relative extent of this semitransparent periphery.) Each septum completely blocks its tracheal passage. Aside from being smaller, in keeping with the size disparity of *A. fasciatus* and *Gryllus* spp., these septa do not differ between the two cricket species.

3. DISCUSSION

It is reasonable to suppose that the purpose of these transverse tracheae is to transmit sound across the body, i.e., there is no respiratory function consistent with the blocking of these passages with a septum. The tracheae seem also overly large for a purely respiratory role. So it is reasonable to regard these air tubes as acoustically adapted.

Michelsen et al. (1994) established that the input to the contralateral spiracle of *G. bimaculatus* was dominant in the localization process, sound from both the ipsilateral spiracle and the contralateral tympanum being of little importance. The morphology of this nemobiine system suggests a much greater role for tympanal access in producing phase changes. The right and left leg tracheae, by being confluent in the midline at an anterior septum, have created an additional sound route: sound entering at a contralateral tympanum can reach and perhaps influence the ipsilateral tympanum more directly than in *Gryllus*.

Crickets globally call with carriers between 3 and 5 kHz (Otte 1992). Though some species, as does *A. fasciatus*, sing with slightly shorter wavelengths, most species are also smaller than field crickets, so the problem of ineffective body diffraction for localization should remain acute.

There are so many kinds of cricket, and to date no comparative anatomical examination of their acoustic tracheae. So it is quite probable that many diverse acoustic tracheal morphologies remain to be discovered among these insects. As for this single example of a distinct nemobiine acoustic tracheal morphology: how dual septa might function by altering phase is unknown.

4. REFERENCES

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