The Cricket Auditory System Responds to Bilateral Phase-Shifts

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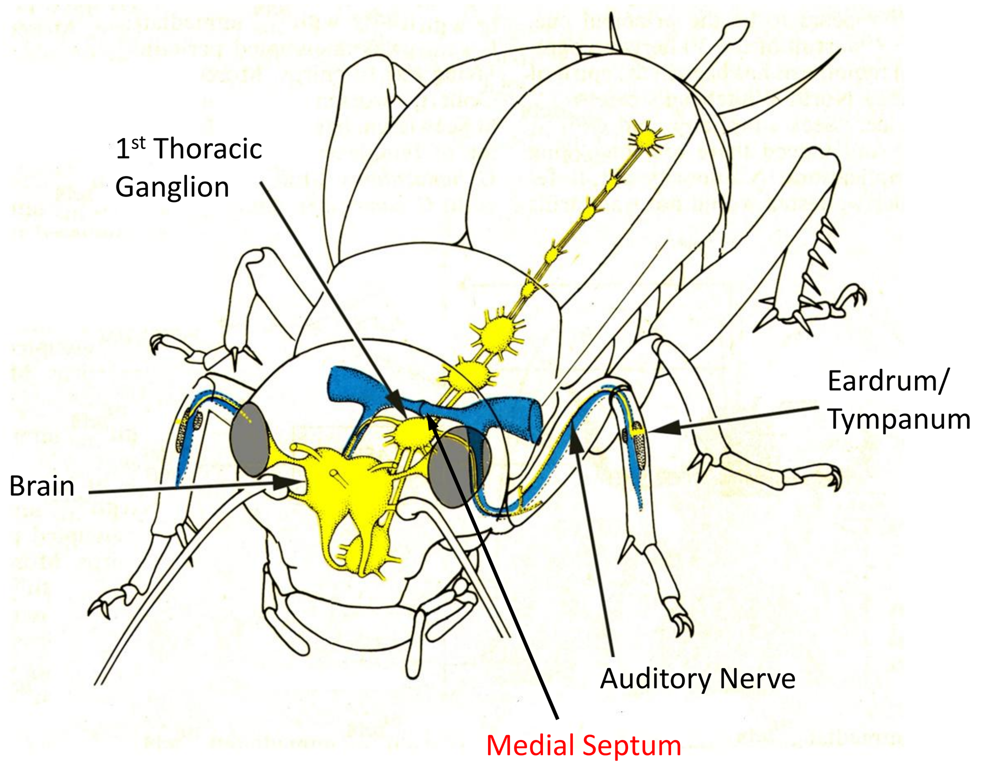
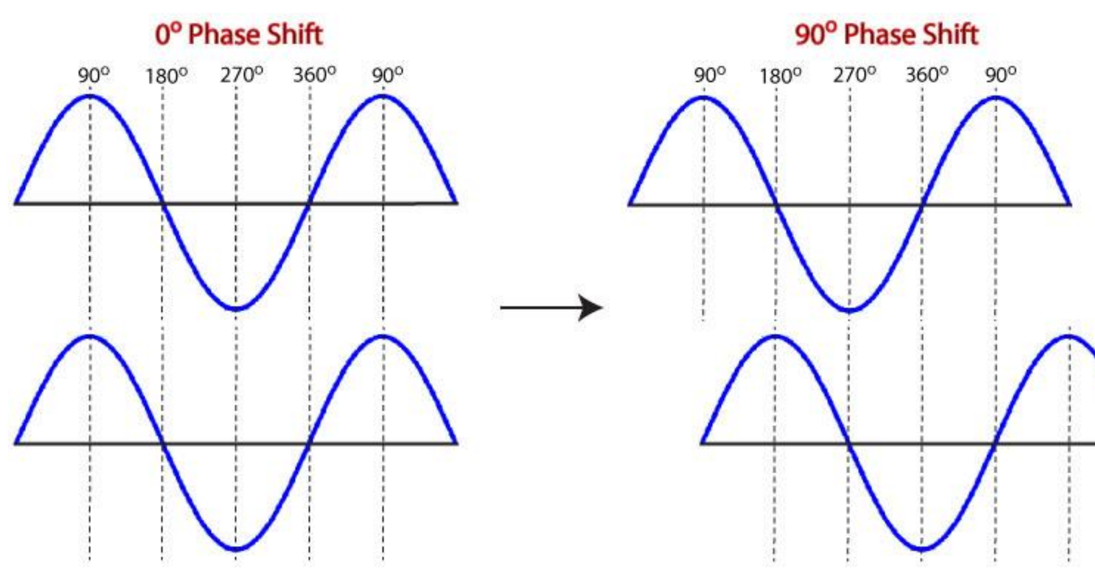
Cricket Auditory System:

The cricket's ears are located on its forelegs. They function as a pressure difference receiver and are connected by an auditory trachea (blue). Sound enters the system through four inputs: the ipsi- and contralateral spiracles located on the prothoracic body segment, and the outer side of the two tympana. The vibration at the tympanum is transduced into neural activity by 50-60 auditory afferents located nearby and is forwarded to the CNS (yellow) for further processing.



Phase-Shifts:

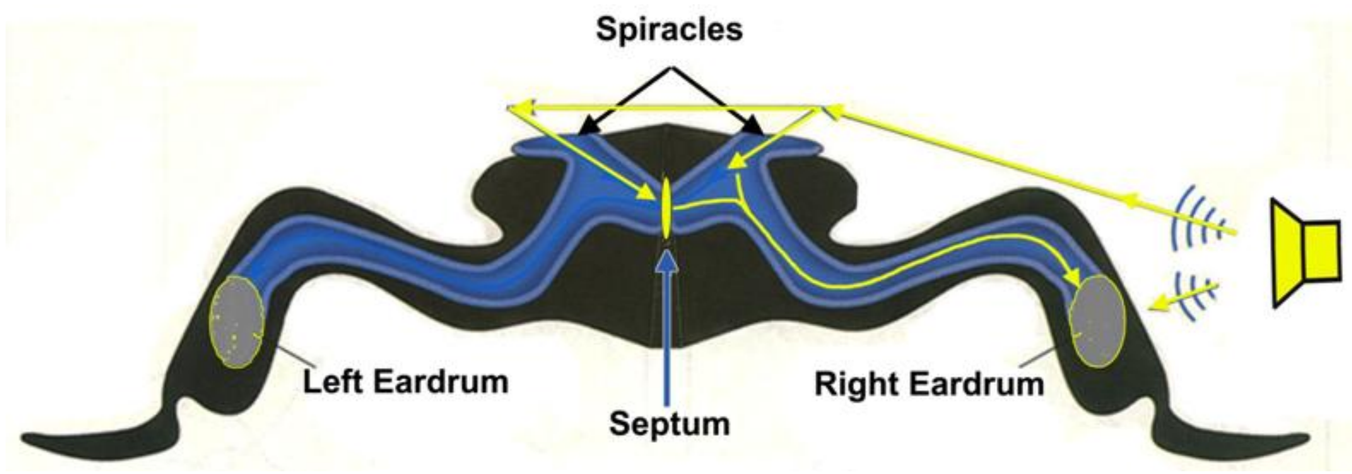
Our experiments looked at how the auditory system responds at different levels to externally applied auditory phase-shifts. Each experimental setup involves a speaker to the left and right side of the animal which simultaneously play the same pure tone pulses, however one speaker is leading in phase by a ninety degree shift.



The upper sound wave becomes shifted forward by 90° relative to the bottom sound wave, and is now considered to be "leading".

Why Phase-Shifts?

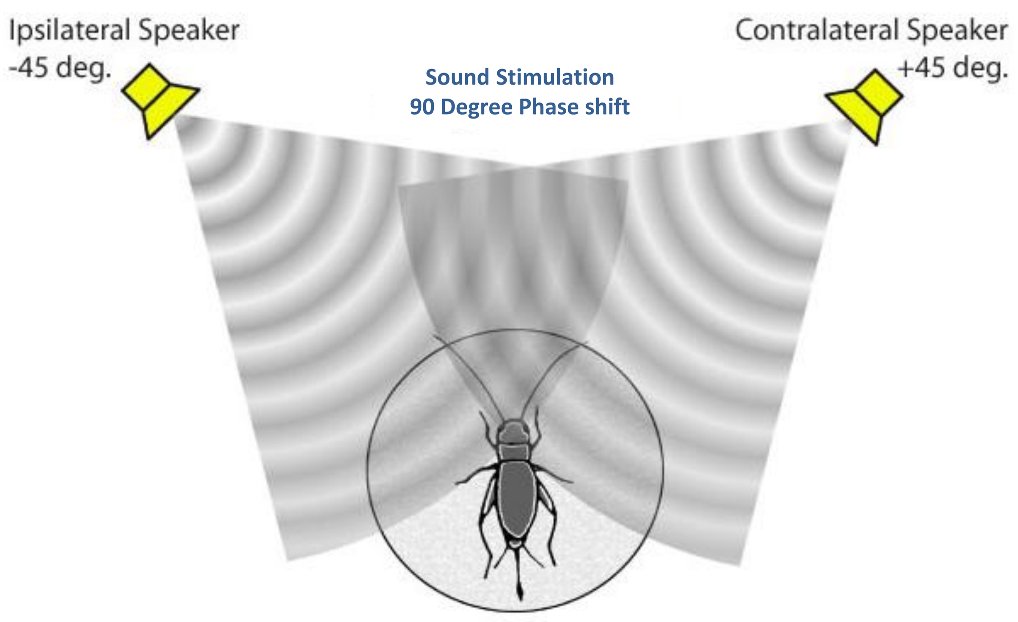
The medial septum, a membrane that separates the two halves of the auditory trachea, is thought to play an important role in creating an internal phase-shift within the cricket auditory system. This phase-shift increases the directionality of the system (Michelsen et al., 1994) for a particular frequency range. However, little is known about the crickets' response to acoustic phase-shifts, which our experiments explore at the levels of behavioral and ear activity.

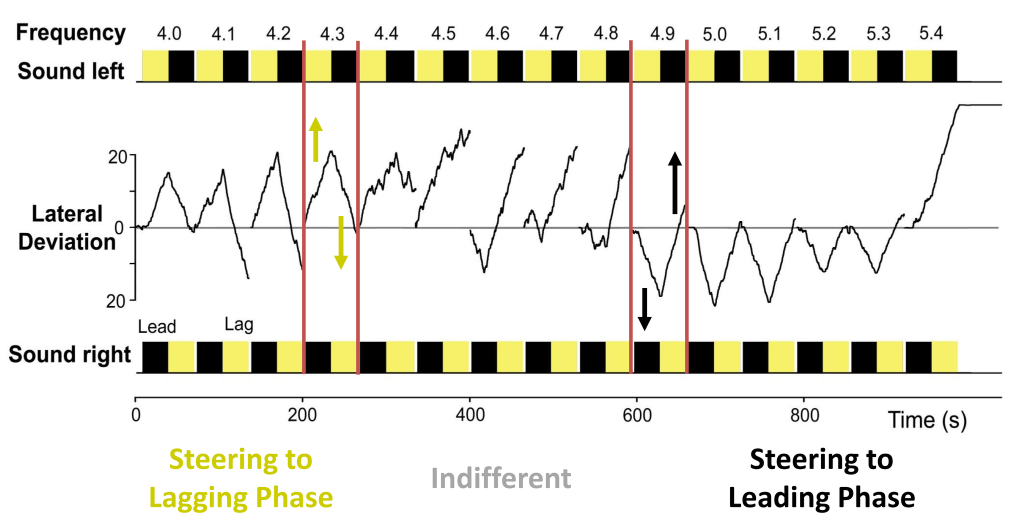


Sound that enters the two spiracles travels through the auditory trachea, and the medial septum, to reach the inner side of the tympanic membrane.

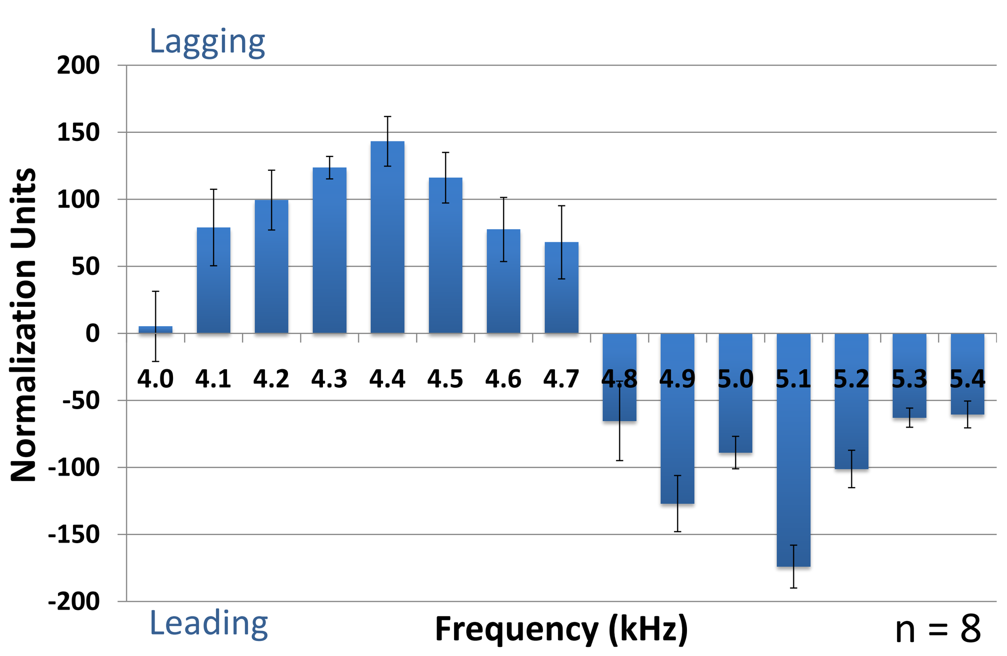
Phonotacic Behavior:

The crickets' behavioral response to a 90° phase-shift between a left and right speaker was tested using a highly sensitive open-loop trackball system.





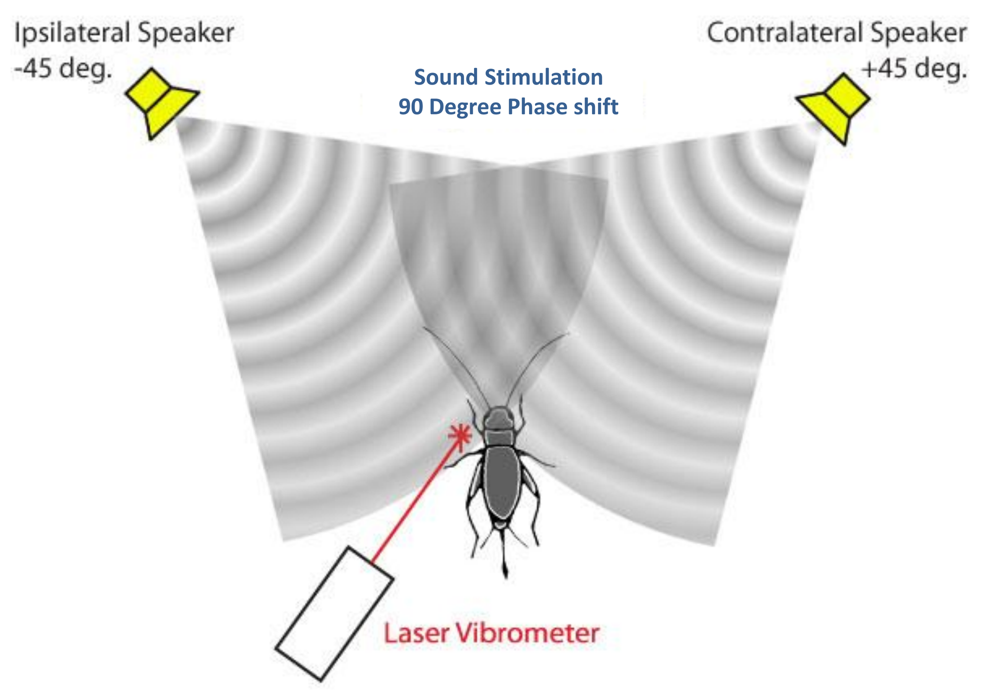
Walking trace of an individual cricket. Below 4.4kHz it is steering towards the lagging side, and above 4.8kHz it is steering towards the leading side.

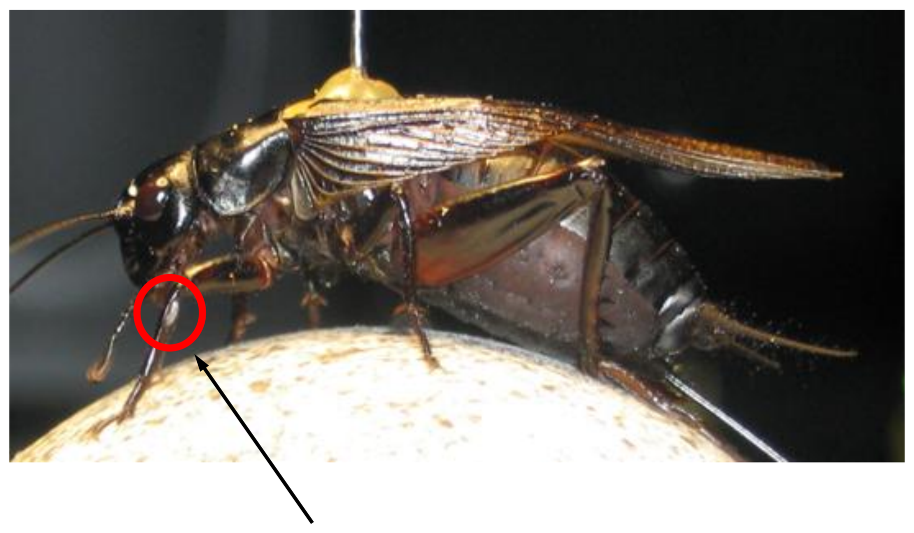


At lower frequencies (4.0-4.7kHz) the crickets steered towards the speaker that was lagging in phase, and at higher frequencies (4.8-5.4 kHz) they steered towards the speaker leading in phase. At the crossing point (N.U. = 0) the crickets had no steering preference.

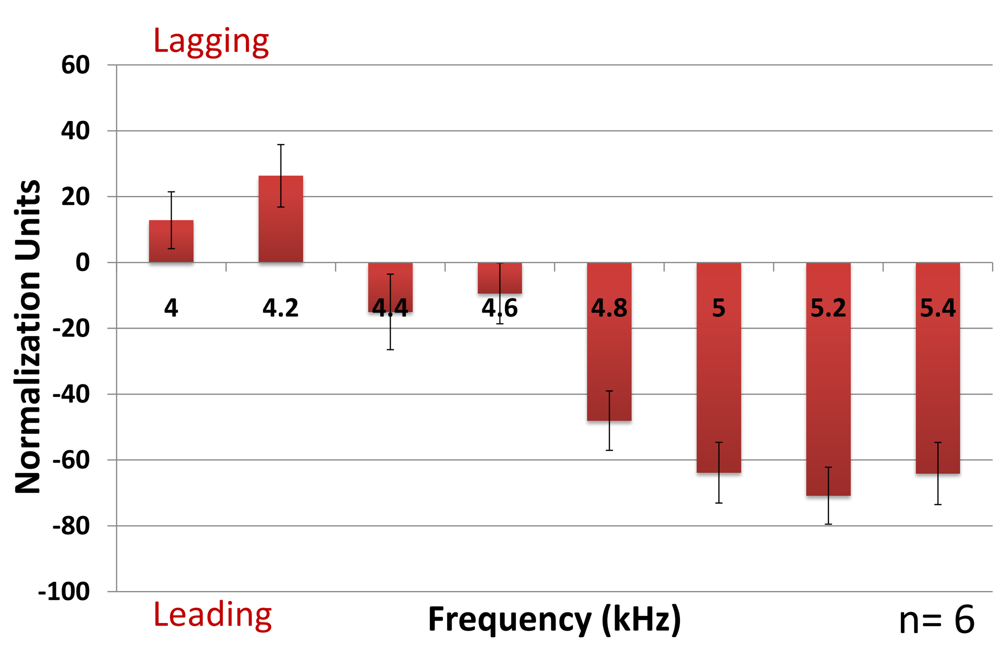
Tympanum Oscillation:

A laser vibrometer was used to measure the amplitude of the tympanic membrane oscillations during the 90° phase-shift paradigm.





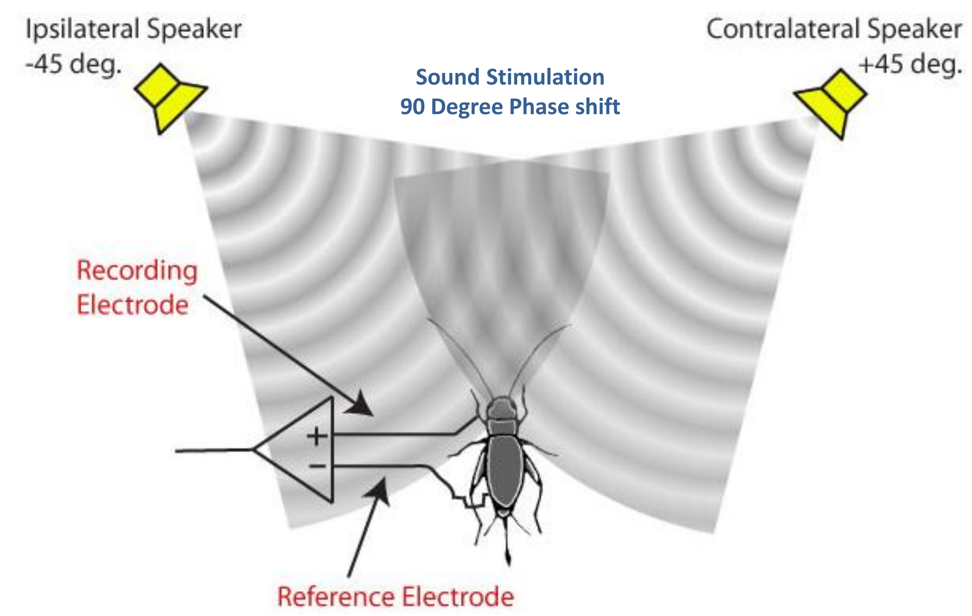
Tympanic membrane, where the laser was pointed.

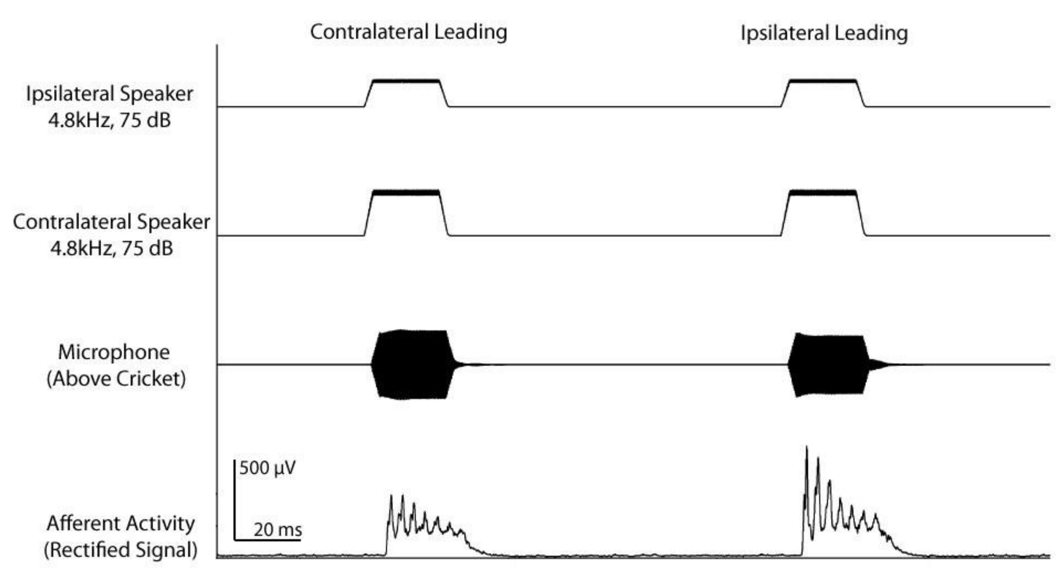


At lower frequencies (4.0-4.2kHz) the tympanic membrane oscillation had a higher amplitude when the ipsilateral speaker was lagging in phase, and at higher frequencies (4.4-5.4kHz) the amplitude was larger when the ipsilateral speaker was leading. At N.U. = 0 the membrane oscillated equally for both leading and lagging conditions.

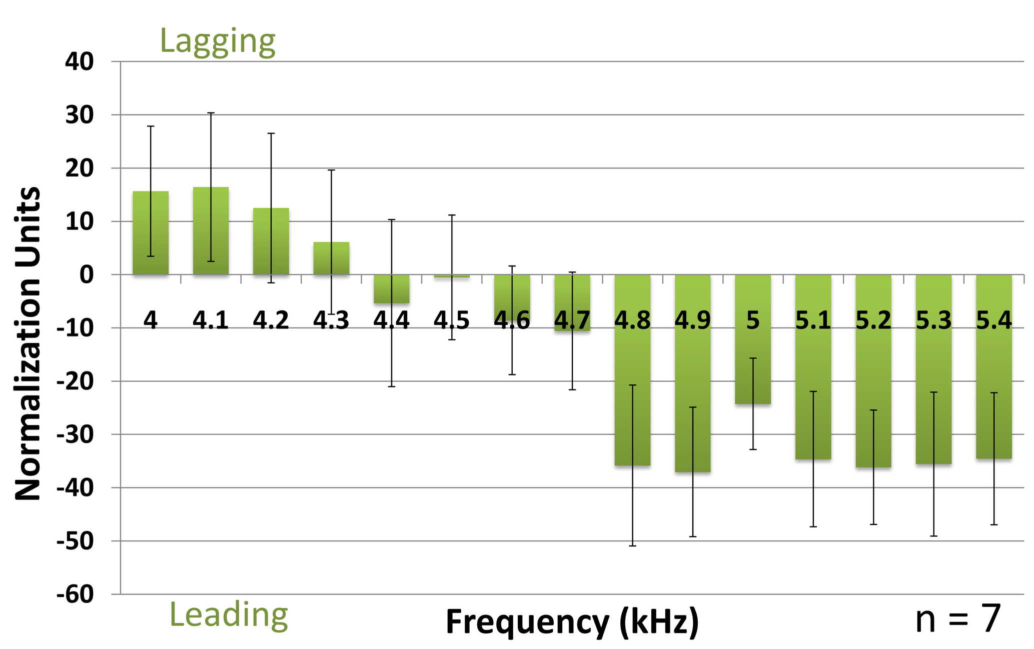
Afferent Activity:

The afferent activity of the crickets' auditory nerve was recorded using a hook electrode. The activity shown represents the summed activity of multiple neurons.





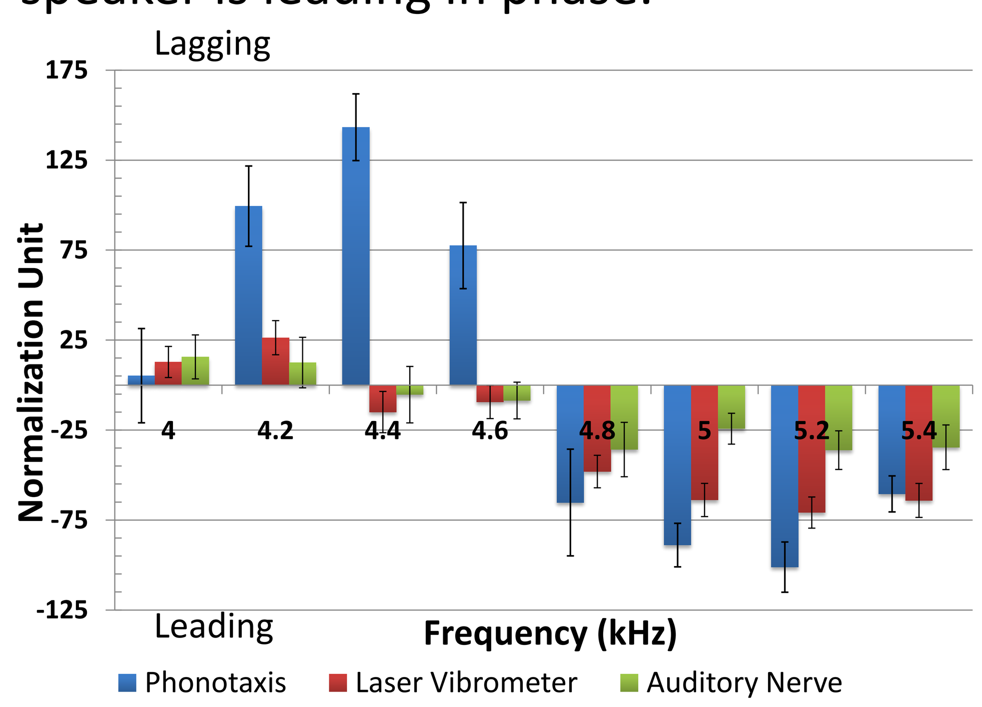
Sample trace of a recording during the 90° phase-shift stimulation.



At lower frequencies (4.0-4.4kHz) the auditory afferent response was stronger when the ipsilateral speaker was lagging in phase, and at higher frequencies (4.4-5.4kHz) the response was stronger when the ipsilateral speaker was leading in phase. At N.U. = 0 the afferent response was equal for both leading and lagging conditions.

Conclusions:

The phonotactic behavior, tympanic membrane oscillations, and afferent auditory nerve activity all reflect a similar response to a 90° phase-shift. At low frequencies each respective level of the auditory system has a greater response when the ipsilateral speaker is lagging in phase, and it has a greater response at higher frequencies when the ipsilateral speaker is leading in phase.



The Next Steps:

- Test the same animals using all three methods in order to more closely compare the response at each level of the auditory system.
- Puncture the medial septum to check its role in increasing the directionality of the system by creating an internal phase-shift.
- Test different degrees of phase-shift to see how different shifts affect the system, and determine the size of the phase shift created by the medial septum.

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