Hearing in the Praying Mantis

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1. Introduction of Hearing Morphology

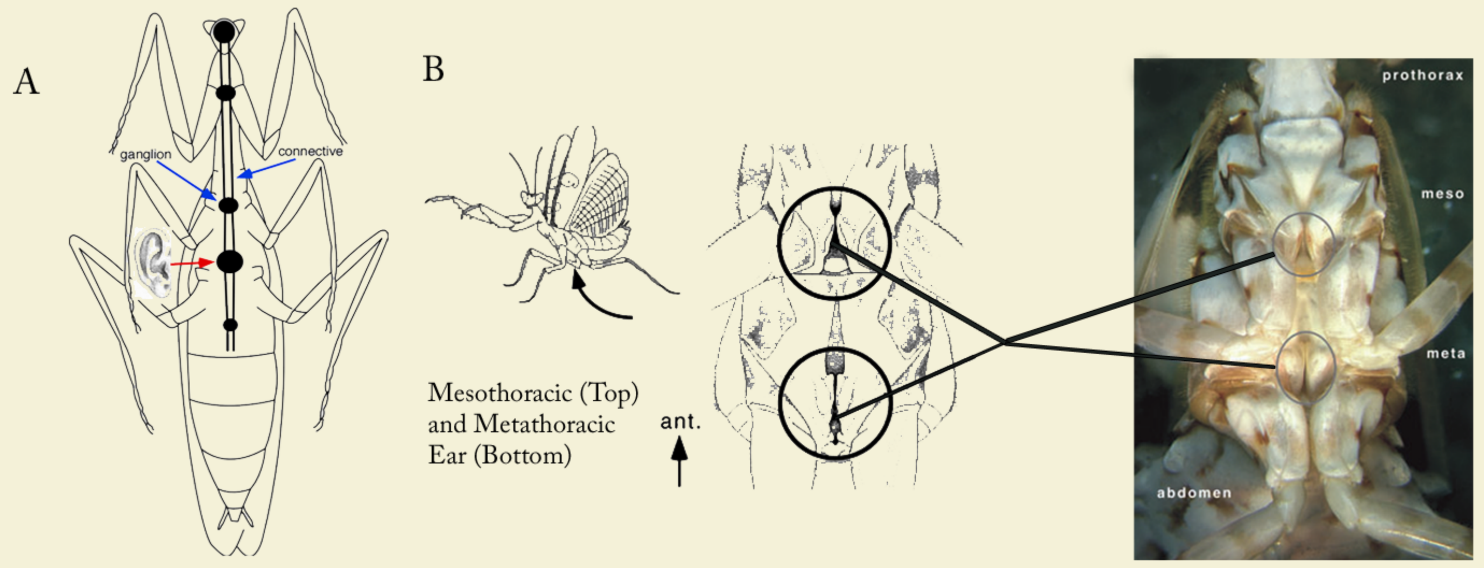

Figure 1: Basic Hearing Model of Praying Mantises
Mantises have a decentralized nervous system composed of several ganglia that connect to unidirectional auditory organ (A). Auditory signals are processed in either the lower metathoracic ear or the higher mesothoracic ear (B).

Our prior research has shown that mantises are able to process auditory signals using ears located on its ventral thorax (Fig. 1A). These ultrasound-sensitive ears are distinguished in structure and function; one ear is located on the metathoracic region and another on the upper mesothoracic region (Fig. 1B).

Most mantises have an ultrasound-sensitive ear in the ventral midline of the metathorax (MT), and a few lineages have additionally evolved a second, serially homologous ear sensitive to 2–4 kHz in the mesothorax (MS). Each auditory organ contains both a tracheal air sac and an eardrum, which are vital for auditory processing. We have set up two approaches to investigate the structure of both tracheal systems: using Mercox to create external casts of the ear, and using x-ray tomography (3–6 μm resolution) to create 3D reconstructions. Casts show a much smaller and shallower invagination of the tympanum (eardrum) which may underlie differences in sensitivity between the MT and MS ears. Reconstructed models show a notable increase in volumetric size of the two bilaterally symmetrical tracheal air sacs, located directly beneath the insect's ears, as the mantis develops. The orientation of the different ear structures and their varying attachments provides a clearer understanding of signals that lead to behavioral responses. Anatomical findings on the tracheal systems can be used to ascertain the interaction of high and low frequency sounds and their effect on each others' response. Threshold values and sensitivity at different frequencies were determined to obtain the typical pattern of the auditory response, then used as a baseline comparison from which to view changes in the response. In addition to investigating the basic structural vs. functional relationships of the mantis' auditory system, understanding what factors influence the underlying neurophysiological response allows us to paint a more comprehensive picture of the mantis' auditory system. Additional work has focused on understanding the multi-modal interaction of visual cues on the auditory response. Both the mantis and its main predator, ultrasound-emitting bats, are nocturnal; thus, we expect to find a strengthened, more sensitive response in dark environments as opposed to light environments. Preliminary findings suggest a complicated scenario: although the auditory response may indeed be longer in the dark, it reacts faster in the light.

2. Mercox Casts /X-Ray Tomography Reveal Intricate Tracheal Patterns

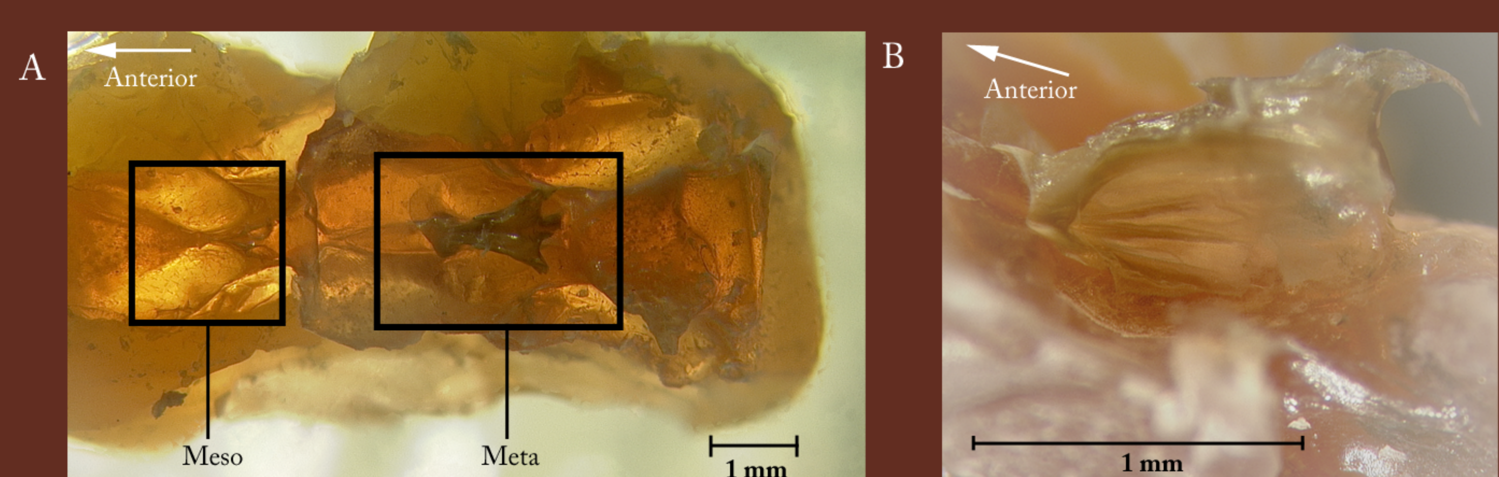

Figure 2. *A full external Mercox cast of the meso and metathoracic ear (A). (B) shows a magnified image of a metathoracic tympanum.*

Casts are created using Mercox II, a catalyst activated polymer with a relatively quick cure time. A wax well is constructed directly on the external cuticle, and the Mercox resin is applied. The prep is immediately placed in a vacuum chamber in order to eliminate any air bubbles. The Mercoxs does not adhere to the cuticle and is readily removed. Any residue tissue attached to the cast is dissolved away in a 5% KOH solution. Once cleaned, the cast is ready for analysis. The MS ear shows a much smaller and shallower groove when compared to the MT ear. The full thoracic cast clearly shows both ears and their relative size along the midline. The MT ear is given support by a hard internal cuticular structure called the furcasternum. Initial examination of the mesothorax has not yielded an analogous structure. The lack of an analogous structure almost certainly accounts for differences in acoustic properties. Further study needs to be done on the exact dimensions of the MS ear as well as on its inherent acoustic properties.

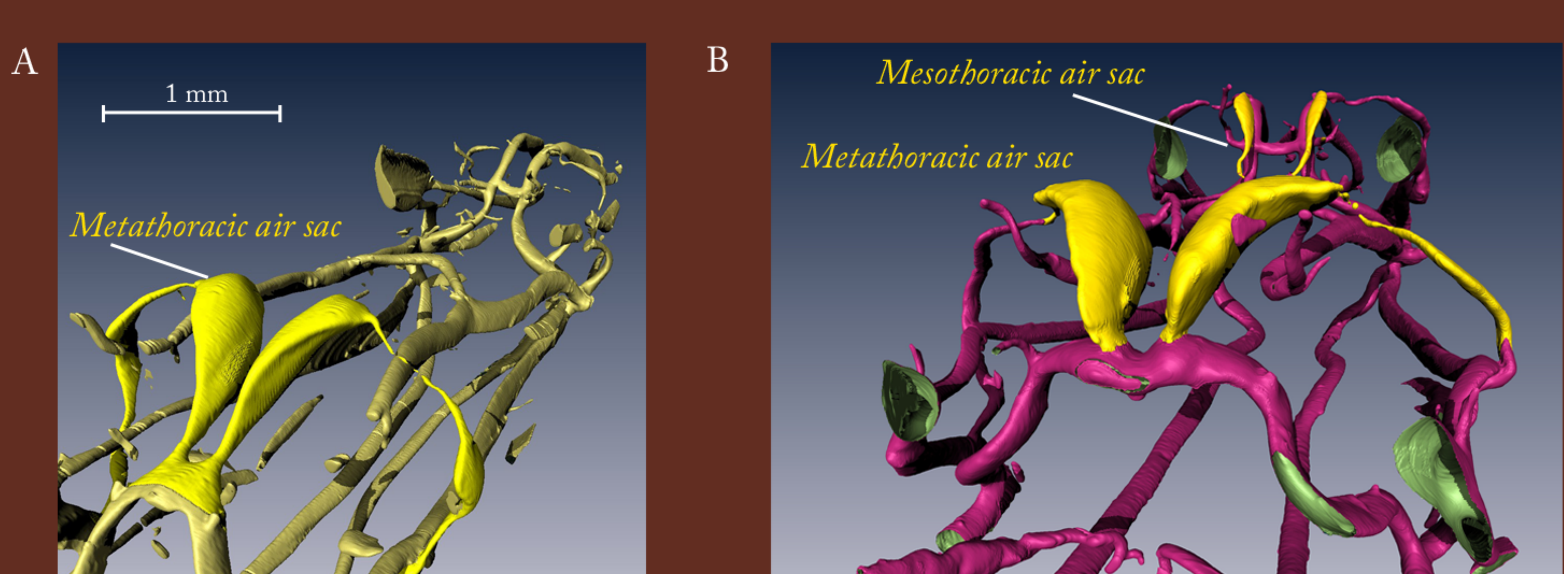

Figure 3. *Tracheal patterns reconstructed using 3D software show bilaterally consistency between a Parasphendale agrionina (A) and a Pseudocreobotra ocellata (B). The Para seems to lack a mesothoracic air sac, while the Pseudo has both a metathoracic and mesothoracic air sac.*

Using X-Ray tomography at 3-6 μm resolutions, cross section slices of the mantis thorax were compostited using 3D software to generate the mantis thoracic tracheal plan. Noticeable patterns emerged from these composites, such as consistent bilateral symmetry and increasing tracheal air sac volume across nymphal stages of development.

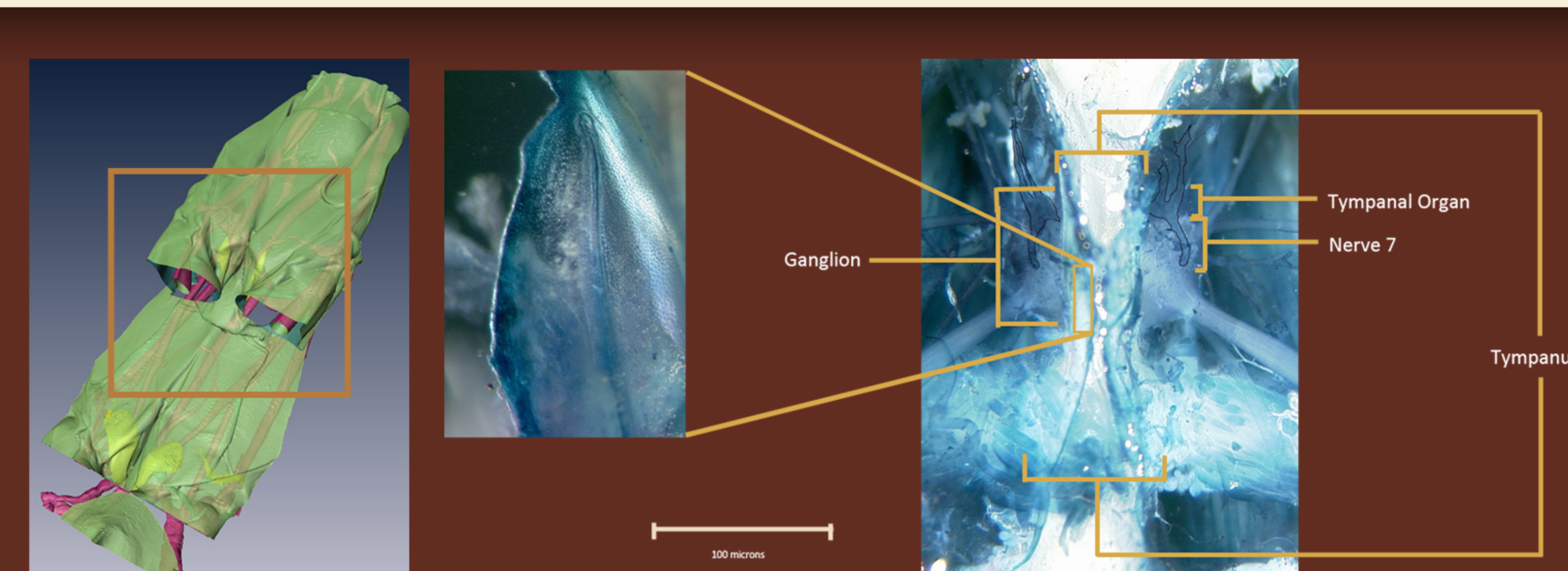

Figure 4. *The bilaterally symmetrical orientation of the mesothoracic ear. The magnified image of the tympanum shows the potential attachment site of the tympanal organ to the tympanum. We believe the spiral pattern leads toward the dimple that the tympanal organ attaches to.*

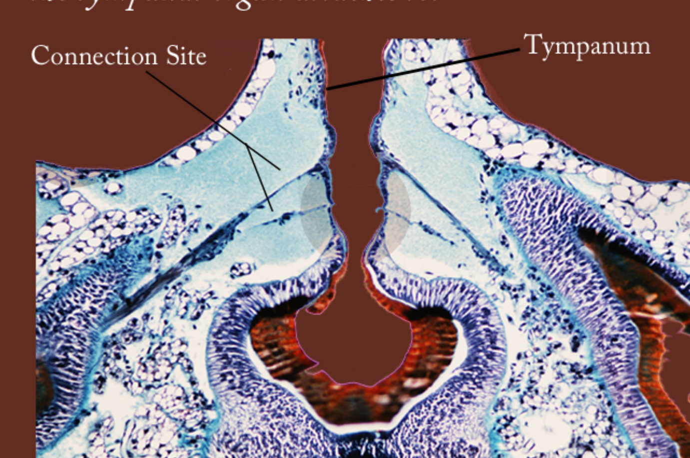

Figure 5. *A microscopic crossection of the mesothoracic ear representing the images used to calculate scolopales within the attachments of the tympanal organ to the tympanum.*

The bilaterally symmetrical mesothoracic ear is structured by the tympanum, a tympanal organ, and a tracheal sac on either slide of a deep slit. The typanmum is hard cuticle that vibrates in accordance to varying pressures between its two walls. At the center of the ear is the mesothoracic ganglion from which nerve 7 relays auditory signals to the rest of the body. Nerve 7 attaches the ganglion to the tympanal organ, which contains chordotonal sensilla that interpret the vibrations coming from the tympanum and send correlating signals through nerve 7. Chordotonal sensilla are made up of a bipolar neuron and a scolopale. By examining numerous cross-sections of the mesothoracic ear we can search for the scolopale caps to locate the presence of a neuron. Calculating the number of scolopales allows us to accumulate an impression of the amount of neural activity in different attachments of the tympanal organ. We have been working to find the exact attachment site and orientation of the tympanal organ to the tympanum because the anatomical information provides a clearer picture of the path neural signals take to receive and interpret stimulus, and thus more broadly how the ear functions.

3. Hearing Sensitivity Varies Between the Meso- and Metathoracic Ears

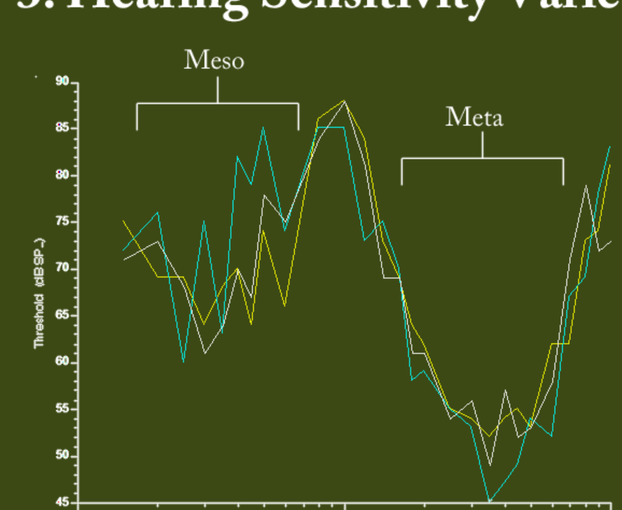

Figure 6. *Threshold values of P. ocellata at various frequencies. The mesothoracic ear is sensitive from 2 to 4 kHz while the metathoracic ear is sensitive from 30–40 kHz.*

Research shows that the mantis has an auditory response in acoustic as well as ultrasound wavelength (2 – 100 kHz). The threshold values of *P. ocellata* exhibit a sharp change in threshold from 10 kHz to 100 kHz. The pattern shows that *P. ocellata* auditory response is most sensitive between 30 to 40 kHz, which relates to metathoracic hearing.

4. Low Frequency Inhibits High Frequency Response

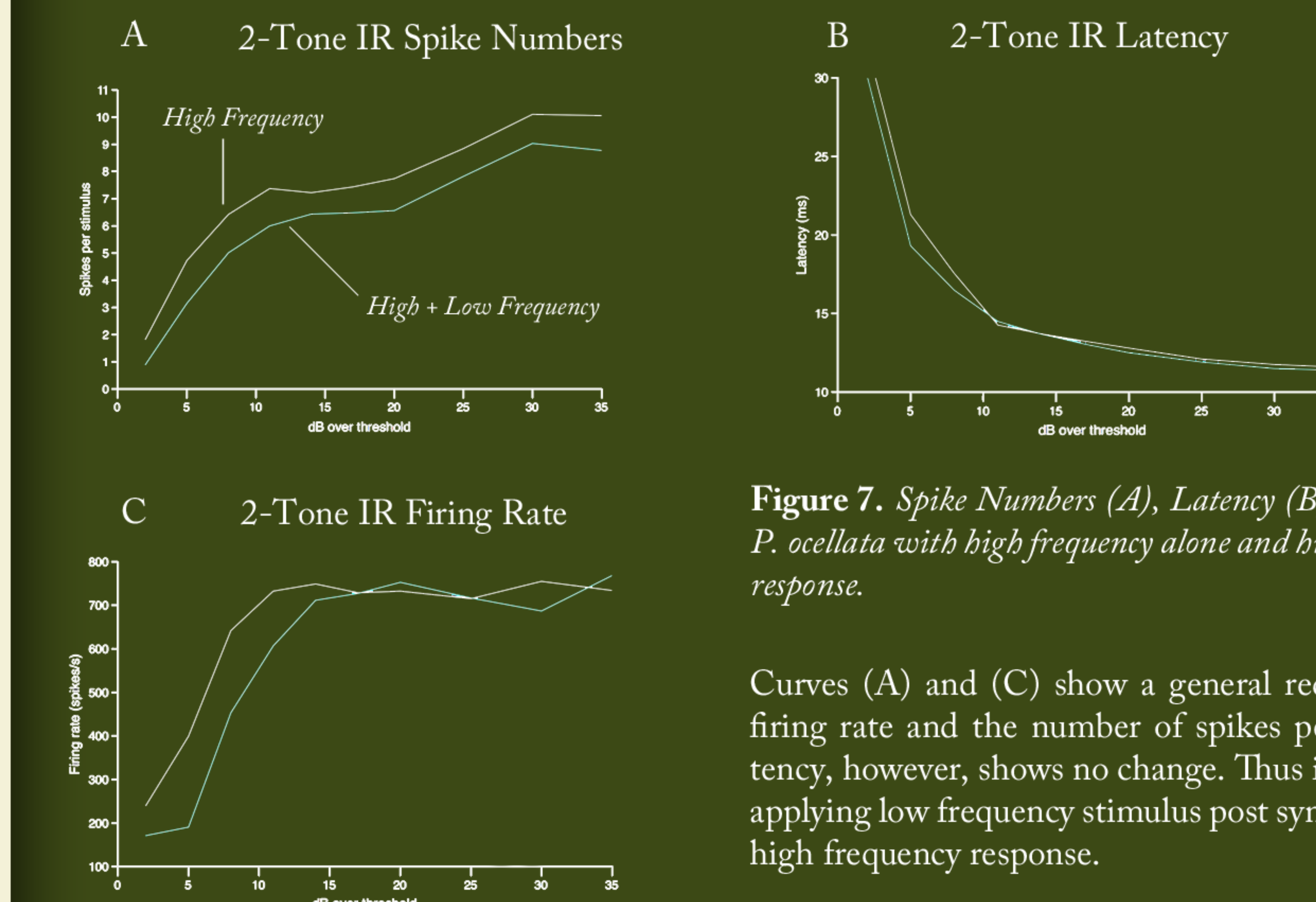

Figure 7. *Spike Numbers (A), Latency (B), Firing Rate (C) of P. ocellata with high frequency alone and high plus low frequency response.*

Curves (A) and (C) show a general reduction in both the firing rate and the number of spikes per stimulus. The latency, however, shows no change. Thus it was theorized that applying low frequency stimulus post synapticaly inhibits the high frequency response.

5. Lighting Condition Affects Descending Auditory Response

Figure 8. *An ultrasound stimulus elicits a stereotyped escape behavior in the mantis.*

Figure 9. *Descending auditory response in the dark is stronger and longer, as opposed to in the light.*

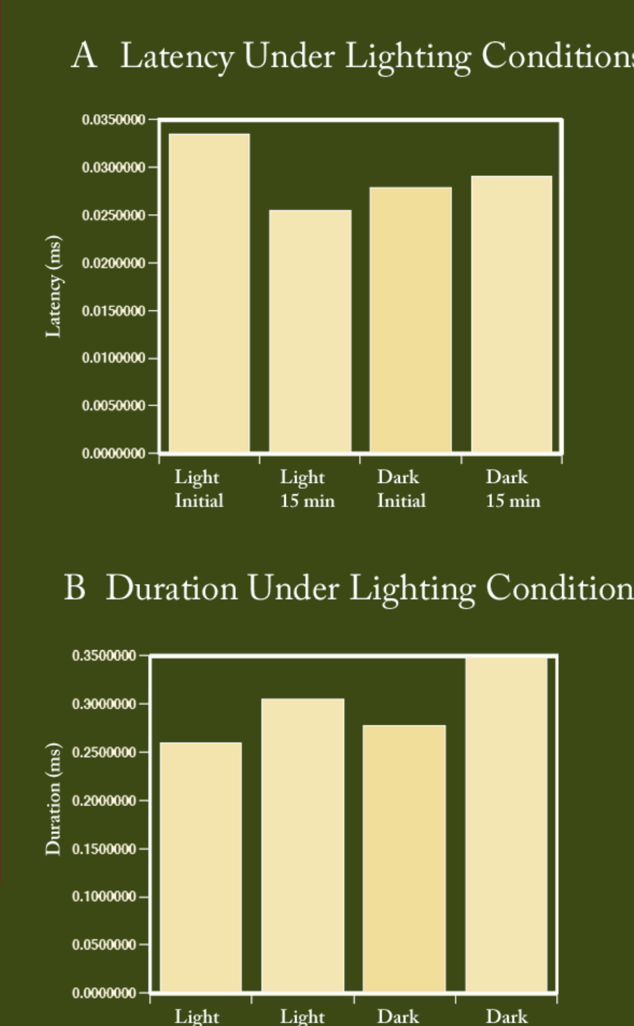

Figure 10. *Two factors 'hide' the short light latency seen in our data (A). 1. There is a carryover from dark trials of delayed latency into light initial trials. 2. One experiment with an abnormally slow reaction time (long latency) is obscuring the means of the light conditions. High variability among the experiments obscures the means seen in graph (B), however, taking into account outliers, preliminary data shows that the response duration is longer in dark conditions.*

Understanding the multi-modal interaction of visual and auditory cues is essential to providing a comprehensive picture of the mantis' auditory system. Differences observed in the auditory response, in the light versus the dark, could impact how future mantis research is conducted; significant differences between the two would strongly imply lighting is a variable that should be controlled across experiments (either conduct all experiments in the dark, or all in the light).

By using an extracellular glass suction electrode, we were able to record the descending auditory response to a 30 kHz, 200ms ultrasound stimulus. We analyzed four aspects of the response: latency, total duration, number of total action potentials (spikes), and the number of different neurons firing. Our findings to date show a longer response duration in the dark, but a significantly faster response (shorter latency) in the light conditions. This latter finding is intriguing as one would naturally expect a nocturnal species with nocturnal predators to react faster in the dark. Although a greater sample size is needed to better explain variability observed, analyzed data concludes that the lighting condition does indeed differentially impact the descending auditory response.

Acknowledgements
We would like to thank Dr. David D. Yager for allowing us to learn and develop under his supervision, and for guiding us each on our specific projects. This research was supported by NSF Grant No. IBN 9808859 (DDY).