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Abstract. Our current understanding of the mating game for many mosquito species is that males aggregate in noisy mating swarms and listen with their Johnston's organs (JOs) for the deeper flight tones of approaching females, to which they are attracted. As has been demonstrated, at least for the most intensely studied vector species, the mechanical resonance of the flagellum and the frequency range of the female's JO is far below that of the male's flight tones. Therefore, it has been assumed that females do not use hearing to detect the presence of males. Here we reveal that this may not be the case, and that the JOs of female *Culex quinquefasciatus* are exquisitely tuned to low frequency distortion products in the vibrations of the antenna due to a nonlinear interaction between her own flight tones and those of a nearby male. She can hear male flight tones by virtue of, and not despite, hearing her own flight tones.

Keywords: Johnston's organ, distortion products, mosquitoes
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INTRODUCTION

The auditory Johnston's organ (JO) of the antennae of male mosquitoes is slightly mistuned to the flight tone of female mosquitoes. The female JO, however, is tuned to frequencies well below the male flight-tone. This led to the tentative conclusion that the female JO has no biologically relevant auditory function [1]. This conclusion was strongly challenged by the finding that tethered, flying, female mosquitoes interact acoustically with each other and with artificial tones [3]. The performance of auditory organs as receivers in antiphonic communication is commonly tested in response to pure tones. The JOs of mosquitoes should, therefore, be tested in response to tone pairs, thereby mimicking the normal acoustic challenge of the mosquito, which is to detect the flight tones of other mosquitoes against the background of its own flight tones. Auditory systems have been shown to behave as nonlinear amplifiers, which tend to distort sounds and generate distortion products when stimulated by pairs of tones (f_1 and f_2). The mosquito JO also behaves as a nonlinear amplifier and is known to produce distortion products [3]. Are audible distortion products produced in a mosquito when its hearing organs are stimulated by tones at frequencies similar to those of their own flight tones and those of a conspecific of opposite sex?

METHODS

Laboratory bred *Culex quinquefasciatus* mosquitoes were anaesthetized by cooling and secured by their dorsal thorax with insect wax to a fine wire for flight tone-recordings or an Ag-AgCl reference block for electrophysiological recordings from the JO with a pair of tungsten electrodes or for mechanical measurements of the flagellum with a self-mixing interferometer [2]. The particle velocity level of the constant tone used in the experiments to mimic the mosquitoes own wing beats was measured with a particle

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velocity microphone (Kowles NR-23158-000) from a flying tethered mosquito. The particle velocity level was calculated in the far field and the sound system calibrated so that known particle velocity levels could be delivered through two Beyer DT770 headphones, in the near field, where the particle velocity level cannot be directly measured.

RESULTS

Isoresponse, mechanical tuning curves based on measuring the particle velocities required to elicit 6 nm displacements of the female antennae, 240 µm from its base, to pure tones revealed that the female JO is most sensitive to frequencies below 200 Hz, but can respond mechanically to frequencies in the range of several kHz. Mechano-electrical transduction by the JO is, however, limited to frequencies below 400 Hz at behaviourally relevant sound intensities. This finding was based on measurements of isoresponse, electrical tuning curves of the particle velocities necessary to evoke a 0.2 µV extracellular receptor potential from the JO. The female's antennae produces large $2f_1 - f_2$ distortion products in response to two stimulus tones (where $f_1 < f_2$). One of the tones (f_1) was held constant at 400 Hz and at a level that mimicked the females own flight tone as detected by her JO. The variable tone mimicked the flight tone of a nearby male mosquito, as would be detected by the JO, which is within range of the mechanical responses of the JO, but beyond the range of the mechanoelectrical transducer. This combination of tones produced low frequency $2f_1 - f_2$ electrical distortion products which peaked sharply at the flight tone frequency of the male.

CONCLUSIONS

The female JO is not tuned to the male flight tone but is very sharply tuned to a product produced between the mixing of her own flight tone with that of a male. The distortion product produced, when she is approached by a male mosquito, lies within the sensitive low frequency region of the electrical and mechanical responses of the JO and flagellum of the antenna.

ACKNOWLEDGMENTS

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COMMENTS AND DISCUSSION

Manuela Nowotny: I really enjoyed your talk, Ben, and I like the idea that not only are we able to use DPOAEs to learn something about hearing but animals also using DPOAEs for communication. Is it right that the mosquito can change its wing tone and thus the frequency of the distortion product?