Directional Hearing in the Locust
Schistocerca gregaria Forskål (Acrididae, Orthoptera)

Lee A. Miller
Institute of Biology, Odense University, DK-5230 Odense, Denmark

Received March 28, 1977

Summary. At 2 kHz, 3.5 kHz and 5 kHz the locust ear functions as a mixed pressure and pressure-gradient receiver. The ear is inherently directional at these frequencies. The directional characteristics are independent of the amount of body tissue (Figs. 6 and 7). At 15 kHz the locust ear functions mostly as a pressure receiver, and is inherently non-directional (Fig. 6d). Hearing is, however, directional at 15 kHz owing to diffraction caused by the body (Fig. 1). Auditory thresholds are influenced by the amount of body tissue at frequencies from 2 to 15 kHz (Fig. 8). At frequencies less than 6 kHz the sound conducted through the body is attenuated by 1 to 8 dB depending on the amount of body tissue. At frequencies greater than 12 kHz the sound conducted through the body is attenuated by up to 18 dB, and the attenuation is only slightly influenced by body tissue (Fig. 2). The attenuation of sound conducted through the body is independent of the direction of sound, but may be affected by the amount of tissue between the ears (Fig. 4). The tissue in the body appears to act as a ‘resistive’ element, which introduces a phase shift in the sound conducted through the body relative to that striking the front side of the tympanum. Body tissue can set the level of sensitivity, but does not influence the receiver characteristics of the ear.

Introduction

Acridid grasshoppers have two bilaterally symmetrical ears (tympanal organs) located in the first abdominal segment. The intact locust ear functions primarily as a pressure receiver at frequencies above about 10 kHz (Michelsen, 1971c). This conclusion is based partly on the fact that very little sound reaches the back side of the tympanum owing to attenuation in the body. Consequently, the ear itself should not contribute to directionality at high frequencies. The situation below about 8 kHz is more complex. A considerable amount of sound can reach the back side of the tympanum suggesting that the ear itself might function more like a pressure-gradient receiver. To what extent the intact locust ear functions
as a pressure-gradient receiver at lower frequencies cannot be determined from existing studies (Katsuki and Suga, 1960; Autrum et al., 1961; Michelsen, 1971 c; Römer, 1976). (For a detailed account of the physiological and biophysical aspects of insect hearing see Michelsen and Nocke, 1974). The amount of tissue in the locust body greatly affects the auditory threshold, with sensitivity being inversely proportional to tissue weight at frequencies below about 10 kHz (Michelsen, 1971 c; Römer, 1976). Michelsen (1971 c) suggests that the low sensitivity is due to internal dampening, which is probably caused by large amounts of tissue in bodies of fat animals. Body tissues, then, may influence the directional characteristics of the ear at frequencies below 10 kHz.

In this paper I describe hearing in the desert locust (Schistocerca gregaria Forskål) as a function of angle of incidence, body tissues, and frequency. I also describe the diffraction of sound caused by the body and the attenuation of sound conducted through the body as a function of body tissue, angle of incidence, and frequency.

**General Methods**

Experiments were performed in a sound tunnel located in a small room, which was insulated with 10 cm of mineral wool. The sound tunnel and sound generating apparatus were identical to that described by Michelsen (1971 a). Sound pressure levels (SPL) are given in dB values relative to $2 \times 10^{-5}$ Newtons/m$^2$ if not otherwise stated.

A holder was designed to rotate the animal in the sound field. It consisted of a fork composed of two hypodermic needles 2 mm in diameter and 15 mm long mounted 15 mm apart in a brass block measuring 25 mm by 8 mm by 5 mm. The brass block was mounted on a brass rod 8 mm in diameter and 153 mm in length. The holder could be rotated continuously through 360°. The holder was grounded and served as the reference electrode in physiological experiments.

Adult Schistocerca gregaria (Forskål) 2 to 11 weeks after the final moult were used in these studies. In some cases individuals were starved for up to 28 days to reduce fatty tissues in the abdomen. In all cases a period of 12 h elapsed between the last feeding and experimentation.

The animals were prepared for experimentation by first removing the head, legs and wings. The gut was not removed. The insects were then impaled on the holder ventral side up through the mesothorax and the second or third abdominal segment. At 0° the ear (or microphone that replaced the ear) faced the sound source, which was placed 70 cm from the preparation. The preparations were rotated counter clockwise when right ears were examined and clockwise when left ears were examined (see inset in Fig. 5b).

The tissue located between the ears was weighed following each directional hearing and conduction experiment. The animals were arbitrarily divided into four weight groups (WG) based on the amount of tissue between the ears.

The sound field was calibrated with a 1/8 inch microphone (free-field) and accessory apparatus (Brüel & Kjaer). The microphone cartridge was mounted on a right angle adaptor such that the preamplifier was located about 10 cm below the preparation. The microphone (together with the right angle adaptor and preamplifier) was omnidirectional to within ±3 dB up to 60 kHz. The sound field around the preparation was uniform to within ±0.5 dB at 5 kHz, and ±1 dB at 15 kHz. dB values are relative to the sound pressure level in the undisturbed sound field at 0°.

An IBM 360/65 digital computer using a standard IBM Fortran IV G level compiler and the Statistical Analysis System (University of Kentucky Computing Center) was used to perform analyses of variance, including two and three-way analyses, on the data. The homogeneity of variances was confirmed using the $F_{max}$ test (Sokal and Rohlf, 1969). Several analyses of variance models were tested on the data to obtain the $P$ values presented below. $P$ represents the chance for obtaining an $F$-value greater than that given by the test.