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Mechanical Time Resolution in Some Insect Ears

I. Impulse Responses and Time Constants

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Summary. 1. The mechanical time resolution is estimated in the ears of noctuid moths (Noctuidae) and locusts (Acrididae). The vibration velocity of small areas on the tympanal membrane is measured by means of laser vibrometry. The impulse response (Figs. 2B and 5A) and the transfer function (Fig. 3) are obtained directly by stimulation with very short impulse sounds and pure tones, respectively. The transfer function is also calculated from the experimentally determined impulse response, and vice versa. Finally, the impulse response is obtained by calculation from the measured vibrations caused by noise. The directly determined and the calculated transfer functions are rather similar (Fig. 3A–B).

2. The impulse response of the attachment area of the receptor cells in the *noctuid* ear is a short, damped vibration with a 'time constant' of about 60 µs (Table 1). The attachment area of the receptor cells can thus separate impulses arriving with time intervals larger than 150–200 µs (Fig. 4).

3. The 'time constant' of the attachment area of the d-cells in the *locust* tympanum is about 90 µs (Table 1). The 'time constant' for other parts of the locust tympanum varies between 50 µs and 200 µs (Fig. 6).

Introduction

The properties of acoustic systems elucidated in experiments depend upon the nature of the sound stimuli used. Long, pure tones cause steady-state vibrations in the hearing organs, and they are ideally suited for exploring how auditory systems receive and handle information about frequency and intensity. Although some animal calls and human sounds consist of long, pure tones, most biological sounds contain rapid modulations of frequency and amplitude. Many insect songs for instance are composed of long series of very short sound impulses, each impulse lasting up to a few hundred µs. In theory, such complicated sound signals may carry a great amount of information, but we are vastly ignorant about the ways, in which auditory systems extract the specific information from such signals.

'Clicks' are often used for determining the auditory 'time resolution', i.e., the dynamic aspects of hearing. But a click is not a well defined stimulus, unless its frequency spectrum is known. Furthermore, the frequency spectra of pairs or series of clicks differ from those of single clicks. It is therefore not easy to interpret the results of most of the experiments, in which such sound stimuli have been used for elucidating the auditory time resolution.

The 'time resolution' of the ear is determined by the dynamic properties of both the mechanical structures and of the receptor cells. The aim of these studies is to investigate the time resolution in the auditory system of some suitable animals, starting in the periphery and moving towards the higher order neurons. Insect ears are well suited for such studies, since they vary greatly in complexity. The ears of noctuid moths contain only two receptor cells attached to a tympanal membrane, and only one of the cells is excited at low sound levels (Roeder and Treat 1957). The locust ear contains four groups of receptor cells attached to four areas on the tympanum, and these groups have different frequency sensitivities (Michelsen 1971). In the ears of crickets and bushcrickets the receptor cells are not attached to the tympanum; furthermore the sound waves may reach the tympanum through different pathways, and the time resolution is therefore even more complicated (paper II – Larsen 1981).

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The vibrations activating the receptor cells can be observed in detail by means of laser vibrometry (Michelsen and Larsen 1978). By simultaneous recordings of neural responses and vibration measurements, it is possible to study the dynamic properties of the mechanical structures and of the receptor cells separately. In this study we measured the vibration velocity of the mechanical parts of the ear, while driving the ear with three kinds of sound stimuli: pure tones, very short impulses, and noise. The response of the ear is described in the frequency domain by means of the *transfer function* ($H(\omega)$), and in the time domain by the *impulse response* ($h(t)$).

The transfer function is easily obtained by measuring the vibration velocity (v), while driving the ear with a sinusoidal sound wave, since $v=H\cdot F$, where F is the driving force. The impulse response may be obtained directly by stimulating the ears with very short sound impulses. Ideally, the sound impulses should have the properties of Dirac's Delta-function, $\delta(t)$; i.e., they should be very short, intense 'clicks' with a duration less than 10% of the time constant of the system under study (see e.g. Varjú 1977).

In linear systems it is possible to calculate the transfer function from the impulse response by means of the Fourier transform. Randall (1977) gives a simple description of these mathematical operations. The impulse response may also be obtained by stimulating the ears with noise and cross-correlating the velocity with the driving force (see e.g. Glaser and Ruchkin 1976). These methods do not apply to non-linear systems, however. One aim of the present study is to investigate, whether the mechanical behaviour of the ears is so close to linearity as to justify such calculations as alternative ways of determining the transfer function and impulse response.

The 'Time Constant'. The impulse response represents, so to speak, the memory of the system. The time constant (τ) is a convenient parameter for describing the oscillatory decay of lightly damped second order systems (e.g., a mass connected to a lightly damped spring), in which the response to a Delta-impulse is given by

$$h(t)=\alpha_o\cdot \mathrm{e}^{-t/\tau}\sin(2\pi f_l\, t) \qquad (1)$$

where α_o is the initial amplitude and t is the time. τ is the time elapsed from the maximum vibration amplitude to the point where the envelope of the impulse response has decreased to 37% ($=\mathrm{e}^{-1}$). f_l is the oscillation frequency (which in lightly damped systems is very close to the resonance frequency of the undamped system).

The behaviour of a membrane vibrating in its basic mode resembles that of a second order system. However, the oscillatory decay of a lightly damped membrane is not described by a simple function (like e^{-kt}), but by a more complex expression containing Bessel functions. The qualitative behaviour is, however, so similar to the type of decay described by (1), that we shall use the time constant τ for describing the decay.

Materials and Methods

Animals and the Properties of the Ears. Noctuid moths, *Agrotis segetum* Schiff., were supplied as pupae by the Danish Plant Pathology Institute. After the final moult the animals were kept at 10 °C and fed on honey-water for up to two weeks. Only male moths more than 4 days old were used in the study. After decapitation and removal of all appendages, the animal was waxed to a small platform. The abdomen was bent to one side, and the tympanal membrane of the ear was exposed by removing the structures protruding over the tympanic recess. This allowed the laser beam to be focused on the opaque patch of tracheal epithelium surrounding the attachment point of the receptor cells in the centre of the tympanum. (For further details on the anatomy, see Ghiradella 1971).

Locusts, *Schistocerca gregaria* Forskål, ph. gregaria, were supplied as adults or larger instars by Bioserv Ltd., Sussex, and used about one month after the final moult. The sclerotized ring encircling the tympanum and a small portion of the surrounding tissue was excised and mounted on a small platform (see Michelsen 1971). The tympanal membrane is bean-shaped and about 1.5 times 2.5 mm at its widest. Most of the membrane is a few μm thick, but part of it is 8–10 μm thick. Four groups of receptor cells (named the a–d cells) attach to four cuticular bodies situated near the border between the thin and the thick parts of the membrane (see Fig. 6). For details concerning the anatomy and the mechanical properties of the preparation, see Gray (1960) and Michelsen (1971). Most of the measurements were taken from the attachment area of the d-cells. These cells respond to 10–20 kHz, whereas the three other groups prefer 2–8 kHz. The d-cells appear to respond to the 3rd and the 4th vibrational mode of the thin part of the tympanum (Michelsen 1971). Their attachment area vibrates perpendicularly to the plane of the membrane, whereas the cell bodies appear to remain stationary at 10–20 kHz (Michelsen 1973).

The noctuid ear was almost intact during the experiments, and – as judged from the phase angles – it was close to being a pressure receiver in the frequency range investigated. The acoustical properties of the *intact* locust ear are rather complicated (Miller 1977). The *isolated* locust ear used in the experiments is a pressure-gradient receiver of known acoustical properties (Michelsen 1971). In both the hearing organs studied here, the amplitude and the phase angle of the force driving the tympanal membrane can therefore be calculated from the sound pressure measured close to the preparation.

Experimental Methods. Most of the apparatus, the acoustical conditions, and the experimental technique are described by Michelsen and Larsen (1978). All sound pressure levels in this paper refer to $2\cdot 10^{-5}$ N/m^2=20 μPa. The signals from the microphone ($^1/_4''$) and the vibrometer were analyzed 'on-like' with a PDP8/e minicomputer equipped with programs for averaging, cross-correlation, and Fourier transformation. In order to handle high-frequency signals we constructed a fast analog-to-digital converter with a peripheral memory (maximum sampling rate 200 kHz, corresponding to a theoretical upper frequency limit of 100 kHz). In a few experiments the apparent sampling rate was increased to 800 kHz by recording the signal on a magnetic tape recorder (HP 3960) and playing it back at one quarter of the recording speed. Before the signals were digitized, they were low-pass filtered (slope 18 dB/octave) to prevent aliasing and to suppress harmonic components (see e.g. Braun 1975).

Pure tone stimuli were generated as described by Michelsen and Larsen (1978). The signals from the vibrometer and the microphone were sampled, digitized, and 100 single records were averaged before the vibration amplitude and the relative phase angle were computed. The phase angle was corrected for the phase distortion in the apparatus (see Michelsen and Larsen 1978), and the amplitude of the vibration velocity corresponding to a constant sound pressure level of 100 dB was calculated. The locust measurements were further corrected for the pressure gradient properties of the isolated ear (see Michelsen 1971). The final results represent the transfer function ('frequency response') between the force and the vibration velocity and could be used for calculating the impulse response (by applying the inverse Fourier transform).

Impulse sound stimuli were produced by a home-made electrostatic loudspeaker. 1024 single records of the tympanal response to loudspeaker generated sounds were averaged to improve the signal-to-noise ratio. For calculating the transfer function the impulse response was smoothed using Hann's weighting function, Fourier transformed, and corrected as indicated above.

The intensity of a short sound impulse cannot be indicated in a simple way. Measures like root-mean-square (RMS) values do not apply to single impulses of short duration. The expression for calculating the RMS-value includes an integration time, the size of which is rather arbitrary. Instead, the sound impulses may be described by means of their shape, peak pressure level, and frequency spectrum. From this information it is possible to calculate the total acoustic energy carried by the impulse. For the present purpose, however, it is not very interesting to know the total amount of energy, since the frequencies outside the frequency range covered by the ear under study will not be effective in causing a response. It is important, however, that the frequency spectrum is reasonably uniform within the frequency range studied. The impulse should be of such intensity as to cause vibrations of a reasonable amplitude (some hundred Ångströms). Very intense impulses should be avoided, since the ears may not behave as linear mechanical systems at large vibration levels. Finally, the total duration of the impulse should ideally be less than 10% of the time constant of the system under study.

The ideal impulse would then be very short and have a uniform frequency spectrum in the entire frequency range covered by the ear. In the case of the *noctuid moth ear* the sound impulses were produced by feeding a saw-tooth pulse (rise time 40 μs, fall time 6 μs) to the electrostatic loudspeaker. The sound impulses thus produced (Fig. 1A) were almost monopolar, of 16 μs duration, and with a uniform spectrum (less than 3 dB variation) between 18 and 38 kHz (the roll-off at high and low frequencies was about 12 and 22 kHz/octave, respectively).

The sound impulses used for the *locust ear* were produced by feeding a 5 μs rectangular impulse from a pulse generator (HP 8011A) into the electrostatic loudspeaker. The impulse sound produced was bipolar (Fig. 1B), of 2 × 13 μs duration, and had a uniform spectrum between 18 and 42 kHz (the roll-off at high and low frequencies was about 24 and 8 dB/octave, respectively).

Noise stimuli were produced by feeding electrical noise (uniform up to 50 kHz) from a noise generator (HP 3722A) into the electrostatic loudspeaker. The frequency spectrum of the noise corresponded to that of the bipolar impulse described above, and the sound pressure level was 80 dB at the position of the preparation.

The simultaneously recorded signals from the microphone (the input) and the vibrometer (the output) were cross-correlated.

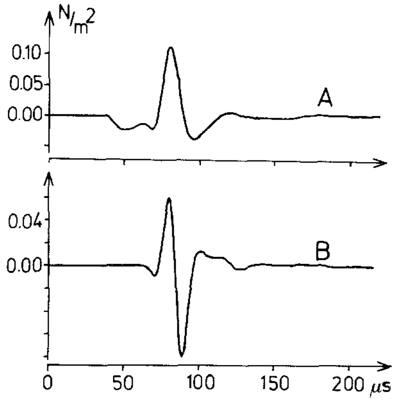

Fig. 1A, B. Impulse sounds used in the study. **A** The impulse sound used for stimulating the noctuid ear. **B** The impulse sound used for the locust ear. The peak sound pressure in **A** and **B** corresponds to 75 and 72 dB SPL

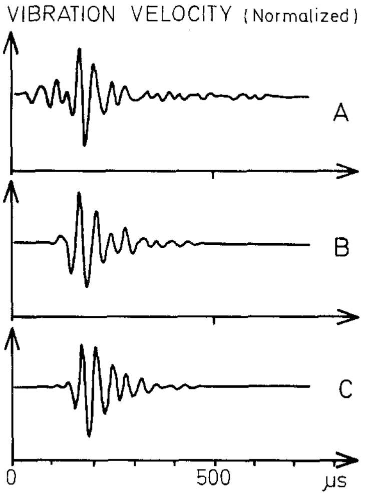

Fig. 2A–C. The impulse response of the *noctuid moth* tympanal membrane measured in three different ways. **A** Calculated from the amplitude- and phase-curves resulting from stimulation with pure tones (o——o in Fig. 3). **B** Produced directly by impulse sounds. **C** Produced by cross-correlating the noise sound input with the resulting membrane vibration velocity and averaging 100 single records. The responses have been normalized for the sake of comparison

100 single records of the cross-correlation function were averaged to improve the signal-to-noise ratio. The final result is the impulse response of the tympanum. From the impulse response the transfer function was calculated as described for impulse sound stimuli.

Results

In the *noctuid ear* the impulse response of the tympanal membrane measured by the three different methods (Fig. 2A–C) are rather similar in duration, period, and decay. The duration is typically 300–400 μs. The oscillation period is about 39 μs, corresponding to a resonance frequency of the tympanum of about 26 kHz. The decay is not quite exponential, but it

Table 1. The behaviour of the attachment areas of the receptor cells in two insect ears in the frequency and time domain, as measured by using three different sound stimuli. The numbers indicate mean value and standard deviation. N number of preparations; f_0 frequency of maximum velocity; Q_{3dB} the quality factor of the membrane determined from the velocity amplitude spectrum; T the dominating period in the impulse response; τ the 'time constant' of the tympanal membrane determined from the impulse response

Object/ preparation	Stimulus	N	f_0 (kHz)	Q_{3dB}	T (μs)	τ (μs)
Noctuid moth A-cells	Pure tones	4	27±2	4.9±0.9	37± 2	66±13
	Impulse sounds	19	25±5	4.8±1.3	40± 7	61±20
	Noise	9	26±5	4.6±1.1	39± 8	57±14
Locust ear d-cells	Pure tones	4	20±4	5.4±1.0	52±17	84±10
	Impulse sounds	13	23±4	6.3±0.8	45± 7	89±11
	Noise	9	20±2	5.6±0.6	52± 4	91± 6

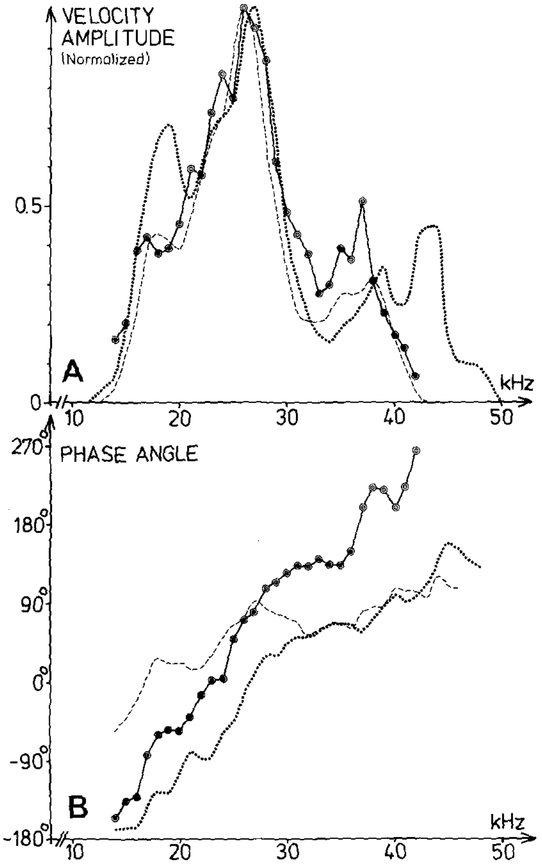

Fig. 3A, B. The transfer function of the *noctuid* tympanal membrane measured in three different ways. **A** The amplitude part of the transfer function (the curves have been normalized to show differences). **B** The phase part of the transfer function. (o—o): curves measured directly with pure tones; (...): curves calculated from the impulse response in Fig. 2B; (---): curves calculated from the impulse response in Fig. 2C

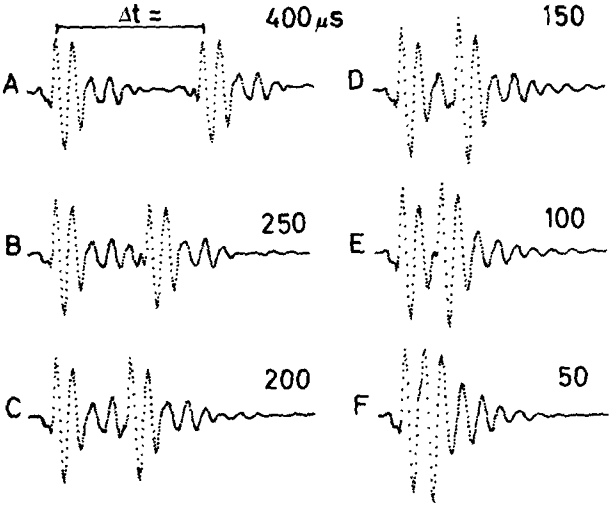

Fig. 4. The tympanal membrane response to double impulse sounds. The different responses have been obtained by varying the time interval, Δt, between the impulse sounds as indicated in the figures

is regular enough to allow a 'time constant' to be calculated. On the average the 'time constant' of the noctuid tympanum is 60 μs (Table 1).

The transfer functions determined with the three kinds of stimuli in the same preparation as in Fig. 2 are shown in Fig. 3. The transfer function ('frequency response') measured directly with pure tones or calculated from the impulse responses is a maximum at about 26 kHz and is moderately tuned ($Q_{3dB} \lesssim 5$). The amplitude curves (Fig. 3A) are rather similar, but typically with some disagreement between 30 and 50 kHz. At a sound pressure of 100 dB the 26 kHz maximum typically corresponds to a velocity of 10 cm/s. The phase curves (the phase angle between the sound pressure and the vibration velocity) determined in the three different ways show the same general development, but they vary as much as 150° from each other. The curves in Fig. 2 and 3 are typical. The results are summarized in Table 1.

Double impulse responses are produced when the membrane is stimulated with pairs of impulse sounds. Due to the small time constant of the noctuid tympanum, the two impulse responses are totally separated when the time interval between the impulse sounds

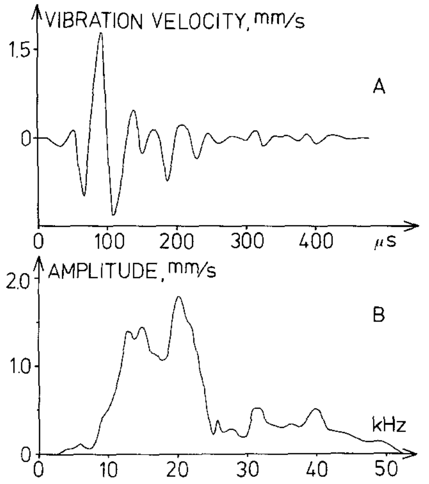

Fig. 5A, B. The impulse response and transfer function of the d-cell attachment area in the *locust* tympanum measured with impulse sounds. **A** The impulse response. **B** The amplitude part of the transfer function obtained from the response in **A**

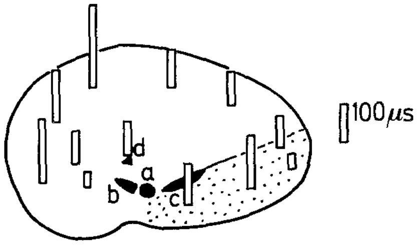

Fig. 6. Variation of local 'time constants' in the *locust* tympanum. The vertical bars represent the magnitude of τ at different positions on the membrane. *a–d* the four cuticular bodies of receptor cell attachment. White area: thin membrane; dotted area: thick membrane

is larger than 300–400 µs (Fig. 4A–B). Visually separate impulse responses are obtained, however, at intervals down to 150–200 µs (Fig. 4C–D). In contrast, if the time interval is smaller than 100 µs the impulse responses are superimposed and only one damped vibration is observed (Fig. 4E–F).

The impulse response of the attachment area of the d-cells in the *locust* tympanum is a damped oscillation about 300 µs in duration and with a 'time constant' of about 90 µs (Fig. 5A). The main period is about 50 µs corresponding to the second peak in the transfer function (20 kHz). The transfer function of the d-cell attachment area (Fig. 5B) has two maxima (resonances), at 12–15 kHz and at about 20 kHz. The results from all preparations and from all three methods are summarized in Table 1.

The locust tympanum vibrates in a complicated way with both basic and higher modes (Michelsen 1971), and the 'time constant' could therefore be expected to vary over the membrane. This is indeed the case (Fig. 6). In some positions only one measurement was obtained, in others measurements were carried out in 3–5 preparations. Recordings from the d-cell attachment area were easily obtained, and the 'time constant' was measured in 13 preparations. The number of successful recordings reflected the variation in optical properties over the membrane which made laser measurements very difficult at certain positions.

Discussion

The auditory time resolution was studied at the most peripheral level of the auditory system in two kinds of insects. Three different kinds of sound stimuli were used for determining the impulse response and transfer function of the tympanal membrane: pure tones, Dirac-impulses, and noise. The results obtained in the *noctuid moth ear* (Figs. 2 and 3) with these three methods are rather similar, both when transformed from the time domain to the frequency domain and vice versa. The experiments show that the amplitude of vibration is linearly related to the sound pressure, at least up to sound pressure levels of 100 dB. The present measurements confirm that the tympanum also behaves in the way expected from the theory of linear systems: for example the Fourier transform of the impulse response is indeed very similar to the transfer function obtained with pure tones. The measurements also demonstrate that these widely different methods give rather similar results, although the sound stimuli used were not quite ideal. This similarity further implies that the determined impulse responses and transfer functions closely approximate the 'real' impulse response and transfer function.

The sound stimuli used here were not quite ideal. The impulse sounds for instance should ideally have a duration of less than 10% of the time constant of the system under test (see e.g. Varjú 1977), i.e., less than 6 µs for the noctuid ear membrane. We were not able to produce such short impulses, but our impulses lasted about 16 µs. Therefore, the impulse response of the tympanum (and consequently the transfer function determined by calculation from the impulse response) are likely to be distorted. In the pure tone measurements, on the other hand, the vibrational response was only determined at some discrete frequencies, and the impulse response calculated from the pure-tone-generated transfer function is therefore inherently distorted. The largest, but systematic, deviations were observed in the phase curves (Fig. 3). This is not surprising, since small errors in the time relation between the sound and the resulting vibration may cause a systematic deviation in phase.

The mechanics of the noctuid ear appears to be rather simple. The tympanum vibrates in its basic mode at least up to 35 kHz, and the vibration has a resonance at 26 kHz. An almost circular and lightly damped, homogeneous membrane vibrating at its basic mode is likely to behave rather like a lightly damped second-order system, in which the time constant (τ) may be estimated from the formula

$$\tau = Q_{3dB}/(\pi \cdot f_o) \quad (2)$$

where f_o is the resonance frequency, and Q_{3dB} is the sharpness of the tuning to the resonance frequency. Using the values for f_o and Q_{3dB} from Table 1 (26 kHz and 4.8) one finds the expected τ to be 56 µs. The observed τ was about 61 µs (Table 1). These values are not significantly different from each other. The small time constant makes it possible for the tympanum to reproduce sound signals rather accurately in the time domain (Fig. 4). It remains to be learned, whether the two receptor cells attaching to the tympanum can make any use of this accurate information. Such studies are now in progress.

The *locust ear* is known to be much more complex. Four groups of receptor cells attach to an inhomogeneous membrane, where they pick up different modes of vibration and thus aquire different frequency sensitivities (Michelsen 1971). The frequency analysis is based partly on the occurrence in the tympanum of two sets of basic and higher modes of vibration. In addition, the receptor organ may vibrate in a complicated way (Michelsen 1973). The present study demonstrates that the mechanical time constant, as measured with impulse sounds with maximum energy at high frequencies, varies over the tympanal membrane. It remains to be learned, whether a similar variation in time constant occurs for other frequency ranges, and whether the receptor cells are able to make use of this variation in mechanical time resolution. The frequency spectrum of the songs produced by acridid grasshoppers has its main components in the same range as the impulse sounds used here, but these animals also appear to use their capacity for frequency analysis in the 2–8 kHz range for obtaining behavioural information (Skovmand and Pedersen 1978). Experiments with sound impulses (electrical sparks) covering the frequency range 3–14 kHz are in progress. The time constants of the impulse responses elicited are around 1 ms. The impulse responses are complicated and variable, but the sound impulses used so far have also been rather variable. Furthermore, we find it difficult to control the sound level of the electrical sparks.

Damping at Low and High Frequencies

The amount of damping (friction) in an oscillatory mechanical system determines both the degree of tuning around the resonance frequency (expressed as Q_{3dB}) and the time constant (τ). Lightly damped systems are inherently well suited as frequency analyzers, but they do not reproduce the time parameters of the sound very accurately. The opposite is true for highly damped systems. Equation 2 suggests that the animals may obtain a reasonable frequency resolution (high Q_{3dB}) and a good time resolution (small τ) by using high frequencies for communication. The time constants observed in the locust ear at low and high frequencies are close to those expected from Eq. 2, although Eq. 2 only applies to second order systems. Two basic modes of vibration are found in the locust tympanum (Michelsen 1971). One basic mode (corresponding to the entire tympanum) has $f_o = 1.8$ kHz and $Q_{3dB} = 2.8$, and the other basic mode (the thin part of the tympanum) has $f_o = 3.4$ kHz and $Q_{3dB} = 4.7$. According to Eq. 2 the time constants should be about 0.5 ms for both modes. The time constants in the preliminary experiments with 'low frequency' spark sounds are of this order of magnitude. The time constant observed at the attachment area of the d-cells by means of the 'high frequency' impulse sounds is also very close to that expected from Eq. 2 (by using $f_o = 21$ kHz and $Q_{3dB} = 6$, $\tau = 90$ µs). The vibration with $f_o = 21$ kHz is probably the fourth mode of the thin part of the tympanum (Michelsen 1971).

The reason for this close agreement between theory and the actual behaviour appears to be that in the locust ear the damping caused by friction is rather independent of frequency. The isolated locust ear when set into oscillation does not re-radiate much sound (in technical terms: the resistive part of the radiation impedance is small within the frequency range of the ear), and the damping is mainly provided by the friction in the tympanum and receptor organ (Michelsen 1971). This may not be the case in all ears. Less damping is to be expected for higher modes of vibration in ears, which are mainly damped by interaction with the medium (see e.g. Morse 1948, p. 200–208). This means that one may find just the opposite development of τ with frequency to that observed here: the higher modes persist in the membrane a long time after the basic mode has died out.

One may speculate that there may exist a wide variety of specialized ears, in which the damping varies in different ways with frequency. Using different degrees of external (radiational) damping may be one way of obtaining a favourable damping (Q_{3dB} and τ) at various frequencies. Alternatively, the frictional losses in the ear itself may be frequency dependent. At present, such thoughts are – of course – only speculations.

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