Oscillatory Nervous Response and Transient Vibration (Ear of *Locusta migratoria* Acrididae, Insecta)

L.-J. Adam, H. Dahmen, and P. Fastrich

Lehrstuhl für Biokybernetik der Universität, Tübingen

(Z. Naturforsch. **32 c**, 309–311 [1977]; received January 10, 1977)

Insect Hearing, Stimulus Slope, Oscillatory Potential, Model

The summed action potential (SAP) of the receptor axons in the tympanic nerve is a very regular, often nearly harmonic oscillation around an average level. The oscillation amplitude depends on the slope of the stimulus ramp, whereas the average level of the response is determined by the plateau of the ramp. Earlier hypotheses upon the tympanic SAP do not explain the above findings. Yet the transient solutions of a simple oscillator model reproduce the tympanic oscillations.

Sound pressure causes vibrations of membrane and inner structures in the tympanic organ and excites some 70–80 attached sensory cells. The lumped activity of their axons, following sound stimuli, *i. e.* the summed action potential (SAP) is described as a more or less oscillating potential with zero-symmetry and varying shape (Horridge [1], Adam, Schwartzkopff [2]).

The SAP, recorded monopolarly in our experiments, shows a nonzero average level (corresponding the the mean activity of axons) and very regular oscillation which after averaging often becomes nearly harmonic (Fig. 1, left). In the present investigations the onset of the stimulus is a ramp: The sound pressure rises linearly with the time and reaches the denoted plateau after a given rise time. In a first series of experiments the plateau level is kept constant, while the slope of the ramp varies: The steeper slope results in a larger amplitude of the oscillation (Fig. 1 a). The DC-level, (the mean activity) is about the same in all records

Requests for reprints should be sent to Dr. L.-J. Adam, Dr. H. Dahmen, Lehrstuhl für Biokybernetik der Universität Tübingen, Biologie II, Auf der Morgenstelle 28, *D-7400 Tübingen*

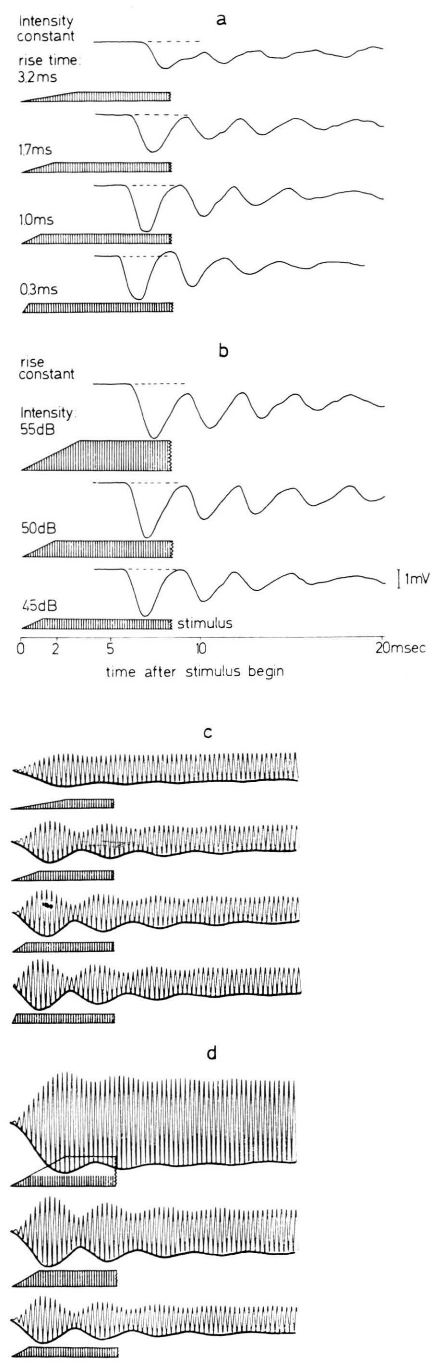

Fig. 1. a, b: The SAPs of the tympanic nerve (upper curves) are nearly harmonic oscillations with decrement c, d: The envelope (thick curves) of the transient vibrations of a simple mechanical oscillator are harmonic oscillations with an accordingly chosen decrement (damping factor). In SAP and model the amplitudes of oscillations are influenced the same way by the slope and not by the height of the stimulus — Methods: a, b monopolar recordings of SAP with two Ag/AgCl hook electrodes, ca. 9 mm apart from the tympanal organ in situ, nerve between electrodes crushed. Hole for electrodes in the metathoracic sternum closed by vaseline. Each SAP, 10 responses added. Negativity down. Stimulus: frequency 3.5 kc/s, in an intensity 45 dB SPL. c, d upper, thin drawn vibrations are solutions y of Eqn (1) to the stimuli $f(t) \sin \omega t$ shown underneath. Stimulus frequency is $\omega = 3.5$ kc/s, linearly rising slopes.

of Fig. 1 a, as can be estimated on the basis of the first oscillation (yet all statements about the DC-level are based on more refined measurements; Adam [3]).

In a second series of experiments the plateau of the stimulus is increased, while the slope of the ramp is kept constant: The DC-level of the SAP increases, yet the amplitude of the oscillation remains constant (Fig. 1 b).

In most afferent nerves, involved in perception of sound or vibration (*i. e.* acoustic nerve of vertebrates, cercal nerve of insects), oscillations of the SAP can be explained as firing of sense cells synchronously with the vibration of the stimulus. In the tympanic SAP the frequency of the oscillation is independent of and much lower than the frequency of the sound. Therefore the tympanic receptors must be synchronized in another way. It is possible that the receptors are simply very similar with respect to their latency and spike rhythm. Yet since strongly oscillating SAPs of sensory receptors are rare, they arouse the suspicion on a special synchronizing mechanism. Two have been given for the tympanic oscillations:

a. Different latencies of fibre groups (Murray [4]) and b. electrical coupling between receptors (Popov, Svetlogorskaja [5]). Yet the variation of conduction velocities of the tympanic fibre groups (Römer, Schwartzkopff [6]) is too small to yield latency differences of 3, 6, 9 and 12 msec (Fig. 1 a, b). Also hypothesis b is unlikely, because the synchronization of fibre activities diminishes by decreasing the slope of the stimulus ramp (Fig. 1 a). Thus we put other mechanisms into question which agree with our experimental findings.

Formerly, transducing mechanisms which may oscillate have not been considered: The tympanic membrane and its attached inner structures are forced to mechanical oscillations by the alternating sound pressure; moreover, an electrical step potential, generated in the tympanic organ and corresponding to the envelope of the stimulus may drive an electrically oscillating circuit. In both cases the transient behaviour might cause the oscillation in the beginning of the SAP.

We regard the case of a simple damped oscillator, which is excited either – in the mechanical cause – by a sine wave, the amplitude of which is modulated by a ramp function (Eqn (1)), or – in the electrical case – by the envelope of the sine wave alone (Eqn (2)):

$$\ddot{y} + b\,\dot{y} + \omega^2 y = \mathrm{f}(t)\,\sin\omega t \qquad (1)$$

$$\ddot{y} + b\,\dot{y} + \omega^2 y = \mathrm{f}(t) \qquad (2)$$

where

$$\mathrm{f}(t) = 0 \text{ for } t = 0$$

$$\mathrm{f}(t) = a\,t \text{ for } 0 \leqq t \leqq t_r$$

$$\mathrm{f}(t) = a\,t_r \text{ for } t \geqq t_r\,.$$

(y = amplitude of the pendulum, b = damping constant, ω_0 = eigenfrequency of the undamped pendulum, ω = exciting frequency, t_r = rise time of the ramp, a = steepness of the ramp). Solutions of Eqns (1) and (2) have been obtained by means of an analogue computer (EAI TR 48).

The solution of Eqn (1) shows pronounced beats, if the damping factor is small and the exciting frequency does not differ too much from ω_0. Under the assumption that the tympanic membrane is vibrating in a similar manner, the mechanoreceptors would be stimulated rhythmically with the beats and the synchronously gated spikes would cause the observed oscillation of the SAP. Thus we have to compare the envelope of the solutions of Eqn (1) with the SAPs. We choose the parameters ω, ω_0 and b so that for one stimulus ramp the envelope resembles the corresponding SAP ($|\omega - \omega_0|/\omega_0 = 0.1$; $Q = \omega_0/b = 30$). With these parameters kept constant the solution to the other stimuli are calculated (Fig. 1 c, d).

The solution of Eqn (2) is a function which shows a transient oscillation around the constant steady state level. It is assumed, that this function describes the time course of the generator potential, which evokes the spikes of the receptors. Thus the parameters ω_0 and b are chosen so that one function equals one SAP ($Q \approx 5$). Again the solutions for all other ramps are evaluated with the same parameters. The solutions are similar to the envelopes in Fig. 1 c, d.

There are remarkable correspondences between the solutions resp. envelopes (Fig. 1 c, d) and the measured SAPs (Fig. 1 a, b):

1. The steeper the stimulus ramp (with constant plateau level) the higher the amplitude of oscillation; the DC-level is unaffected.
2. The higher the stimulus-plateau (with constant steepness) the higher the DC-level; the amplitude of oscillation is not influenced (rise time $\geqq 1$ msec).
3. The durations of successive periods are nearly the same.
4. The duration of the period does not depend on the stimulus slope and the height of its plateau.

Michelsen [7] has reported a Q-value of around 5 which is about 6 times smaller than that of the mechanical oscillator assumed here; however his damping factor might be higher, since he investigated the isolated tympanum in another acridiid. At any rate the mechanical model is extremely simple as compared with the complicated system of three membranes in the tympanic organ (Schumacher [8]). It is the aim of further investigations to examine the concurrent hypotheses in more detail.

Research sponsored by the Deutsche Forschungsgemeinschaft, grant to Prof. D. Varjú.

[1] G. A. Horridge, Proc. Roy. Soc. B **155**, 218 [1961].
[2] L.-J. Adam and J. Schwartzkopff, Z. vergl. Physiol. **54**, 246 [1967].
[3] L.-J. Adam, in preparation.
[4] M. J. Murray, Nature **218**, 95 [1968].
[5] A. V. Popov and I. D. Svetlogorskaja, Zh. evoljucionnoj biochimii i fiziologii (Mosk.) **7**, 516 [1971].
[6] H. Römer and J. Schwartzkopff, Naturwissenschaften **62**, 581 [1975].
[7] A. Michelsen, Z. vergl. Physiol. **71**, 63 [1971].
[8] Schumacher, personal communication.