

CENTRAL MECHANISM OF HEARING IN INSECTS

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INTRODUCTION

The electrical responses to sound stimuli have already been recorded from the auditory nerve bundle in several kinds of insect, in Orthoptera by Pumphrey & Rawdon-Smith (1936) and Haskell (1956, 1957), in Lepidoptera by Haskell & Belton (1956) and Roeder & Treat (1957), and in Hemiptera by Pringle (1953). The central mechanism of hearing, however, has not so far been much explored. Quite recently the present authors (Katsuki & Suga, 1958, 1960) studied electrophysiologically the problems of directional sense and frequency analysis in the tympanic organ of an insect by recording activities of the peripheral auditory neurons. The central mechanism has been further studied, and this paper is concerned with the experimental results. Three problems have particularly been posed: frequency analysis of sound, directional sense and central inhibition.

MATERIAL AND METHOD

The experiments were performed on *Gampsocleis buergeri* (Tettigoniidae), because of its large size and ready availability.

The insect was pinned on its back on a cork board and the ventral exoskeleton covering the nerve cord was removed. The tracheae distributing along the nerve cord were separated from the latter and the non-auditory inputs were also severed. The operated animal was placed about 50 cm from the loud-speakers and the sound was delivered from its left side in a sound-proofed room which was air-conditioned at about 26° C.

The impulses in response to sound stimuli were recorded from the connectives which were hooked up in the air with a 200 μ silver wire electrode mounted on a micro-manipulator. In order to trace the auditory tract in the nerve cord, two different parts of the cord were simultaneously hooked up with two recording silver wire electrodes and the electrical response of each part was led through an amplifier to two beams of an oscilloscope. The sound wave and the time signal were indicated on a third beam simultaneously. The indifferent electrode was a silver wire placed on wet cotton on the abdominal segments from which the exoskeleton was removed.

Most records were photographed on a running film. By such a recording method, the difference in the response pattern and the time delay between the responses recorded from two different parts could be measured with some accuracy and the functional disposition of the auditory tract in the cord could be explored. In order to study the responses from the tympanic and cercal nerves separately, one or other of them was cut in most experiments.

The stimulating and the recording equipment used in the present work was the same as that described in the previous papers (Katsuki, Watanabe & Suga, 1959; Katsuki & Suga, 1960).

RESULTS

(1) *Response in the nerve cord*

When the recording was made from the thoracic connectives of *Gampsocleis buergeri*, spontaneous discharges of several units were always observed, their spike heights being various. The responses to tone bursts were seen only at the onset of sound among spontaneous discharges. Interfering impulses from regions other than the tympanic nerve were eliminated by cutting the rostral and caudal parts of the hooked-up connectives and the other peripheral nerves except the tympanic. Thus only the responses to tone bursts remained, the size of impulses ranging between 1 and 3 mV. In the tympanic nerve, the train of impulses lasted as long as the stimulus sound continued. In contrast, in the thoracic connectives the responses were evoked only at the onset of sound, that is the 'on'-type response. The conduction velocity measured at the suboesophageal-prothoracic connective was found to be about 6 m./sec. Pumphrey & Rawdon-Smith (1937) and Roeder (1948) have already reported that the conduction velocities of the cercal nerve and the giant fibre in a cockroach range from 2 to 3 m./sec. and 6 to 7 m./sec. respectively. Therefore, from the phasic discharge pattern, the large spike height, and the conduction velocity, it may be reasonable to conclude that the impulses originate from the large fibre in the connective.

The hair sensilla on the cerci can, as is already known, respond readily to low-frequency sound and the impulses evoked in the cercal nerve by sound are transmitted to the abdominal cord through the last (6th) abdominal ganglion. Our records, which were obtained from the abdominal nerve cord, always showed the distinct discharges of two units, the sizes of which ranged between 2 and 4 mV. The response pattern of the output of the last abdominal ganglion was more phasic as compared with that of the input. The conduction velocities of the fibres were about 6 m./sec. It was thus confirmed electrophysiologically that there were two auditory large fibres in the abdominal nerve cord.

(2) *Auditory large fibre*

The auditory large fibres in the nerve cord are divided into two: the auditory T large fibre and the auditory C large fibre.

(a) *T large fibre*

The patterns of the responses recorded from the connectives between the brain and the metathoracic ganglion were very similar. The impulses immediately evoked by the activity of the tympanic nerve at the prothoracic ganglion seemed to be conducted to the rostral and caudal ganglia through one and the same large fibre. In the hope of confirming this the impulses were recorded simultaneously from the connectives rostral and caudal to the prothoracic ganglion, that is to say, one recording electrode hooked up the suboesophageal-prothoracic connective and the other the ipsilateral meso-metathoracic connective. The descending impulses from the brain and the ascending impulses from the cercal nerve were excluded by cutting the rostral and,

caudal parts of the connectives beyond the electrodes. The contralateral thoracic connectives and all the peripheral nerves except the ipsilateral tympanic were cut so as to leave only the simple system consisting of the unilateral tympanic nerve and the ipsilateral thoracic connective. The discharge pattern of the ascending impulses from the ganglion was exactly the same as that of the descending ones for any sound stimulus. The impulse sent to the suboesophageal ganglion is always delayed by 0.7 msec., compared with that directed to the mesothoracic ganglion. Thus it was confirmed that the impulses immediately evoked at the prothoracic ganglion were conducted rostrally and caudally on one and the same fibre.

Further attempts were made to discover whether an auditory large fibre of this type extends from the brain to the metathoracic ganglion. One of the electrodes hooked up the brain-suboesophageal connective and the other the meso-metathoracic connective. Fig. 1 represents an example of such simultaneous recordings. In each record of the figure, the upper and middle traces represent respectively the impulses sent up to the brain and down to the metathoracic ganglion, and the lower trace represents the sound stimulus. The frequency of the sound stimulus was changed as shown by the figures at the left side of each column. Good coincidence in the discharge patterns as between the upper and the middle traces is seen for the responses to all frequencies. The time delay between the impulses on the upper and middle traces was always 0.3 msec. and the spike heights were the same. This result shows that the auditory T large fibre runs in the cord as far as from the brain to the metathoracic ganglion and that the impulses in this fibre are initiated at the prothoracic ganglion, probably only by the activity of the tympanic nerve, and are conducted to the brain and to the metathoracic ganglion in exactly the same manner. Thus the information about the sound which stimulated the tympanic organ is sent up to the brain after about 12 msec. and down to the metathoracic ganglion after almost the same time from the arrival of the sound at the tympanic organ. The conduction velocity of this fibre was about 6 m./sec., measured at any part of the nerve cord.

The T large fibre does not extend to the abdominal ganglia, because no response originating from the tympanic organ was found beyond the metathoracic ganglion.

(b) *C large fibre*

The discharge pattern of the response evoked by impulses in the cercal nerve was found to be similar at all connectives from the last abdominal to the mesothoracic ganglion. The simultaneous records obtained from the connectives rostral and caudal to the metathoracic ganglion, however, did not show one-to-one correspondence of impulses. The responses recorded from the two connectives indicated that they consisted of the impulses of two large fibres. The number of impulses was always less at the thoracic connective than at the abdominal one, but the number of spontaneous discharges was just the reverse. From these results it may be said that these large fibres do not extend beyond the metathoracic ganglion, where they have synapses.

The impulses recorded from the metathoracic-abdominal connective, however, showed a perfect one-to-one correspondence with those from the V-VI abdominal connective in responses to sound and also in spontaneous discharges. The impulses at the rostral end of the abdominal cord were always delayed by 2.2 msec. relative to those at the caudal end. The conduction velocities of these fibres were almost the same,

about 5.8 m./sec. Thus the abdominal nerve cord has two pairs of similar auditory large fibres which run to the metathoracic ganglion from the last abdominal ganglion. Those auditory large fibres are called the primary auditory C large fibres in this paper.

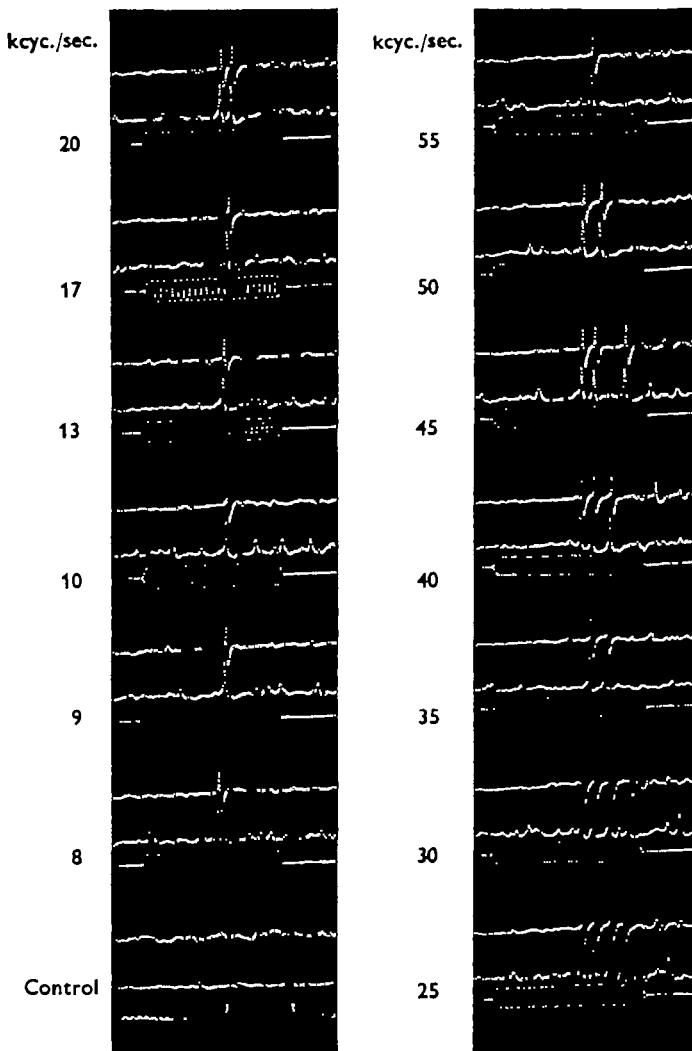


Fig. 1. Responses of the auditory T large fibre to sounds of various frequencies shown at the left side of each column. The upper and middle beams represent the responses recorded from the brain-suboesophageal connective, the ipsilateral meso-metathoracic connective respectively, and the lower beam represents the sound wave. Time signal (at the bottom of the left column), 10 msec.

A pair of auditory large fibres were, as described above, found in the meso-metathoracic connective. These fibres were activated at the metathoracic ganglion by the primary C large fibres. For this reason the auditory large fibres between the meso- and metathoracic ganglia are called the secondary auditory C large fibres. In the

Nerve cord rostral to the mesothoracic ganglion, the C large fibre tract was not found electrophysiologically, but the activities evoked by low-frequency tone bursts were observed on several small fibres.

(3) *Interaction between impulses from the tympanic nerves of opposite sides*

The tympanic nerve in Orthoptera consists of about 100 nerve fibres (Vogel, 1921). When the tympanic nerve was hooked up with a silver wire electrode, the grouped discharges of those fibres were observed as long as the sound lasted. However, in each fibre a sigmoid relation was found between the sound intensity on a decibel scale and the number of impulses per sec. The information about the sound intensity can be thus signalled to the central nerve cord. On the other hand, the responses of the T large fibres were phasic, so it may be that the information about the intensity is not sent to the brain in the same form as it has in the tympanic nerve.

In order to study in detail the responses of the T large fibres, a pair of connectives between the suboesophageal and prothoracic ganglia was hooked up on the electrodes, the ascending impulses from the rear ganglia being eliminated by cutting the connectives. There remained both the tympanic nerves, the prothoracic ganglion, and both the ascending connectives. In Fig. 2 the upper and middle traces show the impulse discharges of the tympanic large fibres of the right and left sides respectively. The lower trace shows the wave form of the delivered sound, the frequency of which is 13 kcyc./sec. A and B represent respectively the responses before and after cutting the left tympanic nerve. The T large fibre of the left side, which was activated by the impulses sent up from the tympanic nerve nearer to the loud-speakers, sent more impulses than that of the right side (A). Here a very interesting phenomenon was found as a result of cutting the left tympanic nerve (B): no impulse discharge was found on the left side but in response to the same sound stimulus a remarkable increase in the number of impulses was found on the right side. When the right tympanic nerve was cut, the reverse effect was observed. When there were many impulses in a response to sound, the increase in number of impulses after cutting the nerve was not so marked, whereas when the number of impulses in the response was fewer, the increase after the cut was more marked. It was found that the impulses delayed by more than 4.6 msec. after the first impulse in the response were suppressed by the impulses of the contralateral tympanic nerve. This phenomenon shows that impulses of the tympanic nerve on one side have an inhibitory effect on the contralateral T large fibre.

In three cases out of twenty-six the impulses in the T large fibre remained even after cutting the ipsilateral tympanic nerve, though the number was small. Disappearance of these remaining impulses after cutting the contralateral tympanic nerve proved that they were evoked by the activity of the contralateral nerve. They were delayed by several milliseconds as compared with the ipsilaterally evoked impulses. The shortest delay was 3.3 msec. When the contralaterally evoked impulse was observed, an attempt was made to discover whether the contralaterally and ipsilaterally evoked impulses converged on the same T large fibre. No difference in the spike height and no summation of spikes were found among them. The delay of the first spike transmitted from the contralateral tympanic nerve was always about 10 msec. from the onset of the sound stimulus, but the spike with this delay was not found

regularly in the response of the T large fibre before cutting the ipsilateral tympanic nerve. These facts suggest that the ipsilaterally and the contralaterally conducted impulses in the tympanic nerves activate one and the same T large fibre. However, there still remains the question of whether the inhibitory effect is exerted upon the tympanic nerve. By recording the electrical activity from the latter it was confirmed that the inhibitory effect of the tympanic nerve on one side does not extend to the tympanic nerve of the opposite side.

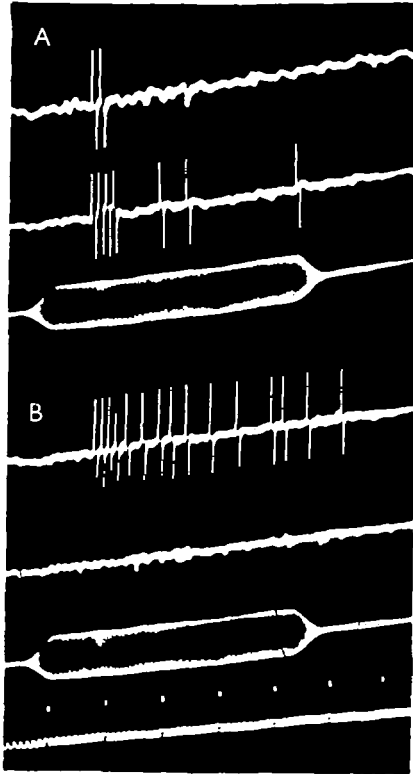


Fig. 2. Inhibitory effect of the tympanic nerve on the contralateral T large fibre. In A and B the upper and middle beams represent impulse discharges of the right and left large fibres respectively. A is before and B is after the elimination of the inhibitory effect by cutting the left tympanic nerve. The sound stimulus on the lower beam is 13 kcyc./sec. in both A and B. Time signal, 10 msec. See text.

Therefore it is highly probable that the T large fibre receives not only the excitatory effect from the ipsilateral tympanic nerve at the prothoracic ganglion but also the inhibitory and weak excitatory effects from the contralateral nerve. The irregularity of the contralaterally evoked impulses tells us that the inhibitory effect may be varied by intrinsic factors.

The discharge pattern of the T large fibre was phasic as described above, but it was due to the inhibitory effect of fibres from the opposite side. When the contralateral tympanic nerve was cut, though the T large fibre responded with increased impulses, the response adapted so that the train of impulses lasted at most only for the

