PERIPHERAL MECHANISM OF HEARING IN LOCUST

Nobuo SUGA*

Department of Physiology, Tokyo Medical and Dental University, Tokyo

Since the production of sound and its reception in insects attracted the interest of entomologists, a number of behavioral and electrophysiological studies on these problems have been performed. It is well known that insects have, as sound receptive organs, the tympanic organs and also the hair sensilla which are distributed over the various regions of the body surface. The anatomical studies on the tympanic organs were performed of *Acridiidae* by SCHWABE[14], *Cicadidae* by VOGEL[16], and *Noctuidae* by EGGERS[2] and they showed that the structure of those organs is fundamentally the same though they locate at the different parts of the body surface in different species.

Since PUMPHREY and RAWDON-SMITH[11], it has been widely accepted that the tympanic organ of insect has almost no ability of analysing the sound frequency, which does not mean the repetition rhythm of pulsatory sounds. Recently KATSUKI and SUGA[6] studied the activities of single tympanic neurons in *Gampsocleis buergeri* by means of a microelectrode technique and offered a neurophysiological evidence for PUMRHREY's hypothesis. They suggested that in some insects rough frequency analysis of the sound is carried out by the action of different sound receptive organs, i.e. the tympanic organ and hair sensilla.

In *Acridiidae* the scolopses in the tympanic organ are arranged in three groups, each of which attaches to a different part of the tympanic membrane. It can therefore be conceived that the frequency analysis may be done if each group of sensory cells is influenced by a different frequency of sound. It is said that PUMPHREY and RAWDON-SMITH found no significant difference on the threshold curve determined before and after the selective destruction of groups of the sensilla. The determination of the response areas of single tympanic neurons is thus expected to offer the conclusive answer to this problem and this is one of the purposes of the present work. Another aim of the experiment is to analyse the slow potential change obtained at the tympanic organ of insects, which will be first described in the present paper. The problem of the generator potential in this organ has not yet been studied successfully, although the fine structure of it was long before

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*菅 乃武男

examined. Compared with the microphonic potential in the cochlea of higher animals this slow potential may be quite interesting even from the view point of the comparative physiology.

MATERIAL AND METHOD

Material used was *Locusta migratoria danica.* A pair of tympanic organs are found at the first abdominal segment of the locust and each of them is composed of a tympanic membrane and a chordotonal organ. A tympanic nerve composed a nerve bundle together with a heart nerve and a stigma nerve, connecting with a metathoracic ganglion (FIG. 1).

Nerve responses were recorded to the sound stimuli with a 200 μ silver wire electrode from the tympanic nerve. In this case the insect was pinned on a cork-board dorsal side down and the metathoracic ganglion as well as the tympanic nerve were exposed by removing the exoskeleton and also by cutting tracheae on them, in order to avoid the break of air sacs which surround the chordotonal organ.

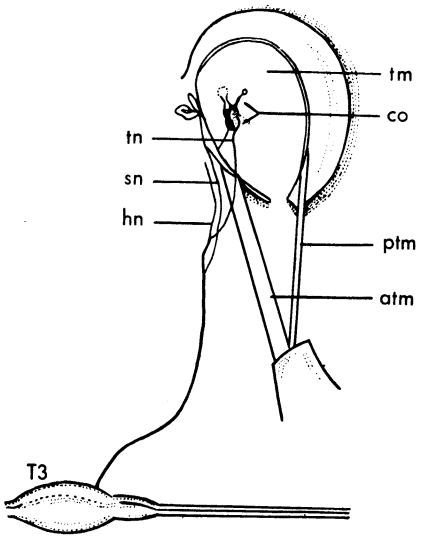

FIG. 1. The schema of the tympanic organ and the tympanic nerve. atm: anterior tympanic muscle, co: chordotonal organ, hn: heart nerve, ptm: posterior tympanic muscle, sn: stigma nerve, T3: metathoracic ganglion, tm: tympanic membrane, tn: tympanic nerve (From SCHWABE).

When the chordotonal organ was studied, the insect was pinned on a cork-board ventral side down and the dorsal exoskeleton of the first abdominal segment was dissected, and further the air sacs surrounding the chordotonal organ was opened. Thus the chordotonal organ and the tympanic nerve were exposed. Since the chordotonal organ showed a slight movement synchronized with respiration, it was not easy to apply a capillary microelectrode to this organ. Therefore, the exoskeleton surrounding the tympanic organ was firmly immobilized with pins to

prevent the movement described above and then a microelectrode was inserted slowly into the organ by the aid of a micromanipulator under the visual control of a binocular microscope. The microelectrode used was a superfine glass capillary, filled with 3 M KCl solution and with a tip diameter less than 0.2 μ. The ohmic resistance of the electrode ranged between 30 and 50 MΩ. An indifferent electrode was a silver wire placed on a wet cotton on the abdominal segment where the exoskeleton was removed. The recording and the stimulating equipment used in the present work were the same with those described in the previous paper[7,8]. The sound stimuli were given to the insect from the direction perpendicular to the body axis and the recording was made from the tympanic organ nearer to the sound source. A condenser-microphone was placed close to the operated insect in order to verify the sound intensity. The threshold curve of a single tympanic neuron and its most sensitive frequency are called "the response area" and "the characteristic frequency" respectively in this paper, in order to distinguish from those of the whole tympanic organ.

RESULTS

(*1*) *Response area.*

When the recording was made from the whole tympanic nerve by means of a fine silver wire electrode, the irregular spontaneous discharge were observed. The delivered tone bursts produced a corresponding increase of the number of discharge when the intensity of sound was sufficiently strong, but the synchronous discharge with the sound frequency as seen on cercal hair sensilla was unrecognizable. The weakest intensity of sound at which the increase of discharge was discernible, in other words the threshold of the tympanic organ was obtained for various frequencies as shown by FIG. 2 (curve A). Curve A represents the mean of the response areas obtained from five specimens. It shows that the tympanic organ is responsive to the sounds from 0.6 to 45 kcps and especially to those from 4 to 9 kcps. It was found that the tympanic organ of *L. migratoria danica* responded even to ultrasonic sounds. The threshold curve was the same before and after the isolation of the tympanic nerve from the metathoracic ganglion.

In order to measure the response area of a single tympanic neuron, the capillary electrode was inserted into the tympanic nerve bundle. The impulses of several tympanic neurons were simultaneously recorded as soon as the capillary electrode was inserted into the nerve, but the isolation of the responses of a single neuron was very difficult. At the chordotonal organ, however, that was not so difficult. The unitary activities of twenty-four neurons were obtained from the organ extracellularly and very rarely intracellularly. Though five of them did not respond to sound stimuli, other nineteen elements did respond to them well. In seven cases among nineteen, the response areas could be fully measured as shown in FIG. 2. It is noted that their response frequency ranges were different whereas

the characteristic frequencies were approximately constant, being between 4 and 9 kcps. A narrower response frequency range was usually found when the threshold was high. The response pattern of those neurons were all slow adaptation and none of them were rapid.

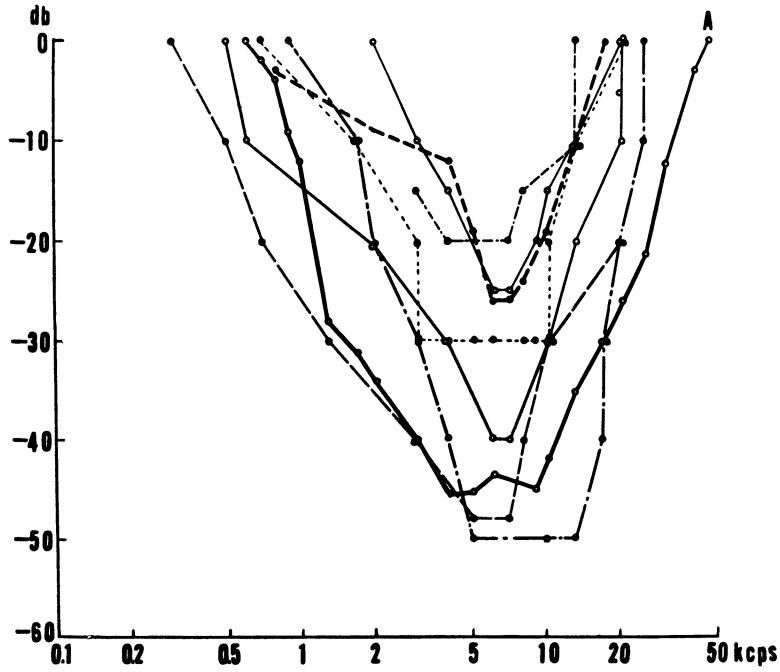

FIG. 2. The threshold curve of the whole tympanic organ (A) and the response areas of single tympanic neurons. The ordinate and the abscissa represent the intensity of the stimulus sound in decibel and its frequency respectively. The characteristic frequency is almost the same from 4 to 9 kcps in all neurons obtained. The largest response area of a single tympanic neuron covers almost all of the threshold curve of the whole tympanic organ.

(*II*) *Impulse frequency of the response evoked by a sound stimulus and spontaneous discharge.*

The number of impulses per second changed with the change of either the intensity or the frequency of sound. The relations between the impulse frequency and the intensity of sound are shown in FIG. 3 for various sound frequencies. They were obtained from the same neuron. The ordinate and the abscissa represent the number of impulses per second and the intensity of sound in decibel unit respectively. The curves for the different frequencies are almost parallel to one another. In this example the highest rate of impulses was obtained for 6 kcps sound and was above 300 per second. For the sounds of lower or higher frequencies than

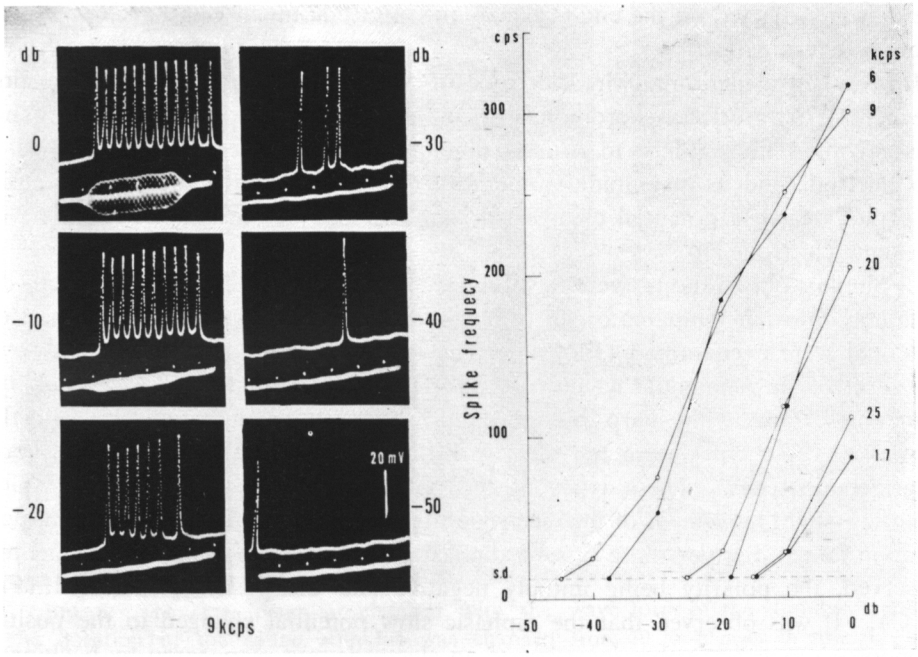

FIG. 3. The relations between the number of spikes per second of the same single tympanic neuron (ordinate) and the intensity of the sound stimulus (abscissa) are shown on the right figure. s. d. represents the frequency of the spontaneous discharges. The frequencies of the sound used are shown on each curve. The left records represent the responses of the same neuron to the stimulus sound of 9 kcps. The intensity of the sound is varied from 0 to −50 db by 10 db step. In each record the upper and the lower beams represent respectively the nerve response to the stimulus sound and the wave form of the sound received by a microphone. The time signals of 10 msec are also represented on the lower beam. The summation of after potentials is recognized in the strong sound stimulation. In −50 db, only a spontaneous discharge is seen.

the most sensitive frequency the spike frequency of the neuron decreases step by step. With decreasing the intensity of sound, the frequency of impulses responding to it went gradually down to the level of the spontaneous discharge which was about 13 per second in the present case. Records in Fig. 3 show one of the examples. The decrease of impulse frequency is seen with decreasing intensity of 9 kcps sound from 0 to −50 db. The pure spontaneous discharge is seen only in the record of the intensity of −50 db in the figure. Such spontaneous discharges were also observed in some other tympanic neurons and the frequencies of them ranged between 3 and 13 per second. As described above five non-responding neurons to sound stimuli were found in five different specimens and the frequency of the spontaneous discharges ranged between 2 and 18 per second. They might be a non-acoustic fiber such as reported on a noctuid moth by ROEDER & TREAT[13] and by TREAT & ROEDER[15]. It was, however, not definitely concluded because

the damage inflicted on the end-organ by the electrode might cause such results on acoustic neurons.

(*III*) When a nichrome wire electrode of 50 μ in diameter was pressed against the central part of the chordotonal organ, a monophasic slow potential change was recorded in response to sound stimulation. The potential was positive at the electrode and its magnitude varied with the change of frequency and intensity of sound. Such a potential change was not obtained at the tympanic nerve with the same electrode.

Similar observations were also made by inserting the capillary electrodes obliquely into the tympanic organ from its dorsal side. Several types of the slow potential were encountered (FIG. 4). The type encountered most frequently was the positive slow potential which rose and fell with a slow rate (FIG. 4, A), but sometimes those with sharp rise and fall were also encountered (FIG. 4, B). However, these types were not clearly distinguishable because there were many intermediate types. These types of the potential change were relatively stable against a slight movement of the electrode tip and could be observed for even more than an hour. Besides those types a diphasic potential change was also sometimes observed, the polarity being initially negative and the positivity followed (FIG. 4, C). It was observed that the diphasic slow potential changed to the positive monophasic one by further insertion of an electrode and reappeared by backing it. The negative monophasic type of slow potential was rarely observed (FIG. 4, D) and very unstable against a slight movement of the electrode tip. The latencies

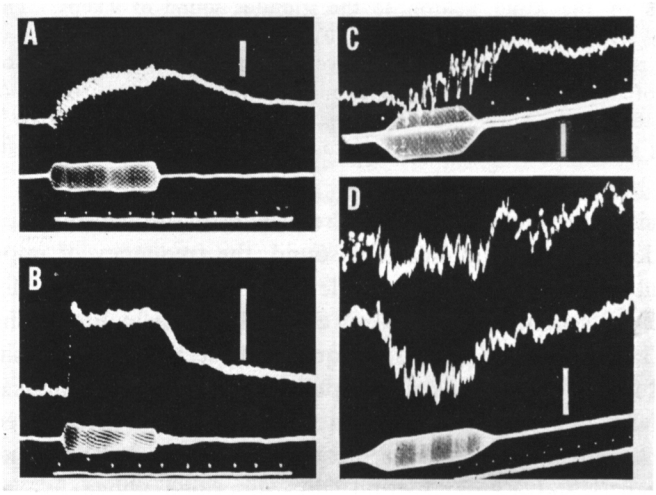

FIG. 4. Four types of slow potentials obtained from the tympanic organ. The vertical line represents 1 mV. Stimulus sounds used are as follows: A: 10 kcps, B: 5 kcps, C: 7 kcps, and D: 8 kcps. In C, negative-positive diphasic spikes superimpose on the diphasic slow potential. The time signals are 10 msec.

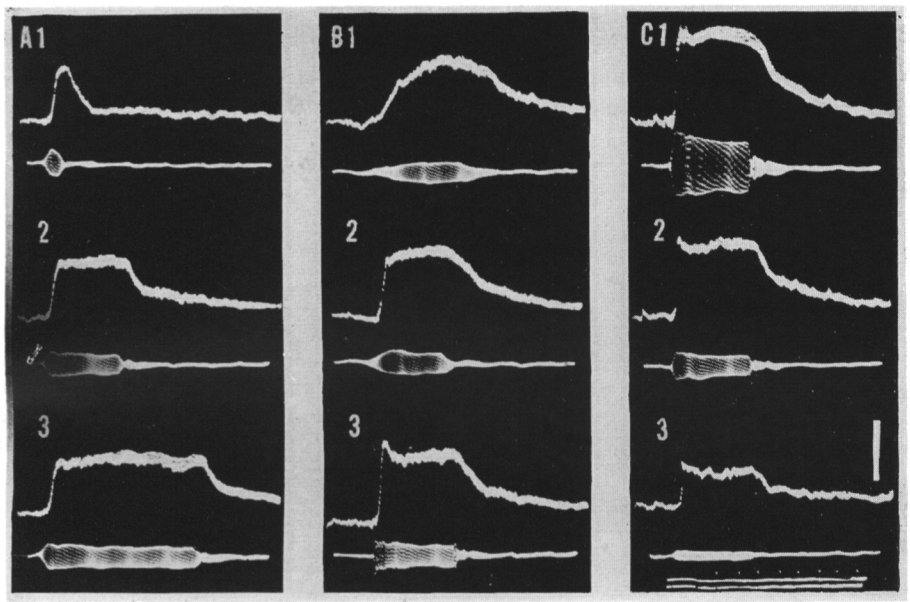

FIG. 5. The slow potential changed with the wave form of the stimulus sound. The duration of the sound stimulus was changed from 10 to 70 msec in row A. In row B, its rising and falling phases were made sharp from 1 to 3. In row C, the intensity was made weak from 0 to −20 db in 10 db step. The frequency of the stimulus sound used is 5 kcps in all cases. The vertical line is 1 mV. The time signals are 10 msec.

were measured between the onset of click and the start of the slow potential and they ranged between 1.3 and 2.0 milliseconds. Since the positive monophasic potential was the most stable type of responses, most of the following observations were done with this type. Records A of Fig. 5 were obtained when the duration of the 5 kcps tone bursts was varied from 10 to 70 msec, showing that the slow potential continued as long as the tone burst continued (A1-3). When the rate of rise or fall of the tone burst was changed, the corresponding changes of the slow potential were always found as shown by records B, 1-3. Record C shows the effect of sound intensity upon the slow potential. Three records were obtained with 5 kcps tone burst of 0, −10, and −20 db respectively (C 1, 2 and 3). The relations between the maximum amplitude of the slow potential and the intensity of sound are illustrated for various frequencies of sound in FIG. 6. Successive insertions of the electrodes into the chordotonal organ often diminished the slow potential and this may be due to the mechanical destruction of the chordotonal organ by the tip of electrode and/or the deterioration of the organ by a concentrated potassium chloride solution which leaked out from the broken tip of an electrode. Application of droplets of RINGER's solution upon the tympanic organ also decreased the amplitude of the slow potential. These results suggest

that the slow potential represents a certain bioelectric phenomenon and not an artifact.

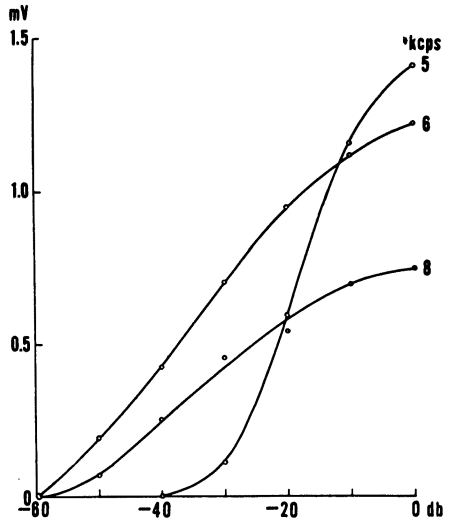

FIG. 6. The relation between the maximum amplitude of the slow potential (ordinate) and the intensity of the sound stimulus (abscissa) obtained from different specimens. The frequencies of the stimulus sound used are shown on each curve.

The effects of several pharmacological agents on the slow potential were examined, but no conclusive result was obtained, because of difficulty of applying test solutions exclusively to the chordotonal organ which was covered with a thin membrane. The effect of 0.2% procaine was examined while the afferent nerve responses were recorded by means of a silver wire electrode placed on the tympanic nerve bundle and the slow potential was simultaneously recorded by a capillary electrode inserted into the chordotonal organ. Several minutes after the application of procaine solution through a micropipett, impulse discharges which were seen at the tympanic nerve were completely abolished. However slow potentials as well as impulse discharges were recorded with a capillary electrode inserted into the chordotonal organ even half an hour after the application. From this result it was conceived that the procaine solution might not diffuse through the membrane which covers the chordotonal organ.

(IV) Responses to two sound stimulation.

A in FIG. 7 represents the response to a prolonged sound. The amplitude of the slow potential increased and reached a steady level after about 300 msec and stayed at this level at least 5 minutes as long as the sound continued. B and C in this figure represent the slow potential produced by two sound stimulation. A short tone burst of 7 kcps was delivered simultaneously with a prolonged background sound of about 5 kcps in B and about 7 kcps in C, the response to the former was superimposed on a long lasting slow potential. But the amplitude of the summated response was smaller than the algebraic sum of those of the

two responses obtained separately. When the background sound produced a slow potential of a very large amplitude, the application of the second short sound did not produce any further additional increase of the amplitude. In other words the amplitude of slow potential was saturated when the intensity of the sound reached a certain high value.

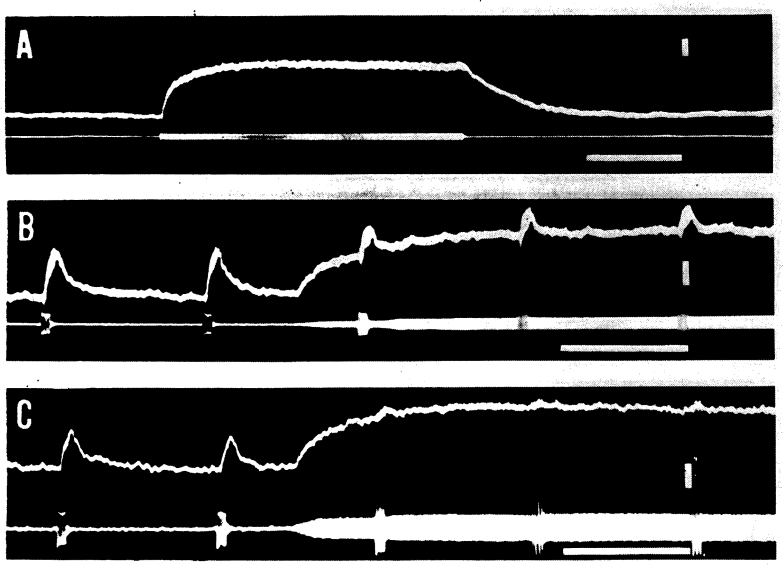

FIG. 7. The slow potential shows very slow adaptation as shown in A. The stimulus sound is 7 kcps. B and C represent the responses to two sound stimulation. One of them is the short sound of 7 kcps, the others are the prolonged sound of about 5 kcps in B and about 7 kcps in C. The vertical lines represent the calibration of 1 mV and the horizontal lines the time scales of 500 msec. (See text).

(V) Slow potential and spike.

The slow potential was not obvious when it was observed on the chordotonal organ near to the tympanal nerve, but positive spikes were often encountered. Sometimes those spikes had pre-potentials, whereas the spikes obtained at the center of the chordotonal organ were almost always accompanied by the positive slow potential and/or pre-potential. Sometimes the negative spikes superimposed on the rising phase of a positive slow potential. During further advancement of the electrode the spikes reversed the polarity (FIG. 8D) and then disappeared. The polarity of the slow potential, however, never reversed during this process and its amplitude scarcely changed. When the spikes superimposed on the rising phase of the positive slow potential, decreasing the intensity of the sound stimulus reduced the amplitude of the positive one as well as the number of spikes, but

even after the spike disappeared completely a small positive slow potential was often observed (FIG. 8 A, B, and C).

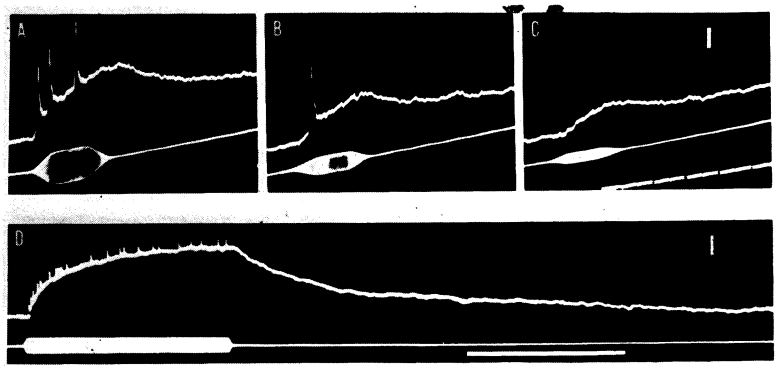

FIG. 8. By weakening the sound stimulus (8 kcps), the positive slow potential decreases with the number of spikes superimposing on it, until only the slow potential remains there (A, B, and C). The time signals are 10 msec. D represents spikes superimposing on the rising phase of the positive slow potential. The horizontal line is the time scale of 500 msec. The vertical lines represent 1 mV.

DISCUSSION

With the use of telephone receiver WEVER and BRAY[18] heard the responses of the tympanic organ to sound stimuli in crickets and katydids and discerned three types of the responses. One of them was the response to sound stimulus and consisted of a sort of "Shushing" noise, of a quality which was in all cases the same regardless of changes in the quality of the stimulus, another was the response reflexly set up on motor nerves, and the third was those of receptors of a tactual kind to air currents. However it is not obvious what potential change they caught. Since their studies were published, there has been no report which has reference to the potential evoked at the tympanic organ of insect[4].

Th present author would like to discuss about two problems here, the ability of frequency analysis of the tympanic organ in insects and the slow potential obtained from the endorgan as described above.

(*I*) *Ability of analysing sound frequency of the tympanic organ.*

It is hardly conceivable that the different parts of a small tympanic membrane of an insect are vibrated differently by different frequencies of sound. However if they should do so, the response area of any one of the tympanic neurons would not be the same as the threshold curve of the whole tympanic nerve, but occupy a part of the threshold curve. However in the tympanic organ that the sensory cells make a group at the center of the tympanic membrane, the largest response area of a tympanic neuron will coincide with the threshold curve of the whole

tympanic nerve and their characteristic frequencies may not be so different to each other. The result obtained by the present study shows that the tympanic organ is the latter case. That is to say, the sensory cells of three groups at the center of the tympanic membrane are almost uniformly stimulated by sound.

On the other hand, there is a possibility that by the mechanical distortion due to the insertion of the electrode the tension of the tympanic membrane might be varied and the thresholds of the sensory cells thus become higher. If that is the case the response areas may slip into either higher or lower frequency side than those under natural condition. The response areas shown in FIG. 2 have approximately the same characteristic frequency, but their thresholds are not the same, some of them are relatively high and some of them low. There is no neuron which has a biased response frequency range and therefore the different characteristic frequency, and the largest response area covers approximately the whole threshold curve of the tympanic organ. Therefore it is concluded that there is no sign of three groups of sensory cells having the different response areas respectively, namely, there is no sign of analyzing sound frequency at the tympanic organ.

(*II*) *Slow potential.*

It has been already described that the slow potentials obtained from the tympanic organ may be the so-called generator potential. They were recorded only from the chordotonal organ and not from the tympanic nerve.

Histological studies have shown that the chordotonal organ is fixed on the tympanic membrane and fundamentally consists of cap cells, enveloping cells, and primary sensory cells. The sensory cell sends peripheralward a scolops and centralward a nerve fiber, many of which form the tympanic nerve.

It has been thought that the function of the chordotonal sensory cells is originally a proprioceptive one to register the displacement of one part of the skeleton with respect to another[5] and that the development of a special proprioceptive function as an enteroceptive function to the tympanic organ which is a kind of exteroceptive one is a subsequent adaptation of a pre-existing system to meet a special need[12]. The endorgan mechanism of proprioception was recently elucidated very extensively on the stretch receptor in frog muscle by KATZ[9,10] and on that in crayfish muscle by EYZAGUIRRE and KUFFLER[3]. The resemblance between the response recorded from the tympanic organ and that obtained from the other receptors mentioned above indicates that the processes of initiating afferent impulses at the receptive organ are of similar nature. It is a matter of interest that the response obtained from the tympanic organ is completely different from those obtained from the cochlea of higher animals although the functions of both organs are quite the same. As is well known the responses obtained from the cochlea to sound stimulation is the microphonic potential which is an alternating potential[17].

Anyhow the origin of both the tympanic organ and the cochlea is believed to be different: the origin of the tympanic organ has been already discussed whereas that of the cochlea is a kind of the cutaneous pressure receptor. Detailed structure

of the cochlea is well elucidated and the origin of the microphonic potential is thought to be the hair cells which are immersed in the special ionic environment. It is the common knowledge that the microphonic potential is the generator potential and initiates the nerve impulse. However in the present case the generator potentials are not alternating and can be distinguished into 4 types. Those four types are explained as follows. Among them the negative monophasic type may have been recorded from just above a certain restricted part of tissues which initially depolarized. This restricted region is probably the group of scolopses. This type was only rarely observed and unstable against a slight movement of the electrode tip. The depolarization evoked here should cause an inward current through membrane of this part (probably of scolops) and the same amount of the current should flow out through the membrane of the sensory cell and also the nerve fiber[1]. The sink of current appears only on this structure, therefore the positive slow potential with a fast rise and fall should be obtained on the cell or nerve fiber at the region which is not far from the sink and the negative-positive diphasic slow potential may be encountered between them. However, on the other hand if the distance between the recorded region and the sink become larger, the time course of the potential change should become slower due to electrotonic spread. The positive slow potential of a slow rate of rise and fall is probably such a potential and since those regions should be larger than those for the negative types, it would be very stable against a movement of the electrode tip. As it is discussed above, the slow potential recorded from the tympanic organ may be the generator potential which initiates the discharges of the tympanic nerve.

SUMMARY

1. The tympanic organ of *L. migratoria danica* was found to accept well even the ultrasonic waves. The response frequency range was from 0.6 to 45 kcps, the most sensitive frequency range being from 5 to 9 kcps.

2. The mode of conveying the information of the tympanic neuron to the central nervous system was found as follows:

A. The tympanic neuron sent impulses in the pattern of slow adaptation and did not discharge synchronously with the sound frequency as seen on cercal hair sensilla. The relations between the number of spikes per second and the intensity of sound in decibel unit were sigmoid and almost parallel to one another for different sound frequencies. A neuron responded with the highest rate of spike discharges to the sound to which the neuron was most sensitive.

B. The largest response area of single tympanic neuron almost covered the threshold curve of the whole tympanic organ and the characteristic frequency of each neuron was almost the same. From those facts it was concluded that in the tympanic organ there was no neuron which had a biased response area and

therefore the tympanic organ might not have the ability of analyzing the sound frequency.

3. The slow potentials were recorded from the chordotonal organ. They were divided into four types: negative monophasic, negative-positive diphasic, positive monophasic with an abrupt rise and fall, and also that with a slow rise and fall.

4. The slow potential changed as if it were the envelope of the sound wave and was almost nonadaptive to prolonged sounds. The relation between its amplitude and the intensity of sound in decibel unit was measured.

5. When a prolonged and a short sound were delivered simultaneously, the slow potential evoked by the short sound superimposed on the long lasting one evoked by the prolonged sound. When the response to the prolonged sound was nearly saturated in amplitude, the response to the short sound delivered simultaneously was almost undiscernible.

6. Positive spikes superimposed on the rising phase of the positive slow potential. By weakening of the stimulus sound, a number of spikes decreased with the slow potential, until only the slow potential remained there.

7. It was discussed that the slow potential change obtained from the tympanic organ might be the so-called generator potential of this organ. Such a potential change as the microphonics was not obtained from the tympanic organ unlike the cochlea of higher animals, although the functions of both organs are the same.

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