

THE AUDITORY SYSTEM OF *HOMOROCORYPHUS* (TETTIGONIOIDEA, ORTHOPTERA)

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INTRODUCTION

The tettigoniid ear is a complex sense organ, situated on the prothoracic legs, below the tibio-femoral joint. Its structure has been described in detail by Schwabe (1966). It contains a minimum of 100 sensilla, and probably a total three times this number. It is more complex than the acridid ear (Gray, 1960) or the lepidopteran ear (Roeder, 1963) and the functional correlate of this complexity is not known.

The presence of a complex auditory receptor is correlated with the acoustic behaviour of the group. In most families the male stridulates and the female is attracted to him. Singing seems to facilitate swarm formation in East African populations of *Homorocoryphus nitidulus vicinus*. Stridulation is by the elythro-elytral method, and wing movements occur at a rate of 140/second. Many tettigoniids emit in the sonic range, i.e. their dominant frequency of emission is audible to the human ear, but these songs also contain ultrasonic components. The amplitude of emission is high. These characteristics correlate with the cryptic and solitary behaviour of many tettigoniids, and a loud high-frequency song enables the female to locate a male accurately over long distances.

The response characteristics of the tettigoniid auditory system have been investigated by several authors (Autrum, 1960; Katsuki & Suga, 1958, 1963). Their findings suggest that sounds are discriminated on the basis of the amplitude modulation pattern, and that the frequency is not important, although Katsuki & Suga (1960) found two types of neurone with different frequency-response ranges, probably central in origin. The central auditory interneurons of *Gampsocleis buergeri* and *Homorocoryphus lineosus* have been investigated by Suga & Katsuki (1961a); Suga (1963). Several auditory interneurons have been recorded, the largest of these being the 'T' fibre, which seems to be T shaped in the ventral cord, although the evidence for this is not strong. This interneurone shows amplitude-discriminating and direction-discriminating properties, but no frequency discrimination. In *G. buergeri*, at least, the fibre responds to the species song.

Autrum (1960) suggested that the tettigoniid ear contained two different types of sensilla, which were responsible for the 'phasic' and 'tonic' responses seen in response to a pulse of sound. These he called the 'phasic' and 'tonic' receptors. Michelsen (1966) showed that the sensilla of the ears of *Schistocerca* and *Locusta* did not behave in either a 'phasic' or 'tonic' fashion, and that the 'on' and subsequent 'tonic'

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components were due to the initial synchrony and subsequent asynchrony of the firing of the sensilla, as was previously suggested by Horridge (1961).

Recent work on the acridid auditory system by Horridge (1961), Popov (1965) and Michelsen (1966) indicates that the acridid ear is frequency-sensitive. In view of the large number of first-order auditory interneurons in the acridid auditory system it would not be surprising to find that different sensilla in the ear drive different interneurons. The idea, first suggested by Pumphrey (1940), that insects discriminate between sounds solely on the basis of the amplitude pattern has been shown to be incomplete, at least, in the acridids. It has often been suggested that the tettigoniid ear may be able to discriminate frequency, on the grounds that the ear contains many sensilla which are graded in size. This paper describes the results of an investigation into the response characteristics of the auditory system of the tettigoniid genus *Homorocoryphus*, with special reference to frequency discrimination.

MATERIALS AND METHODS

Male and female tettigoniids of the genus *Homorocoryphus*, which is common in Uganda, were used. Insects were caught from swarms in the wet season (*H. nitidulus vicinus*) and by sweeping in the grass and forest at other times of the year (*H. subvittatus*, *H. sp. A*). The taxonomy of the group is confused, and the status of the three species used is doubtful.

Both natural and artificial stimuli were used. Artificial stimuli were clicks, continuous sine-wave tones, and sine-wave pulses produced by a circuit which enabled the control of the rise and decay time of the pulse. The songs of *H. nitidulus* and *H. sp. A* were recorded in the field, and from caged insects. The song, which has high-frequency components, was recorded with a Brüel and Kjaer $\frac{1}{2}$ in. microphone (flat to 40 kcy./sec.), amplified, and recorded on a Precision Instrument tape recorder, type 6200 at 37.5 i.p.s. All stimuli were reproduced by a Radford amplifier, and an Ionofane loudspeaker, placed 30 cm from the insect's ear. Stimuli were monitored by placing the microphone in the position of the insect's ear. The response of the ear was recorded in the tympanic nerve with a silver wire electrode. The nerve was cut centrally, and the electrode was placed as close to the ear as possible. First-order central auditory interneurons were recorded from the neck connectives, exposed from the ventral surface and also from split connectives. Recording from small bundles of fibres shows small interneurons, which cannot be recorded from the intact connective. Responses were amplified by an FET pre-amplifier, and data were recorded on tape or film. An electronic counter (Philips type 4032) was used in the analysis of some of the data.

RESULTS

(1) *The ear*

The response characteristics of the ear and also its ability to discriminate between quantitatively different sounds were investigated briefly. It was not possible to record directly from the sensilla of the ear. Analysis of compound potentials recorded from the whole nerve will only indicate gross differences between the responses to stimuli. A negative result will not necessarily mean that discrimination is not occurring, but

ould indicate that the information is carried by the smaller fibres (many are less than 1μ in diameter) which are not discriminated by a hook electrode.

Before a stimulus is presented, there is a low level of activity in the tympanic nerve. This is presumably a response to low-level intensity sound in the environment, and not spontaneous activity, which is unusual in invertebrate sense organs. A sound stimulus elicits a response with a latency of 2 msec., and the conduction velocity of the tympanic nerve as a whole is approximately 1 metre/sec. The ear responds to a continuous sine-wave tone and the response does not adapt. The ear responds to sounds within the range 1–84 kcyc./sec. This is an approximate range due to the limitations of the sound measuring equipment. The dominant frequency of emission of

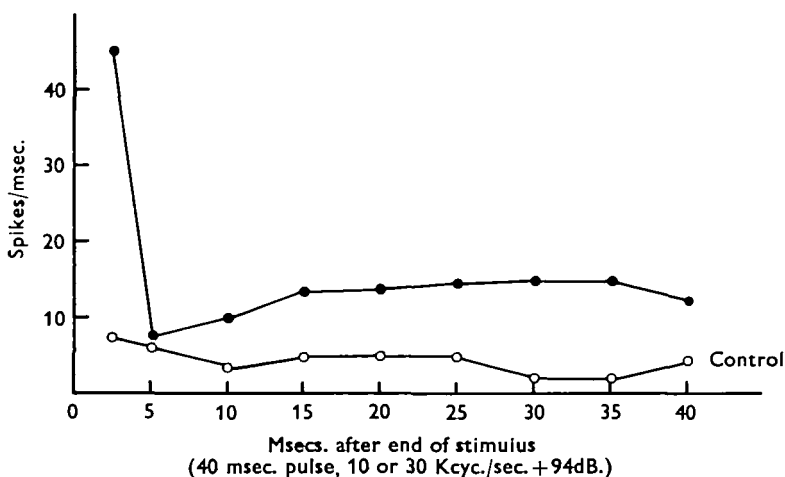


Fig. 1. The post-stimulus response (black circles) of the tympanic nerve shows a sudden drop in the response level at the cessation of the stimulus (pulses of 10 or 30 kcyc./sec., at +90 dB), which reaches the control level (open circles) after 5 msec. The level of the response then rises slightly, and decays over a period of 30 msec. This post-stimulus excitatory effect may reflect an 'off' response by some of the sensilla.

Homorocoryphus is 15 kcyc./sec., with many ultrasonic components, which will be well within the frequency range of the ear. The threshold of response is lowest in the region of 10–15 kcyc./sec., and also low above 30 kcyc./sec., correlating with the different response characteristics of the auditory interneurons described below. Ears are also present in the larval phases, and functional at least from the 4th instar. Larvae were not used routinely in investigations, and the response of the larval ear was not investigated in detail.

The response of the tympanic nerve to clicks suggests that, as in the acridids, the 'on' response is due to synchrony. A single click elicits a single potential which increases in size with the amplitude of the stimulus, indicating that more fibres fire as their threshold is reached. A train of clicks elicits a response to each click, which does not adapt over a minute or more, indicating that the fibres firing are not responding in a 'phasic' way.

The response of the tympanic nerve to a pulse of sound is followed by a period of low-level activity in the nerve, which continues for about 5 msec. after which larger

spikes are seen, diminishing with time. Analysis of the post-stimulus effect shows that the activity drops to pre-stimulus level, and then temporarily increases, so that there is a post-stimulus excitatory effect (Fig. 1). This may reflect an 'off' response by some of the sensilla of the ear.

The ability of the ear to discriminate frequency, amplitude and direction of a stimulus was investigated by presenting stimuli which differed in one parameter only. Analysis of the recorded compound potentials shows that these are essentially the same for all test frequencies. (10–40 kcyc./sec.). The response of the central auditory



Fig. 2. The response of the ear, as recorded in the tympanic nerve (lower trace), to the species song. Time marker, 10 msec.

interneurons, however, indicates that frequency discrimination does occur in the ear, and suggests that the information is carried by small fibres. Statistically significant differences in compound potentials are associated with steps as small as ± 2 dB over the range 80–100 dB. The higher the amplitude, the larger the number of impulses in response to the stimulus.

Experiments concerning the directional sensitivity of the ear confirm Autrum's results (1960), although accurate measurements were hampered by the lack of accurate sound measuring equipment. Directionality is therefore an intrinsic property of the ear.

The response recorded from the tympanic nerve to the species song is a non-adapting compound potential (Fig. 2). A larger component of the response is seen at the beginning of each pulse. The response is presumably species-specific, and this input to the central nervous system (CNS) must drive the interneurons concerned with song recognition.

(2) *Central auditory interneurons*

Four auditory interneurons have been recorded from the neck connectives of *Homorocoryphus*. One is large, and behaves in a similar way to the large T fibre of *G. buergeri* described by Suga & Katsuki (1961a). Although there is no good evidence that the T-shaped fibres in the cord are auditory in function, the nomenclature will be retained as a convenient one. The three smaller fibres have not been described before. Suga (1963) comments on a small fibre in *Homorocoryphus lineosus*, and this may correspond to one of the fibres described below.

(i) *The general response characteristics of the T fibre*

Recordings were made from the neck connectives of the intact animal and also from animals in which the neck connectives had been cut. Fewer fibres are recorded when the head ganglia are disconnected, suggesting that most of the recorded traffic

the neck connectives consists of descending impulses from the head ganglia (see also Rowell, 1969). The response of the T fibre is seen more clearly in such preparations, and little other ascending traffic is recorded. Small changes in response level and rate of response decrement occur as a result of this lesion, but other characteristics of the T fibre response are not affected. The effects of lesions on the level of responsiveness and habituation are considered in a subsequent paper.

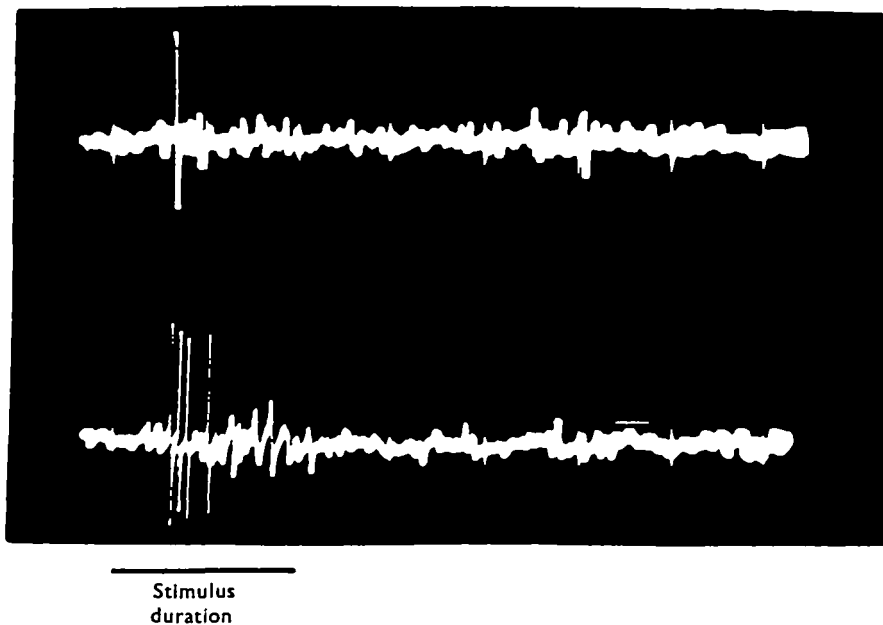


Fig. 3. The response of the ipsilateral (lower) and contralateral (upper) T fibres to a 40 msec. pulse of 10 kcyc./sec. The action potentials are 1 mV in size.

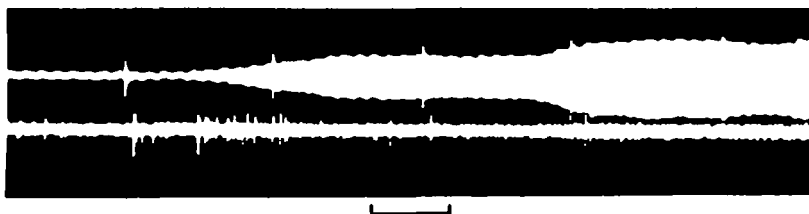


Fig. 4. The response of the T fibre (lower trace) to a continuous sine wave. The T fibre responds only to the onset of the sine wave, and not to subsequent amplitude changes. It continues to respond to transient sounds played simultaneously with the sine wave. Time marker, 100 msec.

The size of the T fibre spike remains constant with changing amplitude of the stimulus, and its short time course (1 msec.) is consistent with the view that it represents the response of a single neurone. The T fibre is driven solely by the tympanic input, and does not respond to sound if the tympanic nerves are cut. It responds to background noise, and a click elicits one or more spikes in both the ipsi- and contralateral fibres. A sine-wave pulse elicits an 'on' response in both fibres (Fig. 3), the response of the contralateral fibre being delayed by 1 msec. with respect to the

ipsilateral fibre. In 1% of the animals observed the response of the contralateral fibre is delayed by 60–80 msec. The T fibres respond only to the beginning of a sound, and therefore give no indication of the length of a stimulus (Fig. 4). The latency of the response of the T fibre with respect to the stimulus varies with the individual, and is between 10 and 20 msec. The delay between the tympanic input to the ganglion and the response of the T fibre, recorded in the connective at the point where it leaves the ganglion, is 6–7 msec. Allowing for conduction time (≈ 3 msec), there is ample time for a complex synapse or synapses to function.

The response of the T fibre can be recorded above and below the prothoracic ganglion, but not below the mesothoracic ganglion as it can be in *G. buergeri*. This may be a species difference, or due to the change in position of the fibre in the nerve cord. The T fibre is also recorded above the suboesophageal ganglion, and sends information to the brain. The ipsilateral T fibre always fires more spikes in response to a stimulus than does the contralateral T fibre (Fig. 3); moving the sound source from one side of the animal to the other alters the numbers of spikes fired by each fibre.

The response of the T fibre to a repeated stimulus decreases very slightly with successive presentations of the stimulus. The habituation characteristics of the T fibre are considered in a subsequent paper.

(ii) *Frequency and amplitude response of the T fibre*

The responses of the T fibre to stimuli differing only in frequency was investigated using a 40 msec. pulse of +94 dB. At 30 kcyc./sec. more spikes are elicited in response to a stimulus than at 10 kcyc./sec., at least in the ipsilateral fibre, but in the contralateral fibre there is little difference between the response at the two frequencies. Directionality is therefore enhanced at 30 kcyc./sec. The response to a pulse of 15 kcyc./sec., the dominant frequency of the song of *Homorocoryphus*, is lower than the response to either 10 or 30 kcyc./sec., and there is very little difference between the response of the ipsi- and contralateral fibres. (Fig. 5). This suggests that the T fibre is perhaps not important in conveying information about the species song, or that the 15 kcyc./sec. component of the song is unimportant. This seems unlikely.

The response of the T fibre to 40 msec. pulses of differing amplitude was investigated at 30, 15 and 10 kcyc./sec. Thresholds were not investigated, as the apparatus for measuring sound was not sufficiently sensitive. At 30 kcyc./sec. there is an increase in the number of spikes fired in response to a pulse as the amplitude is increased, and steps of the order of 2 dB can be discriminated over the range 80–100 dB, paralleling the response of the tympanic nerve. At 10 and 15 kcyc./sec. the response level is lower than at 30 kcyc./sec., and does not change with increasing amplitude. At 30 kcyc./sec. it is the ipsilateral fibre only which increases its response with amplitude, thus increasing directional information about loud sounds (Fig. 6).

(iii) *Directionality*

The ipsilateral T fibre always fires more spikes in response to a sound than does the contralateral fibre, at 10 and 30 kcyc./sec. (Fig. 5). At 15 kcyc./sec. there is no significant difference between the ipsi- and contralateral fibres. The difference between the discharge of the ipsi- and contralateral fibres is greater at 30 kcyc./sec., high amplitude, and low repetition rate.

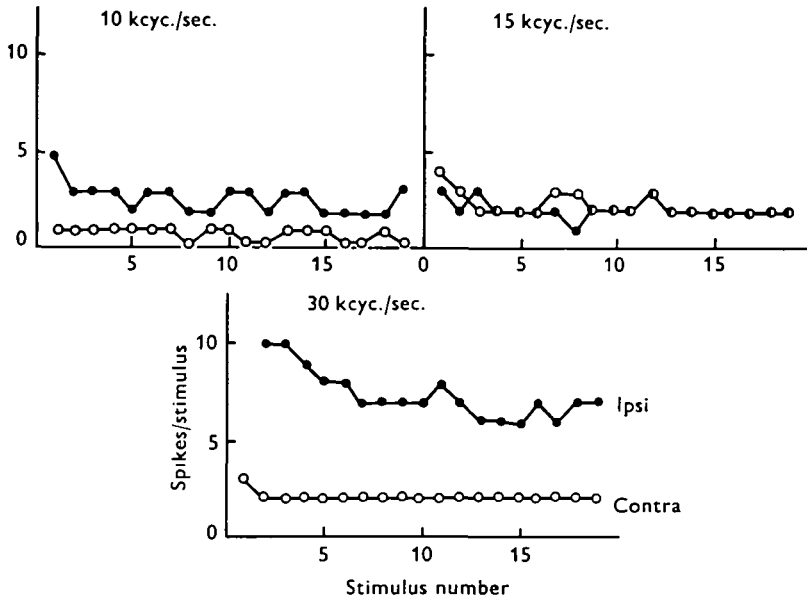


Fig. 5. The response of the ipsilateral (black circles) and contralateral (open circles) T fibres to a train of pulses differing only in frequency. The response level is higher when the stimulus frequency is 30 kcyc./sec., and at 15 kcyc./sec. (the dominant song frequency) the response level is low. There is little difference between the responses of the ipsilateral and contralateral fibres, and the directional information content is low.

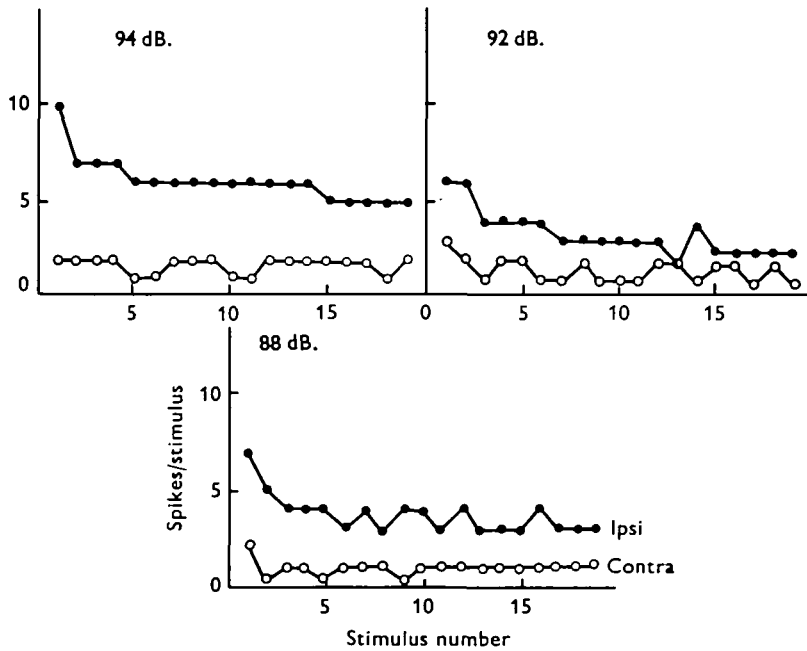


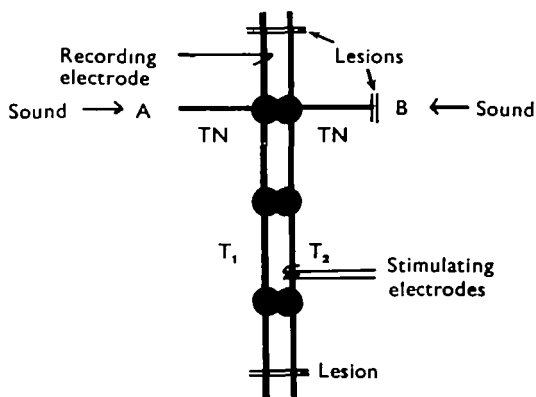
Fig. 6. The response level of the ipsilateral (black circles) and the contralateral (open circles) T fibres to a train of 30 kcyc./sec. pulses played at different amplitudes. The response level increases with the amplitude of the stimulus.

The directional information contained in the tympanic nerve response is enhanced in the central nervous system by the inhibitory effects of the ipsilateral tympanic nerve on the contralateral T fibre. This was also observed in *Gampsocleis buergeri* by Suga & Katsuki (1961). There is also a weak excitatory input from the tympanic nerve to the contralateral T fibre. Some tettigoniids (*Mecopoda elongata*) do not have this inhibitory mechanism, which enhances the directional information carried by the T fibres.

The response of the T fibres of *Homorocoryphus* was investigated before and after tympanic nerve lesions. When the ipsilateral tympanic nerve is cut, there is no response in the ipsilateral T fibre and an increase in the number of spikes in the contralateral fibre over the number fired when both tympanic nerves are intact. This indicates that an inhibitory effect on the contralateral T fibre had been removed by cutting the ipsilateral tympanic nerve. When the contralateral tympanic nerve is cut, there is no response of the contralateral T fibre, although responses in small fibres are sometimes seen. There is an increase in the number of spikes fired by the ipsilateral fibre at 30 kcyc./sec., but at 10 kcyc./sec. the response is variable. At this frequency the discharge of the ipsilateral T fibre may decrease, increase, or show no change. The most commonly observed was a decrease (Table 1). The increase in the response of the ipsilateral fibre was not as great as that in the contralateral fibre when the ipsilateral tympanic nerve was cut, indicating that the inhibitory effect of the ipsilateral tympanic nerve must be greater than that of the contralateral tympanic nerve. This must be due to the difference between the content of the two tympanic nerves, but measurement of this difference was not possible with the apparatus available; it presumably arises from the inherent directionality of the ears.

These observations were made in intact insects, and in those in which the head ganglia had been disconnected. When identical experiments are performed on insects in which the prothoracic ganglion is disconnected from the rest of the central nervous system, the tympanic nerve lesions are observed to have the same effect. This indicates that the inhibitory mechanism is contained within the prothoracic ganglion, and is not affected by inputs from other parts of the central nervous system.

The response of each T fibre is therefore affected by the ipsilateral excitatory input, and by inhibitory and weaker excitatory inputs from the contralateral tympanic nerve. The contralateral excitatory effect is only seen at 10 kcyc./sec. The contralateral inputs may be directly from tympanic nerve fibres, via an interneurone, or from the contralateral T fibre. An attempt to distinguish between these possibilities was made in an experiment which is summarized in Fig. 7. The contralateral tympanic nerve was cut and the response of the T fibre to sound was simulated by electrical stimulation of the connective below the prothoracic ganglion. The response of the ipsilateral T fibre to sound was recorded before, during and after stimulation, and it was seen that the response was not affected by the stimulation of the contralateral connective. Stimulation of the cut tympanic nerve inhibits the response of the opposite T fibre to sound, and it may be concluded that the effect is via the tympanic nerve fibres and that there is no interaction between the T fibres themselves. This experiment, however, does not rule out the possibility of the mediation of an interneurone (Suga & Katsuki, 1961*b*).



TN = tympanic nerves
 T₁, T₂ = T fibres

Fig. 7. This figure summarizes an experiment designed to show the inhibitory and/or excitatory interaction, if any, between the T fibres. The tympanic nerve, B, was cut, and the response of the T fibre, T₂, was simulated by electrical stimulation. The response of the T fibre, T₁, to pulses of sound was recorded before, during and after stimulation. The response of T₁ to sound was not affected by stimulation of T₂. The inhibitory and excitatory effects of the contralateral tympanic nerve in the ipsilateral T fibre must be due to the tympanic nerve fibres synapsing on the T fibre, or acting via an interneurone. There is no T fibre-T fibre interaction.

Table 1. *Summary of the response of the T fibres following specific tympanic nerve lesions*

Effect	No.	Increase %	Decrease %	No change %
10 kcy./sec.				
Cut ipsi TN, contra T Fibre Response	11	91	0	9
Cut contra TN, ipsi T Fibre Response	11	9	64	27
30 kcy./sec.				
Cut ipsi TN, contra T Fibre Response	6	83	17	0
Cut contra TN, ipsi T Fibre Response	6	83	17	0

Stimulus = 40 msec. pulse, +94 dB.

(iv) *The response of the T fibre to bat cries*

The low level of the response of the T fibre to pulses of 15 kcy./sec., the dominant frequency of the species song, suggests that this neurone is not important in song recognition. Its preferential response to 30 kcy./sec. and the increase in directionality with amplitude at this frequency suggests that it has a possible warning function, as high-frequency sounds are associated with the sonar systems of predators such as

bats, and are made involuntarily by rodents when moving through the grass. The neurone responds well to the cries of the Ugandan vesperilionid, *Scotophilus nigrinus*, a known predator of *Homorocoryphus*. There is, however, no behavioural evidence to suggest that an avoidance response is driven by the T fibre.

(v) *Other auditory interneurons*

Two small auditory interneurons have been recorded from the connectives, responding to clicks and pulses. The smaller may be identical with the small fibre observed in *H. lineosus* by Suga (1963). This fibre is sometimes observed in the ipsilateral connective when the ipsilateral tympanic nerve is cut, and must be driven either by the contralateral tympanic nerve, or by an extratympanic input (Fig. 8). Neither of these fibres was observed frequently in the connectives, and they have not, therefore, been characterised in detail. A small fibre which responds to song has been observed in split connective preparation and is described in the following section.

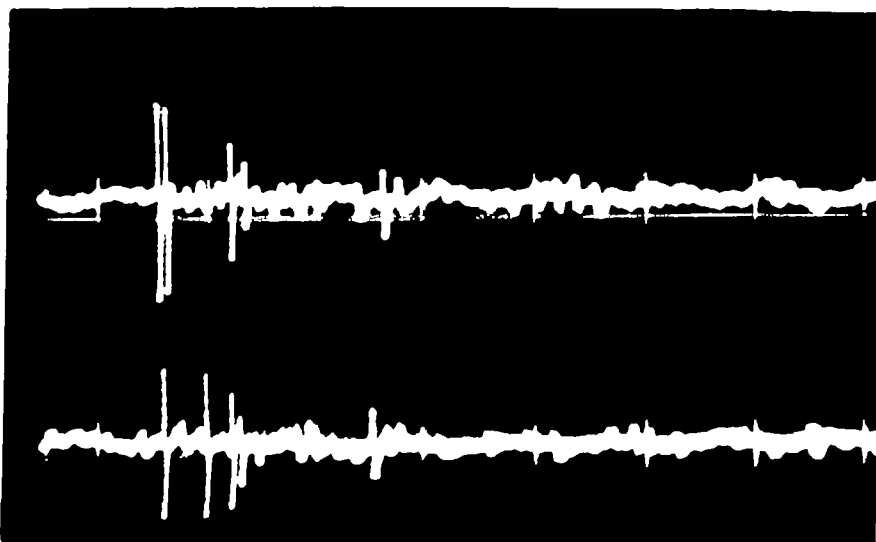


Fig. 8. The response of the ipsilateral (lower trace) and contralateral (upper trace) connectives, showing two small auditory interneurons in addition to the large T fibre. Time scale, 40 msec.

(vi) *The response of central auditory neurones to song*

Unlike the T fibre of *G. buergeri* (Suga, 1963), the T fibre of *Homorocoryphus* does not respond to song (Fig. 9), even when the rise time of the song is very rapid. Further, when the song is played simultaneously with short pulses which approximate to clicks the response of the T fibre to the clicks is inhibited (Fig. 10). The greater the amplitude of the song, the greater the inhibitory effect (Fig. 9). Post-inhibitory rebound is observed after the cessation of the song, a large discharge being observed, which precedes the next pulse (Fig. 11). This post-stimulus effect is unrelated to that seen in the tympanic nerve, which occurs after all short pulses. The discharge of the T fibre is seen only after the cessation of the song, or of a continuous sine wave which

has led to the inhibition of the T fibre. The non-response of the T fibre to the song indicates that there must be at least one other neurone at the level of the prothoracic ganglion which responds to song, as it is unlikely that any motor response is controlled by a thoracic loop, or that the song is signalled in the brain by the absence of activity in the T fibre.



Fig. 9. The response of the T fibre (lower trace) to clicks, and the absence of the response to the species song. Time scale, 100 msec.



Fig. 10. Inhibition, by the species song, of the response of the T fibre (lower trace) to pulses. Time scale, 100 msec.

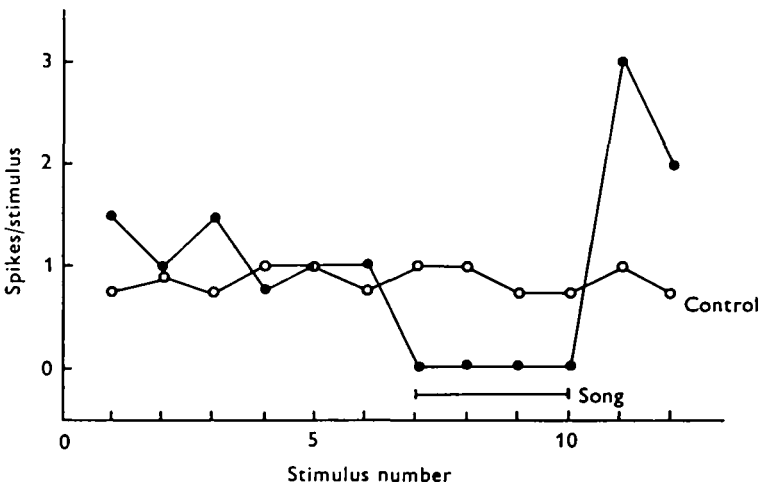


Fig. 11. The responses of the T fibre to pulses (black circles) is inhibited by the species song. When the song stops, there is a large post-inhibitory rebound. The control curve (open circles) shows the response of the T fibre to pulses only.

A small fibre (Fig. 12) which responds to the species song was found by recording from small bundles of fibres in the split connective. This fibre is not easy to find, and has not therefore been investigated in detail. It responds to a continuous sine wave, and to the species song, although there is not a 1:1 correlation between the response and the pulses which constitute the song. There may be another fibre at the level of

the prothoracic ganglion which responds more specifically to the song, but if this is very small the chances of finding it in a split-connective preparation are correspondingly small.

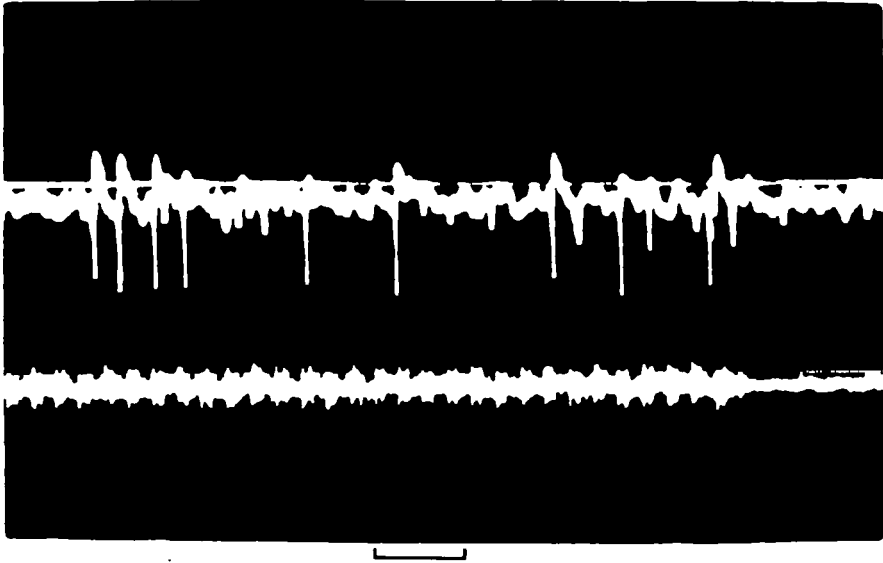


Fig. 12. The response of a small fibre, or a complex of fibres (upper trace) to the species song. The response is not a 1:1 response. Time scale 100 msec.

DISCUSSION

(1) *The ear*

The structural complexity of the ear may be correlated with its ability to respond differentially to stimuli differing in frequency, amplitude and direction. Frequency discrimination is not demonstrated in the recorded tympanic nerve response but can be inferred, as the tympanic input drives one interneurone and others at the level of the prothoracic ganglion which are frequency sensitive, with different frequency response ranges. The threshold of the tympanic nerve is lowest in these areas (10–15 kcyc./sec., and above 30 kcyc./sec.) The amplitude-discriminating ability of the ear is paralleled by the T fibre. The directional response of the ear is an intrinsic property. Differences between the responses of the two ears are almost impossible to measure, but this must result from the different orientation of the legs (normally held at right angles to each other) and the amplitude response properties of the ear. This differential information is enhanced by the T fibre system.

There is, however, no evidence to support Autrum's idea that the sensilla are referable to the 'phasic' and 'tonic' types. As in the acridids (Michelsen, 1966) the 'on' response is a result of initial synchrony, and the 'tonic' response to subsequent asynchrony of fibres with different firing frequencies.

The different response characteristics of the sensilla of the ear are unlikely to be correlated with their size, although it has often been suggested that the smaller sensilla in the tettigoniid ear may respond to high frequencies. The properties of the

Sensilla must be related to the mechanical structure of the ear, which is complex (Schwabe, 1906), and the mechanism of transduction is not understood. The tympanum is very light and vibrates in response to high-frequency sound. As it is fixed at its edges, it is likely that there are different patterns of vibration for different frequencies. This could lead to the differential response of the sensilla, the position of the sensilla on the vibrating column determining in part their response characteristics. The sensilla are not attached to the tympanic membrane but to the tympanal trachea, and it is probably the induced vibration of the air in the trachea which activates the sensilla.

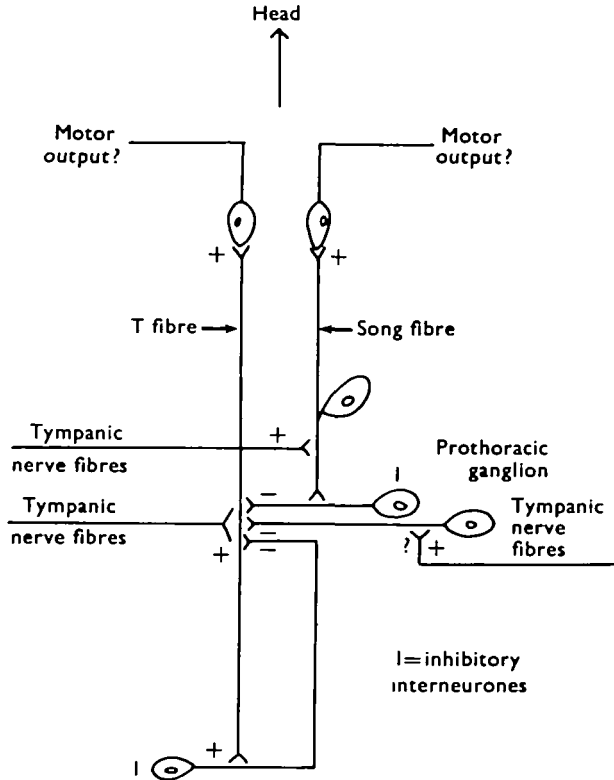


Fig. 13. Possible synapses affecting the T fibre. Only one T fibre is shown, and the site of the cell bodies is unknown. All synapses must act close to one another, as the same signal is sent up and down the T fibre. Inhibition may be pre-synaptic. The inhibitory effect of the song fibre must occur via an interneurone. The contralateral tympanic input may also act via an interneurone. The posterior branch of the T fibre may initiate a negative feed-back system, which is discussed in a subsequent paper.

(2) *The central auditory interneurones*

Four central interneurones have been recorded: the T fibre, a song fibre and two small fibres which are occasionally seen in whole-connective recordings. The response properties of the T fibre suggests that it may function as a warning neurone. *Tetti-goniids* are cryptic and solitary by day, and active by night. They are subject to predation at all times by animals which create ultrasonic noise by moving in their environment, and also by bats, which locate their prey by means of echo-location.

Advance warning of such predators would be advantageous. The T fibre responds preferentially to short, high-frequency sounds, and can discriminate small changes in the amplitude and also in the direction of a sound source. It adapts rapidly to a continuous tone, and does not respond to the species song. There is no 'on' response of the T fibre to the song, suggesting that the T fibre is being actively inhibited. Inhibition is also observed when pulses are played simultaneously with the species song. The degree of inhibition increases with the amplitude of the song. Inhibition is presumably a result of the activity of a neurone which responds to the species song. The absence of an 'on' response of the T fibre to the song suggests that the song fibre responds during the build-up of stridulation, during which time the T fibre would not be expected to respond in the absence of inhibitory factors, because of the slow rise time of the song.

The small fibre responding to the song could inhibit the T fibre. The song fibre presumably plays a part in controlling the intraspecific behaviour of *Homorocoryphus*, the orientation of the females to singing males, and the interaction of singing males. It may be partially responsible for the phasic response of the T fibre.

If the T fibre evokes avoidance behaviour, it is essential that it should be inhibited by the species song, as the same motor apparatus is used for avoidance behaviour, orientation behaviour and singing. In the absence of inhibition, conflicting behaviour patterns might be stimulated. It is quite likely that a song fibre is inhibited by the T fibre (Fig. 13). Inhibition of one fibre by the other may be interpreted as an attention mechanism. Although tettigoniids are observed to take evasive action at the approach of man, this may be mediated via the subgenual organ, and there is as yet no direct evidence that avoidance behaviour is driven by the T fibre.

Tettigoniids are able to locate a sound source, e.g. a singing male, over long distances. Alexander (1956) reports that the female *Neoconcephalus* (closely related to *Homorocoryphus*) can locate a singing male over a distance of 500 metres. In some tettigoniids (although few have been investigated) the T fibre responds to song, and its directional properties probably provide a neural basis for sound location. In *Homorocoryphus*, the directional properties of the T fibre cannot be utilized for this purpose, but would make possible the accurate location of a predator and may drive an evasive behaviour pattern. Differential information regarding the sound source is provided initially by the difference in response of the two ears to a stimulus. This is then enhanced by the inhibitory system of the ipsilateral tympanic nerve on the contralateral T fibre, and vice versa. Direction may be signalled simply by the different number of spikes in the ipsi- and contralateral T fibre. Information about the position of the leg is probably integrated in the neural direction-finding system.

The inhibitory and minor excitatory synapses of the tympanic nerve on the T fibre may be pre- or post-synaptic with respect to the major excitatory synapse, or, if the fibre is T shaped, on the leg of the T. All these situations would lead to the same information being transmitted up and down the cord. The information going down to the mesothoracic ganglion is probably important in regulating the control of the level of responsiveness of the T fibre, and its rate of habituation. This is discussed in detail in a subsequent paper. There is no evidence that the inhibitory or excitatory effects on the contralateral fibre are the result of T fibre-T fibre interaction, although an interneurone may be involved.

At least two auditory pathways exist in the central nervous system of *Homorocoryphus*, and there are probably more. There may be another neurone which responds to song at the level of the prothoracic ganglion. Higher auditory interneurons have not been investigated, and there is no information about the relationship of the auditory input to the motor output.

The auditory system of *Homorocoryphus* differs from that of *Gampsocleis buergeri*, the only other tettigoniid investigated in any detail, in that the T fibre does not respond to the species song. *Mecopoda elongata* does not have the inhibitory circuit which enhances the directional information carried by the T fibre. The T fibre appears to be universal among the tettigoniids, and species differences in its properties may be related to the different roles it may play in controlling the behaviour of different species.

Recordings of auditory interneurons of *Gastrimargus africanus* (Acrididae) by Rowell & McKay (1969) indicate that there are many auditory interneurons at the level of the neck connectives. The large alpha neurone is specialized for the reception of high-frequency sound, as is the T fibre of *Homorocoryphus*, but carries little directional information. It is a tonic fibre, and responds to continuous sound. Directional information is carried by the beta fibre, which is highly specialized for this purpose, and has mutual inhibitory connexions similar to the tettigoniid T fibre such that the contralateral fibre never fires in response to unilateral sound. The insect auditory system as seen in the Orthoptera, probably the most highly developed auditory system among the insects, is not a simple system as it was thought to be. Both tettigoniids and acridids are able to discriminate between qualitatively different sounds at the level of the sense organ and in the central nervous system, and possess several auditory pathways dealing with different types of input.

SUMMARY

1. The responses of the auditory interneurons indicate that the tettigoniid ear discriminates frequencies.
2. The T fibre receives strong ipsilateral and weak contralateral excitatory inputs and a strong contralateral inhibitory input, from the tympanic nerves. These inputs are frequency-sensitive, the response being greatest at 30 kcyc./sec. and above. Responsiveness is low in the region of 15 kcyc./sec., which is the dominant song frequency.
3. At 30 kcyc./sec. the T fibre is most sensitive to amplitude increments, and conveys maximal directional information. Both the T fibre and the ear (as judged by the compound potential in the tympanic nerve) respond to steps of 2 dB. The directionality of the ear is enhanced by the contralateral inhibitory connexions of the T fibre. At 15 kcyc./sec. directionality is poor, but is present at 10 kcyc./sec.
4. The T fibre is inhibited by continuous sounds, including the species song. The extent of the inhibitory effect varies with the amplitude of the continuous sound. This may assist in explaining the 'phasic' response of the T fibre. There is little habituation to repetitive stimuli.
5. A small interneurone seen in split connectives gives a 'tonic' response to song

and to continuous sound. It may inhibit the T fibre. Two other auditory fibres are occasionally recorded in the connectives.

6. The T fibre has all the properties required of a warning system responding to pulsed high-frequency sound, and it responds well to bat cries. There is, however, no evidence that it mediates a behavioural response.

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