

## AUDITION IN THE DESERT LOCUST: BEHAVIOURAL AND NEUROPHYSIOLOGICAL STUDIES

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### INTRODUCTION

The tympanal organ of insects has been the subject of many studies revealing its electrophysiological and physical characteristics in audition (Pumphrey, 1940; Horridge, 1961; Adam & Schwartzkopff, 1967; Michelsen, 1971).

Horridge (1961) suggested that all the effects found at different tones for the primary neurones (of the tympanal organ) could arise from incidental properties of the neurones, in the sense that they may have no significance in the life of the animal. If so, it is unclear why there are separate groups of tympanic sensory cells (Suga, 1960; Horridge, 1960, 1961; Michelsen, 1968). After the discovery of an auditory centre in the insect protocerebrum (Adam & Schwartzkopff, 1967) it is impossible to accept the above idea. The auditory input is also integrated in the insect C.N.S. with some other neuronal pathways shown by multimodal units reacting to visual and auditory stimuli (Horridge *et al.* 1965). This integration has to be reflected in the output site, revealing some kinds of behavioural pattern, like various modes of communication between specimens.

It has already been shown that behavioural reactions to acoustic signals can be elicited in insects (Dumortier, 1963). The common feature of many types of artificial stimuli given to tympanate insects is that they are more or less faithful imitations of real natural sound-emission rate. In the present studies we have shown to what extent a novel acoustic stimulus is effective for the behaviour of a locust. This and the characteristics of the auditory perception of the desert locust *Schistocerca gregaria* were the subject of the present studies.

### METHODS

#### *Electrophysiology*

*Animals.* Adults of the desert locust *Schistocerca gregaria* (Forsk.) were used. Results were obtained for 9 males and 15 females.

Insects were decapitated and cut across the middle of the abdomen. The tympanal organ is located laterally on the first abdominal segment. The operation was therefore done from the dorsal aspect and the tympanal nerve was uncovered between the meta-thoracic ganglion and the tympanal organ.

*Recording and stimulation.* The tympanal nerve was slightly lifted up and put on the

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recording electrode and the indifferent electrode was placed elsewhere on the operate body surface. Stainless-steel entomological pins were used as electrodes.

Impulses from the nerve were fed to a low-level pre-amplifier (type 122, Tektronix) and from there to a dual beam oscilloscope (type 502A, Tektronix) triggered by the stimulus signal, and photographed by a kymograph camera (Grass, C4E). Pure tone signals were driven from a sine/square generator (model IG-82, Heathkit) connected through a time gate to an audio-amplifier (built-in Revox tape recorder, type 77A) and speaker. Two speakers were used for 0.2–10 kcyc/sec and for 15–40 kcyc/sec ranges. The condenser microphone (type 4131-1" or type 4135-1/4" with power supply type 2081, Brüel and Kjaer, Denmark) and speaker were placed 15 cm from the preparation. The microphone was connected to a sound level meter (decibel meter, type 2203, Brüel and Kjaer, Denmark).

The animal preparation, speaker and microphone were placed in a soundproof thermostatic incubator at  $27 \pm 2$  °C. The incubator inside was covered by anti-reflection coat. The background noise obtained was < 30 dB. (The tympanal organs of *S. gregaria* and *Locusta migratoria* responding to sound intensities higher than 40 dB (Horridge, 1960; Michelsen, 1968)).

*Experimental procedure.* The threshold intensity was determined for each tone given. Each stimulus was a 0.5 sec pulse followed by 0.5 sec silent interval. Some pulses were given for each tone in subthreshold, threshold and suprathreshold levels. One to three series of stimuli were given to each preparation. A threshold response was regarded as the smallest intensity in which spikes began to appear.

### Behaviour

*Animals.* Forty animals were used for each stimulus (1, 4, 7, 10, 20 kcyc/sec and 'white' noise), half males and half females. The animals were of some group ages between 5 and 56 days. They were equally divided into treatment and control groups. The control animals were kept separately under the same physiological conditions. Thus the control animals had not experienced the auditory stimulus.

*Techniques.* Insects were attached on the dorsal side of the thorax by means of a wax (Specialvoks, ML-445/2, Dansk Voksfabrik, Copenhagen) to a specially constructed flight mill (Plate 1a, b). The flight-mill arm was connected using a low-load microswitch to an electrical counter counting the number of rounds made by the animal.

The flight mill and the speaker were kept during the tests in the soundproof incubator at  $33 \pm 2$  °C (see electrophysiological methods). The speaker which was connected to the audio-amplifier of the tape recorder was placed 20 cm above the flying animal. For volume calibration a condenser microphone (type 4131, B and K) was placed in the same location of the animal and connected to the sound level meter. A circular fluorescent lamp surrounding the speaker supplied bright and equally dispersed illumination.

For pure tone stimulation the sine/square generator was connected to the audio input of the Revox tape recorder. All the pure tones given were at a volume of  $80 \pm 1$  dB. The tape recorder was used to broadcast a recorded flight sound or 'white' noise using a tape loop 3 m long. 'White' noise tape was prepared using

calibrated 'white' noise generator. Flight-sounds tape was recorded from an insect flown on flight mill under a low-level background noise.

*Experimental procedure.* After the animal had been attached to the flight mill it was allowed to fly freely (clockwise and anticlockwise directions were repeated alternatively) and when it stopped flying a stimulus was given. If the animal reacted the stimulus was stopped. The stimulus continued for 2 min and if no reaction was seen the animal was stimulated arbitrarily to fly. This was done by applying an air stream on the head (wind receptors on the head are excitatory for the flight motor system (Weis-Fogh, 1955-6)). Thus the stimulus preceded the flying period. The control experiments were carried out in the same way, but a silent period was given for 2 min instead of the stimulus. Ten successive repetitions were made for each specimen tested. The time between the onset of the stimulus and the beginning of the response (the delay period) was measured. Then the number of rounds was counted for each positive response by the electrical counter.

When recorded flight noise was used as a stimulus it was presented in normal speed and volume of 80 dB. The stimulus or control durations were 5 min, and five successive repetitions were made for each specimen. Treatment and control stimuli were alternatively presented. When natural flying sounds were used the animal tested was subjected to the flight sounds of four specimens (males or females) attached to another four-armed flight mill. The emitting group was exchanged with the speaker. Five to ten successive repetitions were made for each tested specimen. Treatment and control (silent period) were alternatively given to each specimen. The stimulus period was 2-5 min. The natural flying sounds were of intensity of 60 dB.

## RESULTS

### *Electrophysiology*

The tympanal nerve responded in the range between 0.2 and 40 kcyc/sec with maximum sensitivity between 3 and 5.5 kc/sec (Text-fig. 1). The sensitivity decreased abruptly toward the ultrasonic frequencies and gradually toward small frequencies. The response of both sexes was found to be the same.

The repetition frequency at which the sound receptors in the tympanal organ of *S. gregaria* fail to respond depends on the intensity of the stimulus, its duration and the adaptation state (Michelsen, 1966). This was also found to be true in our experiments for the peripheral nerve (Table 1). Adaptation (changes in the sensitivity as function of time) was found using relatively long intervals between pulses of the same stimulus (Text-fig. 2B).

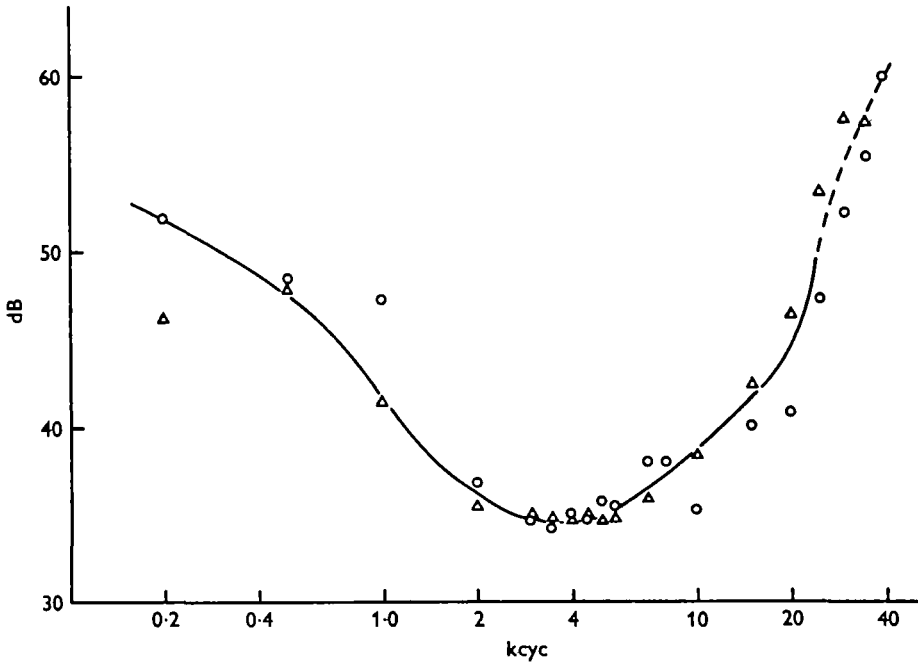
The number of units contributing to the electrophysiological response considerably increased as function of intensity (Text-fig. 3). In some tests responses of single units were obtained (Text-fig. 2A). It is worth mentioning that the single neurones responded to background noise disregarding the tone and intensity of the stimulus given under the experimental conditions.

### *Behaviour*

*Observations on the flight behaviour.* Observations were made on the flight behaviour of tethered flying locusts under the experimental conditions. Some specimens were

gliding on the flight mill or flying with wings of one side only. Some were flying poorly without any forward movement.

Loss of contact with the substratum by the tarsi removes an inhibitory influence on the flight motor system (Weis-Fogh, 1955-6). It was found that the locusts overcome this loss of contact by some 'tricky' ways or simply by catching the wings (Plate 2*b*). Some stopped flying by catching a wing with the leg or by catching the



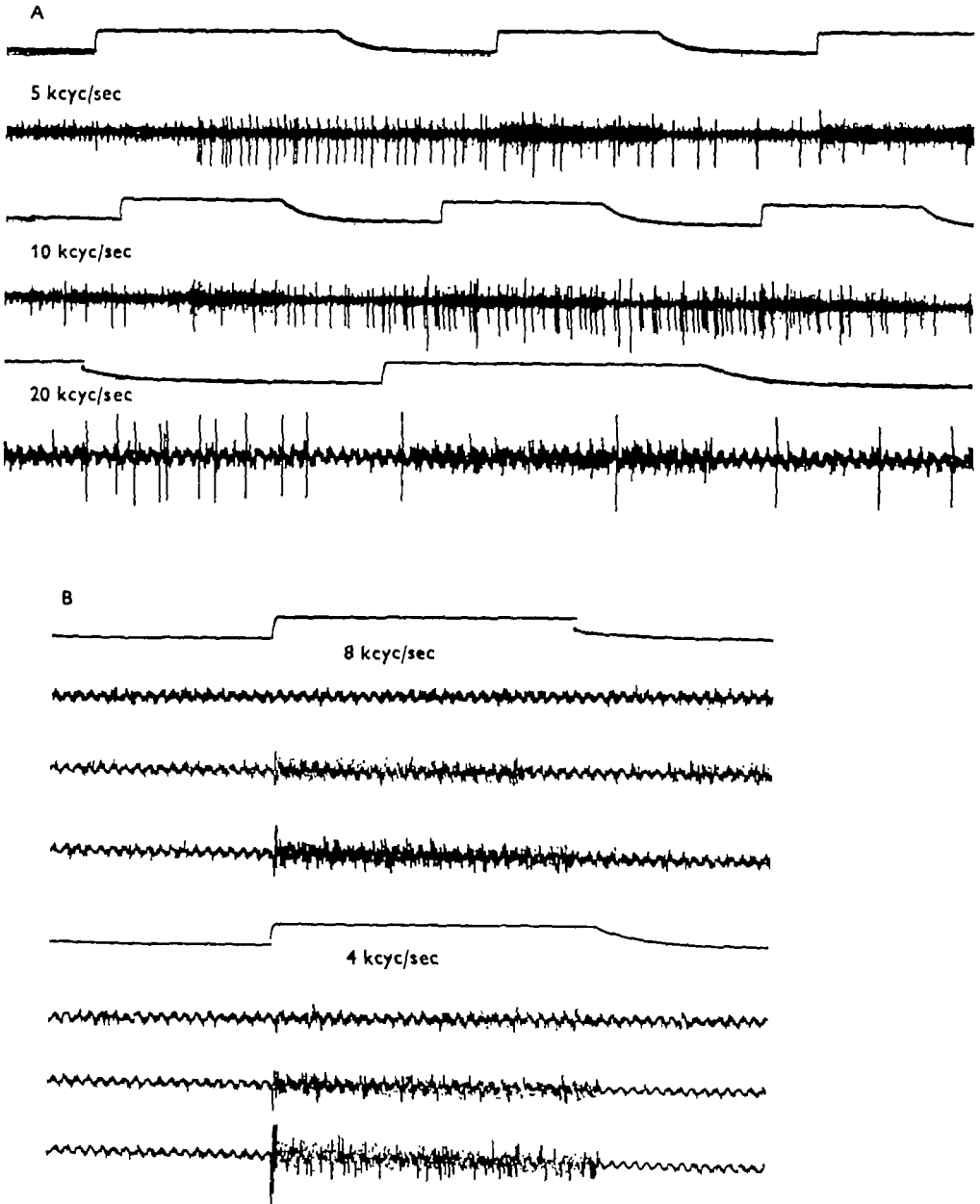
Text-fig. 1. Threshold intensity curve of the response of the tympanal nerve to pure tone stimuli.  $\Delta$ — $\Delta$ , Males;  $\circ$ — $\circ$ , females. (--- sound intensity not fully calibrated.)

Table 1. *The decrease in the sensitivity of the tympanal nerve response of the desert locust under continuous stimulation with sound stimuli*

(1<sub>1</sub> = first stimulus; 2 = last stimulus 1-2 h after successive stimulation with 2-3 frequency series. Calculated for four animals. Compare 1 and 2 at each frequency.)

Frequency (kcyc/sec)	Threshold response (dB)	
	1	2
1	47.5	47.5
2	35.0	36.5
4	34.2	35.0
10	35.0	35.0
20	41.8	43.8
25	47.2	48.0
30	49.5	58.0

ventral side of the abdomen with the middle legs. Some animals put the right tarsus or the two hind tarsi on the abdomen tip. Some put the left fore and hind legs on the wings, or grasp the right fore and hind legs together. The animals were constantly watched during the experiments and these types of behavioural pattern were prevented.

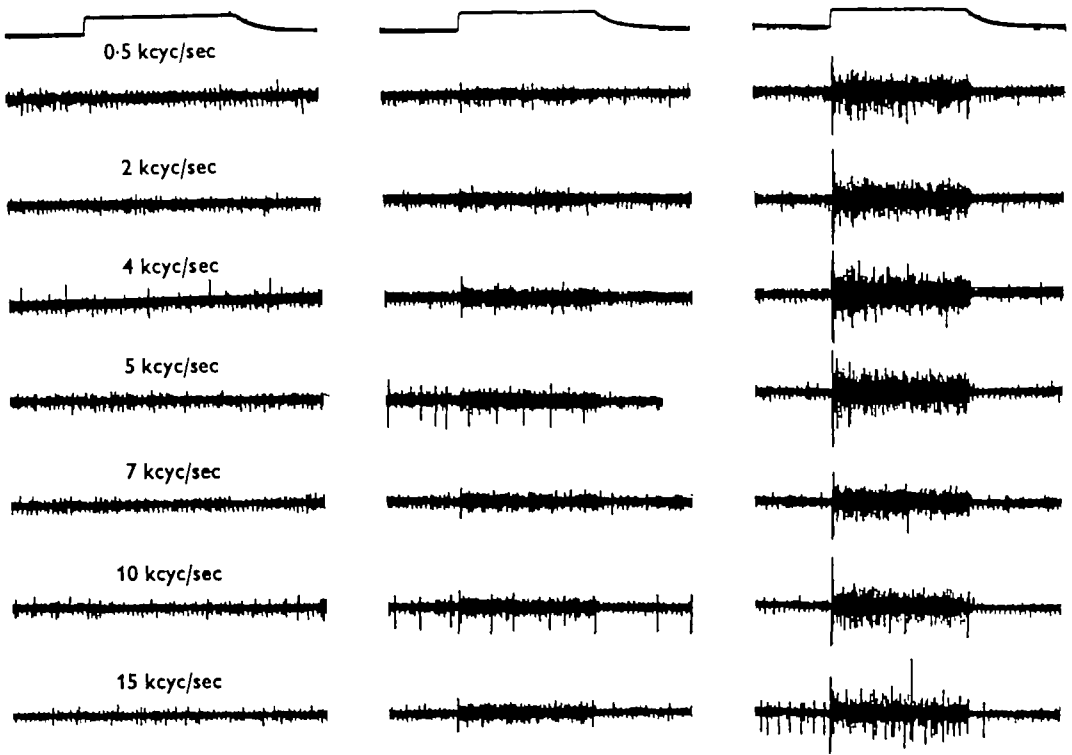


Text-fig. 2. A, Recordings from single units of the tympanal nerve responding to low-frequency background noise superimposed on the response of the whole bundle to pure tone stimuli. Spike potentials are seen in subthreshold and threshold intensities for the whole bundle (at 5 and 20 kcyc) and threshold intensities at 10 kcyc. Stimulus duration 0.5 sec. Threshold intensities (approximations) are seen in Text-fig. 1. B, Adaptation of the tympanal nerve to pure tone stimuli. Impulses were obtained for each tone under successive stimulation (intervals of 2-3 sec) with the same threshold intensity ( $37 \pm 1$  dB). Stimulus duration 0.5 sec.

The change in the rate of flying was determined in order to know the time the animals spent flying on the flight mill during the experiments (Table 2).

*Responses to pure tones.* The total number of animals activated by the stimulus is shown in Text-fig. 4. While males showed positive response to all the frequencies, the females' response was uncertain in 1 and 20 kcyc/sec. The maximum response was ranged between 4 and 10 kcyc for females and between 10 and 20 kcyc for males. 'White' noise was found to be a strong stimulus for both sexes. The 'white' noise is even more effective than the various tones in comparison to the control group.

The delay (the time from the onset of the stimulus to the beginning of the response) was found to range in males between 29.6 and 38.8 sec while for the females the appropriate values are longer, 35.2 and 56.6 sec. In many cases the delay period was



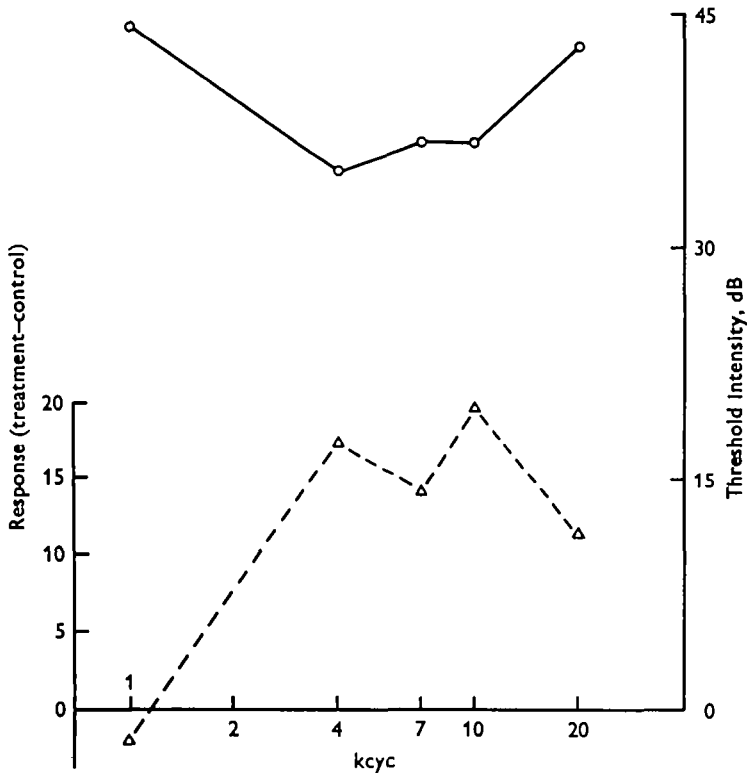
Text-fig. 3. The response of the tympanal nerve to pure tone stimuli. The number of units contributing to the response increased with the intensity. Each impulse begins with on-discharge. Single-unit responses are seen under various tones and intensity levels. Stimulus duration 0.5 sec. Threshold (left) intensities (approximations) are seen in Text-fig. 1, sub-threshold (middle) and suprathreshold (right) intensities were arbitrarily selected.

Table 2. *Changes in the rate of flying of the desert locust under the experimental conditions*

(Total number of rounds completed in each period. Temp.  $29 \pm 1$  °C.  
Five females, two males.)

Time...	1 min	2	4	8	16	30	1 hour	2	4
Males	104.5	203.0	402.0	725.0	1330.0	2356.0	4058.5	6178.0	—
Females	91.0	197.8	411.0	753.0	1386.0	2366.0	4060.0	7730.0	11562.0

1-3 sec, which is clearly different from the electrophysiological one (the latency). The delay period is shorter in the treated animals in 1, 4, 20 kcyc and 'white' noise in males, and 4, 10 and 20 kcyc in females (Table 3). Considering this total average no systematical change is seen in accordance with the various tones given.



Text-fig. 4. Behavioral and electrophysiological (threshold intensity) responses to the same pure tone stimuli. (Average number of flight initiations for both sexes:  $\Delta$ --- $\Delta$  [treatment-control];  $O$ — $O$ , electrophysiological data.).

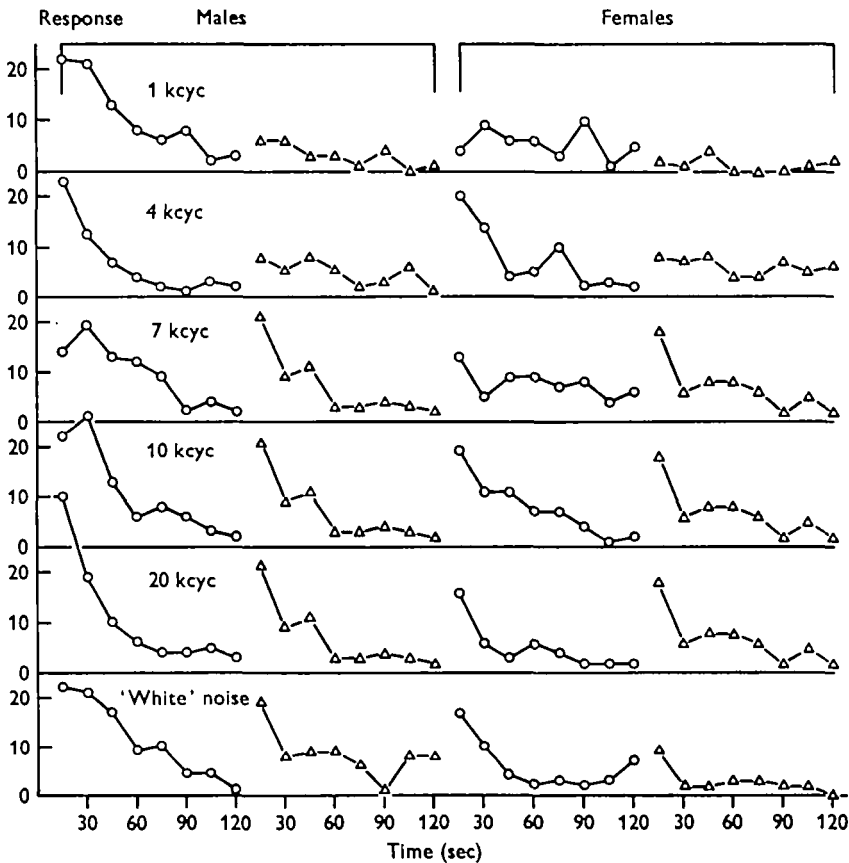
The change in the delay period as a function of the sound stimulus was observed in more detail by examining the distribution of the data (Text-fig. 5). Although animals tend to fly even under silent conditions, there are remarkable differences in the period of time within which they begin to fly in comparison to specimens treated by sound stimulus. Flight was initiated mainly in the first 30 sec in males with maximum response at 10 and 20 kcyc. With the other tones longer delays were found, yielding less steep curves. A far larger number of animals reacted in the first 30 sec to the pure tones than under silent conditions. The 'white' noise was also found to be a sound stimulus. More females began flying in the first 30 sec in 4 and 10 kc than in the appropriate controls. The females' response to 'white' noise is very high. However, the males are much faster than females (shorter delay period), as seen also in Table 3.

The number of rounds flown by the animals as a result of pure tone stimulation is much greater in the treated group than in the control group (Table 4). Thus, they

Table 3. *The delay period before the response of the desert locust to the sound stimuli*

(Total averages, in seconds. The same control used for 7, 10 and 20 kcyc.)

		Frequency (kcyc/sec)					'White' noise
		1	4	7	10	20	
Males	Treatment	37.2	29.6	38.8	35.2	31.2	36.4
	Control	39.6	41.7	33.9	33.9	33.9	47.8
Females	Treatment	56.6	35.2	53.4	35.8	36.7	42.4
	Control	51.7	55.5	40.5	40.5	40.5	39.1



Text-fig. 5. The number of animals responding as function of the delay period. The delay period results were grouped using successive intervals of 15 sec. ○—○, Treatment; △—△, control.

spent longer periods flying under the influence of pure tone stimulation (compare with Table 2). It is worth mentioning that the number of rounds flown by males is higher than that of females. This may be due to sexual differences, especially in behaviour and body weight. There is no systematic influence along the frequency scale of the tones given. It is very interesting to note that while the pure tone stimuli have a positive effect of initiating and maintaining of flight, 'white' noise is inhibitory (Table 4). As mentioned earlier the number of animals that began flying under the



Influence of 'white' noise is equal to or higher than the number that did so under pure tone stimulation. Since the insects fly fewer rounds in 'white' noise (Table 4) we concluded that they stop earlier in comparison to those stimulated by pure tone. This inhibition under 'white' noise shows that the animals differentiate it from pure tone.

Table 4. *Number of rounds completed by the desert locust in response to each sound stimulus (total average)*

		Frequency (kcyc/sec)					'White' noise
		1	4	7	10	20	
Males	Treatment	244.0	97.3	103.4	107.8	128.5	215.0
	Control	64.3	96.3	67.2	67.2	67.2	267.0
Females	Treatment	110.8	65.5	76.2	98.4	60.7	92.8
	Control	75.1	24.7	48.5	48.5	48.5	122.8

Table 5. *The delay period before response of the desert locust after the first (I) and last (II) period of stimulation*

(Results of both sexes were averaged.)

		Frequency (kcyc/sec)					'White' noise
		1	4	7	10	20	
I	Treatment	44.7	24.7	24.6	24.9	45.3	38.1
	Control	42.5	22.5	24.3	24.3	24.3	46.6
II	Treatment	46.3	23.6	62.1	39.2	44.2	32.7
	Control	33.0	56.9	41.4	41.4	41.4	52.6

*Is the sound stimulus learned?* In the experimental procedure the stimulus periods were separated from the response period. This set of activities was repeated ten times with each animal (see methods). When data are grouped as to the repetition number (which is the time scale) the relative number of flight initiations was found to increase as function of time in 7, 10 and 20 kcyc/sec as seen in the difference from the control group (Text-fig. 6). Such an increase may indicate a learning procedure.

While no systematic change as a function of time was found for the delay period (Table 5) the number of rounds flown was very considerably influenced (Text-fig. 7). Animals were responding increasingly to pure tones between 4 and 20 kcyc. Ten and 20 kcyc were the most effective ones while at 1 kc no increase was seen. The response to 1 kcyc is poor in most of the experiments mentioned above, and this is also in accordance with the electrophysiological data. In contrast, under 'white' noise stimulation there is a strong depression (inhibition) along the time axis. This reinforcement of the response with time shown in Text-figs. 6 and 7 may indicate that the appropriate stimulus is learned by the animal. This aspect of learning will be discussed in more detail in the discussion.

*Responses to flight sounds.* The influence on the flight response of natural flying sounds as well as of broadcast ones is seen in Table 6. The response seems to be higher in the treated groups than in the control groups. But in general the differences were small, even using the broadcast stimulus with its higher intensity than the natural one.

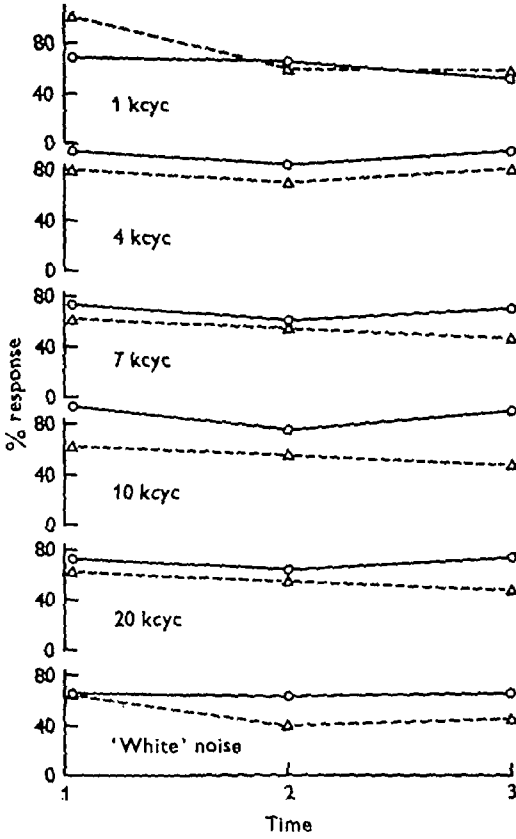


Fig. 6

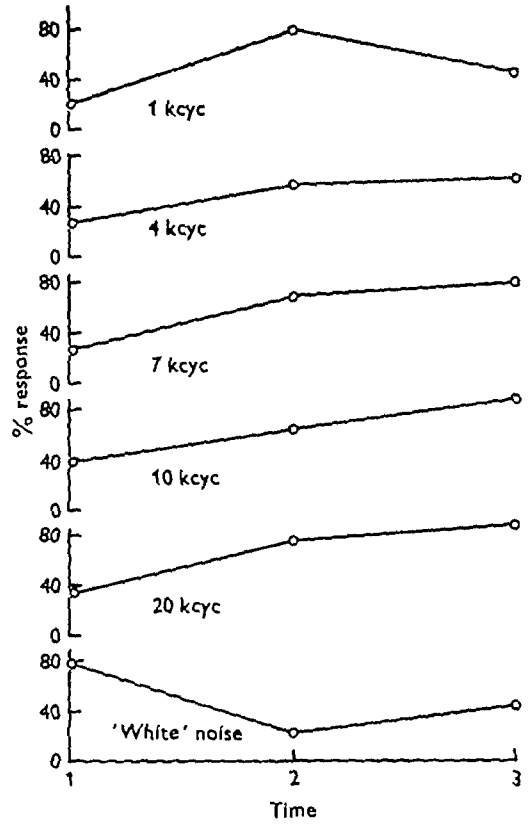


Fig. 7

Text-fig. 6. The percentage of flight initiations as function of time (average for both sexes). Numbers on the abscissa represent the first, fifth and tenth stimulus followed by flying. (The total period varied between 1 and 4 h, depending on the time spent by each animal while flying.) O—O, Treatment;  $\Delta$ --- $\Delta$ , control.

Text-fig. 7. The percentage of rounds completed as a function of time. (As the difference from the control group.) See also legend to Text-fig. 6.

Table 6. *The influence of natural and broadcast flight sounds on the initiation of flight response in the desert locust; calculated from the total number of repetitions in the treated group or in the control group*

	Natural		Broadcast	
	Males	Females	Males	Females
No. of animals	17	12	7	3
Treatment (%)	56.2	53.8	62.8	73.3
Control (%)	52.4	47.4	71.4	40.0

#### DISCUSSION

The auditory range and peak found in our electrophysiological studies (Text-fig. 1) are approximately the same as that found for the tympanal nerve of *S. gregaria* and *Locusta migratoria* (Horridge, 1960, 1961) of *L. migratoria* m. (Adam & Schwartzkopff, 1967; Suga, 1960; Katsuki & Suga, 1960) and in *Paroxya atlantica* (Wever & Vernon, 1959). These results are also in agreement with single-unit recordings from the

Tympanal organ, the thoracic ganglia and the protocerebrum (Suga, 1960; Horridge, 1961; Adam & Schwartzkopff, 1967; Michelsen, 1968). Different results were obtained for *S. gregaria* and *L. migratoria* by Haskell (1957) and Pumphrey & Rawdon-Smith (1936), probably due to technical reasons. Our neural data are in accordance with the behavioural experiments when presented on the basis of auditory efficiency (Text-fig. 4). This adjustment may indicate the function of the hearing organ in relation to the behaviour of tympanate insects.

Behavioural results on sound perception were obtained in some species. Busnel & Busnel (1956) obtained beating of wings and leg movements in *S. gregaria*. For the reflex response of the legs a frequency range of 0.1–17 kcyc was found. In contrast, in our behavioural experiment insects hardly reacted at 1 kcyc and showed strong response at 20 kcyc. Initiation of flight movements and change in the frequency of the wing-beat in some Lepidoptera were found by Treat (1955). Frings & Frings (1956) obtained similar results by using physically defined pure tone stimuli. The Frings' concluded that frequency was not important, provided that intensity was sufficient. This is true if one ignores the kind of behaviour concerned. Looking on our 'classified' flight behaviour of the locust we found that while the delay period is independent of the tone given the number of specimens showing response is dependent on the tone frequency. Thus, by making such a classification one can find the dominant behaviour controlled by the stimulus given.

Hansson (1945) conducted training experiments to tones in bees, but with no results. In contrast in some orthopteran species learning of artificial signals was attributed to their ability to answer a pulsed noise by a certain song (Dumortier, 1963). It seems as if the pure tone given was learned by the insects in our studies – but for different behavioural purpose.

If learning occurred, the excitatory pure tone as well as the inhibitory 'white' noise stimuli were both effective. In order to see this better we conducted some preliminary tests in which insects were stimulated by flight sounds or 'white' noise after they were allowed to fly for a long period in the presence of each stimulus. No difference was found between the treated and the control groups. Because of the known ability of locusts to learn (Ellis, 1959) we can not exclude auditory learning. Conditioning experiments may give better information on the procedure of auditory learning in this animal.

The outstanding ability of locusts to form enormous aggregations while flying in swarms demands a device of communication between individuals or groups. Assuming that the auditory stimuli are responsible for this kind of recognition and cohesion, Haskell (1957) stimulated settled or roosting locusts by playing back wing-beat noise. Although the flight noise has the appropriate spectrum for the auditory apparatus of *S. gregaria* according to Haskell, no systematic response was seen. It may be that the auditory stimulus itself is not strong enough to release the inhibitory effect on flight of tarsal receptors in settled locusts (Weis-Fogh, 1955–6). According to our findings it seems true that flight sounds elicit flying but only when the animal is already in the air, i.e. when the flying mechanism is not inhibited. Thus we can assume that the flight sounds stimulate the animal to initiate flight by shifting it from gliding or passive flying situation to an active one. Flight sound may maintain a certain flying rate or also accelerate flying. The communication device between specimens

during mass take-off has not been explained by this theory. Furthermore, a correlation between the development of wings and the tympanum in various species of Orthoptera (Uvarov, 1966) was found suggesting some function related to flight as a communication apparatus.

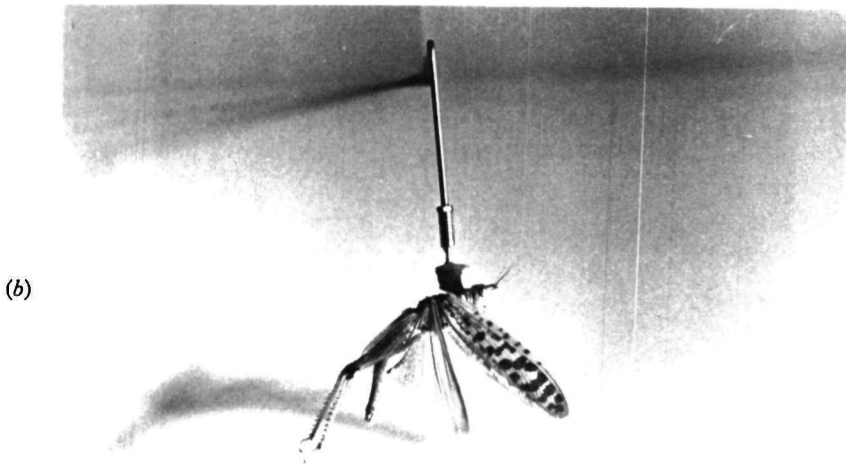
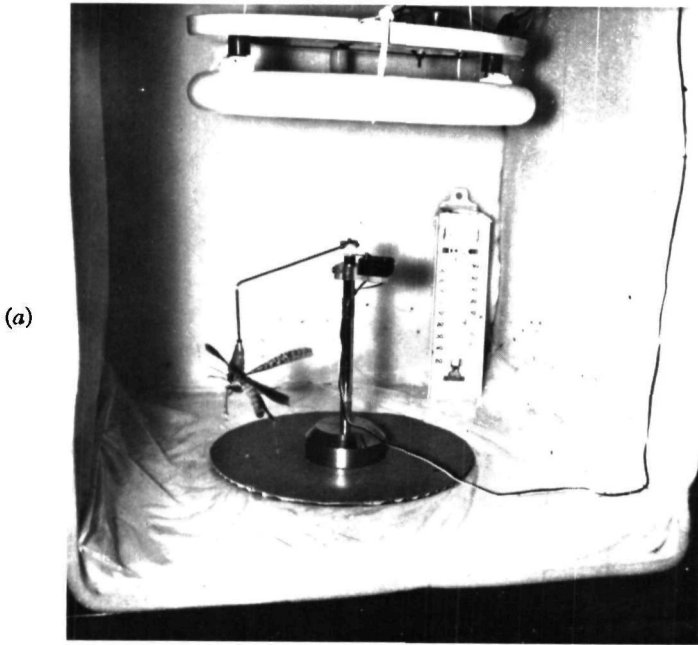
Whether or not external stimuli are used for communication between locusts in swarms has not yet been determined. Some supporting ideas can be obtained from studies which were carried out on the visual system. Flying locusts were found to respond to a rhythmically flashing light by adopting impulse discharge (in the metathoracic ganglion) and a wing-beat frequency equal to the flash frequency, if the flash frequency is not too different from the initial wing-beat frequency (Waldron, 1968; Page, 1970). Motion detection which is very well developed in locusts (Horridge *et al.* 1965) can be simulated by Waldron's model. This input can be integrated or reinforced by the auditory input for communication purposes in swarming locusts. The wing noise emitted by *S. gregaria* during flight is the sound stimulus available for such a purpose. The existence of the appropriate hearing apparatus transducing sound stimulus to a certain neural message lead us to assume that this is the communication device, in addition to the eyes. The present behavioural findings support this theory.

#### SUMMARY

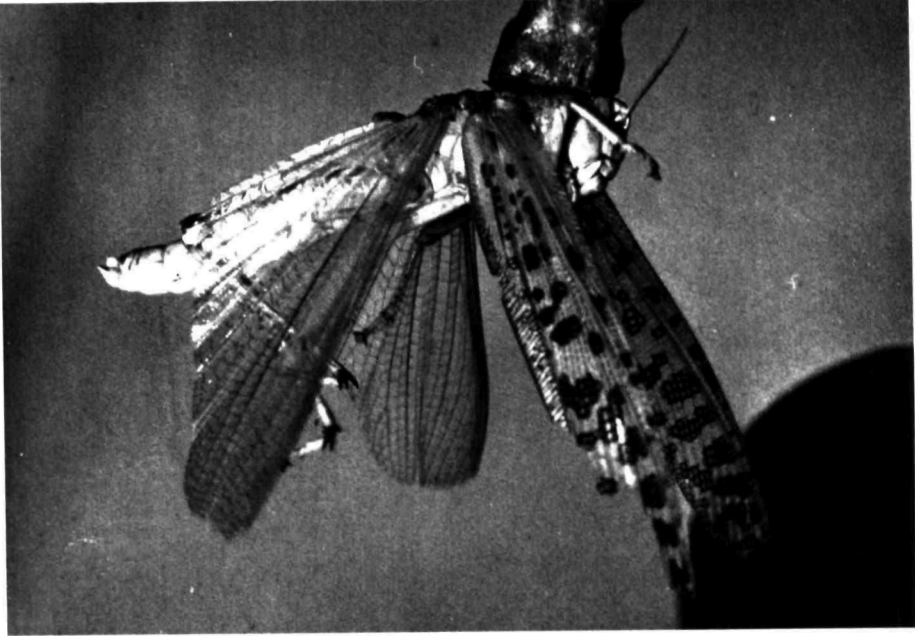
1. The auditory responses of the desert locust *Schistocerca gregaria* were tested using electrophysiological and behavioural methods.
2. The electrical response of the tympanal nerve to pure tone stimuli showed maximum sensitivity between 3 and 5.5 kcyc/sec. The response was the same in both sexes.
3. The flight behaviour was tested as function of pure tone stimuli and measured as the delay period, the number of insects reacting and the time they spent flying.
4. The number of animals which began to fly after the various tones presented was in accordance with the electrophysiological results. The number of animals having a short delay period (under 30 sec) was considerably higher than in the controls for the various sound stimuli.
5. The number of rounds flown (or time spent in flying) was the most affected parameter, although no systematic response was seen as a function of the tone 'excitation' by pure tone stimulus and 'inhibition' by 'white' noise. These two kinds of stimuli were presumably learned by the animal during successive repetition of the stimuli were presumably learned by the animal during successive repetition of the stimulation procedure.
6. The usefulness of sound emission during flight and sound perception (by the hearing organ) was discussed. The auditory neural mechanism of the desert locust is presumably integrated with the visual mechanism for communication purposes between swarming animals.

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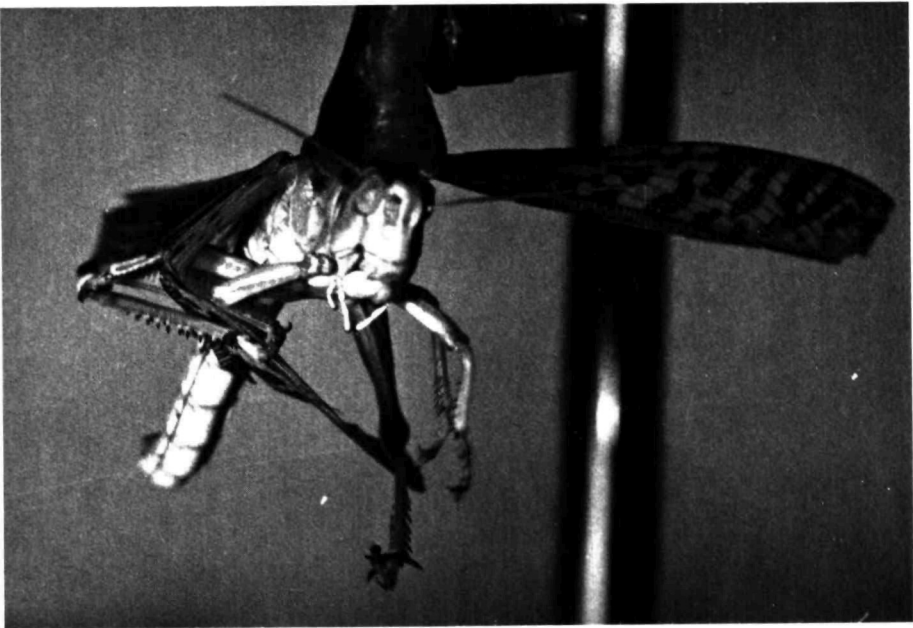
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(a)



(b)



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## EXPLANATION OF PLATES

## PLATE 1

The soundproof chamber used for the electrophysiological and behavioural experiments. The electrophysiological apparatus and the animal preparation were placed inside the chamber during the tests. The flight mill was used for the behavioural tests (height: 20 cm). The fluorescent lamp is seen above the flight mill (a). An insect is shown attached to one arm of the flight mill (b).

## PLATE 2

Position of wing-beat in flying locust. The noise emitted is due to the impact seen between the downward-moving hind wings and the hind legs (a). An animal is seen in the act of inhibiting flight by catching the wings with the legs (b).