

SOUND PRODUCTION AND RECEPTION IN A COCKROACH

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INTRODUCTION

Although Pumphrey & Rawdon-Smith demonstrated as long ago as 1936 that the fine, long hairs of cockroach and cricket cerci form part of auditory receptors, few examples of sound production have been described in cockroaches.

METHODS

Sounds were analysed by means of a WVB Vortexion tape recorder and a Solartron 1440 oscilloscope. Artificial tones were produced by an Advance SG 14 audiofrequency generator calibrated from -20 to 105 db. Sound intensities were monitored by means of a Dawe 1400E meter, and the reference level was taken as $0 = 0.0002$ dyne/cm².

OBSERVATIONS

Henschoutedenia epilamproides (Shelford) is a large species of cockroach (50 mm.) with specialized areas of cuticle (Fig. 1) on the humeral region of the tegmina and lower surface of the posterior margin of the pronotum, which enable it to make a chirping sound. The behavioural circumstances of sound production in this insect suggest that it is part of a defence mechanism. When a shadow passes over the insect a single chirp may be emitted, and if the insect is seized, a series of chirps are produced. The sound, coupled with the vibratory movement of the pronotum necessary for its production, is startling to the human observer when the insect is first held in the hand. Its maximum intensity measured 1 cm. from the microphone is about 70 db.

Recorded and analysed oscillographically the structure of the sound can be described at different time levels. The smallest units are individual sound waves repeated at a frequency of about 5 kcyc./sec. with a greater or lesser degree of regularity (Pl. 1, fig. 2*a*, *b*).

Usually the sound waves are grouped as pulses, the intervals between the pulses appearing simply as reduced amplitude oscillations, so that the basic frequency of 5 kcyc./sec. can be said to be amplitude modulated at 1-2.5 kcyc./sec. (Pl. 1, fig. 2*b*, *c*). The pulses usually comprise two to six sound waves, but occasionally they may extend to fifteen or more waves (Pl. 1, fig. 2*a*).

These sound pulses may follow one another in a fairly regular way to make up the chirps that are the smallest units distinguished by the human ear (Pl. 1, fig. 2*d*), or the pulses may be differently spaced within each chirp forming clearly different subunits of 10-70 msec. duration. Subdivision of successive chirps is illustrated in Fig. 2*e*,

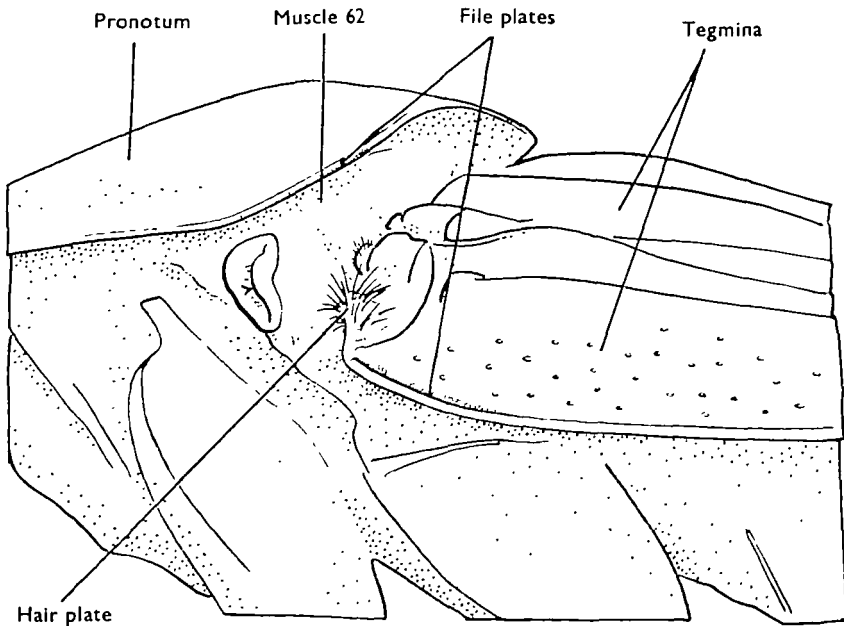


Fig. 1. Lateral view of the thorax and abdomen to show the position of the file plates and the hair plate. The edge of the pronotum has been raised. Muscle 62 is the muscle believed to be mainly responsible for the stridulatory movements.

where three different subunits can be seen to occur in the same order in each of the three chirps. The number of pulses in each subunit varies very widely from three to about sixty.

The duration of a chirp is 20–100 msec., the chirps being emitted singly (Pl. 1, fig. 2*f*), or in groups of three to six (Pl. 1, fig. 2*e, f*). In a group of chirps, the intervals between chirps last 10–20 msec.

Careful examination of the recorded sound reveals other repetitive variations sometimes of considerable regularity (examine Pl. 1, fig. 2*f*), but the appearance of these components cannot be relied on. Each chirp appears to result from a single one-way movement of the pronotum against the tegmina. Rubbing the stridulatory surfaces together by hand at different speeds produces only slight variations in frequency, due to the fact that at very low rates of movement so little energy is put into the system that no recordable sound is emitted. The lowest discernible frequency produced in this way was about 3 kcyc./sec.

The specialized cuticular areas mentioned above have a rather striking reddish orange colour, and are noticeably more opaque than adjoining parts of the cuticle. The surfaces are nearly flat and make intimate contact when they are brought together. Although these surfaces appear quite smooth under a low-power microscope ($\times 20$), the frictional resistance between the two surfaces is quite evident if they are rubbed together in the dead specimen, while no resistance can be felt if one surface is replaced by an unspecialized piece of tegminal cuticle. When examined under a higher power ($100\times - 40\times$), the fine parallel ridges which form the stridulation surface become apparent. There are more than 100 raised striae on the tegminal plate set approxi-

mately 5μ apart. A somewhat similar pair of structures was described by Vosseler (1907) in an East African species of *Rhyparobia* (*Leucophaea*).

The pronotal movement, which looks quite rapid, is largely produced by an oblique muscle arising from the first phragma and running centrally and dorsally to an insertion on the posterior integumental fold of the pronotum. It appears similar to muscle 62 of Carbonell (1947) and its homologous muscles in more posterior segments are involved in flight. A structure that may be important in control of sound production is a cuticular elevation bearing numerous long trichoid sensilla, that lies beneath the pronotum, a millimetre or so nearer the midline than the tegminal plate (Fig. 1). Movement of the pronotum on the mesothorax produces deflexion of the longer hairs.

Attempts were made to find out whether the insects were sensitive to the sounds they produced. Recorded chirps, and pure tones from an audiofrequency generator, had little behavioural effect on an insect moving about in a normal manner. Slight effects were occasionally noticed at artificially generated 'pips' of 5 kcyc./sec., on high intensity (over 80 db.).

Recordings were made from the cercal nerve. The cerci in this species are comparatively small, 4.5 mm. long in a 50 mm. specimen, as compared with 6 mm. in a 35 mm. example of *Periplaneta americana*. The fine hairs (Fadenhaare of Sihler (1924) are about 4μ thick, and generally similar in numbers and distribution to those of *P. americana*, although they appear rather more lightly hinged, and more responsive to air draughts.

Recordings were hampered by the fact that the cercal receptors appear much less silent under no-stimulus conditions than in *P. americana*.

Playing back the recorded stridulation at highest available intensities produced only slight responses in the cercal afferents as shown in Pl. 1, fig. 2*f*. High-intensity clicks due to the turning on and off of apparatus (arrows) produced definite responses. Stimulation with artificially generated tones of $\frac{1}{2}$ –3 sec. duration produced virtually no responses at frequencies over 500 cyc./sec. (500–6000 cyc./sec. This was at intensities of about 100 db. When the frequency of sound stimulation was lowered, responses began to appear at between 300 and 400 cyc./sec., and at 200 cyc./sec. a well-defined non-adapting response could be observed. Responses were evoked readily at intensities between 85 and 100 db. over the frequency range 100–20 cyc./sec. In Fig. 3 responses to different frequencies are shown. At 50 cyc./sec. response height (summed potentials) dropped off with declining intensities until at about 60 db. a response could no longer be distinguished (Fig. 4 *a-c*).

Postsynaptic fibres exhibited little heightened activity below 90 db. at a stimulation frequency of 50 cyc./sec., but at 100 db. a rapidly adapting response occurred (Fig. 5 *a*).

Responses in the cercal receptors were most readily evoked by a frequency of 50 cyc./sec., and this was regarded as the frequency to which they had the lowest threshold. Synchronous responses similar to those described by Pumphrey & Rawdon-Smith (1936) occurred at this frequency (Fig. 3 *e*). As can be seen by examining these records, off-on responses occurred even when the level of sustained response was low.

Although a detailed study of frequency sensitivity was not made, these facts suggest that Pumphrey & Rawdon-Smith's results with *Gryllus* and *Periplaneta* hold substantially for *Henschoutedenia*, with the greatest sensitivity in the low-frequency range of 20–100 cyc./sec. However, Pumphrey & Rawdon-Smith were able to obtain

responses in *Gryllus* up to 4 kcyc./sec., and Katsuki & Suga (1960) up to 3 kcyc./sec. in *Homoeogryllus*, and 2 kcyc./sec. in *Xenogryllus*, using high intensities. *Henschoutedenia* seems unlikely to be able to hear sounds at frequencies similar to the carrier frequency of its own chirp.

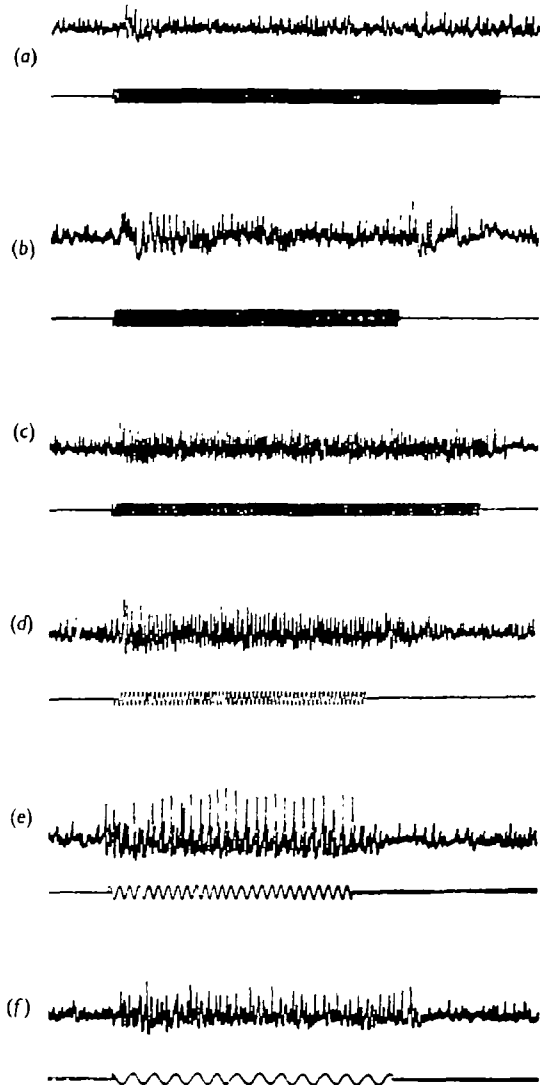


Fig. 3. Cercal receptor responses to different artificial sound frequencies at 100 db (range 8 ft.). (a) 400 cyc./sec. Very little response. (b) 300 cyc./sec. Irregular heightened activity. (c) 200 cyc./sec. Activity greater and more regular, with occasional synchronous periods. (d) 100 cyc./sec. Largely synchronous response showing increased amplitude. (e) 50 cyc./sec. Synchronous response of large amplitude potentials. (f) 20 cyc./sec. Synchronous and asynchronous elements appear to be responding in this record. Calibrations given by sound frequencies.

If the stridulation is part of a defence mechanism, it would be interesting to see whether *Henschoutedenia* chirps were capable of frightening predators. Cockroach chirps were played to laboratory rats while they were being presented with food

pellets or plasticine dummies. Signs of alarm were detectable but slight, but it may be that the behaviour of laboratory rats is so conditioned by noise that this may have reduced any symptoms of fear. Withdrawal movements were most noticeable when the onset of the cockroach sound was sudden.

Experiments with bank voles (*Clethrionomys glareolus*), on the other hand, had different results. These specimens had been recently captured in the field. If the cockroach sound was played to them, they showed alarm and retreated to their nest. This effect was well defined.

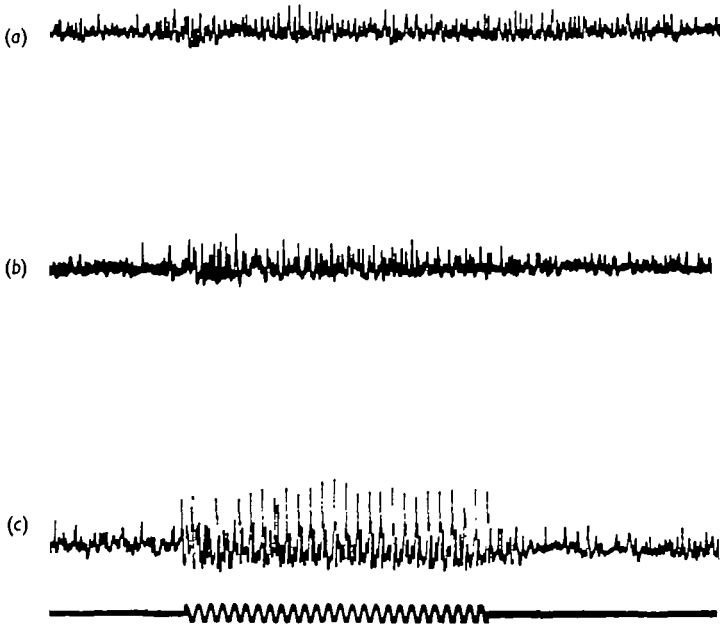


Fig. 4. Response of cercal receptors to different sound intensities at 50 cyc./sec. The loud-speaker was at a range of 8 ft. in all cases. (a) 60 db. Slight 'on' response, then a small amount of heightened activity. (b) 70 db. A well-defined 'on' response followed by irregular activity. (c) 100 db. Maximum synchronous response. Calibration as sound, 20 msec. peak-to-peak intervals.

Finally, the response of this insect to air draughts may be mentioned. Light currents of air produce an immediate behavioural response in *P. americana* when directed against the cerci, but hardly any in the generally more sluggish *H. epilamproides*. And yet recordings from the cercal nerve of the latter insect suggest unusual sensitivity. Slight air movements made with a pipette or an electric hair dryer at a range of 5–6 ft. produced large bursts of afferent-fibre activity. The response in post-synaptic fibres is still more striking (Fig. 5*b*). The level of spontaneous activity in the nerve cord appears rather low as compared with *P. americana*, but giant fibre activity is readily evoked by cercal stimulation, and may be followed by several seconds of generally heightened activity, something which does not appear in *P. americana*.

If recordings are also made from the tibial depressors of the metathorax, activity in slow and fast fibres is readily detected, but the response following cercal stimulation

is a slight one. Small responses occur in both types of fibre, but no general muscular contraction ensues.

It seems that cercal receptors and synapses have low thresholds, but that the thoracic synapses are of so high a threshold that they damp out effective muscular responses.

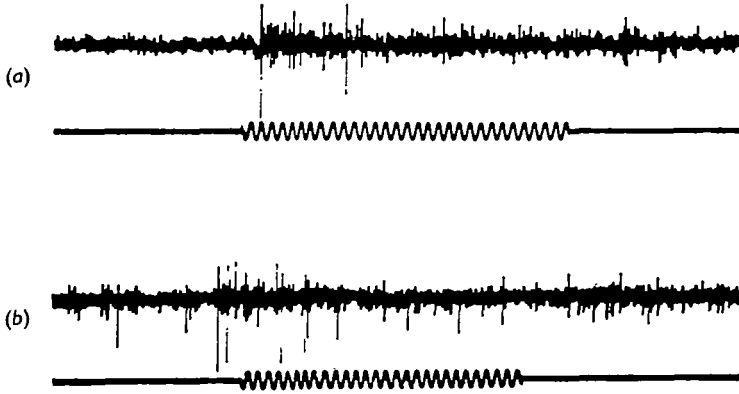


Fig. 5. Post-synaptic responses. (a) Response to 50 cyc./sec. sound (100 db). Response largely adapted out after $\frac{1}{4}$ sec. Two large spikes. (b) Response to brief air current. The time marker here only approximately marks time and duration of stimulus. Large response followed by heightened activity for about 1 second. Eight large spikes. Calibration intervals 20 msec.

DISCUSSION

It seems unlikely that sound production in *Henschoutedenia* plays any part in communication between individual cockroaches, as the frequency response of what is believed to be their only auditory receptors is below the major frequencies of the sound, and the sound is not produced spontaneously.

If the sound has a defensive role, two aspects of its function suggest themselves. First, that the sound is associated with unpleasant properties of the insect, such as noxious substances, an interpretation at one time put forward to explain the ultra sounds of moths by Roeder, and his colleagues (Roeder, personal communication). Or, secondly, that the sound has in itself a more direct effect due to its mimicking mammalian cries of alarm or anger. Withdrawal of the predator would in this case be linked with the normal aggressive behaviour within the species. If the second of these two possibilities is tenable a much closer resemblance between the sound pattern of prey and predator would be expected, than if the sound is a simple warning cry.

Fig. 6a, b illustrates the resemblances between repetitive sound produced by *Rattus rattus* and *Henschoutedenia*.

Recordings of the sounds made by rats show that much of it has a basic frequency of 3.5–5.0 kcyc./sec. (Fig. 6c), and individual chirps may take a similar form to those emitted by *Henschoutedenia* (Fig. 6b, d).

Roth & Willis (1960) list a number of examples of rodent predators of cockroaches. It is perhaps significant that this cockroach is unlike many other species which emit foul-smelling secretions when they are molested.

If the sound pattern is as important as it would seem to be, the provision of the hair plate shown in Fig. 2 may be a means of maintaining the constancy of intervals between chirps and their subunits.

The question of the pitch and speed of onset of the sound may be linked with type of muscle used for stridulation. If each cycle or sound wave is made by a synchronous impact of many equally spaced teeth, then the basic frequency of the sound emitted will be governed by the speed of movement of the stridulatory structure relative to one another, and the spacing of the teeth on these structures. If the teeth are 5μ apart, then the movement must be 25 mm./sec. for a 5 kcyc./sec. tone. Furthermore, if a 20 cyc. subunit of a chirp represents the longest homogeneous unit of sound, then it probably represents a single complete twitch in muscle 62, and will take 4 msec. for completion at 5 kcyc./sec. This represents a very brief twitch. In coxal muscles of *P. americana* Usherwood (1962) found that a maximal twitch response occupied

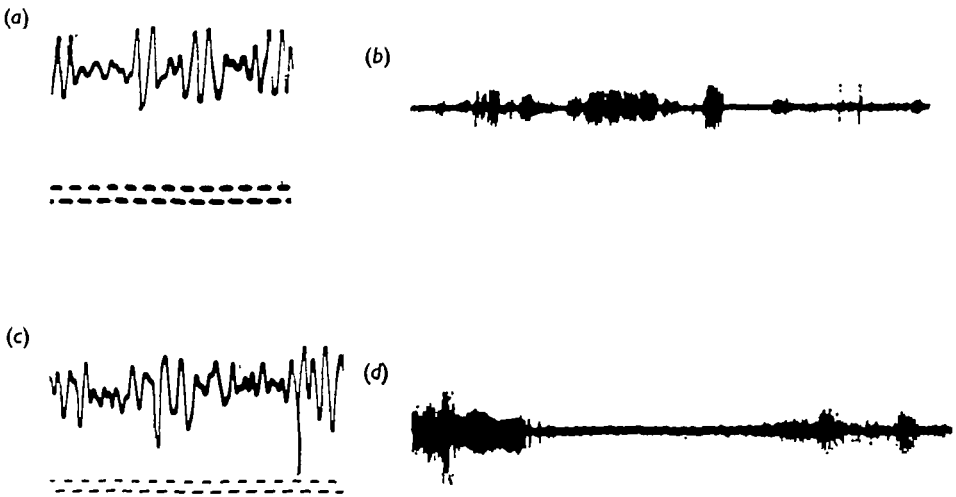


Fig. 6. Sounds made by *Henschoutedenia* (a, b), and *Rattus rattus* (c, d). (a) Sound pulses from the cockroach. Calibration 5 kcyc./sec. (b) Cockroach chirps. Considerable variety in the form of chirps can be seen. (c) Sound pulses from the rat. These tend to be slightly less regular than those of the cockroach. Calibration 5 kcyc./sec. (d) Rat 'chirps'. Chirp durations as in the cockroach 20–100 msec.

from 10 to 16 msec., but Roeder (1953) figures a tergal muscle with a duration of contraction of 5 msec., and the figure he gives of thoracic movements during flight shows an initial phase of this duration (Roeder, 1951). These deductions suggest that *H. epilamproides* utilizes the small, brief contractions of synchronous wing muscle for sound production.

SUMMARY

1. The cockroach *Henschoutedenia epilamproides* produces distinctive patterns of sound, on being disturbed, by means of a stridulatory apparatus. The carrier frequency of the sound is between 4.5 and 5.0 kcyc./sec., and is amplitude-modulated to form pulses. These pulses are grouped to form chirps, which are emitted singly or in a series. The structure of the longer chirps (50–100 msec.) may be quite complex.

2. While the circumstances under which sound is usually produced in the laboratory suggests that it is not important in intraspecific communication, it may be of some importance to the cockroach to hear its own sound. Recordings made from the

cercal nerve show that the cockroach responds hardly at all to its own sound, and very poorly to artificial tones above 400 cyc./sec. The cercal afferents are most sensitive to tones of 50 cyc./sec., and will respond to less than 60 db. at this frequency.

3. Although the auditory performance of *Henschoutedenia* cercal receptors appears poor by comparison with *Periplaneta americana*, their responses to air movements are most striking. Some difficulty was experienced in standardizing this form of stimulation, but it appeared that *Henschoutedenia* was much more sensitive than *Periplaneta* to this form of stimulation.

4. Experiments with rodents (*Rattus rattus* and *Clethrionomys glareolus*) lent some support to the idea that the cockroach sound mimicked the cries of rodent predators, and had some deterrent effect on them.

It is a pleasure to acknowledge the help given by Dr D. R. Ragge of the British Museum in identifying *Henschoutedenia*, and in drawing my attention to other aspects of cockroach sound. I must also record my thanks to Mr L. Panko for his technical assistance, and to Mr M. Stoddart who provided the specimens of the bank vole (*Clethrionomys glareolus*). Finally I owe a debt of gratitude to Dr J. H. Sudd, of the University of Hull, who generously sent me additional specimens of *Henschoutedenia*.

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EXPLANATION OF PLATE

Fig. 2. Cockroach sound. (a) Continuous sound. Calibration 200 μ sec. = 1 cyc. (b) Amplitude-modulated sound. Calibration 200 μ sec. = 1 cyc. (c) Amplitude-modulated sound. Here the pulses are rather more regular than in (b). (d) Two chirps with increasing intervals between pulses in each one. Calibration pulses 50 msec. apart. (e) Three successive pulses in which different subunits can be seen. A subunit of regular pulses is followed by a long subunit of irregular pulses of slightly greater amplitude, terminated by a coda of small pulses. Calibration 50 msec. (f) The response of cercal receptors to cockroach sound. Responses (lower line) to apparatus clicks can be seen, but little evidence of sensitivity to cockroach sound. The upper line displays a variety of chirps. 1 cm = 50 msec.

