NEURONAL MECHANISMS UNDERLYING CONTROL OF SOUND PRODUCTION IN A CRICKET: 
ACHETA DOMESTICUS*

BY ARTHUR EWING† AND GRAHAM HOYLE

Biology Department, University of Oregon

(Received 21 December 1965)

Analyses of neuronal mechanisms underlying instinctive behaviour have long been required (Tinbergen, 1951) but have not been forthcoming. The reason seems to lie in part in a lack of agreement as to suitable experimental animals. There are now signs that certain large insects, which are available in many laboratories, and whose nervous systems are amenable to electrophysiological investigation, have been selected as first-choice subjects for detailed investigations. As examples we may refer to the work of Wilson (1961, 1964) on locust flight mechanisms, Roeder, Tozian & Weiant (1961) on the praying mantis and Hoyle (1964) on general locomotory activity in locusts.

The simplicity of the motor nervous system of insects renders possible an exact interpretation of electromyograms recorded from freely moving, intact animals, thereby permitting a full analysis of the motor output associated with behaviour, provided the latter can be elicited under laboratory conditions.

A possible subject for analysis in the laboratory is the innate behaviour involved in singing in crickets. A good deal of descriptive work has been done by Alexander (1961) on the nature of the songs, their functional significance and probable evolution. What makes this subject particularly appealing, however, is that songs can be elicited by local stimulation of the brain (Huber, 1960, 1962). This means that a form of complex behaviour can be evoked by means (electrical stimulation) which are fully controllable and so should be an aid in investigation of this complex problem.

Some species of crickets give up to four structurally distinct songs, and more are recognized in some species if the context is also taken into account. It is desirable to know the ways in which these are produced, the sites in the nervous systems where the control information is stored, how afferent clues are used to call forth a particular song and so forth.

A necessary preliminary for any of these aims is to establish techniques for examining the motor output to the muscles during natural sound production in the intact animal. The methods used by one of us (Hoyle, 1964) to study the control of locomotion in locusts are adaptable to the problem and have been used successfully in the present work. The species used principally was Acheta domesticus.

Nature of the sounds

Males of Acheta domesticus emit what the human ear can distinguish as four distinct types of song: calling, aggression and two forms of courtship song. Preliminary

* Supported by research grant G 21451 from U.S. National Science Foundation.
† Present address: Department of Zoology, University of Edinburgh.
studies showed that these are structurally distinct. A sound forming part of a song consists of an irregular, relatively high-frequency oscillation in the region of 7000–8000 cyc./sec., which varies in amplitude either regularly or irregularly. The sounds occur on sudden closing of the wings when they are also pressed together. A striker on the edge of the left tegmen (fore-wing) scrapes against a file on the underside of the right tegmen (Fig. 1). Following a long rest the indirect wing muscles have not been active for some time and are relaxed, so that the wings are separate. At the start of the singing there is thus no opening sound, but as the wings press closer together a faint opening rasp occurs, though this is probably not of behavioural significance.

The significant sound appears in a sequence of major units each corresponding to a single wing closure. Such a unit will be termed a pulse of sound. Pulses vary in amplitude through three causes: (1) as a result of differences in the force with which the two wings press against each other; (2) as a result of differences in the velocity of the wing stroke; (3) as a result of different extents of opening of the wings prior to the closing stroke. Differences in velocity and in extent of opening also account for differences in the duration of the pulse.

The second sort of variation must, however, be associated with significant differences in the mean basic frequency, since this is caused by heavily damped oscillations corresponding to one for each jerk of the wing edge (striker) over a unit of the file of the other wing. High-speed recording of a large number of pulses has revealed that variations in basic frequency are rare and so the second variant, wing-closing velocity, may be largely discounted. A sequence of pulses will be referred to as a chirp when it is of short duration (up to 7 pulses) and a trill when the number exceeds 7.

Calling. The commonest song, calling, consists of a series of chirps commonly con-
Sound production in crickets

Raining 2 or 3 pulses given at regular intervals. It is emitted spontaneously by a sexually mature male on his territory.

Aggression. This is exhibited by males in the presence of other sexually mature males. It is signalled by short trills apparently identical with those used in calling, but on average a greater number of pulses is produced (Table 1).

Table 1. Number of pulses per song and intervals between pulses

(Several songs of each of the principal kinds were analysed. The mean interval between the first and second pulses was less than subsequent intervals in all songs and associated with a smaller degree of wing opening, especially evident in courtship song. The distinction made between the songs termed calling and aggression was based upon the context.)

<table>
<thead>
<tr>
<th>Song</th>
<th>Intervals</th>
<th>Pulses</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>No. of songs</td>
<td>Mean intervals</td>
</tr>
<tr>
<td></td>
<td>analysed</td>
<td>Mean 1st–2nd (msec.)</td>
</tr>
<tr>
<td>Courtship</td>
<td>3</td>
<td>44.2</td>
</tr>
<tr>
<td>(43 pulses)</td>
<td></td>
<td>(last interval = 61.6)</td>
</tr>
<tr>
<td>Calling</td>
<td>17</td>
<td>48.5</td>
</tr>
<tr>
<td>Aggression</td>
<td>19</td>
<td>54.0</td>
</tr>
</tbody>
</table>

Courtship. The common form of courtship song is quite different from the others. In it, the component pulses of sound are shorter and emitted at a much lower intensity. The sequences are long, always forming a trill. Interspersed among the weak sounds are single occasional loud pulses. The latter are sometimes absent and probably have no signal value.

The other form of courtship song, which is not very common, consists of moderately long sequences of loud pulses. The individual pulses proved to be structurally identical with the units of aggressive song, and the chirps very similar to those of aggressive song.

The opening movement can be produced only by indirect wing muscles. The principal ones are undoubtedly the tergosternal muscles (see list below). Closing movements can be produced either by indirectly acting dorsal longitudinal muscles or by several direct-acting muscles. The various closing movements evoked by these muscles are not simple or equivalent.

<table>
<thead>
<tr>
<th>No.</th>
<th>Name</th>
<th>Function in wing movement</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Indirect wing muscles</td>
<td></td>
</tr>
<tr>
<td>81</td>
<td>Dorsal longitudinal</td>
<td>Depressor of wings</td>
</tr>
<tr>
<td>83</td>
<td>First tergosternal</td>
<td>Elevator of wings</td>
</tr>
<tr>
<td>84</td>
<td>Second tergosternal</td>
<td>Elevator of wings</td>
</tr>
<tr>
<td>89</td>
<td>Tergal promoter of coxa</td>
<td>Elevator of wings</td>
</tr>
<tr>
<td>90</td>
<td>First tergal remotor</td>
<td>Elevator of wings</td>
</tr>
<tr>
<td>91</td>
<td>Second tergal remotor</td>
<td>Elevator of wings</td>
</tr>
<tr>
<td></td>
<td>Direct wing muscles</td>
<td></td>
</tr>
<tr>
<td>85</td>
<td>Pleuro-alar</td>
<td>Flexor of wing</td>
</tr>
<tr>
<td>97</td>
<td>First basalar</td>
<td>Pronator depressor</td>
</tr>
<tr>
<td>98</td>
<td>Second basalar</td>
<td>Pronator depressor</td>
</tr>
<tr>
<td>99</td>
<td>Subalar</td>
<td>Supinator depressor</td>
</tr>
</tbody>
</table>

* Number from Snodgrass (1929).
The basalar muscles both depress and pronate and the subalar depresses and supinates. Furthermore, muscles 89, 90, 91, 98 and 99 are bifunctional, also affecting leg movement (cf. Wilson, 1962). The general topography of the relevant muscles is illustrated in Fig. 2.

We have been able to record electrical activity in the intact animal from the following muscles: tergosternals, dorsal longitudinal, first and second basalar and subalar.

**METHODS**

Adult *Acheta domesticus* were obtained commercially and the males were kept isolated for a few days in order to lower their threshold for singing when placed in a test situation. The live leads were fine (170 µ diam.) copper wires insulated with a nylon coating. These were cut clean at right angles to the axis and pressed through small holes drilled through the cuticle overlying the relevant muscles. They were held in position by melting a small bead of high-melting-point wax with a cautery wire at the wire/cuticle junction. A lead thus served both as electrode and conducting element. Its tip just entered the muscle underneath. Normally two such electrodes were used, in different muscles. The placement of electrode tips was checked by dissection subsequent to the experiment. The indifferent lead was a thicker copper wire placed centrally in the prothorax. The leads were about 21 in. long, and taken through the roof of a lucite box within which the crickets were released. The movement of the
Crickets was restricted by placing them in a glass dish, 10 cm. in diameter, but within this they were quite free and not noticeably impeded by the wire leads. The box itself was placed on a table in a sound-proof, electrically screened, double-walled room provided with an observation window. Grass P8 pre-amplifiers placed on top of the lucite box amplified the signals, which were then led out of the sound-proof room into a recording bank comprising an Ampex 4-channel direct-coupled tape recorder, Tektronix 502 oscilloscope and Offner ink-writing oscillograph for immediate monitoring. The song itself was picked up by a high-impedance dynamic microphone and recorded simultaneously with the electrical activity in the muscles.

Recordings on magnetic tape were made at 15 in./sec. and played back at 1 in./sec., thereby increasing the effective recording speed.

RESULTS

Interpretation of recordings

No direct investigations on the innervation of the muscles associated with sound production have been made in crickets. In the desert locust the first basalar is considered to receive a single axon and the rest more than one (Wilson & Weis-Fogh, 1962). In some cases there will be both slow (S) axons giving rise to relatively small junctional potentials and moderate speed and force of contractions, and fast (F) axons giving larger ones (Hoyle, 1957, 1964) with contractions correspondingly faster and stronger; in Acheta all the flight muscles concerned with sound production appear to receive both, but have not been checked critically. A muscle may consist of only one unit, in which case its electrical discharges are readily interpreted, even if innervated by both S and F axons. Or it may consist of more than one unit, each with a separate innervation, in which case there can be two or more trains of action potentials occurring together at different frequencies. In the latter case exact interpretation is difficult and may be impossible.

Wing opening

Wing opening is due entirely to activity in muscles 83 and 84, to be referred to collectively as tergosternals. These are the easiest muscles to record from and give large potentials. Their activity is also picked up by leads placed in other muscles owing to conduction through the entire volume of the thorax.

The basic activity seen in all opening consists of bursts of irregular-appearing small electrical potential changes (Fig. 3). This can be interpreted as due to two or more slow (S) axons, probably independently supplying M83 and M84, firing independently, but in a closely similar way, up to six times, at a mean discharge frequency of from 100 to 150 per sec. The opening burst also includes from 1 to 4 large potentials (Figs. 3, 4 and 6). They may mask the appearance of smaller potentials but probably do not replace them. The large action potentials may be interpreted as due to probably two F axons each firing independently a similar number of times, from 1 to 4. The intervals between action potentials are similar and perfect synchronization may occur, but not always.

The opening burst is thus variable and this variation is reflected in various speeds and extents of opening, which in turn are reflected in the closing movements and therefore the song. The interval between the first and second sound pulses is always
less than subsequent ones. This might be accounted for by increased wing opening after the first, in turn reflecting increased output to the tergosternal muscles (Table 1). During courtship song wing opening is usually less extensive than during aggression and calling, and this is reflected in a reduced electrical activity in the tergosternals. There may be only one or two large action potentials, compared with the common 2, 3

Fig. 3. Typical calling and aggressive songs recorded from the same specimen. Electrical activity was recorded simultaneously from the first basalar (1BA, upper traces) and second basalar (2BA, middle traces) muscles. A high level of volume conductor interference from the tergosternals (TS) was experienced; this serves to indicate the wing-opening activity. Simultaneously recorded sound (microphone output) is presented on the lower traces.

Fig. 4. Correlation of activity in first basalar and subalar muscles. Examples of calling and aggressive songs obtained from one specimen whilst recording electrical activity from first basalar muscle (upper trace) and subalar muscle (SA, lower trace). Note volume-conductor interference from tergosternals (TS). Microphone output indicates sound produced on lower trace.
or 4 in vigorous aggressive song. There is, however, no marked difference in many instances and possibly differences in $S$ axon activity distinguish the two opening patterns. The major differences between songs must be associated with differences in wing closing.

Wing closing during calling and aggression

The electrical activity associated with the closing stroke in calling has been examined in all the main wing muscles which may be concerned, by recording from first one pair, then another and so on.

(i) *Dorsal longitudinal muscle (DL).* One, two or three large spikes commonly occur in the dorsal longitudinal muscles for each closing stroke (Fig. 5). Marked steps in some of the records of the large spikes indicate that two $F$ units may be firing an equal number of impulses at similar intervals with synchrony varying from perfect to nearly perfect. Some smaller potentials, possibly indicative of $S$ neuron activity, also occur, some of them in bursts associated with the large potentials, but others which are often more-or-less continuous, at a frequency of about 15 per sec, such as would be associated with tonic background activity. The first of the large potentials in a burst associated with wing closing occurs only 2–3 msec. before the start of the sound pulse (Fig. 5). This is too soon for the resulting contraction of the dorsal longitudinal muscles to be a major cause of the initiation of the wing stroke. It could, however, play a significant part in its completion. Occasionally the burst of impulses in the dorsal longitudinals occurs by as much as 10 msec. before the sound starts without significantly altering the stroke (lower record Fig 5, 2nd pulse). This non-association confirms that some other muscle must initiate the closing. The most probable contenders for the role are the basalars. The two or three spikes in the dorsal longitudinals always fire at about 2 msec. intervals.
First basalar muscle (1 BA). The first basalar discharge is complex, occurring with or without large spikes. In their absence the sound pulse is always short and weak (see first pulse in sequence of Figs. 3, 4 and 7). Such bursts include as many as seven distinct, consecutive, small, probably S axon, responses. It is at present not possible to say how many axons may be responsible for the records but there are at least two, including an S and an F. A variable number of larger spikes appears before the second, third and later sound pulses. Usually there are two, three or four, at 2 msec. intervals, as though a single F axon has fired a few times at 500 per sec. frequency.

Fig. 6. Correlation of loudness with discharge in subalar muscle. Two examples of calling in which the loudness of individual pulses showed marked differences. Note close correlation of loudness and electrical activity in subalar muscle. Cross-talk from tergosternals serves to indicate wing opening. Microphone output on lower traces.

Fig. 7. Correlation of loudness with discharges in basalar and subalar muscles. An example of aggressive song with different loudness of pulses in which recordings were made simultaneously from first basalar (upper trace) and subalar (middle trace) muscles. Note in this record slight opening sound was recorded.
Sound production in crickets

The major portion of the discharge of the first basalar always precedes the sound, by as much as 10 msec. The first basalar is thus a candidate for consideration as prime mover in the wing-return cycle.

(iii) **Second basalar muscle (2BA).** The second basalar muscle always fires at the same time as the first (Fig. 3). When the large spikes are absent the discharges in the two muscles are manifestly different. As spikes become added they can become very similar, or even almost indistinguishable. One possible explanation is that the $F$ axon discharges are closely synchronized. We cannot, however, rule out the possibility that an $F$ axon is shared in common between the two muscles. $S$ axons supply both muscles and are independent.

What is abundantly clear from our results is that the two basalar muscles act synergistically and serve identical functions.

(iv) **Subalar muscle (SA).** The discharge in the subalar muscle is remarkably similar to that in the basalars (Figs. 4, 6 and 7). When the latter give small potentials only, so does the subalar. Large $F$ responses also occur singly, or in two’s and threes, rarely fours. These can be slightly different in timing from the corresponding ones in 1 BA, or they can occur in perfect synchrony with them.

**Determination of closing stroke**

The activity in the three principal direct muscles is thus virtually entirely synchronous in time and correlated also in duration and intensity. By synergistic action the three muscles determine the wing return. They are frequently aided by action in the indirectly acting dorsal longitudinal muscles, giving an extra ‘kick’ to the already moving wings which results in an extra loud sound at about the mid-point of the return. What the antagonistic action of the subalar and basalar muscles in regard to wing twisting may be is problematical. Only a differential action of the sets of muscles on the two sides will cause a tighter pressing together of the ratchet and file and this has not been detected. The more powerful pronation predominates, bending the wings forwards above the body, but the opposed supinating tendency may help to press the wings close together.

**Wing closing during courtship songs**

The specially notable characteristics of courtship songs are the softness of the pulses and the length of the songs. It will be recalled that the wings open less preceding each sound pulse during courtship than during calling and aggression. We have examined the electrical activity in each of the principal closing muscles during courtship song.

(i) **Dorsal longitudinal.** The soft closing sounds are associated with small, irregular potential changes in the dorsal longitudinal (Fig. 8). The simplest interpretation of these is that $S$ axons innervating different bundles of fibres each fire twice at an interval of 4-5 msec. The exact timing changes in each double pair so that varying summations are seen. However, these potentials occur synchronously with, or only 1 msec. before, the onset of recorded sound and so cannot be determining the onset of the stroke. Immediately before each loud pulse during courtship, one or two large spikes occur (Fig. 8). These are sufficiently different in successive sounds for them to be almost certainly due to two $F$ axons firing once each with a separation of just less than 2 msec.
(ii) **First basalar, second basalar and subalar.** These muscles each show a small burst of S axon responses well in advance of the appearance of the recorded soft sound (Fig. 9). There are no large spikes in these muscles preceding soft sounds. Immediately preceding a loud sound the three muscles each receive a single F axon impulse, almost, but not quite, perfectly synchronized, and coinciding with the first F axon response of the dorsal longitudinal muscles. The brief interval, barely 3 msec. (Fig. 9) with

![Diagram showing muscle activity](image)

**Fig. 8.** Courtship song. Two examples of parts of courtship songs in which electrical activity was recorded from the dorsal longitudinal muscles (upper traces) at the same time as the sound pulses (lower traces). Note that sound pulses (a few are indicated by arrows) occur rhythmically and nearly all are faint. Occasional loud pulses occur. These are associated with two large spikes occurring with a slight separation in two different units of the muscle.

![Diagram showing muscle activity](image)

**Fig. 9.** Courtship song. An example of courtship song in which electrical activity was recorded simultaneously with sounds from the first basalar and subalar muscle. Note the absence of large spikes; slow axon discharges (S†) precede soft sounds. Before a loud sound a single additional large spike occurs late in the tergosternal opening discharge (F) causing extra-wide wing opening which is immediately followed by closing. Single large F axon spikes (F†) occur at almost the same time in both the first basalar and the subalar, resulting in the wings pressing together more firmly and producing a loud sound.

which sound intensification follows the onset of these spikes calls for an explanation. The contractile mechanism is already partly activated as a result of the S axon discharges and has overcome the wing inertia and started the return stroke. Under these circumstances markedly increased mechanical response in the wing is realised in barely 2 msec. from the large spike occurring, and this affords a nice example of one of the uses of dual (S and F axons) innervation.

**Mechanical action of the muscles**

The major uncertainty arising out of the foregoing lies in the role of the dorsal longitudinal muscles. In order further to clarify their role it was decided to cut the direct wing muscles and study the effects on wing movement and sound production so as to determine what the dorsal longitudinals, acting alone, could do. Such procedure unfortunately necessitates cutting also the mesothorax, thereby altering the
elastic properties on which the indirect muscles depend for their functioning, but the cutting can be confined to soft regions, so giving rise to minimal effects. Mock operations in which the cuticle only and not the muscles was cut did not lead to changes in the sounds.

All the direct wing muscles on both sides of the mesothorax were cut in ten animals. In spite of the severity of the operation they all survived and attempted to stridulate, making movements of the wings which appeared superficially normal in situations calling forth each type of song. However, the intensity of the sounds of calling and aggression was greatly reduced. That of courtship was not noticeably affected except in regard to the loud pulses, which were judged to be still present but reduced in volume.

Photographs made of operated animals compared with others of normal, intact insects showed that pronation is reduced so that the wings are held flatter than normally. Furthermore, the angle of the tegminal elevation appears to be greater than normal.

The results of the experiments clearly demonstrate the essentially synergistic action of the indirect and the direct closer muscles. It is predicted that should it prove possible to cut the dorsal longitudinals selectively, or indeed any combination of the muscles concerned with wing closing, the remaining ones would perform the closing function adequately. The sounds would, however, be softer. The collective action of all four muscles is evidently necessary to achieve the pressure which is required for loud sounds.

The dorsal longitudinals may influence the sound production indirectly as well as directly. They are probably under continuous $S$ axon barrage resulting in a maintained tonic background contraction. This helps twist the wings forwards and together, aiding the production of loud sounds. The consistent difference between loud and soft sounds lies in the nature of the discharge to the direct muscles. Only when these receive $F$ axon discharges are loud sounds evoked.

**DISCUSSION**

Calling and aggressive chirps sound very similar to the human ear and some individual records of sounds designated aggressive on account of context containing two or three pulses only are indistinguishable from calling. However, if the chirp contains four pulses it is very probably aggressive rather than calling, and if it contains more than four on the present evidence it is definitely aggression. The difference between calling and aggression probably is that the former is appetitive behaviour occurring when a male in the appropriate physiological state establishes a territory. Aggression is associated with a similar state and a similar background, but with the addition of the response to a specific stimulus situation. Evidently the same central mechanism of sound production is switched on. There are no significant differences in: the quality of pulses within the sounds; the intensity of the pulses; their duration; or the intervals between successive pulses, in the two songs. There is, however, a significant difference in the average total number of sound pulses occurring. Probably this can be attributed to the stimulus offered by the presence of another male in the case of aggression. This extra stimulus to internal ‘drive’ serves not only to ‘switch on’ the
central nervous machinery but to keep it going. The neuronal mechanisms utilized in aggressive song may well be the same as those operative during calling. In both songs there is evidently a tendency to cut off the cycle of pulses even in the continued presence of another male, after a few cycles. After similar intervals the cycle resumes.

However, once a female has been attracted and recognized the song changes to the gentle one of courtship and this is continuous for very long periods. To achieve courtship song at least some changes must be achieved in the nervous system. Minimally, these are reduction in the excitation of the centres controlling the action of individual muscles. These are manifested in fewer or none of the large muscle spikes, which are probably due to $F$ axon activity, and in the continuous nature of the song. There are no significant differences in the individual timing of the pulses, beyond the reduced pulse duration which must follow reduced wing opening, which is common in courtship song. The occasional loud pulse of courtship song may be attributable to an occasional excitation of the $F$ axons and it is probably very significant that all four muscles each show a single large spike in association with the loud sound. In these respects there is a close parallel to the use made of the dual innervation in controlling ordinary leg muscles in locomotion (Hoyle, 1964). To explain their use physiologically it is only necessary to suppose that the final motor output channels share common input circuits, and include at least a single $S$ and a single $F$ axon in parallel. The synapses to the former are activated at a lower threshold than the latter, so the $S$ axon fires first. The $F$ axon is brought in automatically in addition if the input excitation is strong enough.

The fact that differences in extent of wing opening occur, notably in the courtship songs, enables us partially to test whether the wing-closing phase is determined peripherally by reflex action following opening, or centrally, independently of wing opening. The intervals should be reduced in proportion to the reduction in wing opening if they are peripherally determined. There is a small reduction in the interval between sound pulses associated with reduced wing opening, but it is not marked. It seems probable that a combination of central factors and peripheral feedback from proprioceptors determines the time of onset of the closing stroke.

The large number of consecutive pulses making up courtship song could be due to the prolonged nature of the stimulation, which is probably chemical, provided by the continuous presence of the female. However, during aggressive song in response to another male which is kept in the presence of the singer and so also provides continuous stimulation, the chirps do not extend into trills. It may be that strong output to the muscles or strong closing action leads to a feedback which briefly inhibits the song-producing mechanism. Such feedback is present in both calling and aggressive song, but not in courtship. Thus it is only necessary for visual and/or chemical stimulation resulting from the presence of the female to cause slight additional effects leading to a continuous mild cycle of opening and closing to explain the different song. It is very significant that the first pulse in a calling or even aggressive chirp is usually mild, and similar to a pulse of courtship song.

We may conclude that it is not necessary to postulate separate neuronal centres independently storing the information required to evoke each characteristic song. A single ‘song centre’ suffices. A speculative simple scheme of the kind of phenomena which may be occurring is given in Fig. 10. It is realized that a full mechanical
Sound production in crickets

and neurophysiological analysis is desirable, but some preliminary postulates will be needed to guide the course of this work and those which follow will serve such a purpose. The mechanical basis of the wing operation is a simple extension followed by a flexion operated by synergists. It is thus analogous to a single step in ordinary locomotion, but involving only one joint. At this stage the problem confronting us for analysis resolves itself to one shared in common with that of general control of muscles in locomotion (cf. Hoyle, 1964).

A highly characteristic feature of the electrical discharges which have been recorded from both the wing opener and the three closers examined is the high basic frequency of firing, and the close similarity of the frequency, in different phases. It is as if there is a sudden switching on of an oscillator followed, after a brief action, by an equally abrupt cutting off.

If this oscillator were starting from zero frequency a progressive decrease in interval between successive pulses (rising frequency) would be expected, partly as a result of the time-constant of the membrane of the neuron or neurons involved. No such change can be seen in the records. An abrupt onset at a high frequency can best be

Fig. 1o. Scheme to illustrate a simple neuronal circuit which could account for the songs produced. The basis of the system is a pair of neurons cross-connected by inhibitory links to form a reciprocating unit driven by an excitatory pacemaker neuron operating at a high basic frequency (300—500 per sec). The pacemaker is normally inhibited continually, but the inhibition is itself inhibited by activity associated with sexual maturity and visual input from another cricket. During relief of inhibition of the pacemaker bursts of activity at a high frequency are sent alternately to wing opener motorneurons and the four synergistically-acting closer motor-neurons as a result of the characteristics of the reciprocating pair. Synapses with S axons are bridged more readily than those with F axons so for weak excitation the S axons alone will fire and will always fire before F axons, which merely act to supplement the contractions caused by the S axons. Feedback from the wings exerts an influence on, but does not determine, the pacemaking. Further details in text.
explained on the basis of a continuous oscillator with an output suppressed by inhibition most of the time. The oscillator may be envisaged, in its simplest form, as a patch of the surface membrane of a single neuron. Inhibition will summate with it in the same cell.

Such an oscillator is the heart of the 'song centre' postulated, and it is excited by purely endogenous factors following the onset of sexual maturity.

Endogenous control has been largely proven to occur in locust flight (Wilson, 1961). The neuronal control of flight and stridulation is probably very similar as would be expected on the grounds that the stridulatory movements are believed to have evolved from flight (Huber, 1962).

In the cricket song the oscillator is postulated to have a frequency of 300–500 cyc./sec. and the inhibition is conceived as continuous, but itself interrupted by inhibition in bursts equal to the duration of the individual song.

The phasing of opening and closing may be determined by the properties of a reciprocating pair driven by the oscillator. The nature of such a pair and its implication have been discussed by Reiss (1961), who devised the system theoretically, by Wilson (1964), who showed that it may be actually utilized in locust flight, and Hoyle (1964), who considered that it may form a general neuronal basis for controlling certain aspects of locomotion in insects. In the cricket singing, the basalar, subalar and dorsal longitudinal muscles acting synergistically receive the output from one member of the reciprocating pair; the tergosternals receive the output from the other member.

Relief of inhibition achieved by internal physiological changes and appropriate external stimulation leads to the oscillator output being passed on to the tergosternal motor neurons. There it easily excites the $S$ axons monosynaptically, causing moderate wing opening. The closer neurons are next excited. Again only the $S$ axons are excited. Feedback from the wings meanwhile adds to the excitatory state, causing the next burst coming from the centre to excite also the $F$ axons and give greater wing opening. In turn the wing-closing burst excites the $F$ as well as the $S$ axons to the direct wing muscles. The progressive introduction of $F$ axon activity, which occurs also in general locomotion (Hoyle, 1964) may be explained simply by postulating that the final motor pathways for $F$ axons are shared in common with those for $S$ axons but that the excitatory synapses to the $F$ motor neurons are less readily bridged than those for $S$ motor neurons.

Somehow the stimulus to produce courtship song causes a suppression of the tendency to excite also the $F$ axons. This could be envisaged as occurring at the centre itself, or more simply at the level of the motor neurons. Indeed, all $F$ axon activity may be blocked at this time so as to reduce the tendency of the animal to jump or run when disturbed. Such behaviour might be inadaptive in that it would interrupt courtship.

Of course, the above is highly speculative, but it may serve to show that neurophysiologically the elements of a nerve centre controlling a superficially complicated kind of instinctive behaviour do not necessarily require a large network of neurons with intricate cross-connexions resulting in a virtually unanalysable complex. This realization should open the way for direct experimental investigation of the detailed neuronal mechanisms underlying instinctive acts.
SUMMARY

1. The singing of the cricket Acheta domesticus has been studied with a view to examining the neuronal control mechanisms underlying the sound production.

2. Electrical activity was recorded from the muscles responsible for wing opening and closing during singing in intact, freely-moving crickets.

3. Three kinds of song which are both structurally distinct and clearly different in behavioural context were studied in detail: calling, aggression and courtship.

4. Each song is composed of a group of pulses of sound and each pulse corresponds to a single wing-closing movement. The songs differ only in regard to either the number of pulses in a group, or the loudness of the pulses.

5. The opening is caused by the tergosternal muscles receiving a brief burst of excitatory nerve impulses. Extra impulses, leading to extra wide opening, occur before loud sounds.

6. The closing movement is initiated by the first and second basalar and subalar muscles acting synergistically. The force, but not the velocity, of the closing stroke is increased by a late burst of activity in the indirectly acting dorsal longitudinal muscles, leading to louder sound.

7. Weak pulses are the result of (probably) only $S$ axons firing. When $F$ axons fire in addition loud sounds result.

8. During courtship songs the sound pulses are mainly weak and a large number of pulses occur consecutively.

9. The kind of neuronal machinery required to produce the observed output is considered theoretically, and a tentative simple scheme proposed.

10. It is not necessary to postulate separate neuronal centres for each sound, and a small number of neurons could, in principle, provide the underlying control of the different kinds of cricket song.

REFERENCES


