J. comp. Physiol. 122, 53–64 (1977)

Journal
of Comparative
Physiology · A

The Stridulatory Movements of Acridid Grasshoppers Recorded with an Opto-electronic Device*

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Received June 23, 1977

Summary. (i) The singing movements of acridid grasshoppers are recorded opto-electronically: a small retroflective "Scotchlite" sheeting (∅2 mm) is attached to the tip of the stridulating femur and illuminated via a semi-transmissive mirror mounted at 45° to the optical axis in front of a photographic object lens. The light retroflected through this mirror is focused by the lens on the surface of a position-sensing photo-detector from which the co-ordinates of the light spot are tapped off instantaneously. Using this principle and having one recording device on each side the stridulatory movements of both hindlegs are monitored simultaneously.

(ii) The grasshoppers *Chorthippus biguttulus* (L.) and *Chorthippus mollis* (Charp.) and their hybrids are studied by this method. Each of the two hindlegs performs a different stridulatory pattern, the movements being considerably phase-shifted. The legs change their patterns from time to time. In the pure species the two patterns are very tightly coupled. Although in the hybrids in principle the same close relationships exist between the two lateral sub-systems, the couplings of the two patterns can be temporarily loosened. In the extreme, one hindleg may stridulate a *Ch. mollis* song-pattern, whereas the other produces a *Ch. biguttulus* pattern.

A. Introduction

Many orthopteran insects produce elaborate songs during intraspecific communication, a behaviour that has attracted much attention both from ethological and neurophysiological aspects (review: Elsner and Huber, 1973). In order to establish the homologies between stridulatory patterns of different species and to have a suitable basis for an electrophysiological approach to the central nervous basis of sound production it has been found necessary to record not

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* Generously supported by the programme "Neurale Mechanismen des Verhaltens" of the Deutsche Forschungsgemeinschaft (Uh 23/4, El 35/8)

only the acoustic patterns produced, but also the corresponding singing movements.

Such recordings are especially needed in acridid grasshoppers which are unique among orthopterans in producing complex sound patterns with *two* stridulatory systems simultaneously. Each of the two hindlegs rubs its stridulatory file against a vein of the ipsilateral tegmen. The two legs often move with considerable phase-shift and may even produce different patterns (Elsner, 1974). Extremely complex song patterns are produced by hybrid grasshoppers (Helversen and Helversen, 1975) and, thus, a device capable of discerning the movements of *both* hindlegs has become urgently necessary.

To date, no method has been available for *instantaneously* recording the sound-producing movements of both hindlegs simultaneously. Therefore, an opto-electronic device has been developed and used to analyse the stridulatory patterns of pure and hybrid grasshopper species. The technique described in this paper is considered to be of general use for monitoring behavioural activities.

B. A Position-sensing Device for Recording the Stridulatory Movements

1. General Design

In developing a technique for recording these movements the prime requirement is that the animal be free to move and choose its own position for stridulation: the device must therefore be easily manoeuvrable, and anything mounted on the leg must be of negligible weight. The system developed resembles a reflex camera, trained upon a very light speculum of illuminated retroflective sheeting attached to the tip of the stridulating femur. The reflected ray is focused by the lens system upon a position-sensing photodetector in place of the film.

Since the grasshoppers stridulate with two legs, two of these instruments are used, mounted facing one another on photographic tripods placed at each side of the animal. However, since each recording device has its own coaxial illumination, the two are inclined at 5° to one another to avoid shining into each other's lenses. The grasshopper is free to move on a small platform, which can be turned after the animal has taken up its stridulating position athwart to the optical axes of the instruments. This adjustment is not critical because of the retroflective characteristics of the sheeting attached to the legs (see below).

The emitted sound is recorded by a 1″ Bruel & Kjaer condenser microphone (type 4145, 2 Hz – 18 kHz) and stored, together with the recordings of the leg movements on an AM/FM instrumentation tape-recorder (Ampex PR 2200).

2. Mechanical and Optical Construction

Figure 1 illustrates the detailed construction of the device. The grasshopper is illuminated by a 50 Watt DC-light source arranged parallel to the object lens. The light is deflected by a normal mirror upon a semi-transmissive mirror

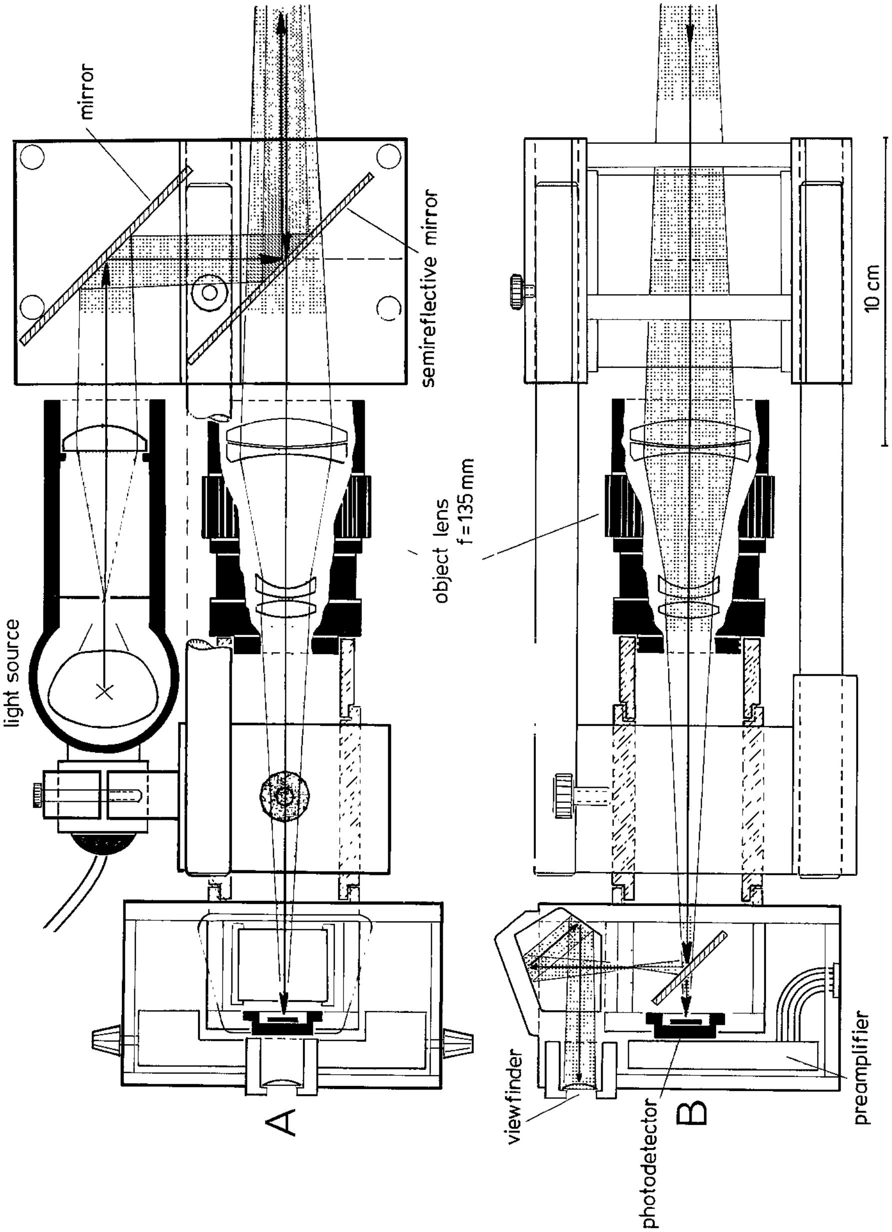

Fig. 1A and B. Diagrams illustrating the mechanical and optical construction of the position sensing device. **A** Top-view; **B** Side-view. Further explanation in the text

(transmission: reflection = 50:50) which is mounted at 45° to the optical axis and in front of the objective. The reflected 50% of the light pass out along the optical axis to illuminate the insect, whereas the transmitted 50% are adsorbed by a black surface. To permit the use of objectives of different focal lengths, the mirror system can be moved towards or away from the front lens.

Because of the properties of the reflective sheeting (see below), the light-beam is returned accurately from the tip of the femur along its own outward path. 50% of the light passes straight through the semi-transmissive mirror (the reflected 50% being wasted), and is focused by the objective (in our case f= 135 mm) upon the photodetector surface. Between objective and photo-detector, another semitransmissive mirror (transmission:reflection=80:20) is placed at 45° to the optical axis. This deflects 20% of the incident light onto a pentagon prism view-finder. The spatial limit of the photodetector is indicated by a graticule engraved on the ground glass screen. The housing of the photo-detector/viewfinder system can be rotated around the optical axis to bring the chord of the arc described by the tip of the femur into coincidence with either axis (x- or y-) of the detector surface.

Two components of the system need to be described in more detail: the position-sensing photo-detector and the retroflective sheeting:

3. The Position-sensing Photo-Detector

We use the Schottky-Barrier photo-detector PIN-SC/10 (United Detector Technology, Santa Monica, Cal., USA). This position-sensing silicon photo-diode has an active area of 10 × 10 mm; one electrode is attached to each of the four sides. A light ray impinging on the surface generates a photo-current which is divided between the four electrodes according to Kirchhoff's laws: the current between any pair of electrodes depends upon the resistance of the path, hence upon the distances from the point of incidence of the light to the insertions of the electrodes. Therefore, the geometric position of the light impact corresponds to a particular combination of the four currents. From the four electrodes two signals can be tapped off reflecting the x- and y-coordinates. These signals are amplified by a two stage-preamplifier, the circuit-diagramm of which is shown in Figure 2A. A bias of 6 V is applied via the potentiomenter P to shift the electrical zero-point if necessary.

The detector is designed to monitor the *centre* of the incident light. Its resolution is therefore independent of both the size of the light spot and the influence of any ambient light that penetrates from the contralateral illumination system.

The photo-detector used in our device responds to light between 300 and 1100 nm. Peak sensitivity is at 850 nm (0.25 μA/μW) which decreases modestly to 80% at 500 nm (specifications given by UDT). Therefore, visible and infra-red light can be used. However, it was found impossible to load the leg of the stridulating grasshopper with a light source (not even a small LED), because of its weight. This is why, instead, a retro-flective sheeting (∅ 2 mm) was attached to the tip of the femur.

4. The Retroflective Sheeting

"Scotchlite" Brand Reflective Sheeting (type "High Gain" No. 7610), manufactured by 3M-Company, was found most suitable for our purpose. The surface of this material is a layer of microscopic glass spheres which function as spherical mirrors focusing and returning light accurately back along its path. It is highly directional: when the sensor is moved only 1° off the axis of the incident light beam, response drops to less than 7% (Fig. 2B). The surface of the sheeting is non-specular and therefore resists glare interference from ambient light. The sheeting retains its accurate directionality up to very oblique angles of incidence (Fig. 2C), and this is why the position of the insect is not critical. In the same way, the small leg movements in stridulation do not impair directionality of the retroflected beam.

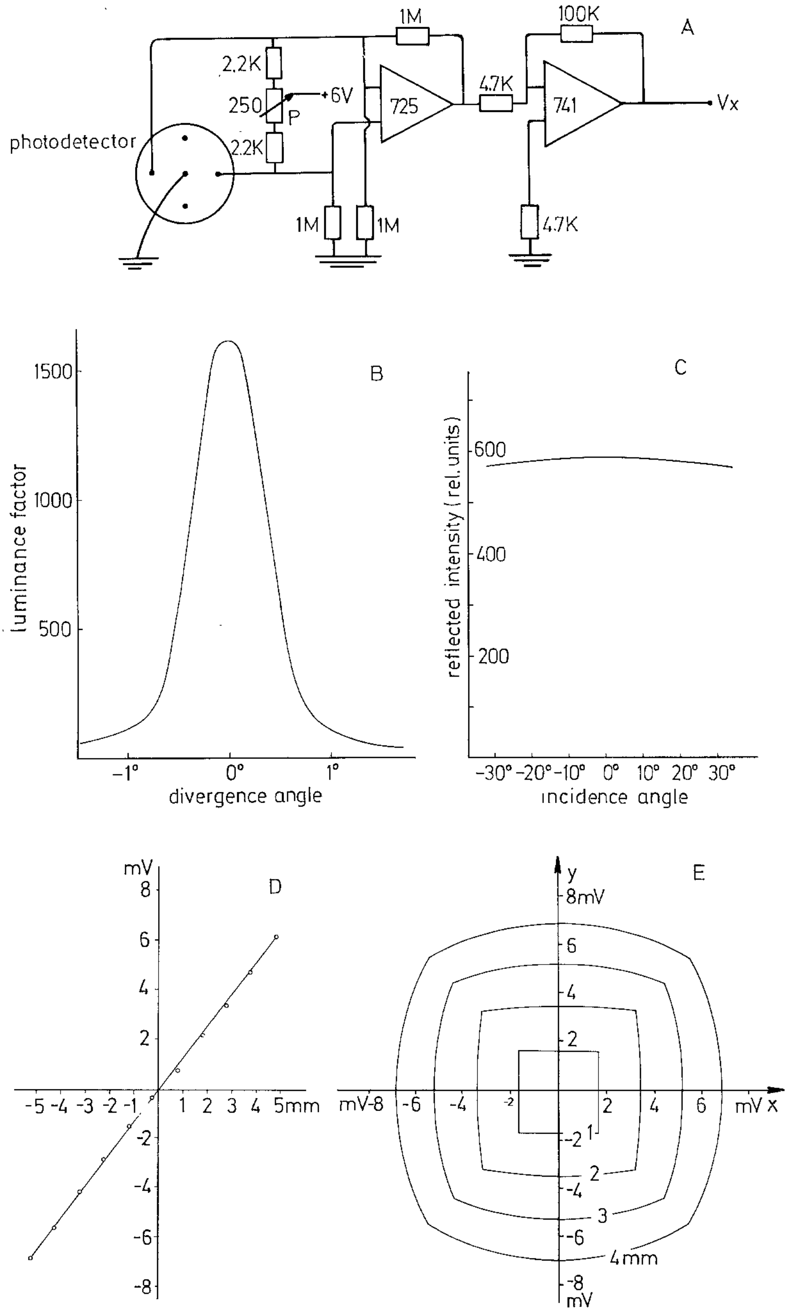

Fig. 2A–E. A Circuit-diagram of the pre-amplifier. **B** and **C** Characteristics of the "Scotchlite" retroflective sheeting No. 7610 (after 3M product bulletin): Luminance factor (multiple of the brightness of a perfect diffuse white surface) and reflected intensity as functions of divergence and incidence angle, respectively. **D** and **E** Diagrams illustrating the linearity of the photodetector: electrical output as a function of moving a light-spot along the x-axis only (**D**) and parallel to the x- and y-axis at distances of 1, 2, 3 and 4 mm (**E**)

5. *Specifications*

(i) Resolving Power. This depends upon the energy of the light incident upon the photodetector surface. In our device, the intensity is only a few μW, which means that, when the light spot moves from the centre to the edge of the detector (i.e., 5 mm), the change of current is less than 1 μA. This gives a signal-to-noise ratio of 55 dB at the output of the pre-amplifier (upper frequency limit set to 1 kHz). This is better than that of the instrumentation tape-recorder (43 dB). Since the amplitude of femoral movement scarcely exceeds ± 5 mm (i.e., the diameter of the detector), an optical magnification of 1:1 can be used, giving a resolution of 20 μm.

(ii) Linearity. If a light spot is moved along the x- or the y-axis, the system works fairly linearily (Fig. 2D). We have therefore brought one of the two axes into coincidence with the cord of the arc described by the tip of the femur, i.e., monitored the projection of the movement on *one* axis only. Recording both x- and y-coordinates was not considered to be necessary, since in our case one coordinate is always determined by the other because the femoral pivot is fixed.

However, other users may need to monitor in two dimensions (for example when tracing a free-moving animal in an orientation experiment), and will want to know the performance in this respect. We found a certain amount of *barrel distortion*, as can be seen from Figure 2E when the light spot is moved parallel to either axis. The manufacturer's data sheets give deviation limits of 1% within 1.25 mm of the centre, and 6% within 3.75 mm; we found 2% and 12% respectively—but this might be due to the low light intensity we have to use.

C. The Stridulatory Movements of the Pure Species and Hybrid Grasshoppers

1. *Pure Species Stridulatory Patterns*

The device has first been used to monitor stridulatory movements of the two grasshopper species *Chorthippus mollis* (Charp.) and *Chorthippus biguttulus* (L.), and their hybrids. Both are species in which the pattern of one hindleg differs from that of the other (Elsner, 1974). To date these two patterns could only be recorded separately and successively, because the devices used (Hall-generators, Elsner, 1970) could not be mounted in pairs bilaterally. This meant that the phase relations of the two legs could only be deduced indirectly by simultaneous electrophysiological recording of the activity of contralaterally homologous muscles. The present device obviates this and permits direct simultaneous comparison.

Chorthippus mollis (Charp.). This grasshopper produces song sequences each lasting 20–30 s, and comprising 60–100 "chirps", two of which are shown in Figure 3A. The "chirps" continuously increase in duration from 280 to 380 ms (37 °C). One hindleg begins with an accentuated downstroke (pattern I, white arrows) followed by a long vibratory up-and-down movement, and finishes with a long upstroke to the initial position. The other hindleg produces a similar pattern but lacks the initial accentuated downstroke (pattern II). The leg producing pattern I is leading the other one.

Chorthippus biguttulus (L.). This species displays series of song sequences; each sequence lasts 2–4 s and comprises a number of 85 ms "chirps" (30 °C) 9 of which are shown in Figure 3B. The left and right movements are basically similar but differ characteristically in detail. On each side, each "chirp" begins with a deep downstroke usually followed by 2 cycles of up-and-down movements of smaller amplitude but rising altitude, so that the leg comes back to the initial position. One leg, however, ends its "chirps" with a short upstroke and remains up for about 10–15 ms (pattern I in Fig. 3B, middle trace), whereas the other continues the movement (pattern II in Fig. 3B, upper trace). Consequently, the "chirps" of one side are separated by pauses, while those of the other are continuously linked. Nevertheless, the combined, bilateral "chirp" is still individually distinguishable in the sound pattern, because the intensity of the final prolonged upstroke (pattern II) is rather weak compared with that of the succeeding initial downstroke (Elsner, 1974). As can be clearly seen from Figure 3B the leg producing pattern I leads.

In each species, the two patterns are produced in a highly stereotyped and regular manner, characterized by the following rules:

(i) If one hindleg produces pattern I, the other performs pattern II; production of the same pattern with both hindlegs simultaneously has been observed in few cases only (Elsner and Helversen, 1976).

(ii) The legs may change their pattern (normally from one sequence to the next), i.e., each leg is able to produce both pattern I and pattern II.

(iii) There is always a phase difference, and it is always the same pattern that leads, here styled pattern I for that reason.

(iv) Although the two patterns differ from each other in characteristic details, a common basic rhythm is maintained: for example, the number of up- and downstroke cycles per "chirp" may change, but it is always the same on both sides.

(v) If one hindleg is amputated at the coxo-trochanteral articulation, the remaining one thereafter produces (in 95% of all cases) only pattern I and does not change to pattern II.

The stridulatory patterns are generated by central nervous networks that send their specifically-patterned commands to the thoracic muscles. It is likely that at least parts of these networks are present bilaterally. The relationships of these two subsystems, each of which controls the movements of one hindleg, are determined by the rules listed above. The neural mechanisms underlying these couplings are under intense study using various neuroethological methods (Review: Elsner and Popow, 1978). In the present paper the result of a *genetic* approach is described.

2. Hybrid Stridulatory Patterns

We have hybridized the two closely related grasshopper species *Chorthippus biguttulus* (L.) and *Ch. mollis* (Charp.). By this means, the motor patterns underlying stridulation may be fragmented into sub-units which may then be connected in a new configuration. The hybridization of *Ch. biguttulus* and *Ch. mollis* was considered to be of particular interest: The stridulatory patterns of these species have presumably certain features which are homologous and others which are not. Recording the stridulatory patterns of hybrid grasshoppers allows us to approach the following questions:

(i) In what way pattern I and pattern II of the two parental species combine to give the hybrid phenotype?

(ii) To what extent are the typical relationships between patterns I and II persistent and modifiable?

(iii) Does the combination of different genomes result in bilaterally symmetrical motor programmes, or may the two hindlegs become more independent of each other than in the pure species?

In the stridulatory patterns of hybrids between *Ch. biguttulus* and *Ch. mollis* the combination of the two parental genomes results in some features having an intermediate form and in a superimposition of others. A considerable variability is observed, both between individuals and between the songs of one individual. This is not known in the parental species.

The songs of hybrids of *Ch. biguttulus* and *Ch. mollis* are illustrated in Figure 3C–F. Those examples have been selected which show particular modifications differentiating the hybrid songs from the parental patterns. Generalizing we may state that the hybrid stridulatory patterns consist of sequences divided into sub-units ("chirps") lasting 0.3 to 1.0 s, two of which are shown in Figure 3C and D, respectively. The length of these sub-units is intermediate between the *Ch. mollis* "chirps" and the *Ch. biguttulus* "sequences". This intermediate inheritance would appear to support the claim of Helversen and Helversen (1975) that the *Ch. mollis* "chirp" is homologous with the *Ch. biguttulus* "sequence".

The beginning of the hybrid sub-units clearly resembles the pattern of *Ch. mollis*: One hindleg performs an accentuated downstroke (pattern I, white arrows in Fig. 3), the other leg lacks this movement (pattern II). Each of the sub-units contains ca. 20–30 cycles of upward and downward movements, each direction being sonorous. These cycles may be continuously linked together in a manner similar to the *Ch. mollis* intra-"chirp" pattern (compare, for example, Fig. 3A and Fig. 3D, *upper* trace) or they may be figured, i.e., be arranged into groups clearly resembling the *Ch. biguttulus* "chirp"-pattern (compare Fig. 3B and

Fig. 3A–F. Stridulatory movements of *Chorthippus mollis, Ch. biguttulus,* and their hybrids. In each case: top trace—left hindleg movements; middle trace—right hindleg movements; bottom trace—right hindleg sound pattern (the left tegmen was removed, sacrificing the sound from that side to have a clear recording from the other). **A** and **B** Stridulatory patterns of *Ch. mollis* (**A**) and *Ch. biguttulus* (**B**) (occasional performance of a "chirp" produced by only 2 cycles of up-and-down movements is marked by an arrow). I, II—Stridulatory patterns I and II; in all recordings the initial downstroke which characterizes pattern I of *Ch. mollis* is marked by a white arrow. **C** The left hindleg of the hybrid produces a combination of *Ch. mollis* pattern II and *Ch. biguttulus* pattern II, the right leg a combination of *Ch. mollis* pattern I (weakly expressed) and *Ch. biguttulus* pattern I. Arrows indicate the characteristic elements of *Ch. biguttulus* patterns I and II (pauses (I) and extended upstrokes (II). **D** The left hindleg stridulates in a manner resembling *Ch. mollis* pattern I (white arrows), whereas the other leg subdivides the song units by producing "chirps" resembling *Ch. biguttulus* pattern II (black arrows). **E** The right hindleg produces a *Ch. mollis* vibratory pattern (continuous series of up-and-downstroke cycles), whereas the other leg inserts a pause clearly resembling *Ch. biguttulus* pattern I (black arrow). **F** Pauses (which characterize *Ch. biguttulus* pattern I) inserted *after* a downward movement (black arrows) and not (as is usual) before (for comparison see **B**, middle trace) Vertical calibration: 3 mm

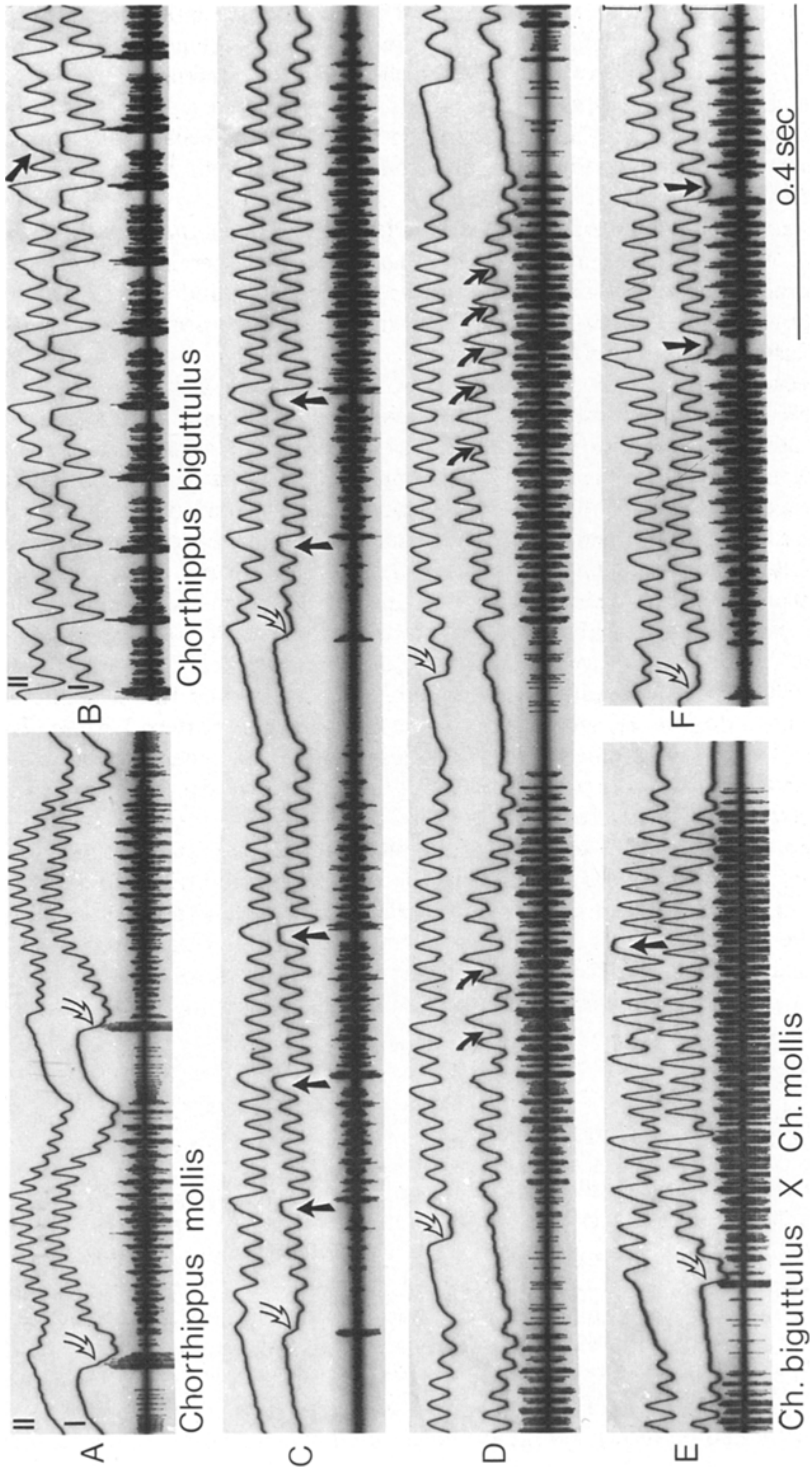
A
II
I
Chorthippus mollis
B
II
I
Chorthippus biguttulus
C
D
E
F
Ch. biguttulus X Ch. mollis
0.4 sec

Fig. 3A–F

Fig. 3C). In the latter case, the typical pattern I and pattern II elements of the *Ch. biguttulus* "chirp", i.e., pauses (pattern I) and extended upstrokes (pattern II), are more or less frequently inserted (Fig. 3C, black arrows). The extent to which the different parental elements are present in a hybrid song varies considerably from one individual hybrid to the other, between one song and another of a single individual, and even in the different parts of one song.

In most cases the features characterizing either pattern I or pattern II of each parental species are connected: One hindleg stridulates a combination of *Ch. mollis* pattern I and *Ch. biguttulus* pattern I, whereas the contralateral leg performs the combination of *Ch. mollis* pattern II and *Ch. biguttulus* pattern II. As in the parental species, the hindleg producing pattern I leads the one performing pattern II (Fig. 3C).

Occasionally, the couplings between *Ch. mollis* and *Ch. biguttulus* patterns I (as well as between the alternative patterns) have been found to be disconnected. For example, *Ch. mollis* pattern I may be connected to *Ch. biguttulus* pattern II. Furthermore, sometimes the rule that one of the two patterns is normally not produced by both hindlegs simultaneously, is suspended: sequences were observed which were subdivided into units beginning on both sides with an accentuated downstroke, the characteristic of *Ch. mollis* pattern I.

Normally, the hybrids perform those movement elements characterizing pattern I and pattern II in the same way as the pure species, sometimes, however, *intermediate* patterns have been observed. For example, *Ch. mollis* pattern I downstrokes at the beginning of the sub-units are carried out with unusually low amplitude (Fig. 3C, white arrows) or *Ch. biguttulus* pattern I pauses lasting atypically short. In a few cases more serious irregularities occurred: For example, *Ch. biguttulus* pattern I pauses inserted *after* a downward movement (Fig. 3F, black arrows), and not before, as is usual.

The most extreme case is that in which the parental patterns are divided *between* the two legs: One produces the *Ch. mollis* type of internal structure (continuous series of movements within each sub-unit, see Fig. 3E, middle trace), the other a *Ch. biguttulus* structure (pattern I pauses, Fig. 3E arrowed; pattern II upstrokes, Fig. 3D, arrowed). When, as here, the pause occurs on one sides only, a phase reversal results: the previously leading leg thereafter lags behind the other.

D. Final Remarks

Using the position sensing device described in this paper the extent of the connections between the stridulatory patterns of the two hindlegs have been revealed. It has been shown that very tight relationships exist between the two sub-systems in pure species. For example, if the pattern of one hindleg is known, then the pattern produced by the other leg can be predicted with confidence. Furthermore, the leg performing pattern I always leads the other. In hybrid grasshoppers these relationships are, in principle, the same. However, the stereotyped relationships may be loosened. Many examples (only a few of which could be shown here) have been found which demonstrate a temporary disconnection of the two lateral sub-systems. One striking example is the simultaneous production of the *Ch. mollis* pattern by one hindleg and the *Ch. biguttulus* pattern by the other. This supports the idea that in these hybrids two parallel, and to some extent independent, pattern-generating neuronal circuits might have been formed according to the species-specific information of the two parental genomes (Helversen and Helversen, 1975; Helversen and Elsner, 1975).

The recordings of the stridulatory movements in pure species and hybrid grasshoppers provide a considerable stimulus for future research on the underlying neuronal mechanisms. It is, for example, of particular interest to know the way in which central nervous and peripheral mechanisms interact to establish the relationships mentioned above. Ablation and stimulation experiments combined with electrophysiological recordings are presently being performed in order to answer this question (Lindberg and Elsner, 1977).

Apart from providing a basis for an electrophysiological approach to the neuronal generation of sound production the opto-electronic device is of general ethological importance. By this method the stridulatory patterns of different species can easily be compared, and false homologies – which may otherwise be made if only the sound patterns are monitored – may be avoided (for example, the false homologizing of the "chirps" of *Ch. biguttulus* and *Ch. mollis*; see Faber, 1957). Movement recordings are therefore essential, especially for phylogenetic considerations. Thus, during the last two years, the singing movements of many acridid grasshoppers have been monitored for the study of evolutionary problems (Elsner et al., in preparation).

Although the recording device has been specifically designed for studying grasshopper stridulation, it is of general usefulness in the behavioural sciences, especially when the animal has to remain free to move and when small amplitudes and high frequencies have to be measured. By choosing appropriate objectives and, if necessary, changing the light sources and optics to illuminate larger areas, the behavioural activities of other animals can be monitored, for example tracing the course of a freely moving animal in an orientation experiment. In that case, the barrel distortion of the system (Fig. 2E) must, of course, be considered. However, the signals can easily be corrected, either digitally, using the previously measured distortion characteristics, or by fitting an appropriate analog network to the output of the amplifier.

We thank Mr. L. Kaltenbach, Mr. W. Mäntele and Mr. H. Schönemann for technical help and gratefully acknowledge the stimulating criticism provided by Dr. W.B. Broughton and Dr. D.B. Lewis.

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