WARM-UP AND STRIDULATION IN THE BUSHCRICKET, *HEXACENTRUS UNICOLOR* SERVILLE (ORTHOPTERA, CONOCEPHALIDAE, LISTROSCELIDINAE)

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SUMMARY

The morphology of the stridulatory organ of the tropical bushcricket *Hexacentrus unicolor* is described and an investigation is made of stridulatory movements and muscle activities.

1. The song is produced by extremely fast stridulatory movements (320–415 Hz), during which, while closing the wings, a highly specialized file is brought into contact with the plectrum to produce sound. The muscles are activated with the same frequency, i.e. they work synchronously (neurogenic).

2. A few minutes before the stridulation starts, the muscles are activated in a similar rhythm to that pertaining during singing (pattern of spike trains and pauses). As a result, the thorax temperature increases considerably (up to approximately 37°C, 13–15°C higher than the ambient temperature). The frequency of the muscle potentials within the spike trains rises during warm-up. There are, however, indications that no phase displacement of antagonistically working muscles takes place.

INTRODUCTION

Many insects increase their body temperature above ambient temperature as a result of muscle activity (for a review see Heinrich, 1974). In most cases this occurs prior to and while flying, but it can also occur during other activities. For example, some bees are able to regulate the temperature of their brood and their nests and maintain a constant body temperature during other activities (e.g. Heinrich, 1979). A variety of beetles, mostly of the family Scarabeidae, exhibit endothermy during flight and when caring for the brood (production and rolling of dung balls; Bartholomew & Heinrich, 1978). Heat is also produced during singing. The bladder cicada *Cystosoma saundersii* Westwood, for example, warms up by approximately 12°C during its evening call and thus increases the volume of its song (Josephson & Young, 1979). Due to its peculiar muscle anatomy – the tymbal is not moved by antagonistically working muscles – it cannot warm up before singing.

Bushcrickets, however, are able to attain an elevated temperature prior to stridulation. Thus *Neoconocephalus robustus* Scudder (Heath & Josephson, 1970) and

probably also *Euconocephalus nasutus* Thunberg (Josephson, 1973), which has not been investigated that extensively, warm up for a few minutes before singing by synchronous excitation of the antagonistically working flying muscles. Another feature common to the two species is that both move their wings with a very high stridulation frequency (160–210 Hz).

In the present study, the bushcricket *Hexacentrus unicolor* is also found to exhibit warm-up behaviour and an extremely fast wing movement, but the neuromuscular programme is shown to be structurally completely different from that in the other species.

MATERIALS AND METHODS

Bushcrickets were collected during March and April 1981 and 1984 in Malaysia in the vicinity of Kuala Lumpur. Further tape-recordings of a single individual were made in the Krau Game Reserve (district Pahang, Malaysia). Altogether seven individuals were investigated: tape-recordings were taken from three individuals, stridulatory movement recordings were obtained from one animal and the muscle activity of another three was measured (using a thermocouple in one case). In addition a Japanese disc-recording of this species was evaluated [King Records SKS(H) 2012].

For a morphological investigation of the stridulatory organs, further to a light microscope examination, the air-dried elytra were sputter-coated with gold and screened in a scanning electron microscope (Etec, Autoscan).

The wing movements during stridulation were recorded by means of an opto-electronic device (Helversen & Elsner, 1977, modified according to Heller, 1984) and recorded with a Racal store 4DS tape-recorder. Recordings of the movements of both elytra were obtained using two detectors, one of which was directed towards the animal from the front, the other from the back. Simultaneously, singing was recorded on a third track (with a Bruel & Kjaer 6·35 mm microphone and a Bruel & Kjaer measuring amplifier 2606). The frequency spectrum of the song was determined using an FFT-analyser (Analogic, Data 6000).

To record the muscle activity, a 50-μm steel wire (insulated except for the tip) was used. The indifferent electrode was inserted at the side region of the anterior abdomen (1·5 mm of its tip was left without insulation). After appropriate amplification the signals were recorded simultaneously with the song on a Uher 4200 IC (in Malaysia) or a Racal store 4DS tape-recorder (FM-track). The position of the electrodes was established *post mortem* by careful dissection.

Body temperatures of the animals during singing were measured with a chromium/nickel–nickel thermoelement (each wire was 100 μm in diameter). This element was fastened within the side of the thorax (right basalar muscle) and the readings of the voltmeter were recorded on another track of the tape-recorder.

Data analysis was in part performed by a computer (Nova 4). Using a special interface (according to the idea of Zarnack & Moehl, 1977) peak amplitude and

corresponding time of a muscle potential were transferred to the computer. In addition, a Siemens oscillograph recorder was used to produce oscillograms.

RESULTS

Hexacentrus unicolor Serville is a long-winged, almost uniformly green-coloured bushcricket of the family Conocephalidae, subfamily Listroscelidinae. It is approximately 45 mm long inclusive of elytral length. Like all members of this subfamily, it is a predatory animal and in captivity lives solely on other insects. In Malaysia both imagines and larvae are relatively numerous in areas with low vegetation, e.g. on the roadside.

The piercing song can be heard from dusk until well into the night. The males exhibit very distinctive spacing: only very rarely are two or more animals found close together. Usually only one animal can be heard at a distance of 20–100 m. Apparently, singing positions are changed frequently (presumably by flying), since most subjects do not maintain their respective singing territories all evening. Acoustic rivalry, as is known from *Hexacentrus mundus* (Lloyd, 1979), is not observed.

Morphology of the stridulatory organs

The stridulatory file is situated, as in most bushcrickets, on the lower side of the left elytron (Fig. 1). It lies straight on the inner border of the mirror without any connection to the longitudinal veins of the wing. It is comparatively short and unusually massive: the teeth are arranged on a thick, broad, chitinous prominence. The form of the lower (*in situ*) edge of this bulge causes a conspicuous bend of the file (Fig. 1A). At the caudal region of the elytron (standing at a 90° angle to the longitudinal axis of the body) this edge has no, or only very small, teeth. A small elevation is followed by a concave central part, which is lined by bigger teeth. This part is bent sharply upwards at its extremity. This structure clearly prevents the slipping of the plectrum during high stridulatory speeds (see below).

The plectrum is extended in a manner similar to that of a bow-string by a massive chitinous structure situated at the caudal edge of the right front wing (Fig. 1B). Both elytra are highly specialized for their different functions.

Singing and stridulatory movements

The song of *Hexacentrus unicolor* consists of short chirps (approximately 50–100 ms long) presented in a rhythm of about 2 Hz (1·6–3·3 Hz). One chirp consists of a crescendoing group of pulses, which follow one another with a frequency of 320–415 Hz. The variation is principally due to different ambient temperatures (22·5–28·5 °C). The frequency spectrum shows two narrow maxima at 11 and 33 kHz and two submaxima at 22 and 44 kHz.

Data known from studies of other bushcrickets (e.g. Busnel, Busnel & Dumortier, 1956) suggest that during one opening and closing sequence one chirp, comprising a
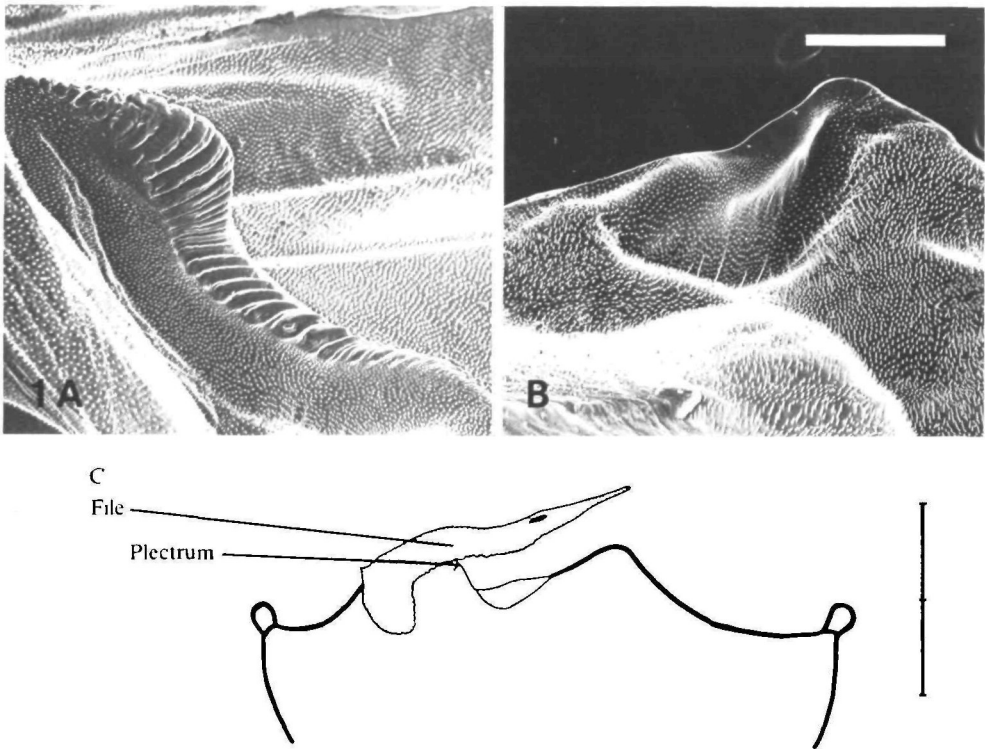
Fig. 1. File (A) and plectrum (B) of *Hexacentrus unicolor*. (C) Schematic cross-section through the elytra in the singing position shown from behind (solid chitinous parts stippled). Scale bars: A,B, 400 μm; C, 2 mm.

group of pulses, is produced. However, recordings of the wing movements show that this is not the case in this species: with each cycle of movement only one pulse is created. Accordingly the frequency of the wing movements is very high (320–415 Hz, see above). The course of the stridulatory movement is shown in Fig. 2. Fig. 2A shows a long recording of the song, Fig. 2B gives a more detailed account of the generation of a chirp. Some time before the generation of sound, the elytra are moved with very high frequency; only after a short period of 'introductory swinging' does the crescendoing tone start. The pulses always emerge during the second half of the closing movement of the wings (Fig. 2C). At the end of a pulse group the wings remain in an opened position for some time. During the successive closure of the wings an isolated sound pulse is created.

Throughout the song the animal is positioned in such a manner that its slightly opened elytra render the alae visible (see fig. 6 of Heller, 1983). The amplitude of the movement is very small and only a vibration is perceptible with the naked eye. An identical wing vibration can be recorded before the song. At this stage the movement is soundless, with almost the same rhythm, frequency and amplitude. The only difference from singing – except for the missing sound production – is that in most cases the elytra spring back without delay to the neutral position at the end of a chirp.
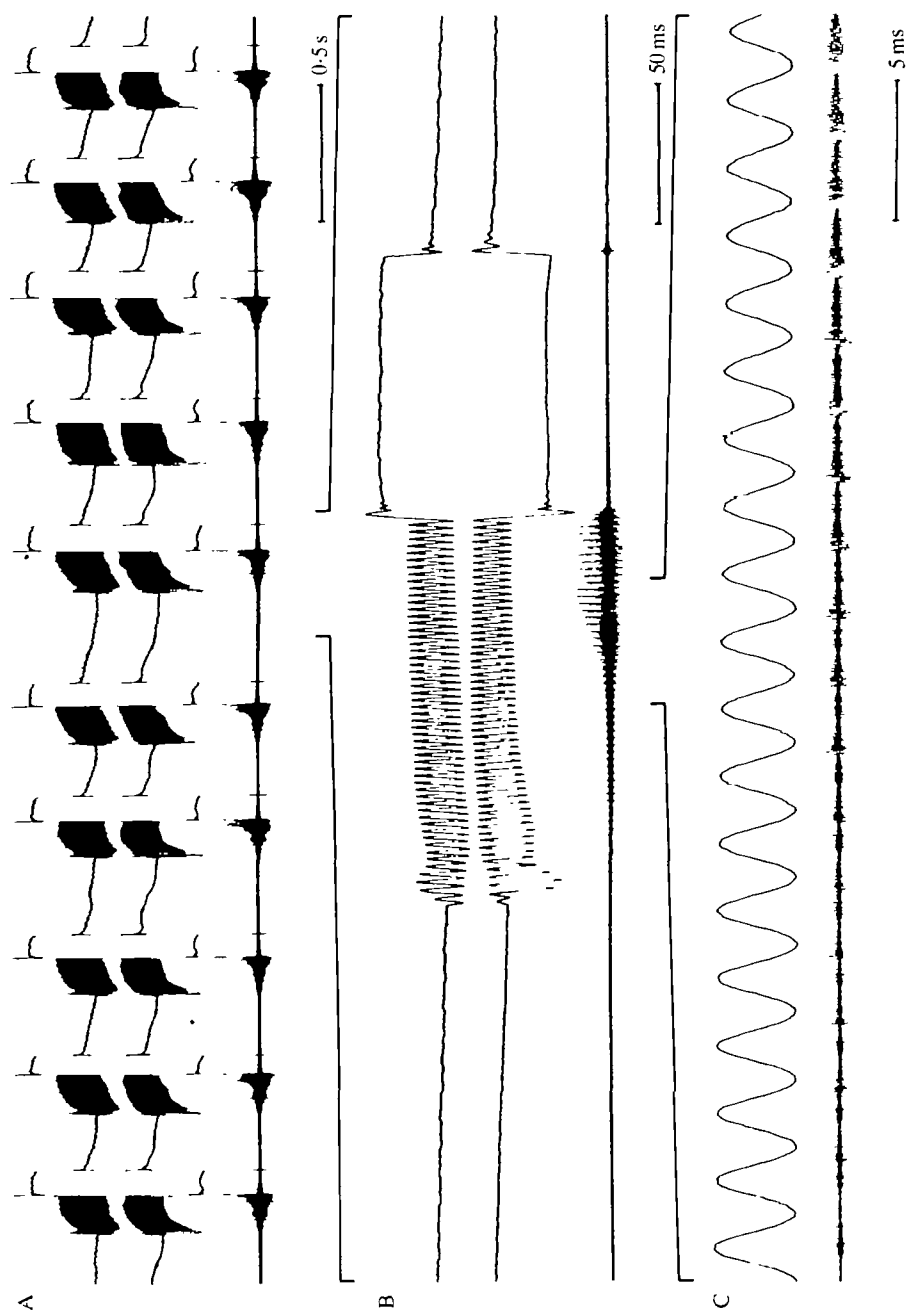
Fig. 2. Oscillograms of the song (lowest track) and stridulatory movements of *Hexacentrus unicolor*. Upper tracks, movement of the left elytron (a deviation of the line to the top indicates an opening, to the bottom a closing movement). Middle track in A,B: movement of the right elytron (a deviation to the bottom means an opening, to the top a closing movement). 28·5 °C; distance to microphone about 10 cm.

The frequency of the wing beat during flight is, as expected, far lower: 22–23 Hz (also measured opto-electronically on two females at 26°C).

Muscle activity and thermogenesis

During the first few recordings it became clear that the muscles are activated long before the onset of the song. This phase, which lasts several minutes, is necessary to raise the thorax to a temperature above that of the environment (see below); the high stridulatory frequency would probably be impossible at the lower temperature. During the warm-up phase, the excitation of the muscles corresponds to the pattern of the song. There are, however, several characteristic differences, not only in the basic rhythm of muscle activity, but also in the frequency of muscle potentials within individual chirps (Fig. 3).

During song generation the pattern of muscle activity is fairly regular. Groups of muscle potentials of constant length alternate with intervals that last considerably longer and exhibit a somewhat greater variation in length (Fig. 3D, from 4 min onwards). These potentials are probably excitatory postsynaptic potentials, as found in *Neoconocephalus robustus* (Josephson & Stokes, 1982). We shall use the term 'spike'. At the beginning of the warm-up phase (i.e. during the first minute), the spike trains are often longer than those occurring during singing (Fig. 3C). The intervals are more irregular and are often very long, but on the whole they have a magnitude similar to those during sound production (Fig. 3D). In the middle of the warm-up (Fig. 3, roughly from 1 to 2 min), both the periods of muscle activity and their intervals are often shorter than at the beginning, even shorter than during singing. This reduction, however, is not readily apparent in Fig. 3. The end of warm-up (Fig. 3, from 2 min onwards) is marked by longer groups of muscle potentials with shorter intervals. During this phase the steepest temperature increment occurs. There is an abrupt extension of the intervals at the transition to singing. The length of the spike trains may either decrease, maintaining an almost invariable rhythm, or change only slightly, slowing the rhythm correspondingly. During the song there is nearly always a slow, but constant, drop in the length of the muscle activity and an increase in the duration of the sound (Fig. 4D,E).

The muscle potential frequency was established at 320–370 Hz during the spike train, i.e. the muscles work neurogenically. Each muscle potential generates one movement of the wing. The difference between the measured 370 Hz of muscle potentials and the 415 Hz of wing movement, taken while singing, is due to different ambient temperatures prevailing at the time of the respective recordings. At the beginning of the warm-up phase the frequency is considerably lower, between 100 and 120 Hz; it then rises more or less continuously. Often there is another abrupt, but small, increase at the onset of the song (Fig. 3B).

The form of the potentials also changes during the warm-up (Fig. 4). At the beginning, in particular, there are bursts of large, regular spikes (Fig. 4A). Here the intratrain frequency does not always rise steadily from one spike train to another; longer intervals are sometimes followed by bursts of higher frequency, which slowly decrease again. In the middle of the warm-up, the frequency increases comparatively

quickly (Fig. 3B). The potentials are more irregular and are often smaller (Fig. 4B). At the end of this phase of warm-up it can sometimes be seen that each spike train ends with regular potentials; their frequency of occurrence increases and, at the end of the warm-up, they are almost completely dominant (Fig. 4C). At the transition to the song hardly any difference between the form of the potentials can be distinguished (Fig. 4C,D). During singing some irregular potentials are followed by long periods of regular muscle activity within one spike train. Such spike trains with irregular beginnings occur occasionally during the early warm-up phase (at a considerably lower spike frequency). Basalar and subalar muscles are activated
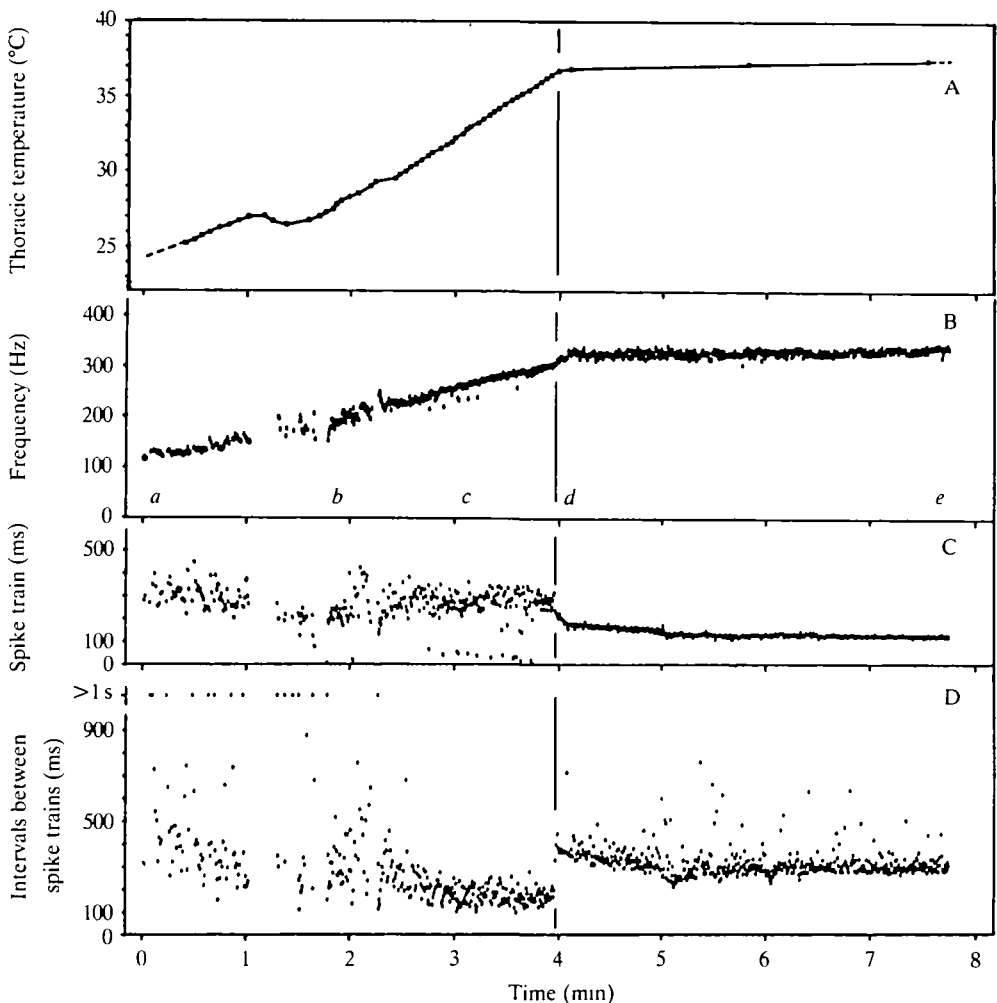

Fig. 3. Thoracic temperature and muscle activity (left basalar muscle) of *Hexacentrus unicolor* during warm-up and stridulation. The vertical line marks the beginning of the song. (A) Thoracic temperature (ambient temperature 23·5 °C); (B) frequency of the muscle potentials in the spike train (letters give the moments of the recordings of Fig. 4); (C) duration of the spike train; (D) duration of the intervals between the spike trains. Note the decreasing temperature during a short break in the muscle activity after 1 min.
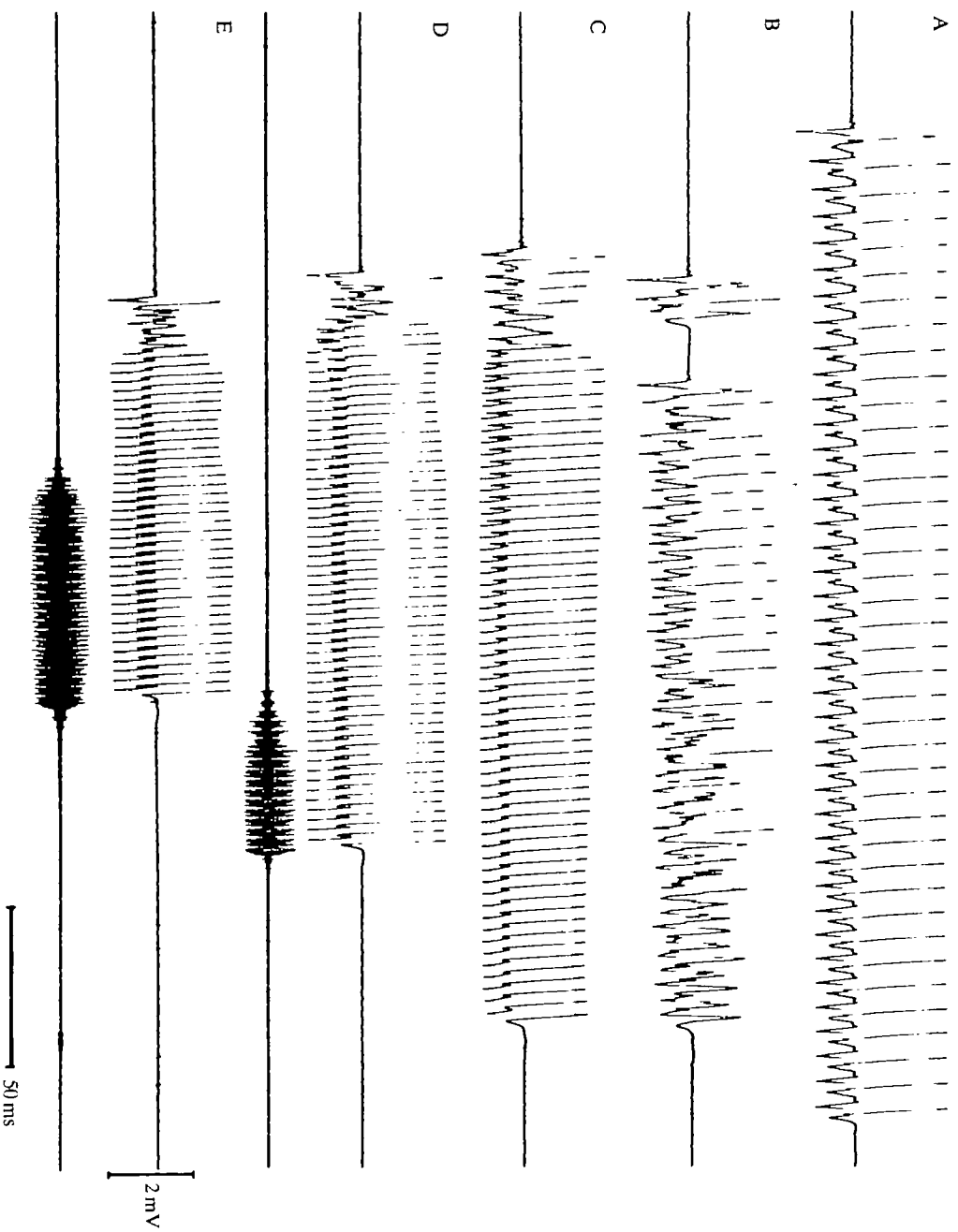
Fig. 4. Muscle activity (individual spike trains of the left basalar muscle) and singing of *Hexacentrus unicolor* while warming up (A–C) and during stridulation (D,E). The times of recording are marked in Fig. 3B (*a–e*). Due to intense echoes in the recording box, only times and duration of sound production can be recorded.

simultaneously, except at the irregular beginning. In one recording, of low quality, antagonists could be discerned which were activated with almost exactly the opposite phase.

The thoracic temperature during singing is approximately 37–37·5°C ($N = 3$), 13–15°C higher than the ambient temperature. The final temperature and the overall increase are similar to those of *Neoconocephalus robustus* (Heath & Josephson, 1970), depending on the ambient temperature. The course of warm-up is linear over extended periods with a rate of increase equal to 3·2–4·7 degrees min^{-1}. The lowest rate of warm-up occurred at the lowest ambient temperature and in the oldest animals. Cooling off is almost exponential until it reaches the ambient temperature. As in *Neoconocephalus robustus* (Stevens & Josephson, 1977), a faster component can also be discerned at the beginning of cooling.

DISCUSSION

Warm-up

Warm-up precedes stridulation in *Hexacentrus unicolor* as in the other bush-crickets which have been investigated, *Neoconocephalus robustus* and *Euconocephalus nasutus* (Heath & Josephson, 1970; Josephson, 1973), but the underlying pattern of muscle activation is strikingly different from that described for *N. robustus* (no such description has been made for *E. nasutus*). The differences suggest that warm-up has a different evolutionary origin in *H. unicolor* (subfamily Listro-scelidinae) from in *N. robustus* (subfamily Copiphorinae of the same family, Conocephalidae; Kevan, 1982).

One major difference between the pattern underlying stridulation in the representatives of the two subfamilies lies in the rhythm employed for warm-up and singing. In *N. robustus*, a much slower rhythm (about 20 Hz) is employed for warm-up than during singing (about 160 Hz; Josephson & Halverson, 1971). In *H. unicolor*, the pattern of spike trains, interrupted at intervals, that is found during warm-up is similar to that observed during singing (Fig. 3). This rhythm appears to be independent of temperature, or to be compensated for it, because during the phase characterized by the steepest temperature increment, the duration of the spike trains and the intermediate intervals hardly change. At the transition to the song, a shift in the ratio of excitation/interval occurs.

A second difference between the two species is found in the transition from warm-up to singing. The frequency of the muscle potentials during warm-up is relatively stable in *N. robustus*, and the transition to singing is marked by a short interval followed by an abrupt increase in the frequency of muscle potentials. In contrast, the frequency of potentials in *H. unicolor* shows a steady rise during warm-up, and there is no obvious change in the frequency or the form of muscle potentials when the song begins.

A further difference concerns muscle phase. In *N. robustus*, the muscles work synchronously during warm-up and antagonistically during the song. In *H. unicolor*, the muscles work in the same phase during both activities, so the elytra are moved by these muscles during warm-up. However, in the middle of the warm-up period,

when muscle potentials are irregular, a reversal of phase might occur. The observation that occasionally a 'cold' animal can produce a song (with a wing movement frequency of about 100 Hz) shows, however, that muscle coordination is possible with the same phase both' at low temperatures and with a warmed-up thorax.

In this last point *H. unicolor* differs from nearly all other insects with neurogenic muscles which have been investigated. The flying muscles of all of them work antagonistically while warming up. Normally, wing movements without a correspondingly high body temperature are ineffective, because cold wing muscles are usually unable to generate enough power at a low frequency. At a high frequency, however, there is an excessive overlap in the duration of their contractions. Additionally, the danger of inadvertently signalling to predators through wing movements exists; this holds equally for a song with a pulse frequency that is unattractive to a conspecific female. *H. unicolor* shows both an unusually low wing-movement amplitude (see above), and its wing movements and sound production are not tightly linked, as is apparent from the late onset of sound in each chirp (Fig. 2). In addition, it may prove relatively difficult to regulate certain phase displacements at such a high muscle potential frequency. It thus seems conceivable that this species uses a different warm-up technique compared to that utilized by other insects with neurogenic muscles. For similar reasons, insects with asynchronous muscles do not need synchronous activation of antagonistic muscles; they are able to uncouple their wings mechanically (Leston, Pringle & White, 1965).

Muscle activity and sound production

The contraction frequency of the stridulatory muscles of *H. unicolor*, which can attain 415 Hz, places them among the fastest known synchronous muscles. They are, however, active intermittently rather than continuously. The cricothyroid muscles of the bat, *Rhinolophus ferrumequinum*, achieve a similar frequency during periods of interrupted excitation, but show a considerably lower tetanus frequency during continuous stimulation (400 Hz compared to 200 Hz; Schuller & Suga, 1976).

Among other insects, synchronous muscles generally show considerably lower contraction frequencies: *Neoconocephalus robustus* at 212 Hz (Heath & Josephson, 1970), the cicada, *Psaltoda claripennis*, at 224 Hz (Young & Josephson, 1983) and the cricket, *Orocharis saltator*, at 280 Hz (measured indirectly *via* its song; Walker, 1969). Only in the cicada, *Okanagana vanduzeei*, have higher frequencies been recorded (550 Hz; Josephson & Young, 1985). Josephson & Halverson (1971) have already pointed out the striking fact that all these muscles characterized by high frequencies are used for sound production. This common feature is presumably due to the short contraction distances and the relatively low amount of energy they require (Josephson, 1985). Thus, although the period of an isometric twitch of *N. robustus* and *N. triops* is relatively short, the contraction speed is not exceptionally high (Josephson, 1984). These and other special properties of the muscles of *N. robustus* (Elder, 1971; Josephson, 1973; Josephson, Stokes & Chen, 1975; Josephson & Stokes, 1982) may also be present in a similar or analogous form in the singing muscles of *H. unicolor*.

The onset of the song or of an individual chirp cannot be attributed to the activity of the large wing muscles, since the elytra are then already in motion. It is also unlikely that it is due to more powerful muscle activation, which is responsible for increasing intensity during cricket song (Kutsch, 1969), since during the transition period between soundless and noisy movements at the beginning of the song no differences occur in the form of the potentials (and the course of the movement). Using similar reasoning, resonance phenomena are also ruled out as causal agents. The structure of the single sound elements (heavily damped pulses) also indicates that file and plectrum are engaged during each movement cycle. It therefore seems highly probable that either a further small adjusting muscle is activated, which changes the position of the elytra slightly, or a 'slow' activation of certain muscle groups is involved. The neuromuscular control of such changes in the elytral position, however, is as yet unknown in all Ensifera.

The evolutionary reasons for warm-up and high-frequency stridulation are still relatively unknown. A direct bearing of the weak 200 Hz component in the song of *N. robustus* (Counter, 1977) or the 400 Hz component of *H. unicolor* on the hearing or recognition of the song seems very unlikely. The hearing organs of *H. unicolor* show no obvious specialization for the reception of low-frequency song (Hsü & Shen, 1952).

It is more likely that closely related species recognize each other by the syllable (or pulse) frequency of the song (Bailey & Robinson, 1971; Bailey, 1976) and that certain species have been 'pushed aside' to very high frequencies (Heath & Josephson, 1970). Many of the *Neoconocephalus* and *Ruspolia* species have simply structured, monotonous songs with different syllable rates [*Neoconocephalus* 10–200 Hz (Walker, 1975) and *Ruspolia* 20–140 Hz (Bailey, 1976)]. In contrast, all other *Hexacentrus* species show high stridulation frequencies [*H. mundus*, 190 Hz (Robinson & Pratt, 1975), 130 Hz (Lloyd, 1979; same species); *H. japonicus*, 270 Hz; *Hexacentrus* species (Malaysia), 275 Hz (K.-G. Heller, unpublished observations)]. In addition, obvious amplitude modulations of these songs suggest that the pulse frequency alone is not sufficient to distinguish different species.

In another hypothesis, Josephson (1973) assumes that females prefer males with the highest pulse rates. Species without warm-up behaviour would therefore choose males calling from the warmest sites. The visiting of these places may also prove to be a useful strategy for females themselves and could promote this behaviour. The advantages of warm-up for flight, catching prey, and territorial and sexual behaviour and their significance for the evolution of this behaviour are completely unknown. However, such animals have an obvious benefit when they are to be caught by the entomologist.

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