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THE NEUROMUSCULAR MECHANISM OF STRIDULATION IN CRICKETS (ORTHOPTERA: GRYLLIDAE)

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INTRODUCTION

Study of the insect neuromuscular system appears very promising as a means of explaining behaviour in terms of cellular operation. The relatively small number of neurons, the ganglionic nature of the nervous system, the simplicity of the neuromuscular arrangement, and the repetitiveness of behavioural sequences all lend themselves to a solution of this problem. As a result, an increasing number ofinvestigators have been turning their attention to insects and especially to the large orthopterans.

Recently, Ewing & Hoyle (1965) and Huber (1965) reported on muscle activity underlying sound production in crickets. The acoustic behaviour is well understood (Alexander, 1961) and in the genera *Gryllus*, *Acheta* and *Gryllodes* communication is mediated by three basic songs composed of three types of pulses. While working independently on this system at the University of Cologne (W.K.) and the University of Michigan (D.B.) using various *Gryllus* species, we found a number of basic differences between the muscle activity in our crickets and that reported by Ewing & Hoyle (1965) for *Acheta domesticus*. These two genera, *Gryllus* and *Acheta*, are so nearly identical that they are distinguished solely by differences in the male genitalia (Chopard, 1961). The present paper constitutes a survey of muscle activity patterns producing stridulation in four species of field crickets. Since the work of the two authors was carried out independently, non-overlapping experiments will be initialled to indicate the investigator.

MATERIALS AND METHODS

Adult male field crickets of the following species were used in these experiments: *Gryllus firmus*, *G. pennsylvanicus* (from Michigan), *G. veletis* (from Michigan; D.B.) and *G. campestris* (W.K.) The first three species are North American and the last is European. The majority of the work was conducted upon freely moving chronic preparations. However, a series of experiments (D.B.) designed to establish the reliability of the chronic recordings and to aid in their interpretation should be examined first.

The mechanical structure of the mesothoracic exoskeleton was investigated to determine the relationship between muscle contraction and movement of the stridulatory apparatus. The tissue was cleaned away and the sclerites were moved at the points of muscle insertion to see how contraction of the muscles affected the forewings. In addition, 100 μ copper wires were fixed bilaterally to the exoskeleton at the insertions of twelve muscles: the subalars, basalars, first tergal promotors of coxa, and

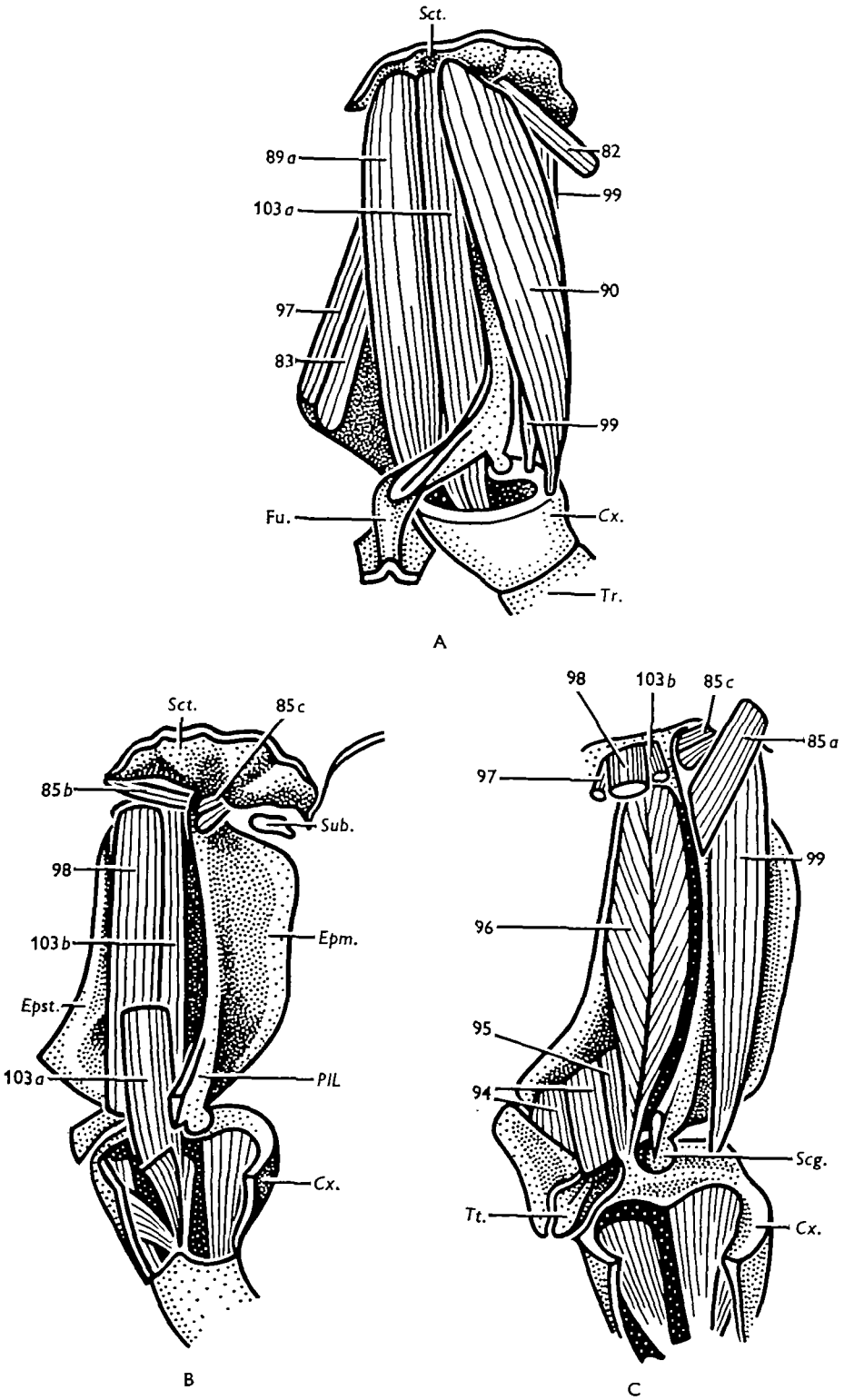

Fig. 1. For legend see foot of facing page.

first tergal remotors of coxa (Fig. 1; the last two muscles along with the tergo-trochanter will be called the medial dorsoventrals). Pulling these in the direction of muscle contraction demonstrated the function of individual muscles and indicated how the contraction of one set of muscles affected operation of the others. Motion pictures were taken to clarify these effects.

Table 1. *Nomenclature of mesothoracic muscles**

Common name	Snodgrass (1929)	Ewing & Hoyle (1965)†	Huber (1960)	Adapted for cricket from Snodgrass
1st dorsal longitudinal	81	81	1	81*a*
2nd dorsal longitudinal	81	81	2	81*b*
Dorsal oblique	82	—	3	82
1st pleuro-alar (wing flexor)	85	—	5	85*a*
2nd pleuro-alar	—	—	4	85*b*
3rd pleuro-alar	—	85	13	85*c*
1st tergo-sternal	83	‡	6‡	83‡
2nd tergo-sternal	84	‡	‡	‡
1st tergal promotor of coxa	89	83	7	89*a*
2nd tergal promotor of coxa	—	—	—	89*b*
1st tergal remotor of coxa	90	90	9	90
2nd tergal remotor of coxa	91	91	—	91
1st pronator extensor of forewing (1st basalar)	97	—	10	97
2nd pronator extensor of forewing (2nd basalar)	98	97	11	98
Depressor-extensor of forewing (subalar)	99	99	12	99
Depressor of trochanter				
1st tergal branch (tergo-trochanter)	103	84	8	103*a*‖
2nd tergal branch (tergo-trochanter)	103	89	—	103*a*‖
Basalar branch (3rd basalar)	—	98	8	103*b*
Sterno-pleural intersegmental	—	—	—	117*b*§

* The animals involved are: Snodgrass, *Dissosteira carolina*; Ewing & Hoyle, *Acheta domesticus*; Huber, *Gryllus campestris*; adaptation for this paper applies to all four of our species. Muscle correlation partly from Wiesend (1957).

† Interpretation of nomenclature is from Fig. 2 (Ewing & Hoyle, 1965). The system was based upon Snodgrass (1929) but includes tergosternals which are not present in the cricket.

‡ Although there are medial *metathoracic* tergo-sternal muscles in the cricket, there are none in the mesothorax; 83 is a small *lateral* muscle originating on the coxo-sternal sclerite.

‖ Since these branches do not appear to be functionally distinct, they will be distinguished as medial or lateral if necessary.

§ This muscle is apparently absent in the grasshopper although there is a pro-mesothoracic sterno-pleural intersegmental. In the cricket it is a large muscle originating on the furca or pleural arm and running dorsally, posteriorly and laterally to a small sclerite joining the meso- and metathoracic terga (in Snodgrass, 1929, 117 is the ventral meso- metathoracic intersegmental).

Fig. 1. Musculature of the right half of the mesothorax of *Gryllus campestris* viewed from inside. In A, B, and C successive layers of muscles have been removed. Common names of muscles involved in stridulation are listed in Table 1. For purposes of clarity, five muscles have been omitted. Muscles 89*b* and 91 attach lateral to 89*a* and 90 respectively. The dorsal longitudinals originate at the junction of the meso- and metathoracic terga and run along the dorsal midline of the mesothorax (Huber, 1960). 81*b* inserts on the tergopleural arm, a narrow sclerite lying along the anterior margin of the mesothoracic tergum from the wing pivot to the midline; 81*a* inserts on the anterior margin of the tergum. Muscle 117*b* is described in Table 1. *Cx.*, coxa; *Epm.*, epimeron; *Epst.*, episternum; *Fu.*, furca; PIL, pleural ridge; *Scg.*, coxal joint; *Sct.*, scutum; *Sub.*, subalar sclerite; *Tr.*, trochanter; *Tt.*, trochantinus. (Adapted from Huber, unpublished.)

In an acute preparation similar to that of Wilson & Weis-Fogh (1962), muscles were stimulated both directly and through their nerves to confirm results obtained in the mechanical experiments. The head and prothorax were removed and the pterothorax was waxed to a rigid support by the sternum. The thorax was perfused with Hoyle's (1955*a*) locust perfusion fluid and could be kept functional for several hours. Individual muscles were stimulated by placing insulated 100 μ Nichrome electrodes at both ends and passing current pulses from a Grass S 5 Stimulator between them at rates from 1/sec. to 150/sec. The dorsal longitudinals, the second basalars, the subalars, the first tergal remotors and the first tergal promotors were stimulated in this manner.

In field crickets relatively long lengths of motor nerve trunks to muscles or synergistic groups of muscles can be isolated. In an acute preparation such nerves were dissected free and placed across two 50 μ silver wires 0·5 mm. apart. The nerves were lifted clear of the thorax into air or mineral oil and stimulated by single pulses or 5 sec. trains up to 150/sec. The effects of the ensuing muscle contraction upon the exoskeleton were observed. By stimulating at the surface of the perfusion fluid, before or after cutting the nerve, it was shown that the muscle contraction was due to neuronal activity. Except for the subalars, all of the muscles which had been stimulated directly were checked by stimulation through their nerves.

In fresh acute preparations, spontaneous wing raising and lowering or opening and closing frequently occurred. When this happened, it was possible to see which muscles were active and to take motion pictures of their activity.

The cricket wing, like other insect wings, has two equilibrium positions, one in which it is flattened and extended for flight and one in which it may stridulate or remain folded. In experiments with normal animals, acute preparations and isolated exoskeletons both wings were 'popped' into either position or one was placed in each position in order to determine the relationship between the upstroke–downstroke movement of flight and the closing–opening movements of stridulation.

Muscle action potentials were recorded in the thorax during flight (D.B.) and during normal stridulation. To accomplish this, a small hole was drilled through the cuticle, and a fine wire electrode insulated to the tip (40 μ stainless steel (W.K.); 100 μ Nichrome (D.B.)) was inserted into the muscle and fixed to the cuticle with adhesive wax. The indifferent electrode was a stainless-steel wire uninsulated for 1 mm. from the tip placed in the abdominal cavity (W.K.) or an uninsulated copper loop in the prothoracic haemolymph cavity (D.B.). The electrodes were clipped to long flexible leads allowing complete freedom of movement. Potentials were amplified by a Tektronix 122 pre-amplifier (W.K.) or a Grass A.C. pre-amplifier (D.B.), and displayed on a Tektronix 502A dual-beam oscilloscope. Sound pulses were picked up by microphone (Beyer M100 (W.K.); Ampex 802 (D.B.)) and displayed synchronously with the muscle potentials on the oscilloscope. Beam displacement was recorded on paper oscilloscope film.

In some animals, recording electrodes were placed in synergistic muscles (with a common indifferent electrode) to determine the degree of synchrony and order of firing (W.K.)

The electrode position was identified by both chemical and physical means. The tip could be fairly accurately located by careful dissection, especially when it was

inserted just through the cuticle. After the end of an experiment, a pulse of current was passed between the electrodes, using the recording electrode as anode, and the cations were either stained with Prussian-blue (W.K.) or precipitated in a bright red nickel-dimethylglyoxime complex (D.B.). The latter method involved anaesthetizing the animal in CO_2, removing the thorax, evacuating it, and placing it for 12 hr. in a solution of 5% sodium acetate, 1% dimethylglyoxime, 7% ammonia, and 87% ethanol (47%). Current was passed after the thorax had been impregnated because a more concentrated precipitate formed and previous experiments had shown that there was no electrode shift during post-mortem manipulation.

Since recording occurred in a volume conductor with a number of concurrently active sources of e.m.f., experiments were carried out to determine the relationship of the electrode tip to potential sources (D.B.). In several animals, four electrodes were placed in the thoracic segments and potentials were recorded sequentially from all pairs (Fig. 2). Tips were marked and their positions and the nature of the tissue around them were determined.

RESULTS

The muscles observed could be placed into two groups according to their activity: those that fire during the opening of the forewings and those that fire during the closing or sound producing (Pierce, 1948) stroke of the forewings (Table 2). This is a chronological as opposed to a functional classification and an 'opener' might, for example, be maintaining the horizontal position of the forewings rather than moving them apart. We found that in our animals muscles fell into the opposite groups from those assigned by Ewing & Hoyle (1965) for *A. domesticus*.

Table 2. *Activity period of mesothoracic muscles of the cricket during stridulation*

Muscle	Kutsch	Bentley	Ewing & Hoyle (1965)
81*a*	Closing	Closing	Closing (81)*
81*b*	Opening	Opening	
89*a*	Closing	Closing	Opening (83)*
90	Closing	Closing	—
98	Opening	Opening	Closing (97)*
99	Opening	Opening	Closing (99)*
103*a*	Closing†	Closing	Opening (89–84)*
103*b*	—	Preliminary‡	Closing (98)*

* Terminology in Ewing & Hoyle (1965).
† Only during the 'tick' in courtship.
‡ Fires when the wings are opened and raised prior to stridulation.

Manipulation of the exoskeleton showed the critical effect of a muscle to be its movement of the exoskeleton with respect to the wing pivot or pleural apodeme. Lowering the tergum or dorsal sclerite of the mesothorax closes the wings; tilting it forward and down raises them. Pushing the tergopleural arms backward medially and pulling them forward laterally spreads the wings. Lowering the subalar sclerite lowers and opens the wings. Pulling down on the basalar sclerite spreads and may lower the wings. Alternate pulling of wires attached to the medial dorsoventral insertion points

and basalar or subalar sclerites produces normal-appearing stridulatory motion and position of the wings.

Direct stimulation, nerve stimulation, and spontaneous activity confirmed the muscle effects indicated by the wire experiments. Anterior medial dorsoventrals raise and close the wings; posterior medial dorsoventrals primarily close them. Dorsal longitudinals inserting on the tergopleural arm, subalars and basalars open the wings while the subalars have an especially strong lowering effect.

Observation of wing action in both equilibrium positions demonstrated clearly that the upstroke of flight is homologous with the closing stroke of stridulation and, conversely, the downstroke corresponds to the opening stroke.

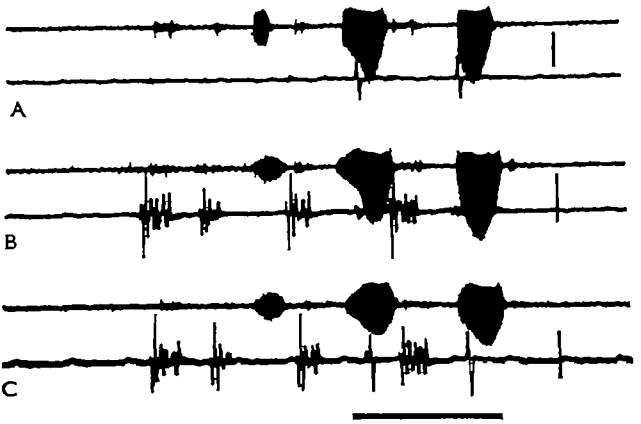

Fig. 2. Multiple electrode recording from *Gryllus firmus* during aggression. A, Recording between remotor (90) and prothoracic indifferent. B, Recording between subalar (99) and prothoracic indifferent. C, Recording between remotor and subalar. The remotor fires during the closing phase; the two subalar units fire during the opening phase. Upper trace in each record displays sound intensity. Time cal., 100 msec. Potential cal., 1 mV.

Recording sequentially from pairs of electrodes showed first that some electrodes record and some do not. The non-recording electrodes were in fat bodies or tracheae or were covered with clotted hemolymph. Of recording electrodes, those completely inside a muscle were unlikely to record from units outside that muscle. If an electrode was on the surface of a muscle it picked up large potentials from that muscle but was subject to interference from other muscles. If an electrode was not directly on the surface of a muscle, it could pick up potentials from muscles some distance away in the thorax. One recording sequence is shown in Fig. 2. This animal had two indifferent electrodes in the prothoracic hemolymph cavity, one electrode inside the first tergal remotor of coxa and one electrode on the lateral surface of the subalar. No sizeable potentials were seen when recording between the indifferent electrodes. While recording between the remotor electrode and an indifferent electrode, large spikes were seen associated with closing activity and there was no interference from outside muscles (Fig. 2A). When recording from the subalar electrode and the same indifferent electrode, opening potentials were seen from the subalar but they were irregular, due to interference from synergists (Fig. 2B). Also, the activity of antagonists, such as the adjacent remotor, was seen as cross-talk during the intense closing pulses.

Fig. 2C was recorded between the two active electrodes. Potentials of opposite polarity appeared as the muscles were alternately active in the opening–closing pattern. In all recordings, spike patterns were consistent with the active electrode position.

Chronic recordings from well over a hundred animals support the conclusions outlined in Table 2. There were no inconsistent results, and patterns were confirmed independently in each laboratory. In the calling or aggressive pulse, closing is produced by the medial row of dorsoventral muscles. The first promotor fires just

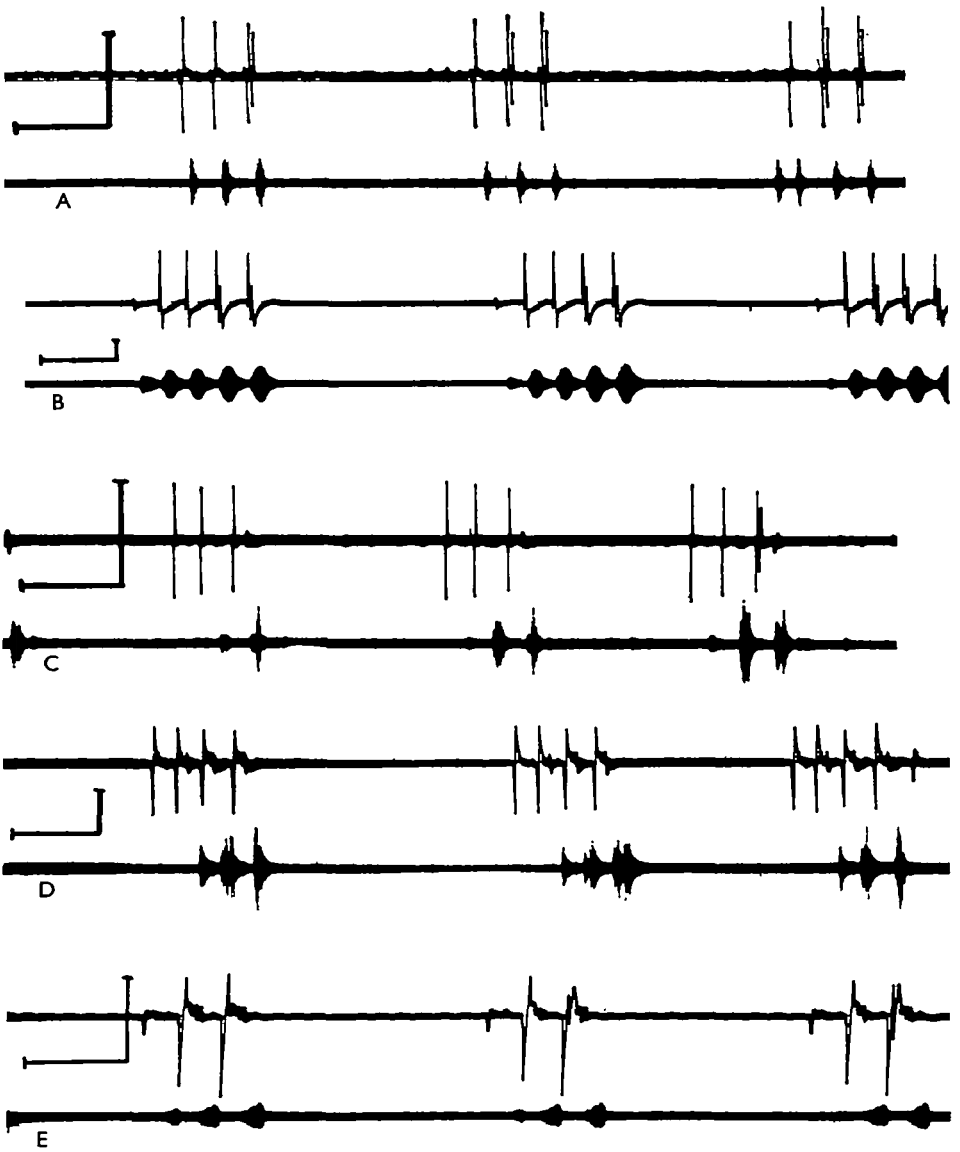

Fig. 3. Potentials recorded from five mesothoracic muscles in *Gryllus campestris* during calling. Lower trace in each record displays sound intensity. A, Promotor (89*a*); B, remotor (90); C, dorsal longitudinal (81*b*); D, 2nd basalar (98); E, subalar (99). The first two muscles fire during the closing phase and the last three during the opening phase. Double units in the 2nd basalar and the subalar can be seen clearly. Time cal., 100 msec. Potential cal., 2 mV.

previous to and during the course of the sound pulse (Fig. 3A, *G. camp.*; Fig. 4B, *G. firmus*). The first remotor fires in the same general pattern (Fig. 3B, *G. camp.*; Fig. 4C, *G. penn.*). In *G. camp.* the tergo-trochanter is not active during this type of pulse; in the North American species it is most active in flight and can fire occasionally when the wings are raised at the beginning of a chirp sequence or during an intense pulse (Fig. 4D, *G. firmus*). Also, in these species, the promotor can fire up to 9 times per pulse and is the most active muscle hitherto observed. Evidently, several of the

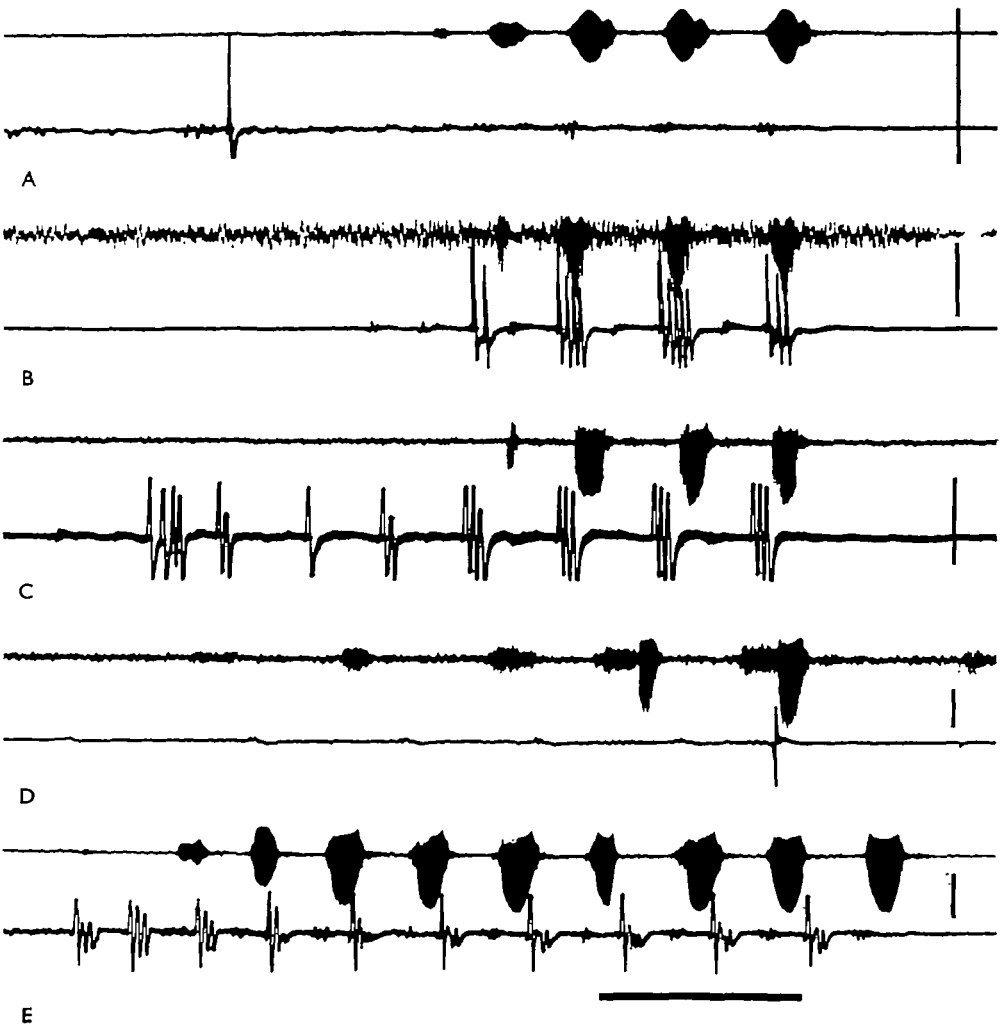

Fig. 4. Potentials recorded from five muscles in *Gryllus pennsylvanicus* or *G. firmus* during aggressive stridulation. The upper trace in each record displays sound intensity. A., 3rd basalar (103*b*), *G. penn.*; B, promotor (89*a*), *G. firmus*; C, remotor (90), *G. penn.*; D, tergo-trochanter (103*a*), *G. firmus*; E, subalar (99), *G. penn.* The 3rd basalar fires prior to the first pulse in a chirp sequence but not during the chirp. The promotor fires during the closing phase as does the remotor. The tergo-trochanter fires during the closing phase of intense pulses. Two units of the subalar can be seen firing during the opening phase. Time cal, 100 msec. Potential cal, 3 mV.

muscles fire more frequently per pulse in the North American species than in the European species although this has not been critically measured.

Wing opening during the aggressive or calling pulse is associated with activity in the dorsal longitudinals inserted on the tergopleural arm, the subalars, and the basalars. The subalar can fire from one to several times beginning in the last phase of the sound pulse or just after its completion (Fig. 2B, *G. firmus*; Fig. 3E, *G. camp.*; Fig. 4E, *G. penn.*). The second basalar fires in a pattern very similar to that of the subalar (Fig. 3D, *G. camp.*); although the third basalar is very active in flight, it does not fire during stridulation except occasionally when the wings are raised and opened for the first time in a chirp sequence (Fig. 4A, *G. penn.*). Simultaneous recordings from the second basalar and the subalar show that although they fire in relative synchrony, the basalar always leads the subalar by a short interval (Fig. 5, *G. camp.*).

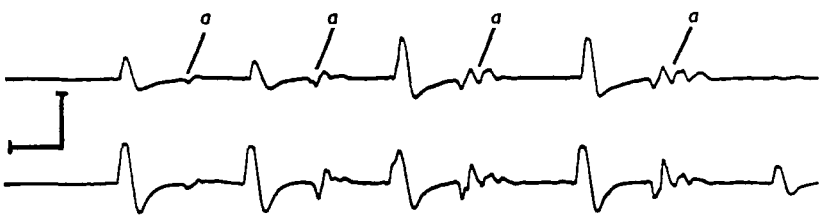

Fig. 5. Simultaneous recording from the subalar (99; upper trace) and the 2nd basalar (98; lower trace) on the same side during calling in *Gryllus campestris*. The basalar fires slightly in advance of the subalar. The large spikes from both muscles display synchronous or slightly out-of-phase firing by two units; small spikes represent single units. Antagonist potentials (*a*) can be seen between the opener spikes. Time cal., 10 msec. Potential cal., 2 mV.

The activity of the muscles alters greatly during the courtship song which is composed of two phases: a series of soft pulses followed by a loud 'tick' at the end of the chirp. In all of the species examined, all of the medial dorsoventral muscles fire synchronously just before the 'tick' (Fig. 6A, B, *G. camp*,; Fig. 7A, *G. veletis*; Fig. 7B, *G. penn.*; Fig. 7C, *G. firmus*). There is no apparent opener activity during this phase but, in contrast to the closers, the openers are very active in the soft pulse phase. The subalars show prolonged firing during this part of the chirp (Fig. 6D, *G. camp.*; Fig. 7F, *G. penn.*). In some cases there is rapid multiple firing of up to fifteen spikes which may produce the vibration of the wings in the open position seen in high-speed motion pictures (D.B.). Second basalar activity is again similar to that of the subalar in *G. camp.* In the North American species the third basalar is inactive.

Analysis of the dorsal longitudinals presents a difficult problem because electrodes fixed to the overlying tergum are moved during stridulation. Since electrodes are marked with the wings lowered, their positions during chirping are not clear. However, it appears that 81*a* and 81*b* are antagonistic. Both originate at the junction of the meso- and metathoracic terga but 81*a* inserts on the front margin of the mesothoracic tergum while 81*b* inserts on the tergopleural arm. Judging from the anatomy the action of 81*b* on the tergopleural arm spreads the wings but movement of the tergum itself by 81*a* may raise the wings or may adjust the rigidity of the thorax in some fashion. Opening activity of 81*b* is shown during the calling-type pulse (Figs. 3C, 6C, *G. camp.*; Fig. 7E, *G. firmus*) and during the soft pulse phase of courtship (Fig.

6C, *G. camp.*; Fig. 7D, E, *G. firmus*). Fig. 7E, a continuation of the stridulation shown in Fig. 7D, illustrates the transition back to calling with the incorporation of both 'ticks' and calling-type pulses. 81*a* is seen firing prior to the 'tick' and during the closing phase of the calling pulse. A similar situation is found in Fig. 6C, although in this particular record 81*b* fires only during the opening prior to the 'tick'.

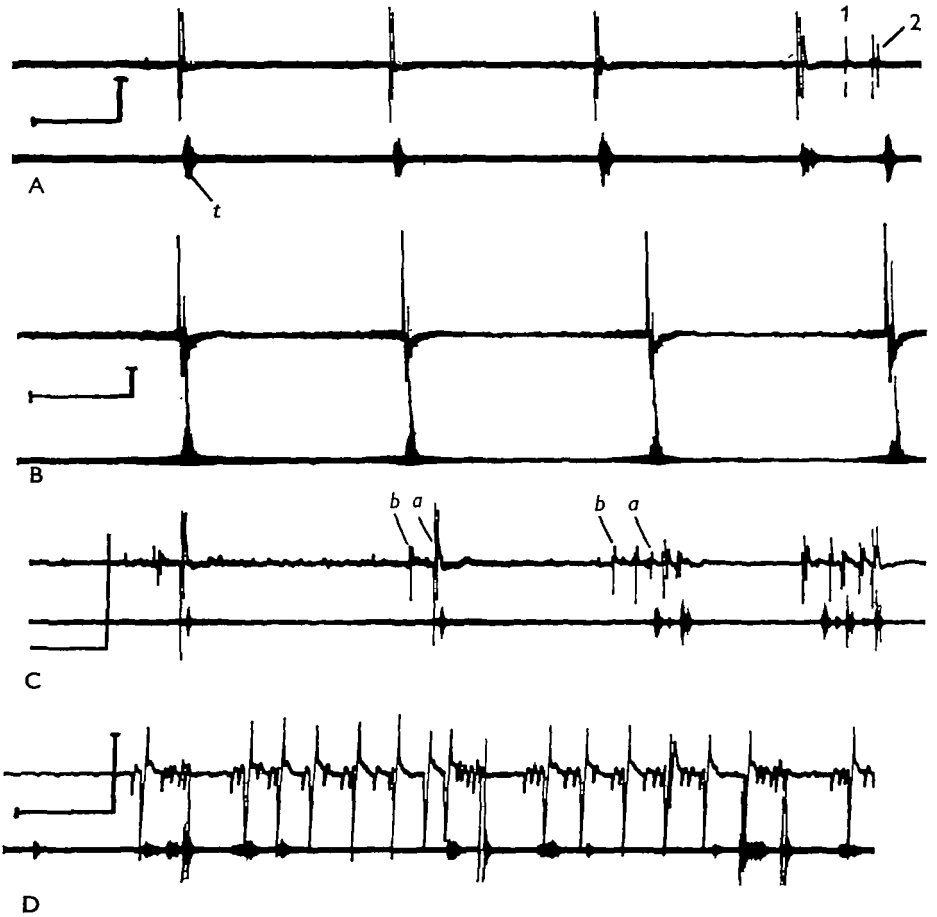

Fig. 6. Potentials recorded from five muscles of *Gryllus campestris* during courtship. Lower trace in each record displays sound intensity. A, Promotor (89*a*); B, remotor (90); C, dorsal longitudinals (81*a*+81*b*); D, subalar (99). The first two muscles fire synchronously before the 'tick' (*t*). Evidently the two dorsal longitudinals are antagonistic: 81*a* fires just prior to the 'tick' or during the closing phase of calling (*a*); 81*b* fires during the soft pulse phase when the wings are opened before the tick or during the opening phase of calling (*b*). The subalar is active in the soft pulse phase. Multiple units can be seen in the promotor, subalar, and dorsal longitudinals. Time cal., 100 msec. Potential cal. A, B, D, 2 mV.; C, 1 mV.

It is difficult to make valid estimates of motor unit distribution. Fast-axon and slow-axon activity cannot be rigorously distinguished without recordings of intracellular or mechanical changes (Hoyle, 1955*b*). However, some units can be separated on the basis of size differences and summation effects. Fig. 8 shows both multiple firing of a single unit and varying degrees of summation of two units in the first

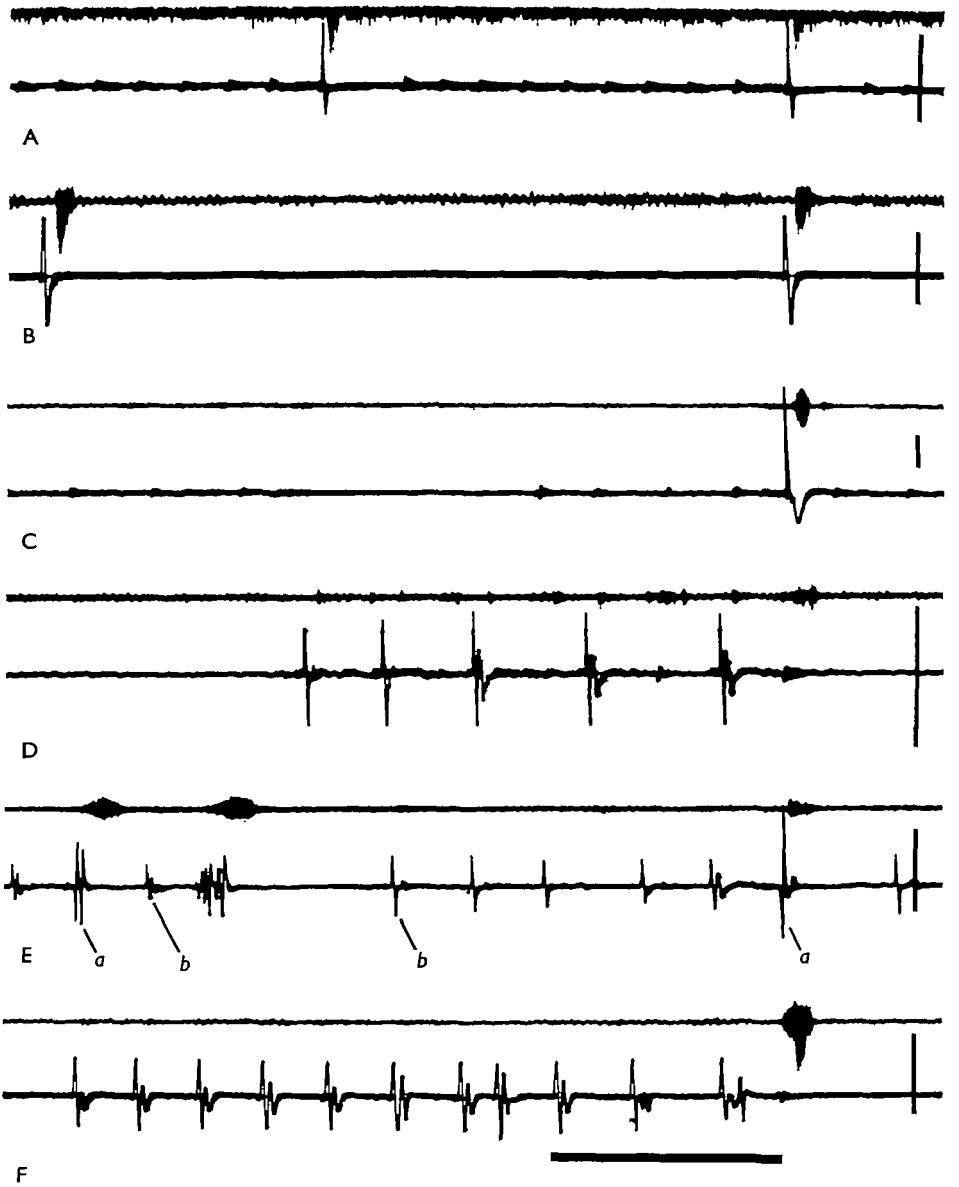

Fig. 7. Potentials recorded from six muscles of *Gryllus firmus*, *G. pennsylvanicus* or *G. veletis* during courtship. Upper trace in each record displays sound intensity. A, Tergotrochanter (103*a*), *G. veletis*; B, remotor (90), *G. penn.*; C, promotor (89*a*), *G. firmus*; D, dorsal longitudinal (81*b*), *G. firmus*; E, dorsal longitudinals (81*a*+81*b*), *G. firmus*; F, subalar (99), *G. penn.* The first three muscles fire synchronously just prior to the 'tick'. Two units can be seen firing in both the subalar and the dorsal longitudinal (81*b*) during the soft-pulse phase. Record E is a continuation at lower gain of the sequence shown in record D. The chirp is during the transition from courtship to calling so the 'tick', the soft-pulse phase and the calling-type pulse can all be seen. 81*b* fires during the opening and the soft-pulse phase (*b*); 81*a* is firing with multiple units of varying synchrony during the closing phase and prior to the 'tick' (*a*). Note opposite polarity of potentials from the two muscles. Time cal., 100 msec. Potential cal., 3 mV.

tergal remotor of *G. camp.* Judged on these grounds, multiple units also occur in the subalar, the second basalar, the third basalar, both dorsal longitudinals, the tergal promotor, the tergal remotor and the tergo-trochanter. Most of the muscles appear to have at least two large units and one or more small. The small units may reflect slow-axon activity.

It has not been possible to correlate changes in pulse intensity directly with activity in any single muscle; increased intensity is usually associated with higher activity levels in all muscles. In some cases, force production can be related to a smaller set of muscles. For example, during the soft-pulse phase of courtship, the forewings are driven by the opener group.

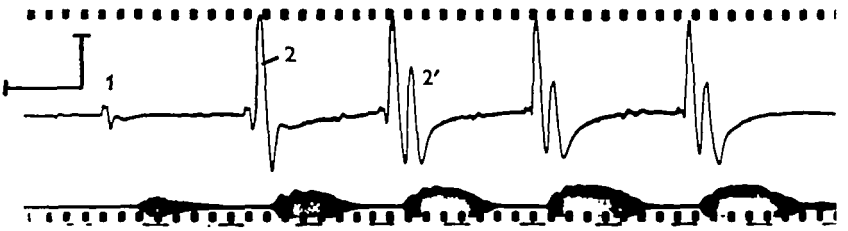

Fig. 8. Potentials recorded from the remotor (90) of *Gryllus campestris* during calling. The lower trace displays sound intensity. Two units (1, 2) can be distinguished which undergo a phase shift toward synchrony during the chirp. Multiple firing (2, 2') of the large unit can be seen prior to the last three pulses. Time cal., 20 msec. Potential cal., 2 mV.

DISCUSSION

If acoustic communication is examined with the intention of analysing behaviour in terms of its smallest functional parts, it is helpful to consider the system as a series of sequentially triggered units. 'Output' arises in supraoesophageal ganglion interneurons (Huber, 1960, 1962, 1965) and passes through premotor interneurons, motor neurons, muscle units, and skeletal movement to produce behaviour. The questions asked in this paper are how movements of the thoracic exoskeleton operate the stridulatory apparatus, how contraction of the muscles moves the mesothoracic exoskeleton, and how force production in the thorax is distributed in time and space by patterning of motor axon activity to produce and modulate stridulation.

Manipulation of the exoskeleton and direct or indirect stimulation of muscles yield relatively straightforward answers to the first two questions. Since muscle action potentials reflect fast-axon acitivity 1:1 in crickets, (Huber, 1965), chronic recording offers a fine tool for analysing ganglionic output patterns. It is worth examining its reliability critically. Chemical stains have been found to be precise indicators of electrode-tip position and, as shown by multiple electrode recordings, potentials can be assigned to muscles in which the tip is embedded. However, the time association of muscle action potentials and sound pulses remains to be fixed. If it can be assumed that the lag between the muscle action potential and the development of mechanical force is similar in the stridulatory muscles of the cricket and the flight muscles of the locust, the work of Neville & Weis-Fogh (1963) gives information on this period. There should be about 1 msec. from the muscle action potential to the onset of

mechanical contraction and 15–20 msec. to the peak. By this criterion the cricket potentials lead by the proper interval to produce the assigned activity. If the single loud pulse in courtship and the synchronous dorsoventral spike preceding it can be causally related, this also gives the correct time-lag. Finally, if both opener and closer activity are being recorded (Fig. 2C, *G. firmus*), the spike that occurs last should be associated with the last wing movement in a chirp (disregarding the possibility of a completely elastic return). Direct observation of stridulation, high-speed motion pictures, and Walker's (1962) analysis of calling show the last movement to be closing. Therefore, the final spike is from a 'closer' and again indicates the proper interval. This being determined, the final question is answered and one can be sure that potentials are being correctly interpreted.

The operation of the exoskeleton by the muscles during insect flight has been examined by a number of investigators. Wilson & Weis-Fogh (1962) have shown that the muscles involved in locust flight can be divided into groups producing upstroke and downstroke. The former is composed of the medial row of dorsoventral muscles, while downstroke is produced partly by elasticity and partly by the dorsal longitudinals and the lateral dorsoventral muscles, the subalars and basalars. Since these are the same two groups involved in stridulation and flight in the cricket, and since stridulation appears to have evolved from flight (Huber, 1962), if the homology between these two wing movements could be established it would indicate which group should be assigned to each stroke. Upstroke has now been shown to be homologous with closing and so one would expect the medial row of dorsoventral muscles to produce closing and the dorsal longitudinals, subalars and basalars to produce opening. Our studies have shown through several lines of evidence that this, excepting the bifunctional dorsal longitudinal, is the case. This conclusion is also supported by Huber's (1965) recordings of activity in the subalar and remotor muscles of *G. camp.* during stridulation.

The critical parameters of behaviour, stridulatory patterns and musculature are either very similar or identical in *A. domesticus* and the *Gryllus* species studied by us. It appears highly unlikely that differences in muscle function of the magnitude outlined in Table 2 could occur. Preliminary recordings from *A. domesticus* substantiate this since subalar activity conforms to the gryllid pattern. Therefore, we find that our results do not confirm those of Ewing & Hoyle (1965) pertaining to the role of muscles in stridulation.

SUMMARY

1. The neuromuscular mechanism of stridulation has been studied in four species of field crickets.

2. The operation of the exoskeleton has been investigated by direct and neuronal stimulation of muscles and by manipulation of the isolated exoskeleton; the wings are closed by lowering the tergum and opened by subalar, basalar and tergopleural sclerites acting outside the wing pivot.

3. Muscle action potentials recorded from freely moving animals during stridulation show the following:

(*a*) In the calling or aggressive song pulses, the closing stroke is produced by the medial dorsoventral muscles; the opening stroke is produced by the basalars and subalars.

(*b*) The 'tick' of the courtship song is produced by simultaneous contraction of the medial dorsoventral muscles; the subalars and some of the basalars are active during the soft pulse phase of the courtship song but not during the 'tick'.

(*c*) Evidently, the first dorsal longitudinal is active during the 'tick' and closing; the second is active in opening and in the soft pulse phase of courtship.

4. The upstroke of flight is homologous to the closing stroke of stridulation.

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REFERENCES

ALEXANDER, R. D. (1961). Aggressiveness, territoriality, and sexual behaviour in field crickets (Orthoptera: Gryllidae). *Behaviour*, **17**, 130–223.

CHOPARD, L. (1961) Les divisions du genre *Gryllus* basees sur l'etude de l'appariel copulateur. *Eos* 37(3), 267–87.

EWING, A. & HOYLE, G. (1965). Neuronal mechanisms underlying control of sound production in a cricket: *Acheta domesticus*. *J. Exp. Biol.* **43**, 139–53.

HOYLE, G. (1955*a*). The effects of some common cations on neuromuscular transmission in insects. *J. Physiol.* **127**, 90–103.

HOYLE, G. (1955*b*). Neuromuscular mechanisms of a locust skeletal muscle. *Proc. Roy. Soc.* B, **143**, 343–67.

HUBER, F. (1960). Untersuchungen über die Funktion des Zentralnervensystems und insbesondere des Gehirnes bei der Fortbewegung und der Lauterzeugung der Grillen. *Z. vergl. Physiol.* **44**, 60–132.

HUBER, F. (1962). Central nervous control of sound production in crickets and some speculations on its evolution. *Evolution*, **16**, 429–42.

HUBER, F. (1965). Aktuelle Probleme in der Physiologie des Nervensystems der Insekten. *Naturw. Rdsch., Stuttg.*, **18**, 143–56.

NEVILLE, A. C. & WEIS-FOGH, T. (1963). The effect of temperature on locust flight muscle. *J. Exp. Biol.* **40**, 111–22.

PIERCE, G. W. (1948). *The Songs of Insects*, pp. 111–12. Harvard University Press.

SNODGRASS, R. E. (1929). The thoracic mechanism of a grasshopper and its antecedents. *Smithson. Misc. Coll.* **82**, no. 2, 1–111.

WALKER, T. J. (1962). Factors responsible for intraspecific variation in the calling songs of crickets. *Evolution*, **16**, 407–28.

WIESEND, P. (1957). Die postembryonale Entwicklung der Thoraxmuskulatur bei einigen Feldheuschrecken mit besonder Berücksichtigung der Flugmuskeln. *Z. Morph. Ökol. Tiere*, **46**, 529–70.

WILSON, D. M. & WEIS-FOGH, T. (1962). Patterned activity of coordinated motor units, studied in flying locusts. *J. Exp. Biol.* **39**, 643–67.