THE FUNCTIONAL MORPHOLOGY OF SINGING IN THE CRICKET

H. K. PFAU AND U. T. KOCH

Fachbereich Biologie, Universität, D-67663 Kaiserslautern, Germany

Accepted 27 June 1994

Summary

We describe the functional morphology of the singing apparatus of the cricket. There are three main functional sections of song mechanics, which partly overlap: (1) preparation for singing (lifting of the wings) and the reverse process (lowering of the wings at the end of the song); (2) singing movements (closing and opening of the wings); and (3) movements that adjust the pressure of the plectrum on the file (engagement force).

In the case of song preparation, the mesotergum + first axillaries + second axillaries + wings form a functional unit. This unit is moved around a transverse hinge axis, which runs through both fulcrum joints. The muscles suitable for wing lifting are the prothoracic furca muscle and the mesothoracic tegula muscle. Those suitable for wing lowering are the prothoracic dorsolongitudinal muscles and the mesothoracic axillary 4, subalar and furca muscles. Lifting and lowering of the wings are superimposed by bistable mechanisms, which are adjustable (mesothoracic medial dorsolongitudinal muscles).

In the case of closing movements (dorsoventral muscles) and opening movements (basalar and subalar muscles), the mesotergum and the wings are moved relative to each other, as for flight movements, but with the wings remaining folded back. The mesotergum is rotated down (closing) and up (opening) around a transverse hinge axis that runs through the caudal joints between the mesotergum and postnota. The path of movement of the wing and its sound-generating structure (i.e. plectrum or file respectively) is determined by an obliquely oriented hinge axis between the mesotergum and first axillary. During opening and closing, the lifted singing position of the wings is stabilized by the medial dorsolongitudinal muscles. We also discuss the role of other muscles that affect singing movements.

The third axillary (and its muscle) and the postnotum [and its muscles, the furca muscle and the lateral (short) dorsolongitudinal muscle] are the main elements in the system that adjusts the engagement force of the wings. When left axillary 3 muscle contracts, the medial part of the left third axillary is rotated caudally (in its vertical hinge joint with the first median plate) against the anal part of the wing. The anal part is bent and rotated upwards, increasing the pressure of the left plectrum against the right file. Conversely, the right axillary 3 muscle, which moves the file away from the plectrum, is able to reduce the pressure. The left furca muscle (the antagonist of left axillary 3 muscle) and the left lateral (short) dorsolongitudinal muscle (the ‘synergist’ of left axillary 3 muscle), and the corresponding muscles on the right side (which have opposite functions), allow a large

Key words: skeletal mechanics, wing movements, muscle functions, adjustment mechanisms, evolution, cricket, Gryllus bimaculatus.
range of different engagement forces. The results are compared with the work of other authors on the functional morphology of this system and with the results of electrophysiological investigations. New aspects of the evolution of the singing mechanisms are discussed.

Introduction

Our present understanding of singing in crickets (more precisely in *Gryllus*, the genus most often investigated) is rather patchy. On the one hand, there are profound insights into physiological (particularly neurophysiological) principles, including the ultrastructure of the ganglia (for a review, see Huber *et al.* 1989). On the other hand, there are morphological studies (for a review, see Matsuda, 1970) and recent papers that describe mechanical aspects of the sound-generating structures (Nocke, 1971; Koch, 1980; Koch and Elliott, 1982; Elliott and Koch, 1985; Koch *et al.* 1988) and the sensory systems that control singing movements (Elliott, 1983; Elliott and Koch, 1983; Schäffner and Koch, 1983, 1987a,b; Schäffner, 1985). Until now, however, an essential link between these fields of knowledge, an analysis of the functional morphology of the cricket’s song apparatus, has largely been neglected.

The few (older) anatomical descriptions demonstrate a complicated mesothoracic musculature. However, the skeletal mechanisms activated by these muscles are treated only vaguely and the descriptions cannot sustain modern research. Work on this subject is complicated by the fact that many muscles in the thoracic system are polyfunctional: i.e. they may participate in singing, flying and/or walking. Therefore, experimental analyses of the cricket’s song urgently require detailed information, ideally about all the skeletal mechanisms of the thorax. Furthermore, one must take into account that there are three different types of songs, rivalry, calling and courtship, which could require different skeletomuscular mechanisms. The present study analyzes mechanisms that concern song initiation (lifting of the wings), the basic singing movements (closing and opening of the wings) and the fine adjustment movements of the wings. We also discuss some aspects of the flight posture and wingstroke of the forewings.

Materials and methods

The anatomy of muscles and skeleton was studied in *Gryllus bimaculatus* (De Geer) fixed in Bouin’s solution. For parallel studies of the skeleton alone, we used preparations macerated in KOH. The mobility of skeletal elements was tested on freshly killed animals. When stored in a refrigerator in a moist atmosphere, these preparations maintain their natural flexibility for several days. Some insights concerning the mechanical function of larger subsystems of the singing apparatus were gained by combining results obtained from smaller systems studied separately. To check these hypotheses, we used a larger preparation that consisted of the mesothorax of a freshly killed animal, which was waxed to a small support after all the soft tissues had been removed. This preparation permitted an unobstructed view of the inner and outer parts of the skeleton during movements mimicked by forces applied with a pair of forceps. Such preparations only lasted for a short time because the joints rapidly dried out.
In addition, hypotheses were checked using working models made from cardboard or using a Märklin metal construction kit. The models were redesigned and refined as our understanding of the anatomy progressed. Further progress is expected from the use of a set of custom-made joints (ball joints and hinge joints) that will be integrated with the Märklin parts.

Figures were prepared using a drawing program (MegaPaint II) running on an Atari Mega ST4.

**Results**

*Principal components underlying wing movements*

Fig. 1 shows an overview of the muscles and sclerites important in singing. The central...
element of the song apparatus is the mesotergum (TII) which, during singing, oscillates up and down between the pleura (PL; Figs 1, 2). At first glance, the forewing (tegmen) seems to articulate with the entire length of the mesotergum. However, the different regions of connection are not of equal importance. Most important for the singing
movements is one particular articulation between the mesotergum and the first axillary + wing, which is situated at the level of the fulcrum joint. This complicated joint is described below. During singing (but not during wing-lifting; see below), mechanical forces are transmitted perpendicular to the longitudinal body axis, from the mesotergum to the wing and vice versa through axillaries 1 and 2 (Ax1, Ax2; Figs 1, 2). The lower side of the second axillary articulates with the fulcrum joint, so the up and down movements of TII are transformed into downward and upward pivoting movements of the wing around point f. Axillary 1 therefore acts like a piston rod and transfers the linear motion of TII into rotations of Ax2 + wing. It also acts partly like a lever, since joint y between Ax1 and Ax2 (Fig. 2) is rather stiff.

The mesotergum (TII) is connected caudally to the metatergum (TIII) in a rather complicated way by an intermediate sclerite on each side: the vestigial (but functionally highly specialized) postnotum (PN, Fig. 1), which probably also contains the remains of the metathoracic prescutum. In a sagittal section, the postnotum has a V-shaped profile (Figs 3–5). There are two joints that connect PN to TII and to TIII: pn1 and pn2, respectively. These joints are point-like and permit movements characteristic of ball joints. Since pn1 is situated lateral and anterior to pn2, the postnota can act as levers in both the sagittal and cross-sectional planes (see below). Joints pn1 and pn2 permit rotational movements of TII (+ wings) relative to TIII, as well as rotational movements of TII relative to PN + TIII and rotation movements of PN itself (see below).

Anteriorly, the mesotergum (TII) is connected to the protergum by membranes and muscles that permit almost free motion of the front of TII.

The prescuta (PS), two narrow sclerites on each side, are connected to the front of the mesotergum. Several prothoracic muscles insert on the PS. Each prescutum is connected to the mesotergum by two joints, ps1 and ps2. There is a third (lateral) joint (ps3) between PS and the anterior flexible ‘horn’ of axillary 1, forming a rather flexible connection between PS and the base of the wing. This flexible connection is important because it permits the lateral end of the prescutum to follow different movement pathways during lifting of the wings and during singing movements (see below).
Fig. 3
Besides the prescutum–axillary 1 connection, there exist further rather flexible connections between the thorax and the wing. There is a tendon s1 (Figs 1, 3A) in the pleural region that originates from the basalar sclerite (BAS) and inserts on the ventral surface of the subcosta of the wing. There is a further ligamentous connection between the postnotum and axillary 3 (s2, Fig. 1; see Fig. 5).

The location and orientation of the individual muscles of the mesothoracic singing apparatus are illustrated in Figs 1–5. It should be mentioned here that the muscles that power the closing stroke of the wing are five dorsoventral muscles on each side, all of which insert onto the mesotergum; they therefore act indirectly. They have been collectively labelled dvm. All these dorsoventral muscles, as well as the basalar and subalar opener muscles [bas1, bas2, sub (except the weak basr, which is pleurosternal)], are tergocoxal and therefore bifunctional: i.e. they are also used for leg movements.

Since the main muscles responsible for the opening of the wing, the basalar (bas) and subalar (sub) muscles, insert onto the wing [bas 1 and 2 by the ligamentous tendon s1; sub by a cuticular tendon (SUB, Fig. 1)], they act directly. The wings are thus moved by an indirect–direct mechanism (Fig. 2), an unusual wing-moving mechanism in the Pterygota. It is also represented, for instance, in the flight mechanism of the Odonata (Pfau, 1986). For a functional interpretation of the (indirect) dorsolongitudinal muscles, see below and the Discussion.

Description of mechanical interactions between the different parts of the song apparatus

Initiation of song: lifting of the wings

At rest, the wings are folded back by flexion of the median plates (Snodgrass, 1935, p. 219f.). They are thus situated so close to the abdomen that singing movements are not possible. Therefore, they must first be brought into the singing position. This lifting activity is clearly different from the activity that prepares the wings for flight.

In the case of flight preparation, the wings are pulled forward and are positioned perpendicular to the body axis, in an approximately horizontal plane. The costal part (CP) and the anal part (AP) of the wing (see Fig. 5) are spread in this position such that they almost form a plane. Likewise, the median plates are spread (unfolded) and secured in this position by bistable mechanisms. The most prominent of these bistable mechanisms is represented by sclerites Ax3 and Ax2, and an elastic U-shaped sclerite (designated as the ‘cup-shaped part of the third axillary’, ‘o’, in Thakare, 1969) that lies between them. Sclerite Ax4 is a locking element. The same bistable mechanisms secure the wings in
their resting configuration in which they are folded back above the abdomen. Here also, Ax4 serves as a locking device.

When the forewings are lifted upwards for singing, the median plates remain folded as in the resting position, so the costal and anal parts remain at an angle of approximately 90° (see Fig. 5). During lifting of the wings into the singing position (Fig. 3), the mesotergum (TII) and the first and second axillaries (Ax1, Ax2), together with the entire wings, are moved as one functional unit. This whole ‘device’ is rotated around a horizontal transverse hinge axis defined by the fulcrum joints f of both sides. Thus, lifting of the wings is also a (‘pronatory’) tilting of the mesotergum. Although the two fulcrum joints (clad with a thick layer of resilin; Fig. 1) are functional ball joints, this property is not used during wing lifting, because both fulcrum joints here define a stable common rotation axis F/F (Fig. 3; c.f. Fig. 1). The reason for the strict coupling between TII and the wings during wing lifting lies in joints t1 and t2 between the mesotergum and first axillaries (Fig. 1; t1 and t2 are simplified to ‘t’ in Fig. 2), because these define (on both sides) hinge axes T1/T2 (Fig. 4), which are almost perpendicular to axis F/F. Therefore, when TII is tilted around F/F there is no relative motion between the wings and mesotergum at the t1/t2 hinges. Thus, the t1/t2 hinges are active only during singing (see below).

Fig. 3 schematically summarizes the roles of the muscles during wing lifting. Arrowheads are used to indicate muscle function: if an arrowhead is close to a moving part (i.e. to a part that moves with respect to another part) and points towards the moving part, then the muscle is stretched in this phase of the movement. If this muscle contracted tonically, it could adjust the amplitude of the movement, acting as a phase-specific antagonistic muscle. In contrast, shortening (passive compression) of a muscle means that this muscle could support this phase of the singing movement by contracting phasically.

Of all the muscles, fu I and teg have the most appropriate insertion points and directions of pull to cause wing lifting. It should be noted that these muscles are located far laterally (approximately in the sagittal planes of the fulcra) and therefore act on both the mesotergum and wings, moving these parts as a unit and not relative to each other (the muscles that cause relative movements of the mesotergum and wings are described below).

Muscles dlmI, ax4, sub and fu are suitable for lowering the wings into the resting position (Fig. 3B→A) (in this study, the different types of dorsolongitudinal muscles of the prothorax are all denoted as dlmI; see Fig. 1).

Lifting of the wings into the singing position (Fig. 3) is influenced by bistable effects. These are caused by the postnota, which connect the mesotergum (TII) with the metatergum (TIII), and the special positions of the two postnotal joints pn1 and pn2. When the mesotergum rotates around axis F/F, the circular path of its caudal edge exerts a force on the metatergum through postnotal points pn2 (which lie caudal to points pn1), pushing it caudally. The metatergum is slightly deformed and stores elastic energy. Since pn1 lies lateral to pn2, the caudal end of the mesotergum (which is arched in a cross-sectional plane; Fig. 1) is also slightly deformed laterally when it moves upwards. This second elastic component of the bistable mechanism is not shown in Fig. 3. On the other side of the unstable centre point of the movement (Fig. 3B), the elastic forces stored in the mesotergum and metatergum start to support the lifting movement, clicking the
Fig. 4. (A,B) Singing movements of the left wing. The left side of the mesothorax and the front of the metatergum are shown in a lateral view; the animal’s front is to the left. The transition from A to B represents wing closing: the sound-producing movement (muscles dvm). The transition from B to A represents wing opening (muscles bas, sub). The main movement axis T1/T2 is oblique. The hinge axis PN1/PN1 of the mesotergum points towards the observer. All shaded muscles may be involved in closing or opening movements, allowing for a wide range of velocities or amplitudes of movement, which may be bilaterally symmetrical or asymmetric. See Fig. 2 and text.
TI + wing unit into the position shown in Fig. 3C, in which it is stabilized by elastic forces. Of course, the bistable mechanisms also come into play when the mesotergum + wings are moved back into the resting position.

The elastic tension between the mesotergum and metatergum could be varied by tonic contraction of special muscles, dlm$m_1$ and dlm$m_2$ (Fig. 1; dlm$\text{n}$ in Fig. 3). These bilateral muscles act approximately in the sagittal planes of joints pn$2$, so they appear to be capable of adjusting the strength of the (first) bistable effect mentioned above.

In addition, wing lifting and lowering may be supported by a further bistable mechanism. Fig. 3 shows that the ligamentous tendon $s_1$ that connects the basalar (BAS) to the wing base (Fig. 3A; see also Fig. 1) moves relative to the rotation axis $F/F$ during lifting of the wing. In the lowered wing position (Fig. 3A), the basalar muscles therefore act to lower the wings, whereas in the lifted position (Fig. 3C) they act to lift the wings. Somewhere between these stable positions there must be an unstable tilt-over point. Thus, apart from being major muscles of the singing mechanism (see below), the basalar muscles seem to contribute to moving the wings into both the singing and resting positions. This hypothesis is supported by the finding that the musculature of the basalar consists of two main parts, bas$1$ and bas$2$ (see Fig. 1; the third, very small part, the rudimentary basr, is not considered), that appear differently coloured in the dissection. This different colouring could indicate a tonic wing-positioning function (bas$2$) and a phasic wing-opening function (bas$1$).

**Singing movements of the wings**

The basic singing mechanism is very similar to a flight mechanism, except that the wings remain folded back as in the resting position (Fig. 5) while they are lifted into the singing position (Fig. 3C). The mesotergum is moved (indirectly) upwards and (directly) downwards between the fulcra, while the wings rotate about their joints $f$ outwards (‘down’ = wing opening: Fig. 2B→A and Fig. 4B→A) and inwards (‘up’ = wing closing: Fig. 2A→B and Fig. 4A→B).

The first axillary (Ax$1$) is linked to the mesotergum by a complicated hinge joint. This joint is defined by joints t$1$ and t$2$ (Fig. 1). The anterior joint t$1$ is a hinge joint itself, with an axis running through the posterior joint t$2$, which is a functional ball joint. The axis T$1$/T$2$ of this whole hinge joint t$1$/t$2$ lies at an angle to both the sagittal and horizontal
Song mechanics of Gryllus
planes, running from ‘posterior–ventral–medial’ to ‘anterior–dorsal–lateral’ (Fig. 4; see also Fig. 1). As a consequence, the wing rotates around an oblique axis parallel to T1/T2 running through fulcrum joint f. The ball joint nature of the fulcrum joint permits this movement, just as it permits lifting and lowering of the wings around F/F (see above), but in the case of singing the stable unit consisting of TII and the wings no longer exists.

It is assumed here that the joint between Ax1 and TII, which is the most important joint for singing movements, represents a stable hinge axis (which, however, is moved together with TII during singing, see below). At first glance, it seems that a small membranous section of the anterior hinge joint t1 offers some play between Ax1 and the edge of the mesotergum (which is bent upwards in this region). During lifting of the wings into the singing position, however, Ax1 is pulled downwards in front of axis F/F (ful and teg pull on the wing through the Ax1 ‘horn’) and Ax1 is pressed tightly onto the surface of the mesotergum, while its edge slightly overlaps the upwardly bent edge of the mesotergum. Therefore, one cannot assume that the membranous play in t1 is actually used during singing: it is locked laterally by the mesotergal edge.

The precise path of motion of the mesotergum during singing remains problematic. During wing closing, TII could, in principle, move parallel to its plane in the downward–forward direction if TII were moved in both joints of the postnotum (pn1 and pn2). This parallel motion, however, is ineffective for closing the wings because of the existence and orientation of the t1/t2 hinge and because it is unfavourable with respect to the pulling direction of the dvm muscles. It must therefore be assumed that TII is rotated downwards at the pn1 joints, around an axis PN1/PN1. This motion corresponds very well to the pulling direction of the dvm (Fig. 4). During rotation of TII around PN1/PN1, hinge axis T1/T2 is moved together with the mesotergum, and its orientation is thus changed. Therefore, the main motion axis of the wing, running through fulcrum joint f parallel to the T1/T2 axis, is not fixed with respect to the animal, but is tilted during wing closure.

The anatomical structure of the postnota appears to permit the rotation of the mesotergum around axis PN1/PN1 as well as around axis PN2/PN2. Experiments using freshly killed animals, however, showed that the pn2 joints are inactive when the wings are in their lifted position, so that rotation of TII must be around axis PN1/PN1.

It is essential to investigate the forces acting on the mesotergum during singing and wing-lifting movements (see above). During singing, the opener muscles (bas, sub) work approximately in a cross-sectional plane containing the fulcra. This ‘neutral’ position of muscles bas and sub with respect to axis F/F comes about only after the wings are lifted (Figs 3C, 4A). The closer muscles (dvm) are more widely distributed along the length of the mesotergum (Fig. 1). In order to give complete balance, the muscles lying anterior and posterior to F/F should contract simultaneously during closing, with similar force. In this case, there is no net torque acting at axis F/F. This means that the power closer muscles would not affect the degree of wing lifting, and singing and lifting movements are mechanically decoupled. Since, however, muscles dlm contract phasically during both closing (dlm1) and opening (dlm2) of the wings (Bentley and Kutsch, 1966; Kutsch, 1969), one can assume that the caudally lifted position of TII [which is equivalent to the lifted position of wings (as described above)] is secured in both phases of wing motion, such that a precise balance of the muscle forces would be unnecessary.
Therefore, there is probably no risk that the triangle consisting of joints ps2–pn1–pn2 could flip down into the other stable position (Fig. 3A) even if the wings were lifted less (as in courtship song), because dlm\textsubscript{m1} is also activated synchronously with muscles dvm just before the ‘tick’.

The long medial dorsolongitudinal muscles therefore have special functions during singing. Bentley and Kutsch (1966) and Kutsch (1969) interpreted these muscles (dlm\textsubscript{m1}=81\textsubscript{a} and dlm\textsubscript{m2}=81\textsubscript{b}) as being antagonistic ‘wing closer’ and ‘wing opener’ muscles. This view, however, does not agree with the functional relationships shown in Fig. 4. According to our results, the mesotergum, which is lifted above the unstable middle position into the singing position, is moved by muscle dlm\textsubscript{m1} at joints pn1 and pn2 in such a way that the angle between TII and PN is reduced, while the angle between the PN and the phragma (PH) is increased (see Fig. 3B,C). This motion, however, does not contribute to wing closure, because it does not cause movement of the mesotergum relative to the wings at hinge joints t1/t2. Thus, muscle dlm\textsubscript{m1} mainly serves to secure the lifted singing position of the wing. In addition, it ensures that muscles dvm only rotate the mesotergum around one stable caudal hinge axis (PN1/PN1; see above). Muscle dlm\textsubscript{m2} has a similar function, securing the lifted wing position during the opening phase, especially when the prescutum is stabilized in its position by the muscle ful. Furthermore, muscle dlm\textsubscript{m2} could lower the prescutum and thus contribute to the opening motion (Fig. 4), because this movement causes a lateral rotation of Ax1 + wing (see the description of the function of muscle teg below). Therefore, although contracting phasically in different phases of the singing movement, muscles dlm\textsubscript{m1} and dlm\textsubscript{m2} must not be considered as antagonists. Rather, they act mainly as synergists.

In addition to the main singing muscles (dvm, bas, sub) and to the ‘tension’ muscles (dlm\textsubscript{m}), Fig. 4 shows a number of other muscles that influence the singing system. The figure shows which of these muscles are stretched or compressed during opening or closing of the wing. Arrows are again used to indicate muscle function (see Fig. 3). In most cases, however, there are no data available to show whether these muscles contract tonically or phasically, so we have marked all these muscles with oblique shading. The ‘tegula muscle’ (teg), for instance, could work as a set point muscle for the closing movement: during wing closing, the prescuta PS (Figs 1, 4B) are rotated upwards, because their anterior lateral joints ps3 are raised by the inward rotation of the first axillaries around T1/T2. Muscle teg is therefore stretched in this phase. If tonically contracted, teg would generate a counterforce to the closing movement, which would allow the amplitude and velocity of the movement to be adjusted. Since the prescuta on each side are mechanically independent of each other, this adjustment could be made separately for each wing. If phasically contracted, teg could support the opening movement of the wing.

The oblique orientation of the hinge joint axis T1/T2, described above, is very important for successful singing. If this axis lay parallel to the body’s longitudinal axis, the wing motion would be essentially a pronation–supination movement, since the wings, when folded back, are oriented nearly parallel to the body axis. This is illustrated in Fig. 2, which shows a very unfavourable configuration of the plectrum and file. In contrast, the oblique axis of wing rotation (running through f, parallel to T1/T2) causes
the plectrum (which is situated on the inner edge of the left wing) to move with a forward component during wing closure. In addition, because the plectrum (and the file) lie caudal to the fulcrum (Fig. 5), the oblique orientation of the axis of rotation means that there is a larger distance between the axis and the plectrum (and the axis and the file, respectively). This distance is much larger than could be attained with a rotation axis running through the fulcrum joint parallel with the body’s longitudinal axis. This distance causes the plectrum and file to move through an arc with a large radius. This permits continuous contact between the plectrum and file throughout a larger section of the motion pathway during wing closing movements. One could assume that plectrum and file stay in contact during the whole closing movement (in contrast to Fig. 2).

It should be mentioned that, if the wings are protracted into the flying position, the oblique hinge axis T1/T2 causes the wing to perform not a pure up-and-down flapping movement, but a composite downward + supination and upward + pronation movement (see Discussion).

Adjustment of the wing engagement force

Among other candidates, the axillary 3 system seems most likely to serve as the system that adjusts the pressure of the plectrum on the file (engagement force). The third axillary (Ax3, Fig. 5) is connected to the first median plate (MP1) by a hinge joint. When the wing is folded back, as in the resting or singing positions, axis Ax3/MP1 of this hinge joint is oriented almost vertically, but when the wing is in the flight position it lies in a horizontal plane at right angles to the body axis.

In Fig. 5, the complicated form of the third axillary (Ax3) has been simplified to show the relevant lever effects. Ax3 is connected to the fulcrum by muscle ax3, which lies lateral to axis Ax3/MP1. Muscle ax3 is presumably a homologue of muscle M85 of Dissosteira carolina and Locusta migratoria (Snodgrass, 1929; Pfau, 1983; Table 1 of Bentley and Kutsch, 1966, erroneously labelled ‘85a’ as a homologue of M85).

Medial to Ax3/MP1, the third axillary is connected to the wing’s anal part (AP) by an intermediate joint. The anal part of the wing carries the sound-generating structures: the harp, the file and the plectrum. In Gryllus, only the left plectrum and the right file (but both harps) are used for sound production and radiation. The third axillary works as a two-sided lever, transmitting muscle forces from its ventrolateral muscle insertion point to cause elastic deformation and rotation of the anal part of the wing. When muscle ax3 contracts, the ventrolateral end of the lever rotates forwards, while its dorsomedial end rotates backwards against the anal part of the wing, thus causing deformation and rotation of the anal part (Fig. 5B).

Whilst the deformation of the anal part can be roughly described as a change of the curvature of the front of the anal part, its rotation takes place in the discrete hinge joint between the costal and anal parts (movement axis CP/AP in Fig. 5). Thus, when ax3 contracts, the anal part is rotated upwards relative to the costal part. Both effects, i.e. the rotation as well as the deformation, cause the plectrum to rise (Fig. 5B). The first median plate (MP1) is stabilized in its position by elastic forces (forces that stabilize the flexed position of the median plates, see above), so it represents a sufficiently stable abutment for the pivoting movements of Ax3.
When muscle ax3 on the left side contracts more strongly, the left plectrum must be pressed more strongly against the right file from below, increasing the engagement force. When the right wing’s axillary 3 muscle contracts, the result is opposite because, in this case, the right file, which is actively used in sound generation, is moved away from the ‘active’ left plectrum. Thus, the left and right axillary 3 muscles can act to change the engagement force of the wings in opposite directions.

However, there are other muscles that work as synergists or antagonists of the axillary 3 muscles. Fig. 5 shows that contraction of muscle ax3 also moves the postnotum (PN). The postnotum is pulled forwards by tendon s2, which connects Ax3 and PN. As a consequence, the postnotum rotates antero-dorso-medially around the oblique axis formed by joints pn1 and pn2 (see Fig. 1). At the same time, the furca muscle (fu) is stretched, while the lateral dorsolongitudinal muscle (dlml) is compressed and passively shortened. If tonically contracted, muscle fu could therefore limit the action of ax3. This direct antagonistic effect is shown in Fig. 5A. In contrast, dlml could ‘loosen’ tendon s2 and thus increase the activity range of ax3. Muscle dlml thus has an indirect synergistic effect (Fig. 5B). This is the reason why information about the amount of contraction of muscles ax3 on both sides is not sufficient for an estimation of the effective wing engagement force. For example, muscles ax3 could contract symmetrically on both sides, but a stronger contraction of muscle fu on the right side could restrict the elevation of the right AP, while the left AP could be raised more strongly by stronger contraction of muscle dlml, causing an increased engagement force between the plectrum and file coming from both wings. When contracted phasically during wing closure, muscle fu can only have an effect during this phase of the wing movement. Otherwise, if contracted tonically, fu may again show phasic influence because its antagonist, muscle dlml, is coupled to the movement of the mesotergum and is passively shortened each time TII moves ventrally during wing closure (see Fig. 4B).

Several muscles of the wing adjustment system could take part not only in the lifting and lowering movements of the wing (Fig. 3) but also in singing movements (Figs 4, 5). It is therefore likely that the same sclerites might be used for different purposes in the different functional sections of the song mechanics. This overlap raises the question as to what degree these functional sections are independent of each other. During the inward–outward singing movements of the wing, the ventral end of the third axillary is moved mainly perpendicular to the direction of pull of muscle ax3, so we conclude that ax3 itself does not markedly influence the opening and closing movements. However, the system adjusting the engagement force depends indirectly on the degree of wing lifting: in the lowered wing position, the postnotum PN is rotated mediocaudally (Fig. 3A). Lifting the wing rotates PN laterofrontally (Fig. 3B,C). This loosens tendon s2 and creates clearance for the activity of muscle ax3. During singing, the postnotum is held in position by the activity of muscles dlmm1 and dlmm2, so the clearance for ax3 is maintained in both phases of the singing movements (see above). The actual effect of ax3 still depends on the activity of the muscles fu and dlml as described above.

There is a bilateral independence of the axillary 3 systems because the postnotum is divided into right and left sclerites (a derived feature within the Orthoptera; see Discussion). This bilateral independence makes muscles ax3, fu and dlml appropriate
unilateral adjustment muscles for the engagement forces of the wings (U. T. Koch and H. K. Pfau, in preparation).

Discussion

Until now, only a few papers have dealt with the functional morphology of the cricket’s song. Recent papers give only very crude information about the function of the mesothoracic muscles; for instance, Furukawa et al. (1983) report only that certain muscles elevate or depress the wing, or rotate a leg to the front or to the back. Our results, therefore, can be compared only with earlier papers (Voss, 1905; DuPorte, 1920) and with information given by Bentley (1966; see Huber et al. 1989).

DuPorte’s (1920) study is almost purely an anatomical investigation. His observations of the function of the mesothoracic musculature can be confirmed only in some aspects. He assumes that the muscle of the third axillary is a ‘depressor of tegmen’ and therefore an antagonist of the basalar muscles. We assume that DuPorte meant that muscle ax3 lowers the wing (which is lifted for singing) into the resting position. This finding does not agree with our functional analysis of the third axillary muscle. DuPorte (1920) generally subdivides all mesotergal muscles into two classes, ‘depressors’ and ‘levators’, depending on whether they lie anterior or posterior to the fulcra. More or less accidentally, this rough classification agrees with our results. DuPorte (1920), however, gives no additional information concerning the underlying skeletal mechanisms or the function of the muscles during song or flight.

Voss (1905) gives a much more detailed description of the function of the muscles. He states that preparation for singing consists of two acts: lifting of the wings and ‘spreading’ of the wings, which (in our terms) means an unfolding of the median plates, moving the wings forward towards the flying position. This forward movement seems not to reach the anteriormost position (Voss, 1905, pp. 676, 678). According to our results, however, the forewings cannot be used for singing even if they are protracted only half way into the flying position. According to Voss (1905), lifting and ‘spreading’ (i.e. protracting) of the wings into the singing position is achieved by a complex cooperation of different muscles. He states that the anterior dorsoventral muscles (‘präscutale Expansoren’, IIdvm5–6), the tergopleural tegula muscles (IIpm10,11) and the basalar muscles (‘episternale Expansoren’, pm1–3) are all engaged in this task. These statements agree only partially (e.g. in the case of the tegula muscles) with our results. According to Voss (1905), IIdvm5–6, IIpm10,11 and pm1–3 muscles are tonically contracted during singing.

Voss (1905) states that the sound-generating closing movement of the wings is caused by the axillary 3 muscles (IIpm12) as a folding-back movement of the wings (i.e. flexion of the median plates). At the same time, the subalar muscles (IIpm6) are said to press the anal parts (‘Analfeldplatten’) of both wings down, to engage the plectrum and file. Voss further states that the reverse (opening) movement (i.e. unfolding and re-squaring of the median plates) is caused by the ‘elastic’ pull of the tonically contracted basalar muscles (pm1–3). When the song ends, the lowering and complete folding back of the wings into the resting position is again stated to be ‘automatic’, caused by elastic forces which, in
this case, are generated by the elasticity of the skeleton (i.e. in the absence of muscle activity). Voss’ description of the mechanisms of the song apparatus is substantially different from our results. This is not surprising, considering the complexity of the system and the absence of electrophysiological information (such as the antagonistic activity of the main opener and closer muscles) at Voss’ time. We will therefore not discuss the numerous further differences between our results and those of Voss. Other parts of Voss’ (1905) paper remain difficult to understand, since it is mainly descriptive and contains only a few drawings explaining function.

The problems with Voss’ (1905) work and the lack of more recent analyses of the functional morphology of the song mechanics have left electrophysiologists without much help in interpreting their recordings. They have had to rely on analysis of the temporal patterns of their recordings and on observations of the functions of homologous muscles during flight. This led to several interpretations that do not agree with the results presented here. For example, Kutsch (1969) assumed that an increase in the activity of the dorsoventral muscles would lead to an increase of the wing engagement force and the loudness of the song. Nevertheless, the patterns of activity that Kutsch (1969) recorded agree with the results presented here. For example, the description of tonic activity of dlmI (58a, 58b) ‘only during courtship song’ agrees with our findings that the function of these muscles is to lower the wings from the lifted singing position. In fact, during courtship song, the wings are not lifted as much as in calling or rivalry song. The stronger tonic contraction of the left muscle ax3 (M85c, as shown in Kutsch’s Fig. 16) also agrees with our results (it would be useful to check whether this recorded asymmetry is the same in each preparation); in addition, however, information is needed on the activity of muscles dlmI and fu.

Bentley (1966) elaborated several details of the functional mechanics of the wings during singing, as shown schematically by Huber et al. (1989, Fig. 9.3). Bentley (1966) assumed that the second axillaries Ax2 (+ wings) move freely on the fulcrum. Our results do not support this mobility, since the hinge joints between Ax1 and the mesotergum (and between Ax1 and Ax2) do not permit it. Furthermore, the motion of the prescutum (tergopleural arm, TPA, in Bentley’s study) does not have the clearance claimed by Bentley, so muscles 58a,b and 81b (and ‘antagonistic’ muscles 49 and 81a) cannot turn the prescutum around a vertical axis through point ps2. Joints ps1 and ps2 permit movement only in a horizontal hinge axis oriented perpendicular to the body axis. Muscles 58a,b (=lateral dlmI) were claimed by Bentley to function as openers. This is not supported by our findings, which indicate that the influence of dlmI on the singing motion should be very small. If any effect could be observed it should support wing closing, since the prescutum is rotated upwards by contraction of dlmI (see Figs 3, 4). Finally, Bentley (1966) assumed that muscle fulI (M59) functions as a wing opener by pulling directly on the wing lateral to the fulcrum (similar to the action of muscles bas and sub). This cannot be confirmed by our results, since this muscle inserts laterally on the prescutum, at about the level of the sagittal plane of the fulcrum or slightly medial to it. The only way this muscle could contribute to an opening movement would be by lowering the prescutum relative to the mesotergum at the ps1/ps2 hinge (see Results for the similar effects of muscles teg and dlmI). However, because of its direction of pull, muscle fulI can turn the
prescutum much less downward than can, for example, muscle teg. Therefore, we assume that the main effect of a ful contraction is to lift the wing.

The long period separating Voss’ (1905) paper and later investigations of the functional morphology of the singing apparatus of the cricket is remarkable. Although there have been many papers dealing with the physiology of the cricket’s song, there have been few efforts to advance our knowledge concerning the underlying mechanisms by explaining the individual functions of the different muscles involved in singing. We think that the great mechanical complexity of the system, mainly concerning the function of the smaller, ‘unimportant’ muscles, reflects the evolution of the cricket’s song apparatus into an optimized system capable of efficient high-intensity sound production. These small muscles therefore belong to adjustment systems that have high adaptive value. It seems worthwhile continuing the functional, morphological and experimental research on these systems, especially with respect to their functional overlap.

A more precise analysis of the functional compromises in the singing apparatus could also lead to further insights into its evolution. We have no doubt that the development of the singing mechanism in the mesothorax of the cricket was at the expense of the ability to fly, because the mechanisms for wing lifting and singing both require mechanical decoupling of the mesotergum and the metatergum. The transformation of the mesotergum into a stiff plate also reduced the ability to fly, because the dorsolongitudinal muscles in the mesothorax could no longer power the flight movement by affecting the arching of the tergum. This means that the tergal arching mechanism (TWM, see Pfau, 1986, 1991), in which the dorsolongitudinal muscles are the main downstroke power muscles, was reduced: only the membranous indentations in the tergal margins at the positions of the first axillaries give an indication of the former ability of the mesotergum to be changed in curvature. These transformations were probably accompanied by another change that further reduced the ability to fly. This change was the development of a stable, oblique hinge joint (t1/t2) between the mesotergum and axillary 1, tightly coupling the wingstroke movement to a pronation–supination movement. In parallel with (i) the loss of the former ability to change the curvature of the mesotergum, (ii) the development of stable hinge joints t1/t2 and (iii) the decoupling of terga, the mesothoracic dorsolongitudinal muscles (dlnm1, dlnm2) acquired new functions as tension muscles between the mesotergum and metatergum. Thus, the former mesothoracic antagonism of indirect–direct downstroke and indirect upstroke flight muscles was transformed into a direct–indirect antagonism of song muscles. The postnotum, hitherto representing the supporting element of the tergal arching mechanism on the pleurum, was presumably freed in the course of these developments to achieve other important functions for singing. It was reduced in size, separated into right and left sclerites, suspended in a movable fashion and brought into close functional contact with the third axillaries. This made possible the differentiation of an efficient adjustment mechanism for the wing engagement force.

This rough reconstruction of the evolution of the complex song apparatus of the cricket shows that the skeletomuscular mechanics underlying singing cannot be derived in a simple way directly from the functions of flight, as had been suggested by an analysis of neural activity (Huber, 1962). This means that we are now able to understand the
evolutionary emergence of the song apparatus of *Gryllus* in more detail and in a new light.

**Abbreviations**

The abbreviations for muscles, tendons and joints are printed in small letters; abbreviations for axes and sclerites are given in capital letters. The axes are named according to the corresponding joints or neighbouring sclerites. In this paper, some muscle names were chosen because the muscles may be homologous with muscles of other groups of insects. However, the ‘tegula muscle’ (teg) and the ‘axillary 4 muscle’ (ax4) do not insert directly onto the tegula or axillary 4 in *Gryllus*. The terminologies of Voss (1905), DuPorte (1920) and Kutsch (1969) have been added in brackets.

**AP** anal part of the wing  
**Ax1** axillary 1  
**Ax2** axillary 2  
**Ax3** axillary 3  
**ax3** axillary 3 muscle [IIpm_{12,13}] [48] [85c]  
**Ax3/MP1** axis through the hinge joint between axillary 3 and the median plate  
**Ax4** axillary 4  
**ax4** axillary 4 muscle [IIpm9] [49] [85a]  
**BAS** basalar  
**bas 1, bas 2** basalar muscles 1 and 2 [IIpm_{1,2, IIpm3}] [41, 40a] [98, 103b]  
**basr** rudimentary (frontal) basalar muscle [IIpm_{14}] [46] [97]  
**CP** costal part of the wing  
**CP/AP** axis through the hinge joint between costal part and anal part  
**dlmI** dorsolongitudinal muscles of the prothorax [0dlm2, Idlm_{3a,b}] [4, 19, 20] [49, 58]  
**dlm1** lateral (short) dorsolongitudinal muscle of the mesothorax [IIIdlm_{3,4}] [XXXVI] [82]  
**dlm_{m1}** first medial dorsolongitudinal muscle of the mesothorax [IIIdlm1] [35] [81a]  
**dlm_{m2}** second medial dorsolongitudinal muscle of the mesothorax [IIIdlm2] [36] [81b]  
**dvm** dorsoventral muscles [IIdvm_{1,2,5,7}] [38–40, 45] [83, 89–91, 103a]  
**F** fulcrum  
**f** joint of the fulcrum; between the pleurum and axillary 2  
**F/F** hinge joint axis through left and right fulcrum joints f  
**Fi** file of the singing apparatus  
**fu** furca muscle of the mesothorax [IIism] [37] [117b]  
**fuI** furca muscle of prothorax [IIism] [21] [59]  
**gr** groove in the fulcrum  
**MP1** first median plate  
**PH** phragma between the mesotergum and metatergum  
**PL** pleurum  
**Ple** plectrum of the singing apparatus
PN postnotum
pn1, pn2 joints of the postnotum (between TII and PN, and TIII and PN, respectively)
PN1/PN1 hinge joint axis through the left and right postnotal joints pn1
PN2/PN2 hinge joint axis through the left and right postnotal joints pn2
PS prescutum
ps1, ps2, ps3 joints of the prescutum; between PS and TII (ps1, ps2), and PS and axillary 1 (ps3), respectively
s1 tendon between the basalare and wing
s2 tendon between the postnotum and axillary 3
SUB subalare
sub subalar muscle [IIpm6] [44] [99]
TII mesotergum
TIII metatergum
t joint between TII and Ax1
t1 anterior joint (hinge joint) between axillary 1 and the mesotergum
t2 posterior joint (ball joint) between axillary 1 and the mesotergum
T1/T2 hinge joint axis through t1 and t2
teg tegula muscle [IIpml] [47] [85b]
y joint between Ax1 and Ax2

We thank Professor F. Huber (Seewiesen) for his constant interest in this work. This study would not have been possible without the support granted by Professor U. Bässler (Kaiserslautern). We gratefully acknowledge funding by the Deutsche Forschungsgemeinschaft (Grants nos Ko 630/4-1 and Ko 630/4-2).

References


