Novel use of hair sensilla in acoustic stridulation by New Zealand giant wetas (Orthoptera: Anostostomatidae)

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Abstract

Sound production in New Zealand giant wetas (Orthoptera: Anostostomatidae) includes a femoro-abdominal mechanism, a ticking sound when alarmed (mechanism unknown) and, in two species (Deinacrida rugosa and Deinacrida parva), a tergo-tergal mechanism on the dorsal overlapping surfaces of abdominal tergites. The tergo-tergal mechanism consists of bilaterally paired patches of short curved spines on the dorsal anterior margins of tergites II–V, rubbed by opposing patches of articulated hair sensilla on the underside of each overlapping tergite. The latter are extremely robust, modified mechanoreceptors inserted at an acute angle onto raised bases which greatly restrict movement. They rub sideways against the underlying spines and produce sound during telescopic abdominal contraction which accompanies defence leg kicking stridulation. Movement analysis showed that the abdominal tergites contract asynchronously during stridulation. Sound is produced during both phases of telescoping. Femoro-abdominal sound comprises loud clicks of broadband sound principally below 10 kHz; tergo-tergal sound is a softer hiss spreading broadly from 10 kHz to the ultrasonic above 20 kHz. We propose that the tergo-tergal mechanism may have evolved under predation pressure by the ground gleaning short tailed bat endemic to New Zealand. The use of mechanosensory hair sensilla for sound production is rare in arthropods.

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1. Introduction

New Zealand wetas are flightless orthopterans (Anostostomatidae) comprising two subfamilies: Henicinae (ground and tusked wetas) and Deinacridinae (tree and giant wetas). All described species bear stridulatory mechanisms which are usually engaged during defence or alarm behaviour, although the tree wetas (Hemideina spp.) also utilise sound production in interspecific communication (reviews; Field, 1993, 2001a,b). The cuticular mechanisms involve a variety of frictional structures on body parts which are rubbed against each other. The following types have been documented: (a) femoro-abdominal, in which metathoracic femoral pegs or spines are rubbed against abdominal ridges or pegs; (b) mandibulo-mandibular, in which mandibular tusk bearing tubercles are abruptly opened while bearing against each other; (c) tergo-tergal, in which fine spines on abdominal tergites are rubbed together during abdominal telescoping. A further putative type, pleuro-coxal, involves minute spines on the hind coxa and on adjacent pleural segments, but this has not been shown to produce sound.

The tergo-tergal stridulatory mechanism occurs on several species of giant wetas in the genus Deinacrida, including: Deinacrida rugosa, Deinacrida parva and Deinacrida fallai. The original description (for D. rugosa) indicated that patches of small spines occur on the anterior dorsal margins of abdominal tergites III, IV, and V, and that these are overlain by opposing spines on the underside of the posterior margins of tergites II, III, and IV (Ramsay, 1953). Hissing sounds were reported during telescopic contractions of the abdomen when the insects were disturbed. An additional report of a tergo-tergal stridulatory mechanism was given for the endangered Deinacrida heteracantha (Richards, 1973), but apparently the full complement of structures is lacking and it is unclear if the mechanism is operational.

We re-investigated the tergo-tergal mechanism for
Deinacrida rugosa and D. parva. We report the discovery of elaborated cuticular structures lacking in the original description, including unusual highly modified hair sensilla which subserve a stridulatory function. Furthermore we present behavioural, mechanical and acoustic analyses of tergo-tergal stridulation by D. parva, as well as an evolutionary rationale for the mechanism.

2. Methods

Descriptions of cuticular structures were made from specimens of D. rugosa \((n = 6)\) and D. parva \((n = 3)\) preserved in 70% ethanol. Visual microscopy and camera lucida tracings were enhanced by staining and clearing excised cuticular regions in 0.1% lignin pink in Amman’s lactophenol. For scanning electron microscopy, cuticle was rehydrated, sonicated in mild detergent solution, transferred through 70, 95 and 100% ethanol to 100% acetone air dried and mounted on stubs with double sided tape. They were sputter coated with gold–palladium and photographed with a Cambridge S600 scanning electron microscope.

Behavioural and acoustic studies were made from two adult D. parva (captured in their native habitat and subsequently released in the same location) and two adult D. rugosa maintained in captivity in the Wellington Zoo. Both are rare and endangered species and are under the protection of the Department of Conservation of New Zealand. Defence behaviour was recorded with a Panasonic GR-DVL9800 digital video camera and subsequently analysed on a Cambridge S600 scanning electron microscope.

An additional modification was found on the intertergite arthrodial membranes of tergites I–VI in both species. This consisted of roughly parallel transverse cuticular ridges \((tcr)\) near the attachment of the membrane to next posterior tergite (Fig. 2A). These ridges were more strongly developed in D. parva than in D. rugosa but in both cases they were covered with micropogs. These pointed pyramidal pegs ranged in width from 10 to 26 \(\mu m\).

A possible adaptation for acoustic amplification of sound from the tergo-tergal mechanism is a marked inflation of the posterior margins of tergites II, III and IV (Fig. 1A, and shown diagrammatically in Fig. 2C). This feature is lacking on non-stridulatory tergites, as well as in Deinacrida species which lack the tergo-tergal mechanism. The inflated margins are filled with tracheal space and could act as reverberatory chambers, as found in the abdominal anatomy of most cicada species.

3. Results

3.1. Cuticular structures

A superficial view of the dorsal surface of the abdominal tergites of both species reveals a bilaterally arranged pair of patches of tiny spines on the anterior margin of tergites II, III, IV, V and VI (white arrows, Fig. 1A). Sparsely distributed spines are also found on the dorsal surface of tergite I. The spines in all patches are approximately 100 \(\mu m\) long, narrow and curved over so that the upper side, rather than the apex, is presented to opposing cuticular structures (Fig. 1B). On tergites III, IV and V the spines are extremely densely packed (approximately 350 mm\(^{-2}\)) and are slightly flared at the base, presumably for structural reinforcement (Fig. 1C).

The spines are rubbed by structures on the underside of the posterior margins of tergites II, III and IV. While originally described as short translucent spines (Ramsay, 1953), we show that these are actually highly modified and robustly constructed hair sensilla. They occur on the arthrodial membrane between pairs of tergites rather than on the cuticular under-surface of the tergite posterior margin. They are more sparsely distributed than the spines (approximately 50 mm\(^{-2}\), Fig. 1D). Each hair sensillum is articulated in a stout base mounted on a raised mound; the sensillum projects from the articulation at an acute angle and appears to have highly restricted lateral and vertical movement (Fig. 1E). The ‘hair’ is modified into a thick and robust blade-like structure approximately 75 \(\mu m\) long, with a narrow upper edge (Fig. 1E and F). Thus, opposing tergal spines and hair sensilla rub against edges rather than apices of the respective structures.

Because the opposing hair sensilla only occur on tergites II, III, and IV, the tergo-tergal stridulatory mechanism is restricted to tergite pairs II–III, III–IV and IV–V. It appears that the additional dorsal spine patches on the anterior margins of tergites I and VI are not involved in sound production.

3.2. Mechanical interaction

The orientations of spines, hair sensilla, and path of travel of these opposing structures were examined by removing and unfolding the overlapping cuticle of two adjacent tergites plus the intervening arthrodial membrane. A camera lucida drawing (Fig. 2A, left half) of one such preparation shows that the structures are oriented with apices approximately facing medially (Fig. 2A, right half). The hair sensilla tend to face posteriorad in vivo, while the spines face transversely except for those near the midline, which face progressively posteriorad. By superimposing traced drawings of the hair sensilla onto the spines in the overlapped, in vivo configuration, it was possible to determine the orientation of the travel path of hairs over spines. This
varied from co-axial orientation to a deviation of up to 45° between the long axes of the interacting structures (Fig. 2D). It is clear, however, that the components generally rub sideways across each other to generate mechanical vibrations for sound.

It was of interest to determine whether the transverse ridges and micropeds on the arthrodial membranes could contact the tergal spine patches and participate in sound production. This was estimated by first measuring the distances of the components and
Fig. 2. Mechanical properties of tergo-tergal stridulatory mechanism. (A) Camera lucida drawing of cleared preparation with normally overlying arthrodial membrane reflected anteriorad (toward top). Stridulatory hairs (top field) and tergal spines (bottom field) shown on left side, and orientation of apices on right side shown by arrows. Horizontal lines indicate tcr covered with micro pegs. Line ‘x–y’ indicates transect measured for model reconstruction in (B–C). (B) Transverse section of diagrammatic reconstructed preparation. Measurements give widths of hair/spine regions and gaps between regions. Thick lines: tergites; thin line: arthrodial membrane; ovate symbols: stridulatory hairs; small bumps: transverse ridges; triangles: tergal spines. (C) Employment of model to reconstruct stridulatory structure overlap in fully extended position (top) and fully contracted position (bottom). Note ineffective amount of micropeg overlap onto tergal spine patch. (D) Composite drawing of axial orientation of stridulatory hair sensilla (white) and spines (shaded) during stridulatory movement (arrows).
3.3. Movement co-ordination of abdominal tergites during stridulation

All three modes of stridulation usually occur while the weta displays the raised-leg defence posture (Fig. 3A). In this highly aroused state, visual, acoustic or tactile provocation elicit a downward sweep of the hind legs which rub against the abdominal ridges to produce loud femoro-abdominal click sounds (Field, 1982). Simultaneously the abdomen is repeatedly telescoped inward and outward to produce tergo-tergal hissing sounds. Lateral views (video) of the wetas showed that the movements consist of dorsal contractions without concomitant ventral contractions of the tergites (Fig. 3B and C). Contractions last from a few hundred ms to about 1.5 s.

The co-ordination of abdominal tergite displacement during sound production was analysed by marking the posterior margin of abdominal tergites I–VI on digitised video frames (Fig. 3D) and then measuring the changes in position of marks during sequential frames. Two questions were addressed: (a) do all abdominal tergites contract against each other or do only those bearing stridulatory structures undergo mutual rubbing? (b) do the tergites move in phase (synchronous contraction of the whole abdomen) or is their displacement more complex?

The data are presented as progressive displacement of each posterior tergite margin relative to that of abdominal tergite I (Al, Fig. 3E (parva), F (rugosa)). One cycle of telescoping is plotted for each species, although eight cycles were analysed from different episodes of the four animals tested. The following trends were seen in all analyses. First, relative movement of tergites against each other only occurred in the first five tergites. Tergite VI maintained a rather constant distance from tergite V and therefore did not participate in stridulatory behaviour (which is consistent with the lack of a V–VI stridulatory mechanism). Second, tergite II usually showed the least displacement. Third, there was not a simple synchronous movement of all tergites during stridulation. Instead, tergite II, or II and III, usually extended (often differentially and thus producing II–III sound), while tergites IV and V contracted inward (often out of phase with II and III). The effect was to produce III–IV and IV–V sound which outlasted the II–III sound. The full cycle therefore usually consisted of a two-phase non-synchronous set of movements (best seen in Fig. 3F) of tergites bearing the sound-producing mechanism, while more posterior tergites did not participate in telescoping. Instead they were passively displaced as the more anterior tergites caused inward telescoping of the abdomen. A further observation is that sound was produced on both inward and outward telescopic movements, inasmuch as velocities were similar in both directions. There was no difference in sounds made by both movements.

3.4. Acoustic analysis

During the defence display, ticking sound production was recorded continuously with little change in rate (small regular pulses, Fig. 4A). Slight tactile stimulation of giant wetas in this posture readily elicited the leg-kick and associated sounds. In Fig. 4A, the largest recorded sounds during two leg kicks represent loud femoro-abdominal clicks, while the prolonged low-amplitude records represent tergo-tergal hisses. The latter usually occurred simultaneously with the femoro-abdominal clicks, as shown in a higher speed trace (Fig. 4B). Here the low level hiss preceded three femoro-abdominal clicks. Occasionally isolated tergo-tergal sounds were recorded. It was then apparent that such sounds were composed of many small pulses of differing sizes (Fig. 4C), as expected from the morphology of the associated stridulatory structures. Note that the record in Fig. 4C includes a second short tergo-tergal hiss following the major one. When single click events from both sounds were displayed with a rapid time base, they showed damped waveforms which indicates the absence of cuticular resonance. The femoro-abdominal clicks were most rapidly damped (Fig. 4D), while those of the tergo-tergal sound were more slowly damped with a shorter period (Fig. 4E).

Spectral analysis was performed using spectrograms and frequency spectra. Both types of sounds were broad-band, which is characteristic of frictional mechanisms. However, isolated tergo-tergal spectra usually had most acoustic energy distributed above 10 kHz (Fig. 5A). It was not possible to record isolated femoro-abdominal clicks, hence we compared the above spectra with those from combined sounds during leg kicks (Fig. 5B). In such examples, the femoro-abdominal clicks added a major broad-band energy component below 5 kHz. The low frequency component of the clicks is particularly noticeable in the spectrogram (Fig. 5B) where the largest femoro-abdominal clicks are linked by arrows from the bottom trace.

3.5. Potential selection pressure from bats

The production of a significant component of ultrasound by the tergo-tergal mechanism may be related to predation by bats. In New Zealand, the short-tailed bat Mysticeta tuberculata preys upon anastostomatids as well as other
ground, and aerial, insects. In a sample of 200 *M. tuberculata* faeces, McCartney and Lloyd classified 18.5% of invertebrate fragments as Anostostomatidae (personal communication, 2002). These remains may well have included henicine ground wetas (*Hemiandrus* spp.), which burrow in the soil. In addition, McCartney found that *M. tuberculata* in captivity readily attacked and ate tree wetas (*H. crassidens*) which were offered, even though the wetas weighed about a third the weight of the bats (6 vs 18 g, respectively). Thus the size of ground dwelling
Deinacrida species (especially nympha! instars, which also produce sounds) is not likely to be a deterrent to bat predation.

4. Discussion

4.1. Morphology

In general, stridulatory structures in insects comprise cuticular ridges, pegs, tubercles and non-articulated spines. These arise from almost any external surface of the body where the protruding cuticular structures can rub against opposing ones (Dumortier, 1963). Normally these structures do not appear to be innervated, and presumably peripheral sensory control of stridulatory movements is mediated by exteroceptors in the region of the stridulatory mechanism. In crickets, for example, nearby hair plates provide regulatory feedback to control wing separation during singing (Elliot and Koch, 1983). In New Zealand wetas, none of the previously described stridulatory structures shows evidence of innervation as a mechanosensory structure. However, scanning electron micrographs indicate that filiform hair sensilla and campaniform sensilla occur at the base of stridulatory pegs and ridges (Field, 2001a). Presumably these serve to signal contact during stridulation and to promote movement co-ordination. We show for the first time that highly modified hair sensilla in wetas serve as sound-producing structures, as well as (presumably) sense organs.

The morphological adaptations of the hairs which promote sound production include (a) a raised, partially enclosing articulation collar which greatly limits the motion of the hair, (b) modification of the hair into a thick blade which is stiff and (c) a cantilevered position of the blade so that its edge is used as a scraper. These features allow each hair to act as a plectrum against the profuse spines on the anterior tergite surfaces. The relatively firm mounting of the hairs and stiff structure ensure that they provide sudden catch-release events as they move laterally across the spines.

Articulated hair sensilla are rarely used in arthropod sound production. Presumably this is because hair sensilla are usually freely moveable within the basal articulation and are not suited as stiff structures for sound emission. Some exceptions have been noted. The aphid Toxoptera rubs short, possibly articulated hind tibial hairs against the 5th and 6th abdominal segments, while the dipteran Dacus has a row of some 20 bristles (apparently articulated) on the 3rd abdominal segment, which rub against the wings to produce short bursts of sound (Dumortier, 1963). In the freshwater crab, Potomon africanum, coxal bristles rub against a patch of marginal bristles on the branchiostegite (Guinot-Dumortier and Dumortier, 1960). The latter are inflated hairs which appear to be articulated. However, the best known example of articulated hairs modified for sound production is found in the peg row on the metathoracic femur of many grasshopper species in the Gomphocerinae (Jacobs, 1953). Here the pegs serve as sound-producing structures which rub against the forewing median radial vein, and are clearly derived from thin, articulated hairs occupying the same location in early instars. The pegs share some of the features noted for the stridulatory hairs of the wetas: a swollen articulation collar limits movement to about 20° and the hair is morphologically strengthened and stiffened. It is modified from a narrow, tapering shaft in early grasshopper instars to a thick peg resembling a pointed mushroom in fourth instar and older males (Hustert et al., 1999). The peg morphology differs amongst the eight genera and 24 gomphocerine species, and is reduced in females in all cases (Jacobs, 1953).

4.2. Sensory role

The significance of articulated, sound producing pegs and hairs is that they also are innervated mechanoreceptors (Hustert et al., 1999). In grasshoppers they signal onset and offset of contact, and rate of movement and pressure of the femur against the wing vein. Their afferent input activates an inhibitory reflex onto one of the leg muscles (Hustert et al., 1999). While other proprioceptors and mechanoreceptor organs may respond to stridulatory movements incidentally, only the femur pegs unequivocally signal ongoing mechanical parameters during stridulatory mechanism engagement. Although the robust hairs of giant wetas have not been analysed histologically for innervation (due to the protected species status), it is almost certain that they too are innervated mechanoreceptor sensilla. This follows because all articulated hair sensilla that have been investigated histologically are innervated by one or more
sensory neurones. It is likely that the weta hairs are involved in feedback control of the motor pattern for tergo-tergal stridulation.

4.3. Role in communication

A previous study (Field, 1982) has shown that the spectral emission band of giant weta species is much wider than that of tree wetas (Hemideina spp.). Sounds from both genera are clearly audible to humans, but for three species of Deinacrida, sound spectra also include ultrasonic frequencies (>20 kHz). While both weta genera use various forms of femoro-abdominal stridulatory mechanisms, the spectra obtained from the above study included sounds from all stridulatory mechanisms used by the recorded specimens during defence behaviour. Some of the energy must have included the tergo-tergal sounds for those Deinacrida species which contain this additional stridulatory mechanism. The published spectrum of D. rugosa had a broad peak from 8 to 25 kHz. Because we could characterize the

Fig. 4. Acoustic recordings from D. parva during defence behaviour. (A) Ongoing ticks are produced during the defence posture at about 4 s⁻¹. Two kicks of the upraised hind legs are accompanied by loud femoro-abdominal clicks and more prolonged, softer tergo-tergal hisses. (B) 20 × expanded sweep of sound recording during single defensive leg kick (different individual). Three loud femoro-abdominal clicks show a lower frequency (longer) waveform than the small high frequency ongoing tergo-tergal sounds, which precede the clicks in this case. (C) Isolated tergo-tergal sound recording showing lack of cyclic pattern during abdominal telescoping. A second short abdominal contraction produced a second brief sound burst. (D) High speed record of two femoro-abdominal clicks showing how the waveform is rapidly damped (period equivalent to 7.3 kHz). (E) Single tergo-tergal click isolated from end of a recording such as that in (C). Damping is less and period is shorter (thus higher frequency, 16 kHz) than clicks in (F).
frequency content of isolated tergo-tergal sounds and showed that they contribute frequencies mainly > 10 kHz, we conclude that much of the ultrasound arises from this mechanism.

It is of interest to explore why some giant wetas evolved this high-frequency stridulatory mechanism. While behavioural studies specifically focussed on giant weta communication are lacking, there is no evidence that sounds produced by species of *Deinacrida* are used in intraspecific communication (Gibbs, 2001). Thus, the role of sound production in giant wetas appears to be interspecific, and limited to predator deterrence.

Documented predators which are likely to have imposed evolutionary selection pressure on giant wetas include harriers (*Circus approximans*), the brown kiwi (*Apteryx australis*), and the tuatara (*Sphenodon punctatus*) (Gibbs, 2001; McIntyre, 2001). All of these animals hear well in the audio band (< 20 kHz), and it is unlikely, but unknown, whether they hear ultrasound (a likely candidate species, the night flying storm petrel *Hydrobates pelagicus*, was found...
to lack ultrasonic signals (Ranft and Slater, 1987)). Most birds hear well up to 10 kHz, and owls hear up to 12 kHz (Warham, 2002). However, New Zealand has one endemic candidate predator which communicates very well in the ultrasonic band: the short-tailed bat M. tuberculata. We propose that this species contributed selection pressure on deinacridine wetas to develop an acoustic deterrent with ultrasonic emission. The short-tailed bat produces pulses with up to three sliding harmonics; the peak fundamental frequency ranges from 20.37 to 38 kHz, with some spread on either side in individual spectra (Parsons, 1997). Since the pulses are used for prey echolocation the bats must hear their own emissions and echoes.

Moreover, short-tailed bats are unusual in that they are surface gleaners which spend large amounts of time hunting and resting on/in the ground litter and adjacent tree trunks (Daniel, 1979). They are likely to have encountered deinacridine wetas (especially the lowland ground dwelling giants D. rugosa and D. parva) while hunting. The use of sudden bursts of audible sound is known to serve as a deterrent against birds which prey upon tree wetas (Field, 2001b), and the same may apply to the use of ultrasound against gleaning bats at night. Other insects, notably lepidopterans and coleopterans, utilise ultrasound emission as a defence against predation by bats (Fullard et al., 1994; Simmons and Connor, 1996; Yager and Spangler, 1997; Greenfield and Weber, 2000).

Henicine wetas and tree wetas seek protection from predators by occupying burrows or tree galleries which are impenetrable by bats, while D. rugosa and D. parva move under rocks or logs for protection (Gibbs, 2001; McIntyre, 2001; personal observations). The arboreal Deiancrida tend to hide in clumps of dead leaves on trees. However, all species emerge at night to forage on leaves or plant matter, and the ground dwelling species are most likely to be at risk from predation by short tailed bats crawling on the ground. We note that ground dwelling henicine wetas also have a large variety of tiny, femoro-abdominal stridulatory structures which may also produce ultrasound (Field, 1993), and may also have been driven by the same selection pressure.

References


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