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Elasticity and movements of the cockroach tarsus in walking

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Abstract Anatomical, kinematic and ablation studies were performed to evaluate the contribution of elasticity in use of the cockroach tarsus (foot) in walking. The distal tarsus (claws and arolium) engages the substrate during the stance phase of walking by the action of a single muscle, the retractor unguis. Kinematic and ablation studies demonstrated that tarsal disengagement occurs at the end of stance, in part via the action of elastic elements at the penultimate tarsal joint. In isolated legs, this joint exhibits very rapid (less than 20 ms duration) recoil to extension when released from the engaged position, and recoil is even more rapid (less than 10 ms) after removal of the retractor tendon (apodeme). The joint also possesses an enlarged cuticular condyle which is the attachment for ligaments and articular membranes, some of which fulfill morphological criteria consistent with the presence of the elastic protein resilin. Measurements of restoring forces generated by joint displacement indicate that they are graded but could readily lift the mass of the distal tarsus. This biomechanical design can facilitate efficient use of the tarsus in walking while under active control by only a single muscle and may also be highly advantageous when cockroaches very rapidly traverse irregular terrain.

Key words Insect · Walking · Elasticity · Tarsus · Joints

Introduction

Elastic elements are now widely viewed as being inherent biomechanical features of appendages used in locomotion of both vertebrates and invertebrates (for review: Alexander 1988; Gronenberg 1996). Elasticity in muscles (Rack and Westbury 1974), tendons (Lochner et al. 1980; Ker 1981), ligaments (Ker et al. 1987) and joints (Alexander et al. 1985) allows these structures to act like springs and exert passive, reactive forces when subject to deformation, and then return to their original shape after recoil. This process permits the storage and release of energy during the step cycle in walking, and it is essential to the efficient performance of rapid locomotion, such as running, galloping or hopping (Farley et al. 1993). Despite considerable anatomical diversity of size, skeletal composition, joint structure and muscle types, the sum of the elastic properties of these structures have permitted the legs of many types of animals to be effectively modeled as springs (Blickhan and Full 1993).

In many systems, specific elastic structures at joints are used as partial or complete antagonists to the active contractions of skeletal muscles (e.g., nuchal ligament of neck, Dimery et al. 1985; wing hinge of dragonfly, Weis-Fogh 1961). The use of elastic membranes or ligaments offers several discrete advantages as substitutes for skeletal muscles performing similar functions (Alexander 1988). First, elastic elements minimize mass (inertia) and conserve metabolic energy, as spring-like structures can be quite light and do not require oxygen or nutrients to function. Second, these elements can generate very rapid movements because, as noted by Gronenberg (1996), the 'greater speed of elastic recoil can overcome the temporal limitations inherent in the contraction of skeletal muscles'. The use of elastic antagonists is also computationally efficient, in that they do not require the precise timing needed for the activation of motoneurons to skeletal muscles that alternate in contractions during rapid repetitive movements. Lastly, although the forces that these structures generate are passive and not under

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independent control by the nervous system, inherent elasticity in muscle tendons and joints can also simplify the problems of feedback control of force in response to perturbations (Rack and Ross 1984).

We have performed anatomical, kinematic and ablation studies to identify and evaluate the functions of elastic elements of the joints of the cockroach tarsus (foot) in walking (Roth and Willis 1952; Arnold 1974). The tarsus contains no intrinsic musculature and movements of the tarsal segments are actively generated by contractions of the single retractor unguis muscle (Radnikow and Bässler 1991). This muscle is located in the proximal leg segments and has a tendon (apodeme) which traverses the tarsus to insert upon the claws and arolium (Wood and Usherwood 1979; Kendall 1970). The retractor muscle depresses these structures and engages them with the substrate (Laurent and Hustert 1988; Wolf 1992), an action that provides stable contact when the animal stands or walks over a variety of terrain (Roth and Willis 1952). The opposite movements of disengagement/elevation are thought to be produced by forces generated by elastic structures in the leg that are stretched during claw engagement (the retractor contraction) (Walther 1969). However, the movements of the tarsus that occur during walking had not been documented nor had locations or specific actions of structures that generate lifting of the tarsus been established. These problems gave impetus to the present studies.

We have utilized an approach to identify and study elastic properties of the tarsal joints that is similar to that used by Weis-Fogh and colleagues in their early studies of insect flight mechanisms (Weis-Fogh and Jensen 1956; Jensen and Weis-Fogh 1962), that is, to characterize these properties in isolated preparations and to compare them with the behavior of intact animals. In locusts, Weis-Fogh (1961) found that the wings in an isolated thorax spontaneously are fully depressed, a position that occurs at the end of a power stroke in flight. Force must be applied to raise the wings to an elevated position, and they exhibit strong elastic recoil when released and very rapidly return to the depressed position. The ability to recoil elastically is retained even after the wing muscles are removed and is therefore an inherent property of the wing joint. This type of analysis, and similar classic studies done in dragonflies, permitted Weis-Fogh to analyze the mechanical properties of the elastic structures associated with the wing joints and led to the identification of the nearly perfectly elastic protein resilin (Weis-Fogh 1960; Anderson and Weis-Fogh 1964; Young and Bennet-Clark 1995), which forms an integral component of the flight mechanism (Weis-Fogh 1959, 1961; Jensen and Weis-Fogh 1962).

Using similar methods, we have confirmed incidental observations of previous authors (Roth and Willis 1952; Arnold 1974) that the tarsus of the cockroach assumes a characteristic default position when denervated or severed from the body, in which the intrinsic joint between

the fourth and fifth tarsal segments (Ta4–Ta5 joint) is greatly elevated (extended). Videotapes of animals during walking have shown that rapid extension of the fifth segment occurs at the end of the stance phase and that the joint is normally held extended during swing. Experiments on isolated legs have shown that the distal tarsus rapidly recoils to this position following passive displacement, through the action of elastic elements associated with the Ta4–Ta5 joint.

The novel aspects of our findings are that (1) distortion of stiff elements of the joint (retractor unguis tendon apodeme) is not requisite for recoil, unlike the mechanism demonstrated for the generation of the locust jump (Heitler 1977), (2) tarsal extension utilizes spring-like properties of the joint ligaments and does not involve a catch mechanism (Heitler 1977; Gronenberg 1996), and (3) the central ligament of the joint, which alone is capable of generating recoil, fulfills the criteria for the presence of resilin (Anderson and Weis-Fogh 1964). We believe this is the first evidence for the presence of resilin as a functioning element in generating movements in intrinsic joints of the leg of an insect. In the course of these sequential studies, we have also shown that the pulvillus (tarsal pad) does not produce recoil through an hydraulic effect.

During walking this elasticity can function to (1) help disengage the contact of the claws with the substrate when the retractor muscle relaxes, and (2) substantially lift the fifth segment, claws and arolium, as a whole, away from the walking surface. This biomechanical design can facilitate the rapid and efficient use of the tarsus in walking while under active control by a single muscle. It may also be considerably advantageous when cockroaches traverse irregular terrain.

Materials and methods

Anatomical studies

The internal and external structures of the tarsus were studied in dissected or wholemount preparations by light microscopy and by examination of the endogenous fluorescence exhibited by the cuticle under UV illumination. For examination by conventional light microscopy, the distal tarsus was severed from the leg at the first tarsal segment and immersed overnight in 4% formalin fixative. Preparations were then either submerged in an aqueous clearing agent, iohalamate meglumine (Conray, Mallinckrodt) for 1 day or dehydrated in a graded series of ethanol solutions and embedded in Permount. Specimens were viewed in an Olympus BH microscope and images were captured on computer through a Cohu 4995 CCD camera using a Matrox Meteor frame-grabber board. To examine UV fluorescence characteristic of resilin (Anderson and Weis-Fogh 1964), the distal leg segments were simply severed or disarticulated (as described below) and placed on a slide on the stage of a conventional Nikon Microphot-5A microscope. They were then viewed and photographed (Kodak Ektachrome 320T film) under fluorescence illumination using a UV2A filter block (excitation 330–380 nm, dichroic mirror 400 nm, emission greater than or equal to 420 nm). Resilin containing structures emitted a distinct blue fluorescence which differed from that observed in the surrounding cuticle (Young and Bennet-Clark 1995).

Kinematic studies

In studies of freely walking animals, adult cockroaches (*Periplaneta americana*; obtained from Carolina Biological Supply) traversed a narrow arena (2 inches wide by 15 inches long) which had Plexiglas walls and a suspended mesh floor (window screen) that served as the walking substrate. Leg movements were videotaped through the arena wall with a video camera (Pulnix Model TM640, 60/120 fields/second; Peak Performance Technologies) placed at the level of the floor.

To examine spontaneous movements of the intrinsic tarsal joints at higher resolution, animals were restrained with staples on a Sylgard resin-coated platform. The left hindleg was positioned so that the most distal tarsal segments projected over the edge of the platform and the proximal segments were immobilized by attaching them with cyanoacrylate adhesive to a small piece of razor blade (placed beneath the tarsus) or to a minuten pin (adjacent to the tarsal joints). Movements of the distal tarsus occurred spontaneously or were evoked by gently touching the abdomen or cerci. However, prolonged mechanical stimulation of the animal was avoided, as it resulted in the distal tarsal segments remaining flexed due to the sustained contraction of the retractor unguis muscle. Tests of recoil of the Ta4–Ta5 tarsal joint were performed after the main leg nerve (n5 of Dresden and Nijenhuis 1958) was cut or after the leg was severed in the distal tibia. After considerable experimentation, it was found that the most reliable method for eliciting recoil was to manually displace the fifth tarsal segment with the closed tips of a pair of forceps. While this method introduced variability in the extent of joint flexion prior to recoil and resulted in some inadvertent lateral displacement of the fifth segment, it was possible to release the fifth segment, under visual observation, in a midline plane to avoid contact of cuticular hairs with the more proximal segment, which impeded free recoil.

Joint movements were recorded with a high speed CCD camera (Redlake Motionscope 500, 500 frames/s; electronic shutter set at 1/10000 s) which was mounted to a photography tube attached to a dissecting microscope. The camera was adjusted so that the view was approximately perpendicular to a plane equivalent to one in which pads of the proximal tarsal segments contact the substrate during walking. Illumination was provided at high intensity by a pair of fiber-optic light guides with a filter (Fostec A0874) at the light source to reduce infrared and concomitant heating (see Results). Image sequences were captured in memory in the Red Lake system and then downloaded to video recorder at a slower speed (10 or 30 frames/s). Video frames from either system were captured from the VCR using a Matrox Meteor board and stored on the computer hard drive as bitmap files.

Joint angles were measured from the digitized graphics images in Image Pro software (Media Cybernetics) and the numerical values were exported to EXCEL and plotted in SigmaPlot. The angle of the joint between the fourth and fifth tarsal segments was measured from the sloping lateral-distal edge of the fourth segment to a line passing through the inferior margin of the fifth segment, near the point at which it joins the claw (auxillae) (Fig. 1). While the cameras were effectively positioned perpendicular to the horizontal plane on which the animal would place the pads of the proximal segments, the long axis of the fifth segment could be perpendicular or point more toward the camera. We gauged the effects of rotation by placing a severed tarsus on the shaft of a potentiometer and rotating through series of angles relative to the camera (the Ta4–Ta5 joint was in the default, extended position, see below). The effects of this rotation were substantial only when the long axis of the fifth segment deviated over 15° from the perpendicular plane (graph in Fig. 1E). This deviation could be gauged by the apparent distance between the claws and data from images which showed larger separation were excluded from analysis. We made no attempt to correct our measurements in images below that deviation.

Force measurements

The leg was severed at the tibio-tarsal joint and the tarsus mounted as in the kinematic studies on elastic recoil. In initial

experiments, the forces needed to displace the distal tarsus at the Ta4–Ta5 joint were monitored using a Grass FT03 force transducer. In subsequent studies, forces were measured with an Akers strain gauge assembly (Senso/Nor Type 801), which gave similar results but had much higher sensitivity. The assembly was mounted to a rod attached to an hydraulic micromanipulator (Narashige model 3333). A small drop of epoxy was placed on its exposed end and allowed to harden. The gauge was then used directly as a probe to depress the fifth tarsal segment. The force signals were amplified and recorded as two channels (one unfiltered, one low-pass filtered (d.c. to 100 Hz)) on a TEAC DAT recorder for subsequent transcription by computer using a Cambridge CED 1401 A/D interface and analysis in Spike2 software. Displacements of the gauge were produced through the micromanipulator and the resultant angle of the Ta4–Ta5 joint was monitored through the Redlake camera, which was mounted to the dissecting microscope. The joint angles were subsequently measured as in the kinematic experiments and then plotted with the corresponding force measurements on a single spreadsheet.

Results

Anatomy and movements of the intrinsic joints of the cockroach tarsus

The cockroach tarsus consists of five tubular segments (numbered Ta1–Ta5) that are linked by intersegmental membranes (Fig. 1A, B). The first tarsal segment is the longest and has a highly mobile joint with the tibia at which the tarsal levator and depressor muscles move the tarsus as a whole. Segments Ta1–Ta4 possess pliant pads (pulvilli) on their ventral sides but the joints between them (Ta1–Ta2, Ta2–Ta3 and Ta3–Ta4) are limited in motion both by the intersegmental membranes and by the extensive overlap between the segments on their lateral walls (Fig. 1C). In contrast, the joint between the fourth and fifth tarsal segments (Ta4–Ta5) allows for extensive movements (Fig. 1D) due to the extreme tapering of the proximal end of segment 5 and the joint specializations described below. The fifth tarsal segment has no pulvillus but bears the tarsal claws and arolium (collectively termed the pre-tarsus) on its distal end at the tarso-pretarsal joint. The claws and arolium are flexed and extended at that joint and the claws can be displaced laterally when they encounter a smooth surface that cannot be penetrated or grasped.

Active movements of the tarsal segments are generated by a single muscle, the retractor unguis (Fig. 1C). The retractor muscle takes origin in the femur and tibia and has a long tendon (apodeme) that traverses the length of the tarsus (Radnikow and Bässler 1991). The apodeme inserts internally upon a broad flat wedge of cuticle, the retractor plate, which is linked to the claws and arolium (Larsen et al. 1997). The direct action of the retractor is to flex those structures at the tarso-pretarsal joint and thus to engage them with the substrate (Fig. 1D). The indirect action of the apodeme is to generally depress the tarsal segments relative to one another at the intrinsic tarsal joints.

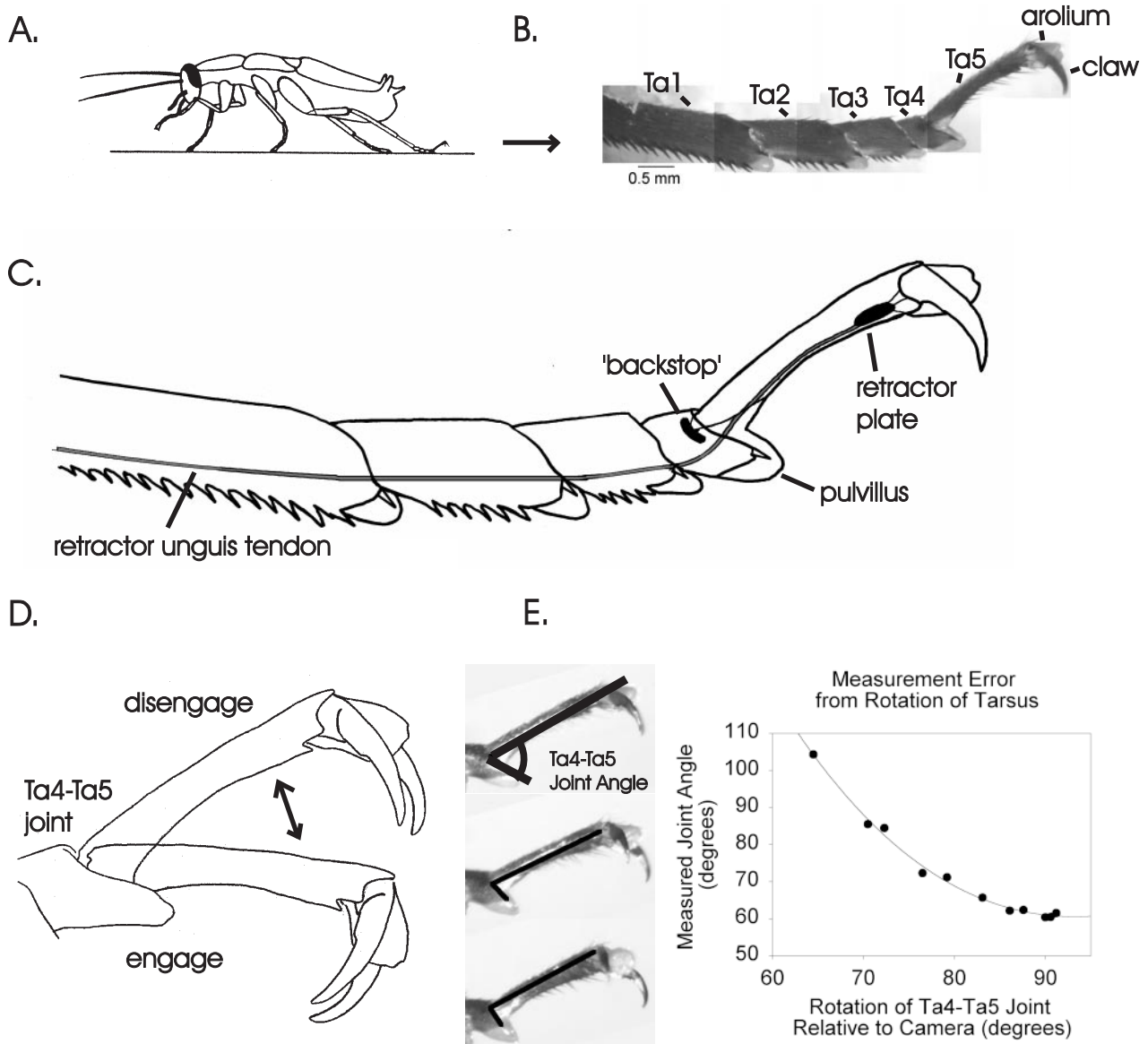


Fig. 1A–E Anatomy of cockroach tarsus and default position. **A** In walking, the cockroach leg contacts and engages the substrate with the tarsus (foot) to provide friction and support. **B** Tarsus in default position – the tarsus consists of five segments (*Ta1–Ta5*) that end distally in the claws and a midline pad, the arolium. When the tarsus is severed from the leg (as shown), it assumes a position in which the fifth segment (*Ta5*) is elevated at its joint with the fourth segment (*Ta4*). **C** Internal anatomy of the tarsus. The tarsal segments are moved via the tendon (apodeme) of the retractor unguis muscle. The apodeme passes through the proximal segments, above the level of the pads (pulvilli) and below the enlarged condyle ('backstop') of the fourth segment. The apodeme attaches distally to the retractor plate, which is linked to the claws and arolium. **D** The retractor apodeme engages the claws with the substrate by flexing them on the fifth segment and also depresses the fifth segment at the *Ta4–Ta5* joint. **E** Evaluation of error in measurements of the *Ta4–Ta5* joint angle – the *Ta4–Ta5* joint angle was measured from video images. As a control, a tarsus in the default, extended position was rotated in a horizontal plane on a platform and the apparent joint angle was measured (*plot at right*). The measurement errors increased as the long axis of the tarsus was directed toward the camera but only exceeded 10% if the perspective deviated beyond 15° from the perpendicular

The 'default' position of the distal tarsal segment

When a leg is severed from the body or when the main leg nerve (n5) is cut, the tarsus immediately assumes the position shown in Fig. 1B, which we have termed the 'default' position. The claws are held extended (Larsen et al. 1997) and the fifth tarsal segment is elevated on the much smaller fourth tarsal segment. We measured the angle of the *Ta4–Ta5* joint in four preparations in which the joint was positioned normal to the camera view, first after severing the leg at the junction between the coxa and body and subsequently when the tarsus was isolated by cutting through the distal tibia. The *Ta4–Ta5* joint angle was $60.5 \pm 2.9^\circ$ (mean \pm SD) after cutting off the leg as a whole and $58.5 \pm 1.9^\circ$ following isolation from the proximal leg segments. That finding implies that the position assumed after denervation of the retractor unguis muscle is retained after severing the linkage of the retractor tendon (apodeme) to its muscle

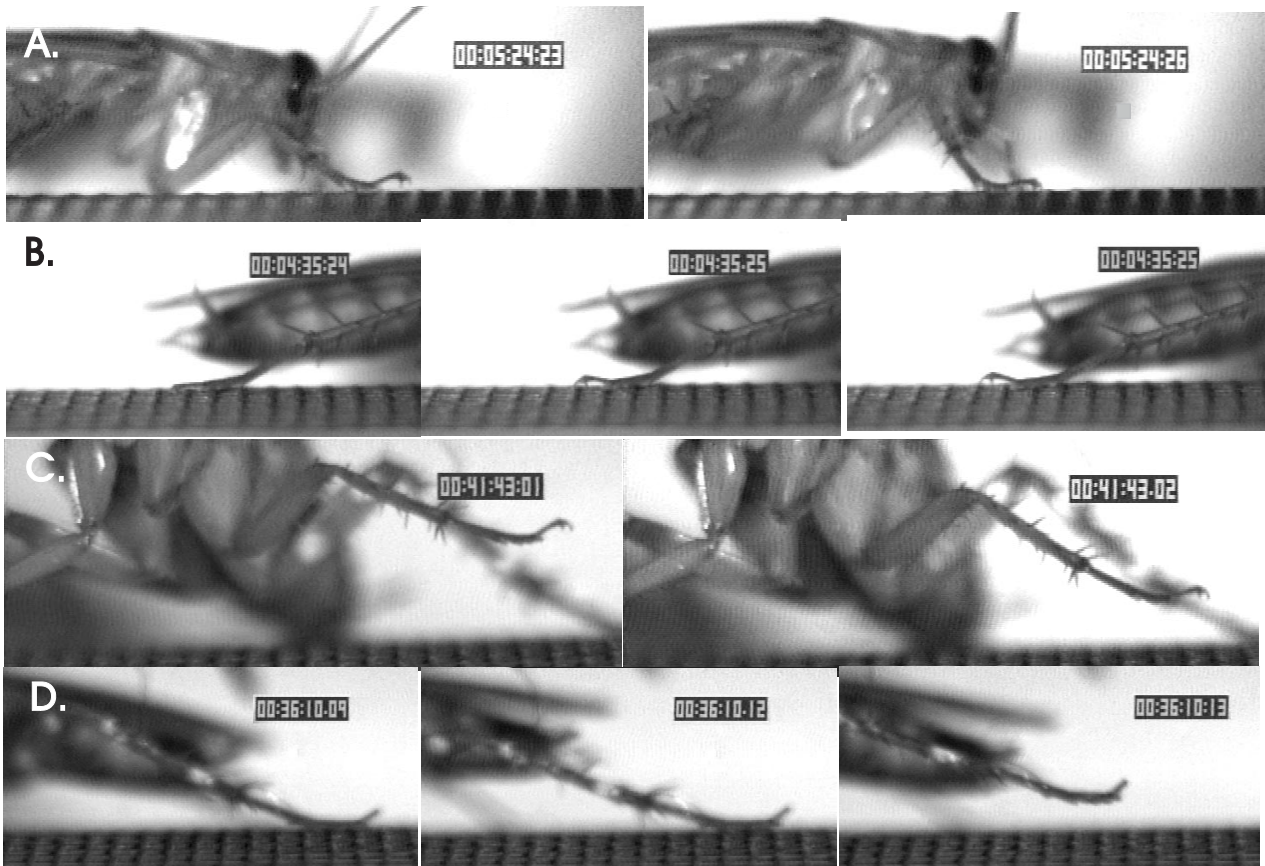


Fig. 2A–D High-speed video images of tarsal movements in freely walking cockroaches. **A** Prothoracic leg at start of stance – the tarsus first contacts the substrate with the proximal segments. The fifth segment is then depressed to engage the claws and arolium. **B** Hindleg at end of stance – the sequence is reversed at the end of stance, and the claw and fifth segment are disengaged prior to the tarsus and leg being lifted in swing. **C** Middle leg during swing – during the swing phase, the distal tarsal segments are held in the default position. **D** Effect of ablating tarsus at distal fifth segment – the fifth segment is continuously held in the default position of the Ta4–Ta5 joint throughout the stance phase (and step cycle as a whole) after removal of the insertion of the retractor unguis muscle

fibers, which are located in the femur and proximal tibia (Walter 1969; Radnikow and Bässler 1991). The default position is, therefore, apparently intrinsic to the distal structures of the cockroach leg.

Observations of the use of the claws and effects of removal of the distal tarsus in freely walking animals

Cockroaches walking on a mesh surface regularly engaged the claws and arolium with the substrate (Fig. 2) (Larsen et al. 1997). While we were only rarely able to resolve the independent movements of the claws and arolium at the more distal tarso-pretarsal joint in freely moving animals, we could often detect and measure movements at the Ta4–Ta5 joint due to the large

excursions they produced in the fifth segment. The magnitude of these joint excursions permitted previous authors to describe tarsal movements based solely upon visual observation (Roth and Willis 1952). Close up views showed that the sequence of placement of the tarsus (Fig. 2A) consisted of first contacting the surface with the pulvilli, often with the segments Ta1–Ta4 held in a horizontal plane when viewed laterally. The Ta4–Ta5 joint was initially held extended with the claws visible above the substrate. Engagement of the claws consisted of a rapid depression of the fifth segment at the Ta4–Ta5 joint and the entrance of the claws through the mesh (where they were no longer visible). This position, with the tarsal segments held in a horizontal plane pressed against the walking surface was apparently maintained throughout the stance phase, when the leg was being used to exert force in support and propulsion. At the end of stance, the sequence was reversed, and the fifth segment and pre-tarsus were typically elevated at the Ta4–Ta5 joint immediately prior to the tarsus and proximal leg segments being lifted in swing (Fig. 2B). This elevation was very rapid and typically occurred within one or two video frames (16–32 ms at 60 frames/s).

We were usually able to successfully image the tarsal joints after the leg had been lifted from the substrate only at the very start and end of the swing phase, or when the animal occasionally fortuitously made a complete turn in front of the video camera (Fig. 2C). In

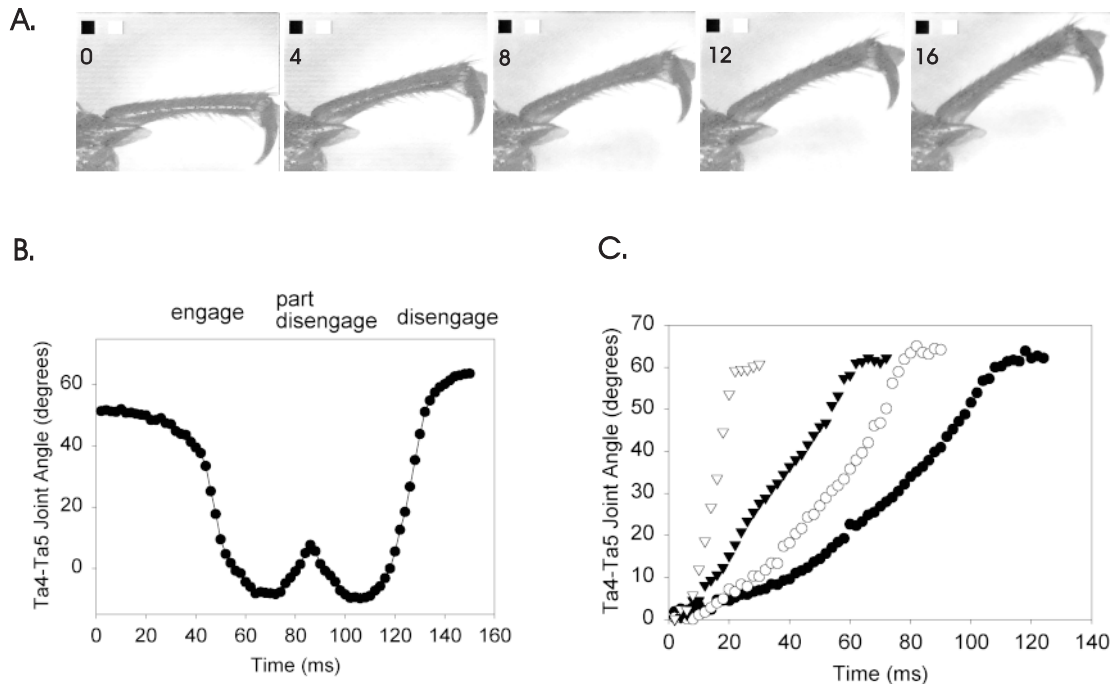


Fig. 3A–C Spontaneous movements of the distal tarsus in restrained preparations. **A** Spontaneous or evoked movements of the Ta4–Ta5 joint were typically quite rapid and joint extensions occurred in less than 20 ms. **B** Plots of Ta4–Ta5 joint angle during a rapid flexion followed by a partial extension, re-flexion and finally complete extension. The maximum rates of change in joint angles during extension (disengagement) could equal those seen during joint flexion (engagement). The resultant movements were generally quite smooth and did not indicate sudden accelerations characteristic of a catch mechanism. **C** Plots of joint angles during different rates of extension also did not show sudden accelerations or decelerations (*symbols* indicate individual events)

those images the segments of the tarsus most often were held rather flatly with the Ta4–Ta5 joint extended.

The sequence of repeated tarsal engagement and disengagement was not seen after removal of the pre-tarsal claws and tarsal plate by severing the fifth tarsal segment perpendicular to its long axis (Fig. 2D). Close-up videotapes of the legs of these animals showed that the stump of the fifth tarsal segment was held in an extended position throughout the step cycle, and the substrate was only contacted via the pulvilli on the proximal tarsal segments. The gross pattern of activities of the animal's other legs were not apparently effected by this ablation in walking on the flat surface. This operation however, severely limited the use of the hindleg in climbing when the substrate was tilted (S.N. Zill, unpublished observations; Larsen et al. 1997) or inverted (Larsen et al. 1995). It should be noted that in all situations no further spontaneous or evoked movements of the fifth segment were observed, even though the stump of that segment could be readily moved manually by the experimenter after a bout of walking. These findings imply that there are no other more proximal attachments of the retractor muscle apodeme that could generate discernible movements at the Ta4–Ta5 joint.

Spontaneous movements at the Ta4–Ta5 joint in intact, restrained preparations

To examine movements of the Ta4–Ta5 joint more closely, we videotaped the distal tarsal segments in animals that were restrained and viewed under a dissecting microscope (Fig. 3A). Spontaneous joint movements were not merely ballistic, all or none events but occurred in a number of patterns and at diverse rates. Movements could be quite rapid but also readily reversed direction in the mid-range. In the sequence plotted in Fig. 3B, which occurred in a period of 160 ms, the Ta4–Ta5 joint angle is first actively flexed as in tarsal engagement, then partially extended and flexed again and finally extended as during disengagement. The strong joint flexions, generated by unresisted contractions of the retractor unguis muscle, resulted in compression of the pulvillus of the fourth tarsal segment so that the joint angle transiently decreased below zero. During this sequence the maximum rate of change of joint angle (measured between successive video images) was approximately equivalent during joint flexion ($4.14^\circ \text{ms}^{-1}$) and extension ($4.35^\circ \text{ms}^{-1}$). Spontaneous disengagement movements occurred at a variety of durations. The durations of single extension movements could vary considerably but in each case, the rate of change of joint angle was relatively constant throughout the midrange (Fig. 3C). As only one muscle acts upon this joint, this diversity is presumably due to the variability in rate of relaxation of the retractor unguis muscle, which has been shown to consist of both slow and fast muscle fibers (Wood and Usherwood 1979) and to be multiply innervated (Walter 1980; Yamaguchi et al. 1993) by fast, slow and inhibitory axons. Also, none of these sequences show initial large accelerations that might be indicative of the

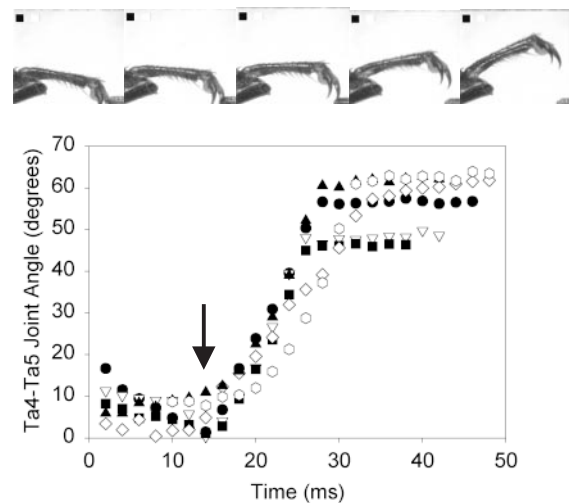
release of a catch mechanism, as occur in the ballistic path of the mandible of trap-jaw ants (Gronenberg 1996) or the femur in the locust defensive kick (Heitler 1977). However, the fastest extension movements at the Ta4–Ta5 joint were quite rapid and produced high rates of joint excursion (mean rate of fastest movement in Fig. 3C is $3.55^\circ \text{ ms}^{-1}$) that resulted in the fifth segment traversing the range between full joint flexion and extension in 16 ms. These measurements are, therefore, consistent with the images of tarsal disengagement obtained in freely walking animals.

Elastic recoil at the Ta4–Ta5 joint

It is possible to readily demonstrate, in an isolated leg, that the tarsus rapidly recoils to an extended position when the fifth tarsal segment is first manually flexed and then suddenly released. In order to study the mechanisms underlying joint recoil, we videotaped movements and plotted the angle of the Ta4–Ta5 joint in preparations in which the main leg nerve was cut and in tarsi in which the leg had been severed in the distal tibia. Figure 4A shows a sequence of video images during a recoil movement and plots of the Ta4–Ta5 joint angle for six successive tests in a single preparation in which the leg was cut near the tibio-tarsal joint. In these tests the joint recoiled to a position of $56.4 \pm 7.3^\circ$ over a mean duration of 18 ms through an arc of 50.0° , resulting in a mean rate of change in joint angle of $2.77^\circ \text{ ms}^{-1}$. The shortest duration was 14 ms and the fastest rate of change of joint angle observed between successive images (at 500 images/s) was $13.1^\circ \text{ ms}^{-1}$. These durations are comparable to those seen at the fastest rates of spontaneous extension in intact animals.

Joint extensions to final positions at smaller angles, as shown in Fig. 4A, were often the result of inadvertent lateral displacements of the fifth segment which could result in the movement being stopped by hairs on the fifth segment becoming caught against the wall of the fourth segment. This could be readily discerned as the fifth segment subsequently moved to full extension when dislodged by the experimenter. Also, in early experiments, in which heat filters were not used on the fiber-optic light sources, the joint could become ‘frozen’ after repeated tests and the fifth segment would remain at any joint position to which it was displaced. This was attributed to desiccation of the joint membranes as the joint could again become mobile if small drops of saline were placed around the Ta4–Ta5 joint soon after the joint immobilization was detected. If this was not done and the preparation was illuminated for longer periods, the joint subsequently became irreversibly immobile. Heat damage was less frequent after IR filters were placed in the light source and tests of recoil resulted in returns to joint extension over many tests (more than a dozen were uniformly performed per session).

A. RECOIL IN ISOLATED LEG



B. RECOIL AFTER REMOVAL OF RETRACTOR APODEME

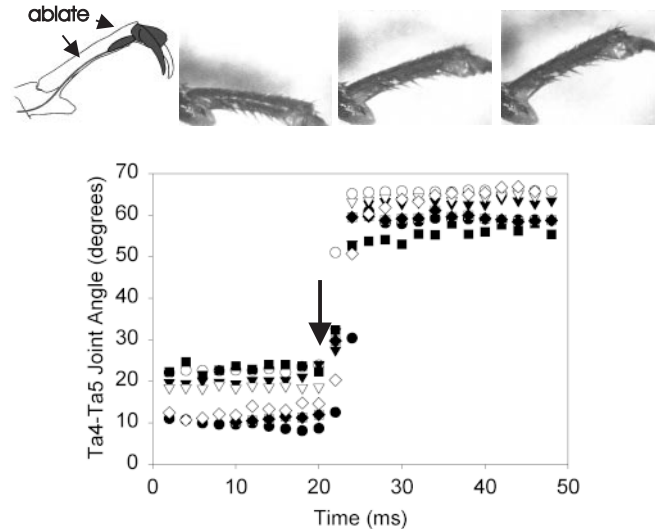


Fig. 4A, B Recoil after displacement of the Ta4–Ta5 joint in isolated legs and following removal of the retractor tendon (apodeme). **A** The fifth segment was displaced manually in the direction of claw engagement and then released in an isolated leg. The joint showed spontaneous and rapid recoil to extension. Plot of the Ta4–Ta5 joint angle during recoil movements (begun at arrow) showed smooth changes in joint angles similar to that seen in intact preparations (symbols indicate individual trials). **B** Recoil was retained after removal of the retractor apodeme, retractor plate and part of the pretarsus (one claw and the arolium). Plots of joint angle after removal of retractor apodeme showed that the ability to recoil occurred even more rapidly after the ablation and that the joint ligaments alone can generate movement to extension

Effects of removal of the pretarsus and retractor unguis tendon (apodeme)

While these tests imply that the Ta4–Ta5 joint is inherently elastic, these findings could be due to stiffness in the apodeme of the retractor unguis which traverses the joint. The retractor apodeme appears kinked or bent (Fig. 6A) in some wholemount preparations of the Ta4–Ta5 joint

that were fixed in extension. If the tendon was similarly bent in intact preparations, it might provide a motive force by acting as a mechanical 'leaf' spring when the joint was flexed. To examine this possibility, we tested the recoil of the joint after complete removal of the retractor apodeme and its insertion (Fig. 4B). In these preparations, we removed the arolium and retractor plate by carefully circumscribing the cuticle of the fifth segment and pulling firmly on the pretarsus or plate itself with very fine forceps. This maneuver extracted a considerable length of retractor apodeme from the tarsus and distal tibia as it remained attached to the pretarsus, as well as the retractor plate, the arolium and one of the tarsal claws.

Following the ablation, the Ta4–Ta5 joint still immediately assumed an extended position. When the fifth segment was displaced ventrally with a probe and then suddenly released, it recoiled to extension even more rapidly than in intact, isolated preparations. This ability occurred immediately following the selective ablation and was retained for some time, provided that small drops of saline were placed on the cut end of the fifth segment to prevent desiccation. Figure 4B is a plot of the joint angle during recoil in seven tests from three different animals. Although the initial positions of release vary somewhat due to difficulty inherent in manually displacing the ablated end of the fifth segment, the joint recoils to extension extremely rapidly. The mean duration of recoil in these tests was 6.0 ms in traversing a mean joint angle of 43.2°, which resulted in a mean rate of 7.2° ms⁻¹.

In order to quantify the effects of apodeme removal on the rate of recoil, we compared groups of tests in which the fifth segment had been displaced, on average, over equivalent ranges of joint angles. Figure 5A plots the mean, normalized change in Ta4–Ta5 joint angle for 10 tests from 4 animals in which the leg had been severed in the tibia and for 13 tests from 3 animals in which the retractor apodeme had been removed. The mean change in joint angle for the two groups were 39.8 ± 10.7° and 39.8 ± 9.0°, respectively. The mean duration of the tests in the severed legs was 13.7 ± 3.1 ms, while it was only 4.6 ± 1.8 ms following removal of the apodeme and pretarsal structures. Figure 5C is a plot of the rates of change of joint angle of the same data set. The mean velocity of joint movement was 3.0 ± 1.0° ms⁻¹ in the severed preparations and rose to 9.06 ± 2.67° ms⁻¹ following the ablation. Both the differences in duration and velocity are significant ($P < 0.01$, Mann-Whitney Ranked Sum test). We have also confirmed these findings by comparing the rate of recoil prior to and following ablation of the retractor apodeme in single preparations, although those tests were technically more difficult to perform.

Thus, the mechanisms which produce both the extended position and the recoil to it are not dependent upon the presence of the retractor apodeme but instead appear to be structural properties of the Ta4–Ta5 joint. Our finding that the joint moves faster after removal of the retractor apodeme and plate at first seems puzzling, particularly when these results are compared to those

obtained from comparable experiments by Weis-Fogh (1961) on recoil in the wings of locusts. Weis-Fogh found that removal of the thoracic flight muscles, which act in parallel with the elastic mechanism associated with the joint hinge, considerably slowed recoil of the wings (Fig. 5B). However, our findings in the cockroach tarsus imply that bending of the apodeme does not assist joint extension and that the enhanced rate of recoil may, instead, be related to the decrease in weight that accompanied the ablation of the retractor apodeme. To assess this possibility, we severed the fifth segment and distal tarsal structures, both in intact preparations and after removal of the retractor apodeme and its associated insertions. The fifth segment and pretarsus in intact preparations had a mean weight of 0.17 ± 0.029 mg ($n=5$), while the mass was 0.093 ± 0.012 mg ($n=6$) following removal of the apodeme, retractor plate and one claw. This represented a decrease of 45% and thus could substantially contribute to the increase in rate following removal of the distal structures.

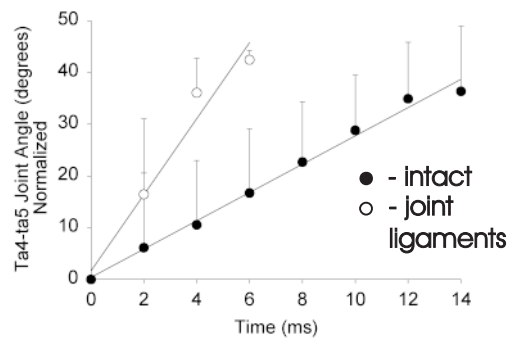
Localization of elasticity by selective ablations

We performed a series of localized ablation experiments to more precisely determine the source of the elasticity within the Ta4–Ta5 joint. First, removal of the pulvillus of the fourth segment, which lies below the joint (Fig. 6A), did not eliminate recoil to extension after manual displacement. This finding argued against an hydraulic or 'balloon' effect from the pulvillus, which is a structure that is highly pliable and can be compressed during extreme joint flexions (Fig. 3B). Partial ablations of the lateral walls of the joint (including the lateral intersegmental joint membranes, Fig. 6B) also did not eliminate recoil, provided that the joint was kept moist. Ablations of the deeper central portions of the joint were more difficult to perform precisely. We were able to completely eliminate recoil at the joint, in some experiments, by cutting through the dorsal and central structures linking the fourth and fifth segments. However, some measure of joint extension, in the absence of imposed displacement, was retained in other experiments. We have not, as yet, systematically confirmed the extent of these ablations morphologically. It is possible that the lateral joint membranes can assist in maintaining the extended position by keeping the segments abutted against each other (see below and Gonyea and Ashworth (1975) for a discussion of comparable results in cat claws). Severing both the lateral and central intersegmental membranes eliminated extension and also produced complete instability of the joint, which tended to completely disarticulate during subsequent tests of recoil.

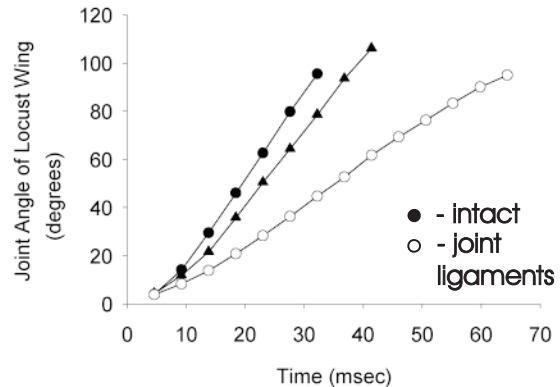
Sources of elasticity within the Ta4–Ta5 joint: evidence for the presence of resilin

The findings of our kinematic studies suggested that the rapid assumption of an extended position is attributable

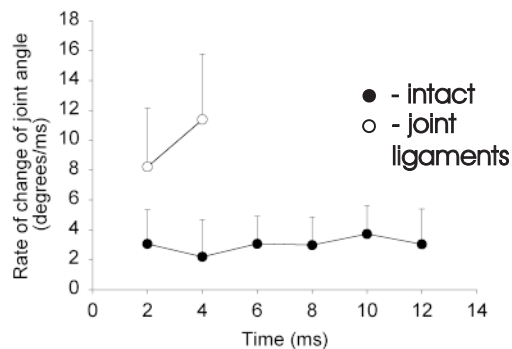
A. RECOIL OF COCKROACH TARSUS



B. RECOIL OF LOCUST WING (data of Weis-Fogh, 1961)



C.



D.

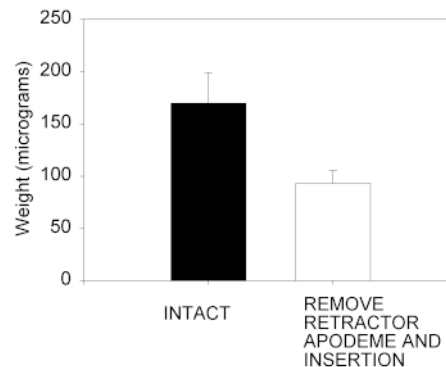
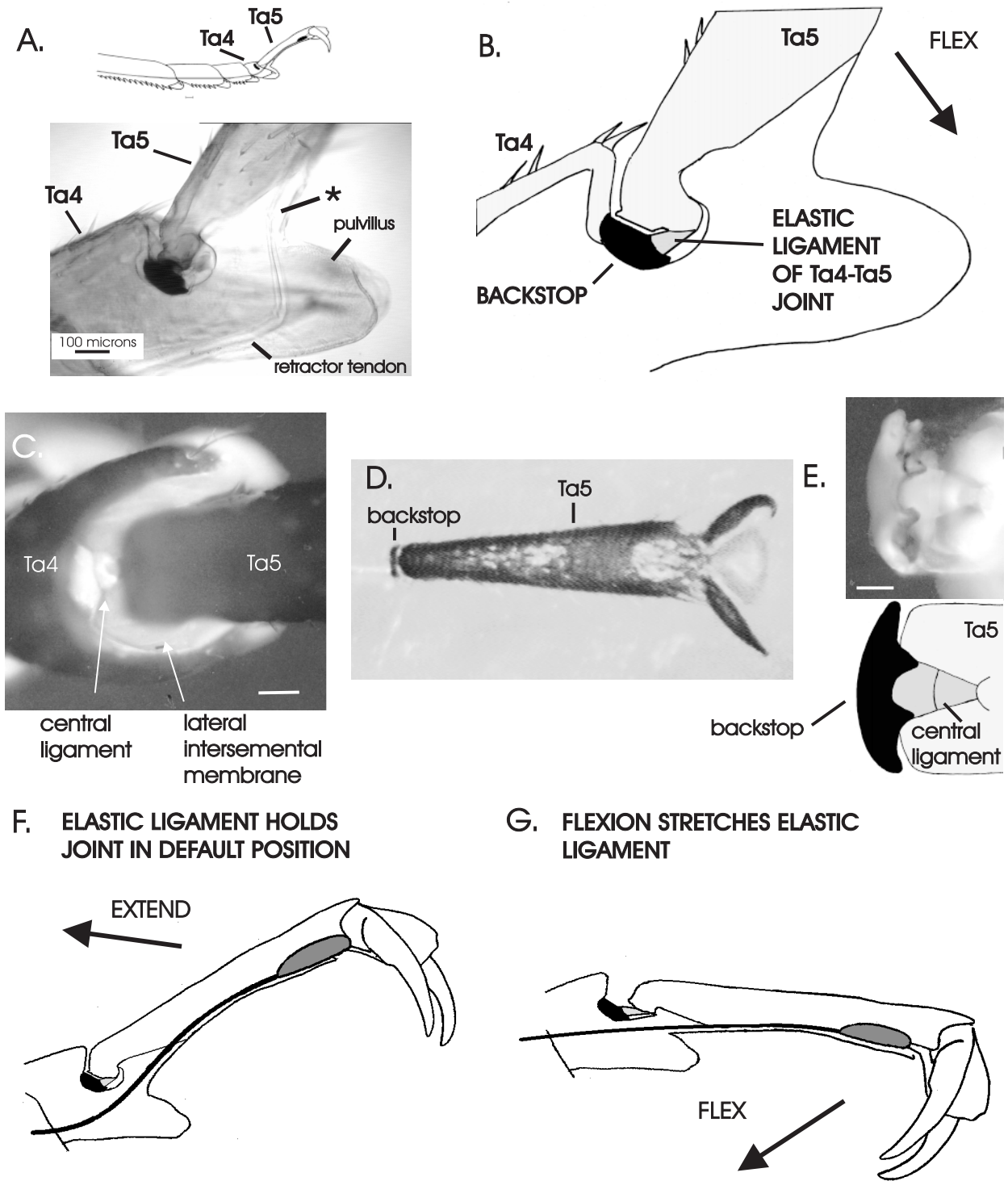


Fig. 5A–D Analysis of rate of joint recoil in cockroach tarsi and locust wings. **A** Normalized plot of changes in angle of Ta4–Ta5 joint in intact isolated legs (*solid dots*) and following removal of the retractor apodeme (*empty dots*). Removal of the apodeme resulted in a significant decrease in duration of recoil. **B** Plot of experiments of Weis-Fogh (1961) on recoil of wings in isolated locust thorax. The duration of recoil was increased after removal of muscles (*triangles*) and after complete isolation of wing hinges (*empty dots*) relative to that seen in intact preparations (*solid dots*), as those structures act as synergists to elastic ligaments. **C** Plot of rate of change of Ta4–Ta5 joint angle in recoil of tarsus. The velocity of recoil was increased by more than twofold after removal of the retractor apodeme, plate and pre-tarsal structures. **D** Mean weight of distal tarsus before and after ablation – ablation of the distal tarsal structures resulted in a 45% decrease in the mass moved by the joint ligaments, which could substantially contribute to the decrease in recoil duration and increase in angular velocity

to elastic structures directly associated with the joint between the fourth and fifth tarsal segments. That joint has a number of anatomical specializations in both its internal and external structure that allow for greater freedom of movement, relative to that seen at the other intrinsic tarsal articulations (S.F. Frazier et al., unpublished observations). First, as we have noted, the fifth segment is considerably tapered, and fits only loosely in the corresponding opening on the distal end of Ta4 (Fig. 6A, B), allowing for the substantial extension and flexion movements we have observed. Furthermore, the

proximal end of Ta5 abuts against a condylar thickening on the dorsal surface of the fourth segment that is greatly enlarged, in comparison to the other tarsal joints. This condyle, which we have termed the ‘backstop’, is heavily sclerotized and appears as a darkened cuticular disk when viewed laterally in wholemount preparations (Fig. 6A) and slopes upward relative to the long axis of the fourth segment. The tapered, proximal end of the fifth tarsal segment is shaped so as to fit snugly in the depression formed above the backstop when that segment is elevated in the default, extended position (Fig. 6B). This arrangement of the articular surfaces implies that when the fifth segment is pulled proximally into the Ta4–Ta5 joint it tends to lift that segment and extend the joint.

We have examined the structures of the joint by fluorescence and light microscopy to test for the presence of the elastic protein resilin by accepted criteria (Weis-Fogh 1960; Andersen and Weis-Fogh 1964; Govindarajan and Rajulu 1975; Young and Bennet-Clark 1995). UV illumination of the tarsus in fresh, unfixed specimens shows extensive fluorescence of structures surrounding the joint, including the lateral intersegmental membranes and pulvilli. However, the lower half of the backstop is the origin for a ligament which provides a short direct linkage between the segments (Fig. 6C). We have been able to study this ligament by isolating the fifth segment



and backstop from the surrounding structures as follows: if the tarsus is held firmly by the proximal segments and the fifth segment is grasped in forceps and vigorously pulled, the fifth segment, with the attached claws and arolium, becomes separated from the leg at the Ta4-Ta5 joint (Fig. 6D). Examination of these isolated specimens has shown that the plane of separation is often in the distal part of the fourth segment, as the backstop remains

attached to the fifth segment via the short ligament described above (Fig. 6E). This ligament emits a blue fluorescence under UV illumination at 420 nm and also stains blue using the toluidine blue-green method of Weis-Fogh. These findings are indicative of the presence of resilin, although conclusive identification of the protein can only be done biochemically (Andersen and Weis-Fogh 1964).



Fig. 6A–G Structures of Ta4–Ta5 joint and model of joint elasticity. **A** Cleared whole mount. **B** Cutaway drawing of Ta4–Ta5 joint. The proximal end of the fifth segment abuts against the enlarged condyle (backstop) of Ta4 and is linked to it by joint membranes. The shape of the articular surfaces are oriented so that the shaft of the fifth segment is drawn upward as the proximal end is pulled toward the backstop. Note (in **A**) the bend in the apodeme of the retractor unguis muscle (*) that courses adjacent to the joint. **C** UV fluorescence of Ta4–Ta5 joint – the Ta4–Ta5 joint is viewed from its dorsal surface with the fifth segment held flexed. In this position, the dorsal ligaments of the joint are stretched and a triangular area between the backstop and the fifth segment strongly fluoresces under UV illumination. **D** Isolation of distal tarsal structures – the backstop remains attached to the fifth segment when the joint is disarticulated. **E** Ventral view of **D** – the backstop is linked to the fifth segment via a triangular ligament. When the backstop is displaced in this preparation, the ligament is stretched. Upon release the backstop recoils to a location equivalent to the default position of the intact joint. **F, G** Model of passive joint recoil – in the default position the fifth segment is held extended by the joint ligaments and articular surface. Joint flexion stretches the elastic ligaments which recoil upon release. Calibration in **C** = 78 μm , in **E** = 50 μm

It is also possible, in these isolated preparations, to manually displace the backstop on the fifth segment and to demonstrate that it recoils back to a position in which it is abutted against that segment. Thus, the central ligament which connects the backstop and fifth segment alone is sufficient to mediate the return of the articular surfaces to a position that would correspond to the default position in the intact animal.

Measurements of forces exerted by elastic structures

The anatomy of the Ta4–Ta5 joint, therefore, indicates that the short ligaments connecting the backstop and fifth segment, that are stretched as the joint is flexed (Fig. 6F, G), could provide motive force for both the assumption of joint extension and for the recoil we observed. Furthermore, the central ligament of the joint, which holds the backstop against the fifth segment should be progressively stretched as the joint is displaced. These findings further imply that restorative forces are exerted upon the fifth segment throughout joint flexion, and that the joint is not propelled ballistically into extension by a mechanism that is stretched only when the joint approaches full flexion. In order to provide data to support these hypotheses, we measured the passive forces exerted upon displacement of the distal tarsus (Jensen and Weis-Fogh 1962). In these experiments, the tarsus was severed from the leg at the tibio-tarsal joint and mounted as in the studies on joint recoil, so that all segments proximal to the Ta4–Ta5 joint were immobilized. The fifth segment was then progressively displaced via a silicon strain gauge assembly mounted to an hydraulic micromanipulator (Fig. 7A). Coupling of the gauge assembly to the segment proved to be somewhat problematic, as the movements of the gauge were linear, while the fifth segment traversed an arc as the joint was flexed and

extended. This was resolved somewhat by placing a small drop of epoxy directly on the free end of the gauge and allowing it to harden. The gauge was calibrated by placing small weights against the hardened drop (Fig. 7B). The gauge was then pressed against Ta5 via the epoxy bead which allowed for the point of contact to roll somewhat while maintaining continuous contact with the leg. The angle of the Ta4–Ta5 joint in these tests was monitored during joint displacements by a high speed video camera mounted to the dissecting microscope.

The passive forces we measured showed a graded increase as the joint was progressively flexed and a subsequent proportional decrease as it was returned to extended positions (Fig. 7B, C). The only discontinuities that were seen occurred in the midrange and were attributed to slipping of the point of contact of the gauge with the leg. This finding again argues against a catch-like mechanism being the motive force for joint recoil, although it should be noted that the retractor apodeme remained intact and attached to the tarsal plate in these tests. During small repetitive displacements (which were generated by manually turning the knob on the micromanipulator) the forces exerted by the joint were relatively smooth and repeatedly reached the same levels at the extremes without measurable hysteresis (Fig. 7B) (see also Jensen and Weis-Fogh 1962). However, the repetitive displacements were relatively slow, being delivered manually, and we have not as yet been able to extend the frequencies of the tests above 1 Hz. Plots of the magnitude of the forces versus the joint angle (Fig. 7D) showed that the maximum force exerted at the joint was 0.15–0.2 mN (approx. 15–20 mg) upon a joint flexion of 30–40° and thus could readily generate recoil and lift the fifth segment and pretarsus which weigh less than 1 mg. The data from each animal were fitted via linear regression and showed slopes of 0.003–0.005 mN force/degree change in joint angle that were similar ($r^2 = 0.89–0.92$). While these tests should be viewed as preliminary, they support the idea that the motive force for recoil lies within the Ta4–Ta5 joint and that it acts like a spring, exerting a continuous restoring force throughout the range of joint movement.

Discussion

The present study has shown that (1) the cockroach tarsus consistently assumes a default position, in which the fifth tarsal segment is extended at its joint with the fourth segment (Ta4–Ta5 joint), after the leg is severed from the body or the main leg nerve is cut; (2) in walking over a wire mesh surface, movements of joint extension occur during each step prior to the onset of the swing phase, when the claws and arolium are disengaged and elevated from the substrate; (3) in isolated preparations, the Ta4–Ta5 joint demonstrates rapid elastic recoil to extension when the fifth segment is manually displaced and released, at rates similar to those seen in walking

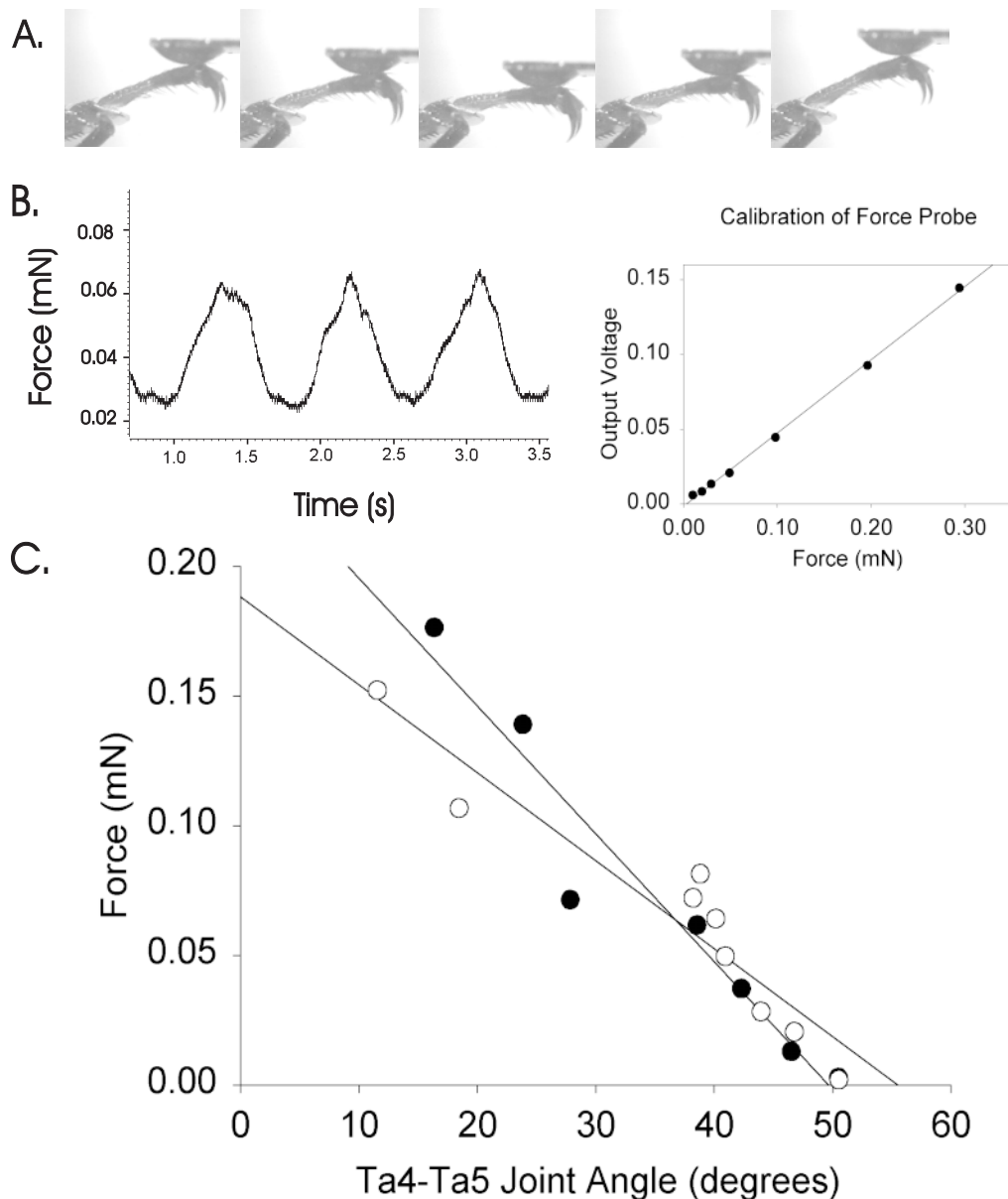


Fig. 7A–C Forces exerted by elastic structures at Ta4–Ta5 joint. **A** Sinusoidal displacement of the Ta4–Ta5 Joint using a silicon gauge – the joint was videotaped during tests in which it was displaced by pushing on the fifth segment with a strain gauge which measured the forces passively generated to return it to the extended position. **B** Forces needed to flex the Ta4–Ta5 joint. *Left* output of the strain gauge during slow sinusoidal displacements (from 35 to 45° joint angle) show a continuous graded force without apparent hysteresis. *Right* calibration of strain gauge with small weights shows that its output is linear. **C** The static force exerted at different sustained joint displacements is plotted relative to the angle of the Ta4–Ta5 joint. The magnitude of the force is proportional to the extent of displacement, as would be expected from a spring-like elastic structure that exerted force throughout the range of joint movement

animals; (4) joint recoil is not dependent upon the presence of the retractor muscle apodeme but instead results from properties of the articular membranes and ligaments that link the fourth and fifth segments, some of which exhibit fluorescence and dye staining consistent

with the presence of the elastic protein, resilin; and (5) force measurements during passive joint displacements indicate that this elasticity is sufficient to lift the distal tarsus from the substrate. It would therefore appear that the movement of pre-tarsal elevation during walking is generated by intrinsic elastic elements within the tarsus.

Model of mechanism of action of Ta4–5 joint and its contribution to movements of the tarsus

Our results support a model of the mechanism of movement of the distal tarsus at the Ta4–Ta5 joint that is shown in the diagram in Fig. 6F, G. In an isolated leg or in an intact animal at rest, the fifth segment is held in the default position by the ligaments of the joint which link it to the base of articular condyle of the fourth

segment (backstop) (Fig. 6F). During experimentally imposed joint flexions, the ligaments are stretched as the segment is displaced and produce the restorative forces that were measured on the distal part of the fifth segment (Fig. 6G). Upon release, the joint ligaments act like springs and pull the fifth segment proximally and it is elevated, in part, due to the orientation of the articular surfaces.

The evidence we have presented supports the idea that these processes also occur during movements that are seen in walking. During the swing phase, the distal tarsal segment and pre-tarsus are held above the substrate by the joint ligaments. At the start of stance, the tarsus as a whole is first depressed, presumably through the action of the tarsal depressor muscles and by extension of the leg as a whole. In walking over rough terrain, the claws and arolium are then actively engaged through the action of the retractor unguis muscle. At the end of stance, tension in the retractor declines and the grip of the claws and arolium relaxes. The distal tarsus is then rapidly elevated by the action of the stretched elastic ligaments. In walking over smooth terrain, in which the friction and adhesion of the pulvilli is sufficient and the pre-tarsus is not engaged, the joint elasticity can hold the distal tarsus elevated throughout the stance phase. During walking this elasticity clearly fulfills two major functions: first, it helps disengage the contact of the claws and arolium with the substrate when the retractor muscle relaxes, and second, it substantially lifts or holds the fifth segment, claws and arolium, as a whole, away from the walking surface. As we discuss below, the elasticity of the Ta4–Ta5 joint most likely serves as a limited antagonist to the retractor unguis muscle, but nonetheless contributes to the production of smooth and graded movements of the pretarsus, such as could occur when the claws and arolium are used in searching for a foothold.

The default position and movements in walking

Our finding that the penultimate tarsal joint is held in extension confirms general observations made by several authors in studies of cockroaches (Arnold 1974) and other insects (Walther 1969). In their seminal study on the cockroach tarsus, Roth and Willis (1952) noted that the claws and arolium were ‘tilted’ away from the surface in the isolated legs of many species, and the ‘default’ position can be noted in several of their published photographs of tarsi (*ibid.*, p 489). Radnikow and Bässler (1991) also found that, in stick insects, the pre-tarsus was fully extended in the absence of tension in the retractor unguis muscle, while a similar position can be observed in the drawing of the tarsal segments in the middle leg of the locust (Laurent and Hustert 1988). The elevated position of the pretarsus is thus characteristic of many types of cockroaches (Arnold 1974) and, potentially, a number of other insects.

We have also documented that the distal tarsus is regularly engaged and then disengaged in the step cycle when walking on (rough) terrain, confirming the descriptions of Roth and Willis (1952) and other authors (Arnold 1974) based upon close visual observation. Engagement of the distal tarsus with the surface is the primary action of the retractor unguis muscle (Snodgrass 1952). While we did not monitor activities of this muscle during tarsal movements, the myographic studies of Laurent and Hustert (1988) in freely walking locusts show bursts of activity in the retractor that are initiated at the start of the stance phase and cease prior to swing. That pattern of activity in the retractor could readily generate the tarsal movements we observed in walking cockroaches.

Further, we have found that after severing the pre-tarsus and tarsal plate, and thus cutting the insertion of the retractor muscle, the fifth segment remained extended throughout the step cycle. This result implies that, in the cockroach, the retractor is the only muscle capable of producing active movements of the distal tarsal joints and supports the conclusion that the tarsus contains no other intrinsic musculature, said by Snodgrass to be the case in all insects (Snodgrass 1927, 1952). However, this result is also important in understanding the mechanism of tarsal movement because several authors (Kendall 1970; Arnold 1974) have noted that the long retractor apodeme is closely approximated, and potentially attached, to the transverse bands of a hemolymph septum that subdivides the tarsal segments. Those postulated linkages could serve as auxiliary attachments for that muscle and produce movements of the proximal tarsus after removal of the distal insertion. Our finding, however, demonstrates that any proximal attachments of the retractor cannot generate discernible movements of the Ta4–Ta5 joint during walking. In sum, these results imply that non-muscular structures located within the tarsus sustain and generate the default position.

Tarsal elasticity and the action of the retractor unguis muscle

The highly flexible and elastic nature of the cockroach tarsus has been recognized by a number of previous authors (Roth and Willis 1952; Arnold 1974). While no other studies have identified the specific sources of tarsal elasticity in the cockroach, the model we propose is in agreement with previous investigations of Walther (1969) and Radnikow and Bässler (1991) on the mechanism of action of the retractor unguis muscle in stick insects. Both of those studies examined the effects of displacements of the retractor apodeme on the position of the tarsus, as a whole. Walther first documented, by optical recording of the position of the tarsal segments, that pulling on the retractor apodeme flexed the tarsus from its extended position at rest in a graded manner. These displacements were countered by elastic forces

that restored it to the extended position. Walther considered that this elasticity was distributed in a number of distal leg structures but identified two potential sources as (1) the tarsus and (2) an elastic band located in the distal tibia which was described as being attached to the retractor apodeme. However, Walther (1969) found that destruction of the elastic band produced little change in the relationship between the retractor unguis position and the angle of the tarsus as a whole. In the present study, we have demonstrated that recoil in the distal tarsal joints persists after complete removal of the tibia, which would eliminate any comparable source of elasticity. Radnikow and Bässler (1991) generally confirmed the findings of Walther and extended them by observing the position of the retractor apodeme through a small window in the tibia while it was manually displaced in the femur. They found that the elasticity present in the tarsus alone (following selective ablation of the tibial band) was sufficient to restore the position of the retractor tendon after displacement. The elasticity we have demonstrated at the Ta4–Ta5 joint could readily contribute to the distal displacement of the retractor apodeme by its indirect action on its insertion in the pre-tarsus.

However, it is also important to note that other elastic structures of the tarsus, such as the flexible intersegmental membranes of the proximal tarsal joints or elastic elements associated with the pre-tarsus (Gorb 1996), can also function as antagonists to the retractor unguis muscles. Walther (1969) measured those forces in stick insects by pulling on the retractor apodeme and moving the unrestrained tarsus as a whole, which as we have noted, included flexing the proximal tarsal joints. He recorded considerably higher levels of force opposing the action of the retractor tendon than those measured in the present study (although those measurements may also have included the force generated upon flexion of the tibio-tarsal joint). Thus, while the ligaments of the Ta4–Ta5 joint function as partial antagonists to the retractor, their contribution may be limited and clearly sums with other elastic elements when the leg is not in contact with the substrate. However, as we have noted, when the proximal tarsal segments are pressed against the walking surface, elastic forces generated in the distal tarsus are apparently sufficient to counter residual tensions in the retractor muscle to permit elevation of the pre-tarsus.

Functions of the default position in posture and locomotion: elasticity confers flexibility of use

The elastic mechanism we have described in the cockroach acts to hold or rapidly elevate the distal tarsus to an extended position. A major advantage of this mechanism is the flexibility it affords in allowing the claws and arolium to be selectively engaged in walking over diverse terrains. The early and extensive behavioral studies of Roth and Willis (1952) provide valuable

insights into the adaptive use of the tarsus in cockroaches. They tested the abilities of animals to traverse different types of surfaces and varied the inclination of those substrates. First, they noted that the claws and arolium were not used in walking over smooth horizontal surfaces but that the pulvilli alone provided sufficient contact and adhesion for support and propulsion (see also Arnold 1974). In traversing rough terrain or in climbing, however, the claws and arolium were regularly engaged. Experiments in which the pretarsus was ablated demonstrated that the claws were essential for vertical climbs or in walking on inverted surfaces, as has been confirmed in later studies (Larsen et al. 1995, 1997). Furthermore, the claws were only effective on surfaces which they could grasp or penetrate but on very hard smooth surfaces the claws could be an impediment (Roth and Willis 1952), although they tended to be displaced laterally through the flexibility of the tarso-pretarsal joint (Kendall 1970; Gorb 1996). Thus, holding the pretarsus away from the walking substrate allows the animal the flexibility to selectively engage the claws when they are necessary and to utilize only the pulvilli when they are sufficient or when the claws might hinder progression.

The arolia of insects are generally considered to function to provide adhesion on smooth surfaces (Snodgrass 1952). However, the mechanism of action of the arolia remains controversial (Wigglesworth 1987; Dixon et al. 1990), despite the fact that the general question of how insects adhere to vertical or inverted surfaces has been investigated for some time, literally since the start of modern biology (Leeuwenhoek 1690 as cited by Stork 1980). Mechanisms of areolar adhesion that seem most accepted are surface tension of compounds secreted by the cuticle (Dixon et al. 1990) and the gripping action of minute setae on the ventral arolium (Stork 1980). The potency of the adhesive mechanism has also been well documented and in some insects it takes forces up to 20 times the animal's body weight to pull it from a surface (Dixon et al. 1990). It has been noted that insects may have problems in detaching themselves and that a surface tension mechanism could be more readily removed or 'peeled from the substrate' by tilting the arolium (Dixon et al. 1990, p 252). It is possible that the elasticity in the Ta4–Ta5 joint produces this type of movement in lifting the arolium from the walking surface, although more experiments are necessary to test this hypothesis (see also Wigglesworth 1987).

Common mechanisms in claws of cockroaches and cats

The elastic mechanisms which allow selective use of the pre-tarsus in cockroaches, and which may be present in a number of types of insects (Radnikow and Bässler 1991; Laurent and Hustert 1988), are remarkably similar to those that underlie use of the claws of cats and other

carnivorous vertebrates (Gonyea and Ashworth 1975; Bryant et al. 1996). In cats, the prehensile claws of the forelimbs are normally withdrawn (retracted), and are protruded (protracted) only in prey capture. In normal use, retraction is maintained without muscle activity, through pairs of elastic ligaments which span the distal interphalangeal joints and the claws are held in a 'default' position of joint extension (Bryant et al. 1996), similar to that shown in the tarsus of the cockroach. These ligaments are yellow colored and stain histologically for the presence of elastin (Gonyea and Ashworth 1975), which is the vertebrate homologue to the protein resilin. Furthermore, protraction of the claws is produced by the action of a single muscle, the flexor digitorum profundus, which acts as the functional antagonist to the elastic ligaments and, like the retractor unguis of insects, has a long apodeme which spans several limb joints. Contraction of this muscle can produce selective protrusion of the claws provided that the more proximal joints are held immobile through co-activation of appropriate limb flexors and extensors. Lastly, the distal interphalangeal joint shows recoil to extension following electrical stimulation of the flexor digitorum profundus (Gonyea and Ashworth 1975), although the movements were not subject to the kinematic analysis done in the present study.

These common characteristics emphasize the advantages offered by use of elastic ligaments as antagonists in the distal joints of appendages. Perhaps the major benefit in these mechanisms is that they result in a substantial decrease in inertia by obviating the need for separate antagonist muscles. The lightness of appendages, relative to body mass, has recently been documented as a common characteristic in many vertebrate and invertebrate animals (Kram et al. 1997). However, in insects such as the cockroach, these mechanisms also allow for very rapid movements, which may be requisite in an animal that can engage and disengage the substrate in traversing terrain at rates up to 20 steps per second. Finally, we would suggest that these advantages of reduced inertia and speed, combined with the simplification of control, that are an apparent common biological strategy may be incorporated in the design of prosthetic limbs and robotic legs to similar advantage.

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