

The femur–tibia control system in a proscopiid (Caelifera, Orthoptera): a test for assumptions on the functional basis and evolution of twig mimesis in stick insects

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Summary

The extremely slow return movements observed in stick insects (phasmids) after imposed changes in posture are termed catalepsy. In the literature, catalepsy is treated as a behavioural component of the twig mimesis observed in walking stick insects. It is produced by the high gain of the velocity-sensitive component of the relevant joint control systems and by the non-linear dependency of its time constant on movement velocity. The high gain, in turn, causes the system to work close to instability, and this may have driven the evolution of gain control mechanisms. Although these statements represent plausible assumptions, based on correlated occurrence, they remain largely hypothetical like many ideas concerning evolutionary tendencies. To test these hypotheses, we studied catalepsy and the relevant properties of the femur–tibia control system in the middle and hind legs of *Prosarthria teretirostris*.

cf. Prosarthria teretirostris is a proscopiid closely related to grasshoppers and locusts. With its slender, green-to-brown body and legs, it shows clear

morphological twig mimesis, which has evolved independently of the well-known twig mimesis in stick insects. The animals show clear catalepsy. The main properties of femur–tibia joint control are remarkably similar between proscopiids and stick insects (e.g. the marked sensitivity to movement velocity rather than to joint position and the non-linear dependency of the time constants of response decay on movement velocity), but there are also important differences (habituation and activity-related mechanisms of gain control are absent). Together, these results validate the main concepts that have been developed concerning the neural basis and evolution of catalepsy in stick insects and its relationship to twig mimesis, while demonstrating that ideas on the role of habituation and gain control should be refined.

Key words: postural control, movement control, catalepsy, gain control, stick insect, *Prosarthria teretirostris*, proscopiid, phytomimesis, evolution, behaviour.

Introduction

Branch- or leaf-like body shapes are the most conspicuous morphological components of twig mimesis in stick insects, but there are also a number of important behavioural adaptations, such as the adaptation of particular resting postures of the body and limbs to give the appearance of a twig. Catalepsy, the extremely slow return movement produced after passive displacement of the legs and other appendages, also appears to be a behavioural component of twig mimesis for two main reasons (see Bässler, 1983, 1993). First, catalepsy appears to correlate well with twig-like body shape, i.e. it is present in all phasmids studied so far, but does not occur in locusts, for example. Second, catalepsy prevents fast movements, and twig mimesis may indeed require very slow movements to evade movement-based visual recognition by predators (e.g. Ewert, 1997).

In the femur–tibia joint of walking stick insects, catalepsy is the result of the opposing effects of velocity- and position-sensitive portions of the postural reflex response in the

femur–tibia joint control system (for details, see Bässler, 1983, 1993). If the femur–tibia joint is brought to a new position, held there for some time and released, the small position-sensitive component of the resistance reflex sustains the return movement. The large velocity-sensitive component, which during the return movement opposes the position component, retards this movement. The tibia thus moves at a (equilibrium) velocity at which both components have the same amplitude, yet opposing directions. Therefore, return velocity decreases with smaller position-sensitive and larger velocity-sensitive components. The non-linear characteristic of the half-life (or time constant) of the velocity-sensitive portion supports catalepsy because it enables the response to decrease rapidly after a fast passive displacement and to maintain a significant amplitude through very slow return movements.

Catalepsy in stick insects thus appears to rely mainly on two properties: the high gain of the velocity-sensitive component of the posture control system and the non-linear dependency

of its time constant on movement velocity (Bässler, 1993). The gain increases after disturbance of the animals, which further slows any return movement as soon as a possible predator approaches. The high gain of the femur–tibia joint control system, as a prerequisite for effective catalepsy, produces a very small phase reserve (see Results) and thus causes the system to work close to instability. To prevent feedback oscillations, which would be conspicuous to a predator, the animals must be able to limit feedback gain according to the behavioural situation. Habituation (Bässler, 1993; Kittmann, 1991, 1997) or habituation-like muscle properties (Bässler and Stein, 1996) provide such gain control, which seems, therefore, to have evolved as a consequence of very effective catalepsy.

Like many ideas concerning evolutionary tendencies, the above concepts are mostly based on plausible assumptions or on correlations rather than on experimentally validated hypotheses. To put these concepts under scrutiny, ideally one would have to study the joint control system in an insect species that has evolved twig mimesis independently. Fortunately, there is a group of orthopteran insects, the proscopiids, that are only distantly related to stick insects and that show clear morphological twig mimesis. Proscopiids show twig mimesis in a manner similar to stick insects and they are of almost the same body size, thus allowing study with the same methods. For the purposes of comparison, there already exist a considerable amount of data, mainly from stick insects and locusts, since the neuronal and cybernetic bases of the femur–tibia joint control system have attracted much attention (for reviews, see Bässler, 1993; Burrows, 1988, 1989, 1996; Büschges, 1995), as has the (evolutionary) relationships between joint control systems in orthopteran insects (Büschges and Wolf, 1995).

In this study, we characterize the femur–tibia control system of cf. *Prosarthria teretirostris*, a medium-sized proscopiid (Fig. 1). As a proscopiid (Proscopiidae, Caelifera, Saltatoria, Orthoptera), cf. *Prosarthria teretirostris* (Flook et al., 1999) (cf. is explained in Materials and methods) is closely related to grasshoppers and locusts. The presumptive sister group of the Proscopiidae is the Eumasticidae (Flook et al., 1999; Dirsh, 1961). As a member of the Saltatoria, *Prosarthria teretirostris* has well-developed, though inconspicuous, legs for jumping (Burrows and Wolf, 2000). With a slender and branch-like shape to its body and legs and brown (adult females) to green (adult males) coloration, this species exhibits clear twig mimesis. This is true for both genders, despite clear sexual dimorphism (Fig. 1A,B). The long body shape is produced by lengthening of the pro- and mesothoraces, in contrast to stick insects which possess long meso- and metathoraces (Fig. 1C). In addition, the orthognath head is elongated, producing an almost opistognath appearance. Stick insects, in contrast, possess prognath heads of normal size. When sitting on feeding plants, the animals are as inconspicuous as stick insects, the classic insect group to display twig mimesis. From the systematics outlined above and from the different ways in which the elongated body shape is produced, it is clear,

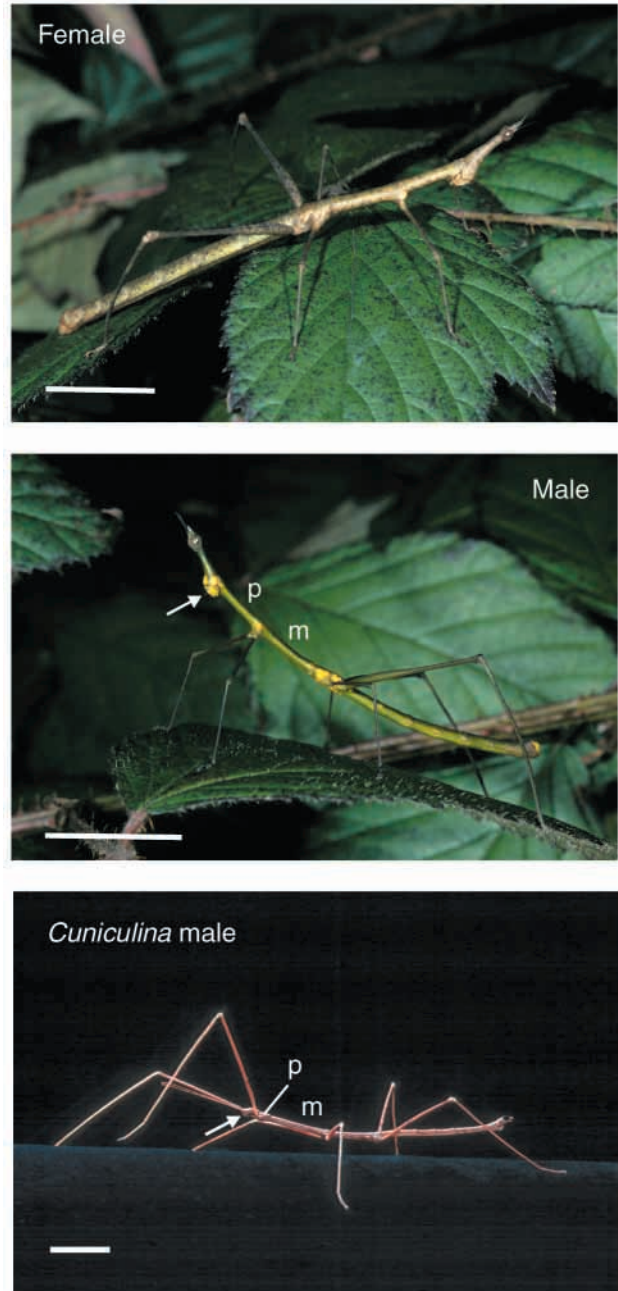


Fig. 1. cf. *Prosarthria teretirostris*, female (A) and male (B) individuals. Note the twig-like shape of the body and legs, elongation of the pro- (p) and mesothoracic (m) segments and of the head (the arrow indicates the mouth of the male) and the brown-to-green coloration. Average body lengths were 10–11 cm for females and 6–7 cm for males. A *Cuniculina impigra* male (C) shown for comparison; labelling as in B. Scale bars, 2 cm.

however, that the two groups have evolved twig mimesis independently

We demonstrate here that *Prosarthria teretirostris* possess catalepsy and that their femur–tibia control systems have remarkable similarities with those of stick insects (such as marked velocity-sensitivity and non-linear dependency of time constants on movement velocity), but we also demonstrate

notable differences (such as the absence of habituation and equivalent mechanisms, independence between reflex gain and the state of activity of the animal). These data confirm the main concepts regarding the neural basis of catalepsy and its evolutionary relationship to twig mimesis and indicate that ideas on evolution and the necessity for gain-limiting mechanisms must be refined.

Materials and methods

Animals and anatomy

Adult cf. *Prosarthria teretirostris* were taken from breeding colonies established at the Universities of Ulm and Konstanz, while adult *Carausius morosus* and *Schistocerca gregaria* were from breeding colonies established at the University of Ulm. The cf. *Prosarthria teretirostris* founder colony was introduced to Germany by Klaus Riede, who deposited a voucher specimen at the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany. The species appears to be restricted to the lowland rainforest of western Amazonia. Preliminary determination of the genus *Prosarthria* was according to Brunner von Wattenwyl (Brunner von Wattenwyl, 1890), and a description of the species *teretirostris* is in preparation (see also Flook et al., 1999), hence the present designation as cf. *Prosarthria teretirostris*. In the following, we refer to the species as *Prosarthria teretirostris*.

Anatomical details were examined by dissecting freshly killed animals. To examine the innervation pattern and anatomy of the femoral chordotonal organ (fCO), the nervous tissue was stained with Ni^{2+} (Bräunig, 1987). The animal was pinned to a cork board, dorsal side up, and opened by a dorsal midline incision, and the nervous system was exposed by removing the gut, salivary glands and fatty tissue. The segmental ganglion of the meso- or metathorax was punctured with a minuten pin, and a glass micropipette was inserted. The pipette contained a 5% NiCl_2 (w/v) solution in distilled water and had a tip diameter of 50–100 μm . The wound in the ganglion sheath was sealed, and the micropipette was fixed in place with a drop of cyanacrylate glue. Ni^{2+} was infused into the nervous system by injecting approximately 10 μA of pulsed current (1 Hz, duty cycle 40–50%) for 24–48 h. Ni^{2+} was precipitated as nickel rubeanate with dithioamide ($\text{H}_2\text{NCSSCNH}_2$, anhydride of rubianic acid) after current injection had been completed. The central nervous system was removed from the animal, dehydrated and cleared according to standard procedures, and the staining was intensified according to Mesce et al. (1993) and Davis (1982) if necessary. Locust saline (Usherwood and Grundfest, 1965) was used for rinsing the preparation where appropriate.

Preparation and experimental procedure

For all experiments, animals were immobilised on a cork board with minuten pins and dentists' glue (Protemp, ESPE). The femur of the middle or hind leg under examination was glued to the cork board such that the femur–tibia joint extended

beyond the edge of the board and the tibia was free to move. The cork board could be arranged in a horizontal or vertical plane, as necessary. Tibial movements were monitored in two ways. First, a semi-circular paper flag was attached to the tibia, in the plane of movement and centred on the femur–tibia joint. This flag cast a shadow on a semi-circular photosensitive diode, with the degree of shading, and hence the voltage output of the diode, being dependent on the femur–tibia angle (Weiland et al., 1986). The paper flag, although weighing little, may noticeably have increased friction in the femur–tibia joint, particularly when the plane of movement was horizontal, as was usually the case. To examine this possibility, we employed a second method of movement recording in which the tibia moved above a semicircular array of light barriers (photodiodes), with neighbouring light barriers being separated by 5° (Kittmann, 1991). The resulting movement record thus had a resolution of 5° and avoided mechanical loading of the tibia. No differences were observed between the results obtained with the two methods (e.g. data in Fig. 3), indicating that joint friction generated by the paper flag was negligible in the present context.

To stimulate the femoral chordotonal organ, a window was cut into the anterior dorsal surface of the femur, sparing the attachment sites of the extensor tibia muscle where possible. This exposed the apodeme of the femoral chordotonal organ, which was clamped into a pair of forceps attached to a transducer (pen motor, Hellige, or modified loudspeaker with feedback system) (Hofmann and Koch, 1985) and cut distally.

The latter preparation exposed not only the fCO tendon but also the nerve supply of the extensor tibiae muscle. Neurograms of slow and fast extensor tibiae motoneurons (SETi, FETi) were recorded by attaching bipolar hook electrodes to a nerve branch entering the extensor muscle. Amplification and storage of electrophysiological data and movement recordings used conventional techniques (custom-made amplifiers, Heinecke, Seewiesen; tape recorder, RACAL store 4DS).

For each species, the relationship between movement of the femur–tibia joint (in degrees) and movement of the fCO receptor apodeme (in μm) was determined in several animals (between three and 10) and double-checked after an experiment where appropriate. A movement of 40° in the middle leg femur–tibia joint corresponded to a movement of the receptor apodeme of approximately 350 μm in *Prosarthria teretirostris* females, 160 μm in *Prosarthria teretirostris* males, 240 μm in *Schistocerca gregaria* and 200 μm in *Carausius morosus*. A movement of 40° in the hind leg joint corresponded to movements of approximately 330 μm and 210 μm of the receptor apodeme in *Prosarthria teretirostris* females and males, respectively. In the text, stimuli delivered to the fCO are usually given in micrometres, instead of degrees, because the stimuli translate slightly differently into angular movement between species and individuals, causing inconsistencies if further calculations were based on degrees (Fig. 7 is an exception where similarly sized individuals could be obtained within species groups).

Data acquisition and evaluation

The data stored on magnetic tape, and sometimes also the original experiments, were run out on a chart recorder (Yokogawa ORP 1200). Movement recordings (amplitudes, half-lives, etc.) were usually evaluated by hand, although the optical movement recordings (Kittmann, 1991) yielded step curves, each step corresponding to a 5° interval, and thus required approximation by exponential functions to determine their time constants. Electrophysiological data were digitised (1401, Cambridge Electronic Design) for further evaluation using the software packages Spike2 (Cambridge Electronic Design) or datapac (RUN Technologies). For statistical assessment of differences between experimental samples, the *U*-test after Wilcoxon, Mann and Whitney was used (significance level 5%). Throughout the text, *N* indicates the number of animals used and *n* the number of measurements carried out in these animals (only stated if more than one measurement was made per animal). Unless stated otherwise, data are given as means with standard deviations (\pm S.D.).

Results*Gross anatomy of the femoral chordotonal organ of Prosarthria teretirostris*

The sensor of the femur–tibia control system is a femoral chordotonal organ (fCO), conforming with that found in other orthopterans and lepidopterans studied (for a review, see Field and Matheson, 1998) with regard to both structure and function. Other sense organs that monitor the femur–tibia angle do not participate in the control of joint angle and posture in stick insects (Bässler, 1977) and are thus not considered here. The gross anatomy of the fCO was investigated by Ni^{2+} staining of the segmental nervous system (see Materials and methods).

In the middle leg ($N=5$), the sensory organ is located in the most proximal part of the femur, just below, and attached to, the anterior-dorsal surface (Fig. 2A,B). The receptor organ consists of two portions. Preliminary electrophysiological recordings suggested that the proximal scoloparium is most sensitive to vibration stimuli, while the distal scoloparium is the transducer for joint angles and movements. This, too, is in agreement with the results of previous studies in stick insects (Kittmann and Schmitz, 1992; Büschges, 1994) and locusts (Field and Pflüger, 1989) (for a review, see Field and Matheson, 1998). Both scoloparia are innervated by branches of leg nerve 5B2 (numbering analogous to the description in the locust) (Snodgrass, 1929). The fCO is attached to the most proximal and dorsal part of the tibia *via* a long tendon, or receptor apodeme. Since the apodeme attaches dorsal to the axis of rotation of the joint (as in all insects examined so far) (e.g. Field and Pflüger, 1989), the sense organ is stretched by flexion movements of the femur–tibia joint and relaxed by joint extension.

In the hind leg ($N=3$), the general structure and innervation patterns of the fCO (Fig. 2C) are similar to those in the middle leg. However, the receptor organ is located more distally,

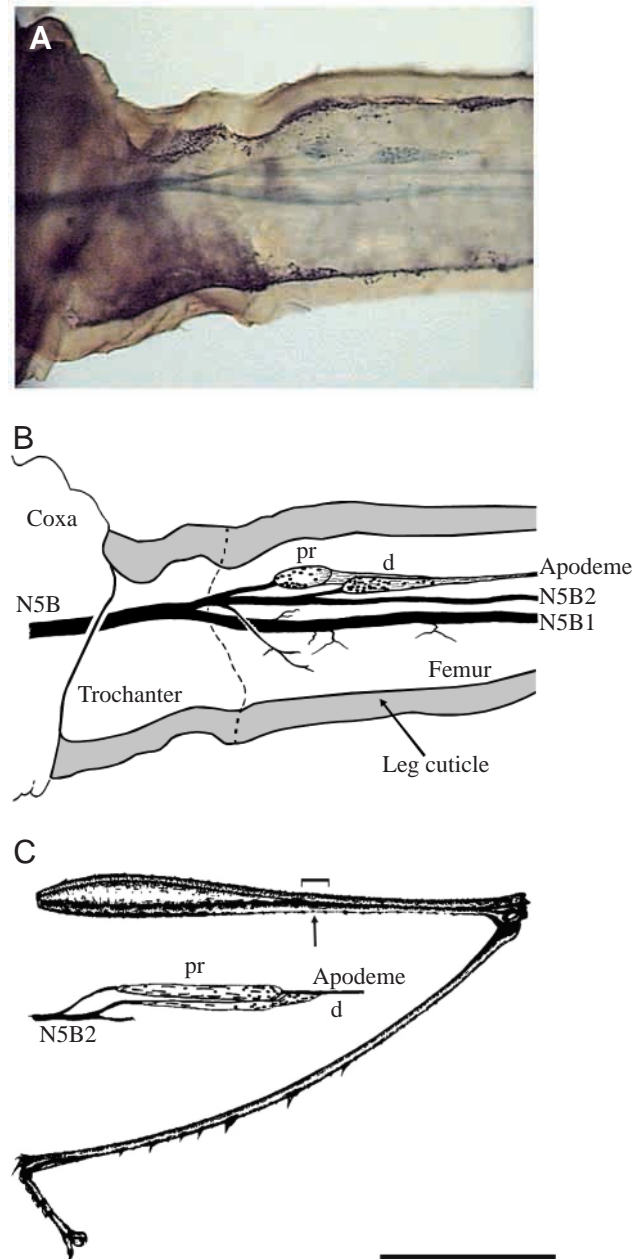


Fig. 2. Anatomy and innervation of the femoral chordotonal organ (fCO). (A) A Ni^{2+} -filled preparation of the middle leg nerves and fCO. The anterior dorsal cuticle of the trochanter and femur has been removed to provide a view of the internal structures. (B) Drawing of the preparation in A, identifying the main structures, named according to Snodgrass (1929) for the locust. Note the proximal (pr) and distal (d) portions of the fCO, the leg nerves 5B1 and 5B2 and the receptor apodeme. Shading indicates the cut surface of the leg cuticle, exposed by removing the anterior-dorsal half of the trochanter and femur (see above). (C) Drawing of a female hind leg and fCO; the arrow indicates the location, and the bracket the size, of the fCO in the leg. Labelling as in B. The inset shows an expanded view of the fCO. Scale bars, 800 μm for A and B, 10 mm for C.

roughly half-way between the (immobile) trochanter–femur and femur–tibia joints. The organ has a more elongated shape

(approximately 1 mm long) and is attached to the anterior-dorsal cuticle in a region where the leg starts to bulge to accommodate the bulk of the large extensor tibiae muscle. It is interesting to note that the location of the fCO in the hind leg of *Prosarthria teretrirostris* is thus intermediate between the situations in a normal insect walking leg (such as the middle leg of *Prosarthria teretrirostris*) and the specialised jumping leg of grasshoppers and locusts, which have very distally located fCOs (Usherwood et al., 1968).

Closed-loop situation: catalepsy

In a first series of experiments, the general characteristics of catalepsy in *Prosarthria teretrirostris* were assessed. Two hind

legs (one male, one female) and three middle legs (two male, one female) were examined with the attached-flag method. 10 min after the animal had been fixed in the experimental apparatus, the femur-tibia joint was bent by hand to a position of approximately 40° (minimum joint angle is between 30° and 40° because of the curved tibia; Fig. 2C), kept there for 15–30 s, and then released. When the leg had reached a constant position after 8–35 min, the joint was passively extended to a position of approximately 175°, again held there for 15–30 s, and released. Between three and 15 such cycles were obtained per leg without major disturbance by active movements.

Fig. 3A shows a sample recording, strongly reminiscent of

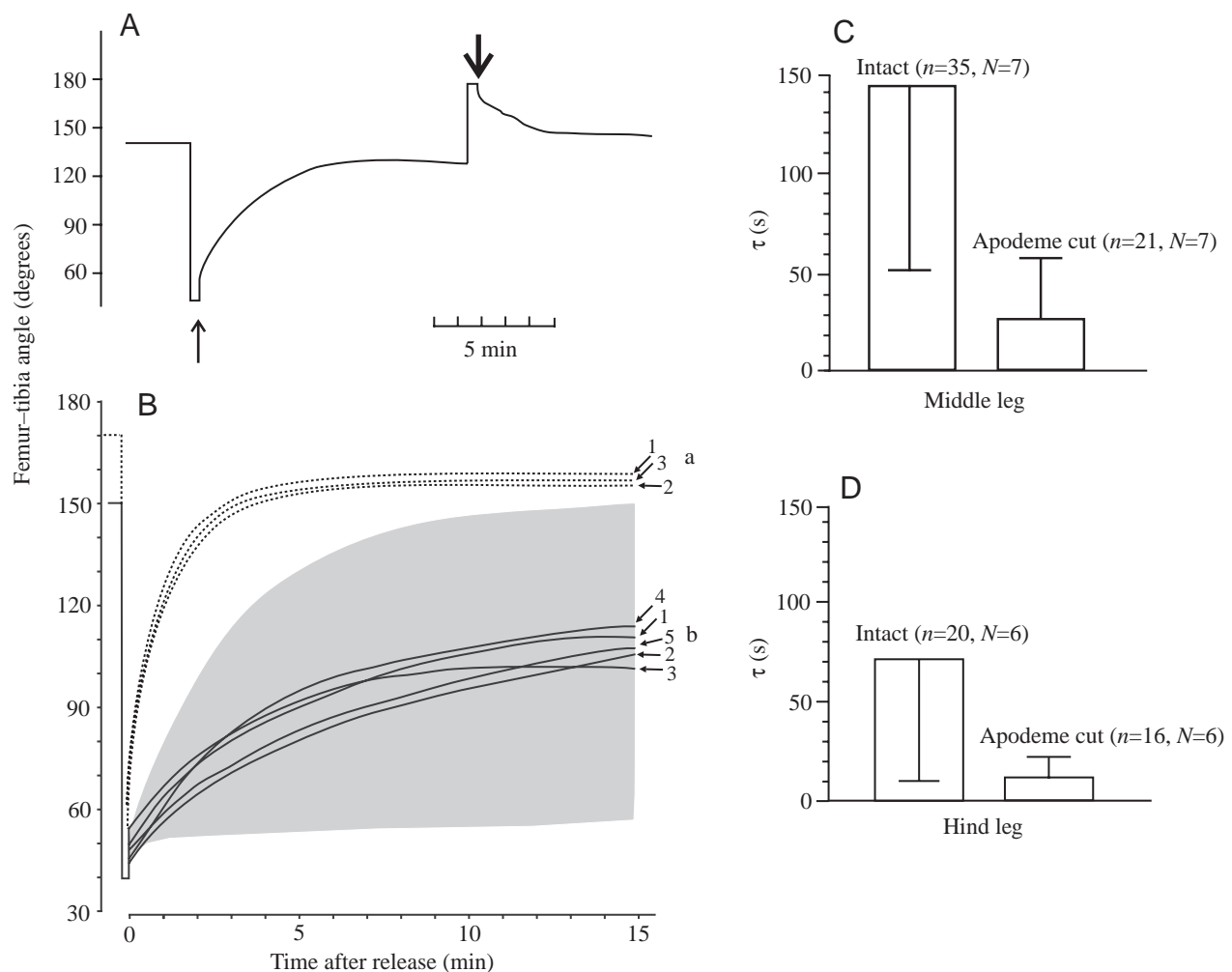


Fig. 3. Catalepsy in *Prosarthria teretrirostris*. (A) Original recording from a female hind leg. Starting from a resting position, the joint was (almost fully) flexed to 40°, kept there for approximately 25 s and released (light arrow). When the leg had reached a constant position, it was (almost fully) extended to 170°, kept there for 25 s and released (heavy arrow). (B) Consecutive return movements of two hind legs recorded after passive flexion to 40°. The movement velocities in animal a (female) were the fastest recorded. The animal was briefly activated by touching its abdomen between return movements 2 and 3. Movement velocities in animal b (male) were the slowest recorded. Between return movements 4 and 5, the animal was briefly activated by touching its abdomen. Other individuals yielded curves located between the sample recordings shown. The shaded area indicates the range of return movements reported for *Carausius morosus* (Bässler, 1972b). (C,D) Time constants (τ) for the return movements (means \pm S.D.) of seven middle (C) and six hind (D) legs of males, before and after cutting the femoral chordotonal organ receptor apodeme. Differences between the intact and operated situations are statistically significant for both hind and middle legs. The leg position was monitored with the attached-flag method in A and B and with the optical method in C and D.

the data obtained in *Carausius morosus* (Bässler, 1972b, 1983, 1993). The characteristics observed in all legs examined are as follows. When released, the leg initially twitched back by 5–30° and then returned more slowly, and with gradually decreasing velocity, towards the starting position. Except for the fastest ones, the return movements were too slow to be visible to the naked eye (see Introduction). The leg usually returned almost to the starting position; this differed from leg to leg but, in most cases, was closer to the fully extended than the fully flexed position. The difference between the final positions reached after imposed flexion and imposed extension was between 10 and 35° ($n=42$). Consecutive return movements from the same release position and the return velocities in a particular leg were in the same range, even over several hours of experimentation, but there were clear differences between legs (Fig. 3B). This is in contrast to *Carausius morosus*, in which consecutive return movements become progressively slower (Bässler, 1972b).

When *Prosarthria teretrirostris* was briefly touched on the abdomen to induce active movements, the subsequent return movements were in the same range as before or became faster ($N=4$, $n=10$; Fig. 3B). This is again in contrast to the situation in *Carausius morosus*, in which the return movements are always much slower following induced active movements (Bässler, 1972b) or disturbances. Return movements in *Carausius morosus* thus cover a broad range of velocities, indicated by the shaded area in Fig. 3B (in this and the following figures, shaded graphs or areas indicate previously published data from phasmids that are included for comparison). In *Prosarthria teretrirostris*, the total range of return velocities is also relatively broad (the two examples in Fig. 3B demonstrate the borders of this range, see also below), although a particular leg covered only a small segment of this range. The slowest return velocities recorded immediately after the initial, fast twitch were 5° min⁻¹ (0.1° min⁻¹ in *Carausius morosus*) (Bässler, 1972b), indicating the threshold range of the velocity-sensitive component of the femur–tibia feedback loop (see Introduction and below).

In a second set of experiments, seven middle and six hind legs of males were examined with the optical recording method (see Materials and methods) (Kittmann, 1991) to make an initial assessment of differences between the closed-loop and open-loop situations. Legs were kept in the extended or flexed positions for 3 min to minimize the amplitude of the initial twitch movement (in *Carausius morosus*, twitch amplitude decreases with holding time) (Godden, 1974; Bässler, 1983). To characterize return movements following the initial twitch, the recorded step curves were approximated by e-functions and the time constants determined. After several cycles of imposed flexion and extension, we cut the receptor apodeme of the fCO (see Fig. 2B) and repeated the measurements. Fig. 3C,D gives the mean values and standard deviations of the time constants for the middle and hind legs. In both sets of legs, the slow return movements were abolished by cutting the receptor apodeme (time constants different; $P<0.05$), that is, by eliminating sensory feedback from the fCO regarding the joint

angle. Sham operations (removing only the cuticle, $N=2$) had no effect. Time constants determined in the closed-loop situation were in the same range as those measured in the preceding set of experiments; for example, the time constants were 22–65 s ($n=11$) in leg a and 230–370 s ($n=12$) in leg b (Fig. 3B).

In summary, the (slow) return movements observed after imposed displacement of the femur–tibia joint of *Prosarthria teretrirostris* (catalepsy) have a course similar to that reported in the stick insect *Carausius morosus*, although the range of return velocities is shifted to larger values, and catalepsy does not improve after disturbances. The scatter in the return movements in *Prosarthria teretrirostris* results mainly from differences among individuals, whereas in *Carausius morosus*, scatter within individuals also plays an important role. Sensory feedback from the fCO is essential for catalepsy.

Open-loop situation: sinusoidal stimuli

The similarities in the cataleptic movements between species suggest that the properties of the femur–tibia joint control system in *Prosarthria teretrirostris* resemble those of stick insects. A first characterization was completed in the open-loop situation, that is, with mechanical stimulation of the femoral chordotonal organ after severing the receptor apodeme.

We first tested the open-loop system with sinusoidal input in three hind legs (all females) and five middle legs (three females, two males) with the attached-flag method. We used long-lasting (2 min) stimuli with amplitudes of 100 µm and frequencies between 0.01 and 2 Hz. The amplitude of tibial movement (the difference between maximum and minimum femur–tibia angle) elicited by the stimulus differed markedly from leg to leg but, in all cases, it was largest at 0.1 Hz. In the three hind legs, maximum movement amplitude ranged from 150 to 20°, and in the five middle legs from 150 to 35°. As examples, the amplitude/frequency characteristics of a strongly responding female's hind and middle leg are shown in Fig. 4 (dotted lines in Fig. 4Ai,Bi; details below).

To assess the habituation characteristics of the feedback loop, we compared the response amplitude of the first stimulus cycle with that of the tenth and twentieth cycles. At 0.1 Hz, the amplitude of the tenth cycle was between 70 and 140% (mean 101%, $n=10$) of that of the first cycle; at 0.5 Hz, the amplitude of the tenth cycle was between 75 and 150% (mean 103%, $n=10$) and that of the twentieth cycle was between 60 and 130% (mean 95%, $n=9$). Stimulus frequencies of 1 and 2 Hz yielded similar results. Thus, there was no habituation with sinusoidal stimulation of the fCO, contrasting with the results obtained in the phasmids *Carausius morosus* (Kittmann, 1991; Bässler and Nothof, 1994) and *Cuniculina impigra* (Bässler and Stein, 1996), which show a pronounced reduction in response amplitude over time.

During ongoing stimulation (0.1, 0.5, 1.0 Hz), the animal was briefly touched on its abdomen to elicit active movements ($N=13$). In seven cases, this slightly increased the amplitude of leg movements, while in six cases, the amplitude remained

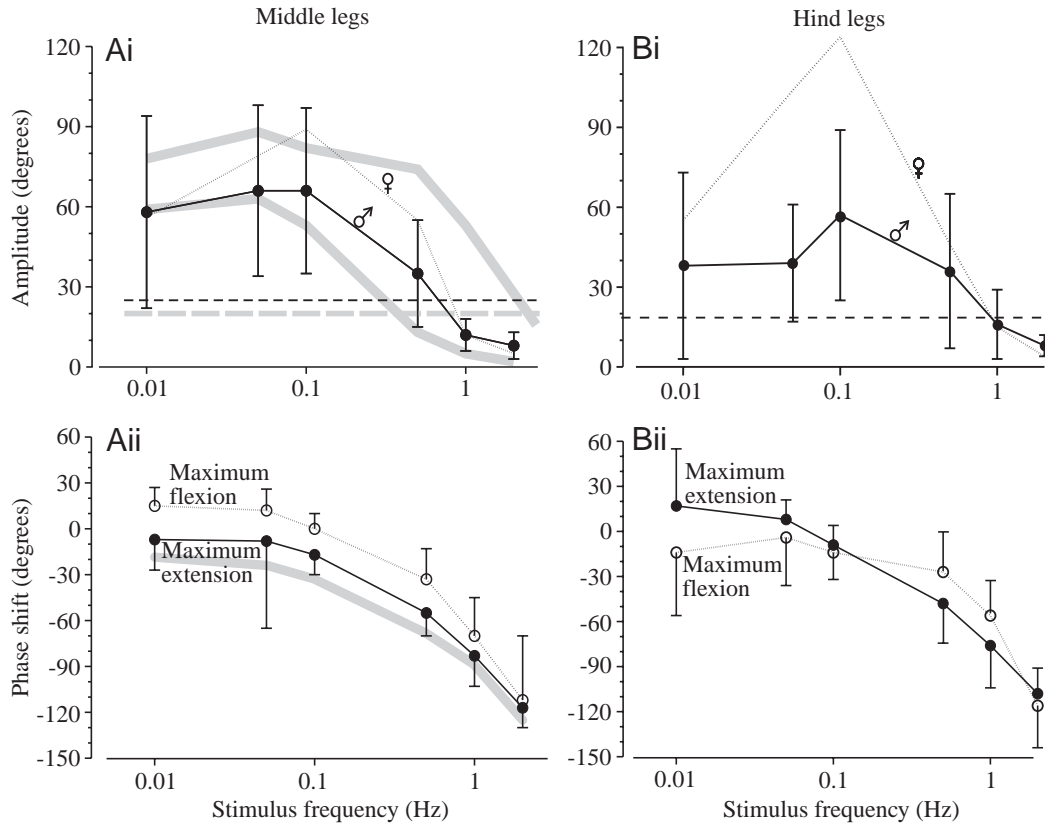


Fig. 4. Sinusoidal stimulation of the femoral chordotonal organ (fCO) (amplitude $100\mu\text{m}$); movement response. (A) Middle legs. (Ai) Relationship between stimulus frequency and response amplitude (tibia movement). Solid line, mean values (\pm s.d.) from seven male middle legs ($n=41\text{--}162$ per data point) (optical recording method). Dotted line, mean values from a strongly responding female (attached-flag method). In both cases, values from the first 10 cycles were used. The shaded lines are the curves for *Carausius morosus* (upper curve, data for the first stimulus cycle) (Kittmann, 1991) and *Cuniculina impigra* (lower curve, habituated situation) (Bässler and Foth, 1982). Horizontal broken lines indicate a gain of 1 (see text). (Aii) The phase shift between the stimulus and the response plotted *versus* stimulus frequency; data from the same animals as in Ai. Values are plotted separately for the relationship maximum joint flexion minus maximum fCO release (open circles) and maximum joint extension minus maximum fCO elongation (filled circles). The shaded line shows the corresponding curve for *Carausius morosus*, as above. (Bi,ii) Corresponding graphs for hind legs (seven males; one female).

constant or even decreased slightly. This is in agreement with the results reported above for the closed feedback loop, where disturbances did not change cataleptic behaviour (but is again in contrast to the situation in stick insects) (Bässler, 1993).

In a second set of experiments, and for a quantitative examination of amplitude/frequency and phase/frequency relationships, seven hind and seven middle legs of males were investigated with the optical recording method. Since tibial movements, in particular those at lower stimulus frequencies, were not exactly sinusoidal, phase shifts were always measured in two ways, first, as the difference between maximum elongation of the fCO and maximum extension of the joint and, second, as the difference between maximum release of the fCO and maximum joint flexion (in degrees, with the cycle period corresponding to 360° ; positive values denote leg movements advancing the stimulus cycle). Values for amplitude and phase shift were averaged for each stimulus frequency and are shown as modified Bode plots in Fig. 4. In intact males, on average, a stimulus amplitude of $100\mu\text{m}$ would signal a joint movement of approximately 25° (for middle legs) and 19° (for hind legs).

Response amplitudes of 25 and 19° therefore represent a gain of 1 (output amplitude equals input amplitude). These values are indicated by horizontal dashed lines in Fig. 4Ai,Bi.

Fig. 4 also shows data from strongly responding females, obtained with the attached-flag method (see above); a gain of 1 corresponds to approximately 15° in the middle and 12° in the hind leg. The data indicate that even strongly responding females possess response characteristics similar to those of males. Values for the other females were well within the standard deviations of values for the males. In particular, a gain of 1 was reached at the same critical frequency, just below 1 Hz, in both genders.

The amplitude/frequency characteristics of *Carausius morosus* (Bässler, 1983, 1993) exhibit slightly higher gains, mainly because gains greater than 1 (upper shaded line in Fig. 4A, valid for *Carausius morosus*, unhabituated situation) are maintained up to higher movement frequencies. Correspondingly, the upper corner frequency is slightly lower in *Prosarthria teretirostris* when compared with *Carausius morosus* (0.1 Hz compared with up to 0.5 Hz) (Bässler, 1983,

1993), while it is in the same range as that of *Cuniculina impigra* (Bässler and Foth, 1982), especially taking into account that the values for *Cuniculina impigra* shown in Fig. 4Ai represent the fully habituated state. The general shape of the characteristics is the same in all species, however, showing a slight increase in gain from the lowest tested frequencies towards a maximum between 0.05 and 0.5 Hz and a steep decrease towards higher frequencies. Phase shift values are indeed almost identical in *Prosarthria teretirostris* and the stick insects.

From the Bode plot determined for an open-loop system, one can estimate whether the closed-loop configuration will be stable or subject to feedback oscillation. If the phase shift is less than 180° at the particular frequency at which the gain equals 1 (intersections between amplitude/frequency graphs and dashed lines in Fig. 4Ai,Bi), the feedback system is stable (Nyquist criterion; strictly speaking, gain has to be below 1 at a phase shift of 180° , which was not measured here). If, however, the phase shift is 180° (input and output in antiphase) or above at this frequency, oscillations will be generated in the closed-loop configuration. The difference between the observed phase shift and 180° is thus termed the 'phase reserve' (Bässler, 1983). The Nyquist criterion, though strictly valid only for linear systems, still provides a first approximation for the non-linear (see below) femur-tibia control loop, and it predicts that the closed-loop system of *Prosarthria teretirostris* is stable, with a phase reserve of $70\text{--}110^\circ$. The phase reserve is thus much larger than in *Carausius morosus* ($30\text{--}40^\circ$) and similar to values in *Cuniculina impigra*.

Schistocerca gregaria middle legs have similar phase shifts to those recorded in *Prosarthria teretirostris* but significantly smaller gains (almost exclusively below 1) (Ebner and Bässler, 1978), resulting in perfectly stable joint control systems.

In a third series of experiments, extracellular recordings were made from the nerve supplying the extensor tibiae muscle during fCO stimulation. This nerve contains the axons of the fast extensor tibiae (FETi), slow extensor tibiae (SETi) and common inhibitor (CI1) motoneurons. The middle legs of six females were used. Stimulus amplitude was $350\ \mu\text{m}$, and stimulus frequencies ranged from 0.0065 to 2 Hz.

In all animals, only SETi was active before as well as during stimulation. This is in contrast to stick insects, in which FETi is often also active, at least during the initial stimulus cycles (see Fig. 7A) (Bässler, 1983). In the absence of stimulation, SETi was spontaneously active, as it is in stick insects. During sinusoidal stimulation, SETi discharge was restricted to the fCO elongation phase (mimicking leg flexion). To characterize the responses, circular phase histograms (Fig. 5A) were prepared (phase 0° corresponding to maximum fCO elongation). These histograms allow the mean vector (its direction characterizing the phase shift; Fig. 5C), mean spike frequency and modulation (Fig. 5B) with respect to stimulus frequency to be calculated. Modulation and mean discharge, rather than maximum spike frequency, were used to characterize the response since they take into account all action

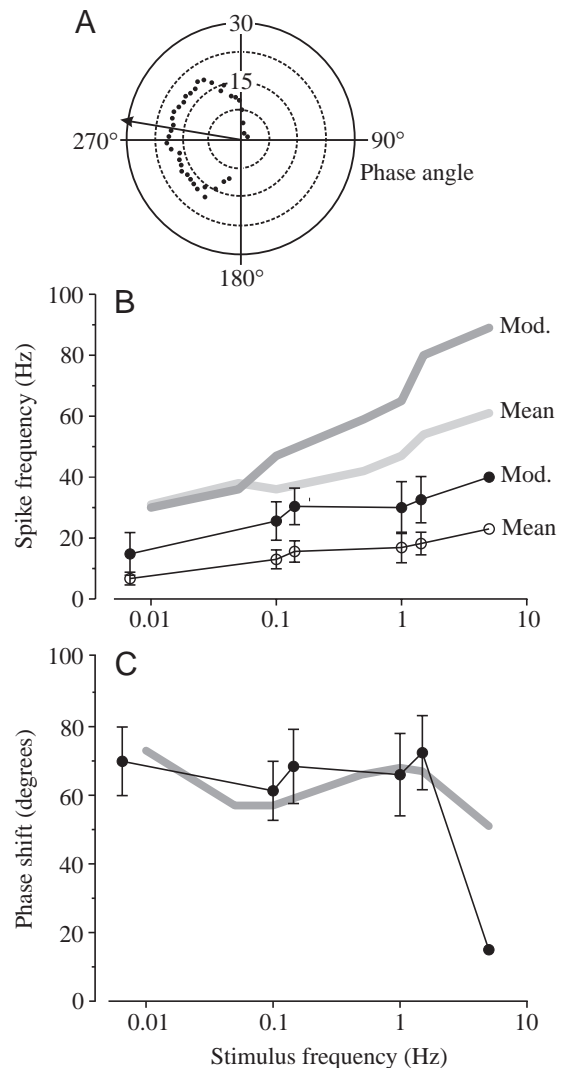


Fig. 5. Sinusoidal stimulation of the femoral chordotonal organ (fCO) (amplitude $350\ \mu\text{m}$); SETi activity (female middle legs). (A) Circular phase histogram (bin width 5°) of SETi spike activity (spikes s^{-1}) recorded during three stimulus cycles at 0.0065 Hz. The mean vector (arrow) is at 280° . (B) Modulation (Mod., filled circles) and mean activity (open circles) of SETi with respect to stimulus frequency (means \pm s.d., $N=6$; except at 5 Hz, where $N=1$). The shaded lines are the corresponding curves for *Carausius morosus* (Kittmann, 1997). (C) Phase shift between maximum fCO elongation and the mean vector (see A; means \pm s.d., $N=6$; except at 5 Hz, where $N=1$). The shaded line shows the corresponding curve for *Carausius morosus*, as in B.

potentials discharged during the stimulus cycle rather than just the shortest spike interval (e.g. Kittmann, 1997). The shaded curves in Fig. 5 again illustrate the corresponding data from *Carausius morosus* (Kittmann, 1997). It is evident that the stick insect shows stronger responses and that these probably persist to higher stimulus frequencies. In addition, FETi discharged during the initial stimulus cycles, as mentioned above.

In summary, the motoneuronal response is significantly

smaller in *Prosarthria teretirostris* than in the phasmids. This corresponds to the lower gain obvious in the movement recordings (Fig. 4A). Phase shift values are similar in all species, again in agreement with the movement recordings. There is no noticeable decrease in the gain of motoneuron responses up to frequencies of 5 Hz, indicating that muscular properties play an important role in the decline in response amplitude observed in the movement recordings above approximately 0.1 Hz (Fig. 4Ai,Bi).

Open-loop situation: ramp-and-hold input

In a first series of experiments, the fCOs of six middle and two hind legs (half from females, half from males) were stimulated with ramp-and-hold stimuli (stimulus amplitude $100\ \mu\text{m}$ and stimulus velocities between 0.1 and $500\ \mu\text{m s}^{-1}$). We used the attached-flag method to monitor tibia movement. In only two legs was the resting position such that both flexion and extension movements were possible with reasonable amplitudes. Fig. 6A shows a sample recording from one of

these animals. In the remaining animals, only the flexion movements were large enough to be evaluated.

Fig. 6A illustrates that there is a prominent velocity-sensitive portion and a smaller position-sensitive portion of the response (explained in the inset of Fig. 6C). The position-sensitive portion is the difference between the steady-state leg positions reached after an extension movement, caused by fCO elongation (note the dotted line), and a flexion movement, elicited by fCO relaxation. It was between 8 and 25° (for a $100\ \mu\text{m}$ stimulus) and thus in the same range as for *Carausius morosus* (Bässler, 1972b), *Cuniculina impigra* (Bässler and Foth, 1982) and *Schistocerca gregaria* middle legs (Ebner and Bässler, 1978).

Thresholds of velocity-sensitivity were between 0.1 and $1\ \mu\text{m s}^{-1}$ for different *Prosarthria teretirostris* legs. Such stimulus velocities would be produced in the closed-loop system by joint movements of 0.1 – $3^\circ\ \text{min}^{-1}$, which agrees well with the slowest initial joint movements observed during catalepsy, which reached $5^\circ\ \text{min}^{-1}$ (see above and Discussion).

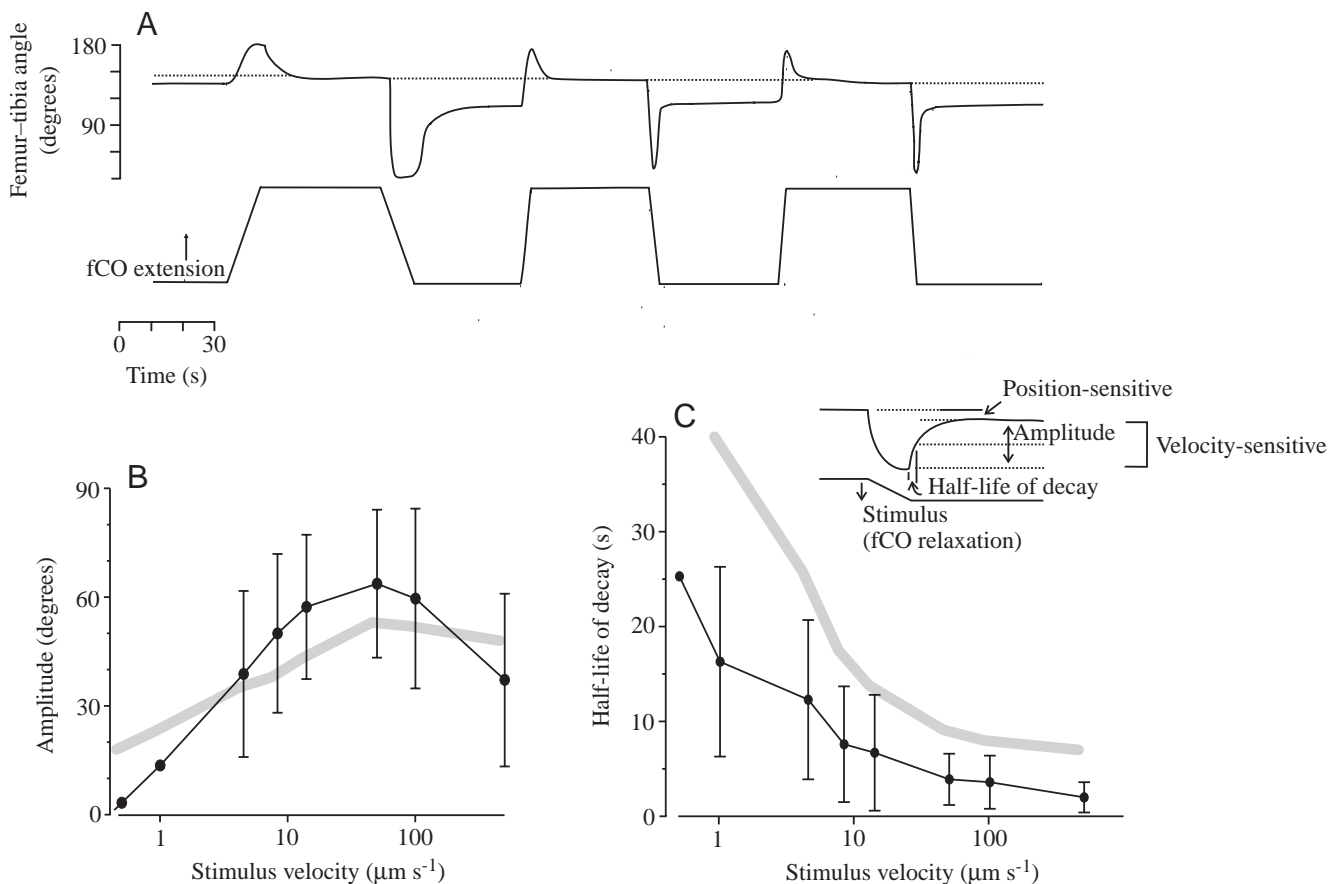


Fig. 6. Ramp-and-hold stimulation of the femoral chordotonal organ (fCO); movement response (attached-flag method). (A) Original recording from a male middle leg. Top trace, femur-tibia angle (the dotted reference line indicates the steady-state position reached after apodeme extension); bottom trace, fCO stimulus (amplitude $100\ \mu\text{m}$). For a definition of the position-sensitive and velocity-sensitive portions of the response, see inset in C. (B) The amplitude of the velocity-sensitive response component (for a definition, see inset in C and text) plotted versus stimulus velocity; pooled data from eight animals (means \pm S.D.; $n=1$ – 4 per animal). With the exception of two animals, only flexion movements were evaluated. The shaded line shows the corresponding curve for *Carausius morosus* (Bässler, 1993). The standard deviation was not calculated for the first (left-hand) two data points because the data were not normally distributed. (C) The half-life of the decrease in the velocity-sensitive portion of the response plotted versus stimulus velocity. Same data set as in B.

This velocity threshold is clearly higher than in *Carausius morosus* ($0.03 \mu\text{m s}^{-1}$, corresponding to $0.005^\circ \text{s}^{-1}$) (Bässler, 1972a) and slightly exceeds that in *Cuniculina impigra* ($<0.1 \mu\text{m s}^{-1}$) (Bässler and Foth, 1982). The amplitude of the velocity-sensitive portion of the response (see inset of Fig. 6C) was largest at moderate velocities ($50\text{--}100 \mu\text{m s}^{-1}$) (Fig. 6B). Absolute values differed greatly among individuals (between 25 and 97° for a stimulus velocity of $50 \mu\text{m s}^{-1}$), but were in the same range as for *Cuniculina impigra* (Bässler and Foth, 1982). The half-lives of decline of the velocity-sensitive response component were dependent on stimulus velocity (Fig. 6C), averages ranging between 25 s (at $0.05 \mu\text{m s}^{-1}$) and 2 s (at $500 \mu\text{m s}^{-1}$). These values are smaller than those reported for *Cuniculina impigra* (Bässler and Foth, 1982). *Carausius*

morosus and locusts were not investigated in this respect (however, see Discussion).

Again, there is good agreement between these data and the observations of cataleptic behaviour (see above). In *Prosarthria teretrirostris*, the velocity-sensitive components decrease with shorter half-lives than in phasmids, while the general dependency of half-life on stimulus velocity is similar. Consequently, the amplitude of the response drops faster when approaching lower stimulus velocities than it does in *Cuniculina impigra*. Therefore, the decelerating effect of the velocity-sensitive portion is less pronounced in *Prosarthria teretrirostris* and, since the position-sensitive part is of the same magnitude, return velocities have to be faster (as shown in Fig. 3B).

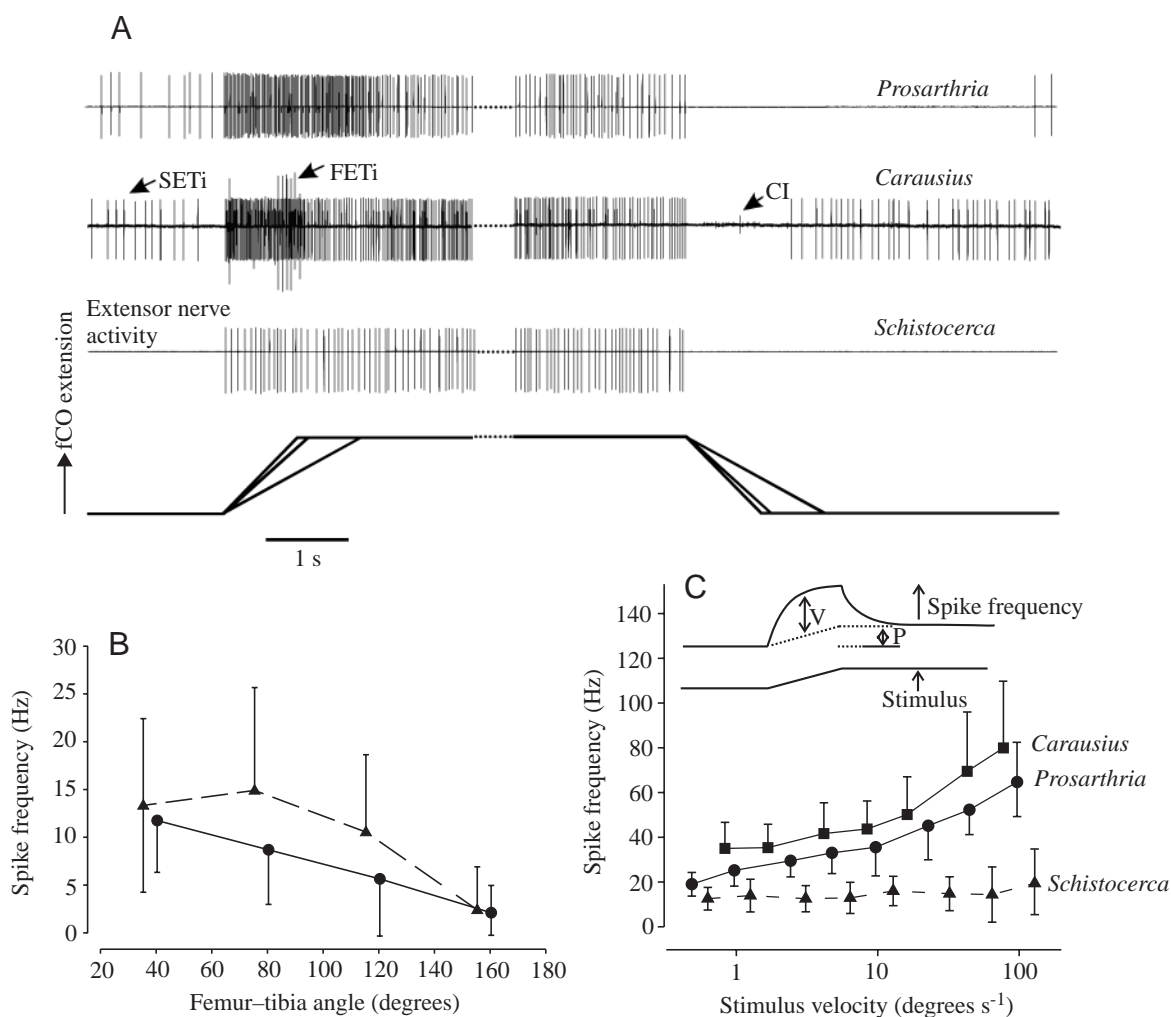


Fig. 7. Ramp-and-hold stimulation of the femoral chordotonal organ (fCO); motoneuron discharge. (A) Sample recordings from the three relevant species: *Prosarthria teretrirostris* (top; stimulus amplitude $350 \mu\text{m}$, corresponding to approximately 40°), *Carausius morosus* (middle, $200 \mu\text{m}$, approximately 40°) and *Schistocerca gregaria* (bottom, $240 \mu\text{m}$, approximately 40°). CI, common inhibitor neuron. (B) Position-sensitive portion of the motoneuron response, P (for a definition of P, see in the inset in C and the text) plotted versus femur-tibia angle. *Prosarthria teretrirostris*, circles ($N=6$); *Schistocerca gregaria*, triangles ($N=5$); means \pm s.d. The data do not differ significantly between species. (C) Velocity-sensitive portion of the response, V (for a definition of V, see the inset and the text) plotted versus stimulus velocity. *Prosarthria teretrirostris*, circles ($N=6$, $n=3$ stimuli per animal); *Carausius morosus*, squares ($N=5$, $n=3$); *Schistocerca gregaria*, triangles ($N=7$, $n=3$); means \pm s.d. A regression line (not shown) through data points for *Schistocerca gregaria* has a slope not significantly different from zero.

In a second series of experiments, SETi activity was recorded during ramp-and-hold stimulation of the fCO in six female middle legs. Stimulus amplitude was 350 μm , and stimulus velocities ranged from 4.5 to 8800 $\mu\text{m s}^{-1}$ (the latter value exceeding physiological values during a jump by approximately twofold). For each stimulus velocity, three measurements were made per animal. To minimize hysteresis effects, we waited at least 60 s between consecutive stimuli. Since comparable data are not available for *Carausius morosus* and locusts, and data for *Cuniculina impigra* (Bässler and Foth, 1982) had been evaluated in a different way, measurements were also made on *Carausius morosus* and *Schistocerca gregaria* middle legs. The stimulus amplitudes were 200 μm in *Carausius morosus* and 240 μm in *Schistocerca gregaria*, both values corresponding to a change of approximately 40° in joint angle (see stimulus curve in Fig. 7A).

In *Prosarthria teretrirostris* and *Schistocerca gregaria*, only SETi fired during the experiments, whereas in *Carausius morosus* FETi spikes were also often observed during rapid elongation stimuli, and CII was frequently active during fCO relaxation. SETi was spontaneously active in all three species, although its discharge frequency was usually very low in *Schistocerca gregaria*. During fCO relaxation, SETi was silent in all three species (Fig. 7A).

Position-sensitivity was examined in *Prosarthria teretrirostris* ($N=6$) and *Schistocerca gregaria* ($N=5$) middle legs. The receptor apodeme was moved in three steps, each corresponding to a change of 40° in joint position, and SETi discharge frequency was determined 50 s after the end of each step (Fig. 7B). The values for the two species are in the same range and not statistically different. The position-sensitive part of the response is apparently similar in these two species (see also movement recordings above).

For a quantitative comparison of the different species, we measured the velocity-sensitive component of the response. To allow for the position-sensitive portion, which develops during the course of a stimulus ramp, we measured the average spike frequency during the ramp (which would be constant if it represented only the velocity-sensitive portion), and subtracted the interpolated position-sensitive component at the middle of this ramp (the mean value of spike frequencies determined at the starting position and 4 s after the final position had been reached; see inset of Fig. 7C). Fig. 7C summarizes the results obtained in all three species. It is obvious that velocity-sensitivity is very low in *Schistocerca gregaria*, as previously demonstrated for *Locusta migratoria* middle legs (Büschges and Wolf, 1995). Velocity-sensitivity is pronounced in *Prosarthria teretrirostris*, although slightly less than in *Carausius morosus*, even when considering only SETi responses (Fig. 7A). In *Carausius morosus*, FETi fires in addition to SETi at higher stimulus velocities, increasing the overall response and making the curve steeper (not shown).

In summary, the responses to ramp-and-hold stimuli are similar in *Prosarthria teretrirostris* and *Cuniculina impigra*

(many variables have not been measured in *Carausius morosus*). The velocity threshold is slightly higher in *Prosarthria teretrirostris*, and the decay of the velocity-sensitive component is faster, while the position-sensitive response components are similar in all three species.

Closed-loop situation: coupling an inert mass

The data reported above suggest that the femur–tibia control loop in *Prosarthria teretrirostris* works relatively close to instability, although not as close as in the phasmids. Coupling an inert mass to the system provides a further test of this assumption. Loading with an inert mass increases phase shift and also gain (the same leg musculature has to move a larger mass) and thus reduces phase reserve, increasing the tendency for oscillation (Bässler, 1983).

In two female and three male hind legs, an inert mass of 10 g (weight suspended from the ceiling; innate frequency of pendulum 0.4 Hz) was coupled to the end to the tibia. The animals were mounted such that the plane of movement in the femur–tibia joint was horizontal. In all cases, oscillations with frequencies of 0.8–1.2 Hz and amplitudes of 5–10° appeared when the legs were free to move. These oscillations lasted for some time (45 s to 20 min, $n=16$) unless terminated by an active kick. When the leg had come to rest, oscillations resumed in response to a brief disturbance of the animal, e.g. touching the abdomen or knocking against the weight. Except in one male, these oscillations again lasted for between 40 s and 5 min ($n=18$). In two female middle legs, the end of the tibia was coupled to an inert mass of 5 g, which also resulted in long-lasting oscillations, with frequencies of 1–1.5 Hz and amplitudes between 5 and 10°. Since the mesothoracic tibia is shorter, the weight often touched the experimental platform, interrupting the oscillations and precluding further analysis.

In a comparison with *Carausius morosus* (Bässler et al., 1974; Pfeiffer et al., 1993; Bässler and Nothof, 1994), we noted smaller oscillation frequencies (1.2–2.5 Hz in *Carausius morosus*) and longer-lasting oscillations (10 s to 2 min in *Carausius morosus*; similar values in *Cuniculina impigra*) (U. Bässler, unpublished data). Oscillation frequencies in all three species were within the range of values expected from the Bode plots, assuming that coupling an inert mass increases the phase shift, and to some extent the gain, of the open-loop system (Bässler, 1983). The lower frequencies observed in *Prosarthria teretrirostris* are thus consistent with the larger phase reserve noted above, and the longer-lasting oscillations attest to less effective gain control mechanisms. However, the amplitude of the observed oscillations was limited to 10°, rather than exploiting the full range of joint movement. This demonstrates the presence of some form of gain control, in the shape of a non-linear relationship between stimulus amplitude and gain, in *Carausius morosus* as well as in *Prosarthria teretrirostris* (Kittmann, 1991). In *Schistocerca gregaria* middle legs, coupling an inert mass to the tibia does not cause feedback oscillations (Ebner and Bässler, 1978).

Discussion

The primary purpose of the experiments reported above was to test a number of plausible assumptions regarding the functional basis and evolution of catalepsy derived from studies in stick insects (see Introduction). *Prosarthria teretirostris* forms a suitable test system because it shows clear morphological twig mimesis, which evolved independently of that in phasmids, and clear cataleptic behaviour. Notable differences are found in the gain control mechanisms, apparent through the absence of habituation, or comparable mechanisms, in *Prosarthria teretirostris* and the failure of disturbances to improve catalepsy. The cybernetic characteristics of the two insect groups are rather similar, namely, the shapes of the Bode plots, the magnitudes of the (large) velocity-sensitive and (small) position-sensitive response components, the phase shift values and the non-linear characteristics of response time constants. In detail, however, *Prosarthria teretirostris* has a slightly larger phase reserve and lower upper corner frequency and a higher velocity threshold and the decay of the velocity-sensitive response component is a little faster. Together, these features result in faster velocities during cataleptic return movements. In the following, we shall discuss the results obtained in *Prosarthria teretirostris* in the light of the assumptions on evolutionary tendencies noted in the Introduction.

Catalepsy has co-evolved with the stick-like body shape and thus is a behavioural component of twig mimesis (Bässler, 1983, 1993; Bässler et al., 1997)

This assumption is based on the correlation between body shape and catalepsy in stick insects and on the absence of catalepsy in *Schistocerca gregaria* middle legs (Ebner and Bässler, 1978) and, by inference, in the remaining appendages of locusts. It is further based on plausibility, namely, that the suppression of fast (return) movements after passive displacement aids twig mimesis and avoids the stimulation of movement-based visual recognition in predators (Ewert, 1997). The presence of catalepsy in *Prosarthria teretirostris* (see Results), which has a twig-like body shape strongly reminiscent of that of phasmids, supports these assumptions.

Catalepsy results from the dominant velocity-sensitive component of the resistance reflex combined with the small position-sensitive component (Bässler, 1983, 1993; Bässler et al., 1997)

This assumption is based on the presence of these properties in the stick insect femur–tibia control systems and on the ability of these insects to induce catalepsy according to cybernetic analysis (in combination with the non-linear time constant of the system, see below). The results obtained in *Prosarthria teretirostris* (see Results) validate this assumption, in particular the combination of high velocity-sensitivity and low (normal) position-sensitivity. However, there may be other ways to generate catalepsy, for example, time-dependent changes in the set point for joint position after passive displacement, combined with a mainly position-

sensitive feedback loop. The combination of variables observed in phasmids and proscopiids may just be the easiest (and evolutionarily the most accessible) way to transform the 'normal' joint control system of orthopteran insects into a feedback system able to generate catalepsy.

The non-linear dependency of the response time constant on stimulus velocity is a prerequisite for catalepsy (Bässler, 1993; Bässler et al., 1997)

This assumption is based on the properties of the stick insect femur–tibia control systems, which can be traced back to the characteristics of identified non-spiking interneurons (Driesang and Büschges, 1993). A non-linear relationship between stimulus (imposed movement) velocity and the time constant of the resulting return movement appears to be advantageous for the reasons outlined above (see Introduction). The initial velocity-sensitive response, resisting the imposed movement, decays rapidly after a fast displacement, while the velocity-sensitive component activated by the (very) slow return movement can maintain a significant amplitude. The results in *Prosarthria teretirostris* clearly support this assumption. Thresholds for velocity-sensitivity prove to be higher (Fig. 6B), and time constants smaller (Fig. 6C), in *Prosarthria teretirostris* than in *Cuniculina impigra*. These differences appear to be responsible for the faster return movements observed in *Prosarthria teretirostris* (Fig. 3B).

In *Schistocerca gregaria* middle legs, a dependency of the time constant on input velocity was noted (Ebner and Bässler, 1978) (half-lives of response increase, rather than decay, were measured, however). This suggests that this property is a plesiomorphic character and was already been present in ancient orthopterans, forming a suitable substratum for the evolution of catalepsy, rather than being produced during the evolution of twig mimesis.

Gain control mechanisms are an evolutionary consequence of the high gain necessary for catalepsy (Bässler, 1993; Bässler and Nothof, 1994; Bässler and Stein, 1996; Kittmann, 1991, 1997)

This assumption is based on the observation that phasmid joint control systems have a high gain and a small phase reserve (see Results). Large increases in gain, brought about by disturbances, for example, may thus drive the control system into instability and induce feedback oscillations (compare Weiland et al., 1986; Bässler and Nothof, 1984; Bässler, 1983), necessitating gain control.

Our results in *Prosarthria teretirostris* refute the assumption that the gain control mechanisms reported in phasmids evolved as a necessary consequence of the high gain essential for catalepsy. *Prosarthria teretirostris* lacks gain control mechanisms such as habituation (as in *Carausius morosus*) or habituation-like features of the muscle/joint system (as in *Cuniculina impigra*), and gain remains unaffected by disturbances (e.g. Fig. 3B). Apparently, the slightly higher phase reserve and lower gain of the *Prosarthria*

teretirostris joint control system (Fig. 4), which is not susceptible to disturbance, are sufficient to protect the system from instability under natural conditions.

These properties of joint control in *Prosarthria teretirostris* result in slightly higher movement velocities (e.g. Fig. 3B) compared with phasmids. Efficient gain control may become necessary only if return movements become as slow as those observed in the stick insects after substantial increases in gain, regardless of the selective forces that bring about further slowing of leg movements. This would be in agreement with the different mechanisms of gain control reported in *Carausius morosus* and *Cuniculina impigra* (Kittmann, 1991, 1997; Bässler and Stein, 1996), suggesting their appearance only after twig mimesis had evolved.

Coupling an inert mass to the tibia demonstrated that the control system of *Prosarthria teretirostris* is able to oscillate, on principle, but this experimental situation is too artificial to suggest a need for gain control under normal conditions. Even in *Carausius morosus*, the existing gain control mechanisms are not sufficient to prevent feedback oscillations if an inert mass is coupled to the tibia. These oscillations are of small amplitude (5–10°), however, and do not cover the full range of joint movement, as would be expected for oscillations caused by positive feedback (equalling negative feedback with a phase shift of 180°). This attests to the presence of some form of gain control, in the shape of a non-linear relationship between stimulus amplitude and gain, in proscopiids as well as phasmids (Kittmann, 1991). This appears to take effect in the high-frequency range 1–2 Hz, rather than over the range of low frequencies and velocities at which cataleptic movements occur (below 0.1 ° s⁻¹ or 0.1 Hz).

Taken together, the data obtained in *Prosarthria teretirostris* demonstrate that, as an alternative to the habituation and habituation-like properties of the muscle/joint system, a slightly higher phase reserve, combined with a gain that is not susceptible to disturbance, is able to prevent feedback oscillation in a high-gain control system.

In summary, it is evident that most assumptions about the neuronal, cybernetic and evolutionary bases of catalepsy, as derived from analyses in stick insects (Bässler, 1983, 1993; Bässler et al., 1997), are verified by the results obtained in *Prosarthria teretirostris*. Only one supposition was falsified, namely, that the evolution of the gain control mechanisms observed in stick insects (Kittmann, 1991, 1997; Bässler and Stein, 1996) is a necessary consequence of high reflex gain. It is now clear that such gain control mechanisms are possible, but not necessary, consequences of the high gain essential for the generation of catalepsy.

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important partner for discussion and put together more than one electrophysiology set-up.

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