

MUSCLE FIRING PATTERNS IN TWO ARACHNIDS USING DIFFERENT METHODS OF PROPULSIVE LEG EXTENSION

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Summary

Activity patterns of six morphologically similar, homologous muscles were recorded from the fourth leg pair in two species of arachnids that use different mechanisms to extend the femur–patella (knee) joint during locomotion. The giant whipscorpion *Mastigoproctus giganteus* (Uropygi) lacks femur–patella extensor muscles but extends this joint with hydraulic pressure, a mechanism that appears to be phylogenetically primitive in arachnids. The black emperor scorpion *Pandinus imperator* (Scorpiones) has an unusual muscle that promotes simultaneous extension at the femur–patella joint and distally adjacent patella–tibia joint. Comparison of electromyograms from freely walking animals revealed similarities in muscle firing patterns of the two species, including asymmetrical alternation of trochanter–femur levator and depressor muscles, transfemoral muscle activation during protraction and abrupt termination just prior to levator activation, and persistence of flexor activity during retraction (extension). These results indicate that the apparent evolutionary transition from hydraulic to muscular extension occurred without substantial alteration of several components of the primitive motor programme. It is suggested that the patterns of extension force generated by hydraulic pressure and by bifunctional extensors are similar and that this similarity is associated with conservation of the motor programme.

Introduction

Propulsive leg extension in most arachnids is accomplished through one of two mechanisms, extrinsically generated hydraulic pressure or contraction of intrinsic extensor muscles. Whipscorpions and spiders lack extensor muscles at the femur–patella (knee) joints of the walking legs, but extend these joints with fluid pressure, a mechanism that appears to be phylogenetically primitive for arachnids (Shultz, 1989, 1990, 1991). Scorpions, opilionids and pseudoscorpions have

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extensor muscles, but many other appendicular muscles are morphologically similar to those of their 'extensorless' relatives (Shultz, 1989). This paper reports results from an electromyographic survey of six morphologically similar, homologous muscles in two arachnids that use different mechanisms to extend their femur–patella joints. My goals are to understand the function of these muscles in arachnids with and without extensor muscles and to gain insight into the evolutionary transition from hydraulic to muscular extension.

This study compares muscle firing patterns in the fourth leg pair of a uropygid whipscorpion and a true scorpion. The femur–patella joint of the giant whipscorpion *Mastigoproctus giganteus* (Uropygi) lacks extensor muscles (Fig. 1A) but is extended by hydraulic pressure generated by compression of the prosoma (Shultz, 1991), a mechanism that has been well documented in spiders (Parry and Brown, 1959; Wilson and Bullock, 1973; Stewart and Martin, 1974; Anderson and Prestwich, 1975; Blickhan and Barth, 1985; Prestwich, 1988; Paul *et al.* 1989). In contrast, the femur–patella joint of the black emperor scorpion *Pandinus imperator* Koch (Scorpiones) is equipped with an unusual muscle (Fig. 1B) that promotes extension at this joint and the more distal patella–tibia joint simultaneously. Despite differences in extension mechanisms of the two arachnids, the morphology of muscles inserting on the femur–patella joint (flexor and transfemoral muscles) and of muscles of the more proximal trochanter–femur joint (levator and depressor) are very similar (Fig. 1). Comparative and phylogenetic studies indicate that the morphologically similar muscles are homologous (i.e. symplesiomorphic) (Shultz, 1989, 1990).

The present analysis reveals that homologous muscles in whipscorpions and scorpions have similar patterns of activity, despite the presence of different extension mechanisms. Firing patterns are essentially the same in the trochanter–femur levator and depressor muscles and very similar in the transfemoral muscle, which spans the trochanter–femur and femur–patella joints. Similarities in the activity of femur–patella flexors are less marked, although flexors in both species are active during both the flexion and extension phases of the step cycle. It is suggested that bifunctional extensor muscles replaced hydraulic pressure in scorpions and their relatives but that these muscles continued to produce mechanical forces similar to those of the primitive hydraulic mechanism. Thus, there may be an association between evolutionary conservation in elements of the motor programme and conservation of mechanical forces used in femur–patella extension.

Materials and methods

Experimental animals

Electromyographic analyses were conducted on 13 whipscorpions *Mastigoproctus giganteus* (Lucas) and 11 scorpions *Pandinus imperator* Koch of both sexes. Carapace lengths in *Mastigoproctus* ranged from 1.80 to 2.08 cm (\bar{x} =1.93 cm); carapace lengths in *Pandinus* ranged from 1.45 to 1.90 cm (\bar{x} =1.71 cm). Whipscor-

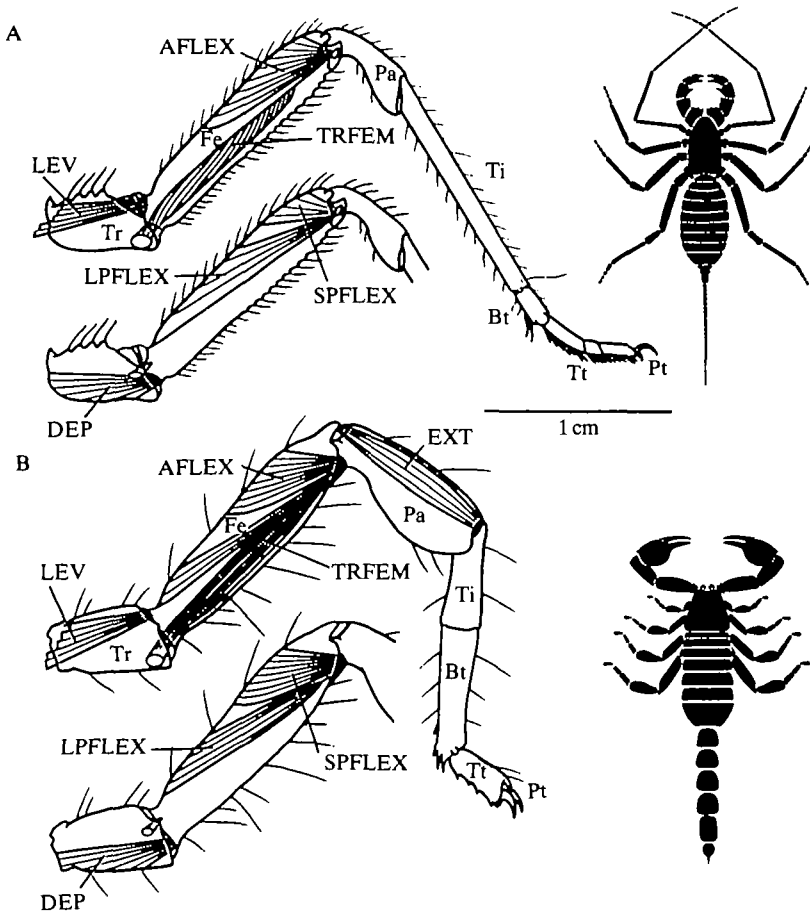


Fig. 1. Skeletomuscular anatomy of walking legs in (A) the giant whipscorpion *Mastigoproctus giganteus* (Uropygi) and (B) the black emperor scorpion *Pandinus imperator* (Scorpiones). Upper diagrams depict an anterior/lateral view of the fourth walking leg from the left side of the body. Lower diagrams depict posterior muscles with anterior muscles removed. AFLEX, anterior flexor; Bt, basitarsus; DEP, depressor; EXT, extensor; Fe, femur; LEV, levator; LPFLEX, long posterior flexor; Pa, patella; Pt, pretarsus (apotele); SPFLEX, short posterior flexor; Ti, tibia; Tr, trochanter; TRFEM, transfemoral muscle; Tt, telotarsus.

pions were collected near Portal, Arizona, USA, and the scorpions were obtained from pet dealers. Animals were housed individually in plastic shoe boxes and given one or two large mealworms or crickets per week. Water was provided *ad libitum* in open Petri dishes. In most cases, an animal was used in two experiments, one focusing on the left member of the fourth leg pair and the other on the right, with a respite of at least 1 week between procedures. The animals were maintained for many weeks after the study and appeared to behave normally.

Electromyography

The activity of three muscles was recorded during each experiment *via* bipolar electrodes fashioned from insulated nichrome wire (A-M Systems, Inc., no. 7620; 50 μm bare). Each electrode consisted of two 50-cm wires glued in parallel, both with about 0.5 mm of insulation removed at one end. The bared ends were inserted just below the cuticle at a site of muscle attachment through a pair of closely spaced holes made with a sterilised minuten pin. A monopolar reference electrode was prepared in a similar way but was inserted through a single hole in the carapace. The free ends were glued together in parallel and anchored to the upper surface of the opisthosoma. Each animal was allowed to walk freely on the cardboard floor of a copper-screen Faraday cage.

Signals from each bipolar electrode were patched into a differential preamplifier (Grass, model 1509), and the monopolar reference electrode was connected to the Faraday cage, which was connected to the common ground of the preamplifiers and recording apparatus. Signals were treated similarly at each preamplifier; the low-pass filter was set at 100 Hz and the high-pass filter at 3 kHz. A 60-Hz notch filter was always in use. Gain varied but generally ranged from 10^3 to 2×10^3 . The treated signals were observed on an oscilloscope and stored on tape using a Honeywell FM tape recorder (model 5600C). After each experiment, the tape speed was reduced by half and the tape was replayed while the signals were observed on an oscilloscope. Those sequences consisting of four or more regular steps were saved on paper using a chart recorder (Gould, model 2400).

Activity of the trochanter–femur levator was recorded during each experiment and used as a reference for all measurements. Experience had shown that the onset of levator activity is well defined and strongly correlated with the start of protraction (the recovery phase of the step cycle) in both *Mastigoproctus* and scorpions (Bowerman, 1981). The interval between the onset of one burst in the levator and the onset of the subsequent burst was regarded as the step period. Three activity parameters were measured for the other muscles: lag, duration and off. The lag of a muscle was defined as the period between the start of a step cycle, indicated by onset of levator activity, and the onset of activity in the muscle. Duration was the period of muscle activity. Off was defined as the period between the end of activity in a muscle and the start of the next step period, indicated by onset of the next levator burst. Data for the trochanter–femur depressor, transfemoral muscle and the three femur–patella flexors were obtained from at least two individuals of each species and from as wide a range of step periods as possible. The firing pattern of the extensor in *Pandinus* was also examined. Onset and end of activity for each muscle were determined by measurement of chart records and were accurate to within ± 5 ms in all preparations.

Statistical analysis

Least-squares regressions for muscle activity parameters and levator cycle period were calculated to describe results from each preparation. However, as

there was little overlap of the levator cycle periods used by the two species, standard methods for testing the homogeneity of slopes, such as analysis of covariance, were not appropriate for statistical comparisons between species. Instead, each activity parameter was divided by levator cycle period to control for the effect of step period. This procedure was considered successful if a least-squares regression indicated the absence of a significant relationship ($P > 0.001$) between the relative value of each parameter and levator cycle period. Mean relative activity parameters (see Tables 1, 2) were compared across individual preparations using analysis of variance followed by *post hoc* comparisons (Tukey test with Tukey–Kramer adjustment for unequal sample sizes) at the 0.001 level of significance. In several instances, there were statistically significant differences in muscle timing parameters in the two species, even though values for preparations of one species fell within the range of individual variation of the other species (see Table 3). As a consequence, it was important to consider the overlap of relative timing parameters among preparations of the two species in addition to strictly statistical comparisons. All statistical analyses were conducted on an IBM-compatible personal computer using SYSTAT, Inc. (1990) software.

Results

General observations

The two species differed in their patterns of locomotor activity. *Mastigoproctus* tended to engage in bouts of uninterrupted locomotion. Individuals displayed a wide range of step periods but tended to use those over about 0.8 s. *Pandinus* generally moved in a stop-and-go pattern consisting of brief bouts of high-frequency stepping interrupted by inactivity of variable duration. This species showed a narrower range of step periods, generally near 0.5 s, and rarely used periods greater than 1.0 s. Because the scorpions *Hadrurus arizonensis* and *Paruroctonus mesaensis* use a wide range of step periods (Bowerman, 1975, 1981), the preference for short step periods in *Pandinus* should not be regarded as characteristic of scorpions in general.

Electromyographic analysis

Levator

Measurements of levator activity were made from electromyograms obtained from four *Mastigoproctus* and three *Pandinus* preparations and were found to be very similar in the two species (Table 1). The onset of levator activity in both species was clearly defined by a sudden burst of high-amplitude spikes. The spike train decreased gradually in both amplitude and frequency and required some subjectivity to determine the point at which levator activity ended. Mean relative values of duration and off were approximately 50% of total step period in most preparations. Thus, levator deactivation generally occurred well after onset of depressor activity (Fig. 2). There was statistically significant overlap among

Table 1. *Relative timing parameters of muscles traversing the trochanter-femur joint of the fourth walking leg in Mastigoproctus and Pandinus preparations*

	<i>Mastigoproctus giganteus</i>				<i>Pandinus imperator</i>		
	1	2	3	4	1	2	3
Levator							
Duration							
Mean	0.455	0.580	0.535	0.500	0.515	0.410	0.435
s.d.	0.050	0.085	0.050	0.095	0.085	0.100	0.140
Off							
Mean	0.545	0.420	0.465	0.500	0.490	0.590	0.565
s.d.	0.050	0.085	0.050	0.095	0.085	0.100	0.140
N	49	33	55	72	54	86	145
Depressor							
Lag							
Mean	0.345	0.345	0.315	0.340	0.350	0.400	0.315
s.d.	0.030	0.025	0.040	0.035	0.045	0.045	0.040
Duration							
Mean	0.610	0.640	0.665	0.620	0.560	0.535	0.585
s.d.	0.045	0.055	0.045	0.040	0.050	0.055	0.055
Off							
Mean	0.045	0.015	0.020	0.035	0.095	0.065	0.100
s.d.	0.030	0.045	0.025	0.025	0.040	0.030	0.045
N	58	66	78	138	106	33	78
Transfemoral muscle							
Lag							
Mean	0.065	0.125	0.100		0.245	0.255	0.230
s.d.	0.025	0.025	0.030		0.060	0.040	0.045
Duration							
Mean	0.815	0.860	0.800		0.620	0.620	0.555
s.d.	0.100	0.030	0.045		0.075	0.050	0.070
Off							
Mean	0.120	0.015	0.100		0.135	0.125	0.215
s.d.	0.095	0.020	0.030		0.055	0.040	0.055
N	27	46	67		147	75	90

Relative values were obtained by dividing the absolute value of a parameter (lag, duration, off) by step period (that is, levator cycle period). Note that data for each muscle were derived from different sets of preparations. For example, the set of individual animals used to obtain data from the levator are not the same as those used to obtain data from the depressor.

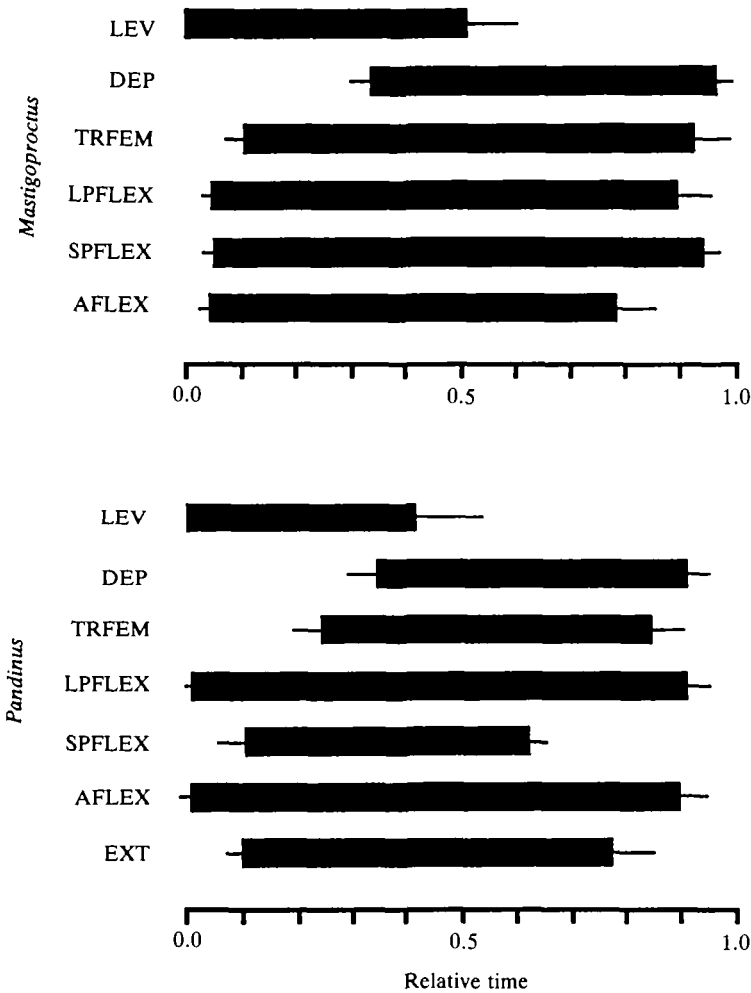


Fig. 2. Electromyogram bar diagrams illustrating mean relative activity parameters for muscles of leg 4 in *Mastigoproctus* and *Pandinus*. Wide black bars indicate the mean relative duration of muscle activity; the error bars indicate one standard deviation. Relative timing values were obtained by dividing absolute values (lag, duration, off) by levator cycle period. Therefore, 0.0 and 1.0 indicate onset of the levator burst. As values for each muscle were derived from data pooled from several individuals, the values presented here should not be used for statistical comparisons. Note that onset of levator (LEV) activity is correlated with onset of protraction and onset of depressor (DEP) activity is correlated with onset of retraction. The femur-patella flexors (LPFLEX, SPFLEX, AFLEX) in both species are active during retraction, that phase of the step cycle when the femur-patella joint undergoes extension. The abbreviations are explained in the legend to Fig. 1.

preparations of the two species for both mean relative duration and mean relative off values (see Table 3).

Depressor

Recordings of depressor activity were obtained from four *Mastigoproctus* and three *Pandinus* preparations (Table 1). Mean relative lag varied between preparations within a species, especially for *Pandinus*. However, there was significant overlap in mean relative lag among representatives of the two species (see Table 3), indicating that relative durations of protraction and retraction were also similar. Mean relative duration of the depressor burst tended to be longer in *Mastigoproctus* (about 63 % of cycle period) than in *Pandinus* (about 55 % of cycle period). The depressor burst consisted of a continuous train of spikes in both species. There was no indication of an internal spiking pattern, although spike frequency and amplitude tended to be more variable in *Pandinus*. Depressor activity was observed to end before onset of the next levator burst in virtually all steps in both species. Relative off values were short in all preparations, but the values observed in two *Pandinus* preparations were higher than in any *Mastigoproctus* preparation (see Table 3).

Transfemoral muscle

Information on the activity of the transfemoral muscle was obtained from three individuals from each species (Table 1). Mean relative lags were similar among individuals within each species but were significantly greater in *Pandinus* (see Table 3). However, the transfemoral muscle in both species was always observed to fire well before the onset of retraction, as indicated by the onset of the depressor burst (Fig. 2). Transfemoral muscle activity began and ended abruptly in both species. Spike amplitude and frequency were somewhat higher during the first half of the spike train in *Mastigoproctus*. As in the depressor, activity in the transfemoral muscle was almost always observed to end before the onset of the next levator burst. However, mean relative off values in the transfemoral muscle in both species were consistently larger than those observed in the depressor (Table 1, Fig. 2). There was substantial overlap in mean relative off values among preparations of the two species.

Long posterior flexor

Data for the long posterior flexor were obtained from two *Mastigoproctus* and three *Pandinus* preparations (Table 2). Mean relative lag was similar among individuals within a species but was significantly greater in *Mastigoproctus* (Table 3). In many instances, the long posterior flexor in *Pandinus* began to fire before onset of levator activity, a feature that was never observed in *Mastigoproctus*. Mean relative duration tended to be slightly greater in *Pandinus*, although the mean in one preparation did not differ significantly from that found in one *Mastigoproctus* preparation (Table 3).

Table 2. *Relative timing parameters of femur-patella flexor muscles of the fourth walking leg in Mastigoproctus and Pandinus preparations*

	<i>Mastigoproctus giganteus</i>		<i>Pandinus imperator</i>		
	1	2	1	2	3
Long posterior flexor					
Lag					
Mean	0.050	0.040	0.010	0.005	0.010
s.d.	0.015	0.015	0.010	0.010	0.010
Duration					
Mean	0.870	0.845	0.885	0.910	0.905
s.d.	0.030	0.070	0.035	0.045	0.030
Off					
Mean	0.080	0.115	0.105	0.085	0.085
s.d.	0.030	0.070	0.035	0.050	0.030
<i>N</i>	29	53	116	98	156
Short posterior flexor					
Lag					
Mean	0.065	0.045	0.075	0.135	
s.d.	0.020	0.015	0.035	0.045	
Duration					
Mean	0.890	0.890	0.525	0.510	
s.d.	0.030	0.040	0.080	0.090	
Off					
Mean	0.045	0.065	0.400	0.355	
s.d.	0.015	0.035	0.085	0.090	
<i>N</i>	23	47	112	99	
Anterior flexor					
Lag					
Mean	0.045	0.045	0.010	-0.010	0.005
s.d.	0.015	0.015	0.020	0.020	0.015
Duration					
Mean	0.775	0.730	0.900	0.860	0.910
s.d.	0.090	0.075	0.035	0.040	0.045
Off					
Mean	0.180	0.225	0.090	0.145	0.085
s.d.	0.090	0.080	0.040	0.040	0.040
<i>N</i>	29	82	44	108	124

Relative values were obtained by dividing the absolute value of a parameter (lag, duration, off) by step period (that is, levator cycle period). Note that data for each muscle were obtained from different sets of preparations. For example, the set of individuals used to obtain data from the long posterior flexor is not the same as those used to obtain data from the anterior flexor.

Table 3. Comparisons of mean relative timing parameters for muscles of the fourth walking leg in *Mastigoproctus* (M) and *Pandinus* (P)

Levator								Long posterior flexor					
Duration	<u>M2</u>	<u>M3</u>	<u>P1</u>	<u>M4</u>	<u>M1</u>	<u>P2</u>	<u>P3</u>	Lag	<u>M1</u>	<u>M2</u>	<u>P1</u>	<u>P3</u>	<u>P2</u>
Off	<u>P2</u>	<u>P3</u>	<u>M1</u>	<u>M4</u>	<u>P1</u>	<u>M3</u>	<u>M2</u>	Duration	<u>P3</u>	<u>P2</u>	<u>P1</u>	<u>M1</u>	<u>M2</u>
								Off	<u>M2</u>	<u>P1</u>	<u>P2</u>	<u>M1</u>	<u>P3</u>
Depressor								Short posterior flexor					
Lag	<u>P2</u>	<u>M1</u>	<u>M2</u>	<u>M4</u>	<u>P1</u>	<u>M3</u>	<u>P3</u>	Lag	<u>P2</u>	<u>P1</u>	<u>M1</u>	<u>M2</u>	
Duration	<u>M3</u>	<u>M2</u>	<u>M4</u>	<u>M1</u>	<u>P3</u>	<u>P1</u>	<u>P2</u>	Duration	<u>M1</u>	<u>M2</u>	<u>P1</u>	<u>P2</u>	
Off	<u>P1</u>	<u>P3</u>	<u>P2</u>	<u>M1</u>	<u>M3</u>	<u>M4</u>	<u>M2</u>	Off	<u>P1</u>	<u>P2</u>	<u>M1</u>	<u>M2</u>	
Transfemoral muscle								Anterior flexor					
Lag	<u>P1</u>	<u>P2</u>	<u>P3</u>	<u>M2</u>	<u>M3</u>	<u>M1</u>		Lag	<u>M1</u>	<u>M2</u>	<u>P1</u>	<u>P3</u>	<u>P2</u>
Duration	<u>M1</u>	<u>M2</u>	<u>M3</u>	<u>P1</u>	<u>P2</u>	<u>P3</u>		Duration	<u>P3</u>	<u>P1</u>	<u>P2</u>	<u>M1</u>	<u>M2</u>
Off	<u>P3</u>	<u>P1</u>	<u>P2</u>	<u>M1</u>	<u>M3</u>	<u>M2</u>		Off	<u>M2</u>	<u>M1</u>	<u>P2</u>	<u>P1</u>	<u>P3</u>

Preparations for each timing parameter are listed in descending order (cf. Tables 1, 2).

Mean relative values were compared across preparations with analysis of variance followed by pairwise comparisons.

Mean relative values showing no significant difference ($P > 0.001$) are underlined.

Two distinct phases were observed in the activity of the long posterior flexor in both species, one burst associated with protraction (flexion phase) and the other with retraction (extension phase) (Fig. 3). Long posterior flexor activity in *Mastigoproctus* began with a well-defined burst of high-amplitude spikes that persisted for about 23% of levator cycle period ($\bar{x} = 0.230$, s.d. = 0.040, $N = 82$), indicating that the burst tended to stop before onset of retraction, as indicated by the onset of the depressor burst. Activity persisted after the flexion burst, but spike amplitude and frequency decreased gradually during the extension phase. As a consequence, it was sometimes difficult to establish the point at which activity ended, and recordings from only two *Mastigoproctus* preparations were obtained with a signal-to-noise ratio sufficiently high to allow a relatively unambiguous measurement of burst termination.

The long posterior flexor in *Pandinus* also showed flexion and extension phases (Fig. 3). The flexion phase was characterised by a train of high-amplitude spikes that lasted for about 21% of the levator cycle period ($\bar{x} = 0.210$, s.d. = 0.040, $N = 90$) and thus ended well before onset of retraction, as indicated by onset of depressor activity. There was a gradual increase in spike amplitude in the extension phase during short step periods, such that the largest spikes occurred just before termination of activity. Consequently, termination of activity was unambiguous at these step periods. However, at longer step periods, such as those

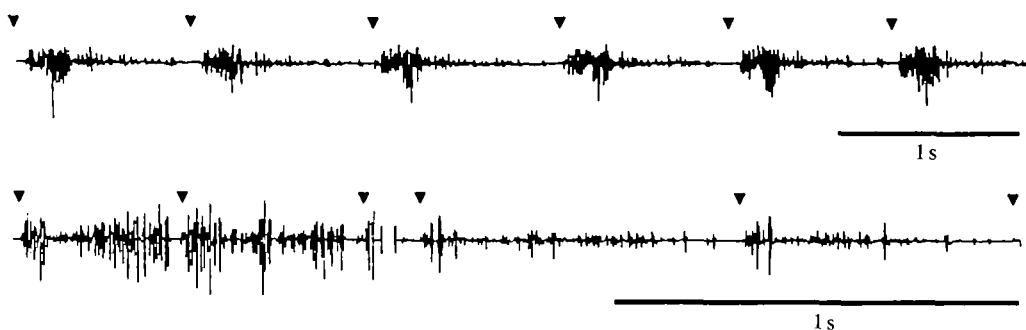


Fig. 3. Representative electromyograms recorded from the long posterior flexor of the femur-patella joint in *Mastigoproctus* (upper trace) and *Pandinus* (lower trace). Arrowheads indicate activation of the reference muscle, the levator. The long posterior flexor has an initial high-amplitude flexion phase and a long extension phase in both species. The spiking pattern of the extension phase in *Pandinus* changes with step period. At long step periods, the spiking pattern of the extension phase in *Pandinus* approximates that of *Mastigoproctus*.

normally used by *Mastigoproctus* (that is, near 0.8 s), the spike train showed a gradual reduction in spike amplitude during the extension phase, such that the differences between the extension phase of the two species became less apparent.

Short posterior flexor

Data on the activity of the short posterior flexor were obtained from two representatives of each species (Table 2). The muscle became active during the early part of the protraction phase in both species and activity persisted into the retraction phase (Fig. 2). The muscle remained active in the *Mastigoproctus* preparations for about 89% of the step period. As in the long posterior flexor, there was an initial burst of high-amplitude spikes (flexion phase) and spike amplitude and frequency decreased gradually through retraction (extension phase). In contrast, the short posterior flexor in *Pandinus* remained active for only about 50% of the step period and activity ended rather abruptly.

Anterior flexor

Information on the activity of the anterior flexor was obtained from two *Mastigoproctus* and three *Pandinus* preparations (Table 2). Mean relative lag values were small in both species but were significantly smaller in *Pandinus* (Table 3). As in the long posterior flexor, the onset of anterior flexor activity in *Pandinus* often occurred before the onset of levator activity, but this pattern was never observed in *Mastigoproctus*. Mean relative duration of muscle activity was significantly greater in *Pandinus*, and the internal structure of the burst differed in the two species. In general, the spike train in *Mastigoproctus* began abruptly with a burst of high-amplitude spikes that diminished gradually during retraction. In some cases, however, the onset of the initial burst of activity was more gradual.

The spike train in the *Pandinus* preparations also began with a burst of high-amplitude spikes, which lasted through about the first half of the step cycle. The spike train during the second half of the step cycle was variable, with no consistent internal pattern from step to step. Mean relative off values tended to be higher in *Mastigoproctus*, although one *Pandinus* preparation did not differ significantly from the *Mastigoproctus* preparations.

Extensor

Data for activity of the extensor were obtained from three *Pandinus* preparations. Mean relative lag differed significantly among the three preparations, where means ranged from 0.075 to 0.125. However, no significant differences were found in mean relative duration of the extensor burst (pooled mean=0.675). Mean relative off values were also similar, but pairwise comparisons reveal a significant difference between two preparations. Mean relative off values ranged from 0.215 to 0.270. Interestingly, the extensor began to fire near the middle of the protraction (flexion) phase of the step cycle and stopped firing well before the end of the retraction (extension) phase (Fig. 2).

Discussion

Comparison of Mastigoproctus and Pandinus

Comparison of skeletomuscular anatomy of *Mastigoproctus* and *Pandinus* with that of other arachnids (Shultz, 1989) indicates that the trochanter–femur joint has undergone little change since the divergence of whipscorpions and scorpions, despite important evolutionary modifications in the structure and mechanics of the femur–patella joint in scorpions (Fig. 1). The firing patterns of muscles associated with the trochanter–femur joint, especially the levator and depressor, are also very similar (Table 2, Fig. 2). These muscles have an alternating firing pattern in both whipscorpions and scorpions, levator activation being associated with onset of protraction and depressor activation with onset of retraction. The absence of statistically significant differences in relative lag of the depressor indicates that the relationship of protraction and retraction with step period is essentially the same in the two species, despite differences in the mechanics of stepping.

The alternating firing pattern of the levator and depressor is asymmetrical in both species. The depressor burst ends abruptly just prior to onset of levator activity, whereas termination of the levator burst is gradual and variable, typically persisting well after onset of activity in the depressor. This pattern has been documented in antagonistic muscles of other arthropods, including arachnids (Bowerman, 1981), insects (Pearson and Iles, 1970; Delcomyn and Usherwood, 1973; Reingold and Camhi, 1977) and crustaceans (Macmillan, 1975; Ayers and Davis, 1977), but the functional significance of this pattern is unclear (Bowerman, 1981). Motor control models of arthropod locomotion attribute stereotypical deactivation of the depressor to inhibition of depressor motoneurons by the same central mechanism that activates the levator (Pearson, 1972; Delcomyn, 1973).

Given the widespread occurrence of asymmetrical alternation in antagonistic muscles, the presence of this pattern in the trochanter–femur levator and depressor in *Mastigoproctus* and *Pandinus* may seem unexceptional. However, the trochanter–femur joint in both species is linked internally to the femur–patella joint by the transfemoral muscle (Fig. 1), such that differences in the mechanics of movement at the femur–patella joint may also be reflected in differences at the trochanter–femur joint. Because femur–patella joint extension is brought about by hydraulic pressure in *Mastigoproctus* and by an extensor muscle in *Pandinus*, the presence of important similarities in activity of the trochanter–femur levator and depressor warrants further explanation. I hypothesise that, despite obvious differences in mechanisms of femur–patella extension in the two species, the patterns of forces generated by the two mechanisms are similar and thus account for the similarities in muscle firing patterns. This hypothesis is developed further below.

The structure and activity of the transfemoral muscle is also similar in *Mastigoproctus* and *Pandinus*. Joint structure and the arrangement of transfemoral origins and insertions in the two species suggest that active shortening of this muscle would promote depression at the trochanter–femur joint and flexion at the femur–patella joint (Shultz, 1989), but these movements do not occur simultaneously during periods of transfemoral muscle activity. The transfemoral muscle in both species is active during late protraction and most of retraction (Fig. 2), periods when the trochanter–femur joint is undergoing depression and the femur–patella joint is extending. This suggests that the length of the muscle does not change substantially during activity, although a more thorough understanding of joint kinematics during locomotion is needed to ascertain precise length changes.

I hypothesise that the transfemoral muscle acts as a mechanical linkage that maintains the proper orientation of the trochanter–femur and femur–patella joints when the animal is moving and when it stops temporarily during locomotion. These functions would appear to have special significance in *Mastigoproctus* and other arachnids that use hydraulic joint extension. Step-coupled fluctuations associated with joint volume changes are normal in walking *Mastigoproctus* (Shultz, 1991) and would be expected to produce variations in extension-promoting force at the femur–patella joint. These fluctuations could disrupt coordination of the trochanter–femur and femur–patella joints during retraction in leg 4 by causing different rates of femur–patella extension during the retraction phase. If extension were to outpace depression, the tarsus would tend to lift from the substratum, removing support and propulsive force provided by that leg. Similarly, the prosomal pressure used during locomotion remains high when the animal stops walking temporarily (J. W. Shultz, personal observation). Isometric contraction of the transfemoral muscle could act to stabilise the femur–patella joint against hydraulic pressure such that the joints within a leg retain an appropriate posture when locomotion is resumed.

Although hydraulic pressure is not used for femur–patella extension in

Pandinus, the transfemoral muscle may play a role similar to that hypothesised for *Mastigoproctus*. Because the bifunctional extensor of scorpions acts as a direct link between the femur–patella and patella–tibia joints (Fig. 1B), variation in movement at the patella–tibia joint has the potential to disrupt coordination between the trochanter–femur and femur–patella joints. In fact, substantial step-to-step variation in the rate of patella–tibia extension has been noted in scorpions (Root and Bowerman, 1978). As in arachnids that use hydraulic joint extension, the transfemoral muscle of scorpions could assist in maintaining coordination between the trochanter–femur and femur–patella joints in the face of perturbations generated elsewhere in the locomotor apparatus.

The principal skeletal innovations associated with the hydraulic-to-muscular transition occurred at the femur–patella joint, but the gross morphology of muscles inserting on the proximal rim of the patella underwent little change. Although few statistically significant, quantitative similarities were found in the firing patterns of the femur–patella flexors in the two species (Table 2), there are several unexpected qualitative similarities. As expected, the flexors in both species were strongly active during protraction, when the femur–patella joint flexes, but they were also active during retraction, when the femur–patella joint extends.

The functional significance of this pattern of flexor activity seems obvious in whipscorpions and other ‘extensorless’ arachnids. Femur–patella extension in whipscorpions is caused by a general increase in haemocoelic pressure brought about by compression of the prosoma (Shultz, 1991), a mechanism similar to that used by spiders (Wilson and Bullock, 1973; Anderson and Prestwich, 1975; Blickhan and Barth, 1985). As a consequence, the rate and degree of extension within a leg are most probably controlled by the action of flexors working against this extrinsically generated pressure. Activity of the femur–patella flexors during extension in *Mastigoproctus* is thus consistent with the apparent mechanical demands of hydraulic extension.

Femur–patella flexor activity during extension is also marked in scorpions (Fig. 2), despite the fact that these arachnids have well-developed femur–patella extensors (Fig. 1B) and lack a method of hydraulic extension (Alexander, 1967). Unlike typical extensor muscles, however, the scorpion extensor acts simultaneously at two joints, the femur–patella and patella–tibia joints. As the muscle has no connection to the patella (Fig. 1B), it cannot control the rate and degree of extension at each joint independently; femur–patella flexors and similar muscles at the patella–tibia joint must be recruited to control extension at each joint. Therefore, forces generated at the femur–patella joint by the bifunctional extensor may be similar to those produced by the hydraulic mechanism, and this similarity may be associated with the apparent conservation of certain components of the primitive ‘hydraulic’ motor programme in scorpions.

Evolutionary conservation in motor patterns

The hydraulic-to-muscular transition of femur–patella extension in arachnids (Shultz, 1989, 1991) appears to represent a substantial change in locomotor

mechanics, but the present analysis suggests that the transition occurred in such a way that many components of the primitive motor programme were preserved. Two explanations for the apparent conservation of the motor programme can be offered. First, it is possible that the actual sequence of skeletomuscular transformations involved in the origin of muscular extension were functionally advantageous in their own right and retention of the structure and firing pattern of more proximal muscles was merely fortuitous. Second, the difficulty of changing a highly integrated motor programme may have limited skeletomuscular evolution to a few functionally viable alternatives, including the evolution of a bifunctional extensor that produces forces similar to those of the hydraulic mechanism. In short, conservation in a motor programme may be regarded as a mere artefact of evolutionary history or as a constraint that acts to canalise skeletomuscular evolution.

Although causal evolutionary hypotheses are notoriously difficult to test, evidence of conservative motor programmes in a variety of taxa and skeletomuscular systems lends some support to the constraint hypothesis (e.g. Goslow *et al.* 1989; Lauder and Schaffer, 1988; Wainwright and Lauder, 1986; for exceptions, see Gordon and Herring, 1987; Lauder, 1983). Wainwright *et al.* (1989) compared activity patterns of homologous muscles during suction feeding in five phylogenetically diverse aquatic vertebrates. The sequence of muscle activation was conserved (a qualitative pattern that has apparently persisted for over 400 million years), but there were statistically significant, interspecific differences in the intensity and duration of activity in most muscles.

The findings of Wainwright *et al.* (1989) are similar to those of the present investigation. The motor programmes of whipscorpions and scorpions have important qualitative similarities (e.g. asymmetrical alternation of levator and depressor activity, transfemoral muscle activation during protraction and abrupt termination just prior to levator activation, persistence of flexor activity throughout much of extension) that appear to have persisted in two separate lineages for over 400 million years and despite a reorganisation of the femur–patella extension mechanism (Fig. 2). Yet there are only a few statistically significant, quantitative similarities in the motor programme of the two species (e.g. relationship of protraction and retraction to step period, relative off values for the transfemoral and long posterior flexor muscles) (Table 2). Given the similarities in the results of Wainwright *et al.* (1989) and the present study, explanations for the long-term evolutionary conservation of ‘qualitative’ over ‘quantitative’ variables must be sufficiently robust to accommodate systems as diverse as arthropod locomotion and vertebrate feeding.

Extensive studies of motor control systems in arthropods and other animals indicate that motor patterns tend to be governed by two basic neural components, a central component and a ‘peripheral feedback’ component (Stein, 1977; Delcomyn, 1980). The central component determines the overall rate of rhythmic activity and the general pattern in which motoneurons are activated and deactivated. In many cases, the central component can generate an essentially

normal motor pattern in the absence of sensory input. The 'peripheral feedback' component modifies the centrally generated pattern in response to sensory cues, such as compressive and tensile loading on the skeleton or muscles. It is tempting to speculate that the conserved elements of motor programmes are those governed by central components of the motor control apparatus while the evolutionarily plastic elements are associated with the 'peripheral feedback' components (e.g. quantitative changes in motor pattern may result from changes in sensory threshold levels). An integration of comparative and physiological approaches may be useful in understanding constraints on neuromuscular and skeletomuscular evolution and the organisation of the motor control apparatus.

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