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STEP-COUPLED FLUCTUATIONS IN PROSOMAL PRESSURE MAY CONSTRAIN STEPPING RATES IN WHIPSCORPIONS (UROPYGI)

Giant whipscorpions, *Mastigoproctus giganteus* (Lucas) (Uropygi), tend to walk slowly, using step cycle periods of about one second or longer, and do not maintain shorter step periods even when stimulated to move faster (Shultz 1992). Results from a recent electrophysiological study (Shultz 1991) suggest a possible explanation for this preference. Whipscorpions lack extensor muscles at the femur-patella joint (Shultz 1989) but extend this joint with hydraulic pressure generated through compression of the prosoma. Baseline prosomal pressure at preferred step periods is maintained at about 60 torr above minimum resting pressure, but there is also a cyclical pressure fluctuation superimposed on the elevated or 'active' baseline (Fig. 1). This fluctuation, which may have a peak amplitude as high as 20 torr over the active baseline, is apparently caused by rapid flexion of the femur-patella joint in members of the fourth leg pair during the recovery phase (protraction) of their step cycles (Shultz 1991). I hypothesize that by maintaining their preferred step periods, whipscorpions avoid flexing the femur-patella joint of one member of the fourth leg pair against the pressure surge caused by flexion in the other member and thereby minimize the mechanical and energetic inefficiencies of hydraulic locomotion. This paper refines quantitative predictions of the hypothesis and presents preliminary supporting evidence derived from a frequency distribution of step periods.

Referring to Fig. 1, the hypothesis predicts that whipscorpions should prefer a step period (T) in which the decay time (hysteresis) of the pressure surge (D) is less than the time between the end of protraction in one member of the fourth leg pair and the beginning of protraction in the other (A_T). To ascertain A_T empirically, one can determine the difference between B_T (the lag time between the onset of protraction in one member of the fourth leg pair and the onset of protraction in the other for a given step period) and C_T (the duration of protraction for a given step period). Thus for a given step period (T)

$$A_T = B_T - C_T \tag{1}$$

Actual values for B_T and C_T were determined from kinematic and electrophysiological analyses of walking whipscorpions. Video analysis revealed that members of the fourth leg pair step 180° out of phase at all step periods (Shultz 1991), as is typical of segmental leg pairs in arthropods. Thus B_T, the time between the onset of protraction in one leg and the onset of protraction of the other, is always equal to about one half the step period; that is, $B_T = 0.5T$.

The value C_T, the duration of protraction for a given step period, was determined by conducting a least-squares regression analysis on selected electromyographic parameters of the trochanter-femur levator and depressor muscles within one member of the fourth leg pair. The levator and depressor are antagonistic muscles, with the levator activating at the onset of protraction (recovery phase) and the depressor activating at the onset of retraction (propulsive phase). Levator cycle duration was regarded as the step period (T) and represented the independent variable. The time between activation of the levator and activation of the depressor was regarded as the duration of protraction (C_T) and represented the dependent variable. All measurements were made in seconds and were accurate to ±0.005 s. Least-squares analysis of 340 steps from four individuals produced the regression equation $C_T = 0.309T + 0.024$ ($r^2 = 0.86$).

Empirically derived values for B_T and C_T were then substituted into Equation 1

$$\begin{aligned} A_T &= 0.5T - (0.309T + 0.024) \\ &= 0.191T - 0.024 \end{aligned} \tag{2}$$

The hypothesis predicts that whipscorpions should prefer step periods in which A_T is greater than D, the decay time of the step-coupled pressure surge. Thus the minimum preferred step period can be predicted by substituting the empirically derived value of D for A_T in Equation 2 and then solving the equation for T. The value for D was determined by recording prosomal

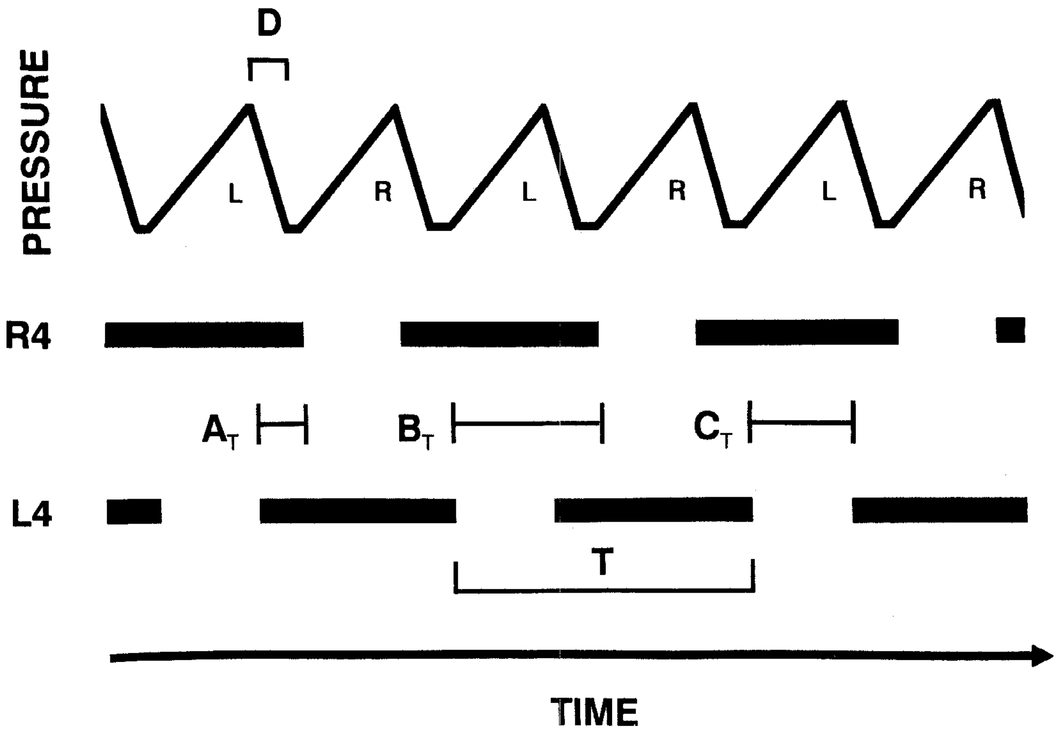

Figure 1.—Diagram illustrating the relationship between step-coupled fluctuations in prosomal pressure and stepping pattern of the fourth leg pair. Each pressure surge is caused by flexion of the femur-patella joint in one of the fourth walking legs during the recovery phase of the step cycle. The pressure surges labled 'L' are caused by flexion of the left fourth leg (L4) and those labled 'R' are caused by flexion in the right fourth leg (R4). The time needed for the pressure surge to decay is indicated by 'D'. In the step diagram for R4 and L4, the black bars represent periods of retraction (propulsive phase) and the open regions represent protraction (recovery phase). Variables associated with the step diagram include A_T (time between end of protraction in one of the fourth legs and beginning of protraction in the other at step period T), B_T (time between beginning of protraction in one of the fourth legs and beginning of protraction in the other at step period T) and C_T (duration of protraction in the fourth leg pair at step period T). The hypothesis developed here predicts that whipscorpions should prefer step cycles (T) in which D is less than A_T, where $A_T = B_T - C_T$. At step periods where D is greater than A_T, pressure surges will overlap causing an increase in the pressure baseline and requiring greater exertion by flexor muscles.

pressure from a freely walking whipscorpion through a pressure transducer affixed to the arthrodial membrane of the femur-patella joint in leg 1 (see Shultz 1991 for details). Pressure decay times were measured in 17 steps where step period was sufficiently long that the pressure surge decayed to the active pressure baseline. Mean decay time of the pressure surge was found to be 0.130 s (SE = 0.006). This value was then substituted for A_T in Equation 2, and the equation was solved for T. On the basis of these data, the hypothesis predicts that whipscorpions should prefer step periods greater than about 0.80 s.

This prediction was compared to a frequency distribution of step periods (n = 483) from electromyographic records of seven whipscorpions. The structure of the distribution is consistent with the predictions of the hypothesis (Fig. 2). The number of steps with 'long' cycle periods (i.e., greater than 0.8 s) is substantially greater than those with 'short' cycle periods (i.e., less than 0.8 s). More importantly, a preference for 'long' over 'short' step periods is suggested by a pronounced increase in the frequency of steps in the 0.80–0.89 s range compared to the 0.70–0.79 s range.

These results are consistent with the hypothesis that *Mastigoproctus* uses long step periods to avoid mechanical and energetic inefficiencies associated with flexing the femur-patella joint of one member of the fourth leg pair against high prosomal pressures generated by flexion in the

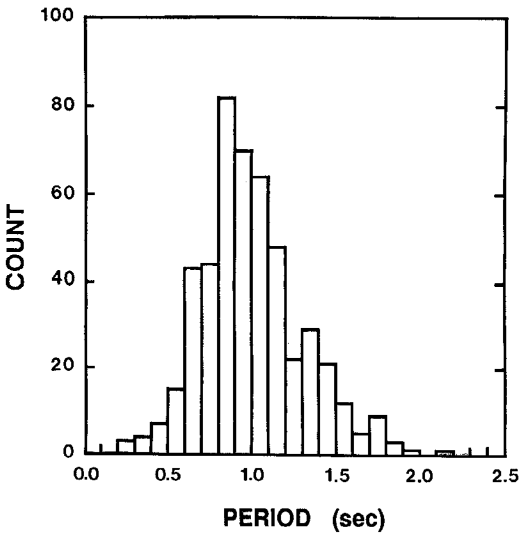

Figure 2.—Frequency distribution of step cycle periods representing 483 steps from seven whipscorpions. The hypothesis developed here predicts that whipscorpions should prefer step periods longer than 0.80 s. The structure of the frequency distribution is consistent with this prediction, but this comparison cannot be regarded as a statistical test of the hypothesis.

other. If whipscorpions were to walk at shorter step periods (i.e., higher speeds), step-coupled pressure surges would overlap thereby increasing the active baseline pressure and requiring greater forces from the flexor muscles. It is not known whether these results apply to spiders and other arachnids that use hydraulic pressure for leg extension.

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