

## AXIAL KINEMATICS AND MUSCLE ACTIVITY DURING TERRESTRIAL LOCOMOTION OF THE CENTIPEDE *SCOLOPENDRA HEROS*

BRUCE D. ANDERSON<sup>1</sup>, JEFFREY W. SHULTZ<sup>2,\*</sup> AND BRUCE C. JAYNE<sup>3</sup>

<sup>1</sup>Department of Integrative Biology, University of California, Berkeley, CA 94720, USA,

<sup>2</sup>Department of Entomology, University of Maryland, College Park, MD 20742-5575, USA and

<sup>3</sup>Department of Biological Sciences, University of Cincinnati, Cincinnati, OH 45221-0006, USA

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### Summary

For centipedes moving steadily on a treadmill at speeds of 0.5, 1.0 and 1.5  $Ls^{-1}$ , where  $L$  is body length, we obtained video tapes of movement that were synchronized with electromyograms (EMGs) from lateral flexor muscles at six standardized longitudinal positions. Field-by-field analysis of video tapes revealed posteriorly propagated waves of bending at all speeds. Muscle activity was also propagated posteriorly at the same speed as the kinematic wave, and EMGs of the lateral flexors were generally unilateral and alternating (between the left and right sides). The timing of EMG activity relative to lateral bending was consistent with electrical activity during the shortening of muscle fibers; therefore, activity of the axial musculature appears to cause lateral bending. Analysis of variance revealed widespread effects of speed on both kinematic and electromyographic variables, whereas longitudinal position within the centipede (between body segments 8 and 18) generally did not have significant effects on the same variables. For example, as speed increased from 0.5 to 1.5  $Ls^{-1}$ , the amplitude of lateral displacement

approximately doubled and the amplitude of lateral bending increased approximately threefold. Lag times (in seconds) indicating the propagation of kinematic and EMG events along the length of the centipede decreased significantly with speed. Phase lags among longitudinal sites decreased significantly with increased speed, indicating that the kinematic and EMG wavelengths increased with increased speed. EMG duration approximated 50% of cycle duration and was unaffected by speed, and the phase of the EMG activity relative to lateral bending was also unaffected by locomotor speed. Hence, all results from all speeds are consistent with active bending of the axial segments during centipede locomotion, conflicting with the widely accepted hypothesis that lateral bending is imposed on the body by the metachronal stepping pattern of the legs and that bending is resisted by axial muscles.

Key words: locomotion, Arthropoda, Chilopoda, muscle, electromyography, centipede, *Scolopendra heros*.

### Introduction

Locomotion in most terrestrial animals is achieved primarily through appendicular movements. However, it is well known that axial movements can enhance locomotion by increasing stride length, and axial movements are often essential for attaining the highest speeds in vertebrates (Howell, 1944; Snyder, 1952; Gray, 1968). Among terrestrial arthropods, the myriapods (centipedes, millipedes, etc.) and some larval insects combine axial and appendicular movements during locomotion and, among these, certain centipedes are the fastest runners (Manton, 1977). In contrast to the apparent synergism characterizing the axial and appendicular movements in running vertebrates, the currently favored view of locomotion in centipedes maintains that lateral undulations are imposed on the body by the high-speed stepping patterns and that

undulations are deleterious and actively resisted by the axial musculature (Manton, 1977).

Many of Manton's views were derived from combined observations of static anatomy and the kinematics of locomotion in scolopendromorph centipedes. During the locomotion of these centipedes, contralateral legs within each body segment step alternately, and increased speeds are attained by decreasing the duration of the propulsive stroke. Many legs contact the ground simultaneously at any given instant during low-speed movement; this number decreases at higher speeds. Similarly, the distance between supporting legs increases with increasing speed, such that only three or four legs may support the animal at the highest stepping rates. Patterns of axial undulation are also correlated with speed.

\*Author for correspondence.

Both the wavelength and amplitude of posteriorly propagated (descending) waves of lateral bending increase with increased speed. The propulsive legs of the animal are located in the concave side of each bent region. On the basis of these observations, Manton reasoned that a lateral force was imposed on the body as it pivoted around each supporting leg, such that the propulsive legs on one side of the body tended to force the body towards the contralateral side. Thus, the descending wave of stepping would produce a descending wave of axial bending. Manton argued that lateral bending was energetically inefficient and that scolopendromorphs attempted to damp lateral undulations through active resistance by the axial muscles, a strategy that succeeded only at the lowest speeds.

Manton concluded that the key to achieving efficient high-speed locomotion in centipedes was to eliminate the propensity for the body to undulate at high stepping rates and she ascribed functional significance to a suite of features (e.g. tergal fusion, longitudinal variation in tergite size, reduced segment number) found in centipedes. Manton's suggestions are now widely accepted in both the primary scientific literature and in textbooks (e.g. Gray, 1968; Wainwright *et al.* 1982; Barnes, 1987). Manton's interpretive approach generated explicit hypotheses which can now be tested experimentally. For example, Full (1989) found that scolopendromorph centipedes actually run more economically (consume less oxygen per unit body mass per unit distance) than other animals of similar mass, a result that seems to be inconsistent with Manton's predictions. Simultaneous recordings of kinematics and *in vivo* muscle activity can similarly provide information to test Manton's hypothesized patterns of axial muscle activity.

The principal goal of our investigation was to test Manton's model for the role of axial structures during the locomotion of scolopendromorph centipedes. Information with which this model may be tested is the timing of lateral flexor muscle activity relative to lateral bending of the axial structures. If axial muscles oppose lateral bending so as to maintain a straight, rigid body throughout forward locomotion, one would predict that activity of the lateral flexors would be either isometric or occur during lengthening of the muscle tissue. In contrast, if axial muscles actively generate sinusoidal descending waves of bending, one would predict that lateral flexor activity should begin when the intersegmental joint is maximally convex towards the side of the flexor muscle and that muscle activity should end when this region is maximally concave (i.e. activity during shortening of the muscle tissue). In the present study, we obtained synchronized video tapes and EMGs from axial muscles of scolopendromorphs running on a treadmill at three standardized speeds. Hence, we could determine whether lateral bending was likely to be resisted or actively produced by axial muscle activity and whether the relationship between bending and muscle activity was speed-dependent. Our results are consistent with the pattern expected for axial muscles promoting, rather than resisting, the formation of lateral bends.

## Materials and methods

### *Experimental animals*

Large scolopendromorph centipedes, *Scolopendra heros* Girard, were collected from the desert in Arizona by a commercial supplier. Four animals were used in our experiments with a mean mass of  $11.56 \pm 0.59$  g (S.E.M.) and a mean length of  $15.2 \pm 0.22$  cm (S.E.M.). Animals were maintained in plastic cages on a 12 h:12 h L:D photoperiod and at the same temperature that was used in the experiments ( $22\text{--}25^\circ\text{C}$ ). Petri dishes were used to provide a continuously accessible source of water, and the animals were fed a maintenance diet of crickets, *Acheta domesticus* (L.).

### *Kinematics*

We placed the animals on a motorized treadmill in order to obtain both video tapes and electromyograms (EMGs) of the animals moving primarily at three standardized speeds (0.5, 1.0 and 1.5 body lengths per second,  $Ls^{-1}$ ). The working section of the treadmill was approximately  $14\text{ cm} \times 32\text{ cm}$ , with the longest dimension being parallel to the motion of the belt of the treadmill. Hence, the tread surface was sufficiently large to allow unhindered movement of the centipedes. The video camera was positioned vertically above the center of the working section of the treadmill. The camera had an imaging rate of 60 Hz and shutter speed of  $1/500$  s. A neon flasher light blinked every 0.5 s within view of the camera and simultaneously sent a signal to the tape recorder to allow synchronization of the video tape and EMG records. The treadmill belt was marked with a reference grid to facilitate kinematic analysis.

We used the Peak 5 digitizing system (Peak Technologies Inc., Boulder, CO, USA) to digitize images (spaced at  $1/60$  s) and to perform a frame-by-frame analysis of the kinematics. We only analyzed sequences for which the centipedes closely matched the treadmill speed and for which the EMGs were of suitable quality. For each treadmill speed, we selected time intervals long enough to encompass four complete cycles of locomotion. We digitized the  $x$ - and  $y$ -coordinates for two points on each body segment including the bases of the antennae, the left and right posterior lateral margin of each tergite and the bases of both legs on the most posterior segment. We also digitized a point on the tread surface in order to include a correction for tread speed when calculating the speed of locomotion of the centipede. In our digitizing scheme, the overall direction of forward movement of the centipede (parallel to the direction of movement of the tread surface) was used to define the  $x$ -axis, and lateral movement to the right was in the positive  $y$  direction.

To calculate the displacement of the middle of each body segment, we used the mean of the digitized  $x$ - and  $y$ -coordinates from both the left and right landmarks on each segment. For each cycle of movement, we calculated the amplitude of lateral displacement ( $y_{\text{max}}$ ) as half of the difference between successive minimum and maximum values of the  $y$ -coordinate. Consequently, because the midline of each

segment oscillated to the left and right during the locomotor cycle,  $y_{\max}$  oscillated between negative and positive values.

Before calculating the angles indicating the amount of lateral bending (flexion) between adjacent body segments ( $\beta$ ), we filtered the digitized coordinates with a Butterworth optimal filter using the Jackson–Knee method. We then measured the amount of flexion as the angle between the two lines determined by the filtered right- and left-side coordinates of two adjacent segments. By convention, positive angles of flexion indicate that the animal was flexed (concave) to the right, and negative angles indicate flexion in the opposite direction. The calculation of the amplitude of lateral flexion ( $\beta_{\max}$ ) was similar to that of lateral displacement. Likewise,  $\beta_{\max}$  oscillated between negative and positive values during the locomotor cycle as the animal flexed alternately to the left and right, respectively.

To determine any propagation of  $y_{\max}$  and  $\beta_{\max}$  along the length of the centipede, we calculated lag times ( $y_{\text{lag}}$  and  $\beta_{\text{lag}}$ ) as the difference between the elapsed times of comparable kinematic events ( $y_{\max}$  or  $\beta_{\max}$ ) for pairs of sites at different longitudinal positions divided by the number of intervening body segments. Positive values of lag time indicate that events at the more posterior sites occurred after those at the more anterior location. We divided lag times by cycle duration to determine the intersegmental phase lags of  $y_{\max}$  and  $\beta_{\max}$ . For each body segment of interest, we also calculated the difference between the elapsed times at  $y_{\max}$  and  $\beta_{\max}$  and divided this difference by cycle duration to yield the phase shift between these two kinematic events ( $y$ – $\beta$  shift).

We determined the duration of each locomotor cycle (rounded to the nearest 0.01 s) as the difference between successive times of  $y_{\max}$ ,  $\beta_{\max}$  and EMG onset for body segments 8, 10, 12, 14, 16 and 18 (see Fig. 1). Preliminary statistical analysis revealed no consistent significant differences between cycle durations calculated using successive times of  $y_{\max}$ ,  $\beta_{\max}$  or EMG onset. Clear periodicity in EMGs was occasionally evident, even when kinematic variables had amplitudes (at  $0.5 \text{ L s}^{-1}$ ) so low that determining cycle duration was difficult. Hence, to use a single value of cycle duration to calculate all phase variables, we used the mean cycle durations determined from all available EMGs within each cycle. The frequency of undulation ( $f$  in Hz) equalled the inverse of cycle duration.

#### Electromyography

Centipedes were maintained under cold anesthesia throughout the implantation of electrodes. Before implantation, the animals were cooled in a refrigerator ( $5^\circ\text{C}$ ) for approximately 10 min and then immobilized on a small metal sheet which was kept on a bed of ice. The implantation procedure generally lasted about 4 h and the animal was allowed at least 30 min to recover before the experiment, during which it appeared to behave normally.

Procedures used in obtaining EMGs were similar to those used in previous studies of arthropod locomotion (e.g. Delcomyn and Usherwood, 1973; Bowerman, 1981; Shultz,

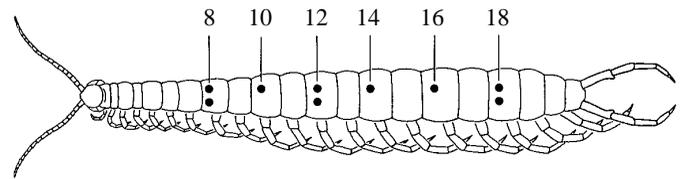


Fig. 1. Dorsal view of *Scolopendra heros*. For the sake of simplicity, most legs on the right side are not shown. The filled circles indicate the locations of the nine bipolar electrodes that were used to record *in vivo* muscle activity. Segments are numbered from anterior to posterior.

1992). We constructed bipolar recording electrodes using 0.05 mm diameter polyurethane-coated, stainless-steel wire with a total length of approximately 1 m. The two strands of each electrode were glued to each other using a plastic cement. We scraped approximately 0.2 mm of insulation off the recording end of the electrode, and approximately 0.3 mm of wire in this region was bent at a right angle relative to the remaining wire. Results of preliminary dissections indicated that this configuration was optimal for ensuring that the electrode tips were embedded within the target muscle.

Nine bipolar electrodes and one ground electrode were implanted in each centipede. Numbering segments from anterior to posterior, implants were made on the right side of the body in segments 8, 10, 12, 14, 16 and 18 and on the left side in segments 8, 12 and 18 (Fig. 1). We inserted electrodes through the cuticle into the anterior attachment of the largest apparent lateral flexor muscle, the deep dorsal oblique muscle (Fig. 2, DDOM), through a pair of closely spaced (approximately 0.3 mm apart) holes made with a minuten insect-mounting pin. The DDOM attachment and fibers could be observed directly through the translucent cuticle. In addition, because muscles are separated by major tracheal trunks, which can also be seen through the cuticle, we were able to use these as landmarks to differentiate one muscle from another. We used a combination of cyanoacrylate glue and plastic cement to attach wires to the tergites in the immediate vicinity of implantation as well as at additional locations along the length of the animal. Sufficient slack was provided along implantation sites and points of attachment so that the centipede could move in an unimpeded fashion. The wires from the ground and all electrodes were glued to each other with plastic cement so that a single collective cable could be attached to a tergite near the mid-body of the animal. Threads suspended from the walls of the treadmill facilitated the positioning of the main cable so that it allowed free movement of the animal and minimized motion artifacts.

EMGs were amplified  $10\,000\times$  with Grass model P511K amplifiers using a 60 Hz notch filter and low- and high-pass filter settings of 100 Hz and 10 kHz, respectively. The amplified EMGs were recorded with a TEAC XR-7000 FM data recorder using a tape speed of  $9.5 \text{ cm s}^{-1}$ . The voltage of the blinking light (in the camera view) was simultaneously recorded with the EMGs to synchronize the EMG and

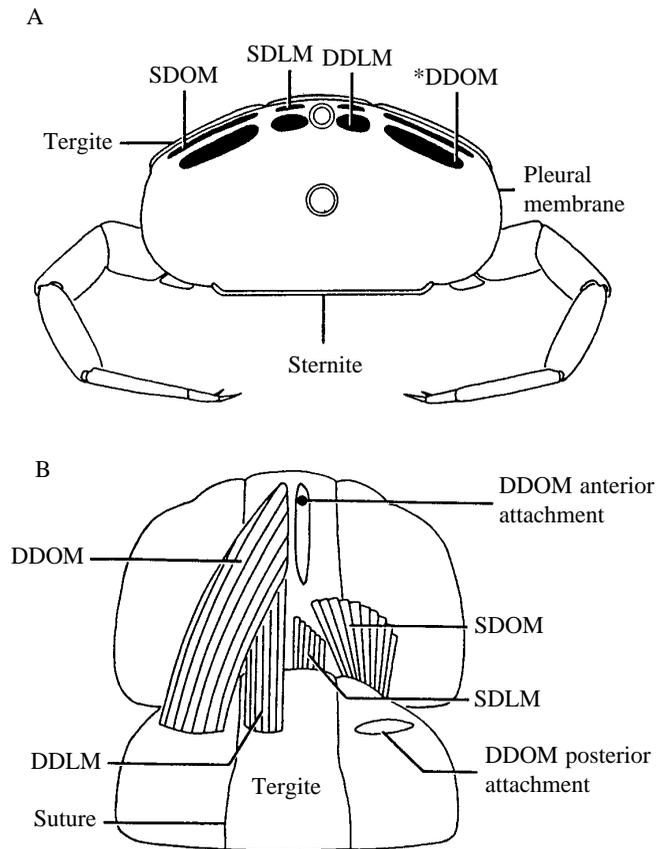


Fig. 2. Centipede musculature in cross-sectional (A) and ventral (B) views. The cross section is through the posterior part of the segment. In the ventral view, anterior is towards the top of the diagram, and the dot indicates the approximate position of the EMG electrode in the deep dorsal oblique muscle (DDOM). SDOM, superficial dorsal oblique muscle; SDLM, superficial dorsal longitudinal muscle; DDLM, deep dorsal longitudinal muscle.

kinematic data. To make hard copies of the EMGs for determining onset and offset times of muscle activity, we used a tape speed of  $1.2 \text{ cm s}^{-1}$  to play back EMGs from the tape recorder to a Gould model RS 3800 chart recorder, such that 1 mm on the hard copy equalled 5 ms of the original time scale.

We determined the times of EMG onset and offset by measuring the hard copies of the signals to the nearest millimeter (5 ms) and omitted bursts that could not be measured reliably. EMG duration equalled offset time minus onset time. We calculated EMG lag times (ONlag and OFFlag) among different longitudinal locations in the same manner as for the kinematic calculations. To facilitate investigation of the effects of speed, EMG durations and lag times were also converted to proportions of the cycle period (ON phase lag and OFF phase lag). We also calculated the phase shifts between the EMG and kinematic variables such that negative values indicate that the time of the EMG event preceded that of the kinematic event. The variable ON- $\gamma$  shift equalled the phase shift between EMG onset and the time of maximal lateral

displacement towards the side containing the electrode, whereas ON- $\beta$  shift was the phase shift relative to the time of maximal extension (convex) towards the side of the electrode. OFF- $\gamma$  shift equalled the phase shift between EMG offset and the time of maximal lateral displacement away from the side containing the electrode, whereas OFF- $\beta$  shift was the phase shift relative to the time of maximal flexion (concave) towards the side of the electrode.

#### Statistical analyses

Although it is desirable to perform statistical analyses that account for variation among different individuals, missing cells (particularly at  $0.5 L s^{-1}$  and at the highly variable posterior sites) within our overall experimental design of four individuals at three speeds and at six longitudinal locations prevented us from using a three-way analysis of variance (ANOVA) that accounted for individual differences. Instead, we used two-way ANOVAs in which both speed and longitudinal location were considered as fixed effects. To minimize the problems associated with pseudo-replication, for each site within each individual at each speed we calculated a mean value from the maximum of four observations (cycles) available for each combination of locomotor speed and anatomical location. Hence, in the two-way ANOVAs, for each combination of speed and longitudinal location, there were a maximum of four observations (=number of individuals). Unless stated otherwise, we used a significance level of  $P < 0.05$ . Because many effects were often highly significant ( $P < 0.001$ ), corrections for multiple comparisons were generally of little consequence. The Bonferroni method (dividing  $P$  by the number of comparisons) is one method of adjusting for multiple comparisons and, in the Results section, we discuss in greater detail the consequences of making such a correction. All statistical analyses were conducted using the software package Systat (Wilkinson, 1992).

## Results

### Morphology

The trunk in scolopendromorph centipedes has 21 leg-bearing segments (Fig. 1), each composed of a dorsal tergite and a ventral sternite (Fig. 2A). The tergites and sternites of adjacent segments are joined by flexible membranes (Fig. 2A). There are no condyles or other sclerotized specializations serving as intersegmental articulations, although the mid-dorsal and mid-ventral membranes tend to be less flexible than the lateral membranes. Tergite size tends to increase towards the posterior end of the animal, but the middle region of the trunk is composed of a staggered series of long and short tergites (Fig. 1). Electrodes implanted in this region were consistently placed in muscles arising from long tergites.

The axial musculature of centipedes is complex (Manton, 1965, 1977), and several trunk muscles may be capable of promoting or resisting lateral flexion. However, among the dorsal muscles, the deep dorsal oblique muscle (DDOM) has morphological features that are both consistent with

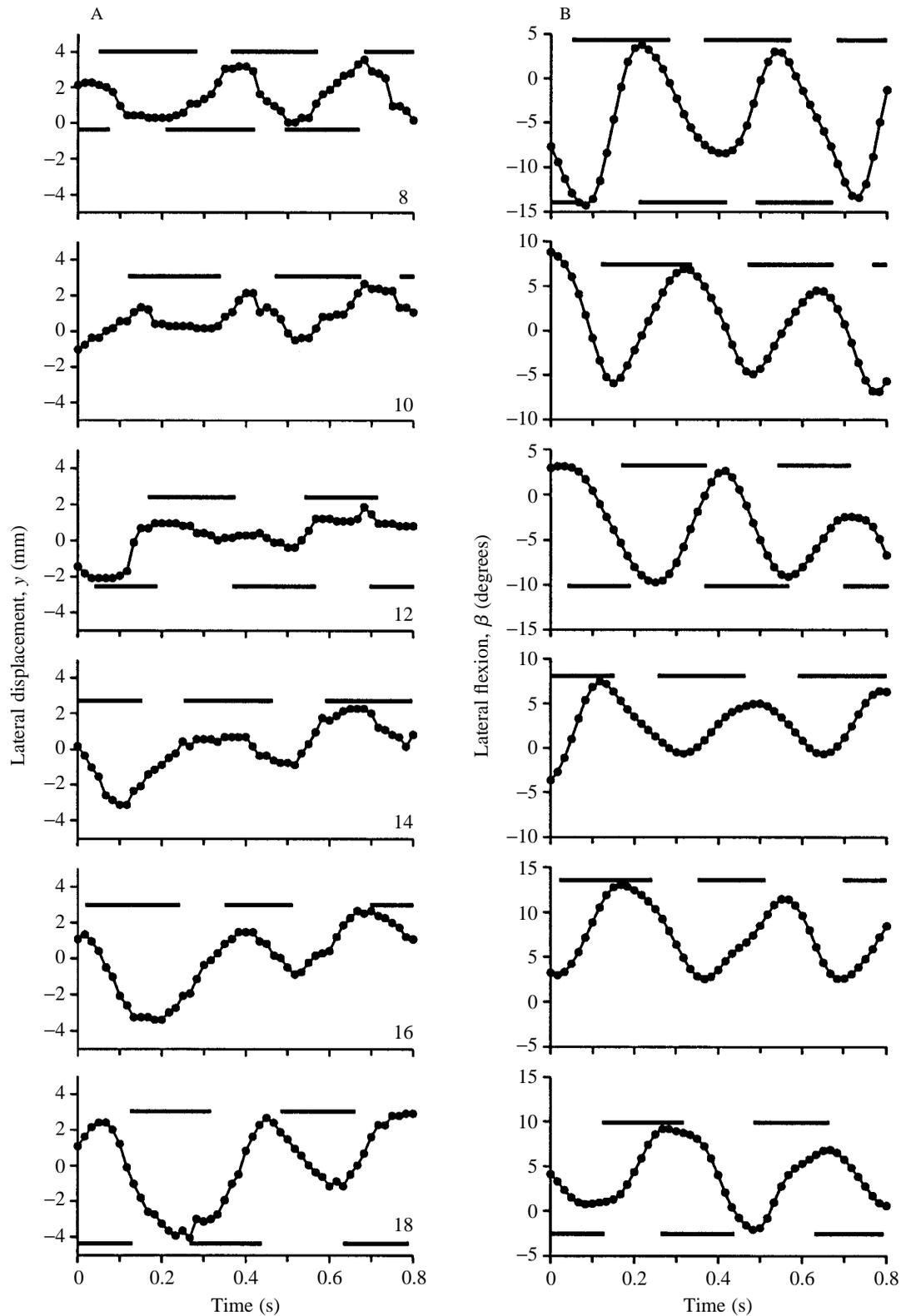


Fig. 3. Lateral displacement  $y$  (A) and lateral flexion  $\beta$  (B) versus time for a centipede moving at  $1.0Ls^{-1}$ , where  $L$  is body length. Positive and negative slopes on the plots of  $y$  versus time indicate movement of the body segment towards the right and left, respectively. Positive and negative slopes on the plots of lateral flexion  $\beta$  versus time indicate flexion towards the right and left, respectively, and positive values of  $\beta$  indicate that the side of the centipede is concave towards the right. The thick horizontal bars indicate the timing of electrical activity of the DDOM on the right side (above each plot), left side (below plots for segments 8, 12 and 18). Segment number is indicated in the lower right-hand corner of each lateral displacement plot.

specialization for lateral flexion and suitable for electromyographic analysis. The DDOM is a large muscle that arises anteriorly from the anteromedial portion of one tergite and inserts near the anterolateral margin of the posteriorly

adjacent tergite (Fig. 2). Consequently, this muscle has a larger mechanical advantage for lateral flexion than either the deep dorsal longitudinal muscle (DDLML) or the superficial dorsal longitudinal muscle (SDLML).

Table 1. Summary of F-values from separate two-way ANOVAs performed on kinematic and EMG variables

Variable	Error d.f.	ANOVA effects		
		Speed	Site	Speed $\times$ site
$y_{\max}$	54	61.9 (<0.001)	3.1 (0.02)	1.4 (0.21)
$\beta_{\max}$	54	18.2 (<0.001)	0.4 (0.82)	0.2 (0.99)
$y_{\text{lag}}$	45	15.0 (<0.001)	0.9 (0.46)	1.1 (0.39)
$\beta_{\text{lag}}$	43	25.9 (<0.001)	2.4 (0.06)	0.8 (0.68)
$y$ phase lag	43	8.8 (<0.001)	2.3 (0.07)	0.7 (0.70)
$\beta$ phase lag	45	6.2 (<0.004)	0.8 (0.52)	1.1 (0.39)
$y$ - $\beta$ shift	49	4.2 (<0.02)	0.9 (0.52)	0.7 (0.69)
Period	42	48.5 (<0.001)	0.2 (0.96)	0.3 (0.96)
EMG	44	39.9 (<0.001)	0.7 (0.63)	0.7 (0.73)
duration				
EMG %	44	2.9 (0.06)	0.9 (0.45)	0.6 (0.79)
duration				
ONlag	29	72.6 (<0.001)	2.0 (0.12)	0.8 (0.58)
ON phase lag	29	35.3 (<0.001)	3.3 (0.024)	1.3 (0.32)
OFFlag	29	18.2 (<0.001)	0.9 (0.46)	0.6 (0.79)
OFF phase lag	29	7.7 (0.002)	1.5 (0.22)	0.6 (0.79)
ON- $y$ shift	33	1.3 (0.30)	1.3 (0.30)	0.9 (0.53)
ON- $\beta$ shift	34	0.4 (0.66)	2.3 (0.08)	5.5 (<0.001)

Site refers to longitudinal location along the length of the centipede.  $P$  is indicated in parentheses after each  $F$ -value.

For all lag and phase lag variables, degrees of freedom for speed, site and speed  $\times$  site were 2, 4 and 8, respectively, and for all other variables degrees of freedom were 2, 5 and 10, respectively.

Degrees of freedom of the error term of the ANOVA are listed to the right of each variable.

### Kinematics

As shown in Fig. 3, both lateral displacement ( $y$ ) and lateral flexion ( $\beta$ ) at a given body segment varied more or less sinusoidally with time, and the regions with  $y_{\max}$  and  $\beta_{\max}$  were propagated posteriorly. Analysis of variance revealed that both  $y_{\text{lag}}$  and  $\beta_{\text{lag}}$  decreased significantly with increased forward speed of the centipede (Table 1). Intersegmental lag times showed no significant effect of longitudinal location (Table 1); therefore, the speeds of posterior propagation of  $y_{\max}$  and  $\beta_{\max}$  appear to be constant among the sites for which these values were determined (Fig. 1, segments 8–18).

The amplitudes of both lateral displacement ( $y_{\max}$ ) and lateral flexion ( $\beta_{\max}$ ) increased significantly with increased speed (Table 1; Fig. 4A,B). Within each locomotor speed, there was no significant pattern of variation in  $\beta_{\max}$  along the length of the centipede (Table 1 site effect; Fig. 4B). In contrast,  $y_{\max}$  showed some marginally significant (Table 1) longitudinal variation such that, at the faster two speeds, the more posterior body segments had greater values of  $y_{\max}$ . However, this trend was not significant when the Bonferroni correction was made. As shown in Fig. 1, the more posterior body segments are longer than some of the anterior body segments. Consequently, it is possible to obtain different amounts of lateral displacement with equal amounts of intersegmental lateral flexion along the length of the centipede.

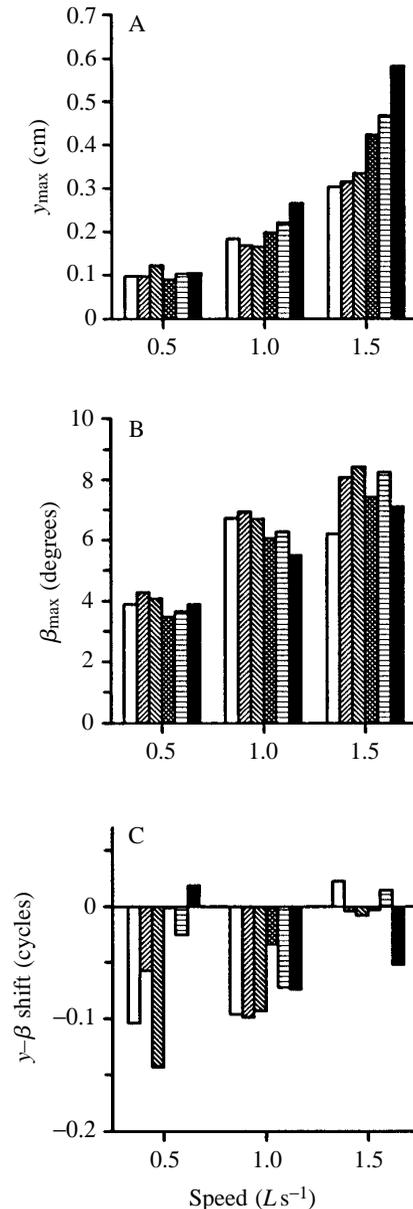


Fig. 4. Cell means from two-way ANOVAs of kinematic variables (Table 1). Amplitude of lateral displacement  $y_{\max}$  (A), amplitude of lateral flexion  $\beta_{\max}$  (B) and the phase shift between lateral displacement and flexion  $y$ - $\beta$  shift (C). For each speed, the white vertical bar represents the mean value for body segment 8, and each successive bar to the right represents a location that is two additional segments more posterior. A negative  $y$ - $\beta$  shift occurs when maximum lateral displacement precedes maximum lateral flexion at a site, and a positive  $y$ - $\beta$  shift occurs when  $\beta_{\max}$  precedes  $y_{\max}$  at a site.  $N=4$  for most samples.

At the fastest locomotor speed, lateral displacement and flexion were almost precisely in phase (Fig. 4C,  $y$ - $\beta$  shift=0). In other words, regions of maximal lateral flexion to the right occurred at the same moment that the region was maximally displaced to the left. As described previously by Manton (1977), the legs of *Scolopendra* contact the ground in these

regions of maximal lateral flexion. There was a marginally significant effect (Table 1) of locomotor speed on  $y$ - $\beta$  shift such that the disparity in the timing of  $y_{\max}$  and  $\beta_{\max}$  was greatest at the slowest speed. However, when  $P$  values were adjusted for multiple comparisons, the effect of speed on  $y$ - $\beta$  shift was not significant.

The phase lags of both  $y$  and  $\beta$  were significantly affected by speed (Table 1). Furthermore, the mean phase lags of  $y$  and  $\beta$  were very similar to each other and showed no regular pattern of differences. Because the intersegmental phase lags are in cycles per body segment, the inverse of these quantities yields an estimate of the wavelength ( $\lambda$ ) of the kinematic wave that is propagated posteriorly along the length of the centipede.

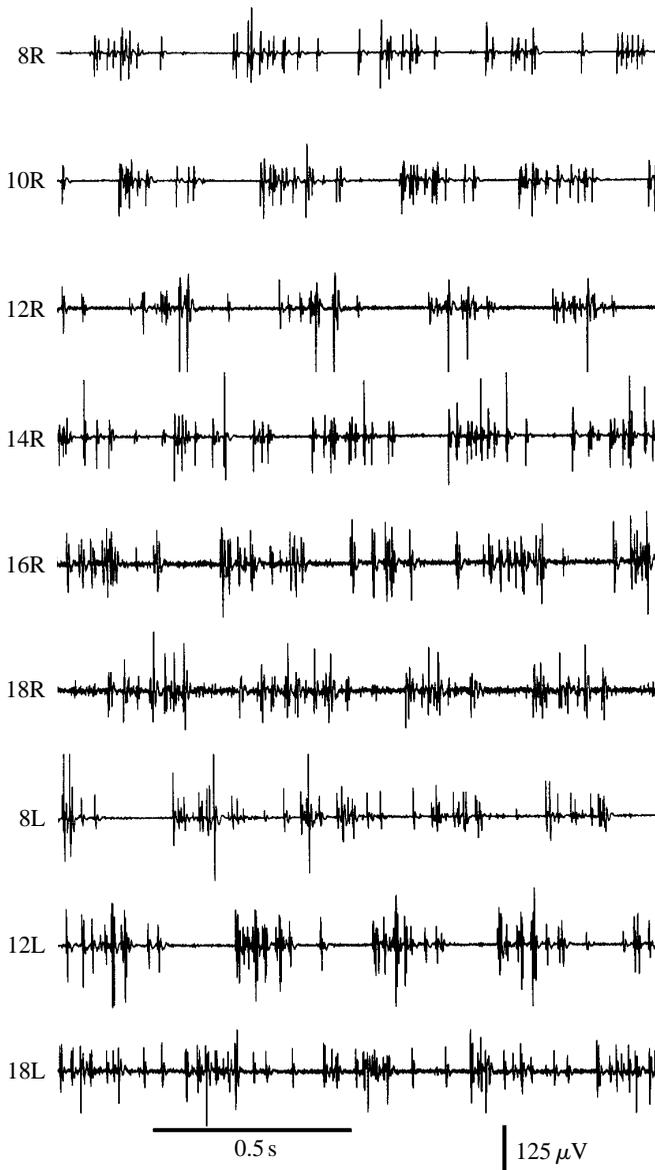


Fig. 5. Representative EMGs recorded simultaneously from the DDOM of a centipede moving at a speed of  $1.0 L s^{-1}$ . Numbers to the left of each recording indicate the number of the body segment (increasing posteriorly, see Fig. 1), and L and R indicate the left and right sides, respectively. Note the posterior propagation of the EMGs.

Using the mean values of  $\beta$  phase lag, the corresponding values of  $\lambda$  were 5.3, 9.4 and 11.0 body segments for forward speeds of 0.5, 1.0 and  $1.5 L s^{-1}$ , respectively.

Cycle duration declined significantly with speed. Mean  $\pm$  s.d. cycle durations were  $0.52 \pm 0.10$ ,  $0.35 \pm 0.04$  and  $0.29 \pm 0.04$  s, and these values correspond to frequencies of undulation ( $f$ ) of 1.92, 2.86 and 3.45 Hz, respectively. The product  $f\lambda$  estimates the speed of propagation of the kinematic wave, and these quantities are 10.2, 26.9 and 37.9 segments  $s^{-1}$  at forward locomotor speeds of 0.5, 1.0 and  $1.5 L s^{-1}$ , respectively.

#### Electromyography

As shown in Fig. 5, muscle activity occurred in relatively discrete bursts which propagated posteriorly. Furthermore, activity alternated between the left and right sides for each body segment (Figs 3, 6). The relative durations of the EMGs

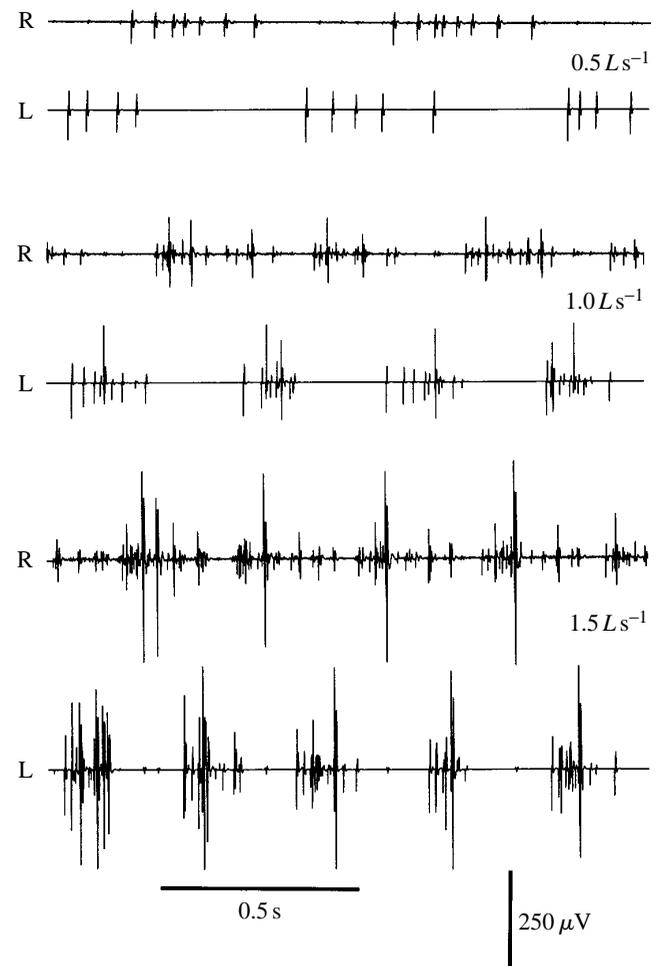
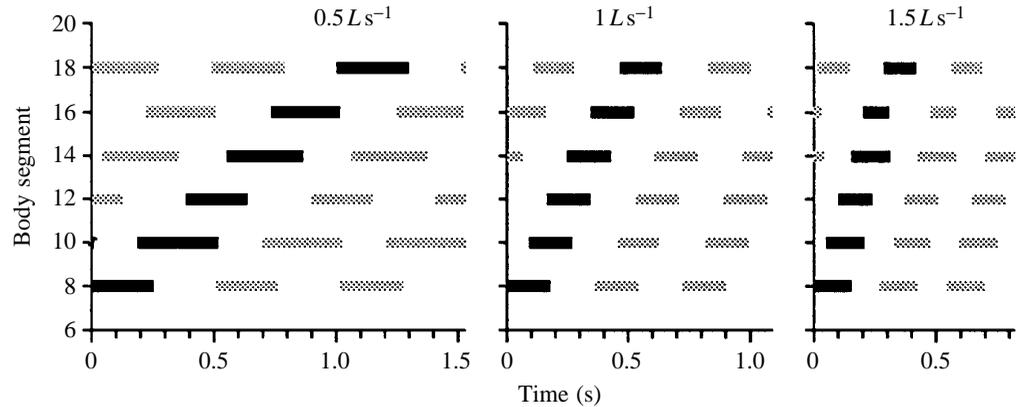


Fig. 6. EMGs from the left and right DDOM in segment 12 of a single individual moving at three speeds. Note that the voltage scale is the same for all EMGs, and the amplitudes and waveforms suggest recruitment of additional motor units with increased speed (see text for more detail). Contralateral EMGs are approximately  $180^\circ$  out of phase and relative EMG durations are approximately 50% of a cycle for all speeds.

Fig. 7. Summary of the timing of EMGs for all longitudinal locations at three locomotor speeds. The horizontal bars indicate activity of the DDOM for each of the longitudinal locations given on the y-axis, and the solid black horizontal bars denote a 'homologous' stimulus as it is propagated posteriorly. The diagram is based on mean values observed for EMG duration (at each site) and intersegmental lag times for the onset of muscle activity (the same values were used for all depicted cycles). Note that the time scale is the same for all three plots, and the time interval shown in each plot equals three cycles. A steeper slope among the onset times of different longitudinal locations indicates a faster rate of posterior propagation. Note that the temporal overlap among the solid black lines increases with increased speed, indicating greater numbers of adjacent body segments with simultaneous ipsilateral activity.



closely approximated 50% of the cycle duration (Figs 5–7), and these values were unaffected by either locomotor speed or longitudinal location within the centipede (Table 1).

The absolute duration of EMG activity decreased significantly with increased speed but did not vary among recording sites (Table 1). Mean  $\pm$  s.d. EMG durations were  $0.28 \pm 0.05$ ,  $0.17 \pm 0.01$  and  $0.14 \pm 0.03$  s for speeds of 0.5, 1.0 and  $1.5 Ls^{-1}$ , respectively. The time interval between onsets of activity at ipsilateral lateral flexors in adjacent body segments (ONlag) decreased significantly with speed but did not vary significantly among sites within each locomotor speed (Table 1). Mean  $\pm$  s.d. values of ONlag were  $0.10 \pm 0.015$ ,  $0.045 \pm 0.01$  and  $0.025 \pm 0.003$  s body segment $^{-1}$  for speeds of 0.5, 1.0 and  $1.5 Ls^{-1}$ , respectively. These positive values of ONlag support the conclusion that lateral flexor muscles had a descending pattern of activation at all speeds. On the basis of the mean ONlag values, the corresponding speeds of posterior EMG propagation were 10.0, 22.2 and 40.0 segments s $^{-1}$ , which were effectively identical to those calculated above for the kinematic wave of axial bending.

When ONlag values were divided by cycle duration, the resulting values of ON phase lag decreased significantly with speed. Longitudinal location had a marginally significant effect on ON phase lag, which would not be considered significant after correcting for multiple comparisons. Mean  $\pm$  s.d. values for ON phase lag (per body segment) were  $0.19 \pm 0.04$ ,  $0.14 \pm 0.02$  and  $0.09 \pm 0.005$  cycles for speeds of 0.5, 1.0 and  $1.5 Ls^{-1}$ , respectively.

Values of both OFFlag and OFF phase lag also decreased significantly with increased speed and did not vary significantly among sites (Table 1). For speeds of 0.5, 1.0 and  $1.5 Ls^{-1}$ , mean  $\pm$  s.d. values of OFFlag and OFF phase lag were  $0.09 \pm 0.04$ ,  $0.045 \pm 0.01$  and  $0.025 \pm 0.01$  s and  $0.17 \pm 0.08$ ,  $0.14 \pm 0.025$  and  $0.09 \pm 0.025$  cycles per body segment, respectively. Thus, the very similar lag times and phase lags indicate the same speeds of posterior propagation of EMG onset and offset.

For each locomotor speed, the longitudinal extent of simultaneous ipsilateral activity of the lateral flexor muscles was estimated from the relative EMG duration (in cycles) divided by the EMG phase lag per segment (since the rate of EMG propagation was constant along the length of the centipede for which we obtained EMGs). On the basis of the mean values of ON phase lag and a relative EMG duration equal to 0.5 cycles, these quantities were 2.6, 3.7 and 5.6 body segments for 0.5, 1.0 and  $1.5 Ls^{-1}$ , respectively. Fig. 8 shows how these relatively large longitudinal regions of ipsilateral muscle activity are propagated along the length of the animal.

In addition to speed affecting many of the EMG timing variables, the intensity of muscle activity increased with increased speed. As shown in Fig. 6, the frequency of spikes constituting an EMG burst increased with increased speed. Furthermore, the amplitude and waveform of many of the observed potentials were highly repeatable, suggesting that such signals were motor unit potentials. At the lowest speed, effectively only one population of spike amplitudes was observed (Fig. 6). At  $1.0 Ls^{-1}$ , the lowest-amplitude spikes were still apparent as well as additional spikes of higher amplitude. At  $1.5 Ls^{-1}$ , there were very high-amplitude potentials in addition to those potentials observed at  $1.0 Ls^{-1}$ . Hence, as centipedes increased their locomotor speed, they appeared to increase the stimulation frequency of individual motor units in addition to recruiting additional motor units in an additive fashion.

None of the variables indicating the phase of EMG activity relative to kinematic events changed significantly with either locomotor speed or longitudinal position (Table 1, ON- $\gamma$  shift and ON- $\beta$  shift). When both ON- $\gamma$  shift and ON- $\beta$  shift equal zero, EMG onset occurs in a region that has maximal lateral displacement and maximal lateral extension (convexity) towards the side containing the electrode (Fig. 3). Values of zero are predicted by the active bending model of undulation. The overall means  $\pm$  s.d. of ON- $\gamma$  shift and ON- $\beta$  shift were  $0.01 \pm 0.06$  and  $0.05 \pm 0.03$  cycles, respectively.

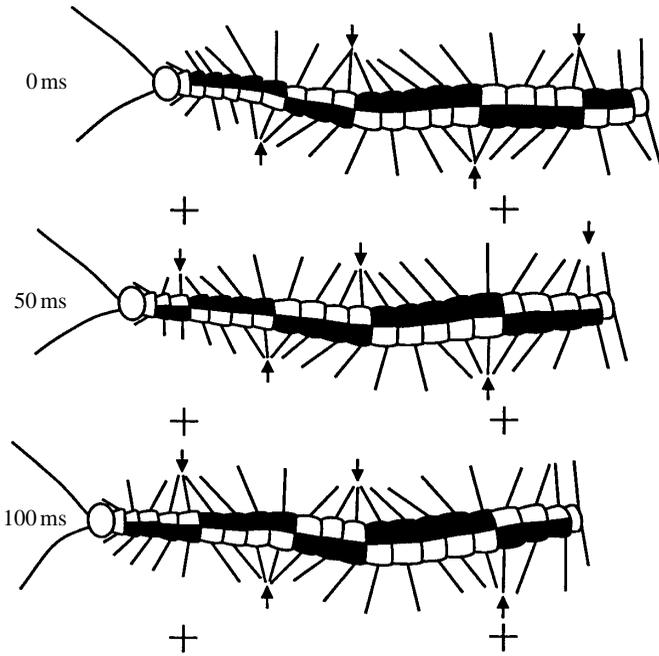


Fig. 8. A drawing of a centipede based on synchronized video tapes and EMGs for locomotion on a treadmill at a forward speed of  $1.0Ls^{-1}$ . Shaded regions indicate activity of the DDOM. The posterior and anterior edges of the each shaded region (including several adjacent ipsilateral locations) represent the onset and offset of muscle activity, respectively, as it is propagated posteriorly. For this illustration, muscle activity was observed directly for the nine electrode locations shown in Fig. 1, and activity at the remaining sites was inferred from mean values of the phase of EMGs relative to kinematic variables. The arrows indicate regions of foot contact with the ground. The legs are represented schematically by a straight line extending from the base of the leg to the distal tip of the limb. Because of varying amounts of flexion within different limbs, the lengths of the schematic limbs are highly variable. The + marks below each diagram indicate reference marks (10 cm apart) on the tread surface which have been aligned so that the forward movement of the centipede proceeds from right to left across the page.

The significant interaction between speed and site in the ANOVA for ON- $\beta$  shift (Table 1) appears to result primarily from the values for site 18 at  $1.0Ls^{-1}$  (Bonferroni *post-hoc* comparison of means). The occasional tendency for the centipedes to lift their posterior region probably accounts for these results, rather than the interaction term reflecting a general trend.

As expected, since EMG duration equalled 50% of the cycle, the ANOVAs of OFF- $\gamma$  shift and OFF- $\beta$  shift (not given in Table 1) revealed no significant effects of speed, site or the interaction term speed  $\times$  site. The grand means  $\pm$  S.D. of OFF- $\gamma$  shift and OFF- $\beta$  shift were  $0.00 \pm 0.05$  and  $0.04 \pm 0.06$  cycles, respectively. Consequently, the offset of muscle activity occurred when a region was maximally flexed (concave) and laterally displaced away from the side containing the electrode. This result is also consistent with predictions of the active bending model.

As shown in Fig. 8, these times of muscle activity also correspond closely to the onset of activity on the side of a body segment that is contralateral to foot contact. In addition, the transitions from left- to right-side and from right- to left-side activity occur in the longitudinal locations of foot contact of the centipede.

### Discussion

The results from our quantitative kinematic analysis of axial bending in scolopendromorph centipedes generally agree with earlier qualitative analyses by Manton (1952, 1965, 1977). Waves of lateral bending passed posteriorly along the length of the body at all speeds, with the speed of longitudinal propagation and the amplitudes of lateral displacement and intersegmental flexion increasing simultaneously with speed. Manton noted that the posterior region of the trunk appeared to undulate at greater amplitudes than the anterior region, and she attributed this to greater flexibility between the posterior segments. In contrast, our results indicated no significant longitudinal differences in intersegmental flexion, and we attributed enhanced posterior undulation to an increase in lateral displacement generated by similar degrees of flexion between longer posterior segments (Figs 1, 4)

Our integrated electromyographic and kinematic results were inconsistent with the mechanical model of lateral bending in centipedes proposed by Manton (1965, 1977). Although Manton did not offer explicit quantitative predictions about the relative timing of muscle activity and the amplitudes of lateral bending, it is clear that she regarded a straight, rigid body as optimal for efficient forward locomotion in centipedes. Manton suggested that lateral bending is imposed on the axial structures by forces generated by the legs and that axial muscles resist rather than promote bending, a process she termed 'facultative rigidity'. This interpretation implies that a lateral flexor on one side of the animal should be active (1) isometrically, (2) or when the muscle tissue is being lengthened during the transition from concave to convex on the side of the active muscle or (3) at any time when the muscle would serve to straighten the body. For the first alternative, no lateral flexion would be observed. For the second alternative, the active resistance model predicts ON- $\beta$  and OFF- $\beta$  phase shifts of  $-0.25$ . For the third alternative, EMG duration would be 0.25 cycles with an ON- $\beta$  phase shift of 0 and an OFF- $\beta$  phase shift of  $-0.25$ . However, our combined mean values observed for ON- $\beta$  shift, OFF- $\beta$  shift and EMG duration differed significantly (one-sample *t*-test, d.f.=3,  $P < 0.005$ ) from the values predicted by both the second and third alternatives.

In contrast to Manton's model, our results indicate that the descending waves of axial bending observed in running scolopendromorph centipedes are actively generated by the axial muscles. In an elongate animal with an actively generated descending wave of axial bending, one would predict that lateral flexor muscles on one side of the animal should become active at, or near, the point of maximal flexion towards the opposite side and that this activity should persist until the body

achieves maximal flexion on the side of the flexor muscle. This active bending model predicts ON- $\beta$  and OFF- $\beta$  shift values near 0. The mean value observed for ON- $\beta$  shift was 0.05, which differs only marginally from 0 (one-sample *t*-test, d.f.=3,  $P=0.048$ ). The mean value for OFF- $\beta$  shift is 0.04 and does not differ significantly from 0 (one-sample *t*-test, d.f.=3,  $P=0.339$ ). Consequently, we conclude that lateral flexor muscles actively promote, rather than resist, axial bending in running scolopendromorph centipedes.

These findings have important implications for the understanding of the locomotor mechanics and evolutionary morphology of centipedes. Using the assumption that lateral bending is imposed by the legs and actively resisted by the axial muscles, Manton offered functional explanations for apparent correlations among the complexity of the axial musculature, variation in tergite length, tergal fusion, segment number, leg length and maximal locomotor speeds that she observed in centipedes and other myriapods. Because of the internal consistency and apparent explanatory power of these mechanical and evolutionary considerations, Manton's work on centipede locomotion has been widely accepted by arthropod biologists. However, our experimental observations of *in vivo* muscle activity contradict the active resistance hypothesis of axial muscle function in scolopendromorphs and suggest that the traditional view of centipede locomotion must be re-examined and that alternative explanations for trends in axial and appendicular evolution should be explored. Similarly, there should be an attempt to find possible mechanical or energetic benefits of descending waves of axial bending at higher speeds, such as increased stride length, greater stability about the center of mass or enhanced tracheal ventilation.

Although lateral undulations appear to be relatively unimportant for the locomotion of the vast majority of terrestrial arthropod taxa other than centipedes, lateral undulations are widespread in ectothermic vertebrate taxa, and numerous studies have experimentally examined the functional basis of these axial movements. One should use caution when making comparisons between vertebrates and centipedes because of the structural and phylogenetic dissimilarities between these groups. However, the combination of vertebrates possessing a segmented body plan (which may or may not include legs) and using lateral bending suggests some utility in comparing axial function in these two groups.

The results of studies on the axial undulatory movements and patterns of muscle activity of ectothermic vertebrates tend to fall into three major categories: (1) terrestrial lateral undulation of snakes, (2) terrestrial locomotion of tetrapods and (3) aquatic lateral undulation. Of these three categories, the terrestrial lateral undulatory locomotion of snakes most closely resembles our findings for the axial movements of centipedes. For snakes performing terrestrial lateral undulatory locomotion past a series of pegs, lateral axial bending and EMG activity in the lateral flexor muscles are both propagated posteriorly (Jayne, 1988). The lateral flexor muscles are activated in an alternating unilateral fashion and the relative

EMG duration approximates 50% of the locomotor cycle. Furthermore, the timing of epaxial muscle activity occurs during lateral flexion towards the side of the active muscle, and the combination of EMG duration and intersegmental lag times is such that several adjacent body segments show simultaneous ipsilateral muscle activity (Jayne, 1988).

One apparent difference between the terrestrial undulation of snakes and centipedes is in the region of the body that transmits forces to the locomotor surface. When a snake crawls past a series of pegs, the pegs are generally located in areas of the snake that are minimally flexed and midway between regions of maximal lateral displacement (Jayne, 1986, 1988). In contrast, the legs of the centipede touch the locomotor surface on the concave side of a region that is maximally displaced to one side while it is maximally flexed (Fig. 8). Perhaps analyses of forces transmitted to the locomotor surface (B. D. Anderson and R. J. Full, unpublished data) will clarify whether these different regions of force application indicate minor or fundamental differences in the mechanisms of centipede *versus* snake locomotion. Unlike the DDOM of centipedes studied here, the EMGs obtained from snakes were from epaxial muscles which spanned several body segments and the species of snakes studied had more than 120 body segments.

Our analysis showed that scolopendromorph centipedes use descending waves of lateral bending and muscle activation at all locomotor speeds, but the situation in vertebrates is more complicated. Whether lizards and salamanders utilize standing or posteriorly propagated kinematic waves in their terrestrial locomotion appears to depend on the species and the speed at which they are moving (Sukhanov, 1974; Edwards, 1977; Ritter, 1992). Traveling kinematic waves in ectothermic tetrapods are more likely to occur at higher locomotor speed and in particular species with relatively elongate bodies (Daan and Belterman, 1968; Edwards, 1977; Ritter, 1992). To date, studies of axial muscle activity during the terrestrial locomotion of salamanders and lizards have found no clear evidence of posteriorly propagated EMG activity (Fig. 5 in Carrier, 1990; Frolich and Biewener, 1992). The coordination of footfalls with lateral displacement of the axial structures is still not thoroughly understood for many species, but it appears that, when a standing kinematic wave occurs for the axial structures, the region of minimal lateral displacement closely approximates the location of the limb girdles (Frolich and Biewener, 1992; Ritter, 1992).

For the aquatic lateral undulation of such diverse vertebrates as eels, trout and snakes, lateral displacement and flexion of the axial structures are propagated posteriorly (Grillner and Kashin, 1976; Williams *et al.* 1989; Jayne, 1988). The activation of the axial musculature during undulatory swimming also proceeds from head to tail; however, the rate of EMG propagation generally exceeds that of the kinematic wave. Consequently, a phase shift occurs between muscle activity and bending, and this phase shift shows a progressive increase posteriorly. In centipedes, however, the descending waves of flexion, lateral displacement and muscle activation are largely coupled and,

except for lateral displacement at higher speeds, show no significant longitudinal variation. Furthermore, for the undulatory swimming of certain vertebrates, EMG duration is commonly less than 50% of the cycle duration, the intersegmental phase lags of EMG onset and offset often differ, and the speed of propagation and the wavelength often show significant longitudinal variation (Williams *et al.* 1989; Van Leeuwen *et al.* 1990; Jayne, 1988).

For diverse modes of animal locomotion involving axial undulations, we still lack a good general understanding of the relative importance of intrinsic (to the organism) *versus* extrinsic factors in determining the axial waveform and its relationship to muscle activity. Despite the uncommon body plan of a pair of legs for each body segment, the axial kinematics and muscle activity of centipedes showed striking parallels to those used by certain limbless vertebrates. A particularly conspicuous feature of the axial muscle activity of centipedes was how EMG activity was phase-locked to the pattern of lateral flexion in a manner that was consistent with active lateral bending. In the future, it might be particularly interesting to determine whether this phase-locking of EMG activity to lateral flexion could be disrupted by altering the environment. For example, one informative experimental manipulation could be to use a very low friction substratum such as glass. Alternatively, one could place a centipede in water (Cloudsley-Thompson, 1982) to see whether the propagation of the axial EMG activity relative to bending would differ from that of terrestrial locomotion and come to resemble that of other undulating swimmers.

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