Helical swimming and body reversal behaviors in *Lumbriculus variegatus* (Annelida: Clitellata: Lumbriculidae)

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Abstract

Two unusual locomotor behaviors (body reversal and helical swimming) are described and related to postembryonic body size in the freshwater oligochaete, *Lumbriculus variegatus* (Annelida: Clitellata: Lumbriculidae). Both behaviors occur as responses to tactile stimulation when worms are on smooth substrates that offer little or no traction or protection. Body reversal, evoked by touch to anterior segments, involves a stereotyped sequence of bending movements that effectively reverse head and tail positions in about 0.4 s in newly hatched worms and 0.6 s in juvenile and adult worms. Though little net shift in the body center occurs, reversal may optimize body positioning in preparation for swimming away from predatory threat. In contrast to reversal, swimming is evoked by touch to posterior segments and consists of a rapid, rhythmic sequence of helical body waves (frequency ≈ 9–11 Hz). Waves alternate between clockwise and counterclockwise helical orientations, with posterior passage of each wave providing forward thrust. Swim velocity and wave velocity increase with body size. Though total distance and duration of each swim episode is short (≈ 1–2 body lengths in < 2 s), swimming may be an important means of predator avoidance in the littoral environment of these worms.

Introduction

Swimming is a relatively uncommon form of locomotion among aquatic oligochaetes (Annelida: Clitellata). It is apparently non-existent in the Family Tubificidae, but relatively common in the Naididae. Sperber (1948), for example, reviewed the systematics and natural history of approximately 100 naidid species, noting more than a dozen that were capable of swimming movements. Although she did not analyze or quantify swim movements, she noted two apparently different patterns of swimming, describing these as 'spiral' movements in some species and 'lateral' (or horizontal) movements in others.

Recently, Drewes & Fourtner (1993) provided the first detailed analysis of swimming behavior in any aquatic oligochaete. They showed that the so-called 'spiral' pattern of movements in the naidid, *Dero digitata* Oken, 1815, actually consisted of a rhythmic series of helical body waves. Curiously, successive waves alternated between left-handed and right-handed helical bending of the body, with posterior passage of each wave along the body providing forward thrust. Swimming in *Dero* occurred spontaneously or in response to posterior touch. However, it only occurred when worms were unconfined, on smooth substrates, or in 'open-water' conditions. Capabilities for touch-evoked swimming were also studied in relation to asexual fission, the normal mode of reproduction in *D. digitata*. Touch-evoked swimming responses occurred in both anterior and posterior zooids immediately after the zooids separated by transverse fission.

Here, I describe helical swimming in *Lumbriculus variegatus* Grube, 1884 (Family Lumbriculidae), the only representative of the Order Lumbriculida in which such behavior has been analyzed. In addition, I document a novel reflex response in which worms rapidly reverse head and tail ends in response to anterior tactile stimulation. Finally, I examine the dynamics of these unusual behaviors in relation to increases in

body size that occur during postembryonic growth from hatching to sexually maturity (cf., Drewes & Brinkhurst, 1990).

Materials and methods

Lumbriculus variegatus were obtained in May from a marsh in Gull Point State Park (West Lake Okoboji, Iowa, U.S.A). *Lumbriculus* cocoons, each containing 4–12 orange embryos, were found attached to submerged, decaying leaves in shallow water at the edge of the marsh. Cocoons were maintained in the laboratory (21–22 °C) for about one week until worms emerged. Maximal length of these hatched worms (at rest) was about 5–6 mm. Juvenile and sexually mature adult worms were collected within the same habitat as cocoons. Resting lengths of these worms ranged from 30–40 mm and 70–85 mm (juvenile and adult, respectively).

Worms were placed in individual shallow containers filled with spring water (21–22 ° C). Containers for juvenile and adult worms were flat-bottomed, white pans (23×23 cm), each containing about 1500 ml water ($\approx$ 3 cm water depth). Containers for newly hatched worms were 5.5 cm diameter Petri dishes containing 20 ml of spring water ($\approx$ 1 cm water depth).

Touch stimuli were delivered with the tip of a hand-held probe. The probe tip consisted of a thin rubber band loop (0.5 thickness for newly hatched worms, or 1.0 mm thickness for juvenile and adult worms). The loop was attached to the end of a wooden applicator stick (2 mm diam) and extended approximately 15 mm beyond the end of the stick. To evoke swimming or reversal responses, the probe was held just above the worm at a 30° angle to its long axis. Then, the head or tail was gently touched with the rubber loop. The flexibility of the loop ensured that worms were not injured when tactile pressure was applied. Touch stimuli were delivered at 15 min intervals to minimize habituation and optimize consistency in evoked responses.

Behavioral responses were recorded on videotape using a color video camera attached to a tripod. The camera lens was directly above the worm and shutter speed was 1/500 s. Jog and shuttle controls on the video cassette recorder allowed single-frame analysis of locomotor movements. Photographs of video images were obtained with a Sony UP1200A video printer.

The following parameters of swimming were examined:

(a) *number of helical body waves* produced per swim episode;
(b) *wave frequency,* expressed in Hz;
(c) *swim distance*, expressed as a percentage of resting body length and measured by determining the net translocation of the worm's head relative to a fixed point in its container; and
(d) *wave velocity*, determined by measuring rearward progress of the helical wave along the worm's body axis during two consecutive video frames.

Parameters related to reversal behavior included:

(a) estimated *angular change* in the worm's longitudinal axis caused by reversal, the maximum possible being 180°;
(b) net positional *change in the worm's body center* caused by reversal, expressed as a percentage of total body length, but without vectorial designation; and
(c) estimated *time from onset to completion of reversal*, as measured by the number of elapsed video frames (0.033 s/frame).

Results

Helical swimming responses

Spontaneous swimming, in the absence of experimenter-applied stimulation, was never seen. However, light tactile stimulation with the stimulus loop anywhere within the posterior one-half of the worm (i.e. between the tail tip and the geometric middle of the body) consistently evoked swimming responses in all sizes of worms. Tactile stimulation slightly anterior to the mid-body sometimes evoked swimming and/or body reversal, as described later. Thus, the sensory field for swimming behavior is slightly greater than one-half the worm's body length.

Swimming movements in all worms consisted of a series of rapid and rhythmic waves of helical body bending. Each wave began at the anterior end and rapidly progressed posteriorly along the body, thus propelling the worm forward (Figure 1). Analysis of freeze-frame video images showed that each successive wave alternated from clockwise (right-handed) to counterclockwise (left-handed) helical orientation. Each episode of swimming was always brief, often lasting less than 1 s. Occasionally, episodes were longer, but none lasted more than 3 s.

As shown in Table 1, the longest swim episodes were seen in juvenile worms in which a mean of

Table 1. Parameters related to swimming in worms of different sizes. Significance of differences between means were determined by *t*-tests

Parameter	(A) Newly hatched			(B) Juvenile			(C) Adult			Significance ($p <$)		
	mean	± SD	(*n*)	mean	± SD	(*n*)	mean	± SD	(*n*)	A–B	B–C	A–C
Number of waves per swim episode	5.9	± 2.4	(29)	14.0	± 6.2	(16)	6.4	± 3.4	(24)	0.001	0.001	ns
Wave frequency (Hz)	11.1	± 1.5	(29)	9.9	± 1.1	(16)	9.5	± 1.5	(21)	0.05	ns	0.001
Swim distance (% of body length)	89	± 45	(17)	128	± 43	(12)	80	± 43	(23)	0.05	0.01	ns
Swim velocity (mm/s)	11	± 2	(15)	47	± 9	(14)	74	± 12	(10)	0.001	0.001	0.001
Wave velocity (mm/s)	40	± 11	(21)	154	± 28	(16)	201	± 48	(16)	0.001	0.01	0.001
Ratio of swim velocity to wave velocity	0.30	± 0.11	(14)	0.31	± 0.08	(14)	0.38	± 0.11	(9)	ns	ns	ns

14 helical waves occurred per episode, or more than twice the number in newly hatched or adult worms. All of these values reflect the most vigorous swimming responses produced by individual worms in each size class. However, some responses to stimulation in every worm, regardless of size, were less vigorous and consisted of as few as 2–3 helical waves.

Despite wide variations in the number of swim waves per episode, the frequency of swim waves was remarkably invariant for all swim episodes in each size class (Table 1). The highest frequency (11.1 Hz) occurred in newly hatched worms. Progressively lower frequencies occurred in juvenile and adult worms. Although frequency in adults was only about 15% less than in hatched worms, this difference was significant ($p < 0.001$). Generally, wave frequency data shown in Table 1 indicate that the inherent frequency of outputs from the central pattern generator for swimming is relatively constant throughout postembryonic growth.

Comparisons of relative swim distance revealed that juvenile worms swam further than either newly hatched or adult worms, and these differences were correspondingly reflected in the number of waves per swim episode. Nevertheless, even juvenile worms rarely swam a distance of more than two body lengths.

A comparison of swim velocity in different worm sizes is shown in Table 1. Velocity significantly increased in relation to body size – there was nearly a seven-fold difference in velocity between the smallest and largest worms. The higher velocity in larger worms may result from greater propulsive forces due to any or all of the following factors:

(a) larger surface area of the body incorporated into the helical wave (i.e. larger stroke size);
(b) greater distance along the body over which each wave acts (i.e. longer stroke length); and
(c) faster wave velocity along the body (Table 1).

The velocity that helical waves move along the body of a worm provides an indirect measure of the rate that the neural excitation controlling swimming propagates along the ventral nerve cord. As shown in Table 1, mean wave velocity in newly hatched worms was 40 mm/s, or about 100 times slower than the conduction velocity of giant nerve fibers in these worms (Drewes & Brinkhurst, 1990). Wave velocity in adult worms was about 200 mm/s, or about 50 times slower than giant nerve fiber velocity in these worms. These differences make it highly unlikely that the worm's giant nerve fibers mediate the wave of central neural excitation that controls swimming.

Calculation of the ratio of swim velocity to wave velocity provides an estimate of the 'efficiency' with which posteriorly directed helical waves translate into forward progress of the body through water. Ratios that approach 1.0 indicate high translational efficiency and low slippage while those approaching 0.0 indicate
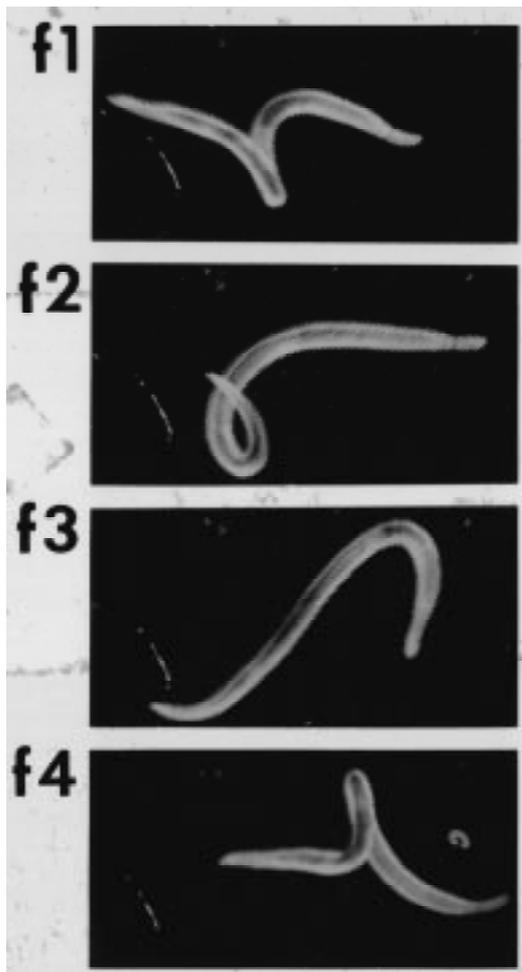
Figure 1. Four consecutive freeze-frame images of body movements during one complete cycle of swimming in a small worm. Frame 1 shows a helical wave (clockwise orientation) at a mid-body position. In frame 2, the same wave has progressed to near the tail end. In frame 3, a second wave begins near the head end. Frame 4 shows this second wave (counter-clockwise orientation) at a mid-body position. Thus, one complete cycle occurs in three video frames, a wave frequency = 10 waves/s.

low efficiency and high slippage. The ratios shown in Table 1 were similar in all sizes, ranging from 0.30–0.38. These values are similar to those derived for helical swimming in *D. digitata* (Drewes & Fourtner, 1993). Comparable values occur in other invertebrates (leeches, certain nematodes, polychaetes and insect larvae), which all utilize two-dimensional, sinusoidal undulatory movements (Taylor, 1952; Gray & Lissmann, 1964; Clark & Hermans, 1976).

Determination of a worm's swim velocity and body length allows calculation of a Reynolds number (R_e), a unit-less measure of the relative influences of viscous and pressure drag during locomotion in fluid or air (Nachtigall, 1983; Vogel, 1994). The R_e for newly hatched worms was 50, a value indicating that both viscous drag and pressure drag influence the dynamics and forward progress of swimming. This R_e is comparable to that of swimming copepods and very small flying insects (Strickler, 1975; Vogel, 1994). It is nearly identical to that in *D. digitata* (Drewes & Fourtner, 1993), a worm whose body size and swim velocity are similar to newly hatched *Lumbriculus*. In contrast, the R_e for swimming in adult *Lumbriculus* was 5000, a value indicative of less viscous drag and relatively stronger influences of pressure drag and inertial forces during its swimming. These values are comparable to those of medium and large flying insects (Nachtigall, 1983).

Body reversal responses

Light tactile stimulation with the stimulus loop anywhere within the anterior-most 30% of the worm's body consistently evoked body reversal responses in all sizes of worms. Tactile stimulation in locations somewhat posterior to this evoked either swimming or reversal, or occasionally both. Thus, the sensory field for reversal behavior is the spatial complement to the field for swimming, although there is an area ($\approx 10\%$ of the worm's body length) in which the two fields overlap and either or both responses may be evoked.

Reversal behavior in newly hatched worms involved three main components of movement (Figure 2). The first component was rapid, end-to-end body shortening that occurred within the first few video frames following delivery of the touch stimulus. The second component was a rapid, J-shaped bending of the posterior end of the body; this bending was concurrent with body shortening. The third component was an anteriorly-directed, wave-like shift in the locus of body bending. As this wave of bending progressed to the mid-body, the worm formed an 'alpha-shaped' loop (see Figure 2, upper frames 4–6). With further progress of the loop, the head end of the worm swung to an open and more straightened position. Passage of this wave of bending was relatively gradual, requiring about 0.3 s (9 video frames) for completion. The net result of reversal was a change of approximately 150° in the longitudinal axis of the body but only a slight translocation in the center point of the worm's body (Table 2).

Juvenile and adult worms also exhibited body reversal in response to anterior touch, although the sequence of reversal movements required significantly
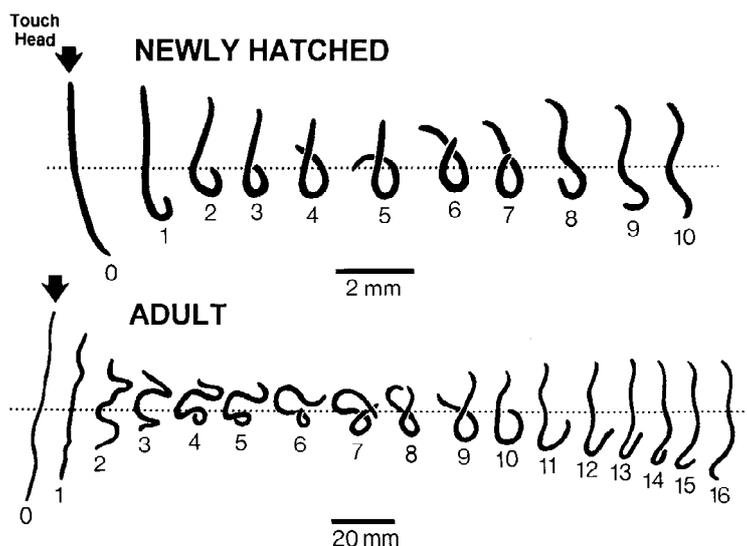
Figure 2. Freeze-frame images (silhouettes) of body reversal responses to head touch in newly hatched and adult worms (upper and lower sequences, respectively). Note the wave of body bending that begins in posterior segments and progresses anteriorly as a moving loop, as shown in frames 3–7 (upper sequence) and 6–10 (lower sequence). Generation of this moving loop is a key event for reversal of the body axis.

more time and was more complex and variable in appearance than in hatched worms (Table 2; Figure 2). Three phases of movement were evident. The first phase was rapid, end-to-end body shortening that occurred within one video frame after the touch stimulus. The second phase involved simultaneous and oppositional body bending in head, mid-body, and tail regions, thus resulting in an 'omega-shaped' appearance of the body. Acquisition of this shape often required several video frames of time. The third phase of movement involved a wave-like, anterior progression of the tail bending initiated during the preceding phase. As this bending progressed anteriorly, it was preceded by straightening (unbending) of mid-body and head regions. Thus, the body formed a moving loop, as shown in Figure 2 (see frames 6–9 in bottom sequence). Gradually, over the next few frames, anterior progression of the wave opened the loop, and reversal was complete.

Execution of the entire reversal sequence required about 0.6 s (18 video frames) in both juvenile and adult worms. The net result of reversal was a change of 140–150° in the longitudinal axis, with only a slight translocation in the center point of the worm's body (Table 2).

Discussion

Adaptive significance of swimming and reversal

Swimming is a rather uncommon means of locomotion in aquatic oligochaetes; it does not occur in tubificids, which often occupy tubes or tunnels in muddy sediments (Stephenson, 1930). However, it is seen in a few naidid species that occupy shallow habitats containing emergent vegetation and vegetable debris (Stephenson, 1930; Sperber, 1948). One possible significance of swimming in such habitats is that it may allow worms to be transiently planktonic. This may provide a faster and more direct means, compared to the alternative of crawling, for escaping adverse conditions and locating more suitable habitat.

Although the mechanics and frequency of helical swimming movements in *Lumbriculus* are similar to those previously described in *D. digitata* (Drewes & Fourtner, 1993), swim behaviors in these two species differ with respect to several important features. First, swimming in *Dero* is often spontaneous, whereas it is always stimulus-evoked in *Lumbriculus*. Second, individual swim episodes in *Dero* were much longer in duration and resulted in much greater swim distances than in *Lumbriculus,* in which swim episodes were brief (usually less than 2 s) and swim distances short (about 1–2 body lengths; Table 1). Thus, in contrast to *Dero*, it seems highly unlikely that the adaptive significance of swimming in *Lumbriculus* is

Table 2. Parameters related to body reversal in worms of different sizes. Significance of differences between means were determined by *t*-tests

Parameter	(A) Newly hatched			(B) Juvenile			(C) Adult			Significance ($p <$)		
	mean	$\pm$ SD	(*n*)	mean	$\pm$ SD	(*n*)	mean	$\pm$ SD	(*n*)	A–B	B–C	A–C
Angular change in body axis (°)	153	$\pm$ 23	(25)	149	$\pm$ 23	(15)	139	$\pm$ 29	(24)	ns	ns	0.05
Change in center of body (% of body length)	16	$\pm$ 13	(25)	13	$\pm$ 8	(15)	12	$\pm$ 10	(24)	ns	ns	ns
Time to reverse (s)	0.37	$\pm$ 0.07	(17)	0.59	$\pm$ 0.19	(12)	0.59	$\pm$ 0.18	(24)	0.001	ns	0.001

related to achieving either sustained vertical movements in the water column (i.e. planktonic existence) or long-distance, horizontal migration.

A more likely explanation is that swimming and reversal responses, separately or in combination, are important behavioral strategies for eluding predators throughout the worm's postembryonic life. Predatory threat to the worm's head results in body reversal so that the worm is well positioned to execute swimming in a direction *away* from the predator. Swimming responses enable rapid, short-distance retreat from a threatening stimulus in instances when worms are on a smooth substrate without the benefit of either protection or traction.

In the laboratory, swimming often occurs when worms are massed together, in the open, around a food source. Then, disturbance by repeated tactile stimulation evokes a relatively rapid and stereotyped sequence of events, which begins with worms executing body reversal responses while still *en masse*; this effectively re-positions the worm's heads away from the food source. The sequence culminates as many worms simultaneously swim away from the food, resulting in rapid dis-aggregation of the assembled mass (Figure 3). The result is an abrupt and dramatic burst of radiating locomotor movements. It seems reasonable to hypothesize that such movements, collectively, may startle or confuse a predator while, at the same time, enhance the probability of the survival of each worm. In summary, helical swimming and body reversal behaviors appear well suited for an oligochaete, such as *Lumbriculus variegatus*, which opportunistically feeds and freely moves about within freshwater, littoral habitats.
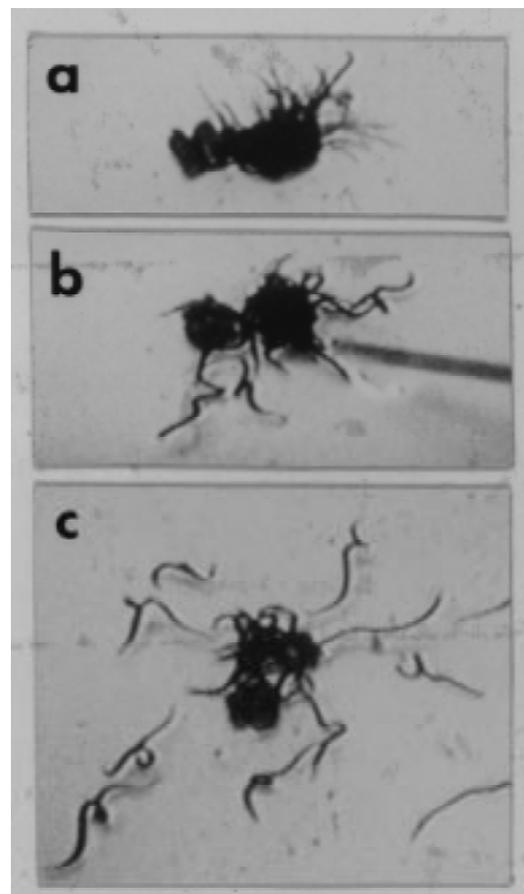

Figure 3. Video images of disaggregation in feeding worms. (a) Before stimulation worms were tightly clustered around a food pellet and their tails were extended outward. (b) After tactile stimulation with an applicator stick, a few worms reversed head and tail positions and began to swim away. (c) With additional stimulation, more worms began to swim, creating an abrupt, radiating burst of swimming movements.

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