RESEARCH ARTICLE

Getting around when you're round: quantitative analysis of the locomotion of the blunt-spined brittle star, *Ophiocoma echinata*

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SUMMARY

Brittle stars (Ophiuroidea, Echinodermata) are pentaradially symmetrical echinoderms that use five multi-jointed limbs to locomote along the seafloor. Prior qualitative descriptions have claimed coordinated movements of the limbs in a manner similar to tetrapod vertebrates, but this has not been evaluated quantitatively. It is uncertain whether the ring-shaped nervous system, which lacks an anatomically defined anterior, is capable of generating rhythmic coordinated movements of multiple limbs. This study tested whether brittle stars possess distinct locomotor modes with strong inter-limb coordination as seen in limbed animals in other phyla (e.g. tetrapods and arthropods), or instead move each limb independently according to local sensory feedback. Limb tips and the body disk were digitized for 56 cycles from 13 individuals moving across sand. Despite their pentaradial anatomy, all individuals were functionally bilateral, moving along the axis of a central limb *via* synchronous motions of contralateral limbs (±~13% phase lag). Two locomotor modes were observed, distinguishable mainly by whether the central limb was directed forwards or backwards. Turning was accomplished without rotation of the body disk by defining a different limb as the center limb and shifting other limb identities correspondingly, and then continuing locomotion in the direction of the newly defined anterior. These observations support the hypothesis that, in spite of their radial body plan, brittle stars employ coordinated, bilaterally symmetrical locomotion.

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INTRODUCTION

The vast majority of animals display bilateral symmetry (Collins, 2001), and most studies on locomotion have focused on bilateral species. However, there are many radially symmetrical animals, displaying either primitive retention of such body plans, as in jellyfish, or secondary convergence on radially symmetrical adult forms, as in echinoderms (Lawrence, 1987). Additionally, early fossil metazoans display a wide array of body plans, including both radial and bilateral symmetry (Knoll and Carroll, 1999). The factors that led to the near-total dominance of the bilaterally symmetrical body plan are unclear and strongly debated, but a common hypothesis is that bilateral symmetry confers a locomotor advantage (Barnes, 1974; Beklemishev, 1969; Buchsbaum, 1976; Meglitsch and Schram, 1972; Willmer, 1990; but see Finnerty, 2005; Grabowsky, 1994). This hypothesis is supported by theoretical arguments on the mechanical advantages of anatomical specialization for movement in one direction (Beklemishev, 1969), *in silico* experimental evolution (Bongard and Paul, 2000) and the relative frequency of various body plans in sessile *versus* locomotory organisms (Beklemishev, 1969; Collins, 2001). Additionally, most radially symmetrical organisms that actively locomote do so by moving along their central (oral–aboral) axis, such as jellyfish and sea cucumbers (Beklemishev, 1969). This orientation allows them to specialize for directional movement even while retaining radial symmetry (Beklemishev, 1969), further underscoring the influence of locomotion on body plan.

In this context, the locomotion of brittle stars (Ophiuroidea) is particularly interesting. Brittle stars display near-perfect pentaradial symmetry with no anatomical or behavioral evidence for an anterior, but move perpendicular to their central (oral–aboral) axis (Lawrence, 1987). Unlike most other echinoderms, brittle stars do not use their tube feet for locomotion (Lawrence, 1987), relying instead on the actions of five long, multi-jointed limbs that apply forces to the substrate (Romanes, 1885). These limbs consist of serially repeated, articulated 'vertebral ossicles' actuated by muscles joining adjacent ossicles (Lawrence, 1987), and represent an independent evolution of muscular, jointed limbs in animals. The nervous system is also radially symmetrical, consisting of a radial nerve cord innervating each limb and a circumoral nerve ring with five ganglia located at the proximal origins of the radial nerve cords, with no centralized control (Cobb and Stubbs, 1981; Lawrence, 1987). Brittle stars can detect and respond to light as well as to tactile and chemical stimuli (Cowles, 1910; Sloan and Campbell, 1982).

Several prior studies qualitatively described the locomotion of brittle stars, often noting the apparent bilateral symmetry and coordination of their locomotion and likening it to tetrapod gaits (Arshavskii et al., 1976a; Arshavskii et al., 1976b; Glaser, 1907; Maier and Schneirla, 1935; Romanes, 1885). However, while qualitative assessment can give insight into locomotion, the high variability in limb movements and the need to simultaneously track multiple identical limbs limits the usefulness of such methods. Furthermore, the natural human tendency to see patterns in

randomness (Zusne and Jones, 1989) combined with the sheer diversity of tetrapod gaits (Hildebrand, 1985b) means that almost any pattern of limb movements could be perceived as a coordinated gait. As such, detailed quantitative analysis is needed to confirm these qualitative observations, and may yield further insights into brittle star locomotion.

Given the variability and complexity of brittle star locomotion, the lack of any central 'brain' (Cobb and Stubbs, 1981), and the presence of photoreceptors, chemoreceptors and mechanoreceptors on the limbs (Lawrence, 1987; Moore and Cobb, 1985), it is possible that brittle stars move without any inter-limb coordination, with each limb responding to purely local stimuli. Isolated limbs of brittle stars are capable of movement (Arshavskii et al., 1976a), and a robotic brittle star has been constructed with movement governed by purely local stimuli (Lal and Yamada, 2008; Lal et al., 2006; Lal et al., 2008). It is therefore possible that the perceived bilaterality in prior studies was due to unknown sensory gradients in the environment, leading limbs facing similar local stimuli to move similarly. However, such uncoordinated movements would result in unequal torques and forces on the body disk, imposing rotations and displacements that do not contribute to forward motion (Lal and Yamada, 2008; Lal et al., 2008).

To test the competing hypotheses of purely locally controlled limb movements *versus* coordinated bilateral locomotion, I quantified the locomotion of brittle stars in a naturalistic test arena and determined the interrelationships between the movement of the limbs and the disk. Coordinated bilaterally symmetrical locomotion was predicted to result in repeatable, consistent patterns of limb movement within and between movement cycles, trials and individuals, whereas no such patterns would be evident if limb movement was locally controlled.

MATERIALS AND METHODS

Thirteen blunt-spined brittle stars [*Ophiocoma echinata* (Lamarck 1816)] measuring 7.7–11.6 cm from the tip of the longest limb to the center of the body disk were collected from the waters of Southwater Caye, Belize (16°49′6′N, 88°4′51′W). All individuals had all five limbs intact, with no noticeable differences in limb length, indicative of recent autotomy and regeneration. Individuals were placed in the center of a 1.5 m diameter test arena filled with fine sand and water from an area near the capture location. There were no strong lighting gradients, and the mixing of the sand during its deposition into the arena presumably eliminated any chemical gradients or scent trails. Because preliminary trials indicated that stimulation *via* contact did not increase speed and frequently disrupted steady locomotion, animals were allowed to move voluntarily for five trials each. All trials were recorded at a minimum of 15 frames s^{-1} *via* either a Fujifilm Finepix S8100fd digital camera (Fujifilm, Tokyo, Japan) or a Pentax Optio W60 digital camera (Pentax, Tokyo, Japan), with a minimum resolution of 640×480 pixels. To prevent distortion by surface ripples, a custom-made floating acrylic tray was held at the surface between the brittle star and the camera during locomotion trials.

For each individual, I selected the longest series of movement cycles in a constant direction and digitized the positions of the body disk and the tips of the limbs using a MATLAB digitizing script, DLTdv3 (Fig. 1) (Hedrick, 2008). A total of 56 cycles were analyzed across all 13 individuals. Qualitative examination of movement trials that were not digitized indicated locomotion similar to that of digitized sequences, punctuated by pauses and turning behavior (see Discussion). Cycles were defined by the start of disk movement relative to the substrate. Displacement per cycle, cycle frequency,
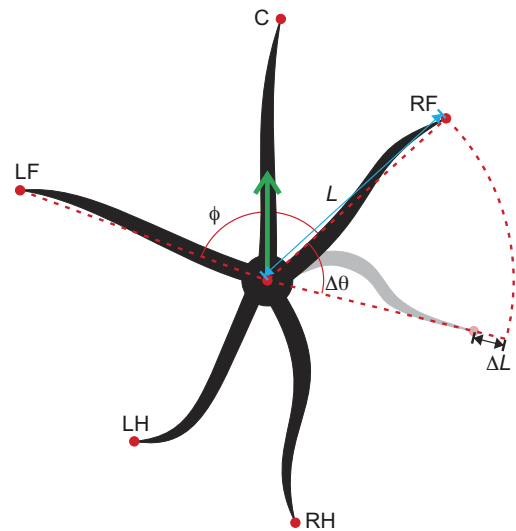

Fig. 1. An illustrative brittle star, showing digitized points and limb variables. The axis of pentaradial symmetry, the oral–aboral axis, is at the center of the body disk and is oriented perpendicular to the plane of the image. The green arrow indicates the direction of movement. Red points indicate digitized points at the limb tips and the center of the body disk. Change in limb length is $\Delta L/L$ (where L is limb length), change in limb angle is $\Delta\theta$ and limb protraction/retraction is (144 deg–ϕ)/2. C, center limb; LF, left forelimb; LH, left hindlimb; RF, right forelimb; RH, right hindlimb.

velocity and duty factor (the proportion of the cycle in which the disk is static) were calculated from disk kinematics. Because brittle stars do not demonstrate an anatomical anterior, the orientation and role of any given limb depended upon the direction of movement. As limb identity and function are variable, limbs were identified relative to the direction of motion of the body disk for each sequence of cycles, with the proximate origin of the center limb on the disk oriented parallel to the direction of motion, and other limbs being identified as right forelimb, left forelimb, right hindlimb and left hindlimb according to their positions (Fig. 1). A consistent center limb was present in all digitized sequences. Each cycle was categorized into one of two locomotor modes based on center limb orientation relative to the direction of movement: rowing and reverse rowing. I collected gait timing variables, consisting of the start and stop of each limb motion relative to the substrate and expressed as a percent of the cycle relative to the start of disk movement. These times were also used to calculate duty factor of each limb. Changes in limb angle and limb length for the swing and stance phases were calculated from the positions of each limb tip and the center of the body disk. Changes in limb length were normalized by the total distance from the limb tip to the center of the body disk. Change in limb angle during stance and swing phases were calculated as the difference between maximum and minimum limb angle during that phase. The protraction and retraction of the forelimbs was calculated by determining the angle between the right and left forelimbs at the start and end of their movement. This value was subtracted from the presumed neutral posture with all five limbs equally spaced (72 deg if forelimbs are adjacent, 144 deg if separated by the center limb), such that limb positions anterior to neutral are positive and those posterior to neutral are negative, and divided by two to account for the simultaneous contributions of both right and left limbs (Fig. 1).

Table 1. Cycle variables and limb symmetries for all trials (means ± s.d.) during each locomotor mode in the brittle star *Ophiocoma echinata*

	Rowing	Reverse rowing
N	42	14
Disk velocity (cm s^{-1})	1.3±0.5	1.5±0.6
Disk frequency (Hz)	0.23±0.08	0.27±0.15
Disk displacement (cm)	5.7±1.2	6.2±1.5
Disk duty factor	0.42±0.12	0.46±0.12
Peak forelimb protraction (deg)	3.2±9.8	9.4±12.9
Peak forelimb retraction (deg)	−30.4±11.2	−35.3±10.3
Synchrony (fore start) (%)	0.7±13	−2.0±11
Synchrony (fore stop) (%)	−2.0±13	−9.2±15
Synchrony (hind start) (%)	1.6±22	5.7±26
Synchrony (hind stop) (%)	4.4±30	16.8±33

Synchrony is the phase lag between a pair of contralateral limbs (hindlimbs or forelimbs) for the same event (start or stop of movement), with percentages closer to zero indicating the event is closer to simultaneous in the right and left limbs. Protraction and retraction are the angles of the forelimbs relative to the neutral posture of evenly spaced limbs. No significant differences are present.

To assess inter-limb coordination, a multiple linear regression was performed between all limb start and stop values (partial correlations yielded qualitatively similar results). Additionally, synchrony (phase lag) was calculated between forelimbs and hindlimbs for both start and stop of movement. To determine the mechanism by which brittle stars modulate speed, regressions were performed between body disk velocity and displacement per cycle, cycle frequency and disk duty factor. The effect of locomotor modes on all variables was assessed using a series of nested MANOVAs for each type of variable (whole-body, limb phase, duty factor, limb length change and limb angle change) to account for correlations between individual limbs, with locomotor mode as a fixed factor and individual nested within it, because the single digitized run of each individual always showed only a single locomotor mode. If locomotor mode had a significant effect on the MANOVA of a type of variables, a series of ANOVAs were conducted to determine which of the variables within the category were significant. Neither size nor velocity was included as a cofactor because of the limited range of values for each. For all tests, significance was defined as $P<0.003$ *via* Bonferroni correction. Alternative statistical methods produced broadly similar results.

RESULTS

Brittle stars displayed coordinated locomotion in all digitized sequences, with no visible rotation of the body disk. Limb start and stop times were strongly correlated within each limb (multivariate $r^2>0.28$, $P<0.0001$ for all). The forelimbs displayed strong coordination. The start of left forelimb movement was correlated to the start ($r^2=0.47$, $P<0.0001$) of the right forelimb. Similarly, the stop of the left forelimb was correlated to the stop ($r^2=0.16$, $P=0.0025$) of the right forelimb. No other correlations were significant. In addition to being tightly correlated, the motions of the right and left forelimbs were highly synchronous (Table 1). Synchronous start of movement was also present for the left and right hindlimbs (Table 1). Duty factor was constant across all limbs and modes (Table 2). These tightly coordinated, highly synchronized movements of the forelimbs (the putative force-generating limbs, see Discussion), combined with the lack of body disk rotation and ubiquity of a center limb, were sufficient to characterize the locomotion of all individuals as bilaterally symmetrical.

Two modes of locomotion were observed during the trials (Fig. 2). In 'rowing', the center limb was oriented in the direction of movement (Fig. 2A,B, supplementary material Movie 1), whereas in 'reverse rowing', the center limb trailed behind (Fig. 2C,D, supplementary material Movie 2). Rowing was the most common locomotor mode, accounting for 75% of digitized trials. Mode was consistent within a trial, even following turns, but all individuals displayed both locomotor modes across trials. In both modes, the body disk displayed cyclic movement and static phases, each comprising approximately half of the cycle (Table 1) and velocity was determined primarily by cycle frequency ($r^2=0.68$, $F_{1,54}=115$, $P<0.0001$; Fig. 3), with little influence of cycle displacement ($r^2=0.02$, $F_{1,54}=1.1$, $P=0.29$) or disk duty factor ($r^2=0.01$, $F_{1,54}=0.5$, $P=0.47$). As is evident from the high standard deviations in most results, both modes were highly variable but clearly distinct.

Rowing, previously described qualitatively (Arshavskii et al., 1976b; Glaser, 1907; Maier and Schneirla, 1935; Romanes, 1885), was characterized by a forward-directed center limb and large angular movements of the right and left forelimbs during swing and stance phases compared with other limbs (Table 2, Fig. 2A,B, Fig. 4A–C, supplementary material Movie 1). Changes in limb length were small for all limbs (Table 2, Fig. 4A–C). Movement of the forelimbs was tightly coupled, as indicated by very low differences between right and left start and stop of movement (Table 1, Fig. 2A,B). Stop of movement of the forelimbs and start

Table 2. Kinematics of individual limbs during each locomotor mode (means ± s.d.) in the brittle star *O. echinata*

	Center limb	Right forelimb	Left forelimb	Right hindlimb	Left hindlimb
Rowing					
Start (%)	−10.2±28.8	−29.6±13.5	−31.0±14.0	12.7±16.7	11.0±14.6
Stop (%)	28.5±32.3	4.5±12.2	6.2±10.7	52.1±22.9	47.7±15.6
Duty factor	0.61±0.15	0.67±0.11	0.64±0.11	0.60±0.17	0.65±0.12
ΔLength (swing) (%)	29.0±12.9	22.5±10.6	26.5±10.2	26.0±10.9	22.2±11.6
ΔLength (stance) (%)	26.6±15.8	**21.8±9.8**	**21.6±10.5**	24.0±11.3	22.1±10.5
ΔAngle (swing) (deg)	32.1±16.2	43.7±21.3	46.0±20.2	14.3±8.6	13.9±7.4
ΔAngle (stance) (deg)	25.2±16.3	43.0±15.6	43.6±16.7	14.1±8.1	12.0±6.2
Reverse rowing					
Start (%)	13.0±13.1	−21.8±15.6	−19.9±20.1	3.7±30.4	−2.0±26.4
Stop (%)	51.0±11.6	1.9±13.1	11.1±18.1	47.3±32.0	30.5±26.7
Duty factor	0.65±0.09	0.76±0.10	0.67±0.13	0.60±0.19	0.68±0.13
ΔLength (swing) (%)	20.4±8.4	26.9±10.9	20.3±10.8	26.2±10.7	13.6±8.8
ΔLength (stance) (%)	18.1±8.5	**34.0±10.2**	**33.7±11.4**	16.9±9.7	20.8±9.0
ΔAngle (swing) (deg)	14.7±10.3	34.0±15.9	35.0±19.4	27.2±18.5	29.2±17.8
ΔAngle (stance) (deg)	6.2±1.5	30.4±11.8	35.3±18.1	19.6±11.3	31.9±17.7

Significant differences between locomotor modes are shown in bold ($P<0.003$).
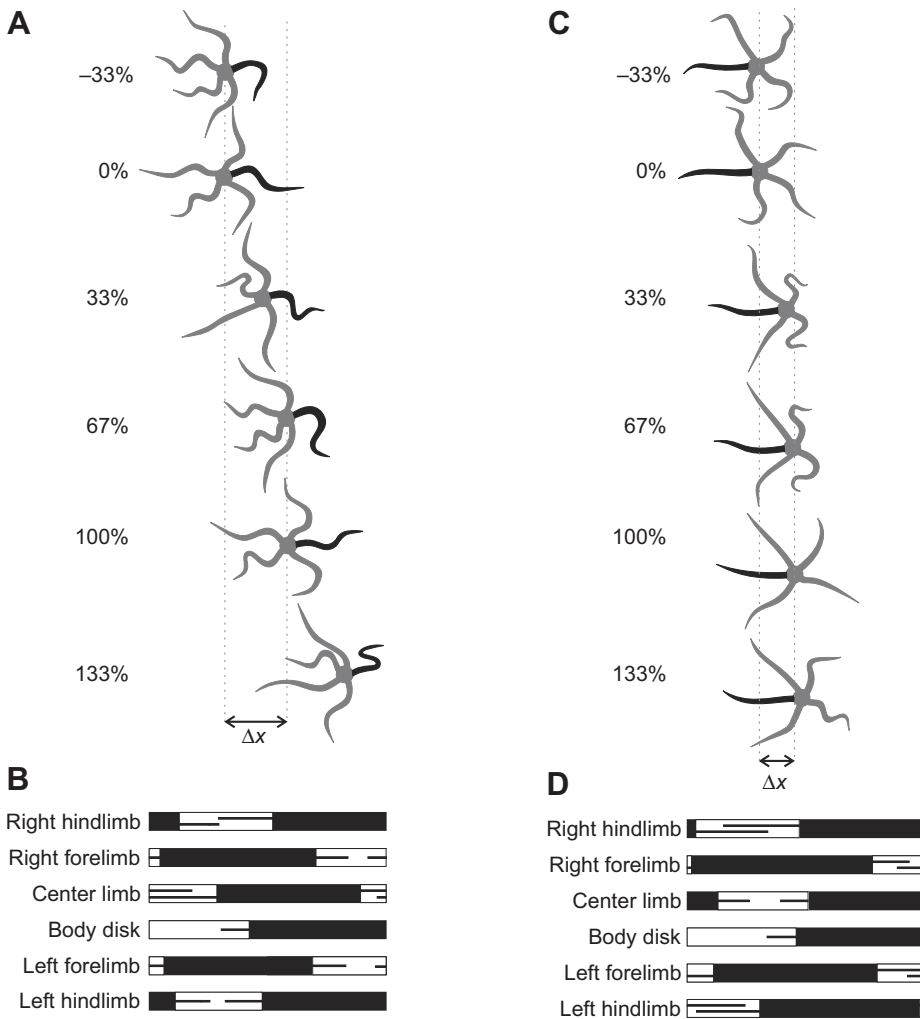
Fig. 2. Locomotor modes of *Ophiocoma echinata*, traced from video (supplementary material Movies 1, 2). The center limb is in black. Times are expressed as percentages of a cycle. The displacement during a single cycle of movement is indicated by Δ*x*. (A) Silhouettes traced from sample video of rowing. (B) Gait plot showing movement patterns of limbs and the body disk during rowing. White and black areas represent movement and stasis of that structure, respectively, with error bars representing 1 s.d. around the mean start and stop time of that element relative to start of body disk movement. (C) Silhouettes traced from sample video of reverse rowing. (D) Gait plot showing movement patterns of limbs and body disk during reverse rowing.

of movement of the hindlimbs both occurred close to the start of disk movement (Table 2, Fig. 2A,B).

Reverse rowing, previously described by Glaser and von Uexkull (Glaser, 1907; von Uexkull, 1905), was characterized by a trailing center limb and large angular movements of the four other limbs during swing and stance phases (Table 2, Fig. 2C,D, Fig. 4D–F, supplementary material Movie 2). Changes in limb length were small, except for the right and left forelimbs (Table 2, Fig. 4D–F). As in rowing locomotion, movement of the right and left forelimbs were tightly coupled (Table 1, Fig. 2) and stop of forelimb movement and start of hindlimb movement occurred close to start of disk movement (Table 2, Fig. 2).

The two modes showed almost no statistically significant differences, likely because of the high variability present in both (Tables 1, 2). Although different orientations resulted in the differences in angle between the forelimbs and the relative to the direction of movement (Fig. 4), this was entirely because of the orientation of the brittle star relative to the axis of movement, as in both cases the limbs only protracted slightly from the neutral posture of equally spaced limbs, and retracted equally as far (Table 1). During reverse rowing, both forelimbs showed greater length change during stance compared with rowing (left: $F_{1,13}=30.6$, $P=0.0001$; right: $F_{1,13}=26.6$, $P=0.0001$; Table 2). Although these variables are significantly different between modes, they cannot be used to categorize the mode of a locomotor trial because of extensively overlapping ranges of values (Table 2).

Additional qualitative observations were made of several changes in direction (Fig. 5, supplementary material Movie 3). Changes in direction were accomplished without rotation of the body disk by redefining the limb identities during the period in which the disk was static. For example, right turns were made by redefining the right forelimb as the center limb, with corresponding shifts in the identity of the other limbs. In all observed turns, locomotor mode remained constant.

DISCUSSION

This study confirms that the brittle star *O. echinata* employs coordinated, bilaterally symmetrical locomotion. Although the anatomy of a bilaterally symmetrical animal confers advantages to locomotion along the body axis and imposes disadvantages for off-axis movement, the radially symmetrical anatomy of a brittle star does not constrain potential locomotor behavior. In spite of this wide range of locomotor options and lack of anatomical predisposition, brittle stars select bilaterally symmetrical locomotion modes. This preference, along with the high velocity compared with other echinoderms (Romanes, 1885), is consistent with prior theories that bilaterality confers a locomotor advantage. However, the use of bilaterally symmetrical locomotion by a radially symmetrical organism also shows that an organism can gain the advantages of bilaterality without departing from a radial body plan, and assumptions about locomotor behavior and capacity based solely on radial *versus* bilateral symmetry may be erroneous (Willmer, 1990).
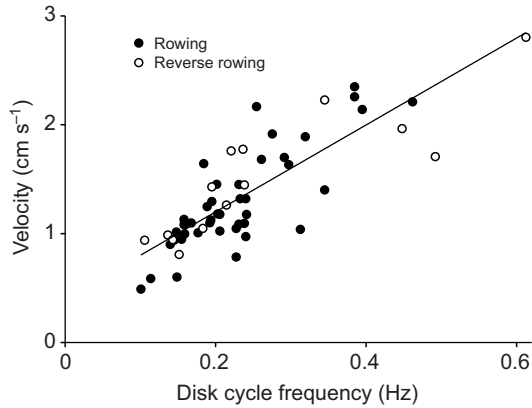
Fig. 3. Velocity *versus* disk cycle frequency in *O. echinata*. Black circles indicate rowing; white circles indicate reverse rowing. The regression equation is: Velocity=4×Frequency+0.4 (r^2= 0.68, $F_{1,54}$=115, P<0.0001).

Locomotor modes

Two locomotor modes were observed during locomotion of this species, both of which corresponded to previous descriptions. Rowing was previously described in qualitative terms by several authors (Arshavskii et al., 1976b; Glaser, 1907; Maier and Schneirla, 1935; Romanes, 1885), and is the most clearly obvious from visual examination. Reverse rowing was also described previously in the literature (Glaser, 1907; von Uexkull, 1905), though not nearly as commonly. Given its infrequency in this study, this may represent a genuine preference for rowing, though further work is needed to confirm this. A previously described 'pulling' mode (Arshavskii et al., 1976b) was not observed, nor was there any evidence of the use of tube feet in locomotion (Arshavskii et al., 1976b). This may be due to errors in prior qualitative assessments or differences in substrate, as in prior studies the brittle stars moved across bare glass of an aquarium rather than natural sand (Arshavskii et al., 1976b). The 'pulling' mode was distinguished solely by movement of the central limb and its hypothesized role in force generation (Arshavskii et al., 1976b), but given the highly variable movement of this appendage and the uncertainty in determining force production from kinematics (see below), this distinction cannot be confirmed without direct force measurements. Additionally, Glaser reports instances of locomotion in which the direction of locomotion does not align with the axis of any limb, leading to the presence of two limbs on one side and three on the other (Glaser, 1907), which was not observed in any trials of this study nor any other qualitative study. Such asymmetrical limb distributions would produce unequal forces and motions on each side of the disk without tight coordination across all limbs, leading to undesirable rotations and off-axis
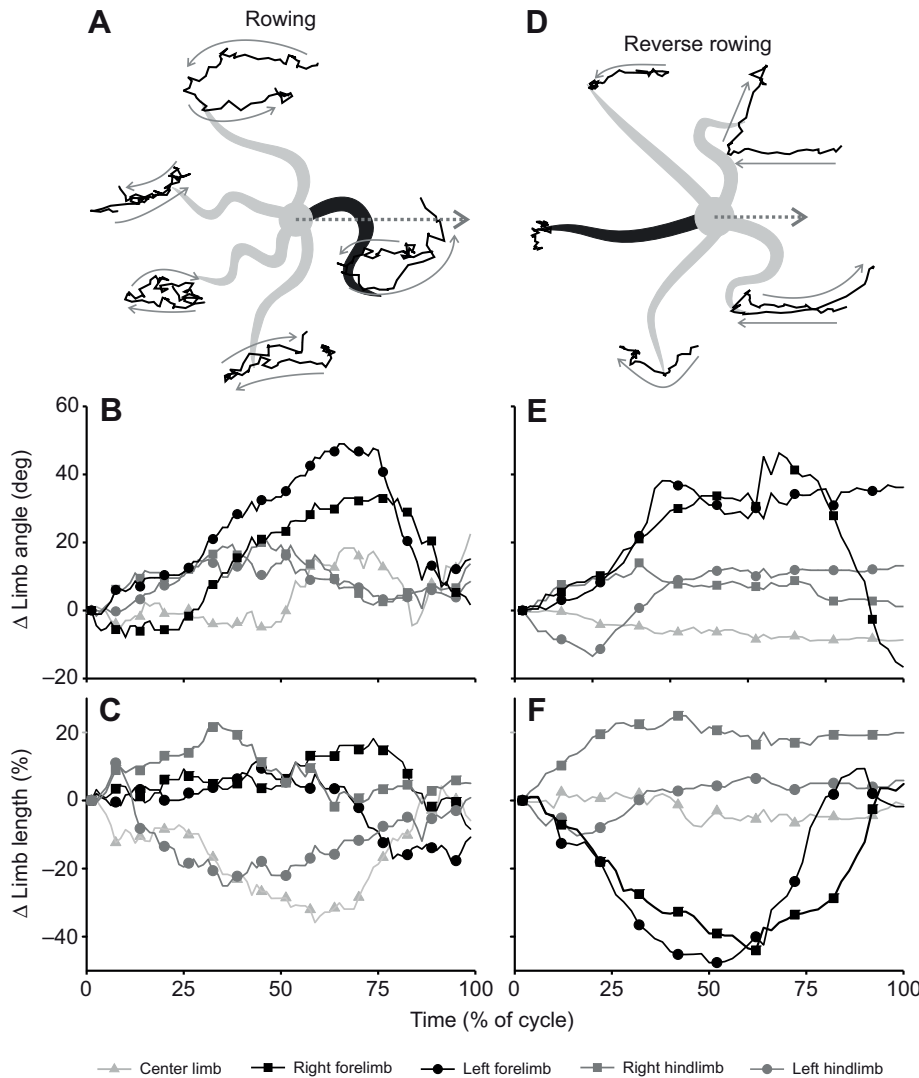

Fig. 4. Limb movements in *O. echinata* during rowing (A–C) and reverse rowing (D–F) from example cycles traced from video (supplementary material Movies 1, 2). The center limb is in black. The dashed grey arrow from the center disk indicates the overall disk trajectory and distance moved, solid black lines indicate the actual limb tip movements and curved grey arrows indicate the direction of limb tip movements. (A) Movement of the limbs relative to the disk during rowing. (B) Angle change of the limbs during rowing. (C) Length change in the limbs during rowing. (D) Movement of the limbs relative to the disk during reverse rowing. (E) Angle change of the limbs during reverse rowing. (F) Length change in the limbs during reverse rowing.
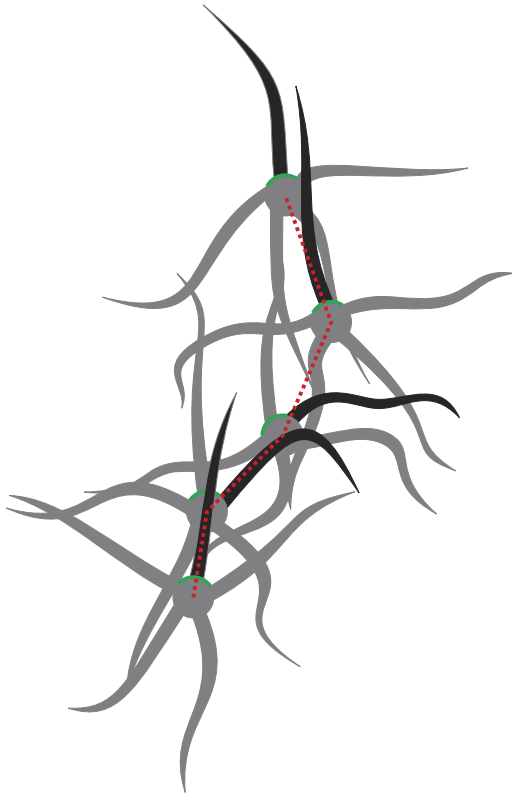
Fig. 5. A series of silhouettes traced from a sample video of two turns in *O. echinata* (supplementary material Movie 3). Each silhouette is at the start of disk movement, with the center limb in black. The red dashed line traces the path of the center disk, whereas the green arcs denote the orientation of the disk relative to the substrate. Turning occurs by designating a new center limb along the new direction of movement and shifting limb identities correspondingly, without substantial rotation of the center disk.

movement. Thus, the described motion is more likely to be a combination of subtle turning behavior and unusual cycles of symmetrical modes. These issues further underscore the necessity of quantitative analysis for accurate understanding of brittle star locomotion.

The two locomotor modes observed present an unusual inversion of the typical concept of limbed animal gaits. In all previously studied limbed taxa, limb identity (right forelimb, left hindlimb, etc.) is permanently defined by anatomy whereas footfall pattern changes, often because of speed (Hildebrand, 1985a). In brittle stars, footfall pattern remains constant but limb identity changes. In rowing, the two synchronous forelimbs are separated by a central limb, whereas they are not in reverse rowing. Because each of the five ganglia of the nerve ring are connected only to the two adjacent ganglia (Cobb and Stubbs, 1981), during rowing, any signals between the tightly coupled forelimbs must pass through the ganglion of the center limb. In reverse rowing, however, the coupled forelimbs are controlled by directly adjacent ganglia. Thus, like the limbs, the ganglia that control each limb perform different functions based on body orientation and locomotor mode. Whether the underlying neural activation patterns differ between modes remains unknown, though some differences in forelimb kinematics suggest this. However, if there are no differences in neural activity and differing forelimb kinematics between modes are entirely due to local sensory cues, these two modes may simply represent the only functionally

effective limb identity states for a given pattern of neural activity. Recent simulations based on brittle star locomotion and neuroanatomy have produced rowing locomotion, but not reverse rowing (Watanabe et al., 2011).

As noted above, locomotion in brittle stars is highly variable, particularly compared with the tightly coupled limb movements observed in tetrapods. There are several possible explanations, some or all of which may combine to produce the observed variability. Mechanistically, the presence of a static period in which the disk rests upon the seafloor frees the limbs from the constraint of providing a base of support at all times, as well as eliminating the need to move the limbs through swing phase quickly enough to either continuously maintain body support or intercept and redirect the center of mass trajectory following a period of unsupported ballistic motion, as in tetrapod walking and running. Limbs that are not used for force generation are further freed of constraints, and their kinematics show greater variability than putatively propulsive limbs (see below; Table 2). Additionally, although the tips of the limbs proved the most useful sites for digitizing, the actual force-generating region of the limb is likely more proximal (see below; Figs 2, 3), and thus the motion of the tips may exhibit extraneous motion relative to the actual contact site, leading to further variability in limb variables. However, it is also possible that the increased variability is neural in origin, either because of heterogeneous sensory feedback in the arena as a result of subtle irregularities in light, substrate or chemical cues, or because of the unique difficulties of producing bilaterally symmetrical locomotion using a radially symmetrical nervous system.

Propulsion

The kinematics of the limbs can give insight into their functional role in locomotion. During both rowing and reverse rowing, the right and left forelimbs are tightly coupled, both to each other and to the motion of the body disk, resulting in low variability in each of these measures, whereas the hindlimbs show considerably greater variability (Table 2). However, variability and coupling are not sufficient to determine which limbs propel the organism forwards, as illustrated by the center limb during reverse rowing, which exhibits tight coupling to the body disk but minimal changes in length or angle (Table 2), suggesting that it simply drags behind the organism (Fig. 2C, Fig. 4D–F). In contrast, the forelimbs in both modes show large changes in angle and length (Table 2). Finally, the occurrence of swing and stance phases relative to the movement and stasis phases of the disk must be considered, as brittle stars are thought to generate propulsive force by substrate reaction forces rather than hydrodynamic forces (Lawrence, 1987). During the motion of the body disk in either mode, the center limb and hindlimbs are only briefly in static contact with the substrate, whereas the forelimbs are in static contact with the substrate for some or all of the period of body disk movement. This combination of kinematics suggests that propulsion is predominantly or exclusively due to the forelimbs in both modes, with the center limb and hindlimbs either trailing passively or being used for sensory exploration.

The mechanism by which the brittle stars employ their forelimbs to generate forward motion differs between the two locomotor modes. During rowing, the forelimbs show little change in length but substantial change in angle during stance, whereas in reverse rowing, the length change is larger (Table 2). Thus, the forelimbs appear to function as a rotating strut during rowing, propelling the body disk *via* the sweeping motions of long limbs (Fig. 2A,

Fig. 4A–C), whereas during reverse rowing the forelimbs appear to both rotate and pull the body disk forward by shortening *via* a series of bends (Fig. 2C, Fig. 4D–F). These differences may be necessitated by the differences in the orientation of the limbs relative to the axis of movement, with the forelimbs oriented almost perpendicular to the axis of movement during rowing (72 deg at neutral posture) whereas the forelimbs are positioned more anteriorly in reverse rowing (36 deg at neutral posture) (Table 1, Figs 2, 3). However, these inferences from kinematics must remain hypothetical until force data can be gathered.

The exclusive reliance on symmetrical movements of the limbs contrasts strongly with the prevalence of alternating motion within a limb pair in tetrapods and arthropods. As all limbs are identical, barring loss and incomplete regrowth, this cannot be due to mechanical inability, though it may be due to the limitations of a radial nervous system in which direct neural connections between non-adjacent limbs do not exist (Cobb and Stubbs, 1981). However, the preference for symmetrical forelimb propulsion may be due to mechanical benefits. Because the body disk periodically rests on the substrate, there is no need for the continuous base of support as in tetrapod gaits, and synchronous movements of symmetrical forelimbs generate symmetrical forces and displacements. In contrast, alternating limb movements without careful coordination would often result in 'wasted' motion because of rotation of the body or movement perpendicular to the direction of overall motion, and limbs may overlap or otherwise interact in detrimental ways during the stride cycle. Locomotion similar to brittle star rowing is seen in the terrestrial locomotion of sea turtles (Renous and Bels, 1993) and mudskippers (Pace and Gibb, 2009), suggesting that this form of locomotion is advantageous even for organisms with bilateral symmetry and sophisticated nervous and muscular systems.

Turning

The lack of fixed limb identities and an anatomical anterior affects turning as well as forward locomotion. Unlike other animals, which must both change their direction and re-orient the body axis, brittle stars simply defined a new central limb and forward axis, with new corresponding limb identities, and continued in the new direction while using the same locomotor mode as before the turn (Fig. 5, supplementary material Movie 3). In addition to freeing the brittle star from the energetic and time costs of re-orienting the entire body, this strategy also obviates the need for a unique motor pattern for inducing body rotation, further simplifying their locomotor repertoire without loss of important functional capabilities. The change in limb identity occurred while the body disk was stationary and after the forelimbs had completed swing phase. Because turns were spontaneous, it remains unknown whether the lack of turns while the body disk is moving represents a genuine functional inability to turn during this period or merely a behavioral preference not to do so. Future work on turning may provide insights into mechanisms of neural control of brittle star locomotion, including the mechanisms and cues for determination of overall direction and limb identity.

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