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Common mechanics of mode switching in locomotion of limbless and legged animals

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Abstract

Crawling using muscular waves is observed in many species including planaria, leeches, nemertea, aplysia, snails, chitons, earthworms, and maggots. Contraction or extension waves propagate along the antero-posterior axis of the body as the crawler pushes the ground substratum backward. However, the observation that locomotory waves can be directed forward or backward has attracted much attention over the past hundred years.

Legged organisms such as centipedes and millipedes exhibit parallel phenomena; leg-tips form density waves that propagate backward or forward. Mechanical considerations reveal that leg-density waves play a similar role to locomotory waves in limbless species, and that locomotory waves are utilized by a mechanism common to both legged and limbless species to achieve crawling.

Here we report that both mode switching of the wave direction and friction control were achieved when backward motion was induced in the laboratory. We show that the many variations of switching in different animals can essentially be classified in two types according to mechanical considerations. We propose that during their evolution, limbless crawlers first moved in a fashion similar to walking before legs were obtained. Therefore, legged crawlers might have learned the mechanical mode of movement involved in walking long before obtaining legs.

Keywords

crawling, mechanics, evolution, worms, gastropoda, myriapoda,

1 Introduction

Crawling is the fundamental method of invertebrate locomotion. Therefore, general insights into the mechanism of crawling are important from an evolutionary point of view if they can be applied to a wide range of organism classes. There are several methods by which crawling on a solid surface can take place, depending on the locomotory equipment available. These methods include ciliary, peristaltic, pedal, undulatory and many-legged locomotion. However, irrespective of differences in equipment, these mechanisms often involve locomotory waves which can be defined as the spatiotemporal coordination of motion of different parts of the body along the longitudinal axis. This allows the crawler to push the ground substratum backward and move itself forward.

A peristaltic wave is one such type of locomotory wave that is often observed in limbless species throughout the phylogenetic tree such as planaria, leeches, nemertea, aplysia, earthworms, and maggots. For example, peristaltic waves in earthworms are generated by successive waves of contraction in the two sets of antagonistic muscles, the circular muscles and longitudinal muscles; part of the body is elongated and thinned by contraction of the circular muscles while another part of the body is contracted and thickened by contraction of the longitudinal muscles [1]. Caterpillars also employ muscular movement involving peristalsis along the body axis. In some species of caterpillar the body is comprised of a gut surrounded by a soft shell, which consists of the body wall (cuticle) and musculature; the former resembles a woven tube and the latter resembles a complicated, repeating series of primarily longitudinal and oblique muscles [2]. In some maggots such as *Neoempheria ferruginea*, the occurrence of peristalsis is not clearly visible due to transparency of the body wall. However, peristalsis becomes apparent if the position of the visible gut with respect to the antero-posterior axis of the whole body is observed.

The pedal wave is another kind of locomotory wave, which appears in the sole of the foot in gastropoda and chitons. In these animals, the foot is responsible for propelling the body over the ground and fixing it to the substratum. Locomotion in these organisms is brought about by waves of contraction or elongation passing along the sole of the foot. These pedal waves are formed by coordinated contraction and relaxation of the muscles immediately under the epithelium of the sole [3]. The part of the foot in the area between pedal waves, known as the interwave, is stationary relative to the substratum and is physically attached to the substrate. The pedal waves may be *monotaxic* in the sense that they occupy the whole breadth of the sole, or *ditaxic* if there are two waves that each occupy half of the sole. In the latter case the waves pass alternately over the right and left-hand sides of the sole and are out of phase with one another.

Parallel phenomena are observed in legged organisms. During the locomotion of myriapoda, each leg rotates around its base with a constant phase difference between adjacent legs. Therefore, density waves are formed by the leg-tip positions, which propagate along the body axis.

Such locomotory waves have been carefully observed in mollusca with a flat ventral foot-like organ, first (for example, in Ref. [4]) in annelida with a limbless worm-like body [1], and subsequently in arthropoda and onychophora [5]. There are two opposite

cases in which the locomotory waves travel forward and backward. The forward waves, which propagate in the same direction as the animal is moving, are termed *direct* waves, whereas waves that propagate in the opposite direction to the movement of the animal are known as *retrograde* waves [6]. It is generally considered that the direction of the waves is fixed for a given species.

The propulsive machinery is very different among crawlers with locomotory waves, but the kinematic similarity of peristaltic waves in annelida to pedal waves in mollusca or leg-density waves in myriapods and onychophora has been correctly pointed out in diagrammatic explanations [7]. Since recently, there are a lot of publications where mechanical and/or mathematical models of locomotion of crawling systems are analysed (for instance, [8, 9, 10, 11]). Tanaka et al. [12] studied the mechanics of peristaltic locomotion and the role of anchoring in locomotory waves by simple mechanical modelling of a peristaltic crawler. Mechanical considerations reveal (1) that leg-density waves play the same role as peristaltic waves in limbless crawlers, and (2) that locomotory waves push the body forward by a common mechanism. A comprehensive understanding of the biomechanics of crawling remains to be found in many species.

Crawlers tend to have a preferred direction, i.e. forward direction, of locomotion which comes from not only asymmetric structure of their bodies along the antero-posterior axis, such as a head with and a tail without sensory organs, but also asymmetric structure of local parts of contact area with the ground, for example backward-sloping bristles such as earthworms have on the ventral surface of the body [13]. To achieve a directional locomotion, the crawlers must perform friction control in which anchorings or unanchorings take place on some parts of the contact area at a suitable timing. The friction control may be helped by the asymmetric structure of the body parts, but is not inevitably provided only by such a static structure. It is more flexible, because the crawlers may have another modes of movement including backward locomotion.

A pioneering study in which limbless and legged crawlers were compared can be found in Gray's book published in 1968 [7]. Thereafter, many reports have been published in which typical forward locomotion modes are described for individual animal species (some reports of note include Refs. [14, 15, 16]). Here we explain that there are several modes of crawling from a mechanical point of view. Taking a broad view of crawling modes over a variety of species, we show that a simple, common rule of biomechanics holds despite differences in physical appearance between species.

In order to consider the general mechanics of invertebrate crawling, including both limbless and many-legged animals, we examine the locomotory waves that propagate during forward/backward migration in more than three phyla and eight classes. We provide a mechanical classification and explanation of the multiple manoeuvres involved in switching between forward and backward locomotion.

Finally, we discuss an evolutionary implication of our findings, namely that legged crawling develops from limbless movement. We focus on this issue from a mechanical point of view, which thus far has not been addressed in any theory of evolution. Inspection of the crawlers that we selected from a wide range of phyla allow us to give a unified viewpoint on this problem. The commonly given explanation of the evolution of legged locomotion is as follows. At some point in time, outgrowths of the body wall orthogonal to the primary body axis appeared by random mutation. A method of

movement using these outgrowths was subsequently acquired. Such organisms then developed leg structures and developed the method of movement through repetition of the mutation and natural selection. In such a scenario, the development of a body structure always precedes its function ("from structure to function"). In contrast, we use the results of our study to propose a different scenario for the acceleration of the evolution in which the function is a precedent for the structure ("from function to structure").

2 Organisms and methods

2.1 Animals

The experiments were performed using two chitons [*Ischnochiton comptus* and *Cryptochiton stelleri*], two kinds of marine gastropods: vetigastropoda [*Monodonta labio* form *confusa*] and limpets [*Lottia cassis*], earthworms [*Pheretima*], polychaete worms [*Eunicida*], maggots (fly larvae) [*Mycetophilidae*], moth larvae [*Marumba gaschkewitschii echephron*], centipedes [*Geophilomorpha* and *Scolopendraomorpha Scolopocryptops*], and millipedes [*Polydesmida Oxidus*]. All specimens were collected in Hakodate or Usujiri, Hokkaido, Japan. All the experiments were performed at room temperature (24 °C). We observed both forward and backward locomotion in all of these animals.

2.2 Measurements

Images were taken using a digital camera: either CASIO Co., type EX-F1 (30 fps or 300 fps) or CANON Co., type EOS 5D MarkII (30 fps). High-speed recordings (300 fps) were used to observe the locomotion of legged animals. The chitons and marine gastropoda were allowed to crawl in lanes on a plastic transparent tray, the widths of which were adjusted to their body widths. The pedal waves were recorded from below. The earthworms and polychaete worms were allowed to crawl in open-ended glass tubes (internal diameters 6 and 12 mm, respectively) and were recorded from above. The moth larvae were allowed to crawl in plastic transparent rectangle tubes, one end of which were closed and the widths and heights of which were adjusted to their body sizes. The centipedes crawled in lanes on a plastic tray, the widths of which were adjusted such that movement was as straight as possible. The millipedes were allowed to crawl in a glass tube (internal diameter 6 mm), one end of which was closed; the movement was recorded from above. The maggot of *Mycetophilidae* is an apodous larva. The specimens were placed on an agar plate (plastic Petri dish with cover, 9 cm in diameter). Several minutes later, the maggots began to create a tubular nest with their transparent sticky mucus. The nest was suspended in the air by sticky mucus strings connecting it to both the plastic ceiling and the agar floor. The maggots moved back and forth freely in their tubular nests, and were recorded from above. It was noted that when they were put on the plastic Petri dish, the maggots also moved freely on the flat surface in the same manner as in the nests. However, we only observed forward locomotion in this case.

2.2.1 Induction of backward locomotion

Backward locomotion of chitons and maggots was spontaneous without the need for any obstacles or stimuli. Backward locomotion was induced in the other animals as follows. The mouths of the marine gastropoda were strongly illuminated using halogen lamps for several minutes when they were at the dead-end of the lane. In *Monodonta labio* form *confusa*, backward movement without rotation was induced by supporting the pedal feet tightly by two bamboo sticks (diameter 2 mm) from both sides. Backward locomotion in earthworms and polychaete worms was induced by poking their mouths when they reached the exit of the glass tube. Millipedes and moth larvae moved backward spontaneously when they reached the closed end of the tubes. Backward locomotion of *Geophilomorpha* was induced by touching their heads lightly. For *Scolopendraomorpha Scolopocryptops*, backward locomotion was induced when their heads were strongly illuminated for several tens of seconds using halogen lamps at the dead ends of the narrow lanes.

2.3 Data analysis

Colour movies were analysed after converting into greyscale. Exceptionally, in the case of *Monodonta labio* form *confusa*, the colour movies were analysed after projecting to blue component. Space-time plots (e.g. figure 1a) were used to visualize and analyze the time development of the wave pattern, where a suitable line was chosen to demonstrate the evolution of the waves. The brightness and contrast of the images were optimized based on analyses of the histograms of the images. All image analysis was performed using either pre-installed plug-ins or our own custom-made plug-in programs for the ImageJ software [17].

3 Results of biological experiment

The animal specimens were classified into three groups depending on their body structure and locomotory apparatus: (1) limbless animals with a foot-like flat muscle sheet (gastropoda and chitons); (2) worm-like limbless animals (earthworms and maggots); (3) multi-legged animals (centipedes and millipedes). The observations made for each group are described in the following section.

3.1 Limbless animals with foot-like flat muscle sheet

Figure 1a shows a space-time plot of the pedal waves of the gastropoda *Monodonta labio* form *confusa*, during forward and backward locomotion. The pedal waves were direct and ditaxic for both the forward and backward locomotion. During forward locomotion the contraction waves propagated from the posterior to the anterior end (figure 1a left panel), whereas during backward locomotion they propagated from the anterior to the posterior end (figure 1a right panel). It should be noted that, during each forward and backward locomotion, the directions of the waves over the right and left hand sides of the sole were identical.

Figure 1b shows the retrograde and monotaxic waves that propagated during the forward locomotion of the chiton *Ischnochiton comptus*. The waves were direct and monotaxic for backward locomotion. During forward locomotion, the anterior edge extended in the anterior direction; this elongation wave ran to the posterior end (figure 1b left panel). Interestingly, backward locomotion involved contraction of the anterior edge in the posterior direction. This contraction wave ran to the posterior end (figure 1b right panel). Although the same wave direction was maintained during forward and backward locomotion, friction control associated with the pedal wave was reversed: the extending part of the foot was lifted from the substratum (to lower frictional resistance) for forward migration, whereas the contracting part was lifted for backward migration. This is typical for chitons and has also been observed in other species including *Fissurella* (by Olmstead [18]) and in *Cryptochiton stelleri* by ourselves. We observed the same combination of waves during forward and backward locomotion in the limpet *Lottia cassis*, but the waves in this case were ditaxic. This has earlier been thoroughly investigated for the limpet *Patella vulgata* [14].

3.2 Worm-like limbless animals

In the maggot, *Mycetophilidae*, direct waves propagated during both forward and backward locomotion. Forward locomotion began with retraction of the posterior end, and this contraction propagated toward the anterior end. The anterior end extended forward just after the wave reached it (figure 2a). During backward locomotion, these processes were reversed both temporally and spatially along the body axis.

In the earthworm, *Pheretima*, the peristaltic waves were retrograde during both forward and backward locomotion (figure 2b).

3.3 Multi-legged animals

The locomotion of multi-legged animals is usually accompanied by density waves formed by the leg-tip positions. Each cycle of the movement of a limb is comprised of a retraction (active stroke) phase and a protraction (recovery stroke) phase. In the case of forward locomotion, the foot moved in the posterior direction during the retraction phase and was lowered to the ground with timing such that almost perfect anchoring made it stationary relative to the ground. Subsequently, during the protraction phase the foot was lifted up from the ground and moved in the anterior direction. In the case of backward locomotion the limb was rotated in reverse fashion, that is, during the retraction and protraction phases it moved in the anterior and posterior directions, respectively.

Figure 3a shows the direct waves observed during both forward and backward locomotion in the millipede *Oxidus*. The spatial interval between adjacent legs was wider in the retraction phase than in the protraction phase, whereas the rotation speed significantly decreased in the retraction phase. In other words, the dense part of the gait wave was observed in the recovery stroke and the sparse part was in the active stroke. The dense and sparse parts appeared in alternating fashion along the body axis and propagated toward the anterior and posterior ends during forward and the backward locomotion, respectively.

	Direct-direct	Retrograde-retrograde	Retrograde-direct
Mollusca	<i>Monodonta labio</i> form <i>confusa</i>		<i>Ischnochiton comptus</i> , <i>Cryptochiton stelleri</i> , <i>Lottia cassis</i>
Annelida and larvae of Insecta	<i>Eunicida</i> , <i>Neoempheria ferruginea</i> , <i>Marumba gaschkewitschii ecephron</i>	<i>Pheretima</i>	
Myriapoda	<i>Oxidus</i>	<i>Geophilomorpha</i> , <i>Scolopocryptops</i>	

Table 1: Summary of wave direction during forward and backward locomotion of all animals studied. The first and second terms connected by a hyphen indicate the wave direction observed for forward and backward locomotion, respectively. For instance, the term *Retrograde-direct* means that a retrograde wave propagated during forward locomotion and a direct wave propagated during backward locomotion.

Figure 3b shows the retrograde waves that were observed during both forward and backward locomotion in the centipede *Geophilomorph*. The spatial interval between adjacent legs was narrower in the retraction phase than in the protraction phase, and the ground speed of the leg tip was almost zero during retraction. In other words, the sparse and dense parts of the wave were found in the protraction phase and the retraction phase, respectively. The dense parts of the wave were observed to be almost stationary relative to the ground because the positions at which the propulsive legs were set down corresponded to common footprints. However, the dense parts propagated in posterior fashion along the body axis during forward locomotion and anterior fashion during backward locomotion. A summary of the wave directions observed during forward and backward locomotion in all of the species studied is given in table 1.

4 Mechanics of crawling

4.1 Multi-block modeling of crawlers

4.1.1 Common mechanics among the three animal groups

Because the locomotory equipment possessed by our three groups of specimens were very different, we will now focus on common features of locomotion among them by focusing on the following two aspects: (1) the intrinsic back and forth motion of a local part of the body that forms an interface in contact with the substrate, and its wave propagation through the entire body; (2) the mechanical interaction (or friction control) between the substrate and the body in relation to the locomotory wave.

We will first consider aspect (1) for each group of animals. In the earthworm, each body segment undergoes a cyclic movement involving extension and contraction. There is a small difference in the phase of oscillation between adjacent segments such that the local cyclic movements result in the propagation of a peristaltic wave (figure

4b). In limbless animals such as gastropoda and chitons, a local part of the sole of the foot undergoes a cyclic movement of contraction and elongation; this local activity forms a pedal wave [19]. This local part of the sole moves both behind and in front of its position in the relaxed state (figure 4a). In multi-legged animals, the leg tip is the interface between the body and the substrate, just as the ventral surface of the foot is the interface in gastropoda. Because each leg repeats a cyclic motion of active and recovery strokes as shown in figure 4c, the leg tip moves both behind and in front of the standard position along the body axis at which the leg is attached to the main body. As described above, every part of the interfacial surface of the body moves periodically back and forth along the body axis for all three groups of animals (figure 4d).

If we focus on the tangential movement of the interface, the conversion of peristaltic waves to or from leg-density waves is possible as follows. Let assume that every legs of a myriapod rotate around their bases with same constant angular velocity as the intrinsic motion (figure 5a). By considering the natural projection of the circular movement of the leg tip with respect to the body axis, it can be envisaged as to-and-fro motion along the body axis. Upper or middle panel of figure 5b schematically shows a snapshot of the circular motion of each leg of a myriapod, where there is a constant phase difference between adjacent legs, respectively. When the tips of all the legs are viewed along the same projection, correspondence is obtained between peristaltic waves and the leg-density waves of myriapoda (figure 5b lower panel).

We now consider aspect (2) above. In earthworms, the body segments are elongated and thinned by contraction of the circular muscles and relaxation of the longitudinal muscles, whereas they are contracted and thickened by contraction of the longitudinal muscles and relaxation of the circular muscles [7]. In relation to this peristaltic wave, the control of ground friction (anchoring control) also takes place: the elongated and thinned segment is lifted up from the substrate, reducing the frictional resistance, while the contracted and thickened segment pushes against the substrate, leading to higher frictional resistance.

In gastropoda and chitons, parts of the sole of the foot adhere to the substrate in the interwave state (zero ground speed) by means of muscular force and mucus viscosity [3, 20, 21]. In the pedal wave state, the frictional resistance decreases as the sole is lifted up from the substratum and/or the liquefaction of mucus is induced by strong shear stress. In myriapoda, the frictional resistance is high and low when a leg-tip is set down and lifted up from the ground, respectively.

4.1.2 Multi-block modelling of crawlers

For the reasons stated above, the three groups of animals have the following features in common (figure 4d):

- (I) [*Multi-block system*] the interfacial body parts to the substrate can be represented as a series of blocks (body-segments) arranged along the body axis;
- (II) [*Oscillator*] the tangential component of the free internal movement of each block is periodic;

- (III) [*Phase wave (density wave)*] there is a constant phase difference between successive blocks, that is, phase (or density) waves propagate along the body axis;
- (IV) [*(Un-)anchoring phase*] (un-)anchoring occurs at specific phases of the oscillation of blocks.

Tanaka et al [12] has proposed a simple mechanical model for peristaltic crawlers with multi-block body which possesses above four common features. From analytical treatments of the model, they showed the directional movement of such crawler can be understood by the following two-step criteria. In the first step, we consider a virtual state in which the (viscous) friction coefficients between the substrate and local parts of the body (blocks) are temporally constant during a complete cycle of motion of the blocks.¹ We call this virtual state *frictional standard state*. Under this condition, we can assume that internal motion of the crawler that satisfies conditions (II) and (III) occurs, but no directional motion takes place. In the next step, we introduce (spatiotemporal) friction control in which condition (IV) is satisfied. If the blocks which have negative (or positive) velocity in the frictional standard state are anchored (or unanchored), the locomotion occurs in the positive direction, because the anchorings reduce the negative velocity component and the unanchorings enhance the positive velocity component. Here, *anchoring* or *unanchoring* on a block means temporarily increase or decrease of the friction coefficient of the block.² In a similar way, locomotion can also occur in the negative direction.

We will now consider the relationship between the direction of locomotion and the timing of friction control with respect to the phase wave in crawlers, in the case where conditions (I) to (IV) above are satisfied. It should be noted that the above criterion on friction control timing for the directional locomotion of a crawler involves the velocity of each block, but is independent of the phase relations between the motions of different blocks [condition (III)]. However, when a phase wave exists, the timing of friction control that is necessary for directional locomotion is naturally associated with the specific phase of the wave because the velocity of each block and the phase of the wave are uniquely coupled. To depict this coupling intuitively, we give a phase space representation of the motion of the blocks in the frictional standard state.

4.2 Phase space description of internal motion of peristaltic crawlers (temporally constant friction coefficient case)

Let $x_n(t) = X_n(t) - O_n(t)$ be the displacement of the n th block from its standard position, $O_n(t)$, to the current position, $X_n(t)$, at time t (figure 6a). The standard

¹In this virtual state, the friction coefficient values need not be identical for all blocks. However, without loss of generality, we can assume they are identical in the following arguments.

²In this modeling, anchoring and unanchoring are symmetrically identical operation. Whatever the friction coefficient in the frictional standard state (called *default value* of friction coefficients) is, they can independently achieve an equivalent effect for a directional locomotion if they occur at their respective suitable timing. However, considering more realistic context, such as physical constraint of crawlers, whether which of them easily operates may change depending on the default value of friction coefficients. The followings are probable. If the default value is sufficiently small or large, anchoring or unanchoring is preferred than the other respectively. On the other hand, if the default values is intermediate, anchoring and unanchoring may be equivalently available for the crawler.

positions of the blocks are assumed to be uniformly arranged and fixed relative to the body, such that $\ell_0 = O_{n+1}(t) - O_n(t)$ is a constant that is independent of n and t . We fix the total number of blocks to be N , and we number the blocks from the tail (x_1) to the head (x_N) as shown in figure 7a.

The positive direction is always from tail to head in this paper. For simplicity, we consider the oscillation of each block along the body axis to be sinusoidal whose angular frequency, ω_0 , is unity. The motion of each block can then be represented as a clockwise rotating point on a circle in the phase space spanned by x_n and $\dot{x}_n (= dx_n/dt)$ (figure 6b).

Next we consider further details of the phase waves that crawlers utilize for locomotion. We assume that the moving distance of the phase wave during one period is same as the whole body length. Figure 7a shows a snapshot of a postero-anterior wave resulting from the sinusoidal motion of each block. We represent this wave in the single phase plane in the manner shown in figure 7b.

The mean distance of adjacent blocks around n th block is $((X_{n+1} - X_n) + (X_n - X_{n-1}))/2 = \ell_0 + (x_{n+1} - x_{n-1})/2$, and the spatial density of the blocks can be estimated as $(\ell_0 + x'_n)^{-1}$, where $x'_n \equiv (x_{n+1} - x_{n-1})/2$. It says that the spatial density becomes lower and higher when x'_n becomes larger and smaller, respectively. The relation between the velocity (\dot{x}_n) and the spatial density $((\ell_0 + x'_n)^{-1})$ of the block depends on the direction of the waves. For example, for the postero-anterior wave in figure 7b, when a block is situated in the lower half of the phase plane ($\dot{x}_n < 0$), the distances from the neighbouring blocks are greater than the mean distance ($x'_n > 0$), so that the bottom of the circle is the most sparse. In a similar way, the top of the circle is the most dense. For a wave propagating in the opposite, antero-posterior direction, the bottom and top of the circle are the most dense and sparse, respectively (figure 7c).

3

4.3 Anchoring / unanchoring phase for forward locomotion

We are now able to formulate conditions for the timing of friction control in the phase waves. In order to realize forward locomotion in a peristaltic crawler, the anchoring should occur in the sparse ($\dot{x}_n < 0$) parts of postero-anterior waves (figure 8a), and in the dense ($\dot{x}_n < 0$) parts of antero-posterior waves (figure 8b), respectively. In the same way, the unanchoring in the dense ($\dot{x}_n > 0$) parts of postero-anterior waves and in the sparse ($\dot{x}_n > 0$) parts of antero-posterior waves can also provide forward locomotion (figure 8).

Based on the theoretical considerations above, we can immediately extract the following facts from our experimental data without any further observations of the contact interfaces of the animals. In the case of forward locomotion with direct waves (*direct*

³This dependency of the relation between \dot{x}_n and x'_n on the direction of the waves can be seen more clearly when more concrete settings are used. For example, we can assume that the phase difference between adjacent blocks is a constant ($\theta_n = \theta_0 + n\Delta\theta$, $-\pi < \Delta\theta \leq \pi$), and that the motion of each block can be represented by $x_n(t) = a_0 \cos(\omega_0 t + \theta_n)$, where the sign of $\Delta\theta$ determines the wave direction (i.e. $\Delta\theta > 0$ and $\Delta\theta < 0$ give antero-posterior wave and postero-anterior wave, respectively). Then, we have $\dot{x}_n = \frac{\omega_0}{\sin(\Delta\theta)} x'_n$. This shows that the relation between the density of the wave and the velocity of the block depends on the direction of the wave, which is determined by the sign of $\Delta\theta$.

forward case), anchoring should take place at the sparse parts of the locomotory wave and unanchoring should occur in the remaining parts of the wave (left-hand panels of figures 1a, 2a and 3a). In contrast, in the case of forward locomotion with retrograde waves (*retrograde forward* case), anchoring should always be at the dense part and unanchoring in the remaining parts of the wave (left-hand panels of figure 1b, 2b and 3b). In all three groups of animals, the locomotory waves are accompanied by the control of ground friction.

4.4 Theoretically possible manoeuvres for mode switching from forward locomotion to backward locomotion

In the same way as for forward locomotion, the timing of friction control for backward locomotion is as follows: anchoring (or unanchoring) should occur in the dense ($\dot{x}_n > 0$) (or sparse ($\dot{x}_n < 0$)) parts of postero-anterior waves, and in the sparse ($\dot{x}_n > 0$) (or dense ($\dot{x}_n < 0$)) parts of antero-posterior waves, respectively. Therefore, the manoeuvres of switching between forward and backward locomotion can roughly be classified into two types. The first manoeuvre is reversal of the wave direction: the direction of the wave for backward locomotion is opposite to that for forward locomotion. Here two cases can be identified, depending on the directions of postero-anterior and antero-posterior waves.

(1) *Direct forward and direct backward case*

Figure 9a shows a single phase space representation before and after mode switching has occurred. In the case of forward locomotion with a direct wave, anchoring (or unanchoring) takes place in the sparse (or dense) part. For backward locomotion, the wave direction is reversed from postero-anterior to antero-posterior and the direct wave is unchanged from that for forward locomotion. Therefore, anchoring (or unanchoring) should take place in the sparse (or dense) part, the same as for forward locomotion.

(2) *Retrograde forward and retrograde backward case*

A retrograde wave is observed for both forward and backward locomotion because the antero-posterior wave is reversed together with reversal of the locomotion direction. When these reversals take place, the anchoring (or unanchoring) is kept in the dense (or sparse) part.

To summarize, animals can reverse their direction of movement by switching the direction of their locomotory waves without any change of the anchoring (or unanchoring) phase in their rotational motion. The direct-direct and retrograde-retrograde cases are perfectly symmetric in a mathematical sense.

The second manoeuvre is inversion of the anchoring phase between the dense and sparse parts while the direction of the wave is kept the same for both forward and backward locomotion. Here two cases can also be identified, depending on the directions of the waves.

(3) *Retrograde forward and direct backward case*

As shown in figure 9b, for forward locomotion with a retrograde wave, anchoring (or unanchoring) takes place in the dense (or sparse) part. For backward locomotion, while the antero-posterior wave remains and the direct wave is observed, the dense part becomes the position for unanchoring instead of anchoring.

(4) *Direct forward and retrograde backward case*

Here a similar inversion of the anchoring phase is carried out. In the case of forward locomotion, anchoring (or unanchoring) occurs in the sparse (or dense) part. For backward locomotion, anchoring (or unanchoring) should occur in the dense (or sparse) part, because in postero-anterior waves the segments move towards the anterior (or posterior) in the dense (or sparse) part, as described for case (2).

Organisms are thus able to reverse their direction of movement by switching the friction control timing in the phase waves without any change in direction of the waves.

4.5 Comparison with real animals and concluding remarks

For a variety of legged and limbless animals across several phyla, we have demonstrated and classified the roles of locomotory waves for movement in the forward and backward directions using phase space analysis of longitudinally-arranged multiple locomotory oscillators and by considering the timing of anchoring in the waves. In particular, the manoeuvre of mode switching from forward to backward locomotion can be classified into two types: (1) changing the direction of the waves; (2) changing the anchoring timing in the waves. Most of our experimental observations fall into the former category. It should be noted that we could not find any specimen that adopts a manoeuvre corresponding to case (4) above, *direct forward but retrograde backward*, although this combination should be possible from our theory; further investigation of this aspect will be left for future studies.

In this study, all the frictional effect involved in animal-substratum contacts were replaced by a binary representation ((un-)anchored state or not). Although the modeling is simple, it seems to be enough to explain the experimental results at the level of detail needed to support the conclusion that all studied animals implement similar motility patterns. However, if we intend to describe locomotion of a particular crawler in more detail, we need to consider a complicated friction law which depends on the texture of the ventral surface and on the structure of the contact interface (e.g. the intermediate material is viscous mucus, soil particles etc.). For example, the mucus - pedal foot interaction in gastropod includes potential dynamical richness, and the details of mucus rheology and the foot geometry can play an important role in dictating gastropod locomotion (see for instance, [8]).

Our results indicate that legged locomotion (i.e. "walking") and limbless locomotion can be considered in the same framework of general peristaltic crawling. In this context, one advantage of legged locomotion over limbless locomotion, in which the animal primarily uses the body itself as a propulsive structure, is the greater ease of friction control during the (un-)anchoring phase. Another is the acquisition of larger stride which is associated with the amplitude in each to-and-fro motion of the contact

interfaces. This enable the legged animals to move faster than the limbless animals even under a condition of same angular speed in each the to-and-fro motion.

5 Discussion

It is probable that in terms of evolution, movement using appendages/outgrowths from the body wall appeared subsequent to limbless crawling such as peristaltic or pedal wave movement [22, 23]. Leg-like appendages with various kinds of anatomical structures were eventually developed, and methods of movement that utilize such appendages then became broadly used by a wide range of animals. Furthermore, it has been discovered that a common gene is involved in the formation of such leg-like appendages in most protostomes and deuterostomes [24].

Here a fundamental question can be raised. How did legged locomotion evolve from limbless locomotion? In the same way that Hamlet cannot be created by the random typing of a monkey, such a complex organ cannot be created only by the repetition of a random mutation. Within the naive framework of evolutionary theory based on the random mutation of genes and natural selection for individuals, evolution of the leg and its use as a method of movement can be summarized as follows: (i) an appendage/outgrowth from the body wall suddenly appeared by means of a mutation; (ii) a method of movement using such appendages (i.e. walking) was subsequently acquired; (iii) further evolution of the legs and the method of movement was achieved through a long sequence of mutations and natural selection. However, in this scenario we encounter difficulties in explaining how the new body component appearing in (i) acquired its adaptive functionality quickly in the face of severe natural selection. The establishment of any complex organ and its function, such as legs and movement, requires the support and cooperation of many other components. Therefore, an organ has a particular function only if there is an existing structure on which to work (a comparison can be made with coadapted genotypes [25]). Based on the results in this study, we propose a hypothetical scenario of the evolution of legged locomotion as follows: when a leg-like appendage appears on the body wall of an animal, the appendage can function immediately because it matches and cooperates with a pre-existing method of movement and its mechanical constraints. That is, chance favors the prepared. Limbless crawlers moved in a manner similar to walking before developing legs. We should note that rigorous ontogenetic or phylogenetic evidences for this scenario still remain to be found.

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Figure Captions

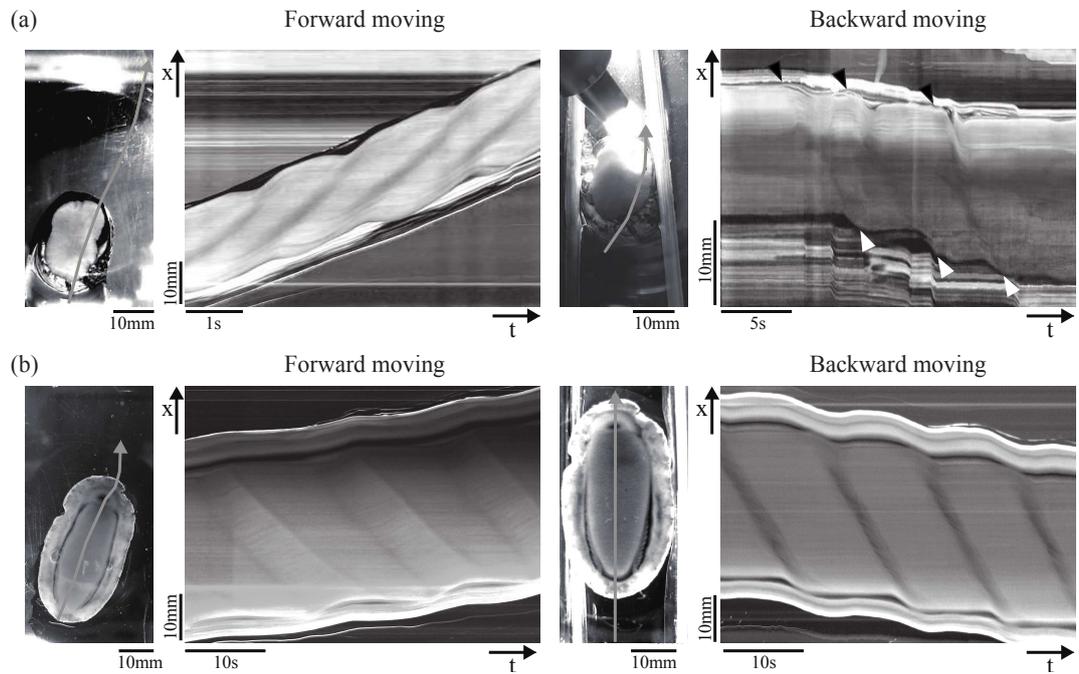


Figure 1: Examples of two types of mode switching for forward/backward movement in gastropoda and polyplacophora. (a) Direct-direct type: direct wave of pedal movement for forward and backward locomotion in Prosobranchia (*monodonta labio form confusa*). Black and white arrowheads on the space-time plot of backward moving (rightmost panel) indicate the beginning and end of the waves, respectively. (b) Retrograde-direct type: retrograde wave for forward locomotion and direct wave for backward locomotion in Polyplacophora (*ischnochiton comptus*).

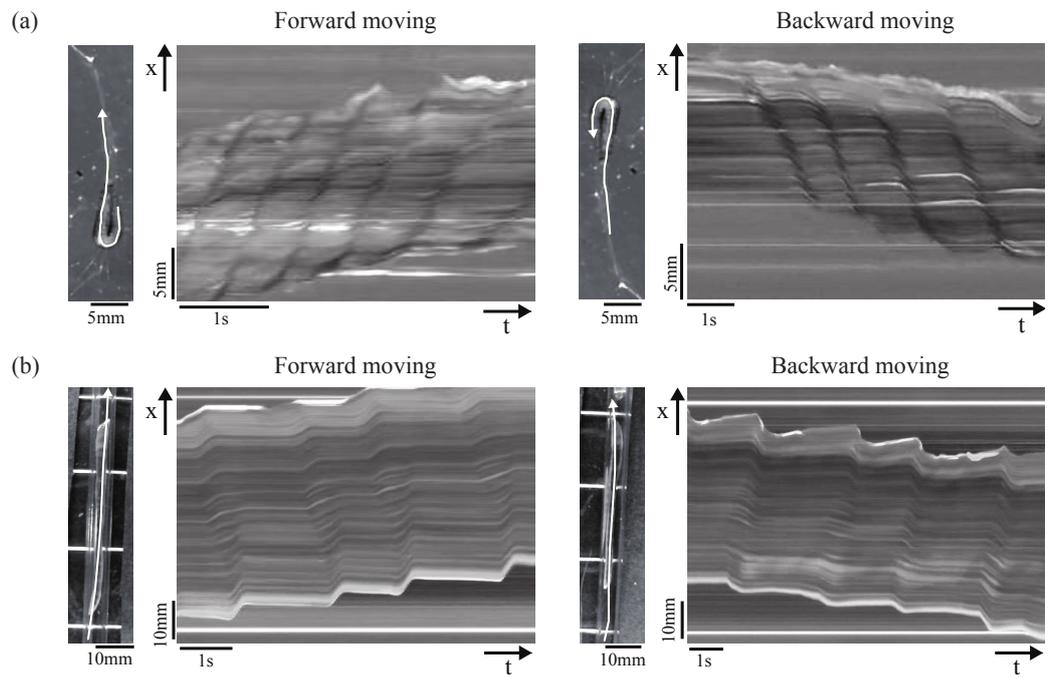


Figure 2: Examples of two types of mode switching for forward/backward locomotion in worms. (a) Direct-direct type for *mycetophilidae* maggots. (b) Retrograde-retrograde type for earthworms (*pheretima*).

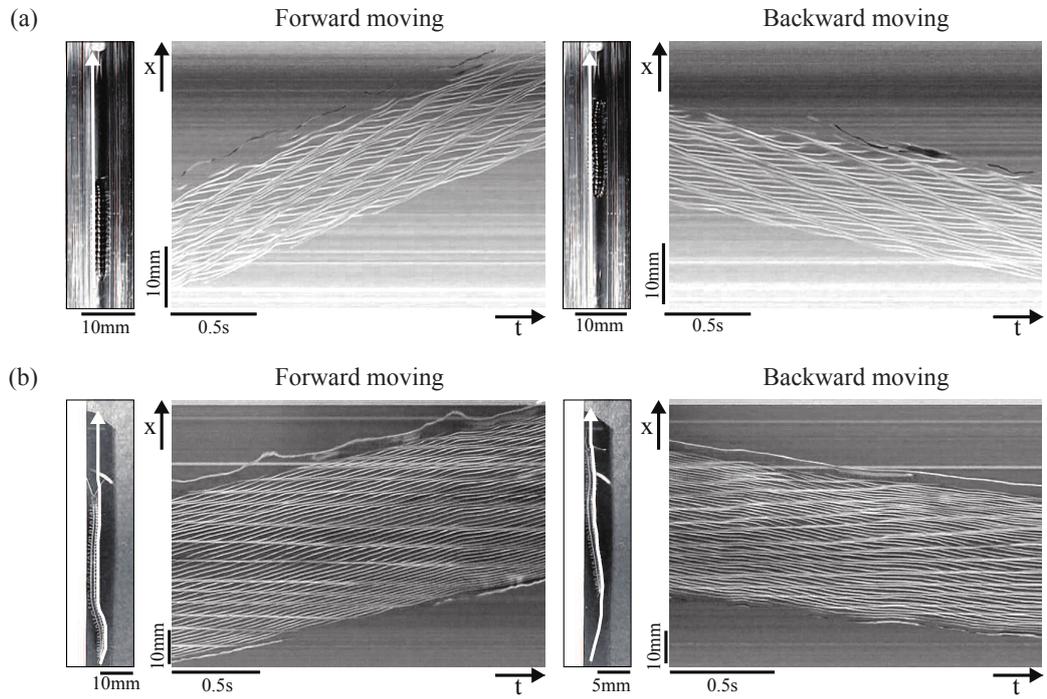


Figure 3: Examples of two types of mode switching for forward/backward locomotion in myriapoda. (a) Direct-direct type in millipedes (*Oxidus*). (b) Retrograde-retrograde type in centipedes (*geophilomorph*).

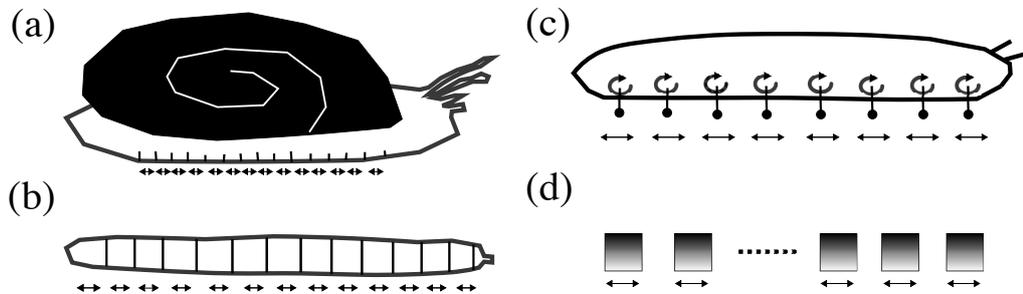


Figure 4: Side view of animals in the three groups and corresponding components of internal motion parallel (or tangential) to the substrate, indicated by the double-headed arrows beneath the body. The heads of all animals are on the right. (a) Limbless animals with flat, foot-like muscle sheet (gastropoda and chitons). (b) Worm-like limbless animals (maggots, earthworms). (c) Multi-legged animals (millipedes, centipedes). Each leg rotates clockwise during forward locomotion and counterclockwise during backward locomotion. (d) Multi-block model for peristaltic movement coupled with friction control.

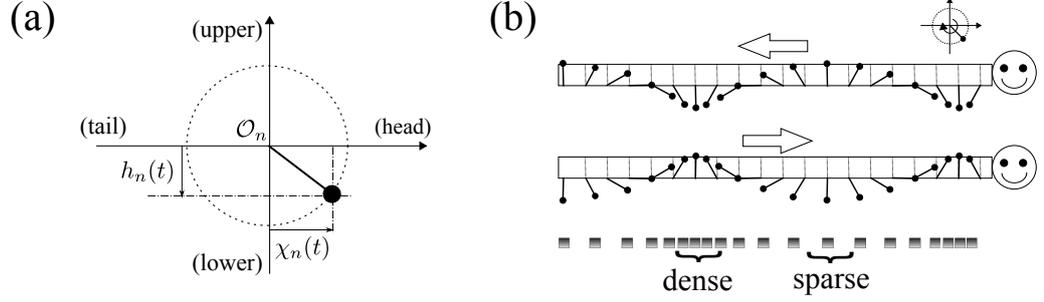


Figure 5: Peristaltic waves to/from legged locomotion. (a) Assumed simple intrinsic rotation of each leg around its base with a constant angular velocity. Set a positive direction of the body axis is taken from tail to head and let $\chi_n(t)$ and $h_n(t)$ be the horizontal and vertical displacements of the n th leg-tip from the base of the leg at time t , respectively. We can observe that $\dot{\chi}_n(t) (= d\chi_n(t)/dt)$ is proportional to $h_n(t)$ when the leg tip rotates clockwise as in forward locomotion. When the leg tip rotates in inverse fashion as in backward locomotion, $\dot{\chi}_n(t)$ is proportional to $-h_n(t)$. (b) Similarities in the mechanical nature of legless crawling and legged walking. The upper and middle panels show snapshots of two types of gait patterns. Every leg tips rotate clockwise as in forward locomotion. The blank arrows indicate directions of the leg-density waves. The anchoring may occur in the dense or sparse part in the upper or middle case, respectively. The lower panel shows the corresponding density waves formed by the leg-tip positions.

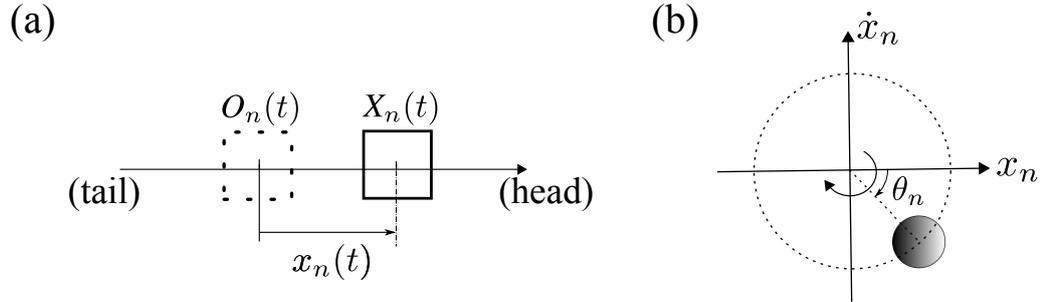


Figure 6: Representation of the oscillatory movement of each segment relative to the body. (a) Displacement $x_n(t)$ of the n th block from its standard position, $O_n(t)$, to the current position, $X_n(t)$, at time t , where $x_n(t) = X_n(t) - O_n(t)$. (b) Phase space representation of the movement of the n th segment in terms of the displacement from its standard position, x_n , and its velocity, \dot{x}_n .

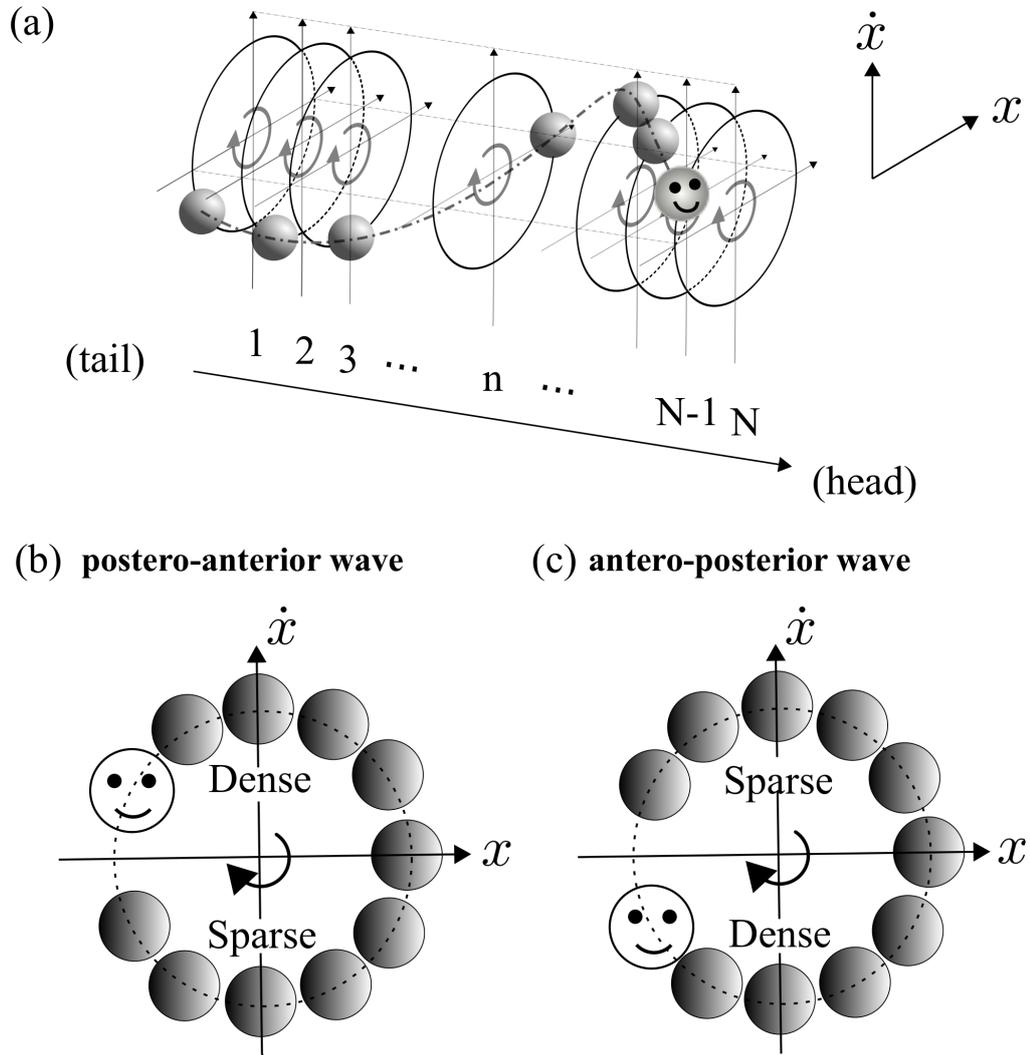


Figure 7: Arrangement of body segments with respect to waves. For simplicity, we assumed that the moving distance of the phase wave during one period is same as the whole body length. unity. (a) Arrangement of body segments in the case of a postero-anterior wave. In the wave, the phase of the n th segment is ahead of the phase of the $n + 1$ th segment. (b) Single phase space representation of movement of all segments comprising a postero-anterior wave. The dense ($x'_n < 0$) and sparse ($x'_n > 0$) parts of the waves are situated in the upper ($\dot{x} > 0$) and lower ($\dot{x} < 0$) regions of this phase space, respectively. (c) Single phase space representation of movement of all segments comprising an antero-posterior wave. The dense ($x'_n < 0$) and sparse ($x'_n > 0$) parts of the waves are situated in the lower ($\dot{x} < 0$) and upper ($\dot{x} > 0$) regions of this phase space, respectively.

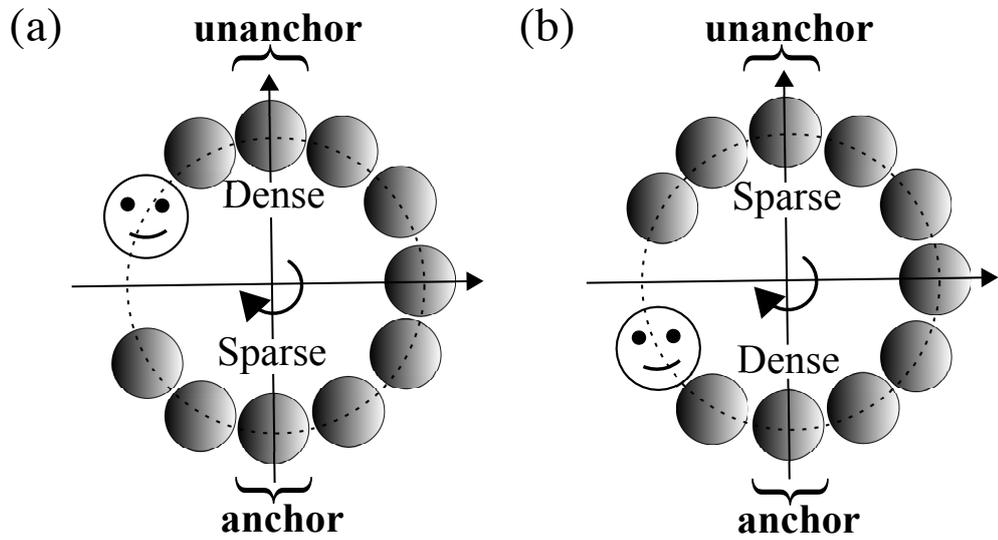


Figure 8: Phase space representation of forward locomotion. The abscissa and the ordinate are x and \dot{x} , respectively. (a) Forward locomotion with a direct wave. Anchoring/unanchoring at the sparse/dense parts induces forward locomotion of the animal. (b) Forward locomotion with a retrograde wave. Anchoring/unanchoring at the dense/sparse parts induces forward locomotion of the animal.

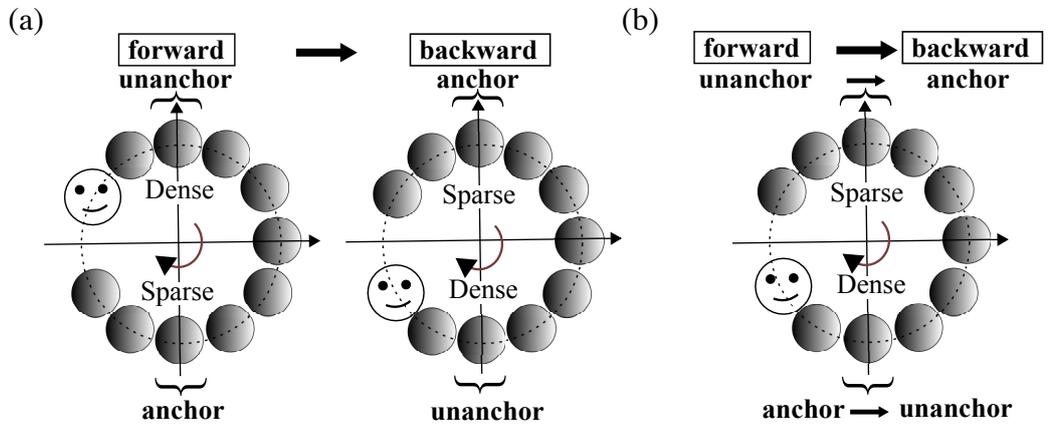


Figure 9: Phase space representation of two types of mode switching from forward to backward locomotion. The abscissa and the ordinate are x and \dot{x} , respectively. (a) Mode switching from forward locomotion with direct waves to backward locomotion with direct waves. (b) Mode switching from forward locomotion with retrograde waves to backward locomotion with direct waves.