The Advantage of Mucus for Adhesive Locomotion in Gastropods

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Abstract

1 For many gastropods, locomotion is driven by a succession of periodic mus-
2 cular waves (contractions and relaxations) moving along the foot. The force
3 generated by these waves is coupled to the substratum by a thin layer of
4 pedal mucus. Gastropod pedal mucus has unusual physical properties: the
5 mucus is a viscoelastic solid at small deformation and shows a sharp yield
6 point; then, at greater strains, the mucus is a viscous liquid, although it
7 will recover its solidity if allowed to heal for a certain period. In this paper,
8 to clarify the role of the mucus and the flexible muscular waves in adhesive
9 locomotion, we use a simple mathematical model to verify that directional
10 migration can be realized through the interaction between the periodic mus-
11 cular waves and the specific physical features of mucus. Our results indicate
12 that the hysteresis property of mucus is essential in controlling kinetic fric-

tion for the realization of crawling locomotion. Furthermore, our numerical calculations show that both the hysteresis property of mucus and the contraction ratio of muscle gives rise to two styles of locomotion, direct waves and retrograde waves, which until now have been explained by different mechanisms. The biomechanical effectiveness of mucus in adhesive locomotion is also discussed.

Keywords: muscular wave, hysteresis loop, viscoelasticity, yield point, mathematical model

1. Introduction

Adhesive locomotion is one of the most fundamental locomotory strategies for many animals without extremities. Gastropods, including snails, slugs, and abalones, are able to crawl steadily by propagating periodic muscular waves (alternating contraction and expansion) along the ventral foot in contact with the substrate^{1–4}. Gastropods interact with the substrate through the viscoelastic mucus released from their foot. It is generally known that gastropod pedal mucus is produced to adjust for humidity and salinity⁵. However, most researchers believe that the nonlinear rheological properties of mucus play an important role in locomotion^{6–9}. Understanding the locomotory mechanism of gastropods has been an interesting endeavor for biologists and biophysicists^{10–20}. In recent years, from the perspective of designing biomimicry robots, adhesive locomotion has become a subject of renewed interest among engineers^{21–23}. Although physical observations and physiological knowledge of gastropod crawling locomotion both exist, the mechanisms of interaction between the muscular waves and the physical features of mucus

35 remain insufficiently elucidated.

36 Although it has long been known that many gastropods crawl on hard
37 substrates by actuating muscular waves along the sole of the foot, many of
38 the earlier studies are simply records of visual observations^{24–26} and classi-
39 fications of the waves according to their direction of propagation²⁷. Direct
40 waves are defined as traveling in the same direction as the movement of the
41 animal. By contrast, retrograde waves are in the opposite direction to that
42 in which the animal moves. Several early studies^{14,26} confirmed that the
43 waves along the foot of a gastropod are concavities. Lissmann was the first
44 to study the kinematics and dynamics of gastropod locomotion in detail, and
45 this enabled improvements in experimental techniques^{2,13}. He proposed that
46 a number of forces are involved in gastropod crawling locomotion, includ-
47 ing external sliding friction in the form of both drag and slip. The basis
48 for understanding the frictional mechanism that enables the creation of the
49 propulsive force was revealed in subsequent studies.

50 Previous research on worm-like peristaltic locomotion^{19,28–34} has been cru-
51 cial in advancing the study of the mechanism of adhesive locomotion in gas-
52 tropods. In particular, studies using a simplified mathematical model of a
53 chain-like body in a resistive medium, including the case of a few degrees
54 of freedom, have indicated that directional migration of the mass center of
55 a body can be realized through nonlinear asymmetric frictional forces^{29–34}.
56 The frictional mechanism of earthworms that actually move by retrograde
57 waves has been solved: anisotropic chaetae that protrude from shortened
58 segments act in the role of spikes. The important fact in the case of earth-
59 worms is that a system with friction against the surrounding environment

60 is controlled without central signals. Because this constitutes an intelligent
61 mechanism for primitive creatures, it would be reasonable to suppose that
62 gastropods also have an automatic system of friction control. However, what
63 is the structure of this friction control in gastropods?

64 Denny was the first to reveal the rheological characteristics of the pedal
65 mucus⁶. Denny and Gosline measured the rheological properties of pedal
66 mucus, including its finite yield stress, and reached the important conclusion
67 that the unusual viscoelastic nature of pedal mucus acts to control friction
68 against the substratum in the generation of the animal's driving force⁶⁻⁹.
69 Although the details of how the propulsive force is generated by mucus are
70 unclear, the indication of a mechanism without a central control is invaluable.

71 With the advent of the 21st century, engineers began to conduct me-
72 chanical studies that support and expand on Denny's hypothesis^{21,22}, and
73 investigated the key features for a complex fluid to be useful in adhesive lo-
74 comotion with direct waves²³. Although their models sufficiently described
75 the rheological features of mucus by putting a strong emphasis on concepts
76 in fluid dynamics, their disadvantage is that the wave motion is prescribed
77 independently of the underlying muscle mechanics.

78 The aim of this study is to prove that crawling locomotion is achieved
79 through an interaction between the propagation of soft-body muscular waves
80 reported by many scientists^{1,2,16,20} and the properties of pedal mucus reported
81 by Denny and Gosline^{6,7}. Hence, a simple mathematical model for crawling
82 locomotion is proposed. This model, which describes the interaction between
83 animals and their environment, is a close representation of the situation that
84 occurs in nature. Our results indicate that crawling locomotion is achieved by

85 this mutual interaction and that the nonlinear hysteresis property of mucus
86 is essential to locomotion. We also find that both direct wave locomotion
87 and retrograde wave locomotion are produced by the same mechanism. As
88 previously shown by Tanaka et al.³⁴, the choice of locomotory style is related
89 to a difference in the timing of anchoring. In our model, the difference can be
90 determined by the properties of mucus and muscle. This means that there
91 is no need for animals to control the friction between their bodies and the
92 substrate.

93 The rest of this paper is structured as follows: The next section introduces
94 a mathematical model for crawling locomotion, and Section 3 presents the
95 results of numerical simulations using this model. Section 4 then discusses
96 the simulation results, draws conclusions, and introduces future work.

97 **2. Modeling of adhesive locomotion**

98 The aim of this paper is to verify that the locomotory mechanism is a mu-
99 tual interaction between periodic muscular wave propagation and the unusual
100 physical properties of pedal mucus. This mechanism was implicitly suggested
101 by Denny and Gosline^{6,7}. Accordingly, we construct a simple mathematical
102 model that captures the essence of this mechanism and is based on experi-
103 mental results reported by Denny and Gosline^{6,7} amongst others^{1,2,16,26}. Our
104 mathematical model is considered an improvement over the model of peri-
105 staltic motion proposed by Tanaka et al.³⁴. We now explain the details of our
106 model. There are two critical factors in this hypothesis of the locomotory
107 mechanism: the propagation of flexible muscular waves and the nonlinear
108 properties of pedal mucus.

109 2.1. Muscular wave propagation

110 As many scientists have reported^{1,2,10–12,16–18,26}, muscular waves are ob-
 111 served during the crawling locomotion of a wide variety of mollusks. One of
 112 the main functions for self-generating a driving force is to excite a muscular
 113 contraction and then propagate the region as a wave. During locomotion,
 114 the ventral foot essentially consists of moving (slipping) regions and adhe-
 115 sive (anchoring) regions, with a few exceptions such as the rim of a slug. A
 116 one-dimensional model is sufficient for our aim of verifying that directional
 117 crawling locomotion is achieved.

118 It is reasonable to use an active spring to represent the flexible muscle
 119 of a mollusk-like gastropod. Although we might consider two types of active
 120 spring (see Appendix A), we use a real-time tunable spring (RTS)³⁵, such
 121 as that in Figure B.1(b), to represent muscle in the mathematical model,
 122 with a view to its utilization in a robot. To mimic animals, we consider
 123 a multi-segment model, as in Figure B.1(a), which can express the prop-
 124 agation of muscular waves. Now, we assume that the ventral foot of the
 125 animal is divided into $(N + 1)$ segments. Similar to the method of previous
 126 studies^{23,30,33,34}, we configure the spring to contract and elongate repeatedly.
 127 In our mathematical model, such an active spring is achieved by periodi-
 128 cally controlling the natural length of the RTS. The natural length of the
 129 $(n + 1/2)$ th RTS, which is one of the elements connected to the n th and
 130 $(n + 1)$ th segments at time t [s], is

$$l_{n+\frac{1}{2}} = l_0(1 + \alpha \sin(\omega t - \beta n)), \quad (1)$$

131 where ω [Hz] is the wave frequency. Using specific properties of the foot,
 132 we set l_0 [m] = L/N and $\beta = 2\pi W/N$, where L [m] is the overall length of
 133 the foot and W is the number of waves along the foot. The muscular force
 134 $F_{n+\frac{1}{2}}$ [N] acting on the n th segment generated by the $(n + 1/2)$ th RTS and
 135 damper is described using $l_{n+\frac{1}{2}}$ [m] as follows:

$$F_{n+\frac{1}{2}} = \kappa_{n+\frac{1}{2}} \left(\frac{x_{n+1} - x_n}{l_{n+\frac{1}{2}}} - 1 \right) + q_{n+\frac{1}{2}} (\dot{x}_{n+1} - \dot{x}_n), \quad (2)$$

136 where x_n [m] is the position of the n th segment in the direction of move-
 137 ment, and a dot over a variable means differentiation with respect to t . The
 138 first term is an elastic force generated by the RTS and the second term is the
 139 damping force. The coefficients $\kappa_{n+\frac{1}{2}}$ [N] and $q_{n+\frac{1}{2}}$ [N·s/m] are constants.
 140 Specifically, $\kappa_{n+\frac{1}{2}}$ is the stiffness of a spring, as determined from material
 141 properties, and has the dimensions of force.

142 2.2. Dynamic viscoelastic properties of pedal mucus

143 The second critical factor consists of the physical properties of pedal mu-
 144 cus reported by Denny and Gosline^{6,7}. Put simply, gastropod pedal mucus
 145 has two states: elastic solid and viscous liquid. The outline of Denny's
 146 experiment⁶ is as follows; the mucus of Pacific banana slugs (*Ariolimax*
 147 *columbianus*) was collected, and its torque against deformation was measured
 148 using a rotary cone-plate instrument for measuring viscoelasticity. First,
 149 when the strain was small, the torque was linear with respect to the defor-
 150 mation, as in Figure B.2(b)A. That is, the mucus behaved as an elastic solid.
 151 The mucus was found to yield when the deformation exceeded some threshold
 152 value, as in Figure B.2(b)B, and the torque became a constant independent

153 of the amount of strain, as in Figure B.2(b)C. According to data reported
 154 by Denny⁶, this torque is linear with respect to the strain rate; that is, the
 155 mucus behaves as a viscous liquid. Thereafter, the increase in strain stops.
 156 More importantly, after a certain period of healing, the mucus recovers its
 157 elasticity, as where A follows D in Figure B.2(b).

158 Based on measurement results, the mucus dynamics under stress can be
 159 pictured as Figure B.3. The chemical bond that is coupled in the elastic state
 160 of the mucus breaks when the muscular contraction waves arrive. After the
 161 wave has passed through this region, the elasticity of the mucus is recovered
 162 by re-coupling of the chemical bond, although this takes a small amount of
 163 time. To describe such a thixotropic nature of mucus under the pedal, we
 164 assume that the mucus is divided into $(N + 1)$, parts similar to the foot in
 165 Figure B.2(a), and define the state of the mucus by a parameter, σ ; i.e., the
 166 mucus behaves as an elastic solid when $\sigma = 1$ and behaves as a viscous liquid
 167 when $\sigma = 0$. It then becomes clear that the pedal mucus system executes a
 168 loop, such as the one in Figure B.2(c). When the force acting on the mucus
 169 is small, the mucus is an elastic solid ($\sigma = 1$). When the force increases (A)
 170 and exceeds an upper threshold F_u , the mucus yields (B). The behavior of
 171 the mucus changes significantly, and it immediately becomes a viscous liquid
 172 ($\sigma = 0$). When the force decreases (C) below a lower threshold F_l , the mucus
 173 recovers its elasticity (D).

174 2.3. Equation of motion for adhesive locomotion

175 Considering the features mentioned above (muscular waves and rheology
 176 of mucus), the equation of motion for each segment can be written as follows:

$$m\ddot{x}_n = F_{n+\frac{1}{2}} - F_{n-\frac{1}{2}} - (1 - \sigma_n)\mu\dot{x}_n - \sigma_n\gamma(x_n - \bar{x}_n), \quad (3)$$

177 where m [kg] is the mass of each segment, and the constants μ [N·s/m]
 178 and γ [N/m] are the viscosity coefficient and elastic coefficient of the mucus,
 179 respectively. It is assumed that $F_{n-\frac{1}{2}} = 0$ if $n = 0$ and that $F_{n+\frac{1}{2}} = 0$
 180 if $n = N$. In this model, the viscoelastic behavior of mucus as friction is
 181 described by a modified Kelvin–Voigt model, where the variable σ_n represents
 182 the state of the mucus under the n th segment. In this model, it is assumed
 183 that the critical position of the n th segment at the moment when the mucus
 184 changes state from a viscous liquid ($\sigma_n = 0$) to an elastic solid ($\sigma_n = 1$), as
 185 in Figure B.2(c)D, is memorized as an anchoring position $\bar{x}_n$. In addition, to
 186 realize the hysteresis loop shown in Figure B.2(c), the variable σ_n is assumed
 187 to satisfy the following conditions:

$$\begin{aligned}
 &\text{if } \sigma_n = 1 \text{ and } |F_{n+\frac{1}{2}} - F_{n-\frac{1}{2}}| > F_u, \\
 &\quad \text{then } \sigma_n \text{ changes to } 0; \\
 &\text{if } \sigma_n = 0 \text{ and } |F_{n+\frac{1}{2}} - F_{n-\frac{1}{2}}| < F_l, \\
 &\quad \text{then } \sigma_n \text{ changes to } 1 \text{ and } \bar{x}_n \text{ is set to } x_n.
 \end{aligned} \quad (4)$$

188 Let $x_n = LW^{-1}\tilde{x}_n$ and $t = \omega^{-1}\tilde{t}$, where $\tilde{x}_n$ and $\tilde{t}$ are the dimension-
 189 less position and time, respectively. Then, we can obtain a system of non-
 190 dimensional equations when $n \neq 0, N$ as

$$\begin{aligned} \tilde{m}\ddot{x}_n = \tilde{\kappa} \left(\frac{\tilde{x}_{n+1} - \tilde{x}_n}{\tilde{l}_{n+\frac{1}{2}}} - \frac{\tilde{x}_n - \tilde{x}_{n-1}}{\tilde{l}_{n-\frac{1}{2}}} \right) + \tilde{q}(\dot{\tilde{x}}_{n+1} - 2\dot{\tilde{x}}_n + \dot{\tilde{x}}_{n-1}) \\ -(1 - \sigma_n)\tilde{\mu}\dot{\tilde{x}}_n - \sigma_n(\tilde{x}_n - \bar{\tilde{x}}_n), \end{aligned} \quad (5)$$

191 where some coefficients are assumed constant, $\kappa_{n+\frac{1}{2}} = \kappa$ and $q_{n+\frac{1}{2}} = q$,
 192 and dimensionless parameters are obtained as

$$\begin{aligned} \tilde{m} = m\omega^2\gamma^{-1}, \quad \tilde{l}_{n+\frac{1}{2}} = 1 + \alpha \sin(\tilde{t} - 2\pi W \frac{n}{N}), \\ \tilde{\kappa} = \kappa N(\gamma L)^{-1}, \quad \tilde{q} = q\omega\gamma^{-1}, \quad \tilde{\mu} = \mu\omega\gamma^{-1}. \end{aligned}$$

193 Similarly, the two mucus thresholds (yield point and healing point) can
 194 be represented in dimensionless form as

$$\tilde{F}_l = F_l W(\gamma L)^{-1}, \quad \tilde{F}_u = F_u W(\gamma L)^{-1}.$$

195 Now, the order of $\tilde{m}$ can be estimated at 10^{-9} that is vanishingly small
 196 compared with the other dimensionless coefficients, e.g., the order of the
 197 dimensionless viscosity $\tilde{\mu}$ is at 10^{-3} , so we can assume that the inertial force is
 198 negligible (see Supplement). This assumption is reasonable in the mechanism
 199 of locomotion for gastropods and their relatives. The dimensionless equations
 200 are then:

$$\begin{aligned} (1 - \sigma_n)\mu\dot{x}_n + \sigma_n(x_n - \bar{x}_n) \\ = \kappa \left\{ \frac{x_{n+1} - x_n}{l_{n+\frac{1}{2}}} - \frac{x_n - x_{n-1}}{l_{n-\frac{1}{2}}} \right\} + q(\dot{x}_{n+1} - 2\dot{x}_n + \dot{x}_{n-1}), \end{aligned} \quad (6)$$

where the tildes are omitted (as in later discussions) for simplicity. Equation (6) is temporally discretized using a finite difference method in order to perform numerical calculations. We confirmed that solutions to the resultant simultaneous equations always exist, because the tridiagonal matrix is diagonally dominant (see Appendix B). The simultaneous equations are solved easily using LU decomposition. In the next section, these simultaneous equations with time evolution are solved using numerical methods.

3. Results of numerical simulations

3.1. Numerical calculations

It is assumed that the initial state of the mucus under each segment is $\sigma_n = 1$ (elasticity), because the animals are adhering to the substratum when the locomotion begins. We can also estimate the scale of some physical quantities from previous research^{6,7,20,36} (see Supplement). First, the order of μ is estimated to be about 10^{-3} . In addition, that of F_u is also estimated to be about 10^{-3} for $W = 1.0$. In our simulations, we divided the foot into 50 segments ($N = 50$), which is sufficient to propagate a wave. The dimensionless parameters of the physical features are set as follows: $W = 1.0$, $\alpha = 0.5$, and $\mu = 0.005$. The parameter F_u ranges from 10^{-3} to 10^{-2} .

Figure B.4(a) shows chronological samples and Figure B.4(c) shows the spatiotemporal dynamics of a simulation using $F_u = 0.35 \times 10^{-2}$, $F_l = 0.001 \times 10^{-2}$, $\kappa = 1.0$, and $q = 0.005$. The mucus under each segment changes its state (viscosity or elasticity) from moment to moment due to the contraction and expansion of muscle. From the results in Figures B.4(a) and B.4(c), it seems that segments of expanded muscle are anchored. In other words, the

regions of contracted muscle move along the body.

Figure B.4(b) shows chronological samples, and Figure B.4(d) shows the spatiotemporal dynamics of a simulation using $F_u = 0.42 \times 10^{-2}$, $F_l = 0.001 \times 10^{-2}$, $\kappa = 1.0$, and $q = 0.005$. That is, the only change from Figures B.4(a) and B.4(c) is the value of F_u . Figure B.4(d) shows with perfect clarity that retrograde wave locomotion is achieved. In this case, it seems that anchoring occurs around the regions of muscle contraction in Figure B.4(b). Hence, the regions of muscle expansion move along the body. Figure B.4(e) is the result of plotting each phase of the natural length of the RTS when each segment is anchored. This result shows that a small change in the yield point can greatly change the phase of anchoring.

Figure B.5 shows the temporal alteration of a segment located in the middle of the body. The upper graphs show the average natural lengths of both sides of the RTS of the 25th segment, $l_{25-1/2}$ and $l_{25+1/2}$, and its average actual length. The lower graphs show the total force acting on the 25th segment, $F_{25+1/2} - F_{25-1/2}$. Panels (a) and (b) represent the cases of direct waves and retrograde waves, respectively. The anchoring clearly occurred in the elongated state of the spring in (a). By contrast, the anchoring occurred in the contracted state of the spring in (b). Although the force generated by one side increases when the difference between natural length and actual length increases, a segment is not able to move without a difference on both sides. Note that the mucus always yields from the left side of the body in the case of either a direct wave or a retrograde wave, as can be seen in Figures B.4(a) and B.4(b). Hence, it is reasonable to focus on the spring between the 24th and 25th segments when the mucus under the 24th segment

250 yields and becomes fluid. The spring is in the contracted state in the case of
 251 a direct wave and the elongated state in the case of a retrograde wave. It is
 252 found that the propulsive force is generated by pushing in the case of a direct
 253 wave. Conversely, the propulsive force is generated by pulling in the case of
 254 a retrograde wave. In a direct wave, the jump (B) of the hysteresis loop
 255 shown in Figure B.2(c) occurs at the positive value F_u , as confirmed by the
 256 graph of force in Figure B.5(a). Moreover, because the total force is positive
 257 when the segment is not anchored, the whole body can move rightward. By
 258 contrast, in a retrograde wave, the jump (B) of the hysteresis loop occurs at
 259 the negative value $-F_u$, as confirmed by Figure B.5(b). As the total force
 260 is negative when the segment is not anchored, the whole body can move
 261 leftward.

262 Figure B.6 is a velocity diagram that shows in detail the effect that some
 263 properties of mucus have on motion. Here, the velocity ratio R is calculated
 264 as the ratio of the velocity of the center of the body to the wave velocity.
 265 Based on previous knowledge^{20,36}, we define an efficient directional motion as
 266 when the absolute value of R is more than 0.1. We see in Figure B.6(a) that
 267 there exist parametric regions of F_u and F_l for achieving valid locomotion.
 268 Figure B.6(a) clearly shows that regions for both direct and retrograde waves
 269 exist. That is, Figure B.6(a) indicates that both F_u and F_l are properties
 270 of mucus that influence the motion of the body. In addition, this study
 271 examines the influence of the viscosity of mucus on locomotion. Figure B.6(b)
 272 is the result of calculations of R with respect to the viscosity of mucus μ for
 273 $F_u = 0.45 \times 10^{-2}$, $F_l = 0.0005 \times 10^{-2}$, $\kappa = 1.0$, and $q = 0.005$. We found that
 274 μ makes a significant contribution to locomotion. Our results indicate that

275 the direct wave appears when μ is either below a lower threshold or above
 276 an upper threshold. Comparing these two regions of the direct wave, R is
 277 larger when μ is smaller. The region of the retrograde wave exists between
 278 the two regions of the direct wave. The diagram shows that the direction
 279 of the body depends strongly on the viscosity of the mucus. The relation
 280 between the velocity ratio R and the average of the anchoring phase can be
 281 seen in Figure B.6(c). The natural length is greater (elongation) when the
 282 phase ($P = t - 2\pi Wn/N$) satisfies $\sin P > 0$. Conversely, the natural length
 283 is less (contraction) when $\sin P < 0$. The results show that the anchoring
 284 phase occurs in the state of elongation when the direct wave is chosen, and
 285 in the state of contraction when the retrograde wave is chosen (i.e., almost
 286 in antiphase with respect to the direct wave).

287 Now, we investigate the influence of muscle features on the style of loco-
 288 motion. Biologically, it would be an important finding if the physical features
 289 of muscle were to have implications for determining the direction of the body.
 290 Figure B.7(a) therefore shows the effects of muscle parameters. The param-
 291 eter κ corresponds to the stiffness of an active spring, and α represents the
 292 ratio of contraction and elongation. Figure B.7(a) illustrates that there is a
 293 parametric region of κ and α in which locomotion can be achieved by crawl-
 294 ing. Furthermore, the nature of the muscle clearly affects the direction of
 295 movement. Figure B.7(b), which is similar to Figure B.6(c), shows the re-
 296 sult of changing the anchoring phase while varying the parameters κ and α .
 297 The two styles of locomotion are realized by changing the anchoring phase
 298 in response to changes in the parameters. Moreover, the black lines in Fig-
 299 ure B.7(a) plot the range of the spring coefficient $r_{sc} (= 2\kappa\alpha/(1 - \alpha^2))$; i.e.,

the difference between the maximum and minimum values of the spring coefficient. The black lines are only drawn when valid locomotion is achieved; that is, when $0.8 \leq r_{sc} \leq 5.2$. We observe that when r_{sc} is relatively small, $0.8 \leq r_{sc} \leq 2.8$, effective locomotion can be realized by means of the retrograde wave as well as the direct wave. When r_{sc} is relatively large, $4.0 \leq r_{sc}$, the direct wave is the only feasible strategy.

4. Discussion and conclusions

The aim of this paper has been to theoretically verify that mutual interaction between muscular contraction and mucus can realize adhesive locomotion. Therefore, we built a mathematical model with two essential assumptions. The first was the active spring (RTS) and the multi-segment body for mimicking the propagation of a muscular wave, and the second was the hysteresis loop for describing changes in the nature of mucus. Our numerical simulations demonstrated that propulsive force adequate for locomotion can be generated by the interaction of muscular wave propagation and viscoelastic mucus. Under this mechanism, the mucus has a role in controlling the friction with the ground.

We first verified that the crawling locomotion is validly simulated by the mechanism: that is, by the mutual interaction between periodic muscular waves of the soft foot and the specific properties of the mucus. At first, the muscle begins to contract and expand periodically, in unison with the phase of the internal oscillators. The mucus under each segment is pulled and pushed depending on the tension induced by the muscular waves. When the tension (force) acting on the mucus becomes larger, the mucus changes to

324 a viscous liquid from an elastic solid working to fix the body to the substrate
325 (anchoring). Beyond this point, the body segments can move smoothly (slip-
326 ping). Both anchoring and slipping regions exist along the foot. Like the
327 muscular wave, these anchoring and slipping regions propagate.

328 Furthermore, two styles of locomotion, the direct wave and the retro-
329 grade wave, are obtained in our numerical simulations. The simple mechan-
330 ical difference between direct and retrograde waves was clarified by Jones
331 and Trueman⁴ after Lissmann¹³ and Miller^{1,15}. The simplified mechanism of
332 direct waves is as follows: the foot adheres to the substratum at maximum
333 extension; then, forward movement occurs when the foot is longitudinally
334 contracted and the contracted portion propagates forward. That is, migra-
335 tion of the center of gravity occurs in the contracted portion of the foot.
336 In contrast, the mechanism of retrograde waves is as follows: the foot is at-
337 tached along its length at its minimum extension; then, the foot is maximally
338 extended forward and the extended portion propagates backward. That is,
339 migration of the center of gravity occurs in the extended portion of the foot.
340 These previous mechanisms were not fundamental mechanisms but merely
341 described the appearance of each style of locomotion based on observations.
342 Our numerical results represent an important progression, as these existing
343 mechanisms were reproduced by considering the underlying principles.

344 Comparing the results of a mathematical model for peristaltic locomo-
345 tion³⁴ makes it easy to understand why these two styles of locomotion can
346 occur. Tanaka et al.³⁴ claimed that the peristaltic locomotion of both the
347 direct wave and the retrograde wave can be realized if the phase of anchor-
348 ing can be changed. Thus, in the simplest terms, it is necessary to vary the

349 anchoring phase in order to realize two styles of locomotion. Based on our nu-
350 merical calculations, we claim that it is possible to change the anchor phase
351 by changing only the properties of the mucus (Figures B.4(e) and B.6(c))
352 or the features of the muscle (Figure B.7(b)). Our study fully supports the
353 conclusions of Tanaka et al. However, we can also say that active control
354 of friction is not required in the case of spontaneous friction transitions by
355 mucus, unlike in the mechanism of peristaltic locomotion.

356 Figure 4 explains why the anchoring phase would change. What is sig-
357 nificant here is the condition of the foot when the jump (B) in Figure B.2(c)
358 occurs; i.e., the moment at which the mucus changes from elastic to viscous.
359 The force can be generated by pushing as well as pulling. In the case of a
360 direct wave, the jump (B) occurs in the segment of foot being pushed. Hence,
361 the mucus becomes a viscous liquid before this portion of foot reaches its full
362 contraction. Therefore, the elongated portions of the foot are anchored. By
363 contrast, in the case of a retrograde wave, the jump (B) occurs in the segment
364 of foot being pulled, and the mucus changes to a viscous liquid before this
365 portion of foot reaches its full elongation. That is, the contracted portions
366 of the foot are anchored.

367 Basically, the choice between two styles is uniquely determined by the
368 parameters F_l and F_u . However, we already know from our additional nu-
369 merical calculations that these two styles of locomotion coexist in the bound-
370 ary regions between direct and retrograde waves, as shown in Figures B.6(a),
371 B.6(b), and B.7(a). In this study, σ_n was initially set to 1 (elasticity) for
372 all n , because this is the condition in nature. Under this assumption, there
373 exist parametric regions where the style of locomotion suddenly changes. It

374 would be reasonable to consider that there are no such boundaries for para-
 375 metric regions of actual animals. From a mathematical perspective, however,
 376 the question is why the sign of the velocity reverses immediately when some
 377 parameter values are changed. This problem, which originates from the exis-
 378 tence of multiple solutions, should be analyzed by improving the description
 379 of the mucus from a discrete model to a continuous model, and by decreasing
 380 the degrees of freedom of the mass system to three. We will investigate this
 381 phenomenon, as a part of future work, by conducting a nonlinear stability
 382 analysis.

383 Finally, let us now consider our results in the context of the research by
 384 Chan et al.²¹. Our study partially supports their results, in that the loco-
 385 motion by direct wave can be achieved through interaction between muscular
 386 contractions and mucus. However, they concluded that spontaneous fric-
 387 tion transitions by mucus cannot produce locomotion by retrograde wave.
 388 Although we cannot say exactly why their conclusion differs from ours, we
 389 suggest a possibility based on Figure B.7(a). That is, their model (and
 390 robots) may impose the condition that the value of either α or r_{sc} is large.
 391 If this is true, we are in agreement with the result that only the direct wave
 392 is obtained. In their study, a mollusk-like flexible body might not have been
 393 considered, because they focused on the properties of mucus. They over-
 394 looked a significant factor: the properties of muscle contribute significantly
 395 to the choice of movement direction in the mechanism of spontaneous friction
 396 transitions by mucus. The two styles of locomotion may be realizable if a
 397 robot is made on the basis of our results. Our study would then serve as a
 398 guideline for the development of such robots.

399 In this study, one deficiency in our mathematical model is the assumption
400 that the recovery is the jump (D) shown in Figure B.2(c). Actually, the
401 recovery of elasticity should be performed slowly in comparison with jump
402 B. It is not yet clear how long the mucus needs to recover its elasticity. As
403 future work, we will build a mathematical model that considers a healing
404 time in the recovery process. Through an improved model, we will be able
405 to investigate how the recovery time affects the locomotion, and how long a
406 time can be valid for effective locomotion.

407 This study reinforces the assertion that mucus has an important role
408 in friction control for adhesive locomotion. Furthermore, we have obtained
409 new insights into the nature of how the mucus and muscles directly affect
410 the style of locomotion. Future experimental research into the yield point
411 of mucus and the ratio of muscle contraction in various species, as well as
412 mathematical investigations into energy efficiency, will reveal the background
413 of the evolutionary acquisition of locomotion strategies in gastropods and
414 related species.

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424 **Appendix A. Device for mimicking a flexible muscle**

425 It is reasonable to use an active spring to describe the flexible muscle of
426 a mollusk-like gastropod. A muscle has two phases (contraction and relax-
427 ation), and its self-driven movement is generated by the actin–myosin system
428 based on control signals. A spring that can alter its natural length in real
429 time is an active device; i.e., it can perform self-driven movement. It is taken
430 for granted that the device also moves passively, because it is a spring. Such
431 an idea has already been proposed in a mathematical model of movement
432 for slime mold³⁷ and earthworms³⁴. Moreover, analogous devices have been
433 developed in robotics, such as the real-time tunable spring (RTS) pioneered
434 by Umedachi et al.³⁵.

435 There are two types of active springs that change in natural length: one
436 is a hinged spring, as assumed in the model of Tanaka et al.³⁴, and the other
437 is a reeling spring with a motor, as used in this study. Essentially, there is
438 not much difference between these two devices, because each is self-driven
439 and describes a flexible body. The difference lies in the way that the natural
440 length is changed. In the case of a hinged spring, only the apparent length
441 is changed (by opening the angle of the hinge). By contrast, in the case of
442 a reeling spring with a motor, the actual length is changed. The description
443 of the force generated by a spring differs between hinged springs and reeled
444 springs, even if the natural lengths $l(t)$ [m] are similarly controlled as follows:

$$l(t) = l_0(1 + \alpha \sin \omega t), \quad (\text{A.1})$$

445 where l_0 [m], α , ω [Hz], and t [s] represent the average natural length,
 446 contraction ratio, wave frequency, and time, respectively. In the case of a
 447 hinged spring, the lengths of parts of the spring do not change, even though
 448 the apparent length does change. Hence, the force F_h [N] acting on segments
 449 generated by the spring is described as follows:

$$F_h(t) = \kappa_h(x_1 - x_0 - l(t)), \quad (\text{A.2})$$

450 where x_0 [m] and x_1 [m] are the position of segments connected by the
 451 hinged spring. In this case, κ_h [N/m] represents the spring constant.

452 In the case of a reeling spring with a motor, the force is slightly different
 453 from that in the case of a hinged spring. In general, a spring becomes softer
 454 as the natural length becomes greater. Therefore, in the case where the
 455 natural length can vary, it is reasonable to suppose that the spring constant
 456 will vary. That is, the spring constant will be inversely proportional to the
 457 natural length. Hence, the force F_r [N] generated by the spring is described
 458 as follows:

$$F_r(t) = \frac{\kappa_r}{l(t)}(x_1 - x_0 - l(t)). \quad (\text{A.3})$$

459 In this case, κ_r [N] represents the stiffness of the spring and is determined
 460 by its materials.

461 **Appendix B. Formulas for numerical calculations**

462 To perform the numerical calculations, the dimensionless equation (6) is
 463 discretized using a finite difference method that makes no assumption as to

464 $\kappa_{n+\frac{1}{2}}$ and $q_{n+\frac{1}{2}}$:

$$\begin{aligned}
& (1-\sigma_i^j)\mu\frac{x_i^j - x_i^{j-1}}{\delta t} + \sigma_i^j(x_i^j - \bar{x}_i^j) \\
&= \frac{\kappa_{i+\frac{1}{2}}}{l_{i+\frac{1}{2}}}(x_{i+1}^j - x_i^j - l_{i+\frac{1}{2}}) + q_{i+\frac{1}{2}}\left(\frac{x_{i+1}^j - x_{i+1}^{j-1}}{\delta t} - \frac{x_i^j - x_i^{j-1}}{\delta t}\right) \\
&\quad - \frac{\kappa_{i-\frac{1}{2}}}{l_{i-\frac{1}{2}}}(x_i^j - x_{i-1}^j - l_{i-\frac{1}{2}}) - q_{i-\frac{1}{2}}\left(\frac{x_i^j - x_i^{j-1}}{\delta t} - \frac{x_{i-1}^j - x_{i-1}^{j-1}}{\delta t}\right), \tag{B.1}
\end{aligned}$$

465 where δt denotes a time step and x_i^j is the position of the i th segment
466 at time j . The following simultaneous equations are obtained by simplifying
467 equation (B.1) in the case of $i \neq 0, N$:

$$\begin{aligned}
& -\left(\frac{\kappa_{i+\frac{1}{2}}}{l_{i+\frac{1}{2}}} + \frac{q_{i+\frac{1}{2}}}{\delta t}\right)x_{i+1}^j \\
& \quad + \left(\sigma_i^j + \frac{(1-\sigma_i^j)\mu + q_{i+\frac{1}{2}} + q_{i-\frac{1}{2}}}{\delta t} + \frac{\kappa_{i+\frac{1}{2}}}{l_{i+\frac{1}{2}}} + \frac{\kappa_{i-\frac{1}{2}}}{l_{i-\frac{1}{2}}}\right)x_i^j \\
& \quad - \left(\frac{\kappa_{i-\frac{1}{2}}}{l_{i-\frac{1}{2}}} + \frac{q_{i-\frac{1}{2}}}{\delta t}\right)x_{i-1}^j \tag{B.2} \\
&= -\kappa_{i+\frac{1}{2}} + \kappa_{i-\frac{1}{2}} + \sigma_i^j\bar{x}_i^j - \frac{q_{i+\frac{1}{2}}}{\delta t}x_{i+1}^{j-1} \\
& \quad + \frac{(1-\sigma_i^j)\mu + q_{i+\frac{1}{2}} + q_{i-\frac{1}{2}}}{\delta t}x_i^{j-1} - \frac{q_{i-\frac{1}{2}}}{\delta t}x_{i-1}^{j-1}.
\end{aligned}$$

468 As a special case, the simultaneous equations for the segments at the
469 end-points of the body are given as follows:

$$\begin{aligned}
& - \left(\frac{\kappa_{0+\frac{1}{2}}}{l_{0+\frac{1}{2}}} + \frac{q_{0+\frac{1}{2}}}{\delta t} \right) x_1^j + \left(\sigma_0^j + \frac{(1 - \sigma_0^j)\mu + q_{0+\frac{1}{2}}}{\delta t} + \frac{\kappa_{0+\frac{1}{2}}}{l_{0+\frac{1}{2}}} \right) x_0^j \\
& = -\kappa_{0+\frac{1}{2}} + \sigma_0^j \bar{x}_0^j - \frac{q_{0+\frac{1}{2}}}{\delta t} x_1^{j-1} + \frac{(1 - \sigma_0^j)\mu + q_{0+\frac{1}{2}}}{\delta t} x_0^{j-1}.
\end{aligned} \tag{B.3}$$

$$\begin{aligned}
& \left(\sigma_N^j + \frac{(1 - \sigma_N^j)\mu + q_{N-\frac{1}{2}}}{\delta t} + \frac{\kappa_{N-\frac{1}{2}}}{l_{N-\frac{1}{2}}} \right) x_N^j - \left(\frac{\kappa_{N-\frac{1}{2}}}{l_{N-\frac{1}{2}}} + \frac{q_{N-\frac{1}{2}}}{\delta t} \right) x_{N-1}^j \\
& = \kappa_{N-\frac{1}{2}} + \sigma_N^j \bar{x}_N^j + \frac{(1 - \sigma_N^j)\mu + q_{N-\frac{1}{2}}}{\delta t} x_N^{j-1} - \frac{q_{N-\frac{1}{2}}}{\delta t} x_{N-1}^{j-1}.
\end{aligned} \tag{B.4}$$

470 Solutions of these simultaneous equations always exist, because the tridiag-
 471 onal matrix is diagonally dominant.

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Figure B.1: Modeling of the ventral foot of gastropods. (a) Multi-segment model that generates muscular wave propagation. Each segment is connected by a real-time tunable spring (RTS) and a damper. (b) Image sketch of RTS³⁵ for simple mimicking of a muscle.

Figure B.2: Modeling of pedal mucus. (a) Pedal mucus under each segment has two states: elastic solid and viscous liquid. (b) Outline of one of the results in the experiments of Denny and Gosline^{6,7}. The parameter F_u corresponds to yield stress, and this is the threshold at which the property of the mucus changes from elasticity to viscosity. The stages A, B, C, and D correspond to those in a hysteresis loop, respectively. (c) Internal hysteresis loop of pedal mucus. The parameter F_l corresponds to the stress when the mucus is healing, and this is the threshold of the change from viscosity to elasticity. The variable σ represents the state of the mucus. When $\sigma = 1$, the mucus behaves as an elastic solid. If the external force on a segment increases (A) and reaches F_u , the mucus yields (B) and behaves as a viscous liquid with $\sigma = 0$. If the external force on a segment then decreases (C) below F_l , the mucus recovers its elasticity (D) and has $\sigma = 1$.

Figure B.3: Image sketch of mucus dynamics under stress.

Figure B.4: Results of simulations with our model. (a), (b) Chronological samples of simulations. In each foot segment, the green regions are expanded muscle and the yellow regions are contracted muscle in comparison to the average length of the RTS. In the mucus under each foot segment, the light blue regions are viscous liquid (slipping) and the dark blue regions are elastic solid (anchoring). The black and red asterisks show the positions of the center at the initial time and subsequent times, respectively. (a) Direct wave for $F_u = 0.35 \times 10^{-2}$, $F_l = 0.001 \times 10^{-2}$, $\kappa = 1.0$, and $q = 0.005$. The waves of contraction propagate in the positive direction and the whole body moves in the same direction. (b) Retrograde wave for $F_u = 0.42 \times 10^{-2}$, $F_l = 0.001 \times 10^{-2}$, $\kappa = 1.0$, and $q = 0.005$. The waves of expansion propagate in the positive direction, but the whole body moves in the opposite direction. (c), (d) Time series plots of the position of each segment using the same parameters as for (a) and (b). (e) Phase plots of $l(t)$, the natural length of the RTS, when the mucus behaves as an elastic solid (anchoring); i.e., the phase of the adhesive region of the foot is indicated. The red stripes are the results with the same parameters as for (a), and the green stripes are with the same parameters as for (b).

Figure B.5: Temporal plots of natural length and actual length of RTS (upper) and force acting on the 25th segment (lower). The yellow regions correspond to the times of anchoring; i.e., the times when the state of the mucus under the 25th segment was an elastic solid ($\sigma = 1$). (a) Direct wave ($F_u = 0.40 \times 10^{-2}$, $F_l = 0.0005 \times 10^{-2}$, $\kappa = 2.0$, and $q = 0.05$). The jump (B) of mucus in the hysteresis loop, as shown in Figure B.2(c), occurs when the force becomes greater than F_u . (b) Retrograde wave ($F_u = 0.45 \times 10^{-2}$, $F_l = 0.0005 \times 10^{-2}$, $\kappa = 2.0$, and $q = 0.05$). The jump (B) occurs when the force becomes less than $-F_u$.

Figure B.6: Effects of properties of mucus on the velocity ratio R for $\kappa = 1.0$ and $q = 0.005$. (a) Color plot of R with respect to F_u and F_l . If the absolute value of R is greater than 0.1, the region is colored blue for a direct wave ($R \geq 0.1$) or red for a retrograde wave ($R \leq -0.1$). (b) Plots of R with respect to the viscosity of mucus μ . (c) Relation between the anchoring phase and R in the case where the absolute value of R is greater than 0.05. The red plots are obtained by varying F_u and F_l , whereas the green plots are obtained by varying μ .

Figure B.7: Effect of muscle features on velocity ratio R . (a) Color plots of R with respect to κ and α . The result is for $F_u = 0.45 \times 10^{-2}$, $F_l = 0.0005 \times 10^{-2}$, and $q = 0.005$. If the absolute value of R is greater than 0.1, the region is colored blue for a direct wave ($R \geq 0.1$) or red for a retrograde wave ($R \leq -0.1$). The black lines are plots of r_{sc} , the range of the spring coefficient of the RTS, and the white arrow indicates the positive direction. The range plotted with the black lines is $0.8 \leq r_{sc} \leq 5.2$. (b) Relation between the average anchoring phase and R in the case where the absolute value of R is greater than 0.05. The plots show results obtained by varying κ and α .