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Cite as: J. Chem. Phys. **156**, 134903 (2022); https://doi.org/10.1063/5.0084490 Submitted: 06 January 2022 • Accepted: 16 March 2022 • Published Online: 05 April 2022

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#### ABSTRACT

Living cells on a substrate with mechanical inhomogeneities often migrate along or against the mechanical gradient, i.e., mechanotaxis, which inspires us to ask how biomimetic cells without biochemical signaling processes respond to environmental inhomogeneity. Here, we perform computer simulations to study the migration of a 2D active colloidal cell (ACC), which consists of active particles enclosed by a passive vesicle, in a heterogeneous environment composed of two adjoining uniform regions with different attributes (influencing the persistent length of the active particle). We find that the ACC can migrate unidirectionally across the interface separating the heterogeneous region and behave tactically. Interestingly, the tactic motion of the ACC is qualitatively different from that of the constituent active particles themselves. In addition, the ACC may also experience a directed drift along the interface of the heterogeneous environment. The tactic behavior of the ACC can be explained by analyzing the pressure distribution on the cell membrane exerted by the enclosed active particles. The findings provide insights into understanding the taxis of biological cells and designing biomimetic cells with environment-sensitive capabilities.

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#### I. INTRODUCTION

Active matter refers to an ensemble of self-propelled units that individually convert their stored or environmental energy into motility or mechanical force.<sup>1–3</sup> Prominent examples include molecular motors walking along a microtubule,<sup>4,5</sup> swimming bacteria,<sup>6,7</sup> self-phoretic colloids,<sup>8,9</sup> macroscopic active granular particles,<sup>10–12</sup> and so on. Because of violating time-reversal symmetry at the single-particle level, active matter is inherently out-of-equilibrium, allowing for diverse exotic phenomena.<sup>10,13–18</sup>

The cell, the basic constituent unit of life, is one of the most important kinds of active particles and can actively sense the surrounding environment and self-adaptively change its shape and motion. The morphology and migration of cells mainly depend on the interactions between the cell membrane, intracellular active components, and adhering substrate or extracellular matrix, which have attracted considerable interest.<sup>19–27</sup> In particular, when a gradient of a certain external stimulus is present, a cell will deform,

polarize, and eventually migrate along or against the gradient. This directed migration is referred to as taxis,  $^{28,29}$  e.g., the chemical gradient-induced chemotaxis<sup>30–32</sup> and the durotaxis<sup>33–36</sup> and hapto-taxis<sup>37</sup> caused separately by the nonuniformities of substrate rigidity and adhesion.

Due to the existence of complex biochemical signaling processes, it is challenging to extract the microscopic physical mechanism of the cell dynamics. Disregarding the signaling processes, active colloidal cells (ACCs) with simple physical interactions are proposed to mimic the shape transformation and migration of a cell in a homogeneous environment.<sup>38–50</sup> In the minimal model, the cell membrane is described as a vesicle, while the intracellular active contents are mimicked by active particles. A recent work<sup>48</sup> revealed a significant increase in the magnitude of the ACC membrane fluctuations, compared with the case of passive vesicles. By tuning the persistent length,<sup>42,44,45,47,49,50</sup> chirality,<sup>38,41</sup> and packing fraction<sup>39,41,42,50</sup> of the encapsulated active particles, the ACC can display a plethora of different shapes, such as capsule, dumbbell, and ruffles in 2D and bola, dumbbell, and tethering in 3D. On the other hand, the simulation results show that the motion behavior of the ACC significantly depends on the aspect ratio, packing friction, activity, and interactions of the enclosed active particles.<sup>39,40</sup> Even in an experiment, a macroscopic artificial cell, consisting of rodlike robots enclosed in a circular arena made of thin paper, is shown to have a clear correlation between its deformation and locomotion.<sup>43</sup> Besides the studies of the individual ACC, the assembly structures of the ACC have also been investigated.<sup>46</sup>

All the above work about the ACC only considers a uniform environment, so it is of great interest to study the dynamics of the ACC in an inhomogeneous environment, especially the possible tactic migration of the ACC. Recently, a variation of ACC "flexocytes" has been employed to simulate the cell motion on a patterned substrate with a smoothed-out step friction<sup>51</sup> and to study the deflection of the ACC trajectory crossing the interface of the heterogeneous substrate. However, it is yet unclear whether and how the ACC in a heterogeneous environment experiences a directed migration.

In this paper, we study the migration of a two-dimensional ACC in a heterogeneous environment with step-type physical attributes. The active particles enclosed in the ACC are taken as circular swimmers,<sup>52-55</sup> which can effectively exploit the inhomogeneity by reciprocally crossing the interface between the heterogeneous regions. Our results show that the ACC can exhibit a distinct tactic motion, whose velocity depends on the properties of the environment and active particles. It not only unidirectionally migrates across the interface between the two regions but also experiences a directed displacement along the interface owing to the broken chiral symmetry. The migration behavior of the ACC can be understood based on the pressure distribution on the cell membrane exerted by the enclosed active particles. For comparison, we also quantify the density distribution of the active particles on the same inhomogeneous substrates in the absence of the membrane constraint. Interestingly, the tactic motion of the constituent active particles themselves significantly differs from that of the ACC, highlighting the vital role of the cell membrane in ACC migration.

#### **II. SIMULATION SYSTEM AND METHOD**

The ACC is composed of an external membrane described by a semiflexible passive ring and intracellular circular swimmers (chiral active particle), as sketched in Fig. 1(a). The circular swimmer is modeled as a disk of diameter  $\sigma$ , subjected to a self-propelling force *F* and torque *M*. We set the number of the active particles  $N_a = 100$  and the packing fraction  $\rho = 0.3$  to avoid clustering. Different active particles interact via the Weeks–Chandler–Andersen potential,  $U(r) = 4[(\sigma/r)^{12} - (\sigma/r)^6] + 1$  if  $r < 2^{1/6}\sigma$  and U(r) = 0otherwise.

The passive ring with a mean radius  $R_v = \sigma \sqrt{N_a/4\rho}$  is constructed by a bead-chain model, consisting of  $N_b = 57$  beads of diameter  $\sigma$ , in which the total bond potential of the passive ring is the summation of harmonic potential between any two adjacent beads, i.e.,

$$U_s = \frac{k_s}{2} \sum_{i=1}^{N_b} \left( \left| \boldsymbol{R}_i \right| - l_s \right)^2$$



**FIG. 1.** (a) Sketch of the active colloidal cell on an inhomogeneous substrate. The ACC consists of a passive vesicle (green) and chiral active particles enclosed inside. The left and right half regions of the environment have different attributes, reflected in the position-dependent quantity A(x). (b) The quantity A(x) as a function of the *x* coordinate, with  $A_I = 2A_r$  remaining fixed.

Here,  $k_s$  is the spring stiffness,  $l_s = 2R_v \sin(\pi/N_b)$  is the equilibrium bond length, and  $\mathbf{R}_i = \mathbf{r}_{i+1} - \mathbf{r}_i$  is the bond vector. We choose  $k_s \sigma^2/k_B T = 80\,000$  to prevent the active particles from escaping out of the ACC and suppress the fluctuation of the ring perimeter. Moreover, the ring also suffers from a bending potential to maintain its round shape,

$$U_b = rac{k_b}{l_s} \sum_{i=1}^{N_b} \left[1 - \cos( heta_i - heta_0)
ight],$$

with  $k_b$  being the bending constant, taken as  $k_b/k_B T \sigma = 500$  unless otherwise specified,  $\theta_i$  being the angle between two neighboring bond vectors  $\mathbf{R}_{i-1}$  and  $\mathbf{R}_i$ , and  $\theta_0 = 2\pi/N_b$  being the equilibrium angle.<sup>56</sup> In addition, there exist the Weeks–Chandler–Andersen interactions between nonbonding beads and between the bead and active particles, similar to the case in the literature.<sup>44,49</sup>

The motion of the chiral active particle *i* with its orientation  $\mathbf{n}_i = [\cos \theta_i, \sin \theta_i]$  (with respect to the *x* axis) obeys the extended overdamped Langevin equation<sup>57</sup> (the Ito convention),

$$\gamma(\mathbf{r}_i)\dot{\mathbf{r}}_i = F(\mathbf{r}_i)\mathbf{n}_i - \nabla_{\mathbf{r}_i}U_t + \gamma(\mathbf{r}_i)\nabla D(\mathbf{r}_i) + \sqrt{2k_BT\gamma(\mathbf{r}_i)}\boldsymbol{\xi}_i,$$

$$\gamma'(\mathbf{r}_i)\dot{\theta}_i = M(\mathbf{r}_i) + \sqrt{2k_BT\gamma'(\mathbf{r}_i)}\boldsymbol{\xi}_i,$$
(1)

with  $U_t$  being the steric interactions between circular swimmer *i* and all other particles (including the swimmers and membrane beads),  $\gamma$ and  $\gamma'(\gamma' = \frac{1}{2}\sigma^2\gamma$  unless otherwise stated) being separately the translational and rotational friction coefficients, and  $D(\mathbf{r}_i) = k_B T / \gamma(\mathbf{r}_i)$ denoting the translational diffusion coefficient with the thermal energy  $k_B T = 1$ . Here,  $\xi$  and  $\zeta$  refer to the Gaussian-distribution white noise of zero mean and unit variance. In general, all physical quantities are the function of the particle position due to the inhomogeneous environment. Particularly, an extra term  $\gamma(\mathbf{r}_i) \nabla D(\mathbf{r}_i)$ is needed to correctly address the multiplicative noise arising from the nonuniform friction.<sup>57</sup> On the other hand, the motion of the constituent bead of the passive membrane is described only by the translational overdamped Langevin equation (1), with a vanishing self-propelled force  $F(\mathbf{r}_i) = 0$  and the total steric interaction  $U_t$  containing the bond potential  $U_s$  and bending potential  $U_b$ . Note that in our model, the hydrodynamic effects are neglected because we focus on the migration of 2D ACC placed at a substrate, which implies that

the momentum is not conserved due to the friction contributed by the substrate. Additionally, the recent experiments<sup>48,49</sup> have shown that the hydrodynamic interactions between the active particles and membrane are not significant for the dynamics of "wet" ACC, presumably due to the permeability of membrane to the water molecule. Hence, we here consider a "dry" active system.

The simulation system has a dimension of  $L_x = L_y = L = 50\sigma$ , with periodic boundary conditions. The environmental inhomogeneity is prescribed in the *x* direction by setting a positiondependent physical parameter A(x). The quantity A(x) may be the self-propelled force or torque and the translational or rotational friction coefficient, resulting in a spatially dependent persistent length of the enclosed active particle. Without loss of the generality, a smoothed-out step function is chosen for A(x), namely,  $A(x) = A_l$  for the left half region and  $A(x) = A_r$  for the right half region, with  $A_l = 2A_r$  fixed, as shown in Fig. 1(b). In the simulations, four different types of inhomogeneities are separately considered: the self-propelled force, torque, translational and rotational friction coefficients. For each inhomogeneity, other quantities are fixed at their reference values  $F\sigma/k_BT = 60$ ,  $M/k_BT = 5$ ,  $\gamma/\gamma_0 = 1$ , and  $\gamma'/\gamma'_0 = 1$  ( $\gamma_0 = 100$  and  $\gamma'_0 = \sigma^2 \gamma_0/3$ ), unless otherwise stated.

The mass center of the ACC is initially placed at the interface of the heterogeneous environment, and the enclosed active particles are initially randomly distributed inside the ACC. Once all particles of the ACC enter the left or right region of the substrate, one simulation run completes. The migration velocity  $v_x$  ( $v_y$ ) is quantified as the ratio of the displacement of the ACC mass center along the x (y) direction to the time and is averaged over 32 different realizations. The obtained migration velocity of the ACC is normalized by the self-propelled velocity of an isolated active particle,  $v_{t0} = F/\gamma$  with  $F = 60k_BT/\sigma$  and  $\gamma = \gamma_0$ .

#### **III. RESULTS AND DISCUSSION**

Inhomogeneous self-propelling force. We first study the migration of the ACC in an inhomogeneous environment with the selfpropelling force F being spatially heterogeneous, i.e., A(x) = F(x). The migration velocity of the ACC crossing the interface of the heterogeneous region along the x and y direction,  $v_x$  and  $v_y$ , are plotted in Figs. 2(a) and 2(b), respectively. It is clearly shown that the ACC migrates to the high-activity region (against the x direction), accompanying a downward migration along the interface. The value of  $v_x$ becomes maximum for a large self-propelling force  $F_l$  (denoting the value of F in the left half region) and small self-propelling torque M, while  $v_y$  reaches its maximum at a large  $F_l$  and moderate M. The migration behavior of the ACC can be understood according to the pressure distribution on the vesicle exerted by enclosed chiral active particles. In the following, we qualitatively analyze this pressure distribution based on the swim pressure of noninteracting linear active particles,

$$P = \frac{F^2}{2\gamma D'}\rho_0,\tag{2}$$

with  $D' = k_B T/\gamma'$  being the rotational friction coefficients and  $\rho_0$  being the bulk density of active particles. Here, the Brownian pressure is not considered because its magnitude is much smaller than the swim pressure. In the presence of chirality, *P* decreases with the



**FIG. 2.** Reduced migration velocity map of the ACC (a)  $v_x/v_{t0}$  and (b)  $v_y/v_{t0}$  in  $(M/k_BT, F_i\sigma/k_BT)$  plane for the case of inhomogeneous self-propelled force. (c) The mechanism of the net displacement of chiral active particles along the vertical dividing line of the heterogeneous region. (d) Density distribution of the chiral active particles without the cell membrane as a function of the x coordinate, with  $F_{1\sigma}/k_BT = 120$  and  $M/k_BT = 1$ . (e) The density map of the active particles within a fixed membrane whose center is located at the dividing line of the heterogeneous environment with  $F_{1\sigma}/k_BT = 120$  and  $M/k_BT = 100$  and  $M/k_BT = 1000$  and  $M/k_BT = 1000$  and  $M/k_BT = 10000$  and the maps of  $v_X/v_{10}$  for (h) soft and (l) rigid vesice membranes.



**FIG. 3.** Reduced migration velocity map of the ACC (a)  $v_x/v_{l0}$  and (b)  $v_y/v_{l0}$  as functions of  $F\sigma/k_BT$  and  $M_l/k_BT$  for the case of inhomogeneous self-propelling torque. (c) Sketch of the coordinate system for a chiral active particle in the vesicle, where the red solid arrow indicates the self-propelling direction of the particle and the vertical dashed line denotes the interface between the heterogeneous regions.  $v_l$ ,  $v_n$ , and  $\Omega$  separately denote the tangential, normal, and the orbital angular velocity of the drift flow. (d) Density distribution of the naked active particles without the vesicle as a function of the x coordinate, with  $F\sigma/k_BT = 120$  and  $M_l/k_BT = 3$ . (e) The density map of the active particles within a fixed membrane whose center is located at the dividing line of the inhomogeneous region with  $F\sigma/k_BT = 120$  and  $M_l/k_BT = 7$ . (f) The corresponding local density profile  $\rho(r)$  of active particles at four regions as a function of distance *r* from the membrane bead. (g) The density map and (h) corresponding local density profile for  $F\sigma/k_BT = 120$  and  $M_l/k_BT = 1$ .

driving torque on the active particle, since increasing M can weaken the accumulation of active particles near the vesicle membrane.<sup>58</sup>

Because the number density of the active particles is inversely linearly proportional to the self-propelling force, <sup>59–62</sup> Eq. (2) means that the local pressure on the vesicle membrane located at the left region is higher than that in the right region. This pressure difference can be verified by the typical density map and local density profile of active particles within the vesicle (taking  $F_l\sigma/k_BT$ = 120 and  $M/k_BT$  = 3 as an example), as separately shown in Figs. 2(e) and 2(f). Obviously, the density of the active particles at the left region of the vesicle is higher than that of the right region, implying a larger swim pressure acting on the left region of the vesicle. The pressure difference increases with F and decreases with the driving torque. As a result, the ACC migrates against the x direction, and the maximum magnitude of  $v_x$  occurs at large  $F_l$  and small M, as shown in Fig. 2(a). On the other hand, the orbital radius  $R_{\omega} = F\gamma'/M\gamma$  (the persistent length) of the circle swimmer at the left region is larger than that at the right region owing to the inhomogeneous F, which on average results in a net downward displacement of the counterclockwise rotating swimmer when it crosses the interface of the two regions, as illustrated in Fig. 2(c). Hence, the chiral active particles more easily accumulate at the bottom of the vesicle, which is confirmed by the density map and local density profile of active particles [see Figs. 2(e) and 2(f)], causing a vertical downward velocity component of the ACC. Nevertheless, for very small or large M, the net vertical displacement of the active particle crossing the interface is negligible, separately due to vanishing chirality or vanishing orbital radius. Therefore, a marked  $v_y$  happens for moderate torques, as displayed in Fig. 2(b).

For comparison, Fig. 2(d) plots the steady density distribution of the chiral active particles without the vesicle (the passive ring) under the same condition, showing that the active particles themselves more likely stay in the region with a low activity, which is consistent with previous work<sup>59,61–64</sup> and is in stark contrast to the case of the ACC. If various *F* are assumed to correspond to different fuel concentrations, then the ACC and the naked active particles will have opposite chemotaxis. This indicates that the confinement from the vesicle membrane plays a critical role in the directed migration of the ACC.

Furthermore, we investigate the effect of the membrane bending rigidity on the migration of the ACC by changing the bending constant  $k_b$ . We find that in the present parameter range the soft  $[k_b/\sigma k_B T = 5$ , Figs. 2(g) and 2(h)] and rigid  $[k_b/\sigma k_B T = 5000$ , Figs. 2(i) and 2(l)] ACCs possess qualitatively the same migration behavior as the ACC of medium rigidity  $[k_b/\sigma k_B T = 500$ , Figs. 2(a) and 2(b)]. The change in  $k_b$  only has a quantitative influence in  $v_x$  and  $v_y$ , which can be understood as follows: In our parameter range, the density is moderate and the persistent length of particles is relatively small, which make the ACC maintain roughly round shape,<sup>39,41,42,44</sup> regardless of the vesicle being soft and hard. As a result, the vesicle fluctuations are similar, and hence, the bending rigidity of the vesicle dose not qualitatively influence the migration of the ACC. Hence, we choose  $k_b/\sigma k_B T = 500$  in the rest simulations.

Inhomogeneous self-propelling torque. We next study the movement of the ACC in an environment with inhomogeneous selfpropelling torque, i.e., A(x) = M(x). Figures 3(a) and 3(b), respectively, plot the corresponding maps of  $v_x$  and  $v_y$ . In this case, the ACC migrates to the low-torque region (the right half region), in



**FIG. 4.** Maps of the reduced migration velocity (a)  $v_x/v_{l0}$  and (b)  $v_y/v_{l0}$  in the  $(M/k_BT, \gamma_l/\gamma_0)$  parameter space for the ACC on a substrate with an inhomogeneous translational friction coefficient. (c) The density distribution of the chiral active particles without the vesicle membrane on the same substrate as in (a), with  $\gamma_l/\gamma_0 = 1$  and  $M/k_BT = 1$ .

contrast to the case of nonuniform self-propelling force. This can be intuitively understood as follows: The heterogeneous self-propelling torque cannot produce a spatially inhomogeneous density distribution of the naked chiral active particles, as shown in Fig. 3(d), such that the cell membrane located in the low-M area is subjected to a higher swimming pressure (longer persistent length), which is directly supported by the density map and local density profile of active particles within the vesicle [see Figs. 3(e) and 3(f)]. Thus, this pressure difference drives the ACC to move rightward. Moreover, given a constant F, a moderate  $M_l$  (representing the value of M in the left half region) can induce a larger difference in the pressure between the left and right parts of the ACC membrane. This is because too small torque renders the persistent motion of the chiral active particles indistinguishable between two confined heterogeneous regions, in which the persistent length  $(R_{\omega} = F\gamma'/M\gamma)$ of the active particle is larger than the cell size  $(R_v \simeq 9.1\sigma)$ , while too large torque trivially disables the persistent motion of the active particle. Hence, the maximum  $v_x$  occurs at moderate  $M_l$ , as shown in Fig. 2(a).

Interestingly, for a relatively large F,  $v_y$  shows a clear direction reversal as the torque changes, implying the existence of two competitive mechanisms contributing to the vertical displacement of the ACC. When M is relatively strong, namely,  $R_{\omega} = Fy'/My$  smaller than or comparable to the cell size  $R_v$ , the similar scenario [Fig. 2(c)] responsible for the nonzero  $v_y$  in Fig. 2(b) can lead to a positive  $v_y$  of the ACC [Fig. 3(b)] because the active particles are more transported to the top region of the vesicle, as shown in Figs. 3(e) and 3(f).

On the other hand, if M is weak, namely,  $R_{\omega}$  much larger than the cell size, a different mechanism will dominate. In this situation,

the active particles all cling to and move counterclockwise along the circular vesicle boundary [Fig. 3(c)] due to its large persistent length. This results in a tangential drift flow along the membrane with the flow velocity  $v_t = F \sin \psi / \gamma$  ( $\psi = \theta - \alpha$  denoting the relative angle between the orientation of the active particle and the local normal of the vesicle), and the corresponding orbital angular velocity of the flow is  $\Omega = v_t/R_v$ . When reaching the steady state, the relative angle  $\psi$  keeps stationary, namely,  $\Omega$  equals to the spin angular velocity of the active particle, yielding  $\Omega = \omega = M/\gamma'$ . Thus, the steady-state drift flow velocity becomes  $v_t = MR_v/\gamma'$ . As sketched in Fig. 3(c), the torque M at point A is larger than that of point B, so the drift flow velocity at point A is larger, thus leading to a density gradient of the active particles from A to B. This density gradient, in turn, generates a diffusive current in the opposite direction to the drift flow in the interval [A, B]. A similar analysis indicates that the drift and diffusive currents have the same direction in the interval [C, D]. Furthermore, since the mean drift flow velocity in the two intervals is the same, the total flow velocity is smaller in [A, B] than in [C, D]. Due to the mass conservation of the boundary flow, the particle density is higher in the interval [A, B] than in [C, D], which is confirmed by the density map and local density profile of particles, as respectively, shown in Figs. 3(g) and 3(h). Consequently, the interval [A, B] suffers from a larger pressure, which drives the ACC to move downward.

Inhomogeneous translational friction coefficient. We now consider the migration of the ACC on a substrate with an inhomogeneous translational friction coefficient  $\gamma$ , i.e.,  $A(x) = \gamma(x)$ . The results are plotted in the space of self-propelling torque M and  $\gamma_1$ (indicating the value of  $\gamma$  in the left half region) [see Figs. 4(a) and 4(b)]. In Fig. 4(a), the presence of the maximum migration



**FIG. 5.** Maps of reduced migration velocity (a)  $v_x/v_{t0}$  and (b)  $v_y/v_{t0}$  of the ACC on a substrate with an inhomogeneous rotational friction coefficient, in a plane of the reduced self-propelled force  $F\sigma/k_BT$  and rotational friction coefficient  $\gamma'_1/\gamma'_0$ . (c) The density distribution of the chiral active particles without the vesicle in the same environment as in (a), with  $\gamma'_1/\gamma'_0$  = 5 and  $F\sigma/k_BT$  = 120.

velocity  $v_x$  at small M and  $y_1$  seems to be similar to that of Fig. 2(a) if we translate the abscissa of both maps into the self-propelling velocity. However, the order-of-magnitude difference in the maximum  $v_x [v_x/v_{t0} \sim 6.5 \times 10^{-2} \text{ in Fig. 2(a) and } v_x/v_{t0} \sim 6.0 \times 10^{-3} \text{ in}$ Fig. 4(a)] implies their migration mechanisms could be different. As stated before, the migration of the ACC arises from the pressure difference between the left and right parts of the vesicle. Since  $\rho_0 \propto 1/v_0 = \gamma/F$ , <sup>59</sup> Eq. (2) means that the swimming pressure is uniform in the present inhomogeneous environment, and hence, the net  $v_x$  of the ACC should vanish. This apparent inconsistence between the simulation and theory presumably originates from the fact that Eq. (2) is not precise for nonideal active particles. A proper explanation for the slow migration of the ACC needs to consider the pressure of interacting active particles. Note that the rectification of active particles, which can also lead to a directed drift of active particle,<sup>64</sup> is not the reason for this present slow migration of the ACC because of the absence of the ratchet-shaped motility.

In addition, the map of  $v_y$  in Fig. 4(b) resembles that in Fig. 2(b) as they share similar mechanisms. For comparison, the density distribution of the naked chiral active particles in the absence of vesicle is provided in Fig. 4(c), with  $\gamma_l/\gamma_0 = 1$  and  $M/k_BT = 1$ . This density difference between the two regions again indicates that the migration directions of the ACC and the active particles themselves are opposite.

Inhomogeneous rotational friction coefficient. Next, we consider a substrate with an inhomogeneous rotational friction coefficient, namely,  $A(x) = \gamma'(x)$ . For the chiral active particle, the effect of the heterogeneous  $\gamma'$  is very similar to that of the heterogeneous selfpropelling torque as both of them influence the rotational angular velocity  $\omega$  (noting that  $\omega = M/\gamma'$ ). It can therefore be expected that the ACCs in such two types of nonuniform environments share similar migration behavior and the underlying mechanism. Figures 5(a) and 5(b) show the maps of  $v_x$  and  $v_y$  in the plane of the dimensionless self-propelling force  $F\sigma/k_BT$  and reduced rotational friction coefficient  $\gamma'_1/\gamma'_0$ , which are indeed consistent with Figs. 3(a) and 3(b), respectively. Figure 5(c) shows that the corresponding density of the active particles without the vesicle is uniformly distributed, which also agrees with the result in Fig. 3(d).

ACC filled with linear active Brownian particles. We have analyzed the migration behaviors of the ACC filled with chiral self-propelled particles in various types of inhomogeneous environments. If the self-propelling torque is zero, the active particles will become the linear active Brownian particles (linear ABPs) and the vertical migration velocity of the ACC will vanish due to the symmetry. To be complete, we also compute the migration velocity  $v_x$ of the ACC filled with linear APBs and the density distribution of the corresponding naked active particles in various inhomogeneous environments, as provided in Figs. 6 and 7.

Figures 6(a) and 6(c) display the  $v_x$  of the ACC containing the linear APBs in the environments with inhomogeneous *F* and *y*, respectively. By comparing with Figs. 2(a) and 4(a) for the cases of chiral active particles, it is obvious that taking M = 0 does not qualitatively change the migration behavior of the ACC in the gradient direction, as well as the distribution of the naked active particles. For the case of inhomogeneous y', the ACC migrates to the high-y'region (the left half region) [Fig. 7(a)] and the density distribution of the naked linear APBs is spatially uniform [Fig. 7(b)], similar to the results in Fig. 5 due to the same mechanism. Nevertheless, in



**FIG. 6.** The migration velocity of the ACC enclosing the linear APBs. (a)  $v_x/v_{t0}$  as a function of the self-propelling force for the inhomogeneous-*F* environment, and (b) the corresponding density distribution of the linear ABPs with  $F_{I\sigma}/k_BT$  = 120. (c)  $v_x/v_{t0}$  as a function of the inhomogeneous- $\gamma$  environment and (d) the corresponding density distribution of the linear ABPs with  $\gamma_I/\gamma_0 = 1$ .



**FIG. 7.** (a) Map of reduced migration velocity  $v_x/v_{t0}$  for the ACC on the same inhomogeneous substrate as Fig. 5, except for M = 0. (b) Density distribution of linear ABPs without the vesicle on the same substrate in (a), with  $y'_1/y'_0 = 1$  and  $F\sigma/k_BT = 120$ .

the parameter range under consideration, the maximum  $v_x$  occurs at small  $\gamma'_l$ , instead of at middle  $\gamma'_l$  as the case of  $M \neq 0$  [see Fig. 5(a)]. This difference arises from the fact that for the same rotational diffusion  $(k_B T/\gamma')$ , the persistent length of the circle swimmer is smaller than that of the linear APB owing to the nonzero M such that the linear ABP with a small  $\gamma'$  is roughly equivalent to the circle swimmer with a middle  $\gamma'$ . When further reducing  $\gamma'$ , the  $v_x$  of the ACC containing the linear APBs will trivially start to decrease, since the persistent length, hence the swimming pressure, becomes too small.

#### **IV. CONCLUSION**

By means of computer simulations, we investigate the migration behaviors of an ACC, consisting of chiral active particles enclosed by a passive vesicle, in various spatially heterogeneous environments. The spatial heterogeneities include nonuniform selfpropelling force/torque and translational/rotational friction coefficient, which all lead to an inhomogenous persistent length of the enclosed active particles. The results reveal that the ACC not only unidirectionally migrates along the gradient of the persistent length but also experiences a directed drift along the interface of the heterogeneous environment due to breaking chiral symmetry. All the results can be intuitively explained based on the pressure distribution on the cell membrane exerted by the active particles. Remarkably, the migration of the naked active particles in such heterogeneous environments is qualitatively different from the corresponding ACC, highlighting the essential role of the passive vesicle in the transport of the ensemble of active particles. In addition, we show that the ACC enclosing the linear ABPs shares similar migration behaviors in the environmental gradient as the case of the ACC containing the chiral active particles. Our findings could provide insights into understanding the taxis of biological cells and designing biomimetic cells with environment-sensitive capabilities and also propose a new way to collectively transport active particles.

#### ACKNOWLEDGMENTS

We thank Hui Li for helpful discussions. We acknowledge the support of the National Natural Science Foundation of China (Grant Nos. 11874397, 11674365, and 11974044) and the Strategic Priority Research Program of Chinese Academy of Sciences (Grant No. XDB33000000).

#### AUTHOR DECLARATIONS

#### **Conflict of Interest**

The authors have no conflicts to disclose.

#### DATA AVAILABILITY

The data that support the findings of this study are available within the article.

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