Volume exclusion and elasticity-driven directional transport: a model inspired by bacterium motility

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Abstract

We present a model to capture the role of strong attractive interaction and volume exclusion inducing super-diffusive transport of small systems in a thermal atmosphere. We characterize such systems on the basis of three dynamic regimes at three different time scales: at very small and large scales the system is diffusive and at the intermediate scales it is super-diffusive. Our model is derived on the basis of some general knowledge about bacterium motility and identifies volume exclusion as a fundamental contributor to the origin of driven directional transport.

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It is widely believed that the basis of driven directional motion of various motor proteins, bacteria, etc. as observed in living systems or in similar environments, is the Brownian Ratchet (BR) mechanism [1–4]. The BR mechanism essentially requires the assistance of noise, a drive which can be periodic in time and directionless over space, and a potential which must have broken reflection symmetry (polar) at a small (microscopic) scale [1]. All these ingredients are pretty much available in the biological world. The biological systems normally perform at room temperatures and thermal noise is always present. The tubular tracks on which the motors move are made up of polar units, and actin monomers are also polar in nature by polymerizing which some bacteria move. The motor proteins and other bio-systems are invariably driven, i.e. are associated with intermittent energy supply to drive them out of equilibrium which is a prerequisite of having directional motion in any system. There have been attempts to model the motion of the bacterium Listeria monocytogenes (LM) [5] and similar bio-mimetic systems [7, 18], which move by polymerizing an actin tail behind them, following the BR paradigm [8–10]. But experimental facts go very much against the basic requirements of the BR theory of such systems. It has been found that the bacterium remains bound to its tail with a strong elastic force (approx. 40 pN) during the course of its motion. The bacterium practically undergoes 20 times less Brownian motion than similar objects in the same environment because of this strong binding [11]. These observations practically rule out the scope of the BR mechanism...
in the conventional form as rectifying Brownian motion to explain the origin of directional transport in actin polymerization-based motile systems like LM.

Following the experimental revelations of limitations of the BR mechanism to account for the origin of motility, a host of activities have been initiated in order to modify the model and to capture the general principle at work in such systems. People are also looking at the microscopic details of the biological and biochemical mechanisms at work. A comprehensive review of such models with the details of what happens at the microscopic scales has been given by Dickinson (see [12] and references therein). An alternative theory of filament end-tracking motors [13], where the actin filament does not require to remain unattached to the membrane of the bacterium for monomer addition, is in keeping with the experiments [11]. It also provides a very reliable microscopic model which has got substantial experimental support subsequently [14–17]. The existence of the strong force of attraction between the bacterium and its tail has inspired observations of the deformation of the membrane and the membrane fluctuations in correlation with resulting motility, and has been extensively explored in [18, 19]. In [18], it has been shown that, depending upon the curvature of the deformed surface of vesicles, there are retractile and propulsive forces while the actin tail remains firmly attached to the vesicle surface. In [19], a substantial deformation of similar vesicles has been detected in a direction orthogonal to the direction of motion while doing force measurements at the actin–membrane interface. An interesting detailed numerical study based on a dendritic nucleation model which looks at the microscopics in detail at a somewhat coarse-grained molecular level also provides interesting insights [20].

A minimalistic model has been proposed by Broeck et al [21], improving on the concept of the intrinsic ratcheting, where the symmetry is broken internally within the system itself. In [22–27], the coupling of an internal degree of freedom with external fields is considered for the symmetry breaking whereas in [21] the internally broken symmetry does not appear as a result of interactions with the environment. In this paper, we also consider a similar structured model with the symmetry broken internally (in a general way) which can account for any of the above-mentioned intrinsic ratchet mechanisms. Here, our main emphasis is on discovering and illustrating the role of volume exclusion as an essential requirement for having elastic forcing to result in directional motion. In doing that, we will develop a very general model being motivated by LM-type systems and only keeping in mind some very gross features such as the existence of elastic interactions, head–tail structure, spreaded tail, etc to systematically understand the role of an important physical constraint—the volume exclusion—which so far has remained unnoticed in this context. An important aspect, as to having directional transport in multidimensional space, which has not been given much attention in the ratchet models is the suppression of the rotational degrees of freedom and how that can be correlated to the gross structural properties of the moving system. In this work, we mainly focus on that to understand the role of attractive interaction and volume exclusion giving rise to directional transport where the drive is basically isotropic. We will show an exactly solvable model in one dimension (1D) to conclusively demonstrate the essential role of volume exclusion in keeping microscopic broken symmetry reflect on macroscopic scales. Then we would numerically extend this model to 2D to confirm the generality of the exact observations in 1D. Its important to note that, within the conventional BR mechanism where the whole system is taken as a point particle, it is impossible to assess the role of volume exclusion and that is why a minimalistic model with an internal structure is needed.

The general result that we get on the basis of the present model, which mimics an LM-type structured object, is that the strong attractive force along with volume exclusion can make it move super-diffusively over a large time scale. If one considers time scales bigger than this range, one eventually observes the system to behave diffusively with an enhanced
diffusivity. There are also smaller scales of time than this intermediate super-diffusive regime where the system shows diffusive motion. This smaller time scale diffusion is an artefact of the system having structures. The fact that different parts of the system can undergo thermal fluctuations, before experiencing appreciable restoring stress, reflects on the existence of this smallest time scale diffusion. In the intermediate time scales, over which the motion is super-diffusive, a correlation is maintained between the orientations of the moving system which do not very often change due to internal resistance to rotational degrees of freedom. We argue that the motile objects like LM directionally operate in this intermediate temporal regime. The transition between different diffusive regimes is a subject of investigation for a number of related systems and in the present context [28] is interesting. The content of the paper is arranged in the following way. In section 1 we put forward the exact analytic calculation for the 1D version of the model. Section 2 uses the knowledge of section 1 to extend the model to 2D and explains the numerical details. In section 3 we present the results of the numerical simulation of the model in 2D. We conclude with a discussion of the present results and comparisons of those with the known facts of LM motions in section 4.

1. 1D model

In 1D, let us consider a model system consisting of two particles connected by a spring. This system when subjected to thermal (white) noise at a particular temperature would come to equilibrium and eventually would never show any directional motion. To drive the system out of equilibrium let us consider that one of the particles has its instantaneous velocity fed back to it just to disturb the fluctuation–dissipation relation that ensures the equilibrium. Application of this velocity feedback is a very general way of driving the system out of equilibrium which in practice can play the role of a variety of forcing that drives the system out of equilibrium as has been considered explicitly in [21]. We are not interested here in investigating the response of the system in relation to the variety of driving mechanisms; we would rather look at the general properties of such driven systems to understand the cooperative working of the minimal ingredients causing directed transport. Note that the instantaneous velocity feedback is also not introducing any directional bias into the forcing. So with the velocity feedback in place, the model will look like

\[
\dot{x}_1 = -\alpha (x_1 - x_2) + \beta \dot{x}_1 + \eta_1 \\
\dot{x}_2 = -\alpha (x_2 - x_1) + \eta_2.
\]  

(1) \hspace{1cm} (2)

Here, \(\alpha\) is the force constant of the spring, \(\beta\) is the feedback coefficient, i.e. a measure of the strength of the velocity feedback. The white noises \(\eta_i\)s have an average \(\langle \eta_i \rangle = 0\) and the second moment \(\langle \eta_i(t_1)\eta_j(t_2) \rangle = 2T \delta_{ij} \delta(t_1 - t_2)\), where the Boltzmann constant \((k_B)\) has been absorbed by fixing the unit of temperature. It is interesting to note that, at \(\beta = 0\), the second moment of the noise can be expressed in terms of \(\alpha\) by adjusting the temperature to explicitly manifest the fluctuation–dissipation relation for the system. A nonzero \(\beta\) breaks this relationship and makes the system go out of equilibrium. The presence of the nonzero \(\beta\) serves another purpose for us, namely breaking the symmetry. For the system to show directional motion in 1D there are two directions for it to move in, to make it take up one of them, the symmetry has to be broken which is achieved by the feedback as well. Now we want to see if the symmetry that has been broken at a microscopic scale, i.e. at the scale of the object which would supposedly move, indeed shows up at global scales at which we expect to measure the directional motion of this model object. In what follows we will always keep \(\beta\) small, in fact \(\beta < 1\), keeping in mind that we are in the overdamped regime of the dynamics. Consideration
of a large $\beta$ would require an inertial term to be taken into account which we do not want to consider in the present context. Similarly, to remain safe within the overdamped regime, we would consider a small $\alpha$. A large $\alpha$ means a smaller characteristic time scale of the relevant dynamics. At that small time scale of the dynamics the overdamped approximation would break down because the damping is an average quantity which requires some time to be felt. For the present model, within its regime of validity, one may consider the two particles to remain in contact with two different heat baths of different temperatures. Similar models have been a subject of intensive investigation for quite some time now [29–31].

Let us change the coordinates of the system and go to the internal coordinates $Z = x_1 - x_2$ and the centre of mass (CM) coordinate $X = (x_1 + x_2)/2$. The model would now be rewritten as

\[
\dot{Z} = -\frac{\alpha(2 - \beta)}{1 - \beta}Z + \xi_Z \\
\dot{X} = -\frac{\alpha\beta}{2(1 - \beta)}Z + \xi_X.
\]

In the above equations, the averages of the noise terms $\xi_i$ are clearly zero and their second moments are $\langle \xi_Z(t_1)\xi_Z(t_2) \rangle = DT_1(1 - \beta)^2$ and $\langle \xi_X(t_1)\xi_X(t_2) \rangle = \frac{D_1}{2T} \delta(t_1 - t_2)$. Equation (3) represents an equilibrium dynamics and we can readily get the probability distribution of the internal coordinate as $P_{eq}(Z) \propto \exp\left(-\frac{\alpha(2 - \beta)}{1 - \beta}Z^2\right)$ for $x_1 > x_2$ due to volume exclusion. For example, if we consider the elastic collision of particles the $Z$ distribution would remain Gaussian and for other collisions there might be deviation from Gaussianity. However, the general result of having a nonzero velocity will hold good in all the cases just because of restricting $Z \geq 0$. Thus, the average internal span $\langle Z \rangle_{eq} = \sqrt{\frac{2T D_1(1 - \beta)}{\pi\alpha(2 - \beta)}}$ immediately gives us, from equation (4), an expression for the average velocity of the CM of the system as

\[
\langle \dot{X} \rangle = -\frac{\alpha\beta}{2(1 - \beta)}(Z)_{eq} = -\frac{\alpha\beta}{2(1 - \beta)} \sqrt{\frac{2T D_1(1 - \beta)}{\pi\alpha(2 - \beta)}}.
\]

The above expression clearly shows, with $\beta \neq 0$, the system would have a nonzero average velocity. Thus, the symmetry broken at the microscopic scale is being reflected at macroscopic scales due to volume exclusion and being driven out of equilibrium. In this connection, a previous work in [27] carried out on mirror symmetry breaking using internal coordinates and exploration of dynamical phases of a similar model is worth mentioning. It is important to mention that the present model, the way it has been conceived, provides an exact analytic result for the velocity of the system unlike the other minimalistic intrinsic ratchet model [21] which despite being minimal in nature gives a perturbative solution for such an average velocity up to the first order in the expansion.

A particular advantage for the system being in 1D is that symmetry once broken would always remain and would not be statistically averaged out over time because the system does not have any rotational degrees of freedom. So a straightforward extension of this model in 2D is bound to fail. One has to think of a differently structured object in 2D, which, due to its very structural properties, can actually suppress the rotational degrees of freedom and thus help broken symmetries at smaller scales reflect on a larger scale. We would like to keep the
basic ingredients of the model such as the strong attraction between parts, volume exclusion, etc. intact in the 2D model as well. In fact, relation (5) also shows that the average velocity is proportional to the strength of the attractive interaction and we recognize the attractive interaction as an important ingredient. Moreover, the experimental observation of LM having a strong attractive interaction between its head and the tail encourages us to think of a model in 2D which is structurally similar to LM and preserves the basic ingredients of our 1D model.

2. 2D model

Keeping in mind the head–tail structure of LM, in 2D we propose a three-body model consisting of three particles (say). The tail of the system consists of two particles which are energetically favoured to remain at a distance (which is tunable) from each other. The third particle, which represents the head of the system, is strongly attracted by spring force towards the other two particles constituting the tail (see the schematic diagram in figure 1). In the absence of any noise the head will stay at the middle of the tail, but in the presence of the noise there will be fluctuations from this position, and the system, on average, would get a triangular shape. To drive the system out of equilibrium we again put an instantaneous velocity feedback on the head of the system. With all these in place, the model looks like

\[
\begin{align*}
\dot{x}_1 &= -\frac{\alpha}{1 - \beta} (x_1 - x_2) - \frac{\alpha}{1 - \beta} (x_1 - x_3) + \frac{\eta_1 \cos \theta_1}{1 - \beta}, \\
\dot{y}_1 &= -\frac{\alpha}{1 - \beta} (y_1 - y_2) - \frac{\alpha}{1 - \beta} (y_1 - y_3) + \frac{\eta_1 \sin \theta_1}{1 - \beta}, \\
\dot{x}_2 &= \alpha (x_1 - x_2) - \left(1 - \frac{\gamma}{\sqrt{(x_2 - x_3)^2 + (y_2 - y_3)^2}}\right) (x_2 - x_3) + \eta_2 \cos \theta_2, \\
\dot{y}_2 &= \alpha (y_1 - y_2) - \left(1 - \frac{\gamma}{\sqrt{(x_2 - x_3)^2 + (y_2 - y_3)^2}}\right) (y_2 - y_3) + \eta_2 \sin \theta_2, \\
\dot{x}_3 &= \alpha (x_1 - x_3) + \left(1 - \frac{\gamma}{\sqrt{(x_2 - x_3)^2 + (y_2 - y_3)^2}}\right) (x_2 - x_3) + \eta_3 \cos \theta_3, \\
\dot{y}_3 &= \alpha (y_1 - y_3) + \left(1 - \frac{\gamma}{\sqrt{(x_2 - x_3)^2 + (y_2 - y_3)^2}}\right) (y_2 - y_3) + \eta_3 \sin \theta_3.
\end{align*}
\]  

(6)

In this 2D model, \(x_1, y_1\) is the centre of the head, the spring constant of the attractive force between the head and the tail is \(\alpha\), the feedback constant is \(\beta\) and the equilibrium separation between the particles in the tail is \(\gamma\). The noises \(\eta_i\) have been applied in such a way that the thermal force remains isotropic and that is why we picked up \(\theta_i\) randomly between the range \(0–2\pi\). All \(\eta_1, \eta_2, \eta_3\) represent the Gaussian white noise. The volume exclusion would be effectively taken by considering that none of the particles can cross the line joining the other two as if all the particles remain tightly tethered to the other two and do not allow any passage through them. Mathematically, this can be achieved by demanding that the quantity \(Q = (x_1 - x_2)(y_1 - y_3) - (x_1 - x_3)(y_1 - y_2)\) would never change sign. If we apply the same analytic procedure as we have done in 1D, i.e. go to the CM and internal coordinates, we will readily see that the average velocity of the CM is again proportional to the average internal coordinate \(\langle V \rangle\) which is a vector from the centre of the tail to the head of the system. But the similar analysis, as in 1D, cannot be done because the volume exclusion constraint is non-holonomic. This non-holonomic constraint makes it extremely difficult (if not impossible) to solve this problem analytically. That is why we will take here the numerical route to investigate
Figure 1. Schematic diagram of the model. Following deviations in the position of the head $(x_1, y_1)$, on either sides of the central position, the direction of the resultant restoring force due to unequal stretching of the sides has been qualitatively represented by the arrows. The central vector, from the CM of the tail to the head, is $\vec{V}$ which determines the direction of motion of the system.

this model and our goal would be to keep this $\vec{V}$ directionally correlated over an appreciable period of time to see directional transport of the system.

To have the constraint in place while evolving the system numerically, we would consider every particle to undergo a reflection, when it tries to cross the line joining the other two and would find out the new positions of all the three particles (consistent with the constraint) from the momentum and energy conservation equations. If such a situation, where the constraint is violated, does not arise, there is no question of going into all these complications. In this process, the particles are considered of the same mass, and the moment of inertia of the two particles connected by a line is that of a dumbbell. Consider the situation when the head (particle 1) hits the line joining the particles on the tail (base line say) with a velocity $u = u_\parallel + u_\perp$ where $u_\parallel$ is the component of $u$ parallel to the base line and $u_\perp$ is the component of $u$ perpendicular to the same base line (from now on all the parallel and perpendicular notations would mean parallel and perpendicular to this line). After suffering reflection, the velocity of particle 1 becomes $v'_1 = v'_\parallel + v'_\perp$, the velocity of the CM of the tail is $v''_\perp$ and the angular velocity of the tail about its CM is $\omega$. Let us also consider that particle 1 has hit the tail at a distance $X$ ($X \leq R$) from its CM and the spread of the tail is $2R$. In such a situation, the momentum conservation gives us

\[
\begin{align*}
    u_\parallel &= v'_\parallel \\
    u_\perp &= -v'_\perp + v''_\perp \\
    u_\perp X &= -v'_\perp X + 2R^2\omega.
\end{align*}
\]

The energy conservation results in the relation

\[
|u|^2 = |v'|^2 + 2|v''_\perp|^2 + 2R^2\omega^2.
\]

We can solve these four equations for the four unknowns, namely $v'_\perp$, $v'_\parallel$, $v''_\perp$, and $\omega$, and that would give the corrections for the positions of the three particles when such a reflection happens to keep the volume exclusion constraint in place. Note that the consideration of this perfectly elastic collision is there to simplify the process of imposing the constraint. We assert that inelasticity would not be in conflict with the generality of the result we will arrive at in the next section. However, the role of inelasticity can later be explored as a specific issue to understand one of the variants of the present model. Another point regarding the limitations
of the present way of imposing the constraint is worth noting—in the simulations we are restricted to take not very large values of $\alpha$ and $\beta$ and not very small value of $\gamma$ so as to keep $\omega$ sufficiently small. Otherwise, the tail will rotate so much that the relative orientations of particles 2 and 3 making the tail, with respect to particle 1, would change and that would again violate the constraint. Nevertheless, we will have a fairly large scale of the parameters mentioned above while following the present scheme of computations to establish the role of elasticity and volume exclusion in producing directional transport.

In figure 1 (the schematic diagram of the model), when the constraint is in place, the thermal fluctuations would on average make the system take the shape of an isosceles triangle. Any deviation of this shape would stretch sides in such a way that the resulting restoring force will try to bring the CM of the tail-to-head vector $\vec{V}$ towards its previous orientation. The origin of this restoring force is the attraction between the head and the tail and one can easily qualitatively understand that the strength of the restoring force should increase with the force constant $\alpha$. This restoring force is responsible for the suppression of the rotational degrees of freedom of the system. But when the volume exclusion is violated, the system undergoes such a dramatic change in its internal structure that $\vec{V}$ cannot be restored to its previous direction and the motion of the system should undergo a drastic irreversible change in directions. Moreover, a wider tail, i.e. a wider base of the triangular system, should prevent an abrupt change in the direction of motion of the system by simply making the volume exclusion apply more frequently and we guess, at this point, to register enhanced directionality in the motion of the system as the width of its tail increases. Thus, we qualitatively understand by looking at the model that strong attractive interactions at least from two different directions between the head and the tail might go against the requirements of the BR model but are instrumental in the suppression of the rotational degrees of freedom of the system and facilitate the average directional motion.

3. Results of the simulation

The system does not show any directional motion when the constraint is not in place. Figure 2(a) shows the space covered by the system (CM has been plotted) over an interval of $10^7$ time steps each step size being 0.0001 in arbitrary units. The spring constant $\alpha = 1.0$, the noise strength $\eta = 0.001$, the feedback constant $\beta = 0.99$ and the width of the tail $\gamma = 0.1$. To have an estimate of how far the system moves compared to the system size one should use the tail width as a reference unit and that shows the system is practically undergoing structural fluctuations sitting at the same place. A dramatic change in the transport occurs when we apply the volume exclusion keeping all other parameters the same. Figure 2(b) shows the trajectories of the system as it evolves over the same period of time with volume exclusion on. To show that the degree of directionality of the average motion of the system indeed increases with the width of the tail, in figure 2(c) and (d) we have plotted the trajectories of the system when $\gamma$ is equal to 0.01 and 0.05 (all other parameters are the same and of course the volume exclusion is there) and we can notice the gradual increase in spread of the system with $\gamma$.

Suppression of the rotational degrees of freedom is clearly manifesting in the system having longer stretches of directional motion with lesser number of turnarounds. At a very large time scale, the motion would definitely be diffusive with an enhanced diffusivity. However, over a range of intermediate time scales, the motion as appears from the nature of the trajectories is probably ballistic. This intermediate time scale is obviously selected by the structural details of the model system. In the case of the bacterium LM one can argue that the size of the cell which the bacterium invades is finite with respect to the size of the bacterium; such an intermediate time scale of effective directional motion would be quite
useful in avoiding frequent collisions with the cell boundaries. Moreover, the diffusive motion at a larger time scale would actually help LM in exploring the whole volume inside the cell for nutrition or whatever. Thus, the model reveals a clear dynamical motive of the structural properties of the actin polymerization propelled bacterium.

In figure 3(a) and (b) we have plotted the directional correlation $C$ of the system without and with volume exclusion, respectively. A vector has been drawn from the CM of the system at $t = t_0$ to $t = t_0 + 1000$ and the correlations between the angles that all such vectors make with the initial one have been numerically calculated for $10^6$ such vectors sequentially appearing over the time of evolution. Without feedback, the correlation falls to zero after showing a peak in the negative direction. This negative peak is an artefact of the model. Since the head is strongly attracted by the tail it would on average regularly change sides through the base line in the absence of the volume exclusion constraint and that gives rise to this peak on the negative side at a characteristic time. However, in figure 3(b) we see a very long range correlation in the average directions of motion of the system and that explains the origin of the intermediate time scale at which the system follows an almost straight path. It is interesting to note that, up to the time where figure 3(a) shows a peak on the negative side, the correlation in figure 3(b) is substantially maintained and only after that it rapidly falls. Every time the system attempts a violation of the volume exclusion it gets reflected back and the restoring forces then come into play to keep the directions of motion correlated. However, with every such reflection, the tail of the system also gets translated and rotated in producing some extra deviation to the central vector $\vec{V}$ to which the direction is to be restored and that is why the correlation falls beyond this time scale appreciably. This fact indicates that, probably, inelastic collisions between the head and the tail or some more spatial stability of the tail would be more effective in preserving the directionality. In the case of LM motion, the tail being an extended actin mesh-work in space is more stable which could always contribute more to the directional correlations.

To understand the present scenario even more clearly, we have plotted (figure 4) the log of the root mean square distance $D$ of the system from its position at $t = 0$ ($\sqrt{\langle (x(t) - x(0))^2 \rangle}$) against the log of time $t$ for three different $\alpha$ values (1.0, 2.0 and 3.0) when the volume

![Figure 2](image-url)
exclusion is on and have compared that with the case when the volume exclusion is absent ($\alpha = 1.0$). When the volume exclusion is absent (call this graph 1) the model system shows three distinct regimes. The first part over a very short length scale is almost diffusive (exponent $\sim 0.45$). This part represents the internal fluctuations of the components of the system before it starts feeling appreciable restoring force. This part should be manifested irrespective of the volume exclusion being there or not and figure 4 clearly demonstrates that. In graph 1, the middle apparently flat part is due to the negative peak on the correlation plot which shows that there is a regular direction reversal, and hence, enhanced suppression of the average motion. At even higher time scales the system eventually starts going diffusive may be due to some rare events that effectively give it some translations. With the volume exclusion on, in this middle regime of time scales, the system shows very much super-diffusive (almost ballistic) transport due to the long directed average stretches of the trajectories we have seen in figure 2. As has been argued before, the transport of the system eventually becomes diffusive at very large time scales. It is interesting to note that with higher $\alpha$, i.e. stronger attractive force between the head and the tail, the rms deviation $D$ of the system would be enhanced by a constant factor since the higher $\alpha$ graphs are lying above practically with the same slope.

Figure 3. Temporal correlations $C$ of directions of motion plotted against time. In (a) it is without volume exclusion and in (b) the plot is the same as with volume exclusion employed.
4. Discussions

The present model, being guided by the essential structural features of LM, reveals a fundamental role of elasticity and volume exclusion in enhancing directional transport of driven micro-systems. It puts forward an alternative scenario to the BR mechanism. The essential role of strong attraction between the head and the tail of LM can be understood as required for the suppression of rotational degrees of freedom, whereas the presence of this strong attraction entirely goes against the requirements of the BR model for such systems. The role of the width of the tail in general is also manifested in enhancing the directed transport.

The transport properties of such systems are clearly characterized by three distinct time scales over which the motions are diffusive, super-diffusive and diffusive, respectively. Qualitatively, in the case of LM, the diffusive regime which manifests internal fluctuations up to the limit the system starts feeling too much of restoring force could help make room for polymerization to take place. In the case of the bacterium LM this regime probably can be tracked in the fluctuations of the membrane near the tail where a whole lot of experimental work is happening [18, 19]. The intermediate regime of the super-diffusive transport is the one that makes the system move directionally. This directional transport is enhanced by the stronger attractive interaction and the wider tail. The dynamical motive of having such a structure is having the directional transport at relatively smaller time scales and diffusive transport at larger time scales. We propose that the identification of the three regimes of motion in the case of LM or similar systems can conclusively prove the validity of the generality of such a driven-transport mechanism.

In trying to understand the origin of directed transport for LM-like systems, the role of elasticity and specially volume exclusion has emerged to be central. The volume exclusion is such a naturally occurring obvious fact that we often overlook its role. However, a clear understanding of the role of volume exclusion in the directed transport would prove extremely
useful in designing small machines. The principle ingredients in designing a class of such micro-motors, as per our present analysis, are a head attracted by a tail at least from two different directions and effective volume exclusion. Such objects would also be interesting to investigate in passive transports because the origin of directionality is totally by the prevention of rotational degrees of freedom and not directly through the forcing, and the object is not structurally isotropic. So passive transport might result in enhanced diffusivity for such objects. We very much hope that the understanding of the present mechanism would be useful in direct applications and engineering of microscopic motile objects.

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