

**Stepping molecular motor amid Lévy white noise**

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We consider a model of a stepping molecular motor consisting of two connected heads. Directional motion of the stepper takes place along a one-dimensional track. Each head is subject to a periodic potential without spatial reflection symmetry. When the potential for one head is switched on, it is switched off for the other head. Additionally, the system is subject to the influence of symmetric, white Lévy noise that mimics the action of external random forcing. The stepper exhibits motion with a preferred direction which is examined by analyzing the median of the displacement of a midpoint between the positions of the two heads. We study the modified dynamics of the stepper by numerical simulations. We find flux reversals as noise parameters are changed. Speed and direction appear to very sensitively depend on characteristics of the noise.

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**I. INTRODUCTION**

Since the late 1980s it has become possible to follow and manipulate moving motor proteins at a molecular level [1]. More recently, such motor proteins have become the moving parts in actual nanotransport machines [2]. In eukaryotic cells the motor protein kinesin is responsible for the transport of organelles and vesicles filled with chemicals. This motor protein literally walks along a biopolymer called “microtubule” as it is fueled by the conversion of adenosine triphosphate (ATP) into adenosine diphosphate (ADP) and inorganic phosphate. The microtubule filaments are periodic structures of a distinct polarity, different at each end.

In a minimal model it is possible to reconstruct the motion of a motor protein on a biopolymer as just the motion of a Brownian particle on an array of dipoles. In such a minimal model the ATP hydrolysis causes the motor to have a fluctuating charge and/or charge distribution. If the array of dipoles is anisotropic, then these nonequilibrium fluctuations will make the motor drift through a “ratchet” mechanism [3–11]. Typically, one assumes that the overall force acting on the particle is a superposition of the Gaussian thermal noise with another periodic or stochastic force due to the ATP hydrolysis [9]. In those cases all moments of

the distribution of the noisy force exist, and the existence of moments of the distribution of the particle’s velocity is guaranteed.

However, as it has been documented in numerical and analytical studies [12–14], the minimal setup for directed transport can also be obtained when taking just the periodic anisotropic potential (see Fig. 1) with added symmetric Lévy noises. Here the term Lévy noise,  $L(t)$ , is used to denote a natural extension of a standard (Gaussian) Brownian-Wiener process [15–17], which includes (a) a general family of stochastic processes with stationary independent increments whose (b) probability distribution belongs to the class of infinitely divisible distributions and satisfies the stability (self-similarity) criterion, i.e.,  $L(\sigma t) \sim \sigma^{1/\alpha} L(t)$  with the stability exponent  $\alpha \in (0, 2]$ . The latter property reflects invariance of the probability density of a random variable under convolution and can be easily rephrased in terms of the Fourier transform of the corresponding probability density function. In analogy to the white Gaussian noise, which is formally represented as the time derivative of the Wiener process, the general Lévy white noise can be defined as the time derivative of the symmetric Lévy process,  $\zeta_L(t) = \dot{L}(t)$ . Asymptotic (tail) properties of the probability distribution function (PDF) of the increments  $\Delta L(t) = L(t+h) - L(t)$  are governed by the stability index  $\alpha$ , i.e.,  $p(l) \sim 1/(|l|^{\alpha+1})$ . Unlike Gaussian noises, Lévy processes may contain random jump discontinuities of arbitrary size (loosely, the intensity measure of its Poissonian jumps [14] is proportional to  $|l|^{-\alpha-1} dl$ ) and therefore are well adapted to account for pulsatory or discrete behavior of natural signals.

It is now known that Lévy noise is useful in understanding the behavior of many biological systems, like bacteria [18],

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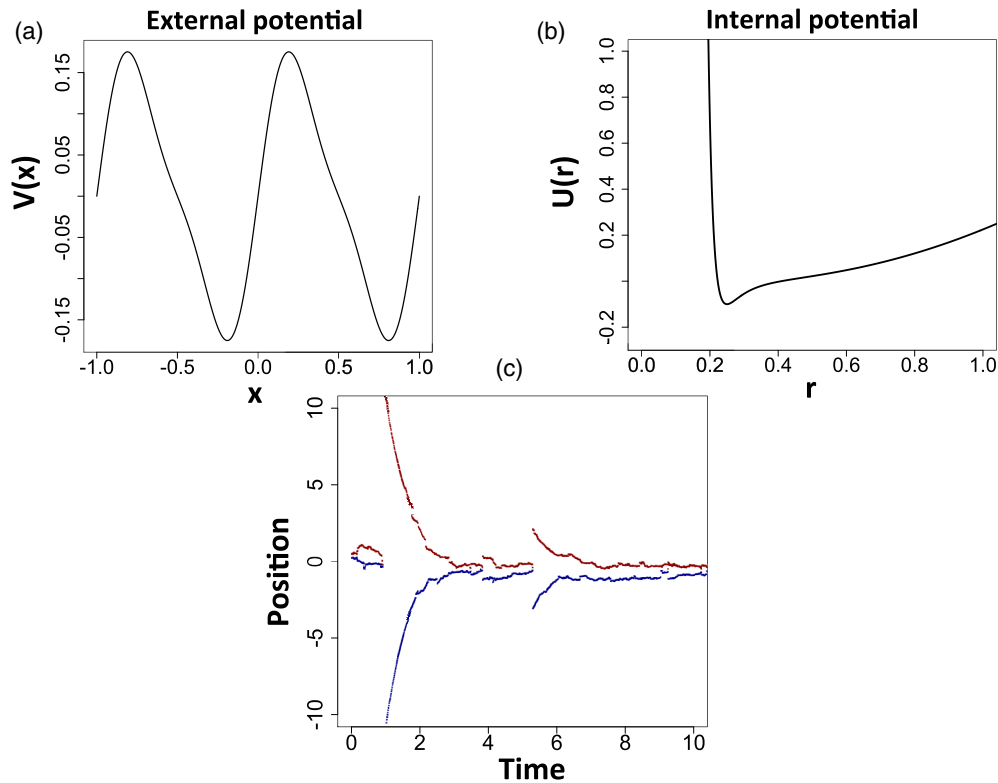


FIG. 1. (Color online) Model system: The heads are subject to an external potential (a) from the filamentous track (e.g., microtubule) and an internal potential (b) due to steric interactions within the motor. The internal potential is the sum of a harmonic and a Lennard-Jones potential [cf. Eqs. (2) and (3)]. In the absence of a constraint on the distance  $|y - x|$  and in the presence of “bursting fluctuations,” the two heads can be pulled apart to an unphysically large distance, i.e., a catastrophe as shown in (c) can occur. Parameter values are  $a = 0.25$ ,  $\epsilon = 0.1$ ,  $\tau = 5$ ,  $k = 0.8$ ,  $L = 1$ ,  $dt = 0.01$ .

predatory fish [19], spider monkeys [20], or human beings [21]. But it came as a great surprise that Brownian diffusion—until recently a model of choice for describing any subcellular processes—was unable to explain a huge amount of experimental data on intracellular motion. Anomalous diffusion, i.e., an unusual nonlinear time dependence of the mean-square displacement (MSD) accompanied by an anomalous scaling behavior [22–25], has become a commonly observed phenomenon in intracellular transport [26–30].

In cell biology, molecular diffusion is recognized as a main form of transport within the cells. Random motion in cytoplasm is usually attributed to thermal fluctuations, which contribute to the dynamics of objects as irregular forcing occurring randomly in time. The latter are commonly modeled as a Gaussian noise source. In a Gaussian distribution the tails of the probability density fall off exponentially and the MSD in the passive motion grows linearly with time.

In contrast to the aforementioned canonical Brownian ratchet powered by Gaussian white noise, we here investigate transport under the action of white Lévy noise. The “heavy” or “fat” tail of the distribution of Lévy noise amplitudes means that large jumps occur more likely than for the Gaussian case. As a consequence, we face a challenge when trying to characterize the ensuing directed motion on the ratchet. This is because the statistical moments of the examined flux of particles can be divergent. In particular, for  $\alpha \in (0, 1]$  neither the dispersion nor even the mean of the corresponding

displacements exist. Therefore, the statistical analysis of the induced flux is no longer possible in terms of standard notions such as mean velocity, standard deviation, and Péclet number [31–33]. New measures to characterize the transport must be introduced [12,13,34].

The  $\alpha$ -stable Lévy noise is associated with systems that are out of thermal equilibrium, and it can occur when conditions leading to the standard fluctuation-dissipation theorem are violated [35–38]. In particular, the Lévy-type statistics is observed in various scientific areas where scale-invariant phenomena take place or can be suspected (for a recent short review see Ref. [16] and references therein). This statistics allows one to describe real situations in which the evolution shows abrupt jumps, called Lévy flights.

The interplay of deterministic dynamics and perturbative Lévy-type noises has been addressed in the literature in various scenarios, including several noise-induced effects like resonant activation [36,37], stochastic resonance [39,40], noise-enhanced stability in Josephson junctions [37], and dynamical hysteresis [39,41]. It has also been studied in the context of population dynamics [40,42], escape from bounded intervals [38,43], barrier crossing problems [44–47], stationary distributions and steady states in confining potentials [48–51]. Also, noise-induced directed motion in spatially periodic potentials has been investigated, although mostly in the presence of Gaussian noise [3,4,7]. In contrast, relatively few research efforts [12,13,34,52,53] have been undertaken

to understand motion in a ratchet potential under the action of jumpy Lévy fluctuations.

On the other hand, increasing experimental evidence has been gathered over the last few years documenting that particles in a living cell perform not only thermal diffusion [23,24,26,27] and significant understanding of the nonequilibrium processes that underlie anomalous diffusion has been gained. It has become possible by developing new microscopy techniques which allow us to follow and identify [54,55] the responsible random forces. According to those studies the cytoskeleton appears to be a very dynamic viscoelastic structure [56] that is subject to a lot of mechanical activity through, for instance, the motor proteins that are connected to it. This *nonequilibrium* activity has been found to generate random fluctuating forces large enough to literally “stir” the cytoplasm [54,57]. The use of Lévy noise in motor protein models is then warranted by the ample evidence of relatively frequent large fluctuations. Their presence, as previously observed, is in fact a signature of Lévy noise.

Here we present a study on a two-headed motor model subject to action of the external Lévy random forcing. We start out, in Sec. I, with the characterization of the noise and formulation of a basic ratchet model. In Sec. II we describe the systems response to external forces. Summary, conclusions, and a discussion of our results are the contents of Sec. III.

## II. METHODS

We let our Lévy noise [15,58,59] consist of subsequent random kicks  $\zeta(t)$ . We restrict ourselves to a case of symmetric stable noises,  $L_\alpha(t) = \int_0^t \zeta(t') dt'$ , where for the characteristic function we have

$$\phi(k,t) = \left\langle \exp[ik \int_0^t \zeta(t') dt'] \right\rangle = \exp[-\sigma^\alpha |k|^\alpha t]. \quad (1)$$

Here the parameter  $\alpha$  ( $\alpha \in (0,2)$ ) denotes the stability index of the distribution whose “fat” power-law tails of the PDF are characterized by  $|\zeta|^{-(1+\alpha)}$  asymptotics. The parameter  $\sigma$  stands for a scale parameter that measures the intensity of the noise. For the special case  $\alpha = 2$ , the Gaussian noise is retrieved with  $\sigma^2$  representing the variance of the corresponding fluctuations. In what follows we will use  $\sigma \in [0.1,0.5]$ , i.e., we consider symmetric, strictly stable distributions for different scale parameters  $\sigma$  [60]. We used the Weron algorithm [61] to generate the Lévy distributed variables in our simulations. The time step in all the simulations is set to  $dt = 0.01$ .

### A. The model

We consider the following overdamped Langevin system:

$$\begin{aligned} \frac{dx}{dt} &= -z_1(t)V'(x) + k(r-a) + U'_{LJ}(r) + \zeta_1(t) \\ \frac{dy}{dt} &= -z_2(t)V'(y) - k(r-a) - U'_{LJ}(r) + \zeta_2(t). \end{aligned} \quad (2)$$

The coordinates  $x$  and  $y$  represent the positions of the two heads of the motor and  $r = |x - y|$  stands for the distance between them. The two heads are coupled by a harmonic spring of a natural length  $a$  and an elasticity constant  $k$ . The functions  $\zeta_i(t)$ , where  $i = 1,2$ , are the independent random

forces modeled by white Lévy noises. As was explained in the Introduction, this non-Gaussian white noises can be thought of as a result of nonequilibrium activity in a viscoelastic cytoskeleton. In order to prevent the two heads from overlapping their positions, we introduce a Lennard-Jones potential as in Refs. [62,63],

$$U_{LJ}(r) = 4\epsilon \left[ \left( \frac{s}{r} \right)^{12} - \left( \frac{s}{r} \right)^6 \right], \quad (3)$$

which becomes strongly repulsive when the heads are too close. Here  $s = 2^{-1/6}a$ , where  $a$  is the location of the minimum of  $U_{LJ}(r)$ . The alternating action of the heads is represented by a dichotomous variable  $z(t)$ , as proposed formerly by Dan *et al.* [63],

$$z_i(t) = \begin{cases} 0 & \text{for } 0 \leq t < \tau/2 \\ 1 & \text{for } \tau/2 \leq t < \tau. \end{cases} \quad (4)$$

Here  $i = 1,2$  denotes the two heads and  $\tau$  is the period of the periodic functions  $z_i(t)$ . The variables  $z_1$  and  $z_2$  are in antiphase: If one of the heads is active (e.g.,  $z_1 = 1$ ), then the other one is turned off (e.g.,  $z_2 = 0$ ). The two heads of the motor interact with the underlying structure of the track (reminiscent of a microtubular trail for kinesins) via a “ratchet” potential  $V(x)$  [see Fig. 1(a)]

$$V(x) = \frac{1}{2\pi} \left[ \sin\left(\frac{2\pi x}{L}\right) + \frac{1}{4} \sin\left(\frac{4\pi x}{L}\right) \right]. \quad (5)$$

In Eq. (5) we set the period  $L = 1$ . It is easily seen that this potential is anisotropic: Going from left to right the slope is characterized by a steeper increase and a slower decrease. According to Curie’s principle [64], net directed flux in a particular direction can only occur if there is a symmetry-breaking feature in the setup. In our case that symmetry-breaking feature is the anisotropy of the potential  $V(x)$ .

The motor protein heads take turns in being attached to the track. In Eqs. (2) this is represented by  $V(x)$  and  $V(y)$ , which alternately take the form of Eq. (5). When a head is unattached, the potential is zero. This switch between heads thus involves an energy difference  $\Delta E = V(x) - V(y)$ . Had the system been at equilibrium,  $\Delta E$  would have determined the ratio of the switching rates. In that case there would have been a Boltzmann relation:

$$\frac{\gamma(x \rightarrow y)}{\gamma(y \rightarrow x)} = \exp[\Delta E/k_B T] \quad (6)$$

between the switching rates  $\gamma$ . Here the rate  $\gamma(x \rightarrow y)$  is for the transition where the  $y$  head attaches and the  $x$  head detaches. The rate  $\gamma(y \rightarrow x)$  is for the transition where the  $x$  head attaches and the  $y$  head detaches. Furthermore,  $k_B$  is Boltzmann’s constant and  $T$  represents the absolute temperature. Note that the harmonic potential  $\frac{1}{2}k(r-a)^2$  and the Lennard-Jones potential  $U_{LJ}(r)$  do not affect Eq. (6) as these energies depend on  $r = |x - y|$  and do not change when a switch occurs. Equation (6) describes the detailed balance that we ought to have at thermal equilibrium. However, in a processive motor protein the attachment-detachment cycle is coupled to ATP hydrolysis. The role of ATP hydrolysis is to break detailed balance and bring the system from Eq. (6) to a situation where the forced switching of Eq. (4) applies.

Equation (4) is a good approximation if the energy that is released in the ATP hydrolysis is significantly larger than  $\Delta E$  [65]. It is valid if the ATP hydrolysis “overwhelms” the  $\Delta E$  that rules the equilibrium behavior.

The forced switching of Eq. (4) would have been the only energy input into the system, if the noise,  $\zeta_i(t)$  [ $i = 1, 2$ , cf. Eqs. (2)], had been thermal, equilibrium noise. In that case, ATP hydrolysis would be 100% accountable for the net motion of the motor. A nonthermal  $\zeta_i(t)$  is a complication since it represents another energy input into the system. Below we will examine the effects of such a  $\zeta_i(t)$ , adhering, however, to the situation when the increments of random forces  $\Delta\zeta_i(t)$  are stationary and statistically independent (i.e.,  $\zeta_i$  has a character of white noise perturbing the system’s dynamics). It should be noted that this approach stands in a clear difference to viscoelastic subdiffusion discussed in a series of papers [66,67] and described by generalized Langevin equation with the memory kernel satisfying the fluctuation-dissipation theorem.

Initially, the two heads of the motor are located so that the distance between them is equal to  $a$ . For time  $t > 0$ , the distributions of the positions  $x, y$  evolve due to the presence of the stochastic forces and the deterministic potentials. As was mentioned before, the mean may diverge when Lévy noise is involved. We therefore characterize the motion of the center of mass of the heads, i.e.,  $X_c(t) = [x(t) + y(t)]/2$ , with the median  $q_{0.5}$ , defined as  $\text{Prob}[X_c(t) \leq q_{0.5}(t)] = 1/2$ . Accordingly, the time derivative of the median,

$$v(t) = \frac{dq_{0.5}(t)}{dt}, \quad (7)$$

may serve as an estimate of the group velocity of the particle “packet” [12,13,34]. With  $v(t)$  we have a quantity that allows us to characterize ensemble transport even in case of unbounded average currents.

### III. STRUCTURAL AND FUNCTIONAL CUTOFFS OF THE FLUCTUATIONS

#### A. Response to bursting fluctuations

With decreasing  $\alpha$ , the probability of longer jumps increases. Consequently, a “bursting fluctuation” may occur that pulls the coupled heads apart over a very long distance [see Fig. 1(c)]. The model is supposed to describe a prototypical nanomotor and it is obvious that constraints must exist to secure the motor’s integrity and function.

The variables  $x$  and  $y$  [cf. Eq. (2)] represent the positions of the two heads of the motor protein. It is the relative distance  $|y - x|$  that has to be limited in course of the action. In order to prevent a “rupture,” as depicted in Fig. 1(c), a response to catastrophic fluctuations has to be imposed in the model.

The elastic properties of a linker structure in typical molecular motors, like kinesins, have been formerly addressed in experimental studies and molecular dynamics simulations using GROMACS software [68,69]. Based on accumulated evidence, it is unlikely that a molecular machine would respond instantaneously to an elongation with an elastic counteraction that resets the linker structure to its equilibrium conformation of length  $a$  or shorter (see Fig. 2).

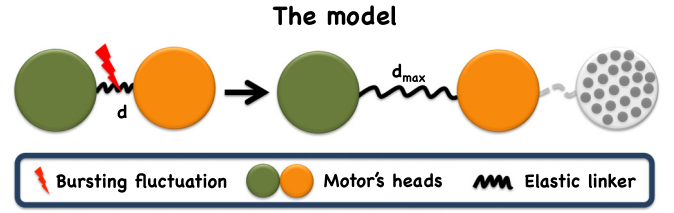


FIG. 2. (Color online) A sketch illustrating the model for the system’s response to bursting fluctuations. If there were no constraint, the leading head would have been in the dotted position. For explanation, see the main text.

Following these observations, we simply “freeze” the distance between the heads when it reaches  $|y - x| = d_{\max}$ , i.e., we leave it at  $|y - x| = d_{\max}$  until a next iteration reduces the distance  $|y - x|$  again. Simulations following this scenario are shown in Figs. 3(a) and 3(b).

Parameters of our model can be categorized as those describing the inner structure and mechanics of the molecular motor and those associated with its chemical activity. Processive motility of molecular motors like kinesin depends on the mechanical transmission of stress through a neck linker which connects the two heads of the molecule. This tension-transmitting element is an unstructured protein segment. In case of kinesin it is 30 amino acids long. It is a simple flexible polypeptide polymer and it is responsible for the internal potential in our model [1,68–70]. In particular, the equilibrium length  $a$  and elasticity constant  $k$  can be seen as characteristics of a neck linker polymer. The distance  $d_{\max}$  represents that maximum allowable extension of the neck linker. The oscillations  $z_i(t)$  [cf. Eq. (4)] are associated with the chemical activity of the motor protein. The mechanical stepping cycle is coupled to the hydrolysis of ATP. The parameter  $\tau$  [cf. Eq. (4)] controls the time for the pertinent conformational changes to occur.

#### B. The effect of noise intensity on the motor’s velocity

We have checked how changing the noise intensity  $\sigma$  affects the motor’s velocity. Figure 4 shows the results of the simulations. The maximal group velocity of the independent motors notably drops for noise departing from Gaussianity. However, the higher the stability index  $\alpha$  of the noise, the lower the intensity  $\sigma$  for which the velocity reaches its maximum value. Also, for  $\alpha = 1.5$  the peak around the maximum is significantly broader than for  $\alpha = 2.0$ , thus reflecting that the maximum velocity range is wider for lower  $\alpha$ . This could be interesting when we use noise as a possible control mechanism for an artificial molecular motor.

#### C. Varying the inner structure

As was pointed out in the Introduction, motor proteins carry cargo, like organelles and vesicles with chemicals, from the cell’s interior to its periphery. Speedy delivery is important for the cell’s survival and it is likely that speed has been optimized in the course of evolution. The linker length  $d_{\max}$  is a variable that is subject to natural selection and likely to have been subject to such optimization.



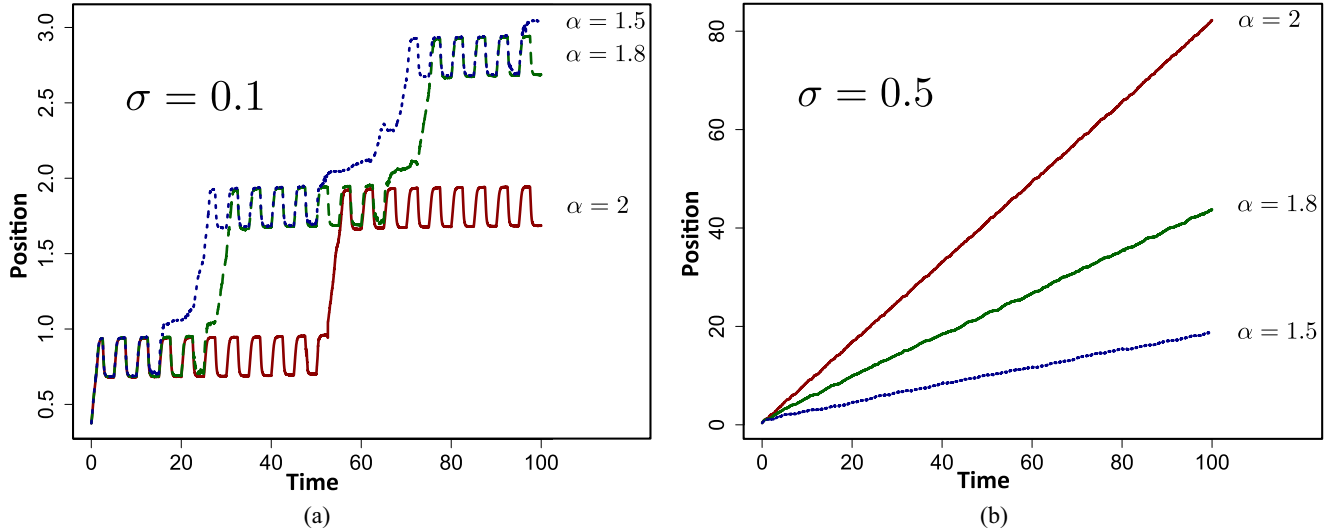


FIG. 3. (Color online) Simulated trajectories [cf. Eq. (2)] showing the displacement of the median  $q_{0.5}$  of the midpoint between  $x$  and  $y$  for 1000 motors. The distance between the heads  $x$  and  $y$  has been limited to  $|y - x| = d_{\max} = 2a$ . The noise parameter is  $\sigma = 0.1$  in panel (a) and  $\sigma = 0.5$  in panel (b). The other parameter values are  $a = 0.25$ ,  $\epsilon = 0.1$ ,  $\tau = 5.0$ , and  $k = 0.8$ . The time step is  $dt = 0.01$ .

Figure 5 shows the results of simulations in which the velocity of the median  $q_{0.5}$  was determined for different values of  $d_{\max}$ . We took 1000 independent motors acting under the constraints of the model and recorded their velocity in the course of 100 time units.

In line with findings discussed in Secs. III A and III B there is a clear nonmonotonic relation between the velocity of the stepper and the maximum linker length  $d_{\max}$ . With an increasing linker length, the group velocity drops rapidly, assumes a minimum, and eventually tends to zero. For an equilibrium linker length  $a = 0.25$  (left panel of Fig. 5) and for Gaussian noise, i.e., stability index  $\alpha = 2$ , the induced current does not change direction as  $d_{\max}$  is varied. In this case derived velocities of the median remain positive within the domain of change of  $d_{\max} \in (0, 8)$ . In contrast, for approximately twice

shorter length  $a = 0.1$  (right panel of Fig. 5) the current becomes inverted in the negative direction (cf. Fig. 6).

What is most remarkable about Fig. 5 is that it shows the possibility of current reversal when a parameter describing noise or internal structure is changed. At small values of  $d_{\max}$ , the directionality can be reversed with a mere change of the stability index  $\alpha$ . On the other hand, for transport subject to non-Gaussian noises of  $\alpha = 1.5$  and  $\alpha = 1.8$ , the current can reverse its direction as the maximum elongation of the linker  $d_{\max}$  is varied. This is a current inversion induced by non-Gaussian Lévy noise, which is akin to that found with non-Gaussian colored noise [71,72]. It is furthermore observed that at  $a = 0.1$  (right panel of Fig. 5) the transport is slowed down and eventually stopped at increasing linker length  $d_{\max}$ . For a longer equilibrium distance between the heads,  $a = 0.5$ , the curves are similar to those observed for  $a = 0.25$ , although velocities are significantly smaller (data not shown).

Altogether, described currents  $v(t) = dq_{0.5}(t)/dt$  are higher for motors subject to Gaussian noises (see Fig. 6) than for steppers influenced by impulsive Lévy fluctuations. The movement depends also on allowable extension of the linker with respect to its equilibrium elongation and becomes suppressed at excessive extensions.

#### D. Varying the enzymatic rate

To examine the impact of the chemical activity on the motor's velocity, we have simulated the motion of 1000 independent walkers under different noise parameters and for different values of  $\tau$ . We have next analyzed the displacement of the median and calculated the group velocity.

In Fig. 7 the normalized velocity as a function of the period  $\tau$  for different values of the stability index  $\alpha = 1.5, 1.8, 2$  is displayed. To estimate the group velocity, the maximum reached by the median  $q_{0.5}$  in course of 100 steps has been divided by the time in which it has been achieved. Furthermore, for each value of the index  $\alpha$  separately, the derived velocity has been normalized with respect to its maximum value. Such

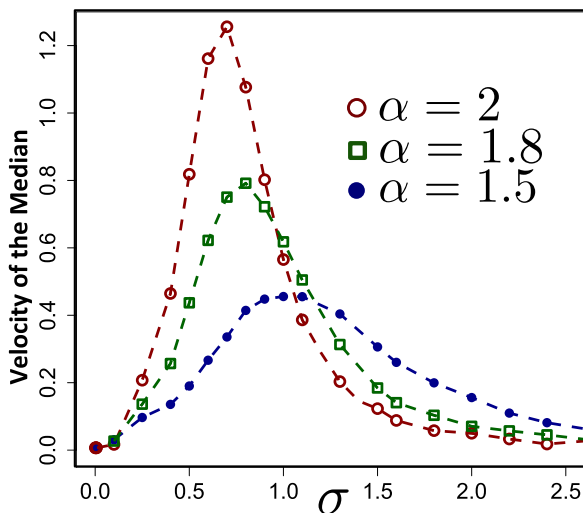


FIG. 4. (Color online) Velocity of the median  $q_{0.5}$  of 1000 independent walkers after 100 time units as a function of noise intensity  $\sigma$ . The parameter values are  $a = 0.25$ ,  $d_{\max} = 0.5$ ,  $\epsilon = 0.1$ ,  $\tau = 5.0$ ,  $k = 0.8$ , and  $dt = 0.01$ .

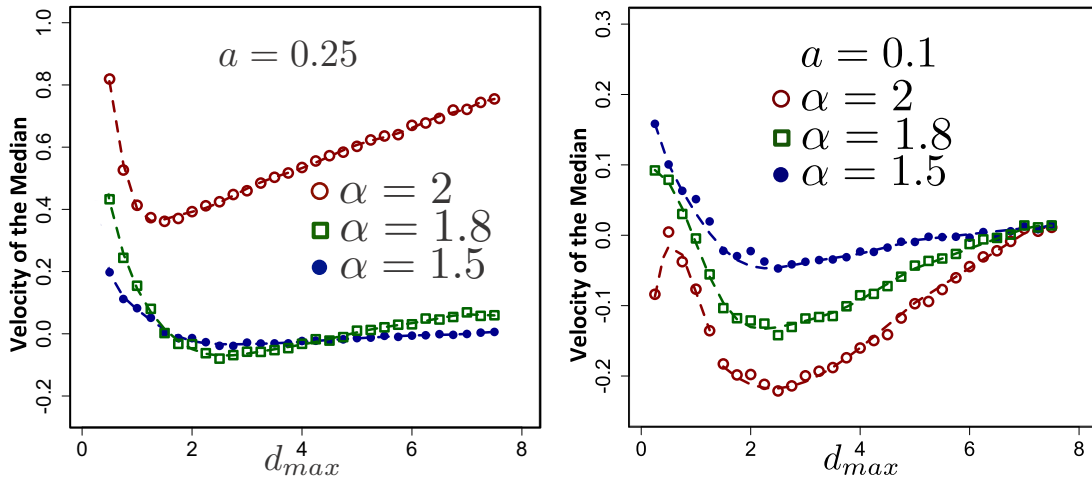


FIG. 5. (Color online) Velocity of the median  $q_{0.5}$  of 1000 independent walkers after 100 time units as a function of  $d_{max}$  for different values of the stability index  $\alpha = 1.5, 1.8, 2.0$  and for different lengths of the fully relaxed linker:  $a = 0.25$  (a) and  $a = 0.1$  (b). The variable  $d_{max}$  represents the maximum allowable distance  $|y - x|$  between the heads. The parameter values are  $\epsilon = 0.1, \tau = 5, k = 0.8, dt = 0.01$ , and  $\sigma = 0.5$ . The duration of the individual motor trajectories has been set to  $t = 100$ . Lines are drawn to guide the eye.

analysis shows (cf. Fig. 7) a clear maximum in the normalized velocity as a function of  $\tau$ , thus indicating an optimal value for the chemical activity rate. As it has been discussed in the existing literature [2,28], fast intracellular transport is important for a living cell and in the course of evolution the

motor protein is likely to have sought out a maximum, similar to the one depicted in Fig. 7. Apparently, the location of the maximum is very sensitive to the noise type: As it can be deduced from Fig. 7, for smaller values of the stability index  $\alpha$ , i.e., when more bursting fluctuations act on the system, the

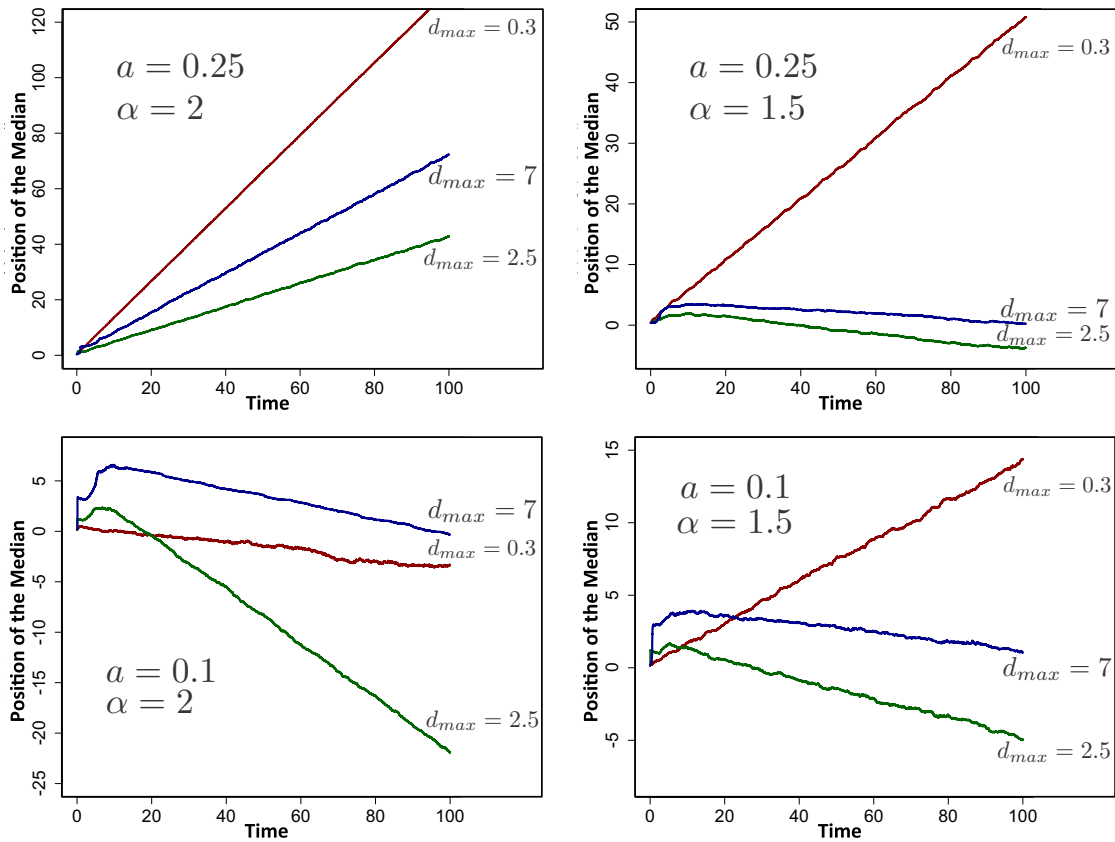


FIG. 6. (Color online) Trajectories of the median  $q_{0.5}$  of 1000 independent walkers. Graphs have been presented for different values of the linker extension  $d_{max}$  close to and beyond the minimum depicted in Fig. 5. Top (bottom) panels refer to linkers characterized by natural (relaxed) lengths  $a = 0.25$  ( $a = 0.1$ ). Stability index is  $\alpha = 2.0$  and  $\alpha = 1.5$  for left and right panels, respectively.

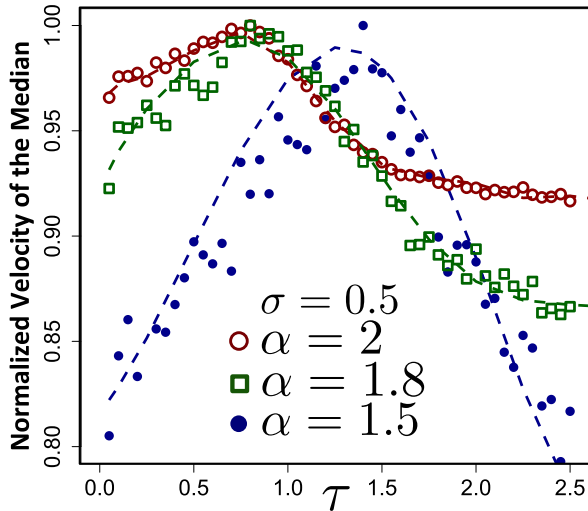


FIG. 7. (Color online) The velocity of the median  $q_{0.5}$  of 1000 independent walkers as a function of the period  $\tau$ , for different values of the stability index  $\alpha$ , namely  $\alpha = 1.5, 1.8, 2$ . The parameter values are  $a = 0.25$ ,  $\epsilon = 0.1$ ,  $d_{\max} = 0.5$ ,  $k = 0.8$ ,  $\sigma = 0.5$ , and  $dt = 0.01$ . Lines, obtained by curve fitting, are drawn to guide the eye.

optimum value of the velocity shifts towards longer turnover times  $\tau$ .

#### IV. DISCUSSION AND CONCLUSIONS

In this paper we have considered a simple model for a stepping motor protein acting under the influence of white stable noises. The model contains parameters that represent the structure and the chemical activity of the motor system. Structural features are denoted by the parameters  $k$ ,  $a$ , and  $d_{\max}$  of the system and have been preliminary analyzed in different dynamic responses, as proposed in Sec. III A. In order to study noise-induced flux, we have focused on the dynamic response of the model (cf. Fig. 2).

It is further shown that noise characteristics and motor parameters control the speed and even the direction of the stepper motion in a nontrivial way. Our results can be significant for understanding of the evolution of motor proteins and for the design of artificial molecular machines.

Dimers, like kinesin, are commonly described by a system of two coupled equations like Eq. (2). The coupling between  $x$  and  $y$  in Eq. (2) should be a reflection of the structure of a real protein. For kinesin the two heads are linked through a polymeric chain that is commonly known as the neck linker. We can examine the model for different equilibrium lengths  $a$  and for different maximum lengths  $d_{\max}$  of the fully extended linker. There is an optimal equilibrium length  $a$  for which the processivity and speed of the motor are maximized. In the case of our motors, that optimal length is around  $a = 0.25$ . A similar result has been reported for Gaussian noise [62].

Results presented in Figs. 4 and 5 document a rich scenario of behaviors emerging when Gaussian noise is replaced by Lévy noise with  $\alpha < 2$ . Specifically, in Fig. 5 current reversals are shown to occur when noise parameters are changed. Additionally, for motors working under the action of impulsive Lévy noises, multiple current reversals are observed when the structure parameter  $d_{\max}$  is varied.

The parameters  $d_{\max}$  and  $a$  characterize the elastic properties of the linker that connects the two heads of the motor. The induced current appears to depend very sensitively on  $d_{\max}$  and  $a$ . This suggests the possibility of a control mechanism through the linker. Experimental results on natural kinesin motors appear consistent with this idea [70].

In a changing environment such as a living cell, it is possible to imagine that noise parameters, such as  $\alpha$ , may differ for different metabolic stages. This leads to an interesting possibility: by changing  $\alpha$  in the course of development, the direction of motor motion may reverse. Natural cytoskeletal molecular motors, like dynein, kinesin, or myosin, walk one way without ever changing direction. However, there are mutants that switch the direction of their motion stochastically [73]. Noise as a possible control mechanism for the motor's flow may also be an important feature for those trying to synthesize artificial molecular motors.

We have shown how motor motion, as described by Eq. (2), depends on chemical properties. Figure 7 shows that there is an optimal time after which the heads should interchange their activity. This value depends on the noise characteristics—the closer the noise is to Gaussian, the faster the reactions should be.

After 20 years of intensive research in the field of molecular transport, we know a lot about the structure of molecular motors [1]. We also know a lot about rates, speeds, step sizes, and load-velocity characteristics [2,4,28,31,69,73]. Yet we have only a limited knowledge of *how* molecular motors work, especially under the action of nonequilibrium, non-Gaussian noises. The ultimate goal of studies like ours is therefore to find and understand relations between motor structure and function. Such insight would be invaluable in, for instance, drug design or constructing artificial molecular motors.

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