**Generalized energy equipartition in harmonic oscillators driven by active baths**

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We study experimentally and numerically the dynamics of colloidal beads confined by a harmonic potential in a bath of swimming *E. coli* bacteria. The resulting dynamics is well approximated by a Langevin equation for an overdamped oscillator driven by the combination of a white thermal noise and an exponentially correlated active noise. This scenario leads to a simple generalization of the equipartition theorem resulting in the coexistence of two different effective temperatures that govern dynamics along the flat and the curved directions in the potential landscape.

*Introduction*- A remarkable result of equilibrium statistical mechanics is the theorem of energy equipartition. In its simplest form, the theorem states that each quadratic term in the Hamiltonian contributes with the same amount of energy \(k_BT/2\) to the average energy of the system\(^3\). In the case of a harmonic oscillator this applies to both kinetic and potential energies. In the colloidal realm, particle motions are strongly overdamped and velocity fluctuates on a timescales that is often hardly accessible\(^2\). However the value of kinetic energy imposed by the equipartition theorem is reflected in a diffusion coefficient that is proportional to the mean squared velocity \(D_T = \mu k_BT\). Therefore, for a colloidal harmonic oscillator the equipartition theorem establishes a link between the thermal diffusion constant \(D_T\) and the average potential energy \(U = D_T/2\mu\). Out of equilibrium system are frequently found in nature and the search for generalized equipartition laws constitutes a very interesting and hot topic\(^4\). In particular there is a growing family of off-equilibrium, active colloidal particles that are able to harness some form of locally stored energy to self propel in persistent random walk\(^5\). An interesting example is provided by passive colloidal tracers suspended in active baths of swimming bacteria. Over time scales that are larger than the persistence time of active forces, those particle display a diffusive behaviour with a diffusivity \(D^*\) that can be order of magnitudes larger than the thermal counterpart \(D_T\).\(^6\) It is found that, whenever the external potential changes smoothly on the characteristic length-scale of the persistent motion, the system is well described by a quasi-Boltzmann distribution with an effective temperature given by \(k_BT_{eff} = D^*/\mu\).\(^7\) In this limiting case the equipartition theorem is recovered in its original form, being a straightforward consequence of Boltzmann statistics. However, when the external potential does not meet these requirements, Boltzmann statistics breaks down\(^8\) and an equilibrium-like picture with one single effective temperature fails. This is particularly evident in the case of rectification effects, as those investigated in Ref.s\(^9\)\(^-\)\(^11\). In these works it has been shown that a bacterial bath can spontaneously induce the unidirectional motion of nano-fabricated asymmetric objects. Similarly, micro-fabricated structures can rectify the motion of motile bacteria and accumulate them in specific spatial region\(^12\).\(^13\). More passive colloidal tracers can be delivered onto target sites by the rectification of fluctuating forces from a bacterial bath\(^14\)\(^-\)\(^15\). Failure of Boltzmann statistics also leads to novel non-equilibrium effects such as the emergence of effective attraction in presence of purely repulsive potentials\(^16\)\(^-\)\(^20\). In this context, a simple generalization of equipartition could seem unlikely.

In this Letter we demonstrate that, in the case of active harmonic oscillators, the average value of potential energy is still linked to the diffusivity by a simple generalization of the equipartition theorem. As a consequence, the effective temperature that associated with the potential energy is always lower than the one obtained from the free diffusion coefficient. We investigate experimentally and numerically the dynamics of colloidal beads, subject to a harmonic potential, suspended in a bath of swimming *E. coli* cells. The elastic force field is obtained experimentally by placing the micro-spheres in a cylindrical microcapillary. Sedimenting colloids fluctuate near the bottom of the capillary where they experience a near-perfect harmonic potential.

*Experiment*- Motile *E. coli* cells are prepared following the protocol described in Ref.\(^21\). Silica beads of radius \(a = 3.5 \mu m\) are first diluted in deionized water and then mixed with bacteria directly on a glass slide. The final bacteria density is estimated to be \(\sim 10^{10} \text{ cells/mL}\). The bacteri-colloids solution is loaded in a microcapillary glass tube (Vitrocom) of internal radius \(R = 25 \mu m\) by capillarity. The sample is left open for few minutes before sealing with index matching oil. This procedure results in the formation of two air bubbles at the edges of the capillary tube as shown in Fig. 1(a). Residual distortions due to the internal glass/water interface have a negligible effect as shown by the absence of anisotropies in both particle shape and diffusion in absence of bacteria (see\(^22\)).

Colloidal beads sediment at the bottom of the capillary and align along the tube axis with an average distance of about \(20 \mu m\). We collect bright field images using a \(20\times\), NA 0.25 microscope objective. After background subtraction and thresholding we obtain particle trajectories

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by center of mass tracking. We report data for 10 beads that were simultaneously tracked for 100 s at a rate of 250 frames/s. The beads span a capillary length of approximately 25 µm probing a local environment characterised by a bacterial activity that decreases as the distance from the trapped air bubble increases.

Simulation- The numerical simulations are performed by considering spherical colloidal particles of radius \( a \) immersed in a bath of self-propelling dumbbells following a “run and tumble” dynamics. Both particles and bacteria are confined in a cylindrical volume as shown in Fig. 1(b) and (c). All interactions are modelled by repulsive steric forces. In addition particles experience a gravitational force \( f_z = -mg \) due to gravity where \( m \) is the buoyant mass of the colloidal particle and \( g \) is the acceleration due to gravity. We include Brownian motion only for particles and neglect hydrodynamic interactions as the dominant force field is then well approximated by an elastic force acting along the \( y \) axis with a spring constant \( k \) defined by \( k = mg/\rho \). The cylindrical geometry of the capillary restricts the colloids to the thermal fluctuations and to the interactions with the swimming bacteria. To account for these we model the dynamics of the beads with the following stochastic differential equation:

\[
\dot{r} = \mu f(r) + \eta^T + \eta^A
\]  

(1)

where \( r(t) = (x(t), y(t)) \), \( f = (0, -k y) \) and \( \mu \) is the mobility of the colloidal particle. We assume that the noise term can be split into two independent components: the standard Langevin thermal noise \( \eta^T \) with \( \langle \eta^T_i(t) \eta^T_j(t') \rangle = 2D_T \delta_{ij} \delta(t - t') \) and \( D_T = \mu k_B T \); an active noise \( \eta^A \) that is exponentially time-correlated, \( \langle \eta^A_i(t) \eta^A_j(t') \rangle = D_A \delta_{ij} \exp(-|t - t'|/\tau)/\tau \), where \( \alpha, \beta \) represent individual Cartesian components. From Eq. (1) we can compute the MSD along \( x \):

\[
\langle \Delta x^2(t) \rangle = 2D_T t + 2D_A \left[ t - \tau(1 - e^{-t/\tau}) \right] 
\]  

(2)

and the MSD of \( y(t) \):

\[
\langle \Delta y^2(t) \rangle = \frac{2D_T}{\mu k}(1 - e^{-\mu kt}) + \frac{2D_A}{\mu k} \frac{1 - e^{-\mu kt} - \mu k\tau(1 - e^{-t/\tau})}{1 - (\mu k\tau)^2}
\]  

(3)

Equations (2) and (3) provide an excellent fit to the MSD along both \( x \) and \( y \) (Fig. 2(a) and (b)). Along both axes the parameter \( D_A \) shows a clear dependence on the average position of the particle (\( x \)) with respect to the edge of air bubble. \( D_A \) is found to decrease from 0.31 to 0.14 µm²/s upon increasing (\( x \)) by few hundreds microns. This suggests that bacterial motility depends on the concentration of oxygen that is progressively consumed by bacteria along the capillary [22]. Differently the fitting parameters \( D_T \), \( \tau \) and \( \mu k \) do not show any clear dependence on the distance from the air bubble. The obtained averages over all particles are \( \tau = 0.093(0.015) \) s, \( D_T \)}
The MSD along $x$ and $y$ of the beads from simulations can be fitted with the same Equations (2) and (3) where this time $D_A$ and $\tau$ are the only free parameters. As seen in Fig. 2(d) and (e) these functions fit very well the simulation data. By fitting the MSD along $x$ with the free parameters $D_A$ and $\tau$ we find that $D_A$ grows continuously from 6.8 to 16.0 $\mu m^2/s$ as we increase the average speed from 15 to 30 $\mu m/s$. The parameter $\tau$ shows also a marked change upon changing the average speed going from $\tau = 0.44$ to 0.23 s.

The $\langle \Delta y^2(t) \rangle$ from simulations is fitted with Eq. (3) with the same free parameters $D_A$ and $\tau$ giving $D_A$ growing from 6.7 to 14.0 $\mu m^2/s$, that is almost identical to the one found from the fitting of $\langle \Delta x^2(t) \rangle$. Also the $\tau$ found from the fit of $\langle \Delta y^2(t) \rangle$ is very close to the one found from the MSD decreasing from $\sim 0.4$ to 0.2 s upon increasing $V$. It has to be noted that simulations are in qualitative agreement with the experiments although a quantitative comparison shows that both $\tau$ and $D_A$ result considerably larger in simulations than in experiments.

It is however clear that the model of Eq. (1) can be used to fit both numerical and experimental curves and that this allows us to make a precise statement on how to generalise equipartition of energy for active particle systems in harmonic potentials. At equilibrium, when only thermal noise is present, the average potential energy of the particle $U = k\langle y^2 \rangle/2$ is simply given by the
that can be obtained taking the limit of (3): when the persistence time \( \tau \) is much shorter than the relaxation time in the potential well \( 1/\mu \), we recover the equilibrium form. This result is direct consequence of the fact that when \( \tau \) is much shorter than any other time scale in the problem, the active noise is practically white and Boltzmann statistics holds with the (unique) effective temperature \( k_B T_{\text{eff}} = (D_A + D_T)/\mu \). However if \( \tau \mu \sim 1 \), even when the stationary distribution deviates strongly from the Boltzmann (as in run and tumble dynamics), the average potential energy will be given by the simple formula (4).

Conclusions- We have investigated, experimentally and numerically, the possibility of generalizing energy equipartition to out of equilibrium systems consisting of colloidal particles that are subject to both a harmonic potential and the interactions with a bath of swimming bacteria. We found that the system obeys a modified energy equipartition law. A harmonic degree of freedom contributes an average potential energy that takes the equilibrium form for small curvatures and decreases when the relaxation time in the harmonic well starts to be comparable to the persistence time of active forces. Based on these observations we expect that using a different type of self propelled colloids, i.e. Janus particles, one could have direct experimental access to higher \( \tau \) values and observe the predicted strong deviations from equilibrium equipartition.

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