

Noise Induced Stability in Fluctuating, Bistable Potentials

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The overdamped motion of a Brownian particle in an asymmetric, bistable, fluctuating potential shows noise induced stability: For intermediate fluctuation rates the mean occupancy of minima with an energy above the absolute minimum is enhanced. The model works as a detector for potential fluctuations being not too fast and not too slow. This effect occurs due to the different time scales in the problem. We present a detailed analysis of this effect using the exact solution of the Fokker-Planck equation for a simple model. Further we show that for not too fast fluctuations the system can be well described by effective rate equations. The results of the rate equations agree quantitatively with the exact results.

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Models of overdamped Brownian particles in potentials with one or more minima and barriers serve as paradigms for many relaxation processes in physical, chemical, and biological systems. The minima represent the stable or metastable states of the system. Transitions from one state to another are induced by the interaction with the environment. This interaction is typically described by a thermal white noise. The dynamics of the system is dominated by characteristic time scales which are given by the mean first passage times for the escape out of the minima of the potential. The simplest system in this class of models is the problem of diffusion over a single potential barrier, pioneered by Kramers [1].

In many situations, the potential fluctuates due to some external fluctuations, chemical reactions, or oscillations. The most prominent model of this kind is a Brownian particle in a symmetric bistable potential, subject to a harmonic force. It serves as the standard model for stochastic resonance [2]. In many other applications one has to consider stochastic, correlated fluctuations of the potential. Doering and Gadoua [3] investigated the situation of a symmetric, bistable fluctuating potential. They found a local minimum in the mean first passage time as a function of the barrier fluctuation rate. This effect has been called resonant activation and has been studied in detail by various people [4–9]. In most of these papers either a symmetric bistable potential or the escape over a single barrier has been studied. Escape rates for general potentials and dichotomous as well as Gaussian fluctuations of the potential have been calculated by Pechukas and Hänggi [6]. Their results support a simple, physical picture of activated processes with fluctuating barriers: If the potential fluctuates fast, the rate for transitions over the barrier is determined by the average barrier. If the potential fluctuations are slow (static limit), the slowest process determines the rate. In an intermediate regime the rate is given by the average rate, which is greater than the rate for fast or slow fluctuations. This picture has already been suggested by Bier and Astumian [5] on the

basis of a simple model with a dichotomously fluctuating linear ramp.

In many applications, one does not have a single barrier or a symmetric, bistable potential. In a more general situation the potential will have several minima of different depths. In equilibrium, the system rests most of the time in the absolute minimum of the potential. But due to potential fluctuations, the position of the absolute minimum may fluctuate. Typical, biological examples of such a situation are membrane proteins like a cell surface receptor or an ion channel. When a ligand binds to the receptor, it changes the potential energy of the receptor and induces a conformational change of the receptor molecule. If the transition from one to the other conformation and back is always more or less the same, a description of this transition by a single coordinate may be sufficient. Then it is possible to model the conformational changes by the motion of a particle in a fluctuating potential.

The effect of a periodic electric field on membrane proteins has been investigated theoretically [10] and experimentally [11]. Astumian and Robertson [10] described such a system by a two-state model with periodically modulated rates. The effect of a periodic modulation can be related to a stochastic, dichotomous modulation [12]. This clearly demonstrates the relevance of our results to such biologically motivated models. We will come back to this point at the end.

The motion of the overdamped particle in a fluctuating potential can be described by a Langevin equation

$$\dot{x} = f(x, t) + \xi(t), \quad (1)$$

where $f = -\frac{\partial V}{\partial x}$. We are using units where the friction constant and k_B are unity. f (and V) depend on t since the potential fluctuates. $\xi(t)$ is a thermal (white) noise, and it satisfies $\langle \xi \rangle = 0$, $\langle \xi(t)\xi(t') \rangle = 2T\delta(t-t')$. In this Letter, we restrict ourselves to the discussion of potentials with two minima, separated by a barrier. The position of the minima is $\pm x_m$ and does not depend on t . The maximum of $V(x)$ is located at $x = 0$. The fluctuation

of the potential is mainly a fluctuation of the depth of the two minima. Let us consider first the simplest, nontrivial version of such a model. Let us assume that the potential fluctuation is a dichotomous process and that $V(x, t)$ takes the two different values $V_+(x)$ and $V_-(x)$. Further we assume that the absolute minimum of $V_+(x)$ ($V_-(x)$) is the right (left) minimum. Such a model contains various time scales: Four mean first passage times for the two minima of $V_+(x)$ and $V_-(x)$, the intrawell relaxation times for $V_+(x)$ and $V_-(x)$, and the characteristic time scales for the fluctuation of the potential. The mean first passage times and the intrawell relaxation times are fixed by the form of the potential; the fluctuation of the potential is an external parameter that can be varied. In a biological model for a cell-surface receptor, as mentioned above, it is determined, e.g., by the concentration of the signaling molecule. Let $V(x) = \frac{1}{2}[V_+(x) + V_-(x)]$, $\Delta V(x) = \frac{1}{2}[V_+(x) - V_-(x)]$. Then $V(x, t) = V(x) + z(t)\Delta V(x)$ where $z(t)$ is a random process that takes two values ± 1 . Its static distribution is $q_0(z) = p_+\delta(z-1) + p_-\delta(z+1)$. Let τ be the correlation time of this process, so that $\langle z(t)z(t') \rangle = \langle z \rangle^2 + (1 - \langle z \rangle^2)\exp(-t/\tau)$. Without loss of generality we restrict ourselves to $p_- \leq 1/2$. What does one expect for such a model? Let us first suppose that the temperature is such that the typical barrier heights of the system are a few T . If τ is small compared to the intrawell relaxation times of the potential, the systems can be described by an effective static potential $\langle V \rangle(x) = V(x) + \langle z \rangle \Delta V(x)$. The stationary distribution is $p_0(x) = C \exp[-\langle V \rangle(x)/T]$. In the static limit, the stationary distribution is $p_0(x) = p_+ \exp[-V_+(x)/T] + p_- \exp[-V_-(x)/T]$. Suppose that p_+ is close to unity. Then the average potential is approximately given by $V_+(x)$ and $p_0(x)$ is approximately the same for small or large τ . In the following we will show that between these two extreme situations an interesting effect occurs: The mean occupancy of the minimum at $-x_m$, which is the minimum that has most of the time the higher energy, may become very large. We will show that this effect is related to resonant activation.

To calculate $p_0(x)$ or dynamic quantities of the system one has to solve the Fokker-Planck equation

$$\frac{\partial \rho(x, z, t)}{\partial t} = - \frac{\partial}{\partial x} \left(f(x, z) - T \frac{\partial}{\partial x} \right) \rho(x, z, t) + M_z \rho(x, z, t) \quad (2)$$

for this model. Here we assumed that the potential fluctuations can be parametrized by a single stochastic variable $z(t)$. $\rho(x, z, t)$ is the joint probability density for the stochastic variables x and z , and M_z is the generator of the stochastic process $z(t)$. To obtain the stationary distribution $p_0(x) = \int dz \rho(x, z)$, it is sufficient to analyze the stationary Fokker-Planck equation. A standard way to solve this equation is to expand $\rho(x, z)$ in the right eigenbasis of M_z . If the potential is piecewise linear, one obtains a set of

coupled differential equations with constant coefficients, which can be solved analytically. The remaining task is to satisfy the continuity conditions for $\rho(x, z)$, which is a simple linear algebraic problem. For the case of a dichotomous process, the force is $f(x, z) = f(x) + z\Delta f(x)$ as discussed above. In Fig. 1 we show results for the probability $\bar{n} = \int_{-\infty}^0 p_0(x) dx$ of the particle to sit in the left minimum of the fluctuating potential as a function of the correlation time τ , and for various values of p_+ . The choice of the potential is arbitrary, and similar results can be obtained for other potentials as well. The results for \bar{n} show that the qualitative discussion for small and large τ given above is valid. But for intermediate τ , \bar{n} is much larger than expected. The system is able to detect fluctuations that are not too fast or not too slow. Such fluctuations enhance the occupancy of the left minimum, although it is most of the time not the absolute minimum of the potential. We thus observe a noise induced stability for the state which has most of the time the higher energy, at least when $p_+ > 1/2$. The results in Fig. 1 show that for large values of p_+ this effect is even stronger.

What is the reason for this effect? How can it be described quantitatively and how does it depend on the potential? To answer these questions, let us go back to the general case (2). If τ is large compared to the intrawell relaxation times for the two minima of $V(x, z)$, the dynamics of the system can be described by an effective rate equation for the probability of the particle to sit in the left minimum, n , or in the right minimum, $1 - n$. The rate equation is given by

$$\frac{dn}{dt} = -r_1(z)n + r_2(z)(1 - n), \quad (3)$$

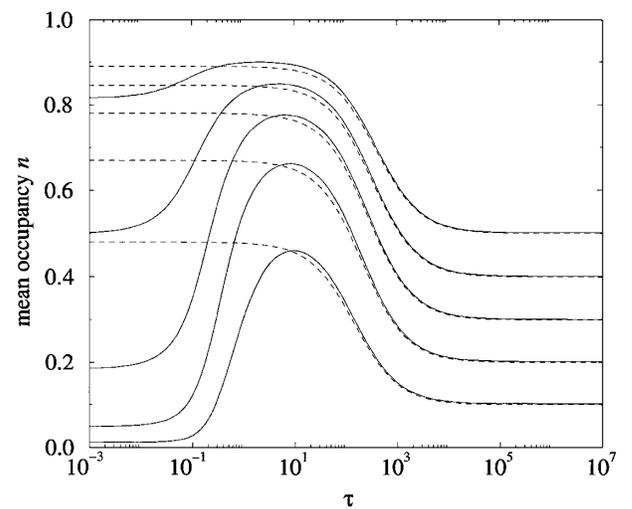


FIG. 1. The mean occupancy in the left minimum of a piecewise linear, dichotomously fluctuating potential as a function of τ for various p_+ . The parameters are $T = 0.3$, $p_+ = 0.5, 0.6, \dots, 0.9$, $f_+(x)$ is piecewise constant and takes the values 10, 1, -1, 2, -2, -10; $f_-(x)$ takes the values 10, 2, -2, 0.5, -0.5, -10. The values of x where $f_{\pm}(x)$ jumps are -4, -2, 0, 2, 4. The dashed lines are the results from (9).

where $r_{1,2}(z)$ is the escape rate for the left or right minimum of $V(x, z)$. If $\Delta V_{1,2}(z) = V(0, z) - V(\mp x_m, z)$ is the depth of the potential, $r_{1,2}(z) \propto \exp[\Delta V_{1,2}(z)/T]$. For (3) we can again discuss the two limiting cases of large or small τ . For large τ , the average occupancy is $\bar{n}(\tau \rightarrow \infty) = n_\infty = \int dz q_0(z)n(z)$ where $n(z) = r_1(z)/[r_1(z) + r_2(z)]$. For small τ , the particle feels average rates and the mean occupancy is $\bar{n}(\tau = 0) = n_0 = \bar{r}_1/(\bar{r}_1 + \bar{r}_2)$ where $\bar{r}_i = \int dz r_i(z)q_0(z)$. For the results presented in Fig. 1 the potential has been chosen such that n_0 is larger than n_∞ and also larger than the occupancy determined by the average potential $\langle V \rangle(x)$. This explains qualitatively the τ dependence of \bar{n} in Fig. 1. Let us now compare the results of the rate Eq. (3) with the results of the Fokker-Planck equation quantitatively. To calculate the stationary probability \bar{n} as a function of τ from (3), we use the Fokker-Planck equation for the density $p(n, z, t)$,

$$\frac{\partial p(n, z, t)}{\partial t} = \frac{\partial}{\partial n} \{ [r_1(z) + r_2(z)]n - r_2(z) \} p(n, z, t) + M_z p(n, z, t). \quad (4)$$

The stationary probability $\bar{n} = \int_0^1 dn np_0(n)$ can be obtained from the stationary distribution $p(n, z)$. It is possible to calculate the stationary distribution $p_0(n) = \int dz p(n, z)$ for a dichotomous process [13],

$$p_0(n) = C(n - \bar{n})(n - n_-)^{\alpha_- - 1}(n_+ - n)^{\alpha_+ - 1}, \quad (5)$$

where

$$\alpha_\pm = \frac{(p_+ r_+ + p_- r_-)(n_\pm - n_0)}{\tau r_+ r_- (n_+ - n_-)}, \quad (6)$$

$$\bar{n} = \frac{r_{2+} - r_{2-}}{r_+ - r_-}. \quad (7)$$

C is a normalization constant. We introduced $r_\pm = r_{1\pm} + r_{2\pm}$. $r_{i\pm}$ are the two values for the fluctuating rates $r_i(z)$, and $n_\pm = r_{2\pm}/r_\pm$. The rates are given by (see [5], where T and L are set to unity; L_{eff} occurs instead of L , since we do not have a linear ramp)

$$r_{i\pm} = \frac{\Delta V_{i\pm}^2 L_{\text{eff}}^2}{T} [\exp(\Delta V_{i\pm}/T) - \Delta V_{i\pm}/T - 1]^{-1}. \quad (8)$$

$p_0(n)$ vanishes outside the interval between n_- and n_+ as it should have been expected. \bar{n} does not lie in this interval. For \bar{n} one obtains

$$\bar{n} = n_0 + (n_\infty - n_0) \frac{\tau}{\bar{\tau} + \tau}, \quad (9)$$

where $\bar{\tau} = \frac{p_+}{r_-} + \frac{p_-}{r_+}$. This shows that for a dichotomous process one always has a monotonic behavior of \bar{n} as a function of τ and the characteristic time scale for the transition from n_0 to n_∞ is given by $\bar{\tau}$. For more general noise processes it is possible to calculate \bar{n} as well. The calculation is much more involved, but the typical behavior of \bar{n} is the same as for the dichotomous case [13]. In Figs. 1

and 2 we compare results of the effective rate equations with results of the fluctuating potential. The agreement is indeed excellent for sufficiently large τ . The value of τ where the transition occurs, and the value of the maximum of \bar{n} agree well with the exact results. The agreement between the rate theory and the exact results becomes better for smaller temperatures (see Fig. 2), which is clear since the rate equations are valid only for low temperatures. The motion in the average potential, i.e., the behavior of the system for small τ , cannot be described this way, since the rates in the average potential differ from the averaged rates. The validity of the two-state model breaks down when τ becomes smaller than the intrawell relaxation times. Nevertheless, we are able to understand why the occupancy \bar{n} in the minimum that has usually the higher energy has the features shown in Fig. 1. Using the average potential, the average rate, and the average occupancy we are able to calculate analytically the three values of \bar{n} . The transition between these values occurs at τ scales given by the intrawell relaxation time and by $\bar{\tau}$. This also explains the results in Fig. 2, which shows how the effect depends on the temperature. For lower values of the temperature, $\bar{\tau}$ becomes larger, and the values of n change due to the dependence of the rates on T .

Comparing the above results with calculations for the mean first passage time shows that the noise induced stability is related to resonant activation. To calculate the mean first passage time, one has to introduce an absorbing boundary at the maximum of the potential and has to solve the Fokker-Planck equation with this boundary. The mean first passage time depends on the initial condition $\rho(x, z, 0)$, but usually the relaxation within the potential well is fast compared to the mean first passage time and the dependence on the initial condition is weak. As the initial condition we choose $\rho(x, z, 0) = \delta(x - x_i)\delta(z - z_i)$

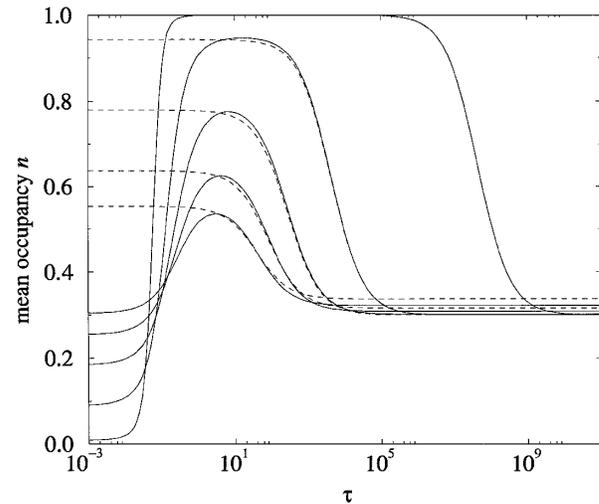


FIG. 2. \bar{n} as a function of τ for $p_+ = 0.7$ and $T = 0.1, 0.2, 0.3, 0.4, 0.5$ (from top to bottom). The potential is the same as in Fig. 1. The dashed lines are the results from (9)

with $x_i = \pm x_m$. Let $x = 0$ be the absorbing boundary. The solution of the Fokker-Planck equation is denoted by $\rho(x, z, t|x_i, z_i, 0)$. The mean first passage time is then given by [14]

$$\tau_{\text{MFPT}} = \int dz \int_{-\infty}^0 dx \rho_1(x, z|x_i), \quad (10)$$

where

$$\rho_1(x, z|x_i) = -\left\langle \int_0^\infty t \frac{\partial}{\partial t} \rho(x, z, t|x_i, z_i, 0) \right\rangle_{z_i}. \quad (11)$$

The average is taken with respect to the stationary distribution of z_i . For a piecewise linear potential $\rho_1(x, z|x_i)$ can be calculated using the same methods as for $\rho(x, z)$ described above. Bier and Astumian [5] calculated the mean first passage time for a linear ramp, which is similar to our situation. They showed that for not too small τ the system is well described by simple rate equations, as in our case as well. Using the rate equations one obtains for the mean first passage times [Eq. (15) in Ref. 5]

$$\tau_{\text{MFPT}}(\tau) = \tau_{0i} + (\tau_{\infty i} - \tau_{0i}) \frac{\tau}{\tau_{\infty i} + \tau}, \quad (12)$$

where $\tau_{0i} = \bar{r}_i^{-1}$ and $\tau_{\infty i} = p_+/r_{i-} + p_-/r_{i+}$. The τ dependence of the mean first passage time is similar to the τ dependence of \bar{n} in (9). The characteristic time $\bar{\tau}$ has the same form as $\tau_{\infty i}$.

As already pointed out, it is possible to extend our calculations to various noise processes. The main qualitative features of the system are the same. Our results show that an asymmetric, fluctuating, bistable system can detect fluctuations that are not too slow and not too fast. For such fluctuations the occupancy of the state that has usually the higher energy is enhanced. The results show that this effect may be very large, depending on the parameters of the system. For the largest value of p_+ in Fig. 1, the mean occupancy in the left minimum is very small for slow and fast fluctuations, but reaches a large value for intermediate values of τ . If one lowers the temperature or modifies the potential it is possible to obtain an even larger effect, as shown in Fig. 2.

To some extent noise induced stability can be compared to noise enhanced stability first found numerically by Dayan et al. [15] and observed experimentally by Mantegna and Spagnolo [16], but there are several differences. The effect called noise enhanced stability in [16] is observed in a periodically driven system with a single, metastable minimum. The system remains in the metastable minimum for some time given by the mean first passage time for the barrier, and the mean first passage time has a maximum at some noise

intensity. This effect is related to stochastic resonance. In our case the potential fluctuates stochastically with some correlation time τ and has two minima. The less stable minimum is the absolute minimum in some configurations of the potential, but most of the time this minimum is metastable. Nevertheless, it can be highly occupied.

As mentioned above Astumian and Robertson investigated a two-state model with periodically modulated rates to describe the effect of an oscillating electric field on membrane proteins. Their results are in qualitative agreement with our results for the model with dichotomously fluctuating rates. One should expect that our results for the motion of a particle in a fluctuating potential, described by a Fokker-Planck equation, are relevant for such biologically motivated models. This is important, because the description by a Fokker-Planck equation is much more general. Furthermore, for large frequencies or small correlation times the system feels an average potential that cannot be described by fluctuating rates.

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