# Escape Problems & Stochastic Resonance

18.S995 - L08 & 09

dunkel@mit.edu

# Examples

Illustration by J.P. Cartailler. Copyright 2007, Symmation LLC.



http://evolutionarysystemsbiology.org/intro/

dunkel@math.mit.edu

#### Reaction-rate theory: fifty years after Kramers

Peter Hänggi

Lehrstuhl für Theoretische Physik, University of Augsburg, D-8900 Augsburg, Federal Republic of Germany

Peter Talkner\*

Department of Physics, University of Basel, CH-4056 Basel, Switzerland

Michal Borkovec

Institut für Lebensmittelwissenschaft, ETH-Zentrum, CH-8092 Zürich, Switzerland



FIG. 3. Potential U(x) with two metastable states A and C. Escape occurs via the forward rate  $k^+$  and the backward rate  $k^-$ , respectively, and  $E_b^{\pm}$  are the corresponding activation energies.

## Arrhenius law

 $k = v \exp(-\beta E_b)$ 



FIG. 2. Van't Hoff-Arrhenius plots of reaction-rate data for two different physical systems in which both thermal activation and tunneling events occur: (a) Rate of CO migration to a separated  $\beta$  chain of hemoglobin (Alberding *et al.*, 1976; Frauenfelder, 1979); (b) diffusion coefficient D of atomic hydrogen moving on the (110) plane of tungsten at a relative *H*-coverage of 0.1 (data taken from DiFoggio and Gomer, 1982). The diffusion D is directly proportional to the hopping rate k.



dunkel@math.mit.edu

0.5

# Using fitness landscapes to visualize evolution in action

A film by Randy Olson and Bjørn Østman

https://www.youtube.com/watch?v=4pdiAneMMhU





#### Freund et al (2002) J Theor Biol



- unu

#### Freund et al (2002) J Theor Biol

mm





Horizontal distance (mm)

Russel et al (1999) Nature

#### Freund et al (2002) J Theor Biol



sensory system. However, stochastic resonance requires an external source of electrical noise in order to function. A swarm of plankton, for example *Daphnia*, can provide the required noise. We hypothesize that juvenile paddlefish can detect and attack single *Daphnia* as outliers in the vicinity of the swarm by using noise from the swarm itself. From the power spectral density of the noise plus the weak signal from a single *Daphnia*, we calculate the signal-to-noise ratio, Fisher information and discriminability at the surface of the paddlefish's rostrum. The results predict a specific attack pattern for the paddlefish that appears to be experimentally testable.

#### 1.4.1 Generic minimal model

Consider the over-damped SDE  $\,$ 

$$dx(t) = -\partial_x U dt + \sqrt{2D} * dB(t)$$
(1.68a)

with a confining potential U(x)

$$\lim_{x \to \pm \infty} U(x) \to \infty \tag{1.68b}$$

that has two (or more) minima and maxima. A typical example is the bistable quartile double-well

$$U(x) = -\frac{a}{2}x^2 + \frac{b}{4}x^4 , \qquad a, b > 0$$
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with minima at  $\pm \sqrt{a/b}$ .

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Generally, we are interested in characterizing the transitions between neighboring minima in terms of a rate k (units of time<sup>-1</sup>) or, equivalently, by the typical time required for escaping from one of the minima. To this end, we shall first dicuss the general structure of the time-dependent solution of the FPE<sup>14</sup> for the corresponding PDF p(t, x), which reads

$$\partial_t p = -\partial_x j$$
,  $j(t,x) = -[(\partial_x U)p + D\partial_x p],$  (1.68d)

and has the stationary zero-current  $(j \equiv 0)$  solution

$$p_s(x) = \frac{e^{-U(x)/D}}{Z}, \qquad Z = \int_{-\infty}^{+\infty} dx \ e^{-U(x)/D}.$$
 (1.69)

## General time-dependent solution

$$\partial_t p = -\partial_x j$$
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To find the time-dependent solution, we can make the ansatz

$$p(t,x) = \varrho(t,x) e^{-U(x)/(2D)}, \qquad (1.70)$$

which leads to a Schrödinger equation in imaginary time

$$-\partial_t \varrho = \left[-D\partial_x^2 + W(x)\right] \varrho =: \mathcal{H}\varrho, \qquad (1.71a)$$

with an effective potential

$$W(x) = \frac{1}{4D} (\partial_x U)^2 - \frac{1}{2} \partial_x^2 U.$$
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Assuming the Hamilton operator  $\mathcal{H}$  has a discrete non-degenerate spectrum,  $\lambda_0 < \lambda_1 < \ldots$ , the general solution p(t, x) may be written as

$$p(t,x) = e^{-U(x)/(2D)} \sum_{n=0}^{\infty} c_n \phi_n(x) e^{-\lambda_n t},$$
(1.72a)

where the eigenfunctions  $\phi_n$  of  $\mathcal{H}$  satisfy

$$\int dx \,\phi_n^*(x) \,\phi_m(x) = \delta_{nm},\tag{1.72b}$$

and the constants  $c_n$  are determined by the initial conditions

$$c_n = \int dx \ \phi_n^*(x) \ e^{U(x)/(2D)} \ p(0,x). \tag{1.72c}$$

## General time-dependent solution

$$p(t,x) = e^{-U(x)/(2D)} \sum_{n=0}^{\infty} c_n \phi_n(x) e^{-\lambda_n t}$$

At large times,  $t \to \infty$ , the solution (1.72a) must approach the stationary solution (1.69), implying that

$$\lambda_0 = 0$$
,  $c_0 = \frac{1}{\sqrt{Z}}$ ,  $\phi_0(x) = \frac{e^{-U(x)/(2D)}}{\sqrt{Z}}$ . (1.73)

Note that  $\lambda_0 = 0$  in particular means that the first non-zero eigenvalue  $\lambda_1 > 0$  dominates the relaxation dynamics at large times and, therefore,

$$\tau_* = 1/\lambda_1 \tag{1.74}$$

is a natural measure of the escape time. In practice, the eigenvalue  $\lambda_1$  can be computed by various standard methods (WKB approximation, Ritz method, techniques exploiting supersymmetry, etc.) depending on the specifics of the effective potential W.

#### 1.4.2 Two-state approximation

We next illustrate a commonly used simplified description of escape problems, which can be related to (1.74). As a specific example, we can again consider the escape of a particle from the left well of a symmetric quartic double well-potential

$$U(x) = -\frac{a}{2}x^2 + \frac{b}{4}x^4 , \qquad p(0,x) = \delta(x - x_-)$$
(1.75a)

where

$$x_{-} = -\sqrt{a/b} \tag{1.75b}$$

is the location of the left minimum, but the general approach is applicable to other types of potentials as well.

The basic idea of the two-state approximation is to project the full FPE dynamics onto simpler set of master equations by considering the probabilities  $P_{\pm}(t)$  of the coarse-grained particle-states 'left well' (-) and 'right well' (+), defined by

$$P_{-}(t) = \int_{-\infty}^{0} dx \, p(t, x), \qquad (1.76a)$$

$$P_{+}(t) = \int_{0}^{\infty} dx \, p(t, x).$$
 (1.76b)





If all particles start in the left well, then

Whilst the exact dynamics of  $P_{\pm}(t)$  is governed by the FPE (1.68d), the two-state approximation assumes that this dynamics can be approximated by the set of master equations<sup>15</sup>

$$\dot{P}_{-} = -k_{+}P_{-} + k_{-}P_{+}, \qquad \dot{P}_{+} = k_{+}P_{-} - k_{-}P_{+}.$$
 (1.78)

For a symmetric potential, U(x) = U(-x), forward and backward rates are equal,  $k_+ = k_- = k$ , and in this case, the solution of Eq. (1.78) is given by

$$P_{\pm}(t) = \frac{1}{2} \mp \frac{1}{2} e^{-2kt}.$$
(1.79)



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For comparison, from the FPE solution (1.72a), we find in the long-time limit

$$p(t,x) \simeq p_s(x) + c_1 e^{-U(x)/2D} \phi_1(x) e^{-\lambda_1 t},$$
 (1.80)

Due to the symmetry of  $p_s(x)$ , we then have

$$P_{-}(t) \simeq \frac{1}{2} + C_1 e^{-\lambda_1 t}$$
 (1.81a)

<sup>15</sup>Note that Eqs. (1.78) conserve the total probability,  $P_{-}(t) + P_{-}(t) = 1$ .



Solution

$$P_{-}(t) \simeq \frac{1}{2} + C_1 e^{-\lambda_1 t}$$

where

$$C_1 = c_1 \int_{-\infty}^0 e^{-U(x)/2D} \phi_1(x) , \qquad c_1 = \phi_1^*(x_-) e^{U(x_-)/(2D)}.$$
(1.81b)

Since Eq. (1.81a) neglects higher-order eigenfunctions,  $C_1$  is in general not exactly equal but usually close to 1/2. But, by comparing the time-dependence of (1.81a) and (1.79), it is natural to identify

$$k \simeq \frac{\lambda_1}{2} = \frac{1}{2\tau_*}.\tag{1.82}$$

We next discuss, by considering in a slightly different setting, how one can obtain an explicit result for the rate k in terms of the parameters of the potential U.



#### 1.4.3 Constant-current solution

Consider a bistable potential as in Eq. (1.75), but now with a particle source at  $x_0 < x_- < 0$ and a sink<sup>16</sup> at  $x_1 > x_b = 0$ . Assuming that particles are injected at  $x_0$  at constant flux  $j(t, x) \equiv J = const$ , the escape rate can be defined by

$$k := \frac{J}{P_-},\tag{1.83}$$

with  $P_{-}$  denoting the probability of being in the left well, as defined in Eq. (1.76a) above. To compute the rate from Eq. (1.83), we need to find a stationary constant flux solution  $p_J(x)$  of Eq. (1.68d), satisfying  $p_J(x_1) = 0$  and

$$J = -(\partial_x U)p_J - D\partial_x p_J \tag{1.84}$$

for some constant J. This solution is given by [HTB90]

$$p_J(x) = \frac{J}{D} e^{-U(x)/D} \int_x^{x_1} dy \ e^{U(y)/D}, \qquad (1.85)$$

as one can verify by differentiation

$$-(\partial_x U)p_J - D\partial_x p_J = -(\partial_x U)p_J - D\partial_x \left[\frac{J}{D}e^{-U(x)/D}\int_x^{x_1} dy \ e^{U(y)/D}\right]$$
$$= -(\partial_x U)p_J - J \left[-\frac{(\partial_x U)}{D}e^{-U(x)/D}\int_x^{x_1} dy \ e^{U(y)/D} - 1\right]$$
$$= J.$$
(1.86)

Therefore, the inverse rate  $k^{-1}$  from Eq. (1.83) can be formally expressed as

$$k^{-1} = \frac{P_{-}}{J} = \frac{1}{D} \int_{-\infty}^{x_{1}} dx \ e^{-U(x)/D} \int_{x}^{x_{1}} dy \ e^{U(y)/D}, \qquad (1.87)$$

and a partial integration yields the equivalent representation

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Assuming a sufficiently steep barrier, the integrals in Eq. (1.88) may be evaluated by adopting steepest descent approximations near the potential minimum at  $x_{-}$  and near the maximum at the barrier position  $x_b$ . More precisely, taking into account that  $U'(x_{-}) =$  $U'(x_b) = 0$ , one can replace the potentials in the exponents by the harmonic approximations

$$U(x) \simeq U(x_{-}) - \frac{1}{2\tau_b}(x - x_{-})^2,$$
 (1.89a)

$$U(y) \simeq U(x_{-}) + \frac{1}{2\tau_{-}}(y - x_{-})^{2},$$
 (1.89b)

where

$$\tau_{-} = -U''(x_0) > 0 , \qquad \tau_b = U''(x_b) > 0$$
 (1.90)

carry units of time. Inserting (1.89) into (1.88) and replacing the upper integral boundaries by  $+\infty$ , one thus obtains the so-called Kramers rate [HTB90, GHJM98]



- 1. a nonlinear measurement device 17,
- 2. a periodic signal weaker than the threshold of measurement device,
- 3. additional input noise, uncorrelated with the signal of interest.



dunkel@math.mit.edu

#### 1.5.1 Generic model

To illustrate SR more quantitatively, consider the periodically driven SDE

$$dX(t) = -\partial_x U \, dt + A \cos(\Omega t) \, dt + \sqrt{2D} * dB(t), \qquad (1.93a)$$

where A is the signal amplitude and

$$U(x) = -\frac{a}{2}x^2 + \frac{b}{4}x^4$$
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$$x' = x/x_*$$
,  $t' = at$ ,  $A' = A/(ax_*)$ ,  $D' = D/(ax_*^2)$ ,  $\Omega' = \Omega/a$ .

and dropping primes. we can rewrite (1.93a) in the dimensionless form

$$dX(t) = (x - x^3) dt + A\cos(\Omega t) dt + \sqrt{2D} * dB(t), \qquad (1.93c)$$

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with a rescaled barrier height  $\Delta U = 1/4$ . The associated FPE reads

$$\partial_t p = -\partial_x \{ [-(\partial_x U) + A\cos(\Omega t)] p - D\partial_x p \}.$$
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$$\partial_t p = -\partial_x \{ [-(\partial_x U) + A\cos(\Omega t)] p - D\partial_x p \}.$$
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For our subsequent discussion, it is useful to rearrange terms on the rhs. as

$$\partial_t p = \partial_x [(\partial_x U)p + D\partial_x p] - A\cos(\Omega t)\partial_x p.$$
(1.95)

## Perturbation theory

$$\partial_t p = \partial_x [(\partial_x U)p + D\partial_x p] - A\cos(\Omega t)\partial_x p.$$
(1.95)

To solve Eq. (1.95) perturbatively, we insert the series ansatz

$$p(t,x) = \sum_{n=0}^{\infty} A^n p_n(t,x),$$
(1.96)

which gives

$$\sum_{n=0}^{\infty} A^n \partial_t p_n = \sum_{n=0}^{\infty} \left\{ A^n \partial_x [(\partial_x U) p_n + D \partial_x p_n] - A^{n+1} \cos(\Omega t) \partial_x p_n \right\}$$
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Focussing on the liner response regime, corresponding to powers  $A^0$  and  $A^1$ , we find

$$\partial_t p_0 = \partial_x [(\partial_x U) p_0 + D \partial_x p_0]$$
 (1.98a)

$$\partial_t p_1 = \partial_x [(\partial_x U)p_1 + D\partial_x p_1] - \cos(\Omega t)\partial_x p_0 \qquad (1.98b)$$

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Equation (1.98a) is just an ordinary time-independent FPE, and we know its stationary solution is just the Boltzmann distribution

$$p_0(x) = \frac{e^{-U(x)/D}}{Z_0}$$
,  $Z_0 = \int dx \, e^{-U(x)/D}$  (1.99)

$$\partial_t p_1 = \partial_x [(\partial_x U)p_1 + D\partial_x p_1] - \cos(\Omega t)\partial_x p_0$$
 (1.98b)

To obtain a formal solution to Eq. (1.98b), we make use of the following ansatz

$$p_1(t,x) = e^{-U(x)/(2D)} \sum_{m=1}^{\infty} a_{1m}(t) \phi_m(x), \qquad (1.100)$$

where  $\phi_m(x)$  are the eigenfunctions of the unperturbed effective Hamiltonian, cf. Eq. (1.71),

$$\mathcal{H}_{0} = -D\partial_{x}^{2} + \frac{1}{4D}(\partial_{x}U)^{2} - \frac{1}{2}\partial_{x}^{2}U.$$
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Inserting (1.100) into Eq. (1.98b) gives

$$\sum_{m=1}^{\infty} \dot{a}_{1m} \phi_m = -\sum_{m=1}^{\infty} \lambda_m a_{1m} \phi_m - \cos(\Omega t) \ e^{U(x)/(2D)} \ \partial_x p_0.$$
(1.102)

$$\partial_t p_1 = \partial_x [(\partial_x U)p_1 + D\partial_x p_1] - \cos(\Omega t)\partial_x p_0$$
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(1.102)

Multiplying this equation by  $\phi_n(x)$ , and integrating from  $-\infty$  to  $+\infty$  while exploiting the orthonormality of the system  $\{\phi_m\}$ , we obtain the coupled ODEs

$$\dot{a}_{1m} = -\lambda_m a_{1m} - M_{m0} \cos(\Omega t), \qquad (1.103)$$

with 'transition matrix' elements

$$M_{m0} = \int dx \ \phi_m \ e^{U(x)/(2D)} \partial_x p_0.$$
 (1.104)

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with 'transition matrix' elements

$$M_{m0} = \int dx \ \phi_m \ e^{U(x)/(2D)} \partial_x p_0.$$
 (1.104)

The asymptotic solution of Eq. (1.103) reads

$$a_{1m}(t) = -M_{m0} \left[ \frac{\Omega}{\lambda_m^2 + \Omega^2} \sin(\Omega t) + \frac{\lambda_m}{\lambda_m^2 + \Omega^2} \cos(\Omega t) \right].$$
(1.105)

Note that, because  $\partial_x p_0$  is an antisymmetric function, the matrix elements  $M_{m0}$  vanish<sup>18</sup> for even values  $m = 0, 2, 4, \ldots$ , so that only the contributions from odd values  $m = 1, 3, 5 \ldots$  are asymptotically relevant.

Focussing on the leading order contribution, m = 1, and noting that  $p_0(x) = p_0(-x)$ , we can estimate the position mean value

$$\mathbb{E}[X(t)] = \int dx \, p(t,x) \, x \tag{1.106}$$

from

$$\mathbb{E}[X(t)] \simeq A \int dx \, p_1(t, x) \, x$$
  
$$\simeq A \int dx \, e^{-U(x)/(2D)} \, a_{11}(t) \, \phi_1(x) \, x$$
  
$$= -AM_{10} \left[ \frac{\Omega}{\lambda_1^2 + \Omega^2} \sin(\Omega t) + \frac{\lambda_1}{\lambda_1^2 + \Omega^2} \cos(\Omega t) \right] \int dx \, e^{-U(x)/(2D)} \, \phi_1(x) \, x$$

Focussing on the leading order contribution, m = 1, and noting that  $p_0(x) = p_0(-x)$ , we can estimate the position mean value

$$\mathbb{E}[X(t)] = \int dx \, p(t, x) \, x \tag{1.106}$$

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Using  $\lambda_1 = 2k_{\rm K}$ , where  $k_{\rm K}$  is the Kramers rate from Eq. (1.91), we can rewrite this more compactly as

$$\mathbb{E}[X(t)] = \overline{X}\cos(\Omega t - \overline{\varphi}) \tag{1.107a}$$

with phase shift

$$\overline{\varphi} = \arctan\left(\frac{\Omega}{2k_{\rm K}}\right) \tag{1.107b}$$

and amplitude

$$\overline{X} = -A \frac{M_{10}}{(4k_{\rm K}^2 + \Omega^2)^{1/2}} \int dx \, e^{-U(x)/(2D)} \, \phi_1(x) \, x.$$
(1.107c)

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The amplitude  $\overline{X}$  depends on the noise strength D through  $k_{\rm K}$ , through the integral factor and also through the matrix element

$$M_{10} = \int dx \,\phi_1 \, e^{U(x)/(2D)} \partial_x p_0. \tag{1.108}$$

To compute  $\overline{X}$ , one first needs to determine the eigenfunction  $\phi_1$  of  $\mathcal{H}_0$  as defined in Eq. (1.101). For the quartic double-well potential (1.93b), this cannot be done analytically but there exist standard techniques (e.g., Ritz method) for approximating  $\phi_1$  by functions that are orthogonal to  $\phi_0 = \sqrt{p_0/Z_0}$ . Depending on the method employed, analytical

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$$\overline{X} \simeq \frac{Aa}{Db} \left( \frac{4k_{\rm K}^2}{4k_{\rm K}^2 + \Omega^2} \right)^{1/2}, \qquad (1.109)$$

which exhibits a maximum for a critical value  $D_*$  determined by

$$4k_{\rm K}^2 = \Omega^2 \left(\frac{\Delta U}{D_*} - 1\right). \tag{1.110}$$

That is, the value  $D_*$  corresponds to the optimal noise strength, for which the mean value  $\mathbb{E}[X(t)]$  shows maximal response to the underlying periodic signal – hence the name 'stochastic resonance' (SR).

#### 1.5.2 Master equation approach

Similar to the case of the escape problem, one can obtain an alternative description of SR by projecting the full FPE dynamics onto a simpler set of master equations for the probabilities  $P_{\pm}(t)$  of the coarse-grained particle-states 'left well' (-) and 'right well' (+), as defined by Eq. (1.76). This approach leads to the following two-state master equations with time-dependent rates

$$\dot{P}_{-}(t) = -k_{+}(t) P_{-} + k_{-}(t) P_{+},$$
 (1.111a)

$$\dot{P}_{+}(t) = k_{+}(t) P_{-} - k_{-}(t) P_{+}.$$
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The general solution of this pair of ODEs is given by [GHJM98]

$$P_{\pm}(t) = g(t) \left[ P_{\pm}(t_0) + \int_{t_0}^t ds \, \frac{k_{\pm}(s)}{g(s)} \right]$$
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where

$$g(t) = \exp\left\{-\int_{t_0}^t ds \left[k_+(s) + k_-(s)\right]\right\}.$$
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To discuss SR within this framework, it is plausible to postulate time-dependent Arrheniustype rates,

$$k_{\pm}(t) = k_{\rm K} \exp\left[\pm \frac{Ax_*}{D} \cos(\Omega t)\right]. \tag{1.113}$$

Adopting these rates and considering the asymptotic limit  $t_0 \to -\infty$ , one can Taylorexpand the exact solution (1.112) for  $Ax_* \ll D$  to obtain

$$P_{\pm}(t) = k_{\rm K} \left[ 1 \pm \frac{Ax_*}{D} \cos(\Omega t) + \left(\frac{Ax_*}{D}\right)^2 \cos^2(\Omega t) \pm \dots \right].$$
(1.114)

These approximations are valid for slow driving (adiabatic regime), and they allow us to compute expectation values to leading order in  $Ax_*/D$ . In particular, one then finds for the mean position the asymptotic linear response result [GHJM98]

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$$\mathbb{E}[X(t)] = \overline{X}\cos(\Omega t - \overline{\varphi}) \tag{1.115a}$$

where

$$\overline{X} = \frac{Ax_*^2}{D} \left(\frac{4k_{\rm K}^2}{4k_{\rm K}^2 + \Omega^2}\right)^{1/2} , \qquad \overline{\varphi} = \arctan\left(\frac{\Omega}{2k_{\rm K}}\right) \tag{1.115b}$$

with  $k_{\rm K}$  denoting Kramers rate as defined in Eq. (1.91). Note that Eqs. (1.115) are consistent with our earlier result (1.107).