Stochastic Equations and Processes in physics and biology

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Examples of stochastic processes

Random walk in one dimension

A walker moves along a line and makes one step at a time of a fixed length Δ either to the left or to the right with equal probability of $1/2$. The time intervals between two subsequent steps is δt.
Transitional probability $p(x, t+1|y, t)$

$$p(x, t+\delta t|y, t) = \begin{cases} \frac{1}{2}, & \text{if} \quad \mid x - y \mid = \Delta \\ 0, & \text{otherwise} \end{cases}$$

For simplicity assume

$$\Delta = \pm 1, \quad \delta t = 1, \quad x_0 = 0, \quad t_0 = 0$$

Random walk in one dimension

Master equation

$$p(i, t+1|0,0) = \frac{1}{2}(p(i-1, t|0,0) + p(i+1, t|0,0)).$$

Random walk in 1D

TIME \ x	-8	-7	-6	-5	-4	-3	-2	-1	0	1	2	3	4	5	6	7	8
0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	$\frac{1}{2}$	0	$\frac{1}{2}$	0	0	0	0	0	0	0
2	0	0	0	0	0	0	$\frac{1}{4}$	0	$\frac{2}{4}$	0	$\frac{1}{4}$	0	0	0	0	0	0
3	0	0	0	0	0	$\frac{1}{8}$	0	$\frac{3}{8}$	0	$\frac{3}{8}$	0	$\frac{1}{8}$	0	0	0	0	0
4	0	0	0	0	$\frac{1}{16}$	0	$\frac{4}{16}$	0	$\frac{6}{16}$	0	$\frac{4}{16}$	0	$\frac{1}{16}$	0	0	0	0
5	0	0	0	$\frac{1}{32}$	0	$\frac{5}{32}$	0	$\frac{10}{32}$	0	$\frac{10}{32}$	0	$\frac{5}{32}$	0	$\frac{1}{32}$	0	0	0
6	0	0	$\frac{1}{64}$	0	$\frac{6}{64}$	0	$\frac{15}{64}$	0	$\frac{20}{64}$	0	$\frac{15}{64}$	0	$\frac{6}{64}$	0	$\frac{1}{64}$	0	0
7	0	$\frac{1}{128}$	0	$\frac{7}{128}$	0	$\frac{21}{128}$	0	$\frac{35}{128}$	0	$\frac{35}{128}$	0	$\frac{21}{128}$	0	$\frac{7}{128}$	0	$\frac{1}{128}$	0

Binomial coefficients: $C_n^k = \frac{n!}{k!\,(n-k)!}$

Random walk in one dimension

Pascal's triangle

$$
\begin{array}{ccccccccccc}
 & & & & & 1 & & & & & \\
 & & & & 1 & & 1 & & & & \\
 & & & 1 & & 2 & & 1 & & & \\
 & & 1 & & 3 & & 3 & & 1 & & \\
 & 1 & & 4 & & 6 & & 4 & & 1 & \\
1 & & 5 & & 10 & & 10 & & 5 & & 1
\end{array}
$$

Binomial coefficients

$$C_n^k = \frac{n!}{k!(n-k)!} = \binom{k}{n}$$

Random walk in one dimension

General solution

$$p(i,t|0,0) = \left(\frac{1}{2}\right)^t C_t^{(i+t)/2},$$

with

$$C_n^k = \begin{cases} \frac{n!}{k!(n-k)!}, & \text{integer } n \geq k \\ 0, & \text{otherwise} \end{cases}$$

$$\begin{aligned} t &= 0 \ldots p_0 = C_0^0 = 1 \\ t &= 1 \ldots p_0 = C_1^{1/2} = 0, \;\; p_1 = C_1^1 = p_{-1} = C_1^0 = 1/2 \end{aligned}$$

Solution using discrete Fourier transfrom

Discrete Fourier transform

$$p(i,t|0,0)=\sum_k \hat{p}_k(t)e^{-Iik}, \quad I=\sqrt{-1}$$

Note that

$$p(i+1,t|0,0)=\sum_k \hat{p}_k(t)e^{-Iik}e^{-Ik},\ p(i-1,t|0,0)=\sum_k \hat{p}_k(t)e^{-Iik}e^{Ik}$$

Master equation

$$\sum_k \hat{p}_k(t+1)e^{-Iik}=\sum_k \frac{1}{2}\hat{p}_k(t)e^{-Iik}\left(e^{-Ik}+e^{Ik}\right).$$

In the Fourier space: geometric series for $\hat{p}_k(t)$

$$\hat{p}_k(t+1)=\frac{1}{2}\hat{p}_k(t)\left(e^{-Ik}+e^{Ik}\right).$$

Solution using discrete Fourier transfrom

Solution in the Fourier space

$$\hat{p}_k(t) = \hat{p}^{(0)}(k)\left(\frac{e^{-Ik}+e^{Ik}}{2}\right)^t.$$

Back to the real space

$$p(i,t|0,0) = \sum_k e^{Iik}\hat{p}^{(0)}(k)\left(\frac{e^{-Ik}+e^{Ik}}{2}\right)^t.$$

Initial conditions: $p(i,t|0,0) = \delta_{i,0}$

$$p(i,t|0,0) = \sum_k e^{Iik}\hat{p}^{(0)}(k) = \delta_{i,0} = \left\{\begin{array}{ll} 0, & i \neq 0 \\ 1, & i = 0 \end{array}\right.$$

Solution using discrete Fourier transfrom

Binomial formulae

$$(a+b)^t = \sum_{m=0}^{t} C_t^m a^m b^{t-m}$$

Discrete times

$$t = 0, 1, 2, 3, 4, \ldots$$

Solution using discrete Fourier transfrom

In the real space

$$p(i,t|0,0) = \sum_k \hat{p}^{(0)}(k) \sum_{m=0}^{t} \left(\frac{1}{2}\right)^t C_t^m \, e^{Iik - Ikm + Ik(t-m)}.$$

Note that

$$\sum_k \hat{p}^{(0)}(k) e^{Ik(i-m+t-m)} = \begin{cases} 0, & m \neq (i+t)/2 \\ 1, & m = (i+t)/2 \end{cases}$$

Final answer

$$p(i,t|0,0) = \sum_{m=0}^{t} \delta_{m,(i+t)/2} \left(\frac{1}{2}\right)^t C_t^m = \left(\frac{1}{2}\right)^t C_t^{(i+t)/2}$$

Exercise: random walk on a circle

Example

Solve the master equation for a random walk on a circle. Hint: use discrete Fuorier transform of a finite length array:

Forward transformation

$$\hat{p}_k = \sum_{i=0}^{N} p_i \exp\left(\frac{2\pi I i k}{N}\right).$$

Backward transformation

$$p_i = \frac{1}{N} \sum_{i=0}^{N} \hat{p}_k \exp\left(\frac{-2\pi I i k}{N}\right).$$

Normalization and completeness

$$\frac{1}{N} \sum_{i=0}^{N} \exp\left(\frac{2\pi I i k}{N}\right) = \delta_{k,0}.$$

Mean exit time

Stochastic process $x(t) \in [a, b]$ **with absorbing boundaries** a, b

$$\Pr(x = a) = \Pr(x = b) = 0 \;\text{ at all times}$$

Initial conditions

$$x(t = 0) = x_0 \in [a, b]$$

Exit time

$t \ldots$ time that it takes to exit the interval $[a, b]$ (random variable)

$$\Pr(t \le \tau) = \int_0^\tau \mathrm{pdf}_{\mathrm{exit}}(t)\, dt$$

Survival probability

$P_s(\tau) \ldots$ Probability that $x(t)$ is still in $[a, b]$ after τ seconds.

Mean exit time

Relation between survival and exit probabilities

$$\begin{aligned} P_s(\tau) &= 1 - \Pr(t \le \tau) \\ P_s(\tau) &= \int_0^\tau \mathrm{pdf}_s(t)\, dt \\ \Pr(t \le \tau) &= \int_0^\tau \mathrm{pdf}_{\mathrm{exit}}(t)\, dt \\ \mathrm{pdf}_s(\tau) &= P_s(\tau)' = -\mathrm{pdf}_{\mathrm{exit}}(\tau) \end{aligned}$$

Mean exit time

$$\begin{aligned} \langle t \rangle &= \int_0^\infty t\, \mathrm{pdf}_{\mathrm{exit}}(t)\, dt \\ &= t\, \mathrm{pdf}_{\mathrm{exit}}(t)|_0^\infty - \int_0^\infty P \left(\int \mathrm{pdf}_{\mathrm{exit}}(t)\, dt \right) dt \\ &= \int_0^\infty P_s(t)\, dt \end{aligned}$$

RANDOM WALK WITH ABSORBING BOUNDARIES

$x = 0$ and $x = 6$ are two absorbing boundaries: $P_r(x=0) = 0$, $P_r(x=6) = 0$ at all times!

TIME \ x	0	1	2	3	4	5	6	SURVIVAL PROBABILITY
0	0	0	0	1	0	0	0	1
1	0	0	$\frac{1}{2}$	0	$\frac{1}{2}$	0	0	1
2	0	$\frac{1}{4}$	0	$\frac{1}{2}$	0	$\frac{1}{4}$	0	1
⇒ 3	0	0	$\frac{3}{8}$	0	$\frac{3}{8}$	0	0	$\frac{6}{8}$
4	0	$\frac{3}{16}$	0	$\frac{6}{16}$	0	$\frac{3}{16}$	0	$\frac{6}{8}$
5	0	0	$\frac{9}{32}$	0	$\frac{9}{32}$	0	0	$\frac{18}{32}$
6	0	$\frac{9}{64}$	0	$\frac{18}{64}$	0	$\frac{9}{64}$	0	$\frac{18}{32}$
7	0	0	$\frac{27}{128}$	0	$\frac{27}{128}$	0	0	$\frac{54}{128}$
8	0	$\frac{27}{256}$	0	$\frac{54}{256}$	0	$\frac{27}{256}$	0	$\frac{54}{128}$

Gambling and the ruin problem

Biased random walk

- Walker starts at $x \in [0, a]$
- Absorbing boundaries $x = 0$ and $x = a$.
- Right and left transition probabilities: p and $q = 1 - p$, respectively.

Gambler's ruin problem

$x \ldots$ associated with gambler's wealth
$p \ldots$ the probability to win in each game
$q = 1 - p, \ (q > p) \ldots$ the probability to lose in each game

Starting at x, what is the probability P_x of reaching $x = 0$ (ruin) before reaching $x = a$ (infinite wealth)?

Gambling and the ruin problem

The master equation for P_x

$$P_x = pP_{x+1} + qP_{x-1}$$

boundary conditions

$$q_0 = 1, \;\; q_a = 0$$

General solution of the difference equation

$$\begin{aligned} q_x &= C_1 + C_2 (q/p)^x, \quad \text{if} \quad q \neq p, \\ q_x &= C_1 + C_2 x \quad \text{if} \quad q = p. \end{aligned}$$

Gambling and the ruin problem

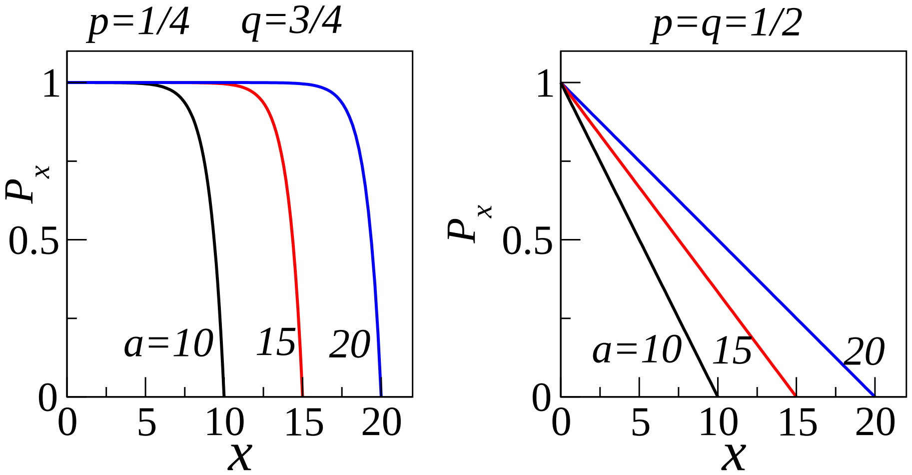
From the boundary conditions, we obtain

$$P_x = \frac{(q/p)^a - (q/p)^x}{(q/p)^a - 1}, \quad \text{if} \quad q \neq p,$$
$$P_x = 1 - x/a \quad \text{if} \quad q = p.$$

What happens if $a \to \infty$?

Gambling and the ruin problem

Plots of P_x



Gambling and the ruin problem

Starting with wealth x, what is the probability of reaching a total fortune of a before going bankrupt?

$$
\begin{aligned}
F_x &= 1 - P_x = \frac{1-(q/p)^x}{1-(q/p)^a}, \quad \text{if} \quad q \neq p, \\
F_x &= 1 - P_x = x/a \quad \text{if} \quad q = p.
\end{aligned}
$$

Applications in

- Risk insurance
- Stock markets

Gambling and the ruin problem

Example

Insurance company earns $\$10$ per day from premiums. However, independent of the past, it suffers a claim of $\$20$ per day with probability q.
Question: If the initial reserve of the company is $\$A$, what is the probability that the company will eventually go bankrupt?

Solution:
Each day the total fortune of the company either increases by $\$10$ if no claims occured, or decreases by $\$20 - \$10 = \$10$ if claims have occured. The respective probabilities are q (decrease of fortune) and $1 - q$ (increase of fortune).

Gambling and the ruin problem

Solution continued:

Assume $q < 1 - q$,

$$P_{x=\$A} = \lim_{a\to\infty} \frac{(q/(1-q))^a - (q/(1-q))^{\$A}}{(q/(1-q))^a - 1} = \left(\frac{q}{1-q}\right)^{\$A}$$

Finite but small, if the initial fortune $\$A$ is large.

Assume $q > 1 - q$,

$$P_{x=\$A} = \lim_{a\to\infty} \frac{(q/(1-q))^a - (q/(1-q))^{\$A}}{(q/(1-q))^a - 1} = 1$$

Ruin will certainly occur

Gambling and the ruin problem

Average duration of the game (Mean exit time)

Average number of steps (played games) before reaching either $x = 0$, or $x = a$.

Master equation for the mean exit time D_x if the walker starts in x

$$D_x = pD_{x+1} + qD_{x-1} + 1$$

Boundary conditions

$$D_0 = D_a = 0$$

General solution

$$\begin{aligned} D_x &= \frac{x}{q-p} + C_1 + C_2(q/p)^x, \quad \text{if} \quad q \neq p, \\ D_x &= C_1 + C_2 x - x^2 \quad \text{if} \quad q = p. \end{aligned}$$

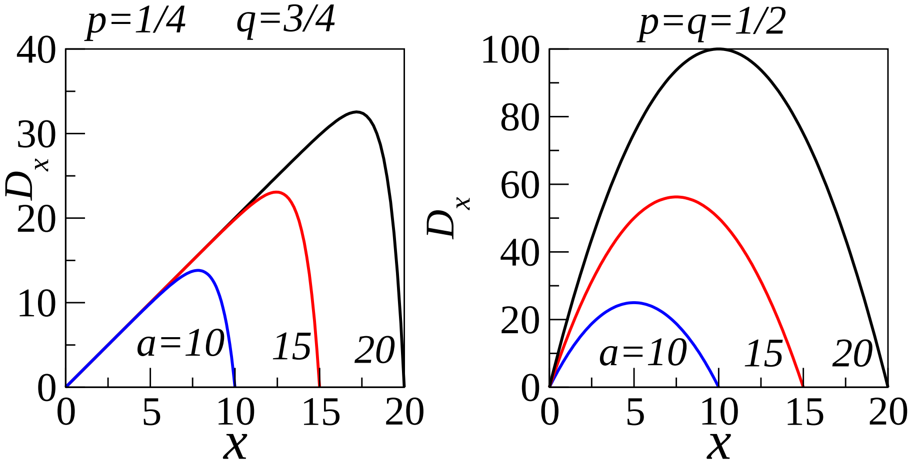
Gambling and the ruin problem

From the boundary conditions

$$D_x = \frac{x}{q-p} - \frac{a}{q-p}\frac{1-(q/p)^x}{1-(q/p)^a}, \quad \text{if} \quad q \neq p,$$
$$D_x = x(a-x) \quad \text{if} \quad q = p.$$

Gambling and the ruin problem

Plots of D_x



Continuous limit

Master equation

$$p(x, t + \delta t | x_0, t_0) = \frac{1}{2}(p(x - \Delta, t | x_0, t_0) + p(x + \Delta, t | x_0, t_0)).$$

Let $\delta t,\ \Delta \to 0$

$$\begin{aligned} p(x, t + \delta t | x_0, t_0) &\approx p(x, t | x_0, t_0) + \partial_t p(x, t | x_0, t_0)\delta t \\ &= \frac{1}{2}(p(x - \Delta, t | x_0, t_0) + p(x + \Delta, t | x_0, t_0)), \end{aligned}$$

$$\partial_t p(x, t | x_0, t_0) =$$

$$\frac{\Delta^2}{2\delta t} \frac{[(p(x - \Delta, t | x_0, t_0) + p(x + \Delta, t | x_0, t_0) - 2p(x, t | x_0, t_0)]}{\Delta^2}$$

$$\approx \quad \frac{\Delta^2}{2\delta t} \frac{\partial^2 p(x, t | x_0, t_0)}{\partial x^2}.$$

Continuous limit

The Fokker-Planck equation

If $\lim_{(\delta t,\,\Delta\to 0)} \frac{\Delta^2}{2\delta t} = constant$, random walk corresponds to diffusion.

$$\frac{\partial p}{\partial t} = D\frac{\partial^2 p}{\partial x^2}$$

Diffusion coefficient

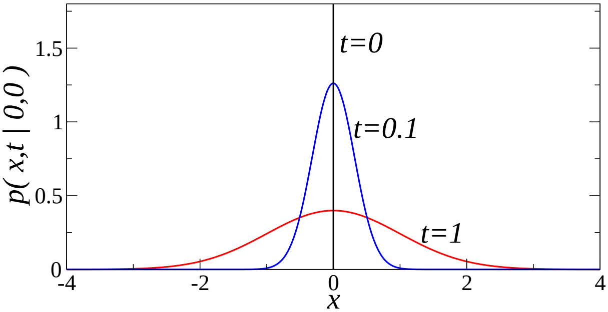
$$D = \frac{\Delta^2}{2\delta t}$$

Solution of the Fokker-Planck equation

$$p(x,t|x_0,t_0) = \frac{1}{\sqrt{4\pi D(t-t_0)}}\exp\left(-\frac{(x-x_0)^2}{4D(t-t_0)}\right).$$

Diffusional spreading

Example distribution $D = 1$, $x_0 = t_0 = 0$



Stationary process?

Random walk on a line and diffusion along a line are not stationary:

$$\lim_{t_0 \to -\infty} p(x, t | x_0, t_0) = 0$$

Diffusion coefficient

Ensemble averaged position

$$\langle x | x_0, t_0 \rangle = \int_{-\infty}^{\infty} \frac{x\,dx}{\sqrt{4\pi D(t-t_0)}} \exp\left(-\frac{(x-x_0)^2}{4D(t-t_0)}\right) = x_0$$

Ensemble averaged square coordinate

$$\langle x^2 | x_0, t_0 \rangle = \int_{-\infty}^{\infty} \frac{x^2\,dx}{\sqrt{4\pi D(t-t_0)}} \exp\left(-\frac{(x-x_0)^2}{4D(t-t_0)}\right) = x_0^2 + 2D(t-t_0)$$

Diffusion coefficient of a 1D stochastic process $x(t)$

$$D = \lim_{t-t_0 \to \infty} \frac{\langle x^2 | x_0, t_0 \rangle - x_0^2}{2(t-t_0)}$$

Diffusion in higher dimensions

n dimensional random walk

In an n-dimensional space the diffusion process (or random walk) is a superposition of independent and identical diffusion processes (random walks) along each of the n dimensions.

in 3D the diffusion equation is

$$\frac{\partial p(x,y,z,t)}{\partial t} = D\Delta p(x,y,z,t) = D\left(\frac{\partial^2}{\partial x^2} + \frac{\partial^2}{\partial y^2} + \frac{\partial^2}{\partial z^2}\right) p(x,y,z,t)$$

Diffusion coefficient in n dimensional space

$$D = \lim_{t-t_0\to\infty}\left(\frac{1}{n}\right)\frac{\langle \boldsymbol{r}^2 | x_0, t_0\rangle - x_0^2}{2(t-t_0)},$$

with

$$\boldsymbol{r}^2 = x_1^2 + x_2^2 + x_3^2 + \cdots + x_n^2.$$

Recurrence and transitivity of a random walk

Returning probability

It is possible to show that the probability to return to the initial position after n steps is given by

$$1D: \ \Pr(i=0, t=n|0,0) \sim \frac{1}{n^{1/2}}, \qquad \sum_{n=N}^{\infty} \Pr(i=0, t=n|0,0) = \infty$$

$$2D: \ \Pr(i=0, t=n|0,0) \sim \frac{1}{n}, \qquad \sum_{n=N}^{\infty} \Pr(i=0, t=n|0,0) = \infty$$

$$3D: \ \Pr(i=0, t=n|0,0) \sim \frac{1}{n^{3/2}}, \qquad \sum_{n=N}^{\infty} \Pr(i=0, t=n|0,0) < \infty$$

1D vs 2D vs 3D

Random walk is recurrent in 1D and 2D and transient in 3D

Autocorrelation function (ACF)

Recall the definition of the ACF

$$\mathrm{ACF}(t,t'|x_0,t_0) = \langle x(t)x'(t')|x_0,t_0\rangle = \int\int dx\,dx' x\,x' p(x,t;x',t'|x_0,t_0)$$

Diffusion process is Markovian

$$p(x,t;x',t'|x_0,t_0) = p(x,t|x',t')p(x',t'|x_0,t_0), \quad (t \geq t' \geq t_0)$$

Using the solution of the diffusion equation

$$\begin{aligned} p(x,t|x',t') &= \frac{1}{\sqrt{4\pi D(t-t')}} \exp\left(-\frac{(x-x')^2}{4D(t-t')}\right) \\ p(x',t'|x_0,t_0) &= \frac{1}{\sqrt{4\pi D(t'-t_0)}} \exp\left(-\frac{(x'-x_0)^2}{4D(t'-t_0)}\right) \end{aligned}$$

Autocorrelation function (ACF)

Calculating ACF

$$\begin{aligned}\mathrm{ACF}(t, t'|x_0, t_0) &= \int\int dx\, dx' \frac{x\, x'}{4\pi D\sqrt{(t-t')(t'-t_0)}} \times \\ &\exp\left(-\frac{(x-x')^2}{4D(t-t')}\right)\exp\left(-\frac{(x'-x_0)^2}{4D(t'-t_0)}\right)\end{aligned}$$

Changing the integration variables

$$x - x' = y\Big|_{-\infty}^{\infty},\;\; x' = x'\Big|_{-\infty}^{\infty}$$

Autocorrelation function (ACF)

$$
\begin{aligned}
\mathrm{ACF}(t, t'|x_0, t_0) &= \int\int dy\, dx' \frac{x'\,(y + x')}{\sqrt{4\pi D(t - t')}} \frac{1}{4\pi D(t' - t_0)} \times \\
&\quad \exp\left(-\frac{y^2}{4D(t - t')}\right) \exp\left(-\frac{(x' - x_0)^2}{4D(t' - t_0)}\right) \\
&= \langle x'(t')^2 | x_0, t_0\rangle \langle 1|0, t'\rangle + \langle y(t)|0, t'\rangle \langle x'(t')|x_0, t_0\rangle
\end{aligned}
$$

Absence of the stationary limit

ACF does not depend on $(t - t')$:

$$
\mathrm{ACF}(t, t'|x_0, t_0) = 2D(t' - t_0), \quad t \geq t' \geq t_0
$$

Biased random walk: continuous limit

Master equation for $q \neq p$

$$P(x,t+\delta t|x_0,t_0) = pP(x-\Delta,t|x_0,t_0) + qP(x+\Delta,t|x_0,t_0).$$

Fokker-Planck equation in continuous limit δt, $\Delta \to 0$

$$\partial_t P \approx \frac{1}{\delta t}\left(pP(x-\Delta,t) + qP(x+\Delta,t) - P(x,t)\right)$$
$$= \frac{1}{\delta t}\Big(p(P - \Delta\partial_x P + \Delta^2/2\partial_x^2 P) + q(P + \Delta\partial_x P + \Delta^2/2\partial_x^2 P) - P\Big)$$
$$= \frac{1}{\delta t}\Big(-(p-q)\Delta\partial_x P + (p+q)\Delta^2/2\partial_x^2 P\Big)$$
$$= \frac{-(p-q)\Delta}{\delta t}\partial_x P + \frac{\Delta^2}{2\delta t}\partial_x^2 P$$

Biased random walk: continuous limit

Exercise: inhomogeneous biased random walk

Show that in case of the position dependent $p(x)$ and $q(x)$, the Fokker-Planck eqiation is given by

$$\partial_t P(x,t) = -\partial_x (f(x)P(x,t)) + D\partial_x^2 P(x,t),$$

with
$f(x) = \Delta \frac{p(x)-q(x)}{\delta t} \ldots$ drift force
$D = \frac{\Delta^2}{2\delta t} \ldots$ diffusion coefficient

Biased random walk: continuous limit

Continuity of the probability

$$\partial_t P(x,t) + \partial_x J(x,t) \quad = \quad 0$$

Probability current

$$J(x,t) = f(x)P(x,t) - D\partial_x P(x,t)$$

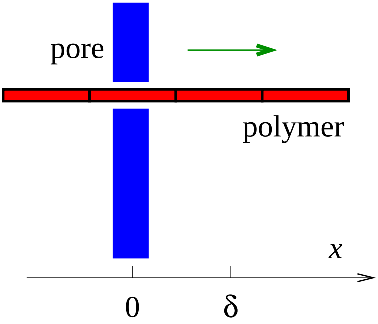
Drift force

Note that $f(x)$ is equivalent to a force, acting on the Brownian particle in the positive x-direction.

Translocation of polymers through cell membrane

Example

A protein passes through a translocation pore of a cell (see Fig.). The rod is made of identical sections (segments) of the length δ. The pore acts as a perfect ratchet, only allowing the motion to the right.
C. S. Peskin et al, "Cellular Motion and Thermal Fluctuations: The Brownian Ratchet", Biophysical Journal **65** *316-324 (1993)*



Translocation of polymers through cell membrane

Probability flux

$$J(x,t) = -\mu f P(x,t) - D\partial_x P(x,t),$$

$P(x,t)\dots$ probability density of the right end of the rod
$\mu f \dots$ load force, acting against the drift
Boundary conditions
$P(x=\delta,t)\dots$ absorbing boundary at $x=\delta$
$J(0,t)=J(\delta,t)\dots$ periodicity of the probability flux:

Conservation of mass

The number of monomers that enter the cell equals the number of monomers, removed from the system at $x=\delta$.

Translocation of polymers through cell membrane

Stationary regime:

$$\begin{aligned} J(x) &= J_0 = constant \\ P_s(x) &= Ae^{(-\mu f x/D)} - \frac{J_0}{\mu f}, \end{aligned}$$

From the bounadry conditions

$$A = \frac{J_0}{\mu f} e^{(\mu f \delta/D)}.$$

Normalizing the density to the number of Brownian particles N

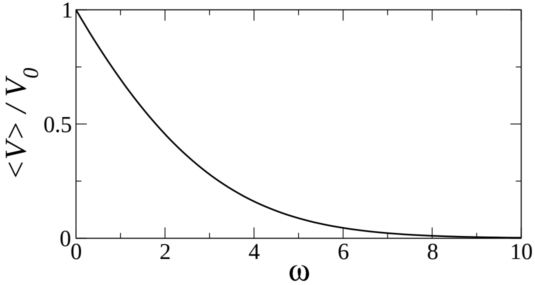
$$\begin{aligned} \int_0^\delta P_s(x)\, dx &= N, \quad \text{or} \\ \frac{J_0}{\mu f}\left[\frac{D}{\mu f}\left(e^{\mu f \delta/D} - 1\right) - \delta\right] &= N \end{aligned}$$

Translocation of polymers through cell membrane

Realtion between average drift velocity and flux

$$\text{flux} = \frac{\langle dN \rangle}{dt} = \frac{\langle V \rangle dt \text{ average } N \text{ per length}}{dt} = \frac{\langle V \rangle dt}{dt}\frac{N}{\delta} = \frac{\langle V \rangle N}{\delta}$$

$$\langle V \rangle = \frac{D}{\delta}\frac{\omega^2}{e^{\omega} - 1 - \omega}, \quad \text{with} \;\; \omega = \delta \mu f / D$$



Translocation of polymers through cell membrane

Limit of zero load

$$V_0 = \lim_{\omega \to 0} \frac{D}{\delta} \frac{\omega^2}{e^\omega - 1 - \omega} = \frac{D}{\delta} \frac{\omega^2}{1 + \omega + \omega^2/2 + \cdots - 1 - \omega} = \frac{2D}{\delta}$$

Relation to Feynman's ratchet

Ratchet mechanism is fueled by chemical reactions. System is out of equilibrium.

For imperfect translocation ratchet as well as the polymerization ratchets, see the original paper.