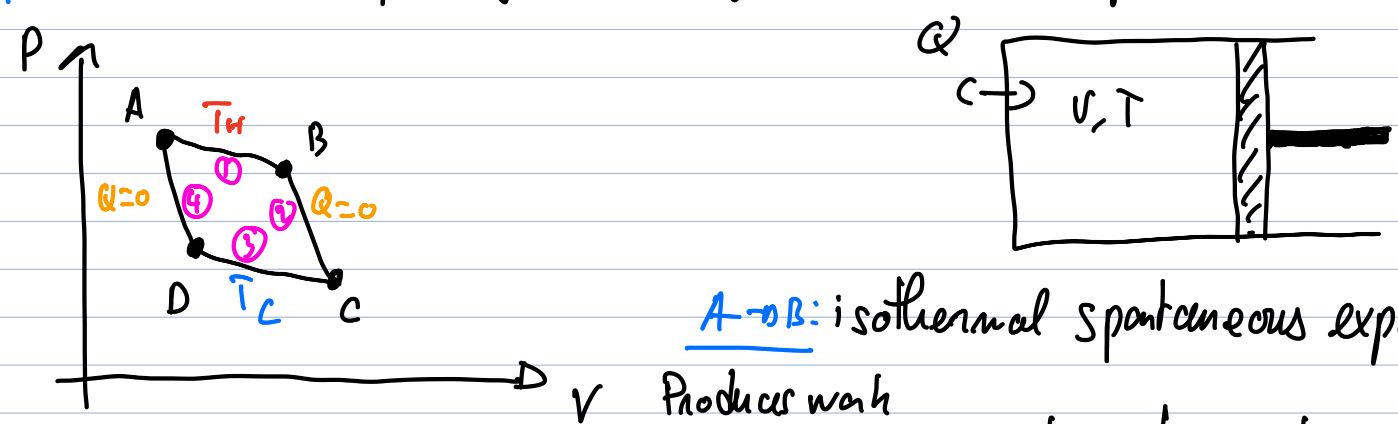
Chapter V: From Brownian ratchet to molecular motor

Q: If equilibrium is contagious (Chapter 2) and leads to Boltzmann weight (chap. 4) and time-reversal symmetry, how can one produce microscopic motors & persistent motion, as commonly observed in biology?

1) Carnot cycle & the lack of equilibrium isothermal motor

Hypothesis: macroscopic system subject to the laws of thermodynamics



A→B: isothermal spontaneous expansion.
Produces work
Requires heat to maintain temperature

B→C: isolate the engine & let the expansion continue.
Adiabatic cooling ($Q=\Delta S=0$) & $W>0$

C→D: isothermal compression, produces heat, cost work.

D→A: adiabatic compression to close the cycle.

1st law of thermodynamics: $dE = TdS - pdV$

$$\int_{cycle} dE = 0 = \underbrace{\int TdS}_{\text{Heat}} - \underbrace{\int pdV}_{\text{work}} \Rightarrow \text{Work } W = \int_{①} TdS + \underbrace{\int_{②} TdS}_{=0} + \int_{③} TdS + \underbrace{\int_{④} TdS}_{=0}$$

since $\Delta Q = 0$

$$\left.\begin{aligned} ①&: Q_H = T_H(S_B - S_A) \\ ③&: Q_C = T_C(S_D - S_C) = T_C(S_A - S_B) \end{aligned}\right\} W = (T_H - T_S)(S_B - S_A) > 0$$

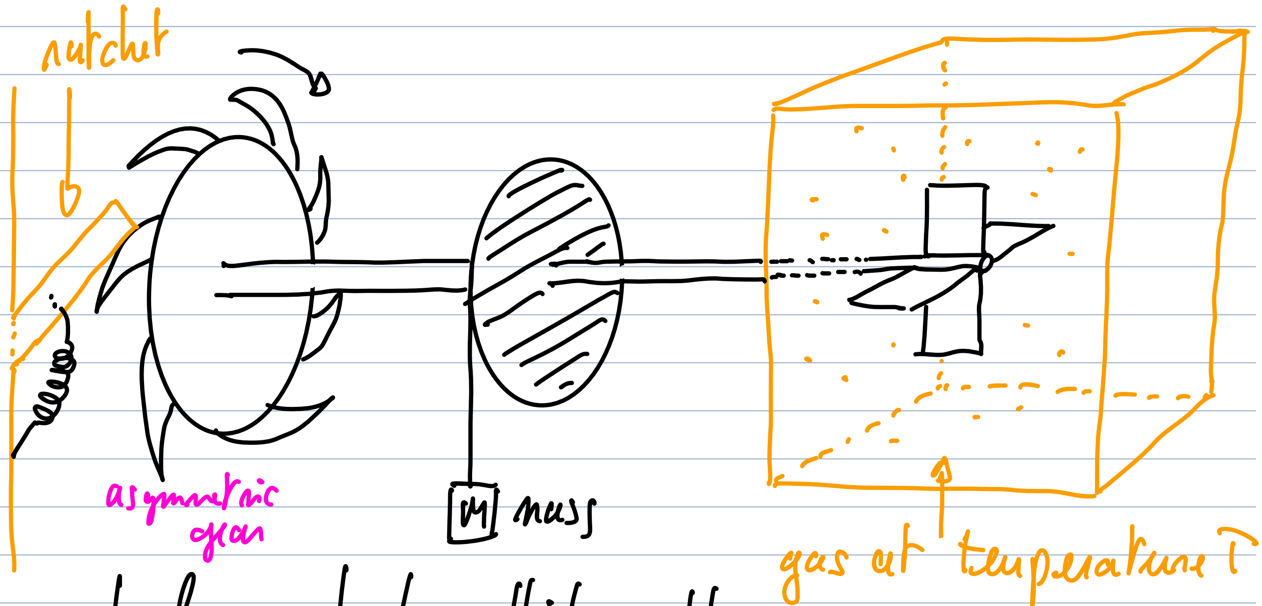
Cost: $Q_H > 0$; Efficiency $\eta = \frac{W}{Q_H} = 1 - \frac{T_C}{T_H}$

When $T_C \to T_H$, $\eta \to 0$ and one cannot extract energy from a single temperature macroscopic motor ruled by equilibrium thermodynamics.

Idea: Maybe, in a small system, fluctuations can help?

2) Thermal Ratchets

* Smolukowsky, Phys. Z. 13, 1069 (1912)
* Feynman, Mecanics, Chap. 46, lectures on Physics



Idea: The gas molecules randomly collide with the paws, which promotes clockwise (cw) & counterclockwise (ccw) rotations of the axis.

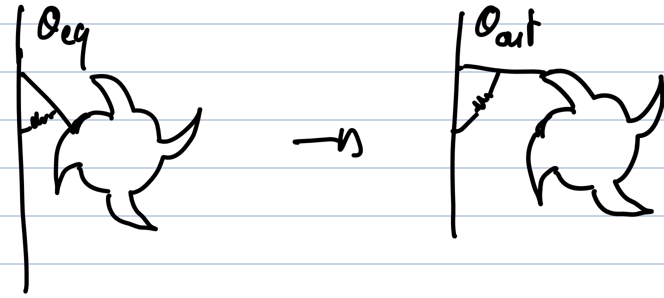
The ratchet allows for the cw rotations of the gear, but prevents its counterclockwise rotation.

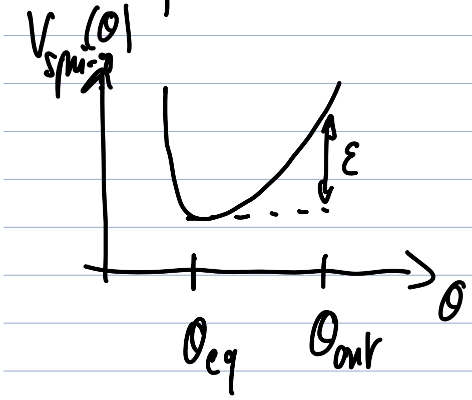
The overall system should thus rectifies the motion of the gear, leading to an isothermal stochastic motor that can exert work & lift the mass M.

Problem: it does not work. Why?

To make the gear rotate, we need to lift the ratchet from its rest angle θ_{eq} up to the angle θ_{out} which releases the wheel.

(1)





This requires an increase of energy of the spring, which is then dissipated once the wheel has rotated $\Rightarrow$ heats up the spring.
$\Rightarrow$ The whole system equilibrates at temperature T.

Then, the probability that the ratchet opens spontaneously is $e^{-\beta\varepsilon}$, which is the same as the probability that the gas particles make the wheel rotate. The mass then makes the gear go CCW on average $\Rightarrow$ no motor, except if $T_{spring} < T$

[Parrondo, Español, Am. J. Phys. 64, 1125 (1996)]

Conclusion: No isothermal motor in equilibrium.

Symmetry: breaking $\theta \to -\theta$ symmetry, as the asymmetric gear does, is not sufficient $\Rightarrow$ need to break time reversal symmetry to allow for a non-vanishing steady-state J_θ current

Several different strategies:

(i) Non isothermal systems.

(ii) Two-state systems, with transition rates between states that drive the system out of equilibrium (of molecular motor).

(iii) Break FDR with temporal correlations

$$\dot{p}(t) = -\int_{-\infty}^{t} ds\, \gamma(t-s)\, p(s) - V'(x(t)) + \sqrt{2\gamma k T}\, \eta(t)$$

with $\langle \eta(t)\eta(t')\rangle \neq \gamma(t-t')$

3) Fluctuating drive: not treated in class

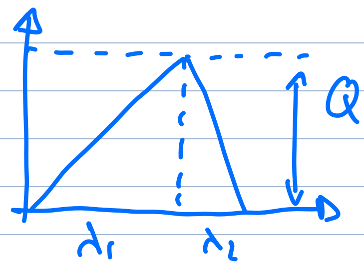
[Magnasco, Phys. Rev. Lett. 71, 1477 (1993)]

See also [C. R. Acad. Sci. Paris, t.315, p.1635-1639, (1992)]

Model: * Brownian particle in an asymmetric potential

$\lambda = \lambda_1 + \lambda_2$

$\Delta\lambda = \lambda_1 - \lambda_2$



$\dot{x} = -V'(x) + \xi(t) + F(t)$

$\xi(t)$ a GWN $\langle \xi \rangle = 0$

$\langle \xi(t)\xi(t')\rangle = 2kT\,\delta(t-t')$

* $F(t)$ is a symmetric fluctuating force of zero mean

* Periodic boundary conditions.

Question: can there be a nonzero current?

3.1) Constant force F

FPE: $\partial_t P = kT\,\partial_{xx} P + \partial_x\left[V'(x)P - FP\right] = -\partial_x J;\quad J = -kT\partial_x P + FP - V'(x)P(x)$ (1)

Steady-state: $\partial_t P = 0 \Rightarrow J$ constant

$\Rightarrow$ Solve (1) $\Leftrightarrow \partial_x P = -\beta J + \beta F P - \beta P \partial_x V$

for constant J & use $P(L) = P(0)$ & $\int_0^L dx\, P(x) = 1$

Homogeneous solution: $P_H(x) = \alpha\, e^{\beta[Fx - V(x)]}$

Look for $P_J(x) = \alpha(x)\, e^{\beta[Fx - V(x)]} \Rightarrow \alpha'(x) = -\beta J\, e^{-\beta[Fx - V(x)]}$

General solution:

$$\boxed{P(x) = P(0)\, e^{\beta[Fx - V(x)]} - \beta J \int_0^x du\, e^{-\beta[V(x) - Fx]}\, e^{\beta[V(u) - Fu]}}$$

where: $x \le \lambda_1$; $V(x) = \frac{Qx}{\lambda_1}$

$\lambda_1 \le x \le \lambda$; $V(x) = \frac{\lambda - x}{\lambda_2} Q$

Two unknowns J & $P(0)$ $\to$ two equations $P(\lambda) = P(0)$ & $\int_0^\lambda dx\, P(x) = 1$

$$P(\lambda) = 0 \Rightarrow J = \frac{2P(0) \sinh\left(\beta \frac{\lambda F}{2}\right)}{\frac{\lambda_1}{Q - \lambda_1 F}\left(e^{\beta(Q - \frac{\Delta F}{2})} - e^{\beta\frac{\lambda F}{2}}\right) + \frac{\lambda_2}{Q + \lambda_2 F}\left(e^{\beta(Q - \frac{\Delta F}{2})} - e^{-\beta\frac{\lambda F}{2}}\right)}$$

Proof:

$$P(0) = P(0)\, e^{\beta\lambda F} - \beta J\, e^{\beta F \lambda}\left[\int_0^{\lambda_1} du\, e^{\beta\left[\frac{Q}{\lambda_1} - F\right]u} + \int_{\lambda_1}^{\lambda} du\, e^{\beta\frac{\lambda}{\lambda_2}Q}\, e^{-\beta\left[\frac{Q}{\lambda_2} + F\right]u}\right]$$

$$P(0)\left[1 - e^{\beta\lambda F}\right] = -\cancel{\beta} J e^{\beta F \lambda}\left\{\frac{e^{\beta[Q - F\lambda_1]} - 1}{\cancel{\beta}\left[\frac{Q}{\lambda_1} - F\right]} + e^{\beta\frac{\lambda}{\lambda_2}Q}\, \frac{e^{-\beta\left[\frac{Q}{\lambda_2} + F\right]\lambda} - e^{-\beta\left[\frac{Q}{\lambda_2} + F\right]\lambda_1}}{-\cancel{\beta}\left[\frac{Q}{\lambda_2} + F\right]}\right\}$$

$$= -J\left\{\lambda_1 \frac{e^{\beta[Q + F\lambda_2]} - e^{\beta\lambda F}}{Q - \lambda_1 F} - \lambda_2 \frac{1 - e^{\beta F \lambda_2 + \beta Q}}{Q + \lambda_2 F}\right\}$$

$\times e^{-\frac{\lambda F}{2}}$

$$2P(0)\sinh\left(\beta\frac{\lambda F}{2}\right) = J\left\{\lambda_1 \frac{e^{\beta[Q - \frac{\Delta F}{2}]} - e^{\beta\frac{\lambda}{2}F}}{Q - \lambda_1 F} + \lambda_2 \frac{e^{\beta[Q - \frac{\Delta F}{2}]} - e^{-\beta\frac{\lambda F}{2}}}{Q + \lambda_2 F}\right\}$$

3.2) The limit of large T

$$\bar{J} = \frac{1}{T}\int_0^T ds\, J(F(s))$$

As $F(t)$ flips, so does $J(t)$, with some relaxation time τ.

When $T \gg \tau$; $\bar{J} \simeq \frac{1}{2}\left[J(F_0)+J(-F_0)\right]$

Q: Under what conditions is $\bar{J} \neq 0$?

① $\lambda_1 = \lambda_2$, $J(F) \equiv \frac{N(F)}{D(F)}$

* symmetric potential $\Rightarrow P_0(F) = P_0(-F)$; $\sinh\left(\beta \frac{\lambda F}{2}\right)$ is odd

$\Rightarrow N(F) = 2P_0 \sinh(\beta\lambda F)$ is odd

* $$D(F,\Delta=0) = \underbrace{\frac{\lambda}{2Q-\lambda F}\left(e^{\beta Q} - e^{\beta\frac{\lambda F}{2}}\right)}_{f(F)} + \underbrace{\frac{\lambda}{2Q+\lambda F}\left(e^{\beta Q} - e^{-\beta\frac{\lambda F}{2}}\right)}_{f(-F)} \quad (*)$$

$= f(F) + f(-F) \Rightarrow$ even

overall $J(F)$ is odd & $\bar{J} = \frac{1}{2}\left(J(F)+J(-F)\right) = 0$

Because of the left-right symmetry, the system cannot "choose" a direction and $\bar{J} = 0$.

② $\lambda_1 \neq \lambda_2$. In principle, need to compute $P_0(F)$, as in Magnasco's PRL.
Work to leading order for small Δ & F.

$N(F) \simeq P_0^0 \beta F \lambda$ where $P_0(\Delta,F) = P_0^0 + o(\Delta,F)$

$$D(F) = \frac{\lambda+\Delta}{2Q-(\lambda+\Delta)F}\left[e^{\beta Q}\left(1-\beta\frac{\Delta F}{2}\right) - e^{\beta\frac{\lambda F}{2}}\right] + \frac{\lambda-\Delta}{2Q+(\lambda-\Delta)F}\left[e^{\beta Q}\left(1-\beta\frac{\Delta F}{2}\right) - e^{-\beta\frac{\lambda F}{2}}\right]$$

$$D(F) = \frac{(\lambda+\Delta)}{2Q-\lambda F}\cdot\left(1+\frac{\Delta F}{2Q-\lambda F}\right)\left[e^{\beta Q}-e^{\beta\frac{\lambda F}{2}}-\beta e^{\beta Q}\frac{\Delta F}{2}\right]$$

$$+\frac{(\lambda-\Delta)}{2Q+\lambda F}\left(1+\frac{\Delta F}{2Q+\lambda F}\right)\left[e^{\beta Q}-e^{-\beta\frac{\lambda F}{2}}-\beta e^{\beta Q}\frac{\Delta F}{2}\right]$$

$$D(F) = D_0(F) + D_1(F)\Delta$$

$D_0(F) = (*) \Rightarrow$ even

$$D_1(F) = \frac{1}{2Q-\lambda F}\left(e^{\beta Q}-e^{\beta\frac{\lambda F}{2}}\right)-\frac{1}{2Q+\lambda F}\left(e^{\beta Q}-e^{-\beta\frac{\lambda F}{2}}\right)$$

$$+\frac{\lambda F}{(2Q-\lambda F)^2}\left(e^{\beta Q}-e^{\beta\frac{\lambda F}{2}}\right)-\frac{-\lambda F}{(2Q+\lambda F)^2}\left(e^{\beta Q}-e^{-\beta\frac{\lambda F}{2}}\right)$$

$$\underbrace{-\frac{\beta\frac{\lambda F}{2}}{2Q-\lambda F}e^{\beta Q}}+\frac{-\beta\frac{\lambda F}{2}}{2Q+\lambda F}e^{\beta Q}$$

$D_1(F) = g(F) - g(-F) \Rightarrow$ odd

$$J(F) \simeq \frac{N(F)}{D_0(F)+\Delta D_1(F)} \simeq \frac{N(F)}{D_0(F)}\left(1-\Delta\frac{D_1(F)}{D_0(F)}\right) = \underbrace{\frac{N(F)}{D_0(F)}}_{\text{odd in } F} - \Delta\underbrace{\frac{N(F)D_1(F)}{D_0(F)^2}}_{\text{even in } F}$$

$$\Rightarrow \bar{J}(F) = -\Delta\frac{N(F)D_1(F)}{D_0(F)^2} \neq 0 \text{ whenever } \Delta\neq 0$$

Here, breaking left-right symmetry suffice to generate a current.

Breakdown of FDR:

We can recast this problem into

$\dot{x} = -V'(x) + \tilde{\eta}(t)$; when $\tilde{\eta}(t) = \sqrt{2T}\,\eta(t) + F(t)$

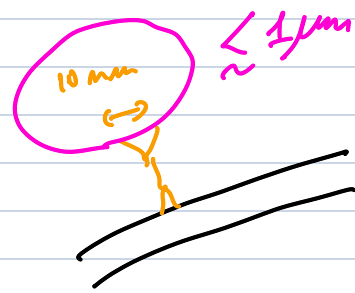
$$\langle \tilde{\eta}(t)\,\tilde{\eta}(t')\rangle = \underbrace{2T\,\delta(t-t')}_{\text{FDR abiding noise}} + \underbrace{\langle F(t)\,F(t')\rangle}_{\text{non equilibrium driving}}$$

4) Molecular motors

4.1) Introduction

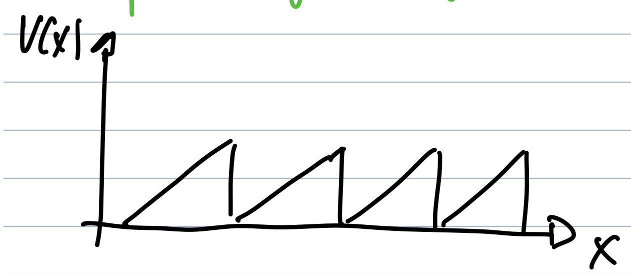
Molecular motors are proteins capable of exerting a non-zero average work.

Ex: . kinesin & dynein transport vesicles along microtubules
. Myosin exert forces on actin filaments



Q: how is it possible?
At the scale of molecular motors, temperature equilibrates in μs while motors step ~1ms ⇒ isothermal motion.

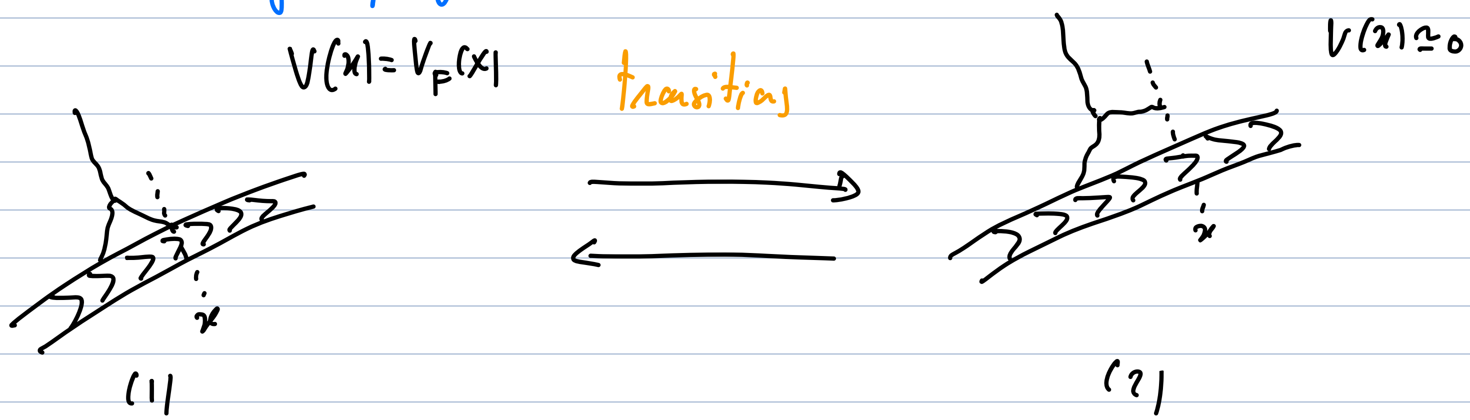
① Spatial symmetry is broken because filaments are polar



⇒ left-right asymmetry.
But if $P \propto e^{-\beta V(x)}$
then $J(x) = T\partial_x P + V' P = 0$
⇒ NOT SUFFICIENT

② Two-state model breaks detailed balance

State 1: strong coupling   State 2: weak coupling



Idea: In each state, the dynamics would relax to $e^{-\beta V(x)}$ and thus leads to vanishing current, but the transitions between the states prevents that. $\Rightarrow$ How?

4.2) Model and dynamics

We consider Brownian dynamics in each state and transitions at rates ω_1 and ω_2 from (1) to (2) and (2) to (1), respectively.

$P_i(x,t)$: probability to find the system in state i and at position x at time t.

$P(x,t) = P_1(x,t) + P_2(x,t)$ the proba to find the system at x at time t, whatever its state.

Q: time evolution of $P_i(x,t)$?

Idea: $\partial_t P_i(x,t) = \lim_{dt \to 0} \frac{P_i(x,t+dt) - P_i(x,t)}{dt}$ $\Rightarrow$ compute $P_i(x,t+dt) - P_i(x,t)$ to order dt.

rates ω_i: proba to go from $1 \to 2$ in $[t, t+dt] \underset{dt \to 0}{=} \omega_1 dt$

Two state changes $\propto (\omega_1 dt) \times (\omega_2 dt) \sim dt^2 \Rightarrow$ no need to consider

* $P(i,x,t+dt \mid j,y,t)$ the proba to find the system in state i & position x at time $t+dt$ given that it was in state j & position y at t. 6

$$\boxed{P(1,x,t+dt) = \int dy\, P_1(y,t)\, P(1,x,t+dt \mid 1,y,t) + \int dy\, P_2(y,t)\, P(1,x,t+dt \mid 2,y,t)}$$

$\Rightarrow$ we need to compute the conditional probabilities (a.k.a. "propagators")

1) $P(1,x,t+dt \mid 1,y,t) = P(\text{stay in state } 1) \times P(y \to x \text{ in } [t,t+dt]) + \mathcal{O}(dt^2)$

$\hookrightarrow 1 \xrightarrow{\omega_1 dt} 2 \xrightarrow{\omega_2 dt} 1$

* As $dt \to 0$ $P(1,x,t+dt \mid i,y,t) \to 0$ if $x-y = \mathcal{O}(1) \Rightarrow y$ needs to be close to x only $y = x + dt^\alpha ; \alpha > 0$ contribute.

$\Rightarrow$ proba to stay in $(1) = 1 - \omega_1(x)dt + \mathcal{O}(dt^{1+\alpha})$

since $\omega_1(y') = \omega_1(x) + \underbrace{(x-y')}_{\mathcal{O}(dt^\alpha)}\omega_1'(x)$

* $P(y \to x \text{ in } [t,t+dt]) = P_1(x,t+dt \mid y,t) \simeq P_1(x,t \mid y,t) + dt\, \partial_{\tilde t} P_1(x,\tilde t \mid y,t)\big|_{\tilde t = t}$

but $P_1(x,t \mid y,t) = \delta(x-y)$

and $\partial_{\tilde t} P_1(x,\tilde t \mid y,t)\big|_{\tilde t = t} = -H_{FP}^1 P_1$; where $H_{FP}^1 = -\frac{\partial}{\partial x}\left[\mu T \frac{\partial}{\partial x} + U_1'(x)\right]$

[also works with $H_{FP}^{1\,+}(y)$]

$\Rightarrow P(y \to x \text{ in } [t,t+dt]) = (1 - dt\, H_{FP}^1)\,\delta(x-y)$

* Together: $P(1,x,t+dt \mid 1,y,t) = (1-\omega_1(x)dt)(1 - dt H_{FP}^1)\,\delta(x-y)$

$\simeq (1 - \omega_1(x)dt - dt H_{FP}^1)\,\delta(x-y)$

$$\Rightarrow \boxed{\int dy\, P(1,x,t+dt \mid 1,y,t) P_1(y,t) = (1 - \omega_1(x)dt - dt H_{FP}^1)\, P_1(x,t)}$$

② $P(1,x,t+dt|2,y,t) = (\text{proba } 2\to 1)\times(\text{proba } y\to x)$

$$= \left[\omega_2(x)dt + O(dt^2)\right]\left[1 - dt\, H_{FP}\right]\delta(x-y)$$

$$\simeq \omega_2(x)\, dt\, \delta(x-y)$$

$$\Rightarrow \boxed{\int dy\, P(1,x,t+dt|2,y,t)\, P_2(y,t) \simeq \omega_2(x)\, dt\, P_2(x,t)}$$

All in all:

$$P_1(x,t+dt) = P_1(x,t) - dt\left(H_{FP}^1 + \omega_1(x)\right)P_1 + \omega_2\, dt\, P_2$$

$$\Rightarrow \begin{cases} \underbrace{\partial_t P_1(x,t) =}_{\substack{\text{rate of change of the}\\ \text{probability to be in}\\ \text{state } i \text{ at } x,t}} & \underbrace{-H_{FP}^1 P_1(x,t)}_{\substack{\text{Motion within}\\ \text{the state.}\\ \Rightarrow -\partial_x J_i}} & \underbrace{-\omega_1(x)P_1}_{\substack{\text{loss or gain}\\ \text{due to hops}\\ \text{from 1 to 2}}} & \underbrace{+\omega_2(x)P_2}_{\substack{\text{loss or gain}\\ \text{due to hops}\\ \text{from 2 to 1.}}} \\ \partial_t P_2(x,t) = & -H_{FP}^2 P_2(x,t) & +\omega_1(x)P_1 & -\omega_2(x_2)P_2 \end{cases}$$

Switching rates:

Let us forget space and focus on $\underset{V_1(x)}{\text{State } 1} \underset{W_2(x)}{\overset{W_1(x)}{\rightleftarrows}} \underset{V_2(x)}{\text{State } 2}$

Dynamics $\partial_t P_1 = -\omega_1 P_1 + \omega_2 P_2$ & $\partial_t P_2 = +\omega_1 P_1 - \omega_2 P_2$

Steady state $\omega_1 P_1 = \omega_2 P_2$

① Thermally activated switch:

$$\left.\begin{aligned} \omega_1^{th}(x) &= \omega(x)\, e^{\beta V_1(x)} \\ \omega_2^{th}(x) &= \omega(x)\, e^{\beta V_2(x)} \end{aligned}\right\} \quad P_i = \frac{1}{Z_1} e^{-\beta V_i(x)} \quad \text{such that } P_i\, \omega_i = \omega(x)$$

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② Chemically activated switch: $(1), ATP \underset{\omega_1}{\overset{\omega_2}{\rightleftharpoons}} (2), ADP+P$

$\omega_1^{ch}(x) = \gamma(x)\, \omega_1^{th}(x)\, e^{\beta \Delta\mu_{ATP}}$

$\omega_2^{ch}(x) = \gamma(x)\, \omega_2^{th}(x)\, e^{\beta[\Delta\mu_{ADP}+\Delta\mu_P]}$; $\Delta\mu_i = \mu_i - \mu_i^{eq}$; $\mu_i = \mu_i^{std} + \ln [i]$

Excess of ATP favors $1 \to 2$ while excess of ADP favors $2 \to 1$

If $\Delta\mu_{ATP} \neq \Delta\mu_{ADP}+\Delta\mu_P$, then $\frac{\omega_1^{ch}}{\omega_2^{ch}} \neq \frac{\omega_1^{th}}{\omega_2^{th}}$ which leads to a competition between the steady states

$\to$ the system will be out of equilibrium.

③ In practice, both processes: $\omega_i(x) = \omega_i^{th}(x) + \omega_i^{ch}(x)$

④ Diffusion:

In the presence of diffusion in each state, the Brownian dynamics is also trying to lead to $\frac{1}{Z} e^{-\beta V_i(x)}$, which is compatible with $\omega_i^{th}(x)$ but not with $\omega_i^{ch}(x)$ if $\Delta\mu \equiv \Delta\mu_{ATP} - \Delta\mu_{ADP}+\Delta\mu_P > 0$

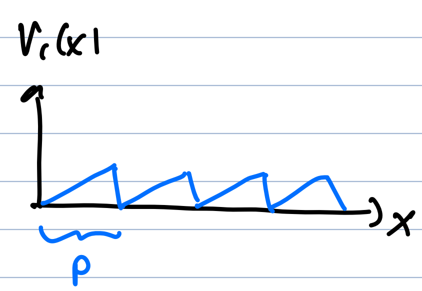
Comment: As time goes on, $[ATP] \to [ATP]^{eq}$ & the environment relaxes to equilibrium $\Rightarrow$ need to maintain $\Delta\mu > 0$. This is why we eat & breathe.

Conclusion: $\Delta\mu \neq 0$ drives the system out of equilibrium $\Rightarrow$ is this sufficient to induce a current?

4.3) A simple example

[Jülicher, Ajdari, Prost ; RMP 69, 1269, (1997)]

$V_2 = 0$, ω_1 & ω_2 constant, $V_1(x)$ periodic with period p



Dynamics: $\partial_t P_1(x,t) = \frac{\partial}{\partial x}\left[T\frac{\partial}{\partial x} + V_1'(x)\right]P_1 - \omega_1 P_1 + \omega_2 P_2$

$$\partial_t P_2(x,t) = T\frac{\partial^2}{\partial x^2}P_2 + \omega_1 P_1 - \omega_2 P_2$$

$$P_{tot}(x) = P_1(x) + P_2(x) \Rightarrow \partial_t P_{tot}(x) = T\frac{\partial^2}{\partial x^2}P_{tot} + \frac{\partial}{\partial x}\left[V_1'(x)P_1(x)\right]$$

$$= T\frac{\partial^2}{\partial x^2}P_{tot} + \frac{\partial}{\partial x}\left[V_{eff}'(x)P_{tot}(x)\right]$$

when $V_{eff}'(x) = \lambda(x)V_1'(x)$ & $\lambda(x) = \frac{P_1(x)}{P_{eff}(x)}$

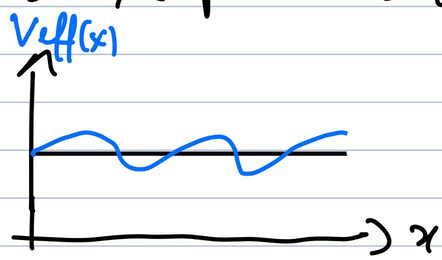
$\Rightarrow$ Brownian dynamics in an effective potential

$$\boxed{V_{eff}(x) = V_{eff}(0) + \int_0^x du\,\lambda(u)\,V_1'(u)}$$

Let $\Delta = \int_0^p dx\,\lambda(x)\,V_1'(x)$

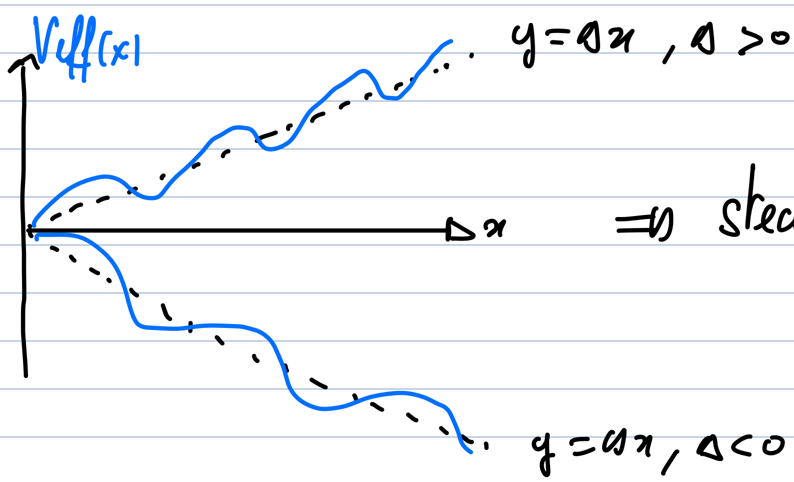
V_1, V_2 periodic $\Rightarrow P_1, P_2$ periodic $\Rightarrow \lambda(x)$ periodic

If $\Delta = 0$ then



$\Rightarrow$ no current.

If $\Delta \neq 0$, then



$\Rightarrow$ steady current.

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What is the condition for $\Delta = 0$?

(i) if $V_1(x) = V_1(-x) \Rightarrow P_1 \,\&\, P_2$ even $\Rightarrow \lambda(x) = \lambda(-x)$ and $V_1'(x)$ odd $\Big\}$ $\lambda V_1'$ odd & $\Delta = 0$

(ii) otherwise, Δ is generically non-zero & the dynamics leads to a non-zero current

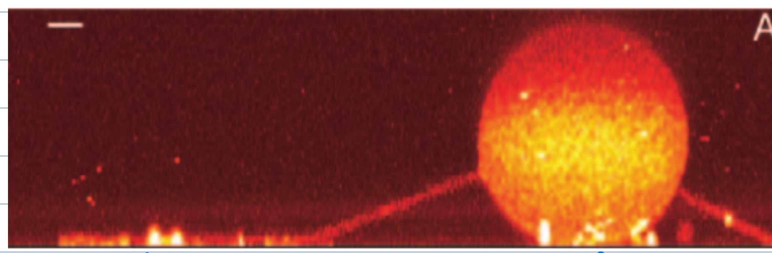
Comment: $\partial_t P_i = -H_{FP}^i P_i$ satisfies detailed balance with $P_i^s = \frac{1}{Z} e^{-\beta V_i}$

$$\partial_t P_i = -\omega_i P_i + \omega_j P_j \;\text{———}\; \frac{P_i}{P_j} = \frac{\omega_j}{\omega_i}$$

It is the competition between the two processes that prevents the relaxation towards a time-reversal symmetric steady state.

4.4) Collective behaviors of molecular motors

Idea: Model the collective behavior of molecular motors, e.g. when they pull on membrane tubes.



molecular motors pulling membrane tubes

microtubules

Giant unilamellar vesicle

[Roux et al., PNAS 99, 5394 (2002)]

Problem: The model above is useful to understand why motors walk processively but it is far too detailed to study the large scale properties of $N \gg 1$ interacting motors.