# Energetics
# at mesoscopic scale

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# Introduction

A few key papers of theory of fluctuations …

1905 – *Einstein's relation* (Fluctuation and dissipation)
1906 – Smoluchowski (diffusion process)
1908 – Langevin's equation (equation of *stochastic* motion)
1915 – Fokker (diffusion process)
1917 – Planck (diffusion process)
…
1940 – Kramers' equation (Brownian motion and chemical reaction)
1951 – Itô; "*On stochastic differential equations*" (mathematization!)
1960 – Zwanzig's *projection method* (from Liouville eq. to *diffusion*)
1963 – Feyman's ratchet wheel and pawl (mesoscopic heat engine)
1965 – *Mori's formula* (from Hamiltonian to linear Langevin eq.)
1973 – *Kawasaki's identity* (non-linear extension of *Mori's formula*)
…
1990's – Jarzynski's equality, Fluctuation Theorems, *StEng*

# Introduction

**A few key papers of mesoscopic experiments …**

1827 – Robert *Brown*
1913 – Perrin; *Les Atomes* (experimental proofs)
1960 – Perutz *et al.* (X-ray structure of protein)
1960's – Shimomura (Green Fluorescent Protein; GFP)
1970 – Ashkin (optical tweezer)
1980's – Bennig *et al.* (STM, AFM)
1984 – Yanagida, *et al.* (dynamics of single filament)
1993 – Rayment (X-ray structure of *myosin*)
1990's – (single protein probe)

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**Perrin 1913**

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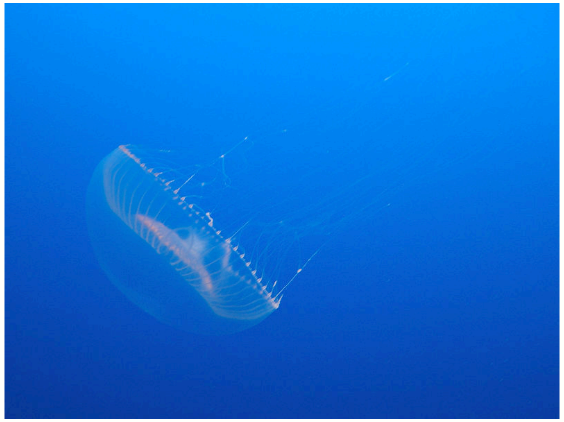

**(GFP)**

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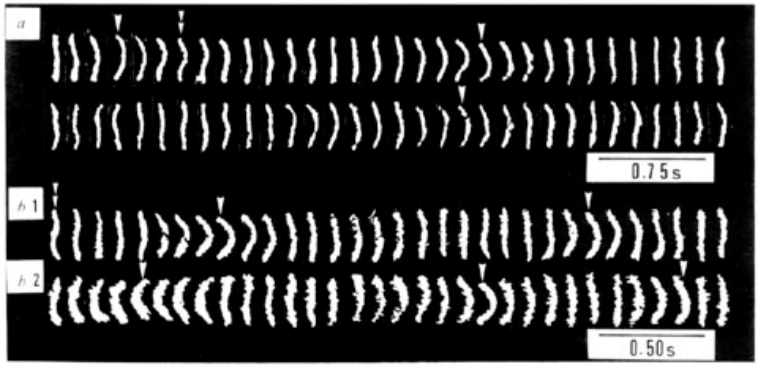


**Yanagida *et al.* 1984**

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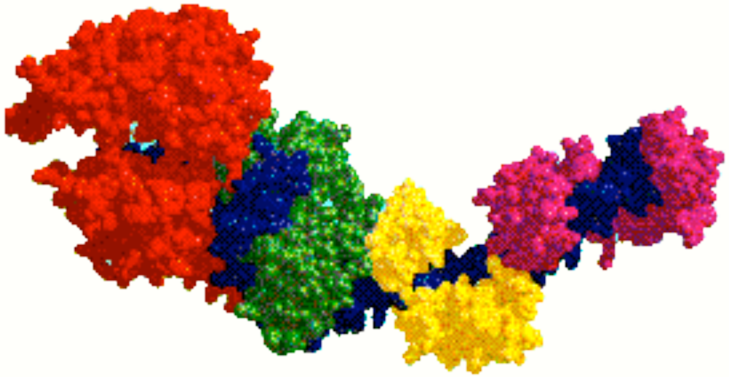

**Rayment et al. 1993**

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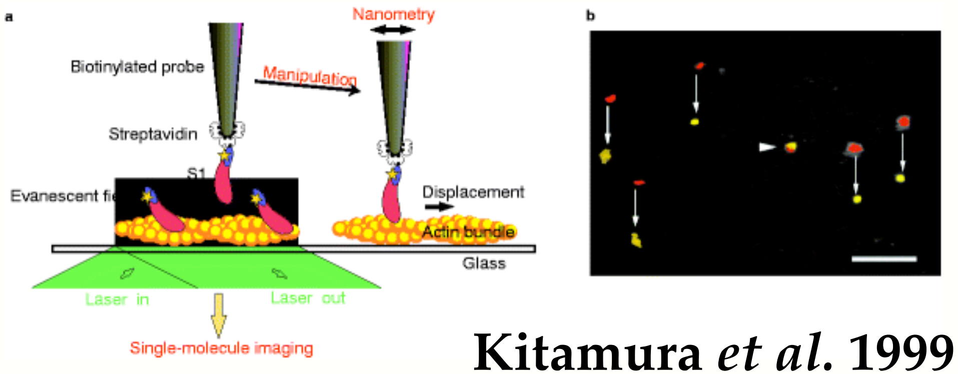
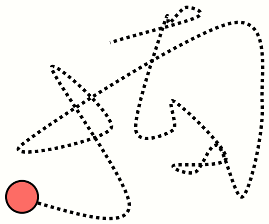



**Kitamura *et al.* 1999**

# Introduction

## Short summary

More and more *mesoscopic* phenomena
— described by Langevin equations



## Reminder : **Langevin equation**

"Newton's 1st law" ➔ *Free Brownian motion without external field*

$$0 = -\gamma \frac{dx}{dt} + \sqrt{2\gamma k_{\mathrm{B}} T}\, \theta(t), \quad \langle \theta(t) \rangle = 0, \quad \langle \theta(t)\theta(t') \rangle = \delta(t - t')$$

*forces from environment*

$\theta(t)$ : white Gaussian process
($\int_0^t \theta(s)ds = B_t$ : Wiener process)

"Newton's 2nd law" ➔ *Brownian motion under external field*

$$0 = -\frac{\partial U(x,a)}{\partial x} - \gamma \frac{dx}{dt} + \sqrt{2\gamma k_{\mathrm{B}} T}\, \theta(t)$$

***a*** : control parameter (by an external system)

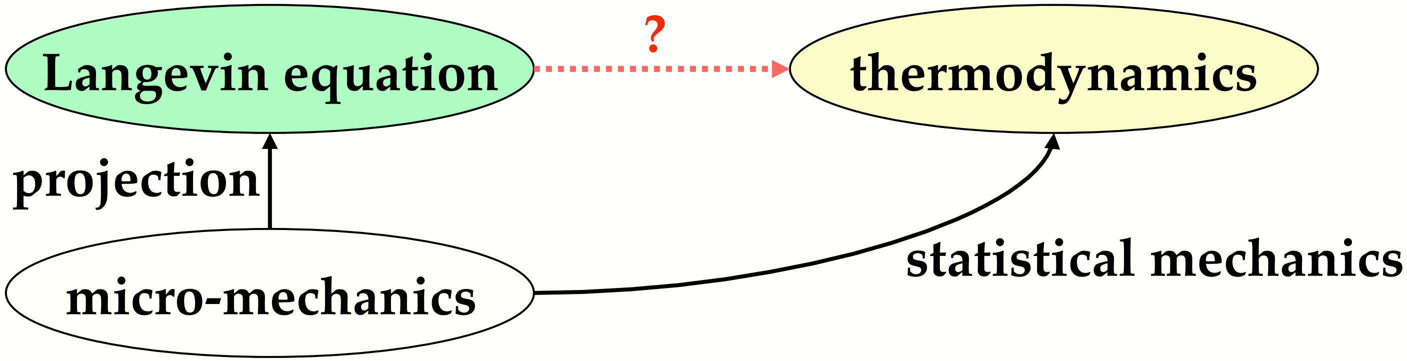
\+ many generalizations *e.g.* *D*-dim, inertia, memory, manifold,…

# Introduction

**What have been *less* disscused ?**

1. Missing link – energetics absent (cf. QM, hydro, Newton, gen-rel)

cf. Known : steady-state of Langevin eq ←→ canocnical ensemble



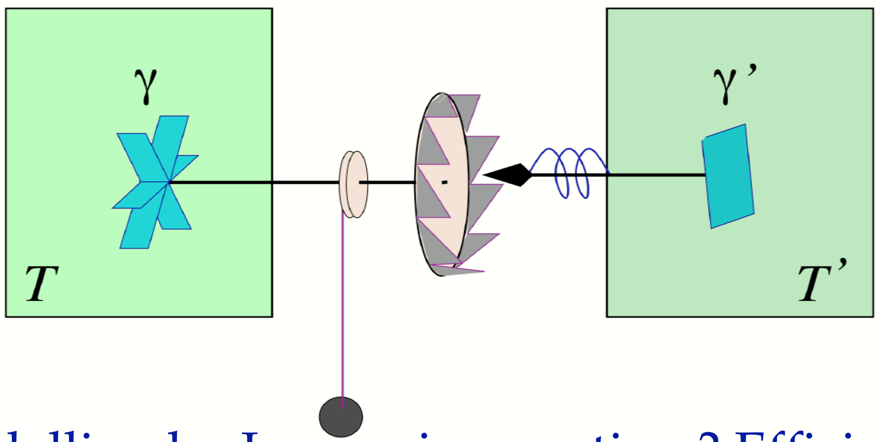

? = stochastic energetics

# Introduction

**What have been *less* disscused ?**

1. Missing link (cf. QM,hydro,Newton,GR) – energetics absent

e.g. *Feynman's ratchet wheel and pawl*



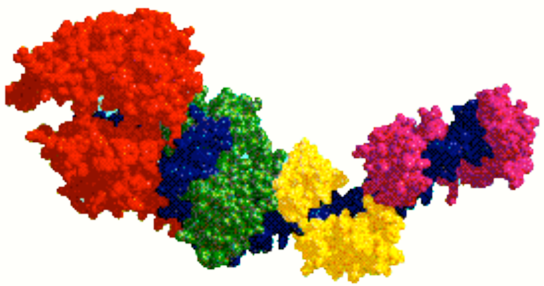

Modelling by Langevin equation ? Efficiency ? (ks 1997)

# Introduction

**What have been *less* disscused ?**

1. Missing link (cf. QM,hydro,Newton,GR) – energetics absent

e.g. *Protein motors*



cf.
ATPase free energy
~70% : ***entropic***
~30% : *energetic*

# Introduction

**What have been *less* disscused ?**

1.Missing link (cf. QM,hydro,Newton,GR) – energetics absent

2. How do the fluctuations look ***at*** mesoscale ?

a) Analyses along a single realisations (cf. ensemble properties)

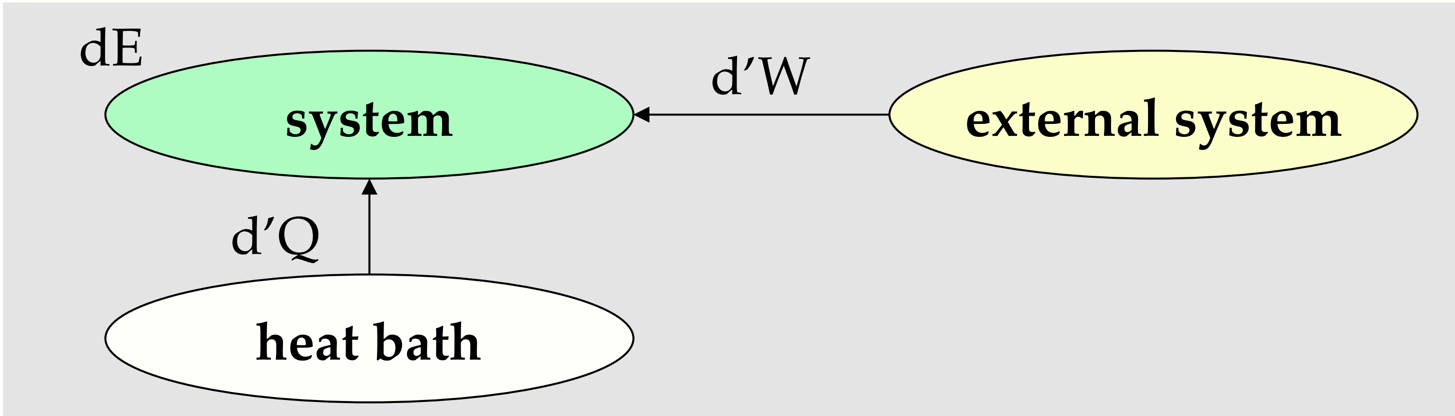
$$0 = -\frac{\partial U(x,a)}{\partial x} - \gamma\frac{dx}{dt} + \sqrt{2\gamma k_{\mathrm{B}} T}\,\theta(t)$$

b) "Newton's 3rd law" ➔ [force from environment]

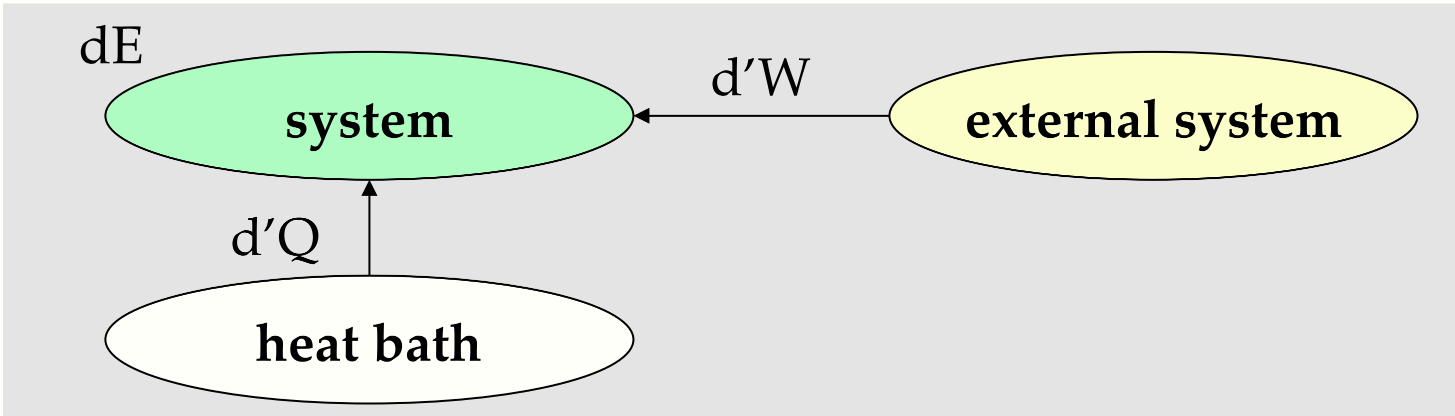
= –[force onto environment]

# Energetics at mesoscopic scales

## Thermodynamics




## Langevin equation (single trajectory)



# Energetics at mesoscopic scales

$$0 = -\frac{\partial U(x,a)}{\partial x} - \gamma \frac{dx}{dt} + \sqrt{2\gamma k_{\mathrm{B}} T}\theta(t)$$

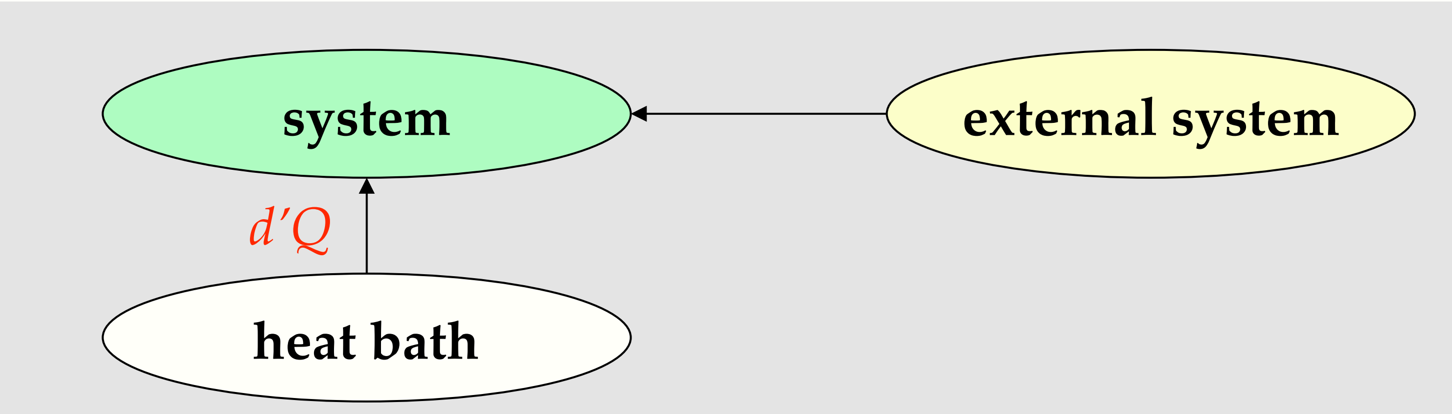
## Definition of *mesoscopic* heat

heat, $d'Q$ : work done by the heat bath
through a (true) displacement, $dx$

$$d'Q \equiv \left( -\gamma \frac{\partial x}{\partial t} + \sqrt{2\gamma k_{\mathrm{B}} T}\,\theta(t) \right) \circ dx(t)$$

$$A(t) \circ dx(t) \equiv \frac{A(t+dt) + A(t)}{2} [x(t+dt) - x(t)]$$

STRATONOVICH type product




e.g. Free Brownian motion; $d'Q = 0$ (for overdamped case).

# Energetics at mesoscopic scales

**1st law of stochastic energetics**

heat : $d'Q \equiv \left(-\gamma\frac{\partial x}{\partial t} + \sqrt{2\gamma k_{\mathrm{B}}T}\,\theta(t)\right) \circ dx(t) = \frac{\partial U}{\partial x} \circ dx(t)$

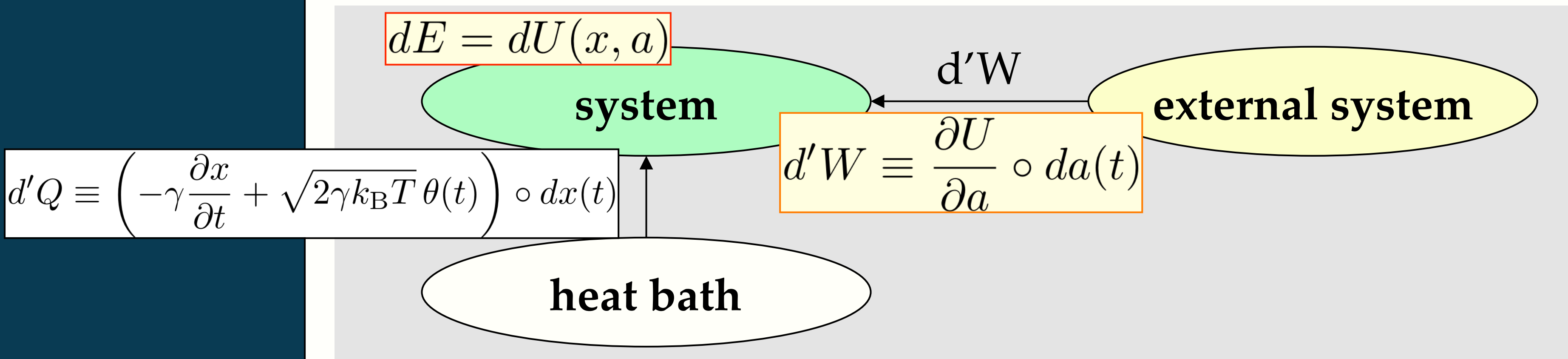
$$0 = -\frac{\partial U(x,a)}{\partial x} - \gamma\frac{dx}{dt} + \sqrt{2\gamma k_{\mathrm{B}}T}\theta(t)$$

energy change : $dE = dU(x,a)$

work by external system : $d'W \equiv \frac{\partial U}{\partial a} \circ da(t)$

➔ $dE = d'Q + d'W$

Energy balance (along a single trajectory)



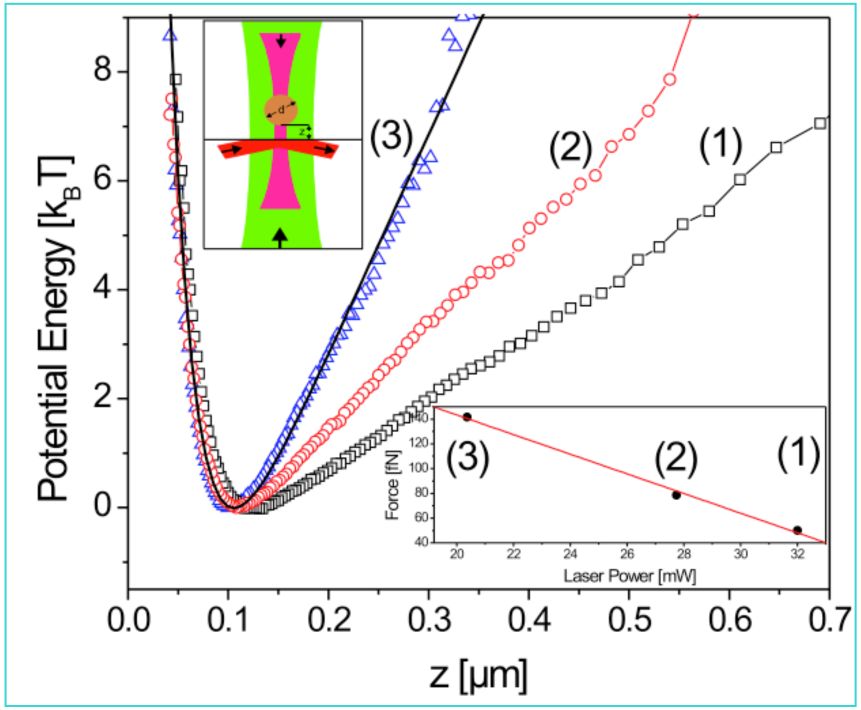
# Energetics at mesoscopic scales

Experimental demonstrations of ***energy balance***

PRL **96,** 070603 (2006) PHYSICAL REVIEW LETTERS week ending 24 FEBRUARY 2006

**Thermodynamics of a Colloidal Particle in a Time-Dependent Nonharmonic Potential**

V. Blickle,[1] T. Speck,[2] L. Helden,[1] U. Seifert,[2] and C. Bechinger[1]



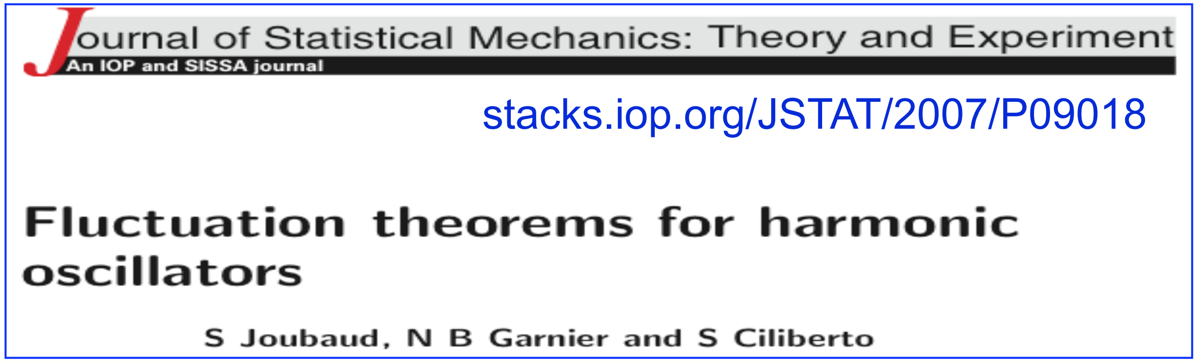

***z*(*t*)** : Single-Particle Tracking (SPT)

***a*** **:** laser force ↑

***U*(*z*,*a*)** : equilibrium distribution data

# Energetics at mesoscopic scales

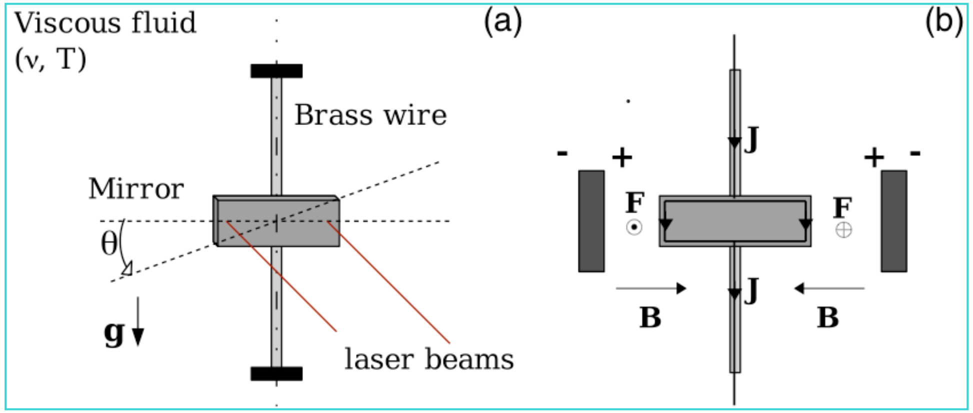
Experimental demonstrations of ***energy balance***


Journal of Statistical Mechanics: Theory and Experiment
An IOP and SISSA journal

stacks.iop.org/JSTAT/2007/P09018

**Fluctuation theorems for harmonic oscillators**

S Joubaud, N B Garnier and S Ciliberto




$\boldsymbol{\theta(t)}$: tilt angle

$$I_{\text{eff}}\frac{\mathrm{d}^2\theta}{\mathrm{d}t^2}+\nu\frac{\mathrm{d}\theta}{\mathrm{d}t}+C\theta=M+\sqrt{2k_{\mathrm{B}}T\nu}\eta,$$

$$\begin{aligned}Q_\tau &= \Delta U_\tau - W_\tau\\ &= -\frac{1}{k_{\mathrm{B}}T}\int_{t_i}^{t_i+\tau}\nu\left[\frac{\mathrm{d}\theta}{\mathrm{d}t}(t')\right]^2\mathrm{d}t' + \frac{\sqrt{2k_{\mathrm{B}}T\nu}}{k_{\mathrm{B}}T}\int_{t_i}^{t_i+\tau}\eta(t')\frac{\mathrm{d}\theta}{\mathrm{d}t}(t')\,\mathrm{d}t'.\end{aligned}$$

Introduction

**Stochastic Energetics**

# Energetics at mesoscopic scales

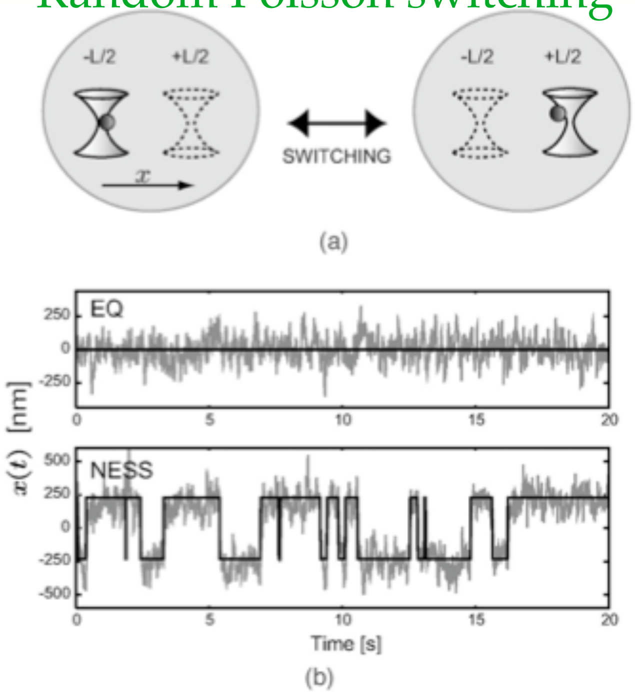
Experimental demonstrations of ***energy balance***

PHYSICAL REVIEW E **75**, 011122 (2007)

**Experimental test of a new equality: Measuring heat dissipation in an optically driven colloidal system**

Shoichi Toyabe,[1,*] Hong-Ren Jiang,[1] Takenobu Nakamura,[2] Yoshihiro Murayama,[1] and Masaki Sano[1,†]

Random Poisson switching




Harada-Sasa* identity : (*PRL '05)

$$\langle J\rangle_0 = \gamma \int_{-\infty}^{\infty} [\tilde{C}(\omega) - 2k_B T \tilde{R}'(\omega)] \frac{d\omega}{2\pi},$$

deviation from equilibrium F-D relation

$f^p$ :probe force

$$\gamma \dot{x}(t) = F(x(t),t) + \varepsilon f^p(t) + \hat{\xi}(t),$$

heat : $\langle J\rangle = \langle F(x(t),t)\circ v(t)\rangle,$

correlation : $C(t) \equiv \langle \dot{x}(t)\dot{x}(0)\rangle_0.$

response :

$$\langle \dot{x}(t)\rangle_\varepsilon - v_s = \varepsilon \int_{-\infty}^{t} R(t-s) f^p(s) ds + o(\varepsilon^2),$$

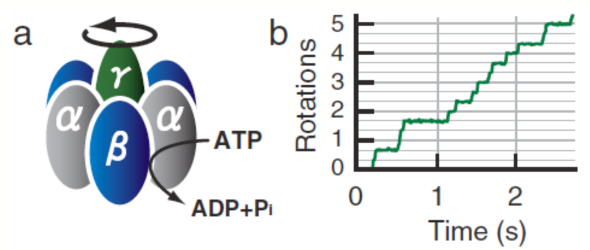
# Energetics at mesoscopic scales

Experimental demonstrations of ***energy balance***

PRL **104**, 198103 (2010) PHYSICAL REVIEW LETTERS week ending 14 MAY 2010

**Nonequilibrium Energetics of a Single $F_1$-ATPase Molecule**

Shoichi Toyabe,[1] Tetsuaki Okamoto,[1] Takahiro Watanabe-Nakayama,[2] Hiroshi Taketani,[1]
Seishi Kudo,[3] and Eiro Muneyuki[1,*]

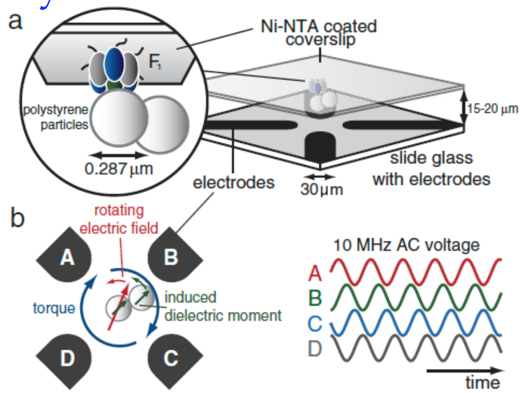


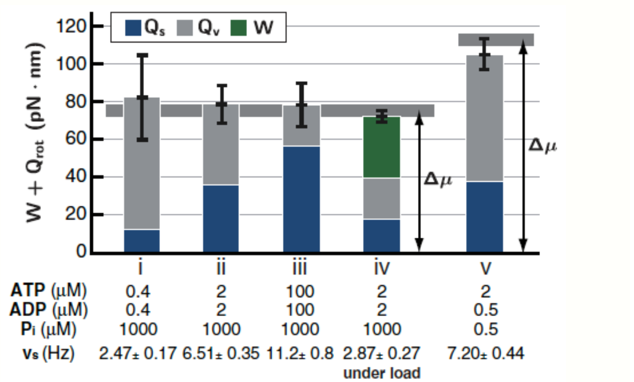

*heat* : $J \equiv \langle [\Gamma v(t) - \xi(t)] \circ v(t) \rangle = \left\langle \frac{d'Q}{dt} \right\rangle$

Harada-Sasa *equality* :

$$J = \Gamma v_s^2 + \Gamma \int_{-\infty}^{\infty} df[\tilde{C}(f) - 2T\tilde{R}'(f)],$$

Torque by electric field :



# Energetics at mesoscopic scales

**2nd law of stochastic energetics**

$$a(t_0) = a_{\rm i} \quad \downarrow \quad a(t_1) = a_{\rm f}$$

Irreversible work :
$$W_{\rm irr} \equiv W - \Delta F = \int_{a_{\rm i}}^{a_{\rm f}} \left\{ \frac{\partial U(x(t),a(t))}{\partial a} - \left\langle \frac{\partial U(x,a(t))}{\partial a} \right\rangle_{{\rm can};T} \right\} da(t).$$

$$F: \; e^{-F/k_{\rm B}T} = \int e^{-U(x,a)/k_{\rm B}T} dx$$

Quasi-static limit : $W_{\rm irr} \to 0, \quad (prob.1)$

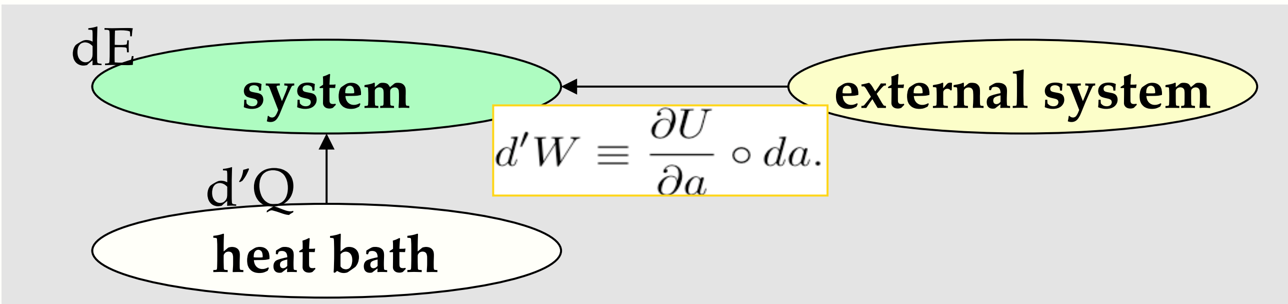
i.e. $W \to \Delta F$ *without ensemble averages*

*Jarzynski equality* ( Jarzynski, PRL97, Crooks, JSP98)

$$1 = \left\langle e^{-\beta W_{\rm irr}} \right\rangle_{\text{eq.at } t=0} \quad \Rightarrow \quad \langle W_{\rm irr} \rangle_{\text{eq.at } t=0} \geq 0$$

Complementarity: $\langle W_{\rm irr} \rangle \, \Delta t \geq S(a_{\rm i}, a_{\rm f}) \qquad (\Delta t \to \infty)$

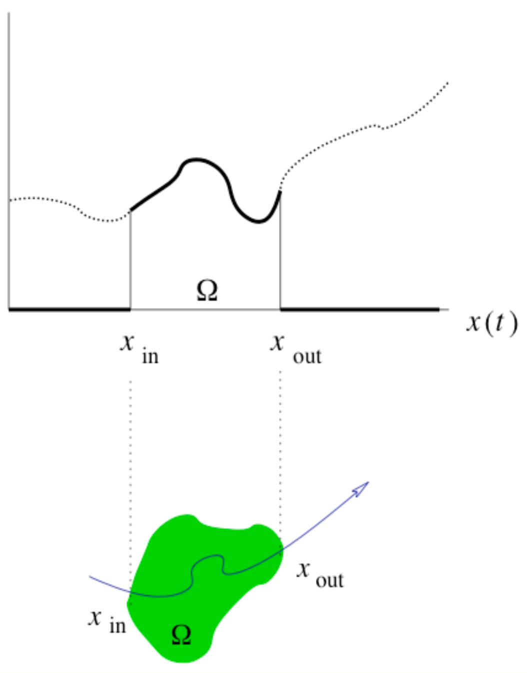
(correction : initial condition sensitive)



# Energetics at mesoscopic scales

**Remark** : energetics of *open system* can also be formulated.

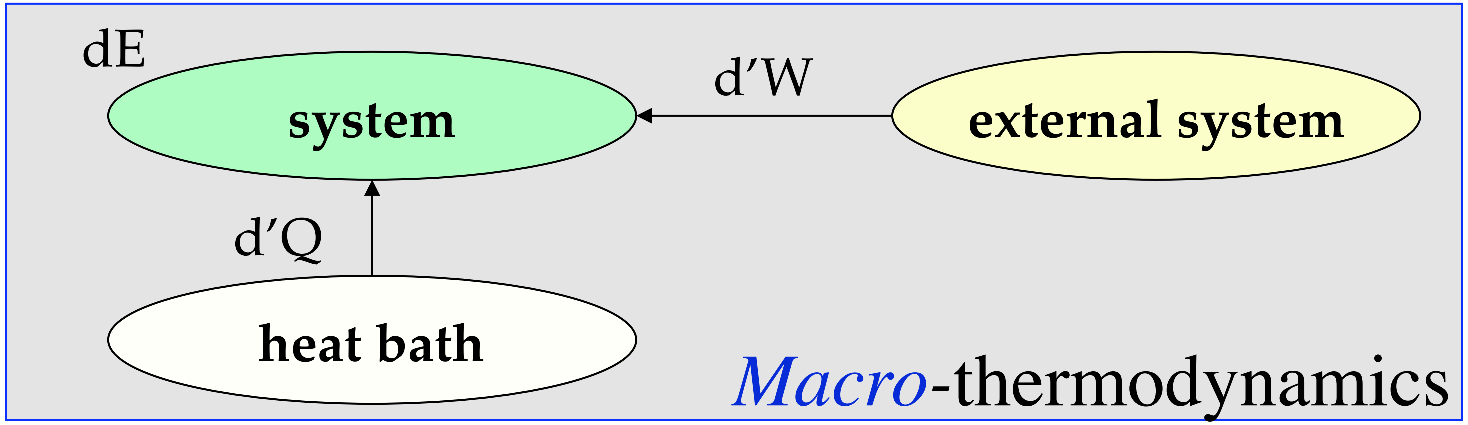
Base : *energy of the open system*

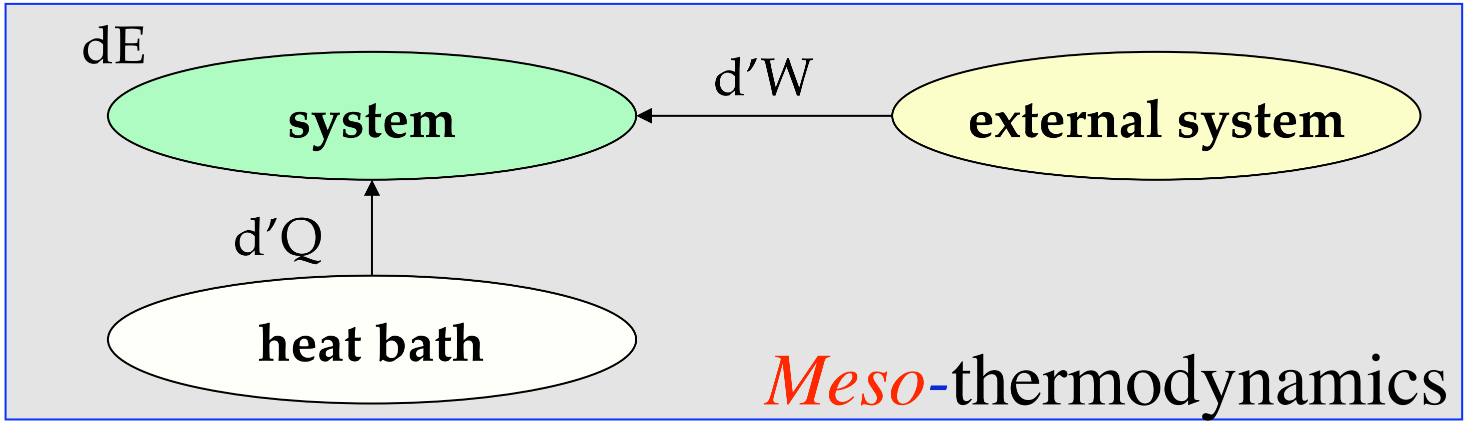



*Individual* particles do *not* carry the chemical potential μ.

# Energetics at mesoscopic scales

**RESUMÉ : "thermodynamic structure"**




(cf. steady-state thermodyn., Q'm entangling,…)

# Misconceptions about the fluctuations

*Are Langevin equations* always *irreversible ?*

"*the mesoscopic equations are therefore irreversible*"
(van Kampen's book "Stochastic Processes in Physics and Chemistry")

## Yes & No :

Yes — microscopic viewpoint
The heat bath does not accumulate the memory*.
(**temperature* [energy] & *mean-flow* [momentum])

No — mesoscopic viewpoint
The trajectories can describe quasi-equilibrium process.

*cf*. thermodynamic adiabatic process of chaotic Hamiltonian system
(macro) (micro)

# Misconceptions about the fluctuations

*Numerical convergence of Langevin eq.*

$$0 = -\frac{\partial U(x,a)}{\partial x} - \gamma\frac{dx}{dt} + \sqrt{2\gamma k_{\rm B}T}\theta(t)$$ under a given $\theta(t)$; $B_t = \int_0^t \theta(s)ds$

**1st order Euler scheme** for Langevin equation ($t_0 < t < t_1$):

$$0 = -\frac{\partial U(x_t,a_t)}{\partial x} - \gamma\frac{x_{t+\Delta t}-x_t}{\Delta t} + \sqrt{2\gamma k_{\rm B}T}\,(B_{t+\Delta t}-B_t)$$

convergence at $\mathcal{O}(\Delta t^{\frac{1}{2}})$ ➡ solution $x(t)$

But error of $\mathcal{O}(1)$ for energy balance.

Implication :

*Apparent equilibrium state* can *dissipate heat.*

*Order* $\mathcal{O}(\Delta t)$ *convergence required for correct energy balance.*

# Misconceptions about the fluctuations

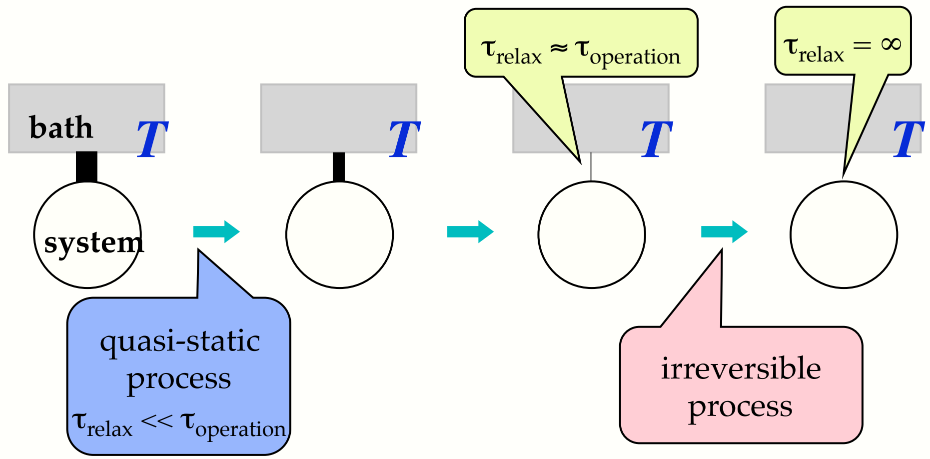
*Can* Carnot cycle *be reversible* ?

Yes & No :

Yes — macroscopic [thermodynamic] limit

No — mesoscopic case (with some exceptions)

Detachment from heat baths




* **divergence of relaxation time** ➔ Impossibility of *quasi-static* operations

associated irreversible work : *non-extensive* & arbitrarily small

Introduction

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**Misconceptions**

# Misconceptions about the fluctuations

*Can* Carnot cycle *be reversible* ?

## Yes & No :

Yes — macroscopic [thermodynamic] limit

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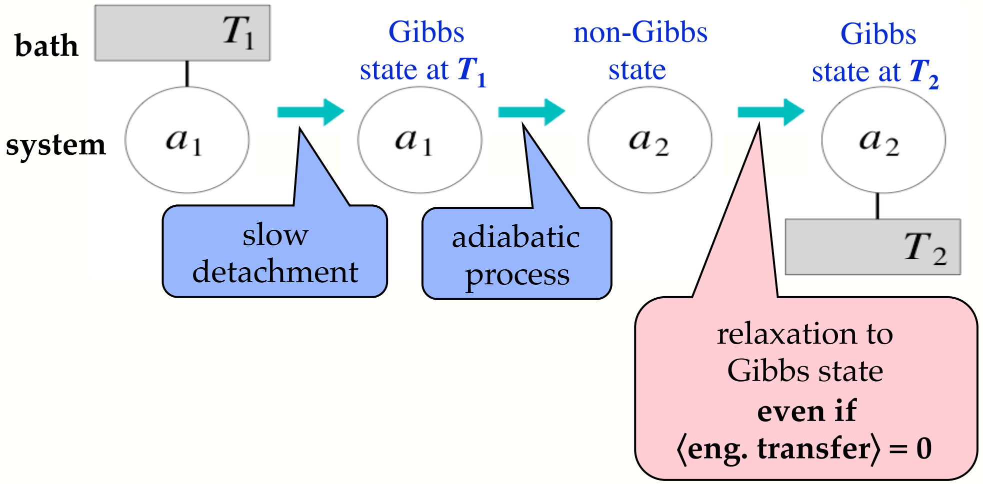
Adiabatic process




* relaxation from **non-gibbs distribution** ➔ Irreversible information loss

associated irreversible work : non retrievable otherwise

# Misconceptions about the fluctuations

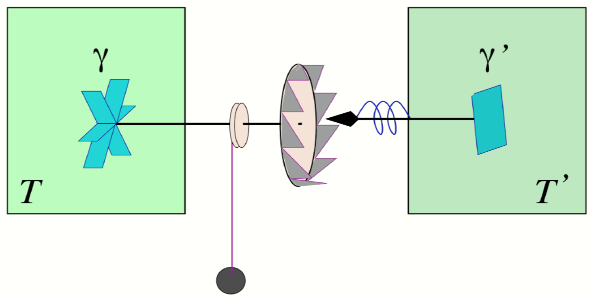
*Can* Feynman's ratchet wheel and pawl *attain* Carnot efficiency?

"*… our device cannot extract more work than this* [$(T_1 - T_2)/T_1$], *operating reversibly*."
— Feynman's lecture 46-3 (1963)

No :

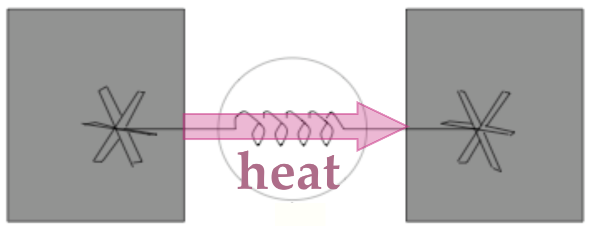
wiggling between the "jumps"

Feynman's ratchet




≅

mechanical *heat* conductor




"stall state" (jump frequency=0) ≠ Carnot efficiency
= **null** efficiency

(Parrondo 1996, KS 1997)

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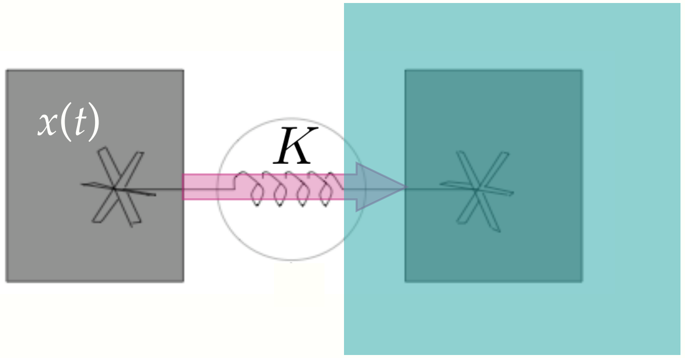
Stochastic Energetics

Misconceptions

# Misconceptions about the fluctuations

**Remark :** mechanical *heat* conductor

➔ "random motion" can absorb heat (cf. Joule's law)




*cf.* "Maxwell's demon"

$T'$=0 case :

$$\gamma\dot{x}(t) = -K\left[x(t) - \frac{K}{\gamma'}\int_0^\infty e^{-\frac{K}{\gamma'}s}\underline{x(t-s)}ds\right] + \sqrt{2\gamma k_\mathrm{B}T}\,\theta(t)$$

*feed-back as 0-K bath*

# Misconceptions about the fluctuations

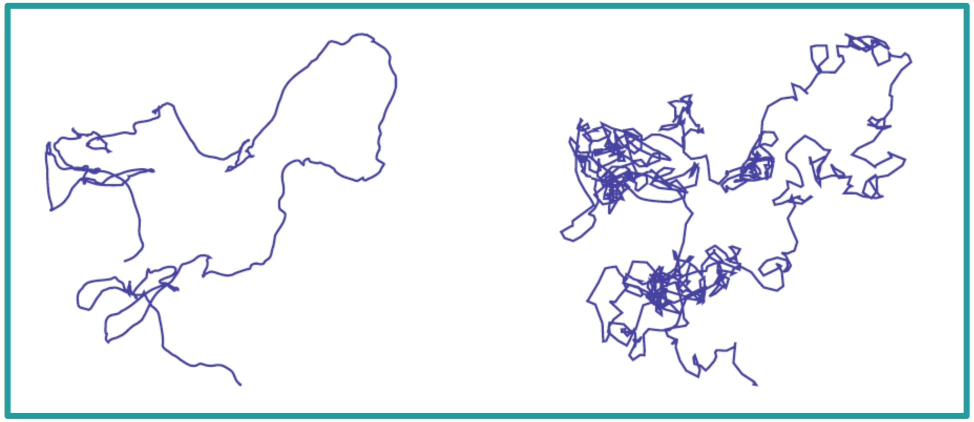
Is the over-damped limit $m \to 0$ *regular* in energetics ?

under-damped : $\frac{dp}{dt} = -\frac{\partial U(x,a)}{\partial x} - \gamma \frac{dx}{dt} + \sqrt{2\gamma k_{\mathrm{B}} T}\,\theta(t), \qquad \frac{dp}{dt} = \frac{p}{m}$

time coarse graining

$$\gamma[x(t+\Delta t) - x(t)] = \sqrt{2\gamma k_{\mathrm{B}} T(x(t))}[B_{t+\Delta t} - B_t] - \frac{\partial U(x(t), a(t))}{\partial x}\Delta t$$
$$+ k_{\mathrm{B}} T'(x(t))\{[B_{t+\Delta t} - B_t]^2 - \Delta t\} + o(\Delta t),$$

over-dumped : $0 = -\frac{\partial U(x,a)}{\partial x} - \gamma \frac{dx}{dt} + \sqrt{2\gamma k_{\mathrm{B}} T}\,\theta(t)$



under-damped　　　　over-damped

Introduction

Stochastic Energetics

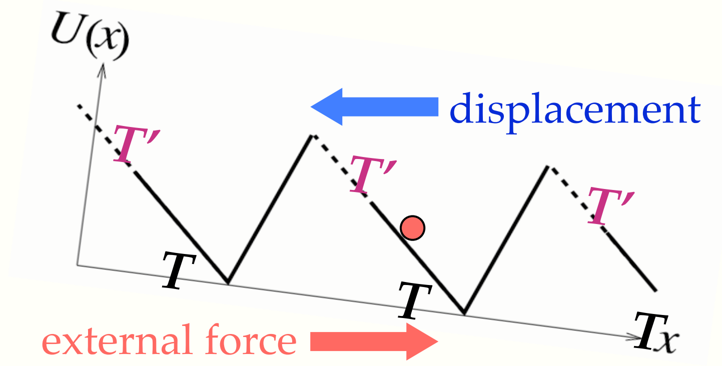
Misconceptions

# Misconceptions about the fluctuations

Is the over-damped limit $m \to 0$ *regular* in energetics ?

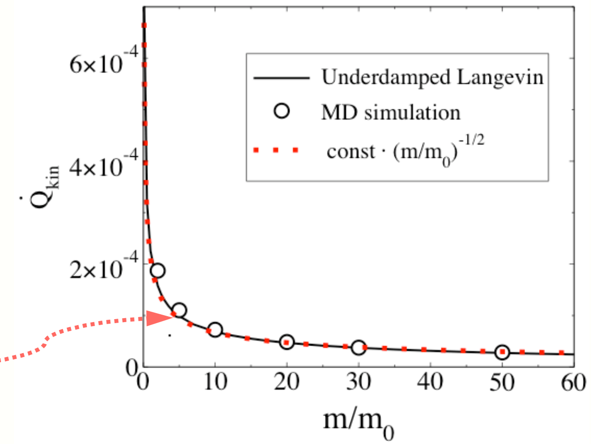
## No, sometimes :

Büttiker-Landauer ratchet (1961)




~~Model : $m = 0$~~
~~"Carnot's limit efficiency" $\frac{T' - T}{T'}$~~
~~at *stalled* state ($v$=0).~~

Model : $m \to 0$
divergence of heat leak $\propto \frac{1}{\sqrt{m}}$
($\Rightarrow$ zero efficiency)




(Benjamin-Kawai, PRE 08)

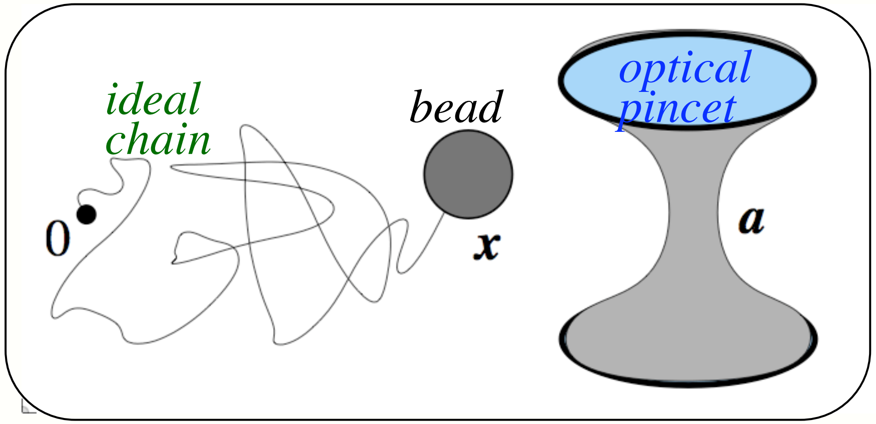
# Misconceptions about the fluctuations

QUESTION :

Relation between **mesoscopic heat** AND "calorimetric heat" ?

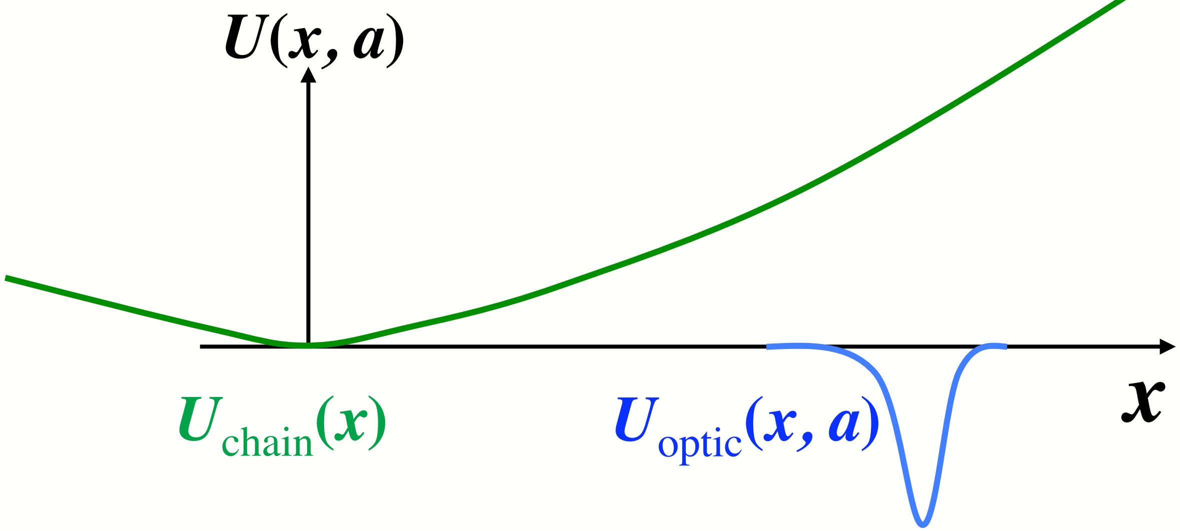
# What is the heat ?

Example




$$U(x,a) = U_{\text{chain}}(x) + U_{\text{optic}}(x,a)$$

$$0 = -\frac{\partial U(x,a)}{\partial x} - \gamma \frac{dx}{dt} + \sqrt{2\gamma k_{\mathrm{B}} T}\theta(t)$$



# What is the heat ?

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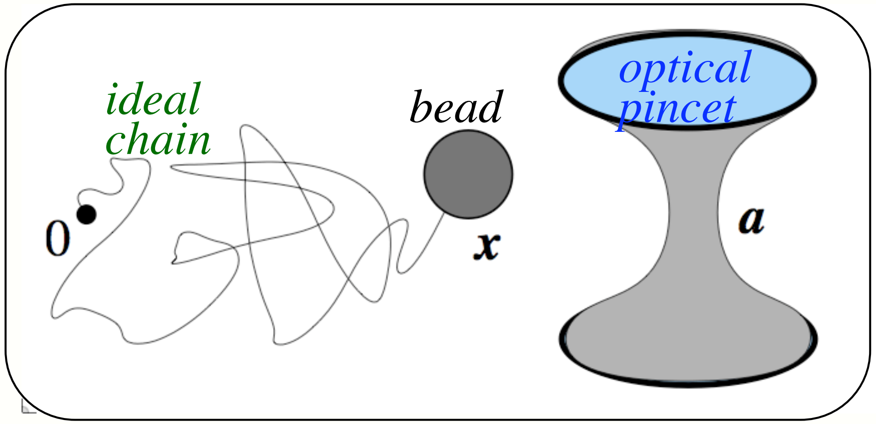


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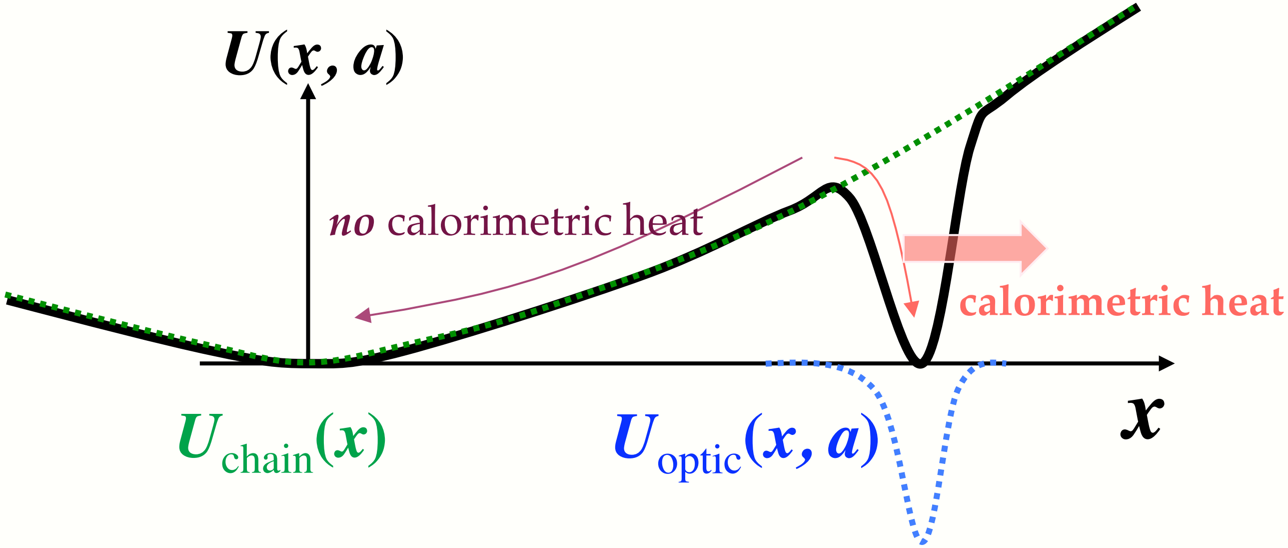


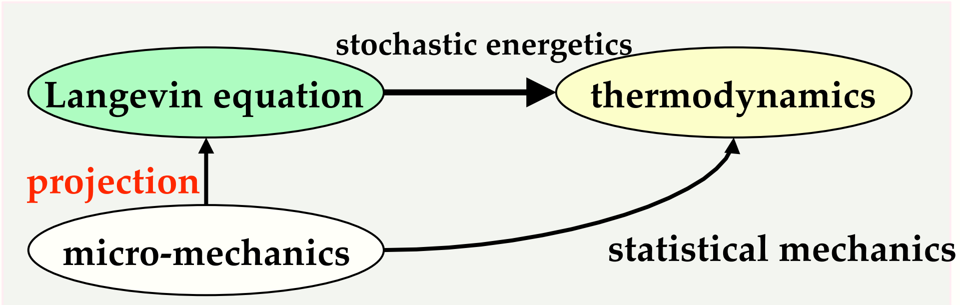
# What is the heat ?

Is **mesoscopic heat** = "calorimetric heat" $d'Q_{\mathrm{m}}$ ?

$$d'Q \equiv \left(-\gamma\frac{\partial x}{\partial t} + \sqrt{2\gamma k_{\mathrm{B}}T}\,\theta(t)\right)\circ dx(t)$$

$$0 = -\frac{\partial U(x,a)}{\partial x} - \gamma\frac{dx}{dt} + \sqrt{2\gamma k_{\mathrm{B}}T}\theta(t)$$

No in general




$U(x,a)$ : free energy — entropy renormalized
$d'W$ : scale independent
energy balance for calorimetric heat

⇒ relation between **mesoscopic heat** AND "calorimetric heat"

# What is the heat ?

Is **mesoscopic heat** = "calorimetric heat" $d'Q_{\mathrm{m}}$ ?

$$d'Q \equiv \left( -\gamma \frac{\partial x}{\partial t} + \sqrt{2\gamma k_{\mathrm{B}} T}\, \theta(t) \right) \circ dx(t)$$

$$0 = -\frac{\partial U(x,a)}{\partial x} - \gamma \frac{dx}{dt} + \sqrt{2\gamma k_{\mathrm{B}} T}\theta(t)$$

No in general

$$dE - T\frac{\partial U}{\partial T} \mapsto dE_{\mathrm{m}}$$

$$dQ - T\frac{\partial U}{\partial T} \mapsto dQ_{\mathrm{m}}$$

**mesoscopic** energy balance

$$dE = d'Q + d'W$$

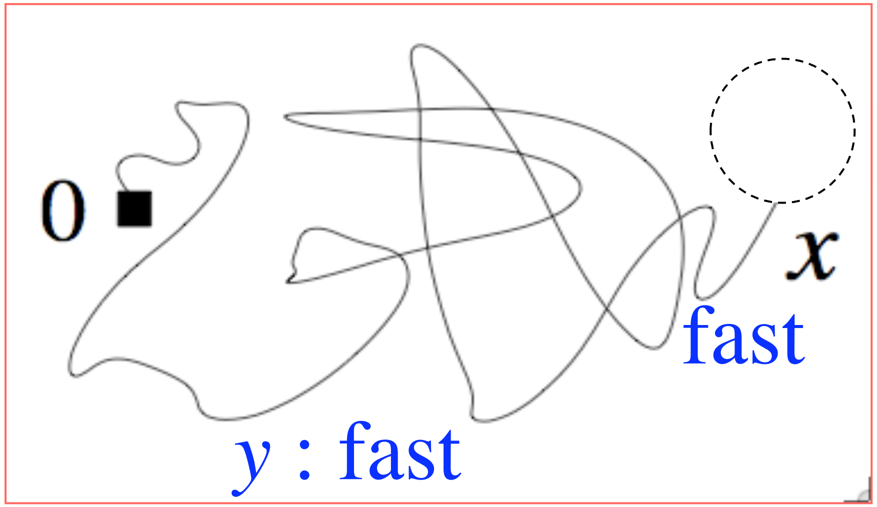
→

calorimetric energy balance

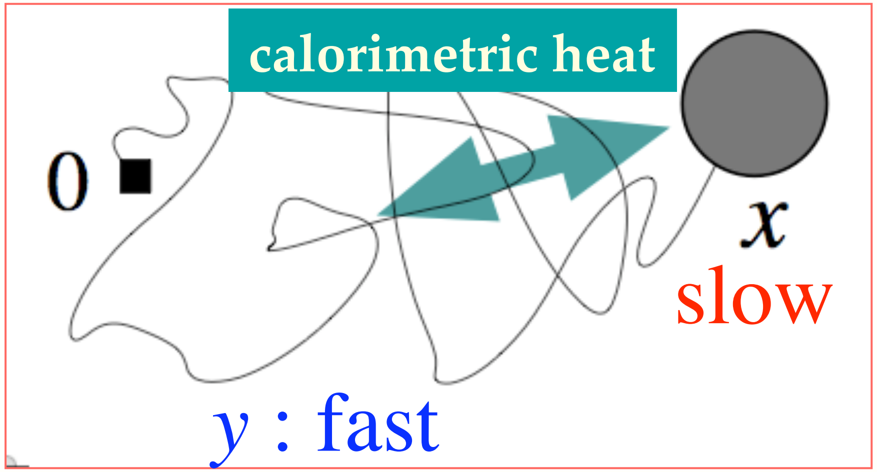
$$dE_m = d'Q_m + d'W$$

# What is the heat ?

**Implication** : local energy transfer *in the environment*

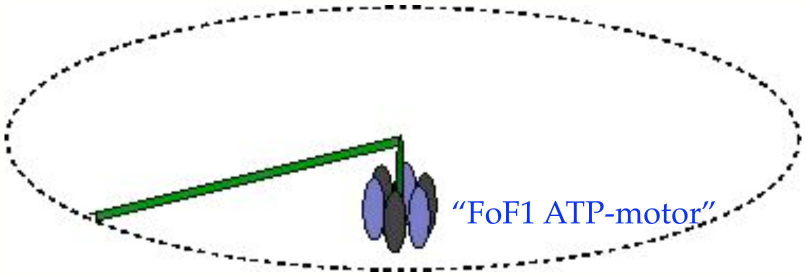



**No calorimetric heat**



# What is the heat ?

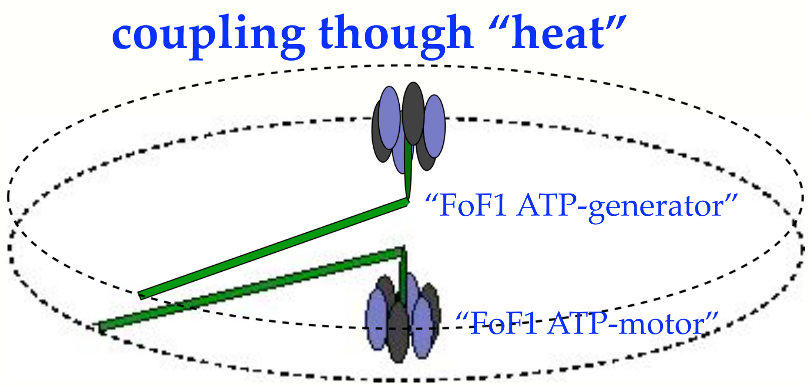
IMPLICATION : scale cascade of heat




(controversy ~2000)
does the filament generate a ***work*** or a ***heat*** ?

# What is the heat ?

Implication : scale cascade of heat




(controversy ~2000)
does the filament generate a ***work*** or a ***heat*** ?

# Project

**Résumé :**

**stochastic energetics**
=> new perspectives of fluctuation phenomena

What can we do with thise perspectives ?

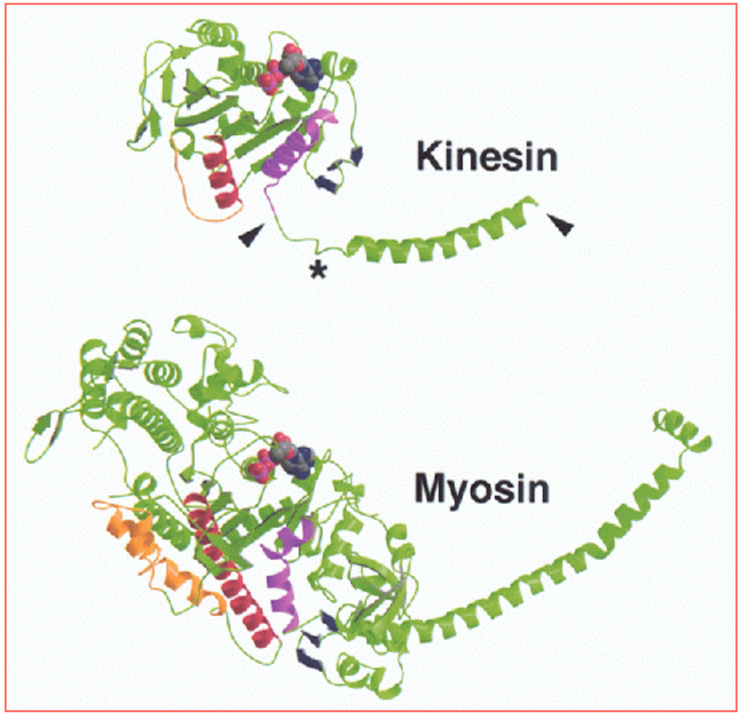
> exploration of structure-function relation of proteins

> mesoscopic mechanism of *motor proteins*

> modelling common to ***myosin*** & ***kinesin***

— similar / different

# Project




(Vale, J. Cell Biol. '96)

Introduction

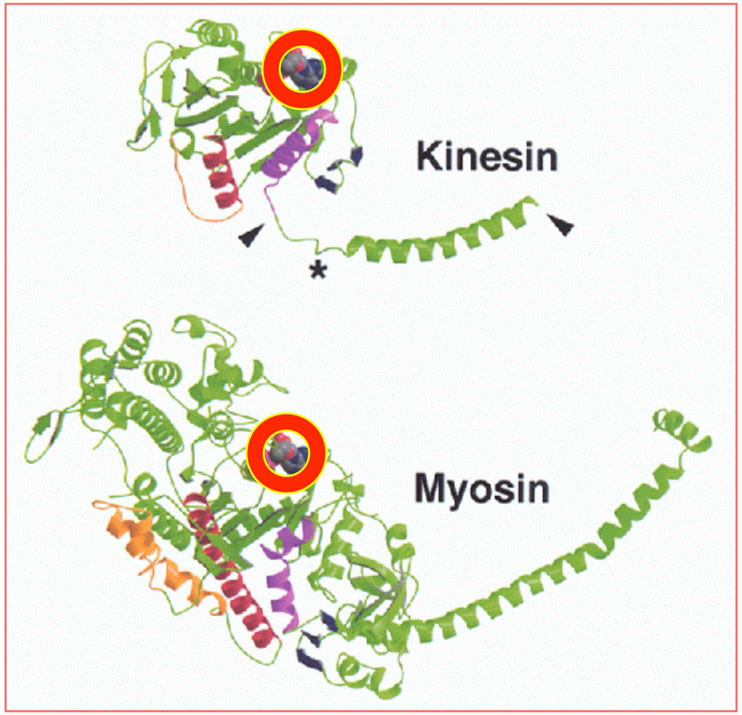
Stochastic
Energetics

Misconceptions

Different heats

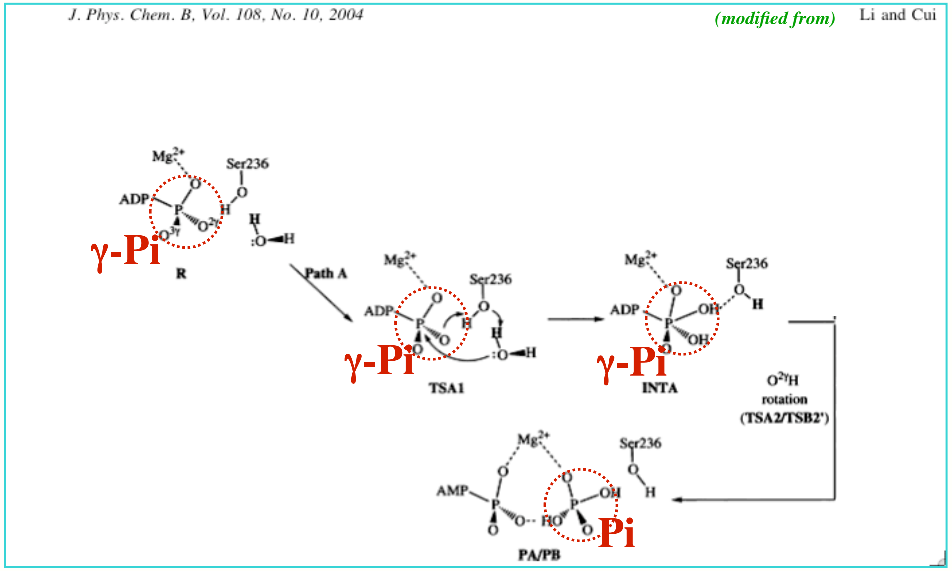
Project

# Project




(Vale, J. Cell Biol. '96)

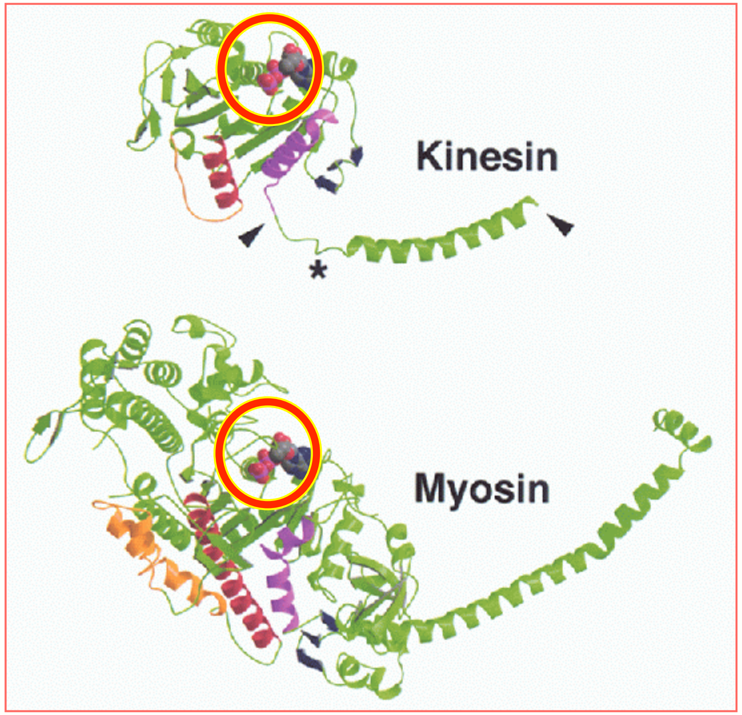
## Identical *QM* reaction




$Pi = H_2PO_4$

(*cf.* protein kinase; γ-Pi is given to Se, which looses a proton)

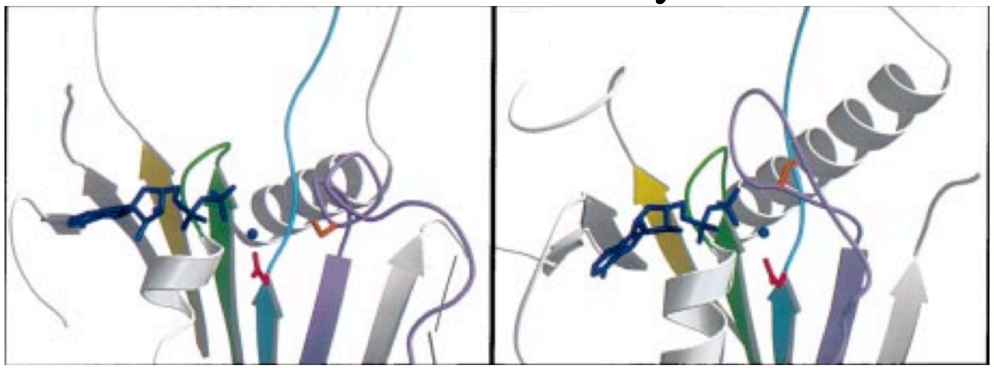
# Project




(Vale, J. Cell Biol. ‘96)

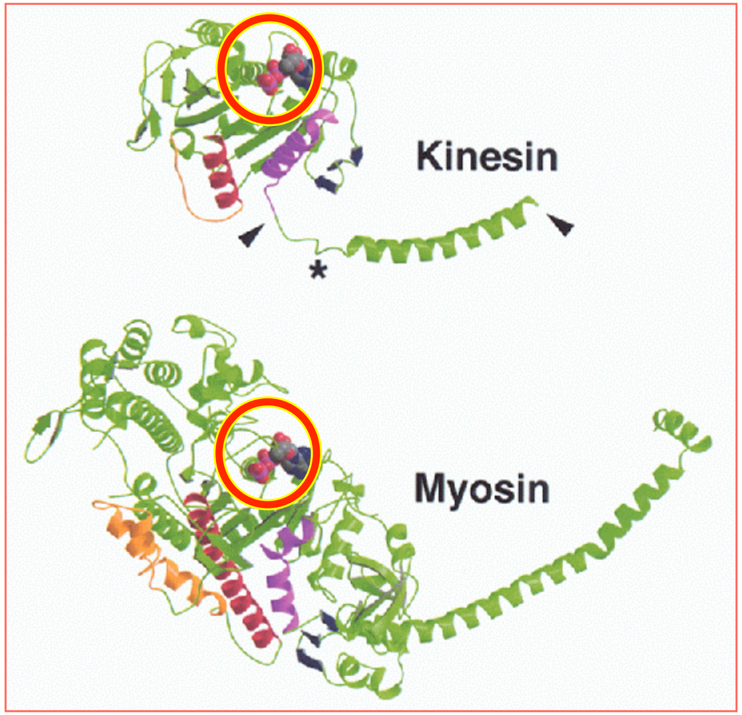
## Very similar 3D atomic structure

kinesin myosin



F. J. Kull, R. D.Vale and R.J.Fletterick
J. Muscle Research and Cell Motility 19, 877-886 (1998)

# Project




(Vale, J. Cell Biol. ‘96)

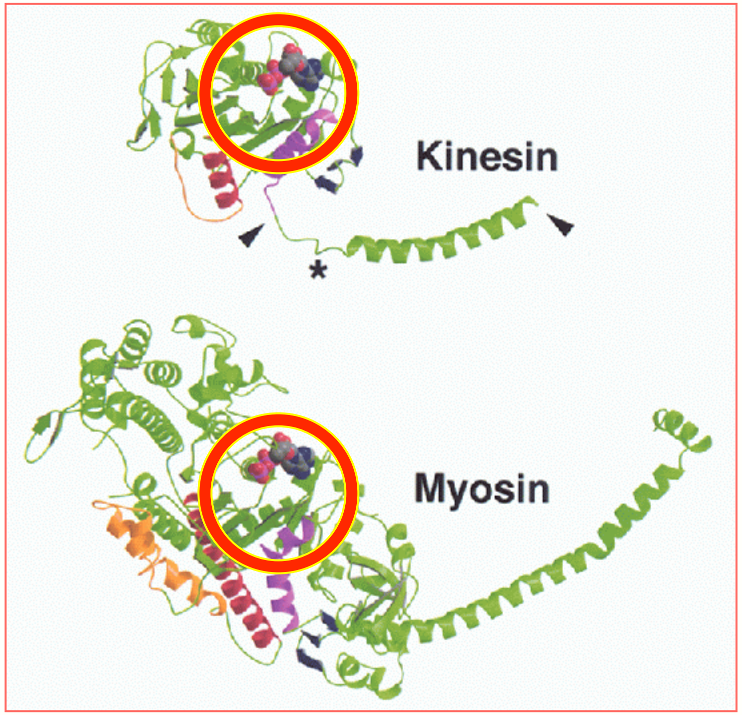
## Very similar AA sequences

Nucleotide Binding Motifs

| | α,β-PO$_4$ N-1 | γ-PO$_4$ N-2 | γ-PO$_4$ N-3 | Purine N-4 |
|---|---|---|---|---|
| G Proteins | GxxGxGKS/T | T | DxxG | NKxD |
| Kinesins | GQTxxGKS/T | NxxSSR | DxxGxE | RxRP |
| Myosins | GESxxGKS/T | NxxSSR | DxxGxE | NP |

(Vale, J. Cell Biol. ‘96)

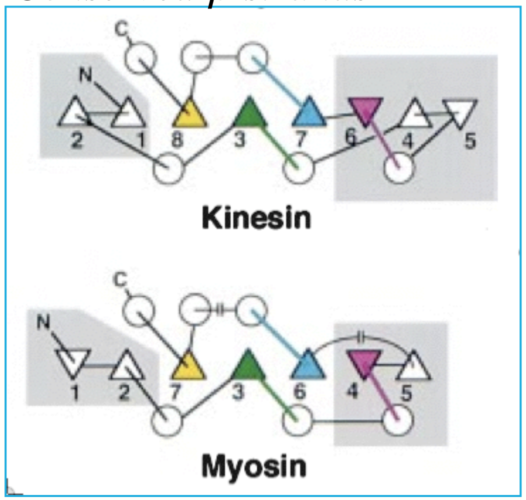
# Project




(Vale, J. Cell Biol. '96)

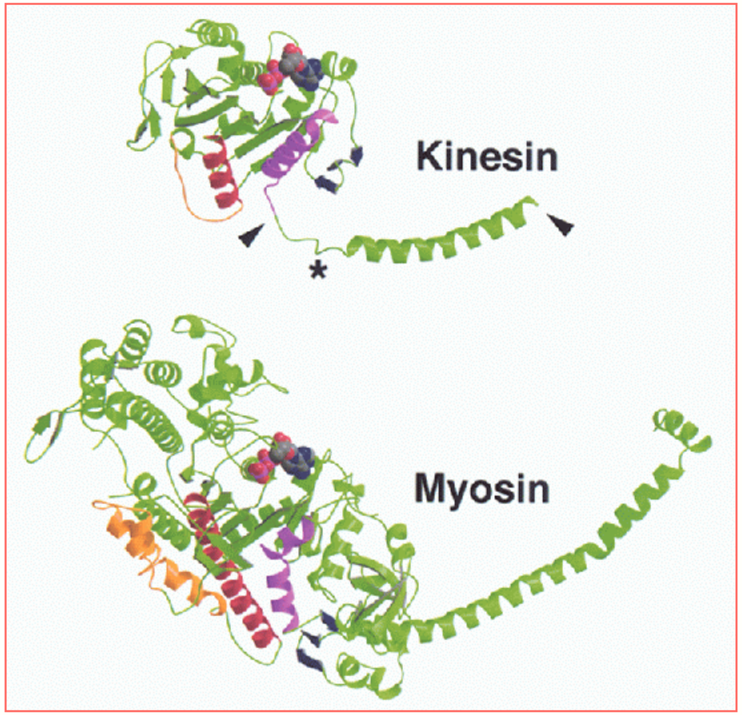
## Similar folding modules

*Conserved β-strands*




Kull, Vale Fletterick
J.Muscle Res. Cell Motility 1998

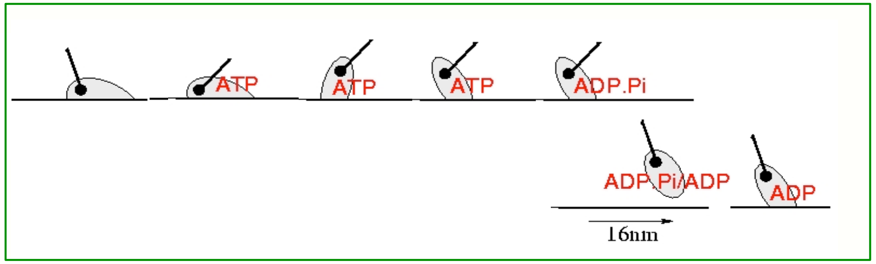
# Project



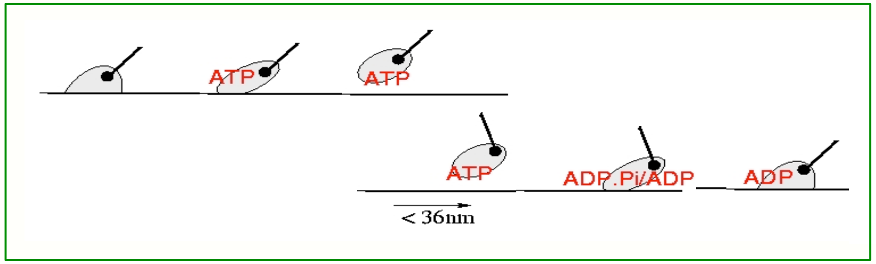

(Vale, J. Cell Biol. '96)

## Different chemo-mechanical cycles

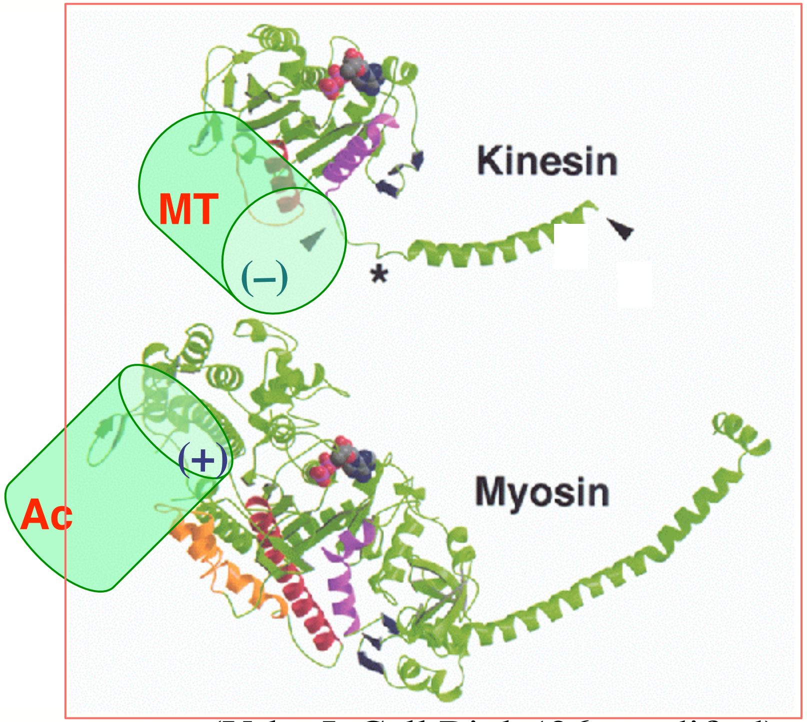
kinesin - microtubule




myosin – F-actin



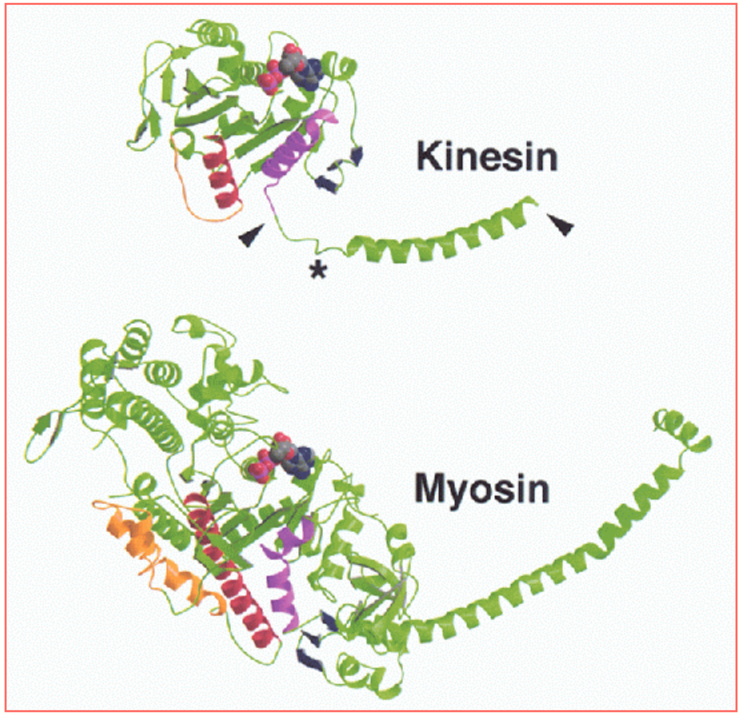
# Project




(Vale, J. Cell Biol. '96, modified)

Different filament binding

# Project



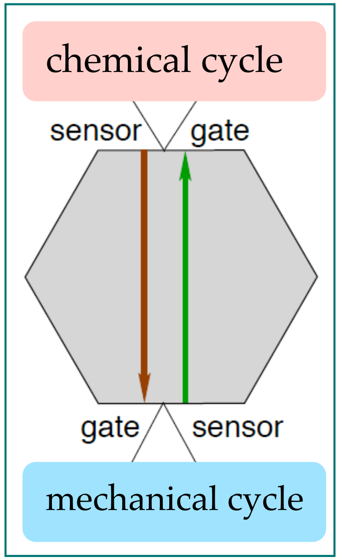

(Vale, J. Cell Biol. '96)

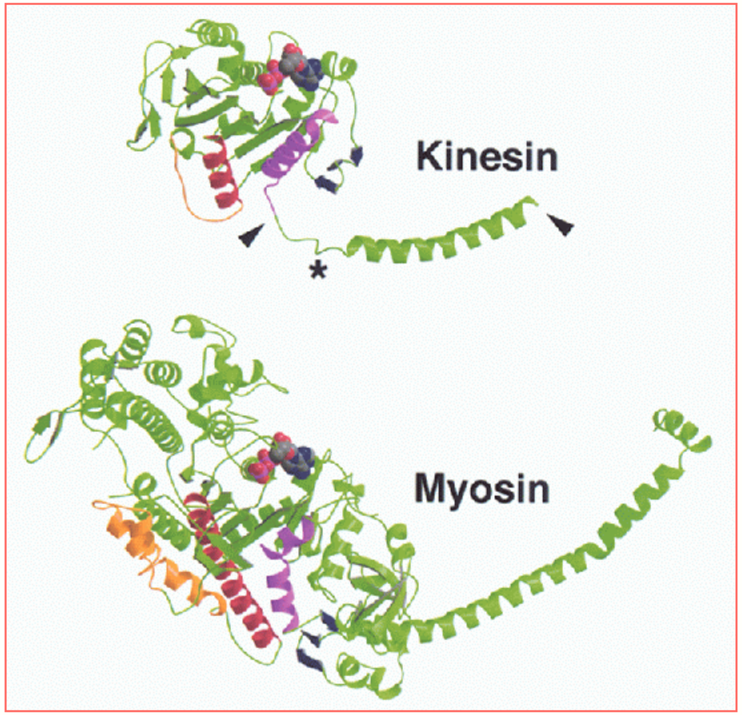
**Designing principle :**

— common *core mechanism* & different attachments

# Project

**Working hypothesis :**
— bidirectional control



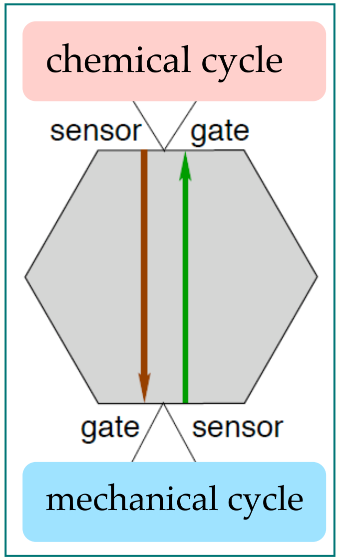




(Vale, J. Cell Biol. '96)

2 "allosteric" couplings (sensor → gate)

# Project

**Working hypothesis :**
— bidirectional control




(KS: 2005,2007, work in progress)

**kinesin**

**myosin**

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Project

# Summary

*Welcome*
*to*
*fluctuating world*
*and*
*stochastic energetics*