Lecture 3: Statistical Basis for Macroscopic Phenomena
Winter 2017

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Probability, the three central distributions, and qualitative behavior of dynamical systems. The power of sketching global behaviors

Pierre-Simon LaPlace
1749 - 1827

Carl Friederich Gauss
1777 - 1855

Simeon Denis Poisson
1781 - 1840

So, today we do two things: consider the **statistics** of systems of various size, and we learn to **think qualitatively** about behaviors of linear dynamical systems.

	n = 1	n = 2 or 3	n >> 1	continuum
Linear	exponential growth and decay single step conformational change fluorescence emission pseudo first order kinetics	second order reaction kinetics linear harmonic oscillators simple feedback control sequences of conformational change	electrical circuits molecular dynamics systems of coupled harmonic oscillators equilibrium thermodynamics diffraction, Fourier transforms	Diffusion Wave propagation quantum mechanics viscoelastic systems
Nonlinear	fixed points bifurcations, multi stability irreversible hysteresis overdamped oscillators	anharmonic oscillators relaxation oscillations predator-prey models van der Pol systems Chaotic systems	systems of non-linear oscillators non-equilibrium thermodynamics protein structure/ function neural networks the cell ecosystems	Nonlinear wave propagation Reaction-diffusion in dissipative systems Turbulent/chaotic flows

adapted from S. Strogatz

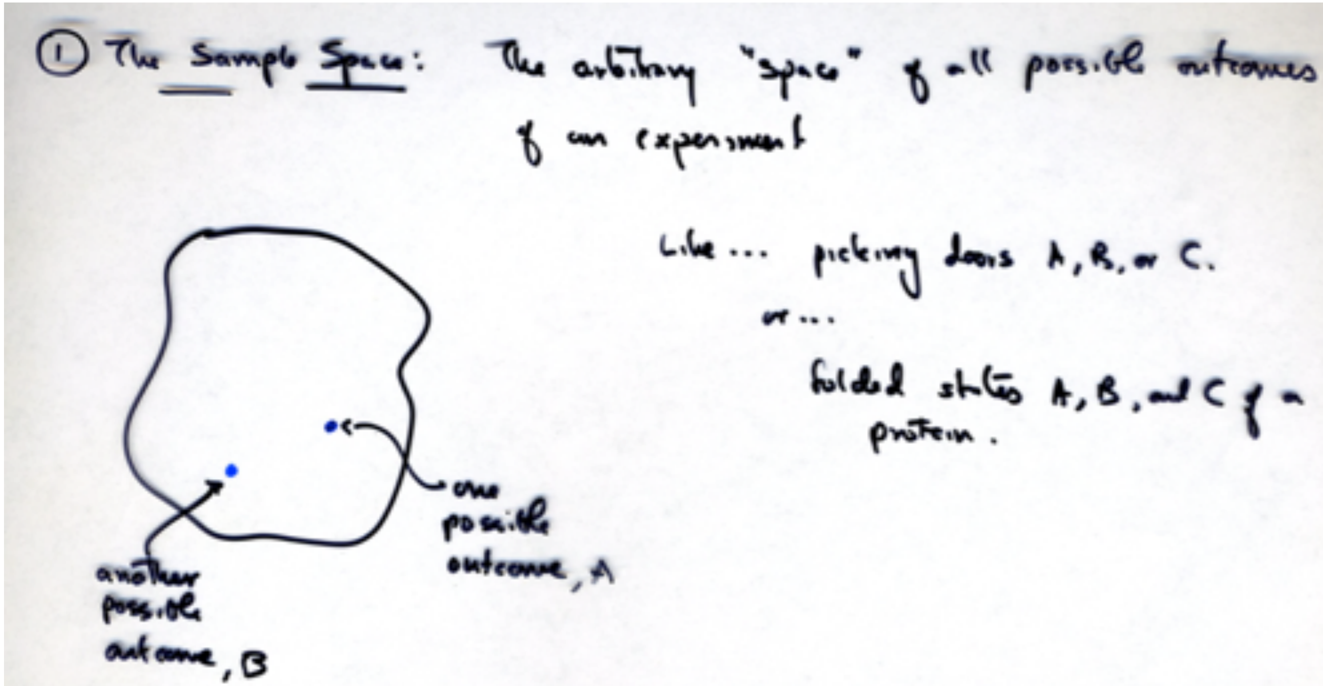
So, today we do two things: consider the **statistics** of linear systems of various size, and we consider **a few examples** of such dynamical systems.

The goals will be two-fold:

(1) Review the essentials probability theory….what are probabilities, ways of counting, the three central distributions of primary importance….the **binomial**, **Poisson**, and **Gaussian**.

(2) See how probability theory provides a powerful basis for **predicting the behavior** of simple systems. And, reinforces the importance of fluctuations in driving reactions.

Probability theory….starting with the basics.



Probability theory….starting with the basics.

① **The Sample Space**: The arbitrary "space" of all possible outcomes of an experiment

Like… picking doors A, B, or C.

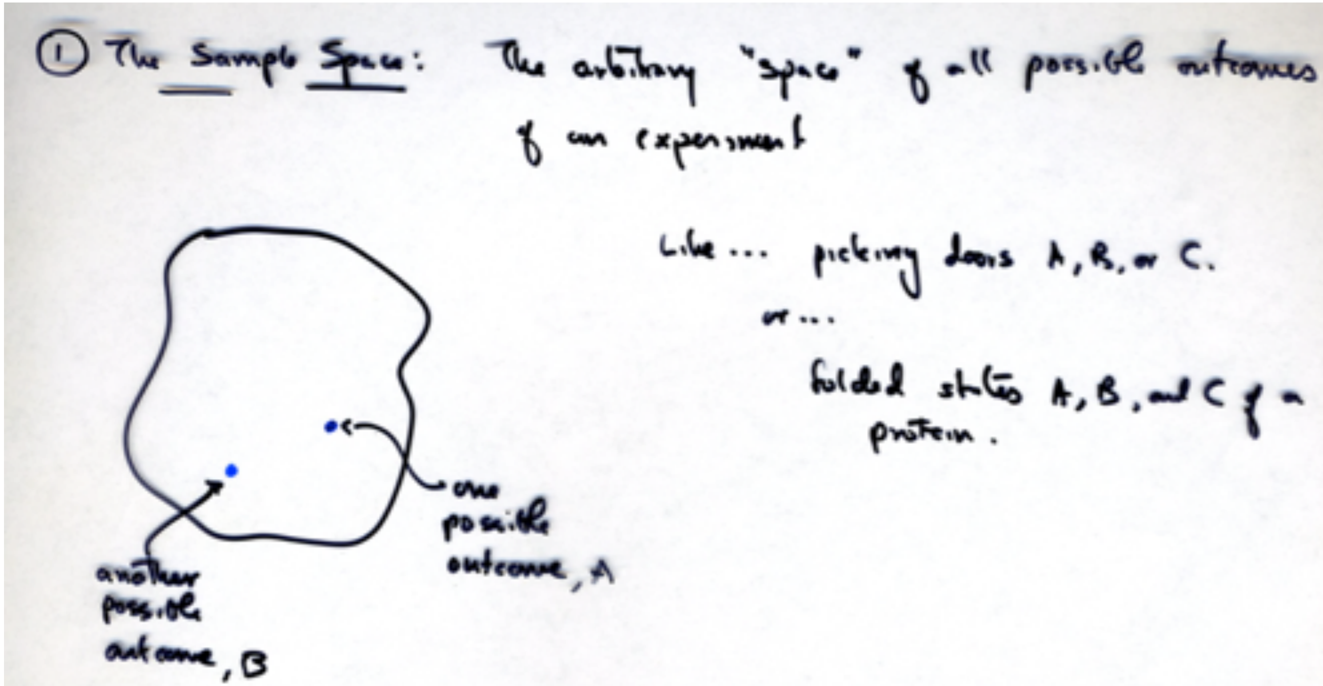
or…

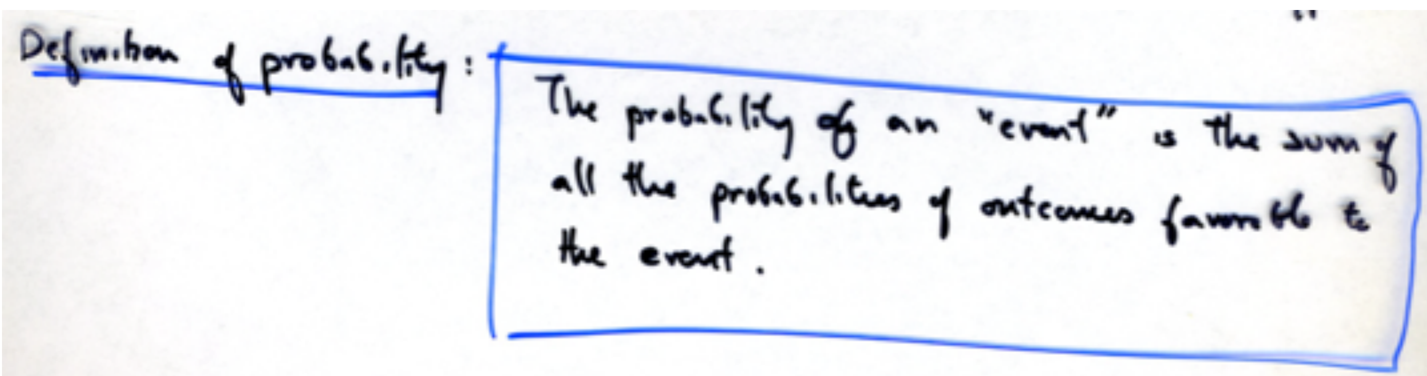
folded states A, B, and C of a protein.

Now… a uniform sample space is one where the likelihood of each outcome is the same

a non-uniform space is one where the likelihoods of outcomes could be different

Probability theory….starting with the basics.





or **stated mathematically**…

Probability theory….starting with the basics.

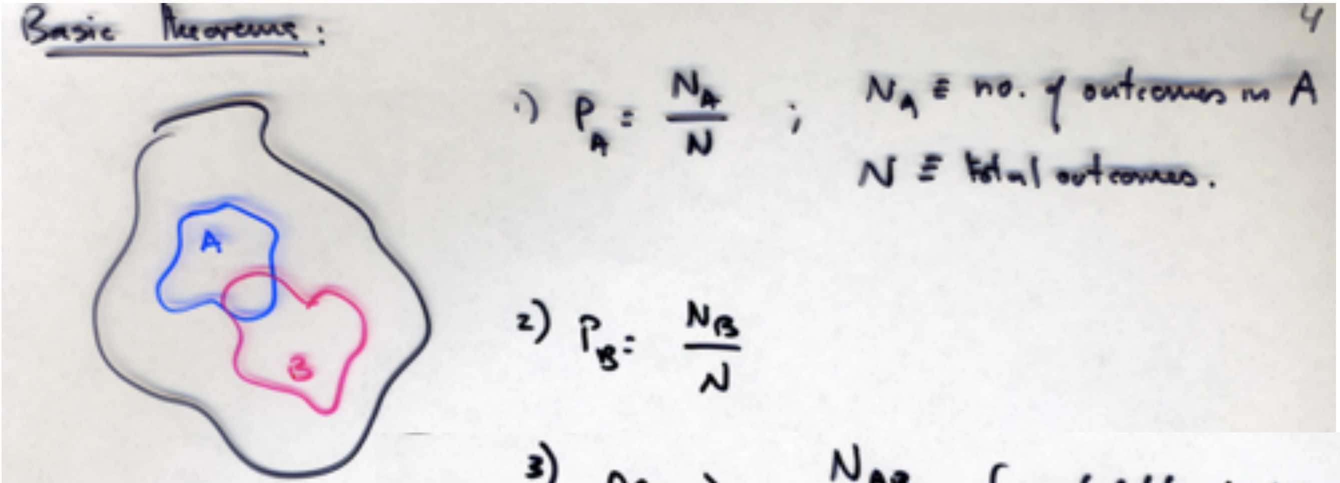
Basic Theorems:

1) $P_A = \frac{N_A}{N}$; $N_A \equiv$ no. of outcomes in A

$N \equiv$ total outcomes.

2) $P_B = \frac{N_B}{N}$

Probability theory….starting with the basics.



Basic Theorems:

4

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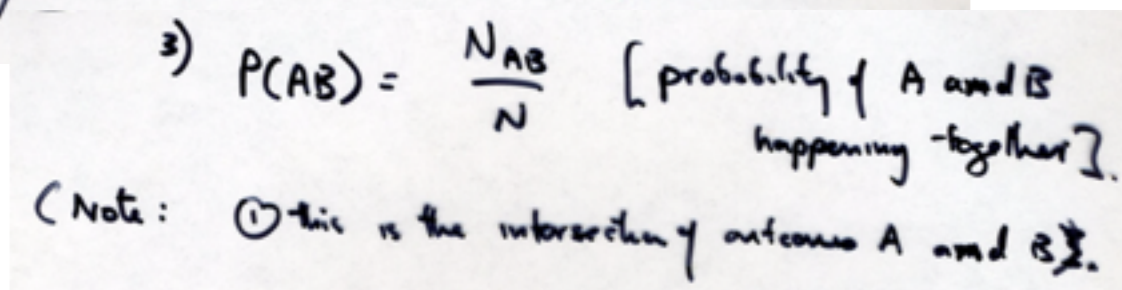

3) $P(AB) = \frac{N_{AB}}{N}$ [probability of A and B happening together].

(Note: ① this is the intersection of outcomes A and B).

the concept of <u>joint probability</u>…

Probability theory….starting with the basics.

Basic Theorems:

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3) $P(AB) = \frac{N_{AB}}{N}$ [probability of A and B happening together].

(Note: ① this is the intersection of outcomes A and B).

…and then the conditional probability…

4)

$$P(B|A) = \frac{N_{AB}}{N_A}$$

[probability of B happening given A has happened].

$$= P(AB) \cdot \frac{1}{P_A}$$

Probability theory….starting with the basics.

4)

$$P(B|A) = \frac{N_{AB}}{N_A}$$ [probability of B happening given A has happened].

$$= P(AB) \cdot \frac{1}{P_A}$$

This leads to the general definition of statistical independence…

$$P(AB) = P(A)\,P(B|A)$$

Probability theory….starting with the basics.

Basic Theorems:

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This leads to the general definition of statistical independence…

$$P(AB) = P(A)\,P(B|A)$$

if A and B independent… then $P(B|A) = P(B)$ and…

$P(AB) = P(A)\,P(B)$ ⇒ statistical independence

Probability theory….starting with the basics.

Basic Theorems:

4)

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$$= P(AB) \cdot \frac{1}{P_A}$$

This leads to the general definition of statistical independence…

$$P(AB) = P(A)\,P(B|A)$$

if A and B independent… then $P(B|A) = P(B)$ and…

$$P(AB) = P(A)\,P(B) \Rightarrow \text{statistical independence}$$

Also…

$$P(AB) = P(B)\,P(A|B)$$, thus…

Probability theory….starting with the basics.

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$$P(A|B) = \frac{P(A)\,P(B|A)}{P(B)}$$ Bayes' theorem.

Probability theory….starting with the basics.

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2) $P_B = \frac{N_B}{N}$

$$P(AB) = P(A)\,P(B|A)$$

…and finally the <u>combined probability</u>…

3) $P(A+B) = P_A + P_B - P(AB)$ (probability of A or B or both).

if A and B are mutually exclusive,

$$P(A+B) = P(A) + P(B)$$

Counting statistics…permutations and combinations

Say we have n things in a row. How many ways are there of arranging them?

or…

1 2 3	1 3 2
2 1 3	2 3 1
3 1 2	3 2 1

This is called the number of permutations of n things n at a time and is given by…

$$P(n,n) = n!$$

$$= n(n-1)(n-2)\ldots.(2)(1)$$

Counting statistics…<u>permutations</u> and <u>combinations</u>

Say we have n things in a row. How many ways are there of arranging them?

or …

1 2 3	1 3 2
2 1 3	2 3 1
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But we can also ask for the number of permutations of n things taken r at a time:

$$P(n,r) = n(n-1)(n-2)\cdots(n-r+1)$$

We can simplify this….

Counting statistics…permutations and combinations

But we can also ask for the number of permutations of n things taken r at a time:

$$P(n,r) = n(n-1)(n-2)\cdots(n-r+1)$$

Multiply and divide by $(n-r)!$

$$P(n,r) = n(n-1)(n-2)\cdots(n-r+1)\left[\frac{(n-r)!}{(n-r)!}\right]$$

$$= \frac{n(n-1)(n-2)\cdots(n-r+1)(n-r)(n-r-1)\cdots(2)(1)}{(n-r)!}$$

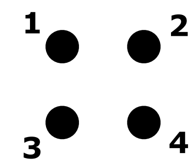
$$= \frac{n!}{(n-r)!}$$

This is the number of ways of taking **n** things **r** at a time….

Counting statistics…permutations and combinations

$$P(n,r) = \frac{n!}{(n-r)!}$$

For example, if we have a tetrameric channel, we can ask how many ways are there of taking two subunits at a time….



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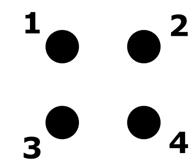
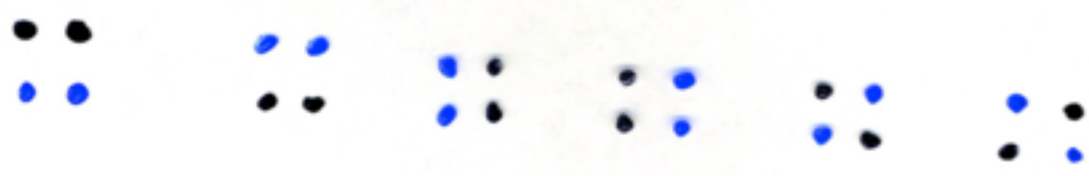




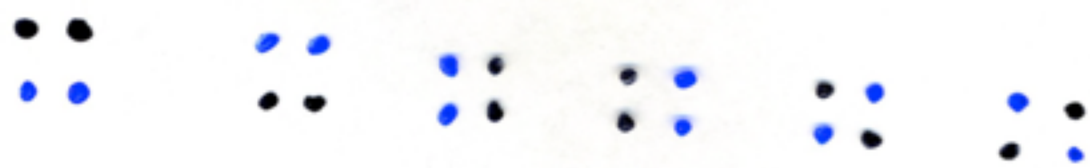
12 ways of taking pairs!

Let's see …

$$\frac{4!}{2!} = 12$$

This is the number of **permutations**…

Counting statistics…permutations and combinations



$$P(n,r) = \frac{n!}{(n-r)!}$$

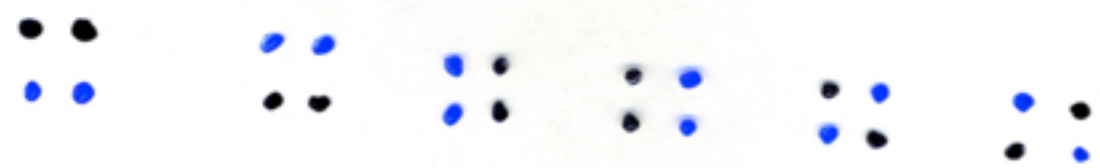
This is the number of **permutations**…

But if we don't care about the order of taking pairs, then this is called the number of combinations of **n** things taken **r** at a time…

$$C(n,r) = \frac{n!}{(n-r)!\,r!} = \binom{n}{r}$$

This is the number of **combinations**…

Counting statistics…permutations and combinations



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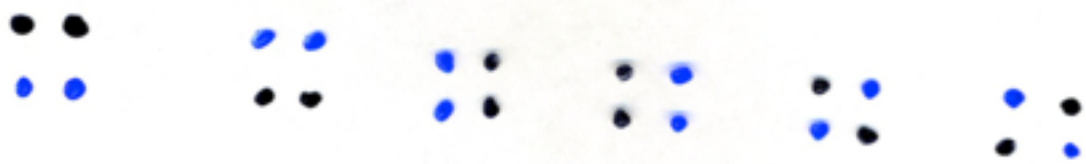
$$C(n,r) = \frac{n!}{(n-r)!\,r!} = \binom{n}{r}$$

This is the number of **combinations**…

So for the tetrameric channel….**12** permutations but only **6** combinations

Counting statistics…<u>permutations</u> and <u>combinations</u>

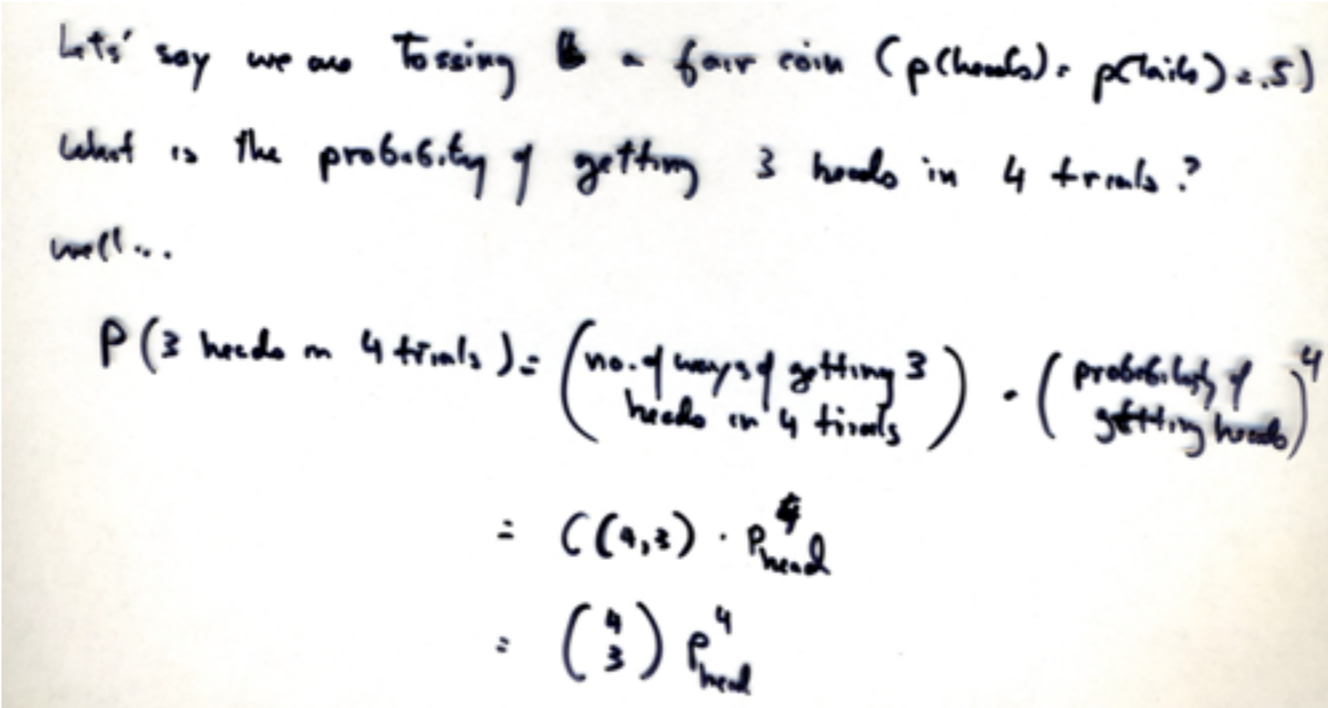


So . . .

<u>permutations</u> are the number of ways of arranging things in a <u>definite order</u>

<u>Combinations</u> are the number of ways of arranging things without caring about the order.

This gets us to the **binomial distribution…**



Lets' say we are tossing a fair coin ($p(\text{heads}) = p(\text{tails}) = .5$)

What is the probability of getting 3 heads in 4 trials?

well...

$$P(3 \text{ heads in } 4 \text{ trials}) = \left(\begin{array}{c}\text{no. of ways of getting 3} \\ \text{heads in 4 trials}\end{array}\right) \cdot \left(\begin{array}{c}\text{probability of} \\ \text{getting heads}\end{array}\right)^4$$

$$= C(4,3) \cdot p_{head}^4$$

$$= \binom{4}{3} p_{head}^4$$

And in general, for getting **r** heads in **n** tries….

This gets us to the **binomial distribution…**

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And in general, for getting **r** heads in **n** tries….

$$P(\text{r heads in n trials}) = \binom{n}{r} (0.5)^n$$

But, what if p(head) is not same as p(tail)?

This gets us to the **binomial distribution…**

$$P(r \text{ events in } n \text{ trials}) = \binom{n}{r} p_{event}^{r} \left(p_{not\ event}^{n-r}\right)$$

$$= \binom{n}{r} p_{event}^{r} \left(1 - p_{event}\right)^{n-r}$$

This is the binomial probability density function….

This gets us to the **binomial distribution…**

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This is the **binomial probability density function**….

It gives us the probability of getting **r** events out of **n** trials given a fixed probability of the event with each trial.

This gets us to the **binomial distribution…**

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This is the **binomial probability density function**….

It gives us the probability of getting **r** events out of **n** trials given a fixed probability of the event with each trial.

In general, it is used in cases where the total number of trials is not large, and the probability of the event is relatively high

General shape of the **binomial distribution…**

$$P(k; n, p) = \frac{n!}{k!(n-k)!} p^k q^{n-k}$$

So…the probability of getting **k** events out of **n** trials given a mean probability of events of **p**

General shape of the **binomial distribution…**

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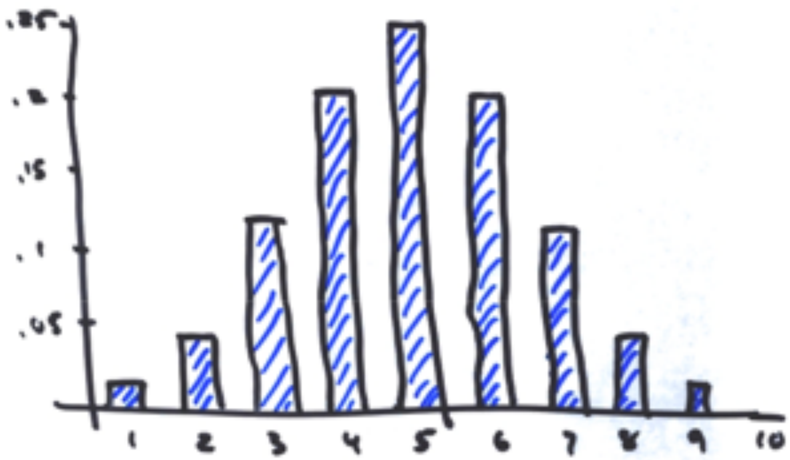
So…the probability of getting **k** events out of **n** trials given a mean probability of events of **p**

Say p=0.5. Out of 10 trials what is the probability of getting 1 success? 2? 3? ... 10?



Quite reasonably, the most likely outcome is the case of k = 5. In general…the mean is **np**.

There are two interesting limits to the Binomial distribution….first the **Poisson distribution**

$$P(k; n, p) = \frac{n!}{k!(n-k)!} p^k (1-p)^{n-k}$$

Now what happens if **n** approaches infinity and **p** is small?

There are two interesting limits to the Binomial distribution….first the **Poisson distribution**

$$P(k;n,p) = \frac{n!}{k!(n-k)!} p^k (1-p)^{n-k}$$

Now take the limit as $n \to \infty$, and noting that $p = \frac{\lambda}{n}$ ← mean no. of events.

$$\lim_{n\to\infty} P(k;n,p) = \lim_{n\to\infty}\left[\frac{n!}{k!(n-k)!}\left(\frac{\lambda}{n}\right)^k\left(1-\frac{\lambda}{n}\right)^{n-k}\right]$$

$$= \frac{\lambda^k}{k!}\lim_{n\to\infty}\left[\frac{\frac{n!}{(n-k)!}}{n^k}\left(1-\frac{\lambda}{n}\right)^n\left(1-\frac{\lambda}{n}\right)^{-k}\right]$$

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Now… (i) $\frac{\frac{n!}{(n-k)!}}{n^k} = \frac{n.(n-1)(n-2)\ldots(n-(k-1))}{n^k} \underset{n\to\infty}{\approx} \frac{n^k}{n^k} = 1$

This is probably not so obvious….

There are two interesting limits to the Binomial distribution….first the **Poisson distribution**

Now...

$$(1) \quad \frac{\frac{n!}{(n-k)!}}{n^k} = \frac{n\cdot(n-1)\cdots(n-(k-1))}{n^k} \underset{n\to\infty}{\approx} \frac{n^k}{n^k} = 1$$

$$\frac{n!}{(n-k)!} = \frac{n(n-1)(n-2)\cdots(n-k)(n-k-1)\cdots(1)}{(n-k)(n-k-1)\cdots(1)}$$

$$= \underbrace{n(n-1)(n-2)\cdots(n-k+1)}$$

$$\lim_{n\to\infty}\left(\;\right) = \underbrace{n\cdot n\cdot n\cdots}_{k \text{ times}}$$

$$= n^k$$

There are two interesting limits to the Binomial distribution….first the **Poisson distribution**

$$P(k;n,p) = \frac{n!}{k!(n-k)!} p^k (1-p)^{n-k}$$

Now take the limit as $n \to \infty$, and noting that $p = \frac{\lambda}{n}$ ← mean no. of events.

$$\lim_{n\to\infty} P(k;n,p) = \lim_{n\to\infty} \left[\frac{n!}{k!(n-k)!} \left(\frac{\lambda}{n}\right)^k \left(1-\frac{\lambda}{n}\right)^{n-k} \right]$$

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Now…

$$① \quad \frac{\frac{n!}{(n-k)!}}{n^k} = \frac{n.(n-1)(n-2)\ldots(n-(k-1))}{n^k} \underset{n\to\infty}{\approx} \frac{n^k}{n^k} = 1$$

And….

There are two interesting limits to the Binomial distribution….first the **Poisson distribution**

$$P(k;n,p) = \frac{n!}{k!(n-k)!} p^k (1-p)^{n-k}$$

Now take the limit as $n \to \infty$, and noting that $p = \frac{\lambda}{n}$ ← mean no. of events.

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Now…

① $$\frac{\frac{n!}{(n-k)!}}{n^k} = \frac{n.(n-1)(n-2)\ldots(n-(k-1))}{n^k} \underset{n\to\infty}{\approx} \frac{n^k}{n^k} = 1$$

② $$\lim_{n\to\infty} \left(1-\frac{\lambda}{n}\right)^n = e^{-\lambda}$$

③ $$\lim_{n\to\infty} \left(1-\frac{\lambda}{n}\right)^{-k} = 1$$

Putting it all together….

There are two interesting limits to the Binomial distribution….first the **Poisson distribution**

$$P(k;n,p) = \frac{n!}{k!(n-k)!} p^k (1-p)^{n-k}$$

Now take the limit as $n \to \infty$, and noting that $p = \frac{\lambda}{n}$ ← mean no. of events.

$$\lim_{n\to\infty} P(k;n,p) = \lim_{n\to\infty} \left[\frac{n!}{k!(n-k)!} \left(\frac{\lambda}{n}\right)^k \left(1-\frac{\lambda}{n}\right)^{n-k} \right]$$

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So…

$$\lim_{n\to\infty} P(k;n,p) = \frac{\lambda^k}{k!} \cdot 1 \cdot e^{-\lambda} \cdot 1$$

$$P(k;\lambda) = \frac{\lambda^k}{k!} e^{-\lambda}$$ → the poission density function

The nearly universal importance of the **Poisson distribution**

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The nearly universal importance of the **Poisson distribution**…**example 1**

$$P(k;\lambda) = \frac{\lambda^k}{k!} e^{-\lambda}$$ → the poission density function

$$A \xrightarrow{\lambda} A^*$$

Single-step molecular conformational change.
An example of a first order process…

Consider its microscopic characteristics….

The nearly universal importance of the **Poisson distribution**…**example 1**

$$P(k;\lambda) = \frac{\lambda^k}{k!} e^{-\lambda}$$ → the poission density function

$$A \xrightarrow{\lambda} A^*$$

Single-step molecular conformational change.
An example of a first order process…

(1) the number of trials is large (and not directly observed)

(2) the probability of barrier crossing is even unknown….all we know is the mean number of events per time (the rate constant).

The nearly universal importance of the **Poisson distribution**…**example 1**

$$P(k;\lambda) = \frac{\lambda^k}{k!} e^{-\lambda}$$ → the poission density function

$$A \xrightarrow{\lambda} A^*$$

Single-step molecular conformational change.
An example of a first order process…

So…

$$P(k \text{ crossings}, \lambda) = \frac{\lambda^k e^{-\lambda}}{k!}$$

The nearly universal importance of the **Poisson distribution**…**example 1**

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$$A \xrightarrow{\lambda} A^*$$

Single-step molecular conformational change.
An example of a first order process…

So…

$$P(k \text{ crossings}, \lambda) = \frac{\lambda^k e^{-\lambda}}{k!}$$

This is the microscopic (stochastic) view of nearly all reactions!
The key assuptions…

1. events are statistically independent
2. events are rare relative to number of trials.

Two solutions to the first order process!

$$A \xrightarrow{k} A^*$$

The **deterministic** solution….

$$\frac{dA}{dt} = -kA$$

with initial conditions and specified range…

$$A(0) = A_0 \quad ; \quad 0 \le \tau \le t$$

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$$A = A_0 e^{-kt}$$

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with initial conditions and specified range…

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$$A = A_0 e^{-kt}$$

The **stochastic** solution….

$$P(n \text{ events}, k, t) = \frac{(kt)^n e^{-kt}}{n!}$$

→ mean no. of events in t is kt

$$P(0, k, t) = \frac{(kt)^0 e^{-kt}}{0!}$$

$$= e^{-kt}$$

But what is $P(0)$?

Two solutions to the first order process!

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The **deterministic** solution….

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$$A(0) = A_0 \quad ; \quad 0 \leq \tau \leq t$$

$$A = A_0 e^{-kt}$$

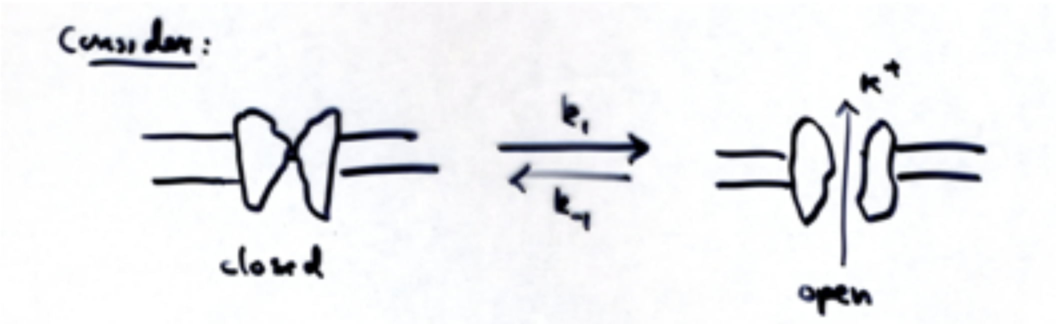
The **stochastic** solution….

$$\frac{N_A(t)}{N_0} = e^{-kt}$$

$$\boxed{N_A(t) = N_0 e^{-kt}}$$

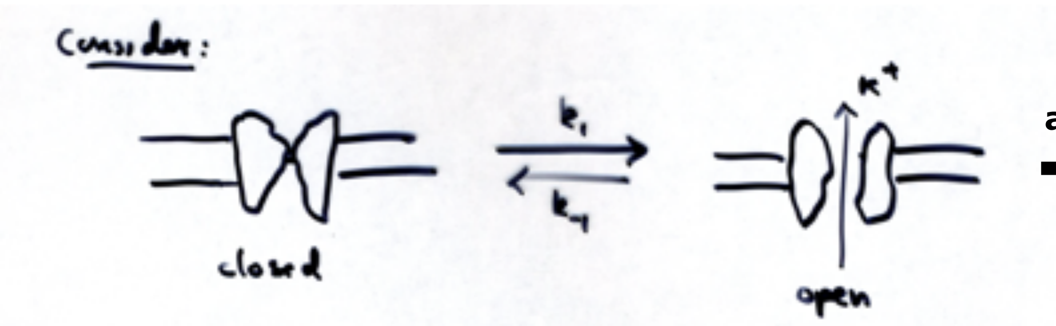
the **microscopic basis** for all single-exponential processes…. a large number of **random**, **independent** trials with a single characteristic wait time.

Example 2: Ion channel gating

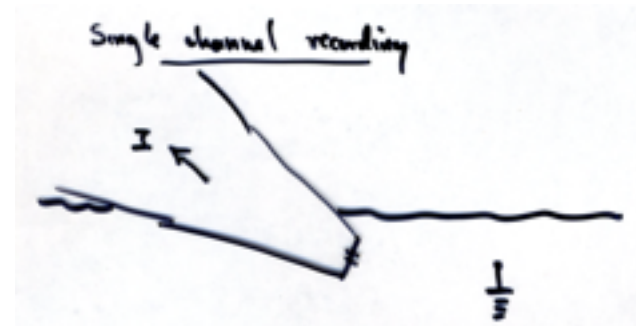


The stochastic opening and closing of single ion channels….

Example 2: Ion channel gating



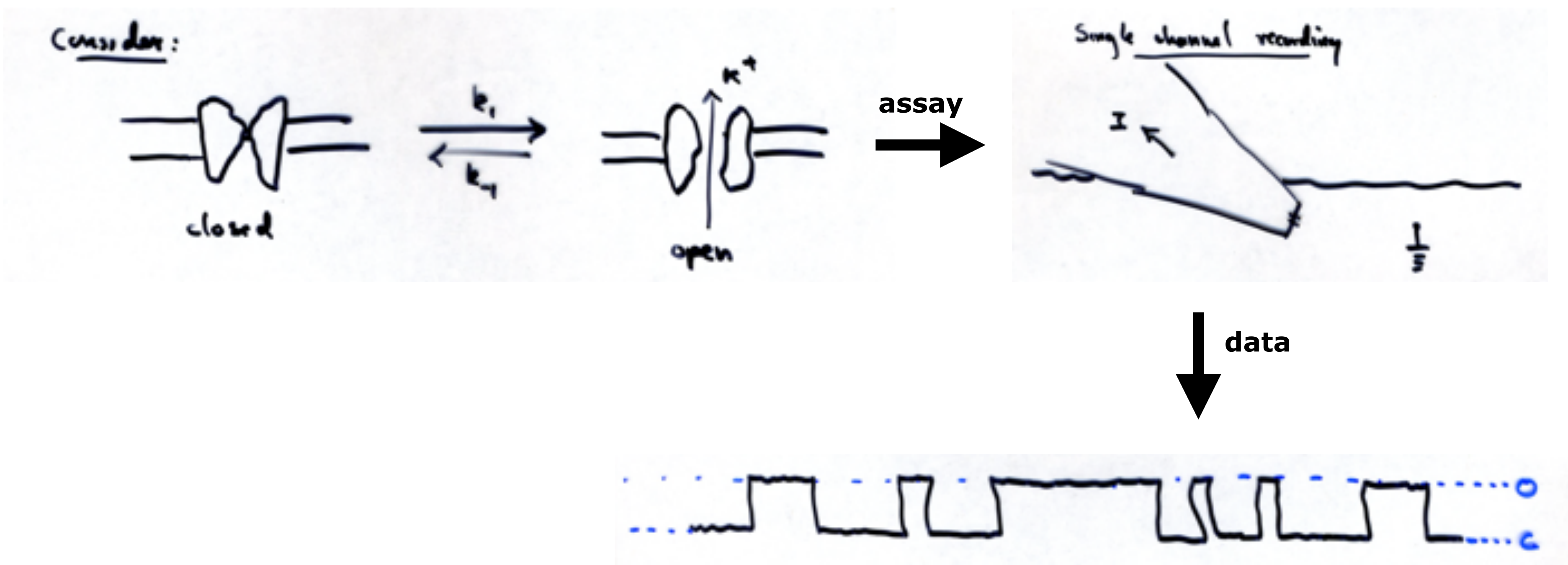
assay



data

With single channel recording…

Example 2: Ion channel gating



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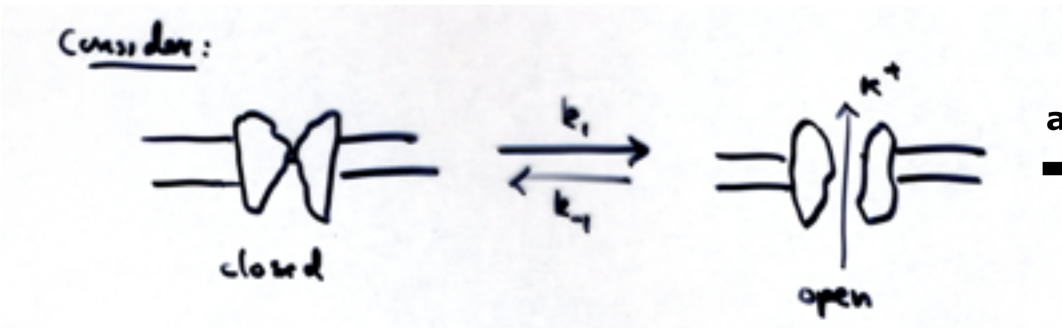
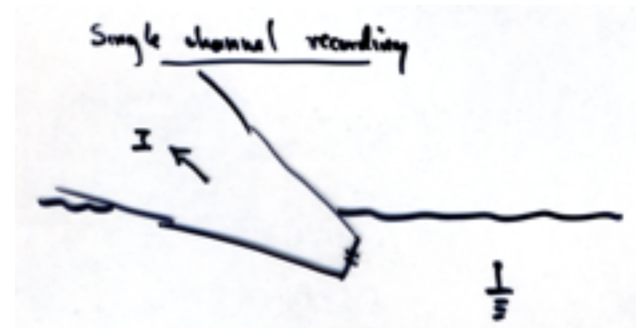
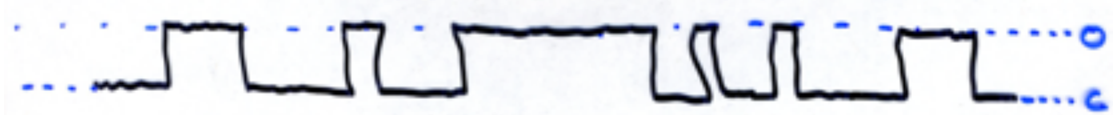


assay

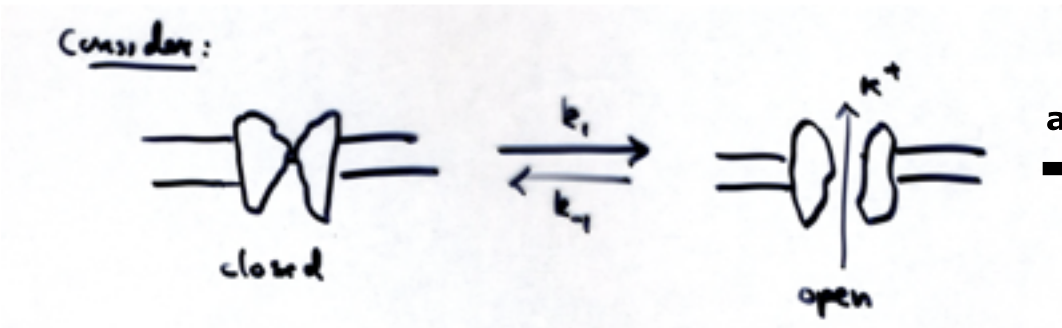


data

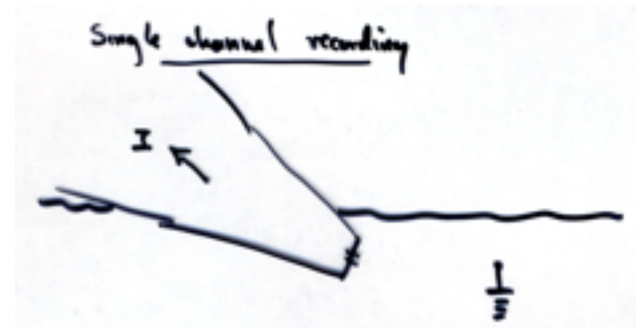


The principles of the Poisson process tells us that the histogram of open times should be exponentially distributed with a characteristic time of $1/k_1$ ...

Example 2: Ion channel gating



assay



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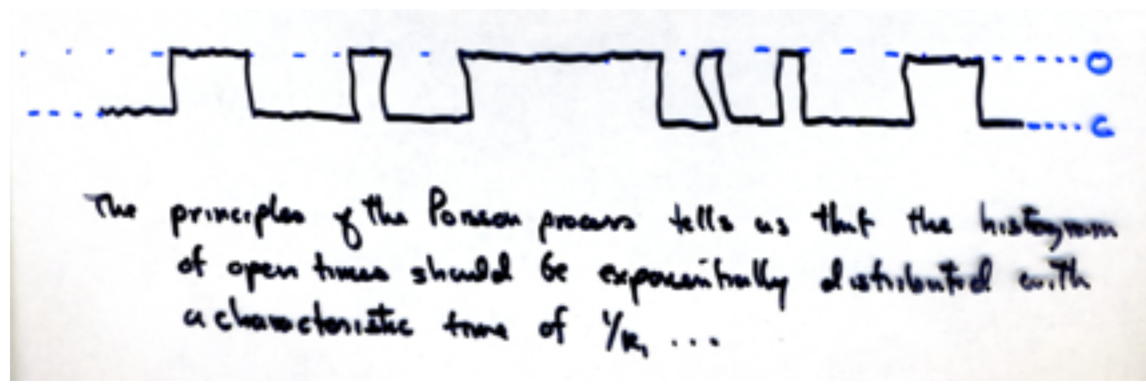
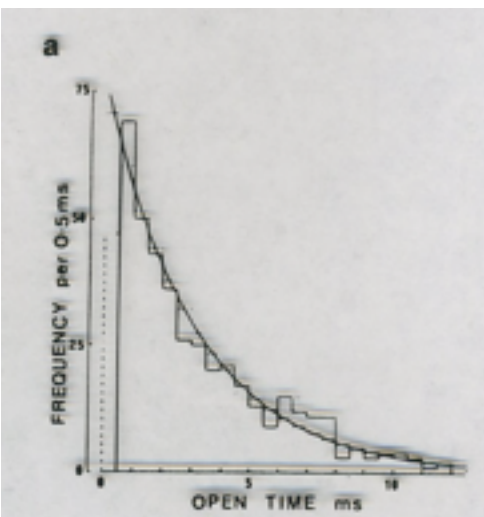
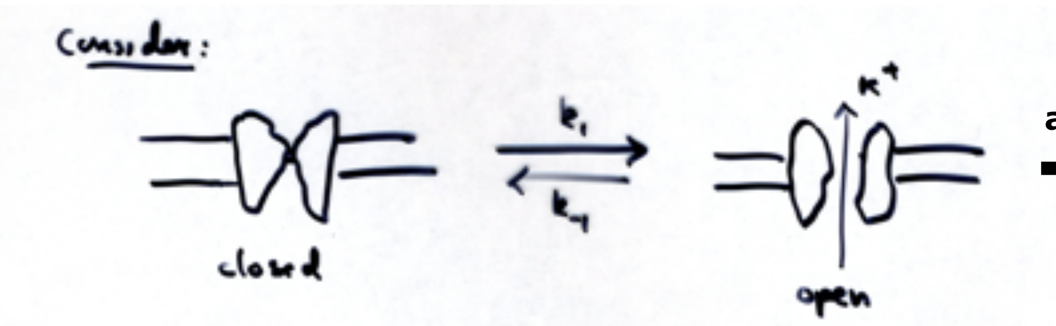


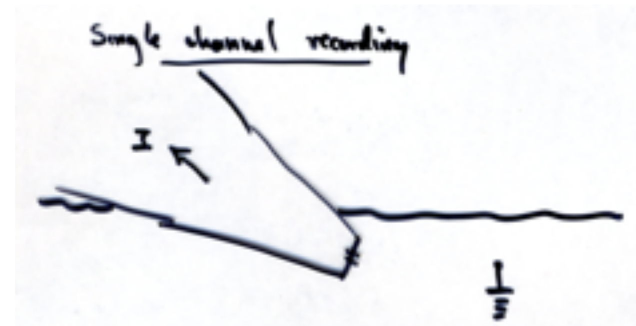
fitting to theory



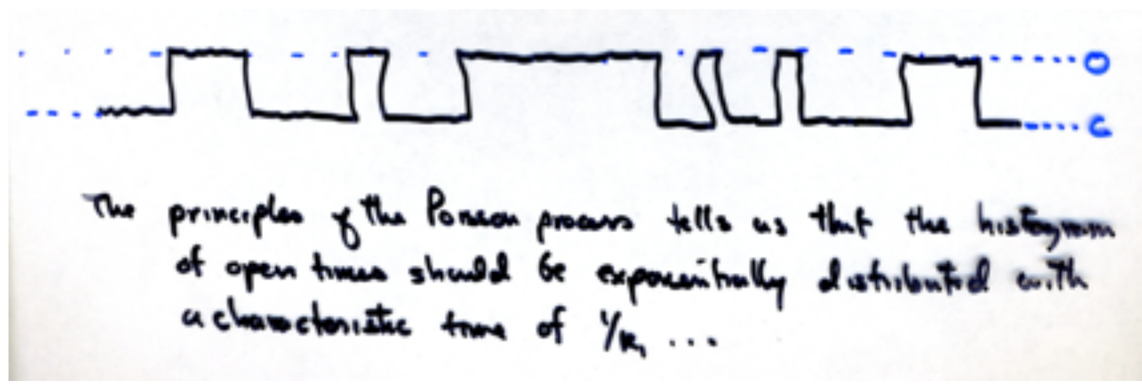
Example 2: Ion channel gating



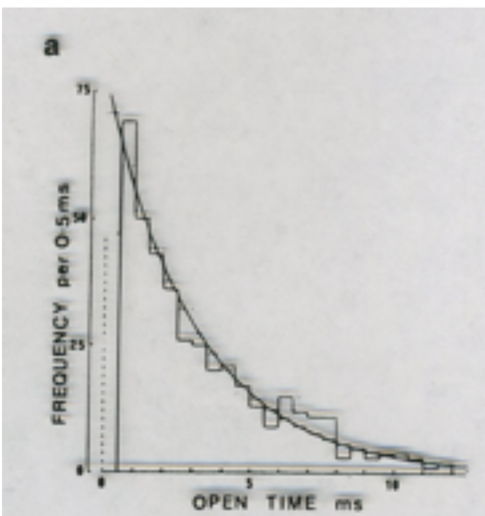
assay



data

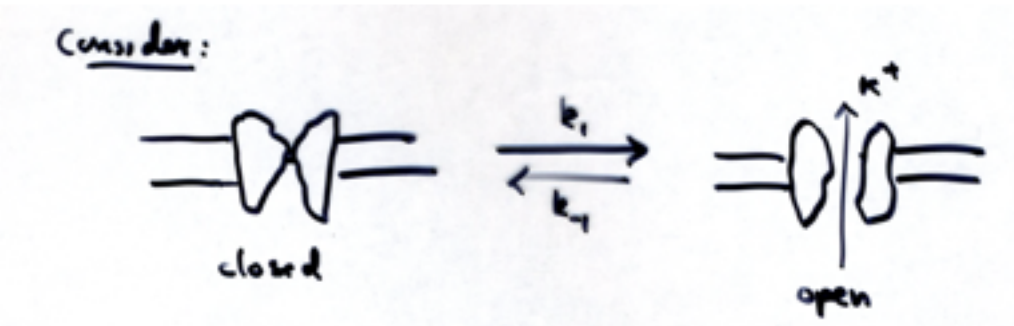


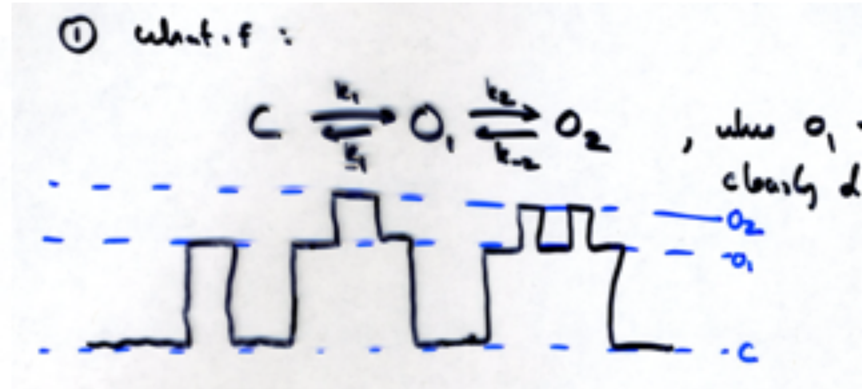
fitting to theory



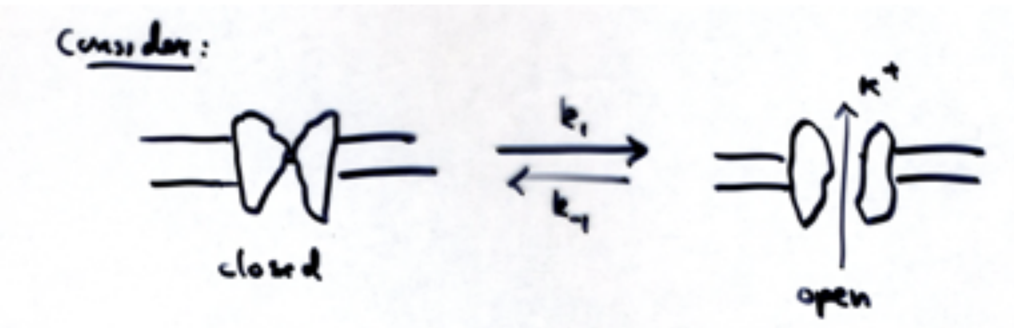
Another example of our process of modeling….

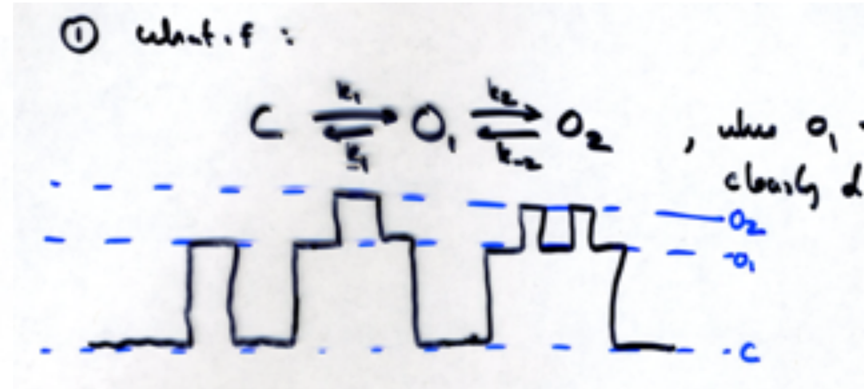
Example 2: Ion channel gating

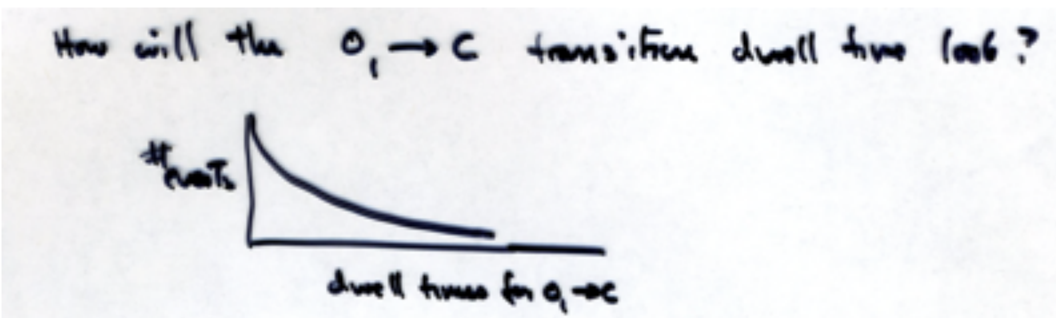




Example 2: Ion channel gating







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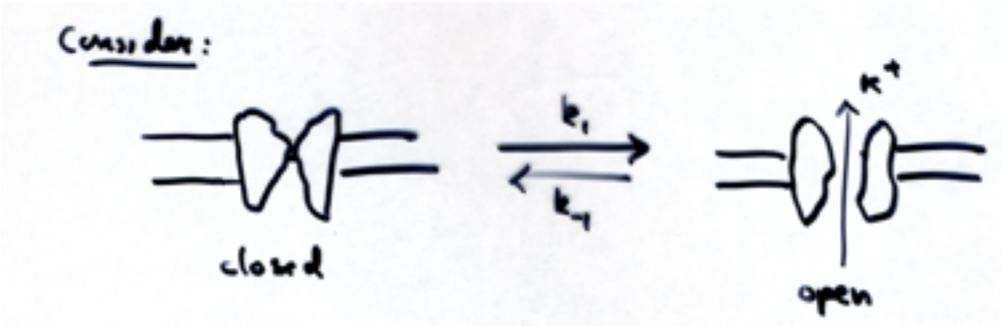

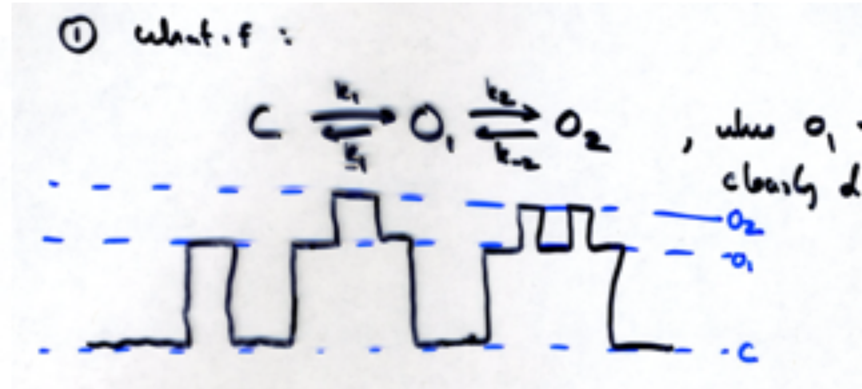

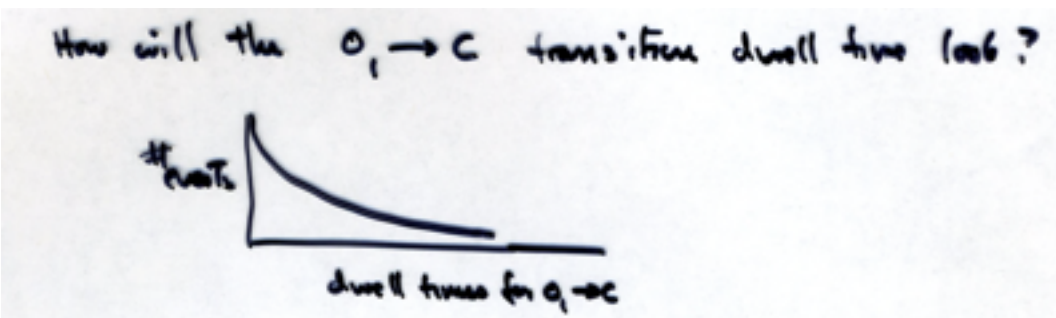

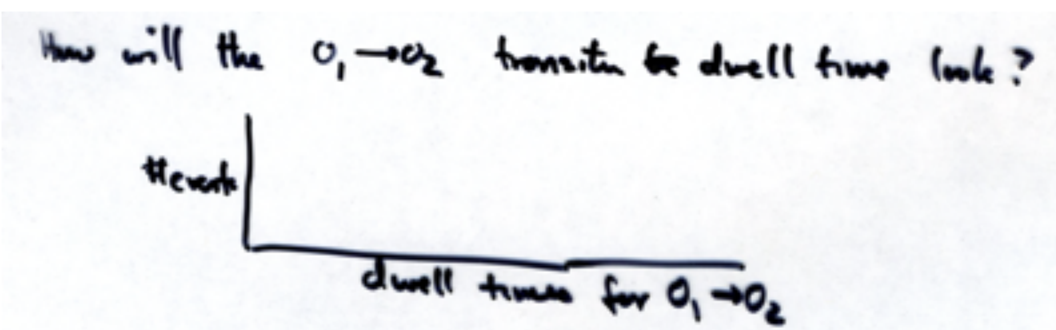

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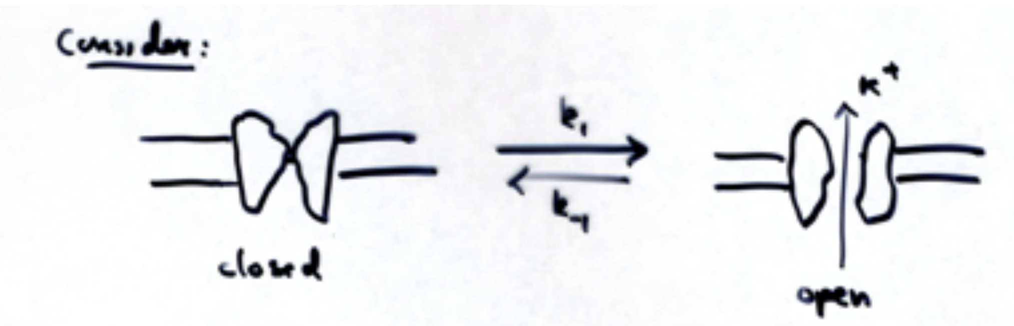
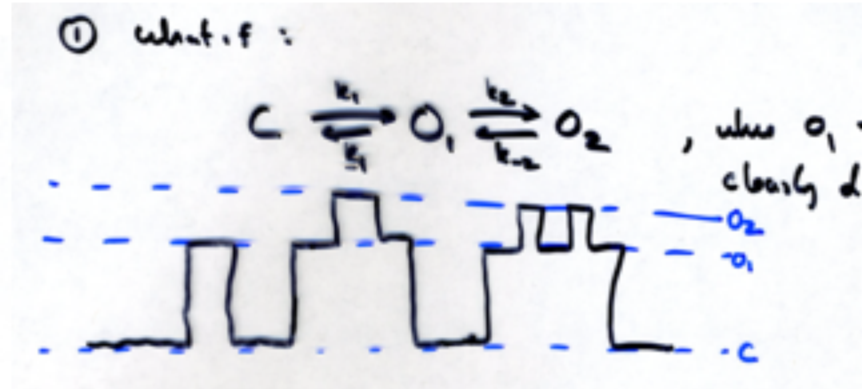
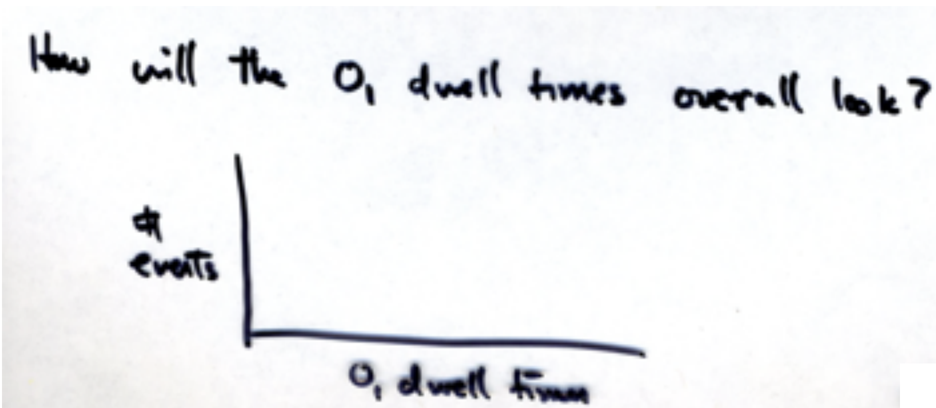
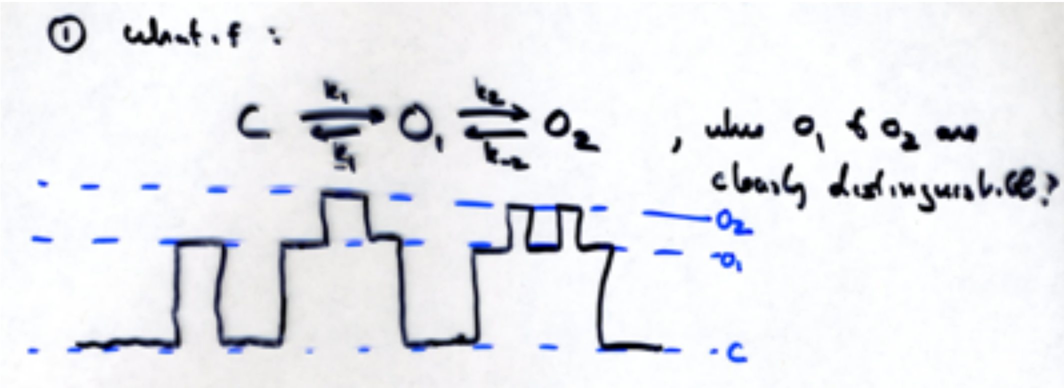






Why?

Example 2: Ion channel gating



$$C \xleftarrow{k_{-1}} O_1 \xrightarrow{k_2} O_2$$

$$\frac{dO_1}{dt} = -k_{-1}O_1 - k_2 O_1$$

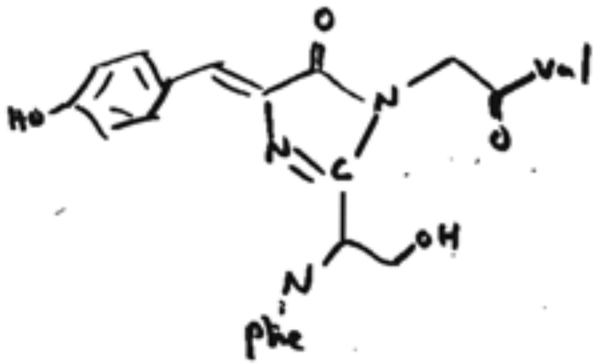
$$= -(k_{-1} + k_2)\, O_1$$

$$\vdots$$

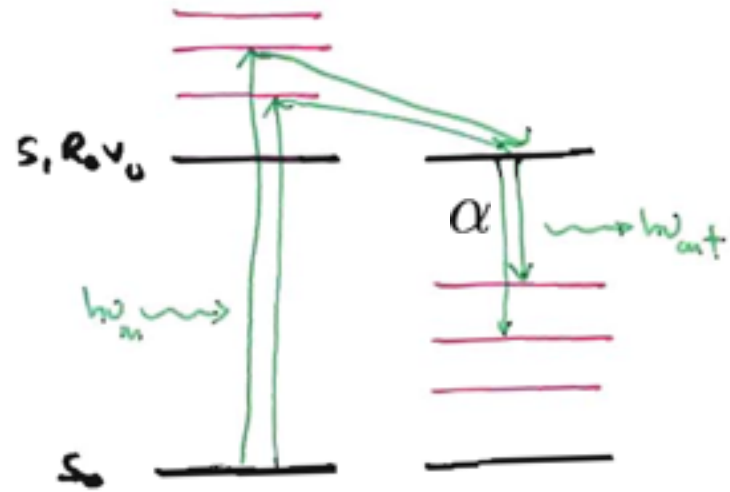
$$O_1(t) = O_0(t)\, e^{-(k_{-1}+k_2)t}$$

So, the **sum of many Poisson processes** is itself a Poisson process with a mean rate equal to the sum of rates

Example 3: **fluorescence emission**….



fluorescence



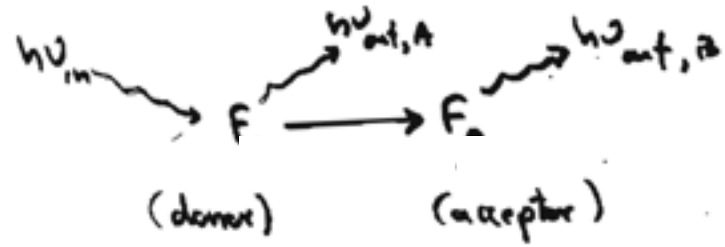
The GFP chromophore

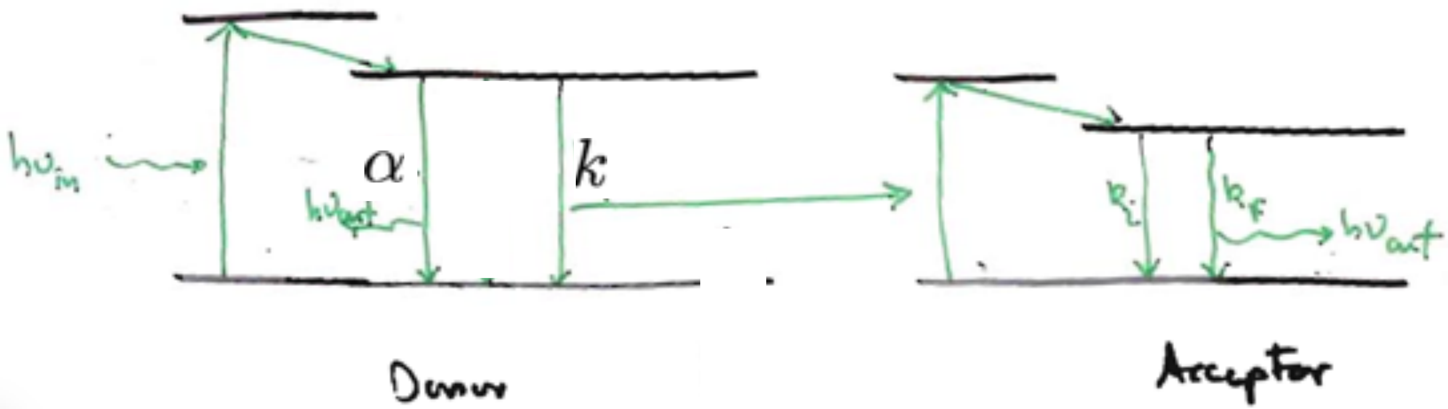
The Jabolinski diagram….

Fluorescence emission comes out of the thermally equilibrated "singlet" state. The relaxation of molecules is a Poisson process. Thus….

$$N = N_0 e^{-t/\tau} \quad \text{where} \quad \tau = 1/\alpha$$

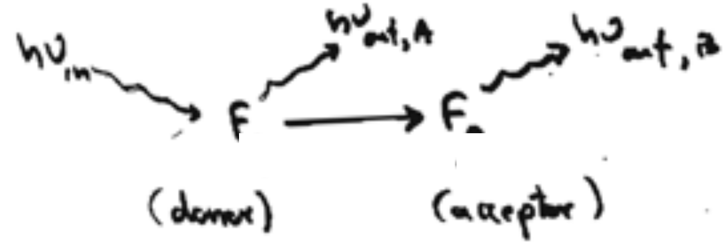
And **fluorescence resonance energy transfer** (FRET)….

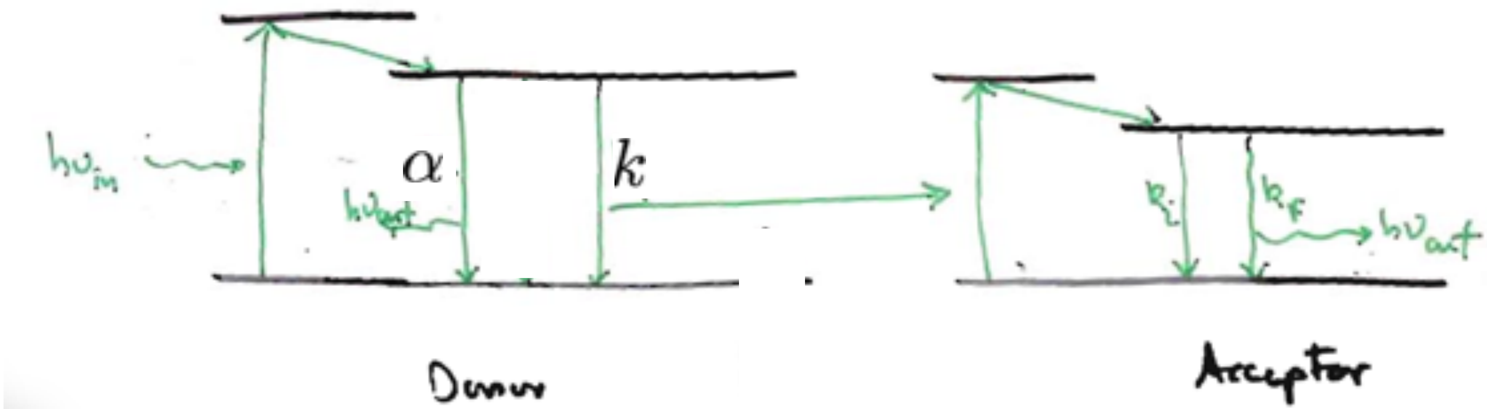




What is the effect of FRET for the fluorescence lifetime of the donor?

And **fluorescence resonance energy transfer** (FRET)….





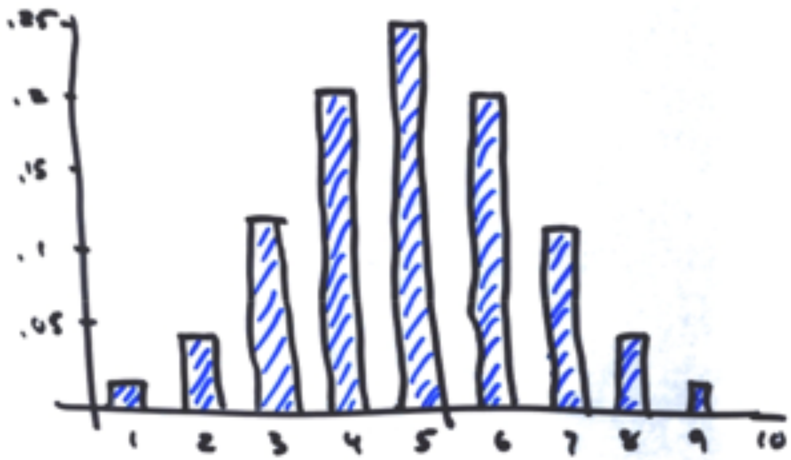
$$N(t) = N_0 e^{-t/\tau}$$ where $$\tau = \frac{1}{\alpha + k}$$

Donor emission is **still a single exponential** but with a faster rate (shorter lifetime) due to FRET…

The other interesting limit of the Binomial distribution….first the **Gaussian distribution**

$$P(k; n, p) = \frac{n!}{k!\,(n-k)!}\, p^{k} (1-p)^{n-k}$$

Say p=0.5. Out of 10 trials what is the probability of getting 1 success? 2? 3? ... 10?



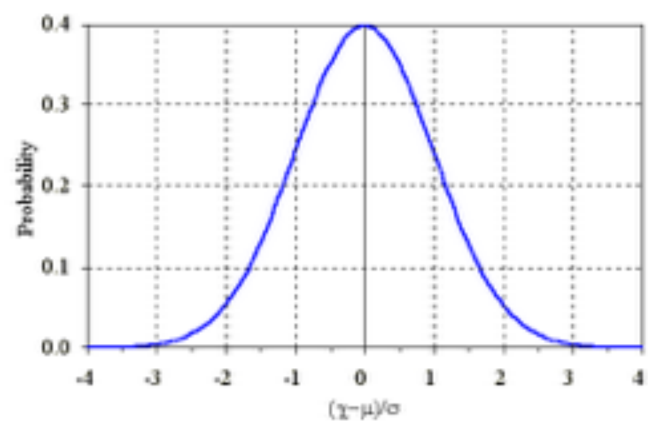
The binomial density function for p = 0.5 and n = 10. Now what happens if **n** approaches infinity but **p** is NOT small?

The other interesting limit of the Binomial distribution….first the **Gaussian distribution**

$$P(k;n,p) = \frac{n!}{k!(n-k)!} p^k (1-p)^{n-k}$$

Then the binomial distribution is well approximated by the Gaussian (or normal) distribution….the bell-shaped curve

$$P(k) = \frac{1}{\sqrt{2\pi\sigma^2}} e^{-\frac{(k-\mu)^2}{2\sigma^2}}$$



What's so special about the **Gaussian distribution**?

what types of processes generate Gaussian distributions?

The central limit theorem

What's so special about the **Gaussian distribution**?

Consider a random variable z_i drawn from some arbitrary distribution of numbers. No constraint is placed on the nature of the distribution from which z_i comes ~~from~~, but we will insist that each draw of z_i be statistically independent of other draws.

What's so special about the **Gaussian distribution**?

Consider a random variable z_i drawn from some arbitrary distribution of numbers. No constraint is placed on the nature of the distribution from which z_i comes ~~from~~, but we will insist that each draw of z_i be statistically independent of other draws.

Now consider a partial sum of k independent draws of z_i:

$$x_k = \sum_{i=1}^{k} z_i$$

Now the mean & variance of x_k will keep going up as $k \to \infty$, so we will just normalize x_k:

$$y_k = \frac{x_k - \text{mean}(x_k)}{\sigma_{x_k}}$$

What's so special about the **Gaussian distribution**?

$$y_k = \frac{x_k - mean(x_k)}{\sigma_{x_k}}$$

```
%1000 vars from the uniform dist.
j1=rand(1,1000);
[yhist,xhist]=hist(j1,20);figure(101);bar(xhist,yhist)
xlabel('value','FontSize',14);ylabel('number','FontSize',14)
%%
```

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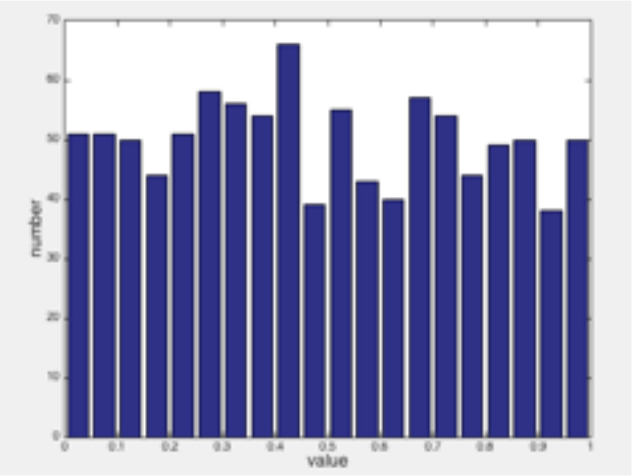

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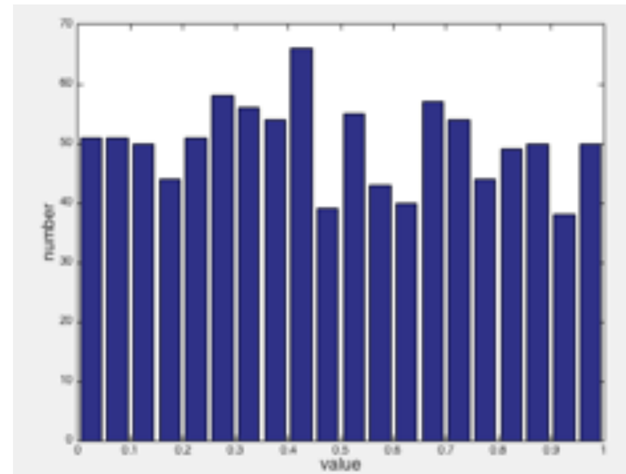


```
%now a 1000 trials of partial summations from uniform dist.
for i=1:2000;Z(i)=sum(rand(1,1000));end
brand=(Z-mean(Z))./var(Z);
[yhist,xhist]=hist(brand,20);figure(100);bar(xhist,yhist)
[fit1]=fit(xhist',yhist','gauss1');
[model1]=gauss1_fittrace(fit1,[-.4:.01:.4]);
figure(100);hold on;plot(model1(:,1),model1(:,2),'-r','LineWidth',2);hold off
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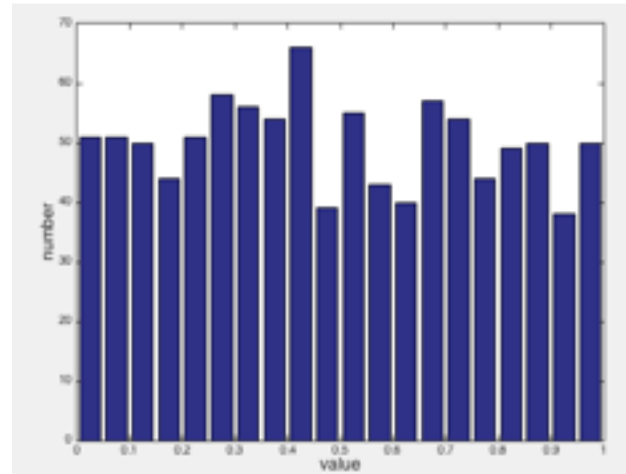


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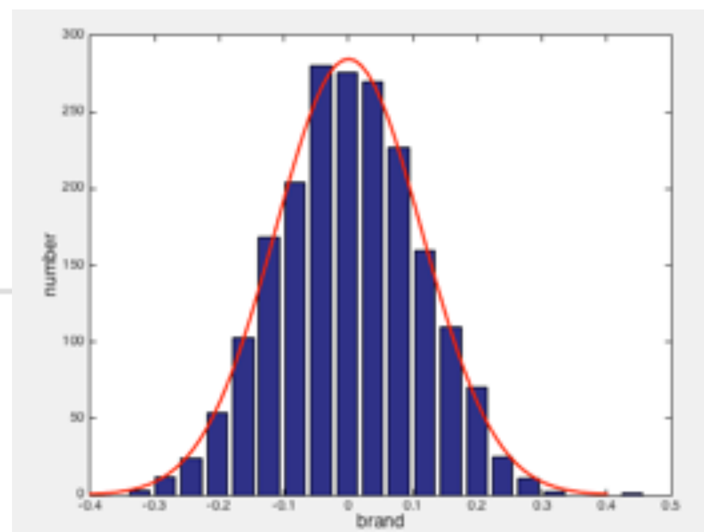

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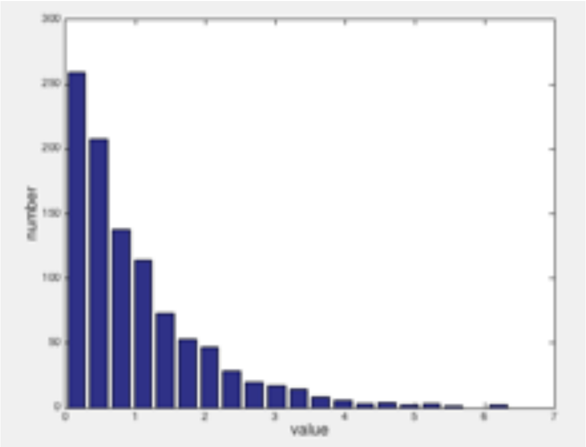
$$y_k = \frac{x_k - mean(x_k)}{\sigma_{x_k}}$$

```
%1000 vars from the exp dist.
j1=exprnd(1,[1 1000]);
[yhist,xhist]=hist(j1,20);figure(101);bar(xhist,yhist)
%%
```



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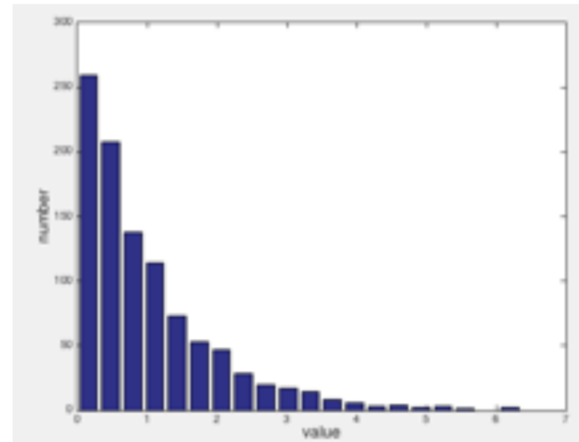
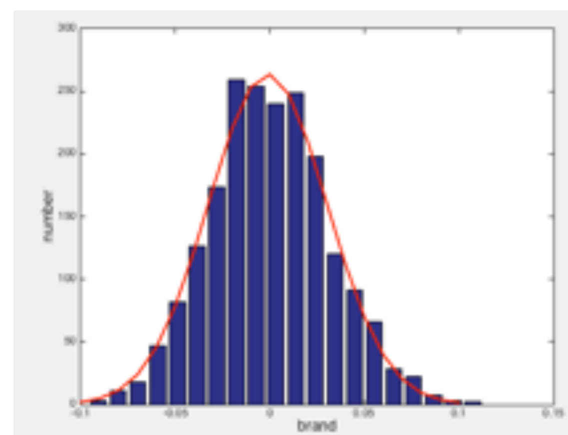



```
%now a 1000 trials of partial summation from the exp dist.
for i=1:2000;Z(i)=sum(exprnd(1,[1 1000]));end
brand=(Z-mean(Z))./var(Z);
[yhist,xhist]=hist(brand,20);figure(100);bar(xhist,yhist)
[fit1]=fit(xhist',yhist','gauss1');
[model1]=gauss1_fittrace(fit1,[-.1:.01:.1]);
figure(100);hold on;plot(model1(:,1),model1(:,2),'-r','LineWidth',2);hold off
```



What's so special about the **Gaussian distribution**?

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We will not prove it here, but it turns out that if we make many observations of y_k, the distribution of y_k as $k \to \infty$ converges to a Gaussian. This is the central limit theorem. It is the reason why models of ~~all~~ many random phenomena apply this distribution, and why we call this the "error distribution".

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the fundamental (and only) constraint that went into the generation of the Gaussian distribution was statistical independence of the variables being additively combined....

each draw was independent of previous draws.

Next time…an analysis of **n >> 1 linear systems**…diffusion and the thermodynamic limit

	n = 1	n = 2 or 3	n >> 1	continuum
Linear	exponential growth and decay single step conformational change fluorescence emission pseudo first order kinetics	second order reaction kinetics linear harmonic oscillators simple feedback control sequences of conformational change	electrical circuits molecular dynamics systems of coupled harmonic oscillators equilibrium thermodynamics diffraction, Fourier transforms	Diffusion Wave propagation quantum mechanics viscoelastic systems
Nonlinear	fixed points bifurcations, multi stability irreversible hysteresis overdamped oscillators	anharmonic oscillators relaxation oscillations predator-prey models van der Pol systems Chaotic systems	systems of non-linear oscillators non-equilibrium thermodynamics protein structure/ function neural networks the cell ecosystems	Nonlinear wave propagation Reaction-diffusion in dissipative systems Turbulent/chaotic flows

adapted from S. Strogatz