

Lecture 12:

Probabilistic & Stochastic Modeling (Part II)

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Random Arrivals

Examples of random arrivals: (i) Shot noise in radio receivers; (ii) Hospital admissions; (iii) Automobile accidents in a community; (iv) Radioactive decay, and so forth. We will in particular later consider photon arrivals at the retina and synaptic arrivals at the neuromuscular junctions.

An immediate interest in each case is the time of the next arrival.

Surely for (i) & (iv) the processes can be regarded as being time stationary.¹ Further, in these two cases we can suppose with confidence that, for example, the waiting times are independent of one another.

Imagine that we have taken data in a particular situation and can therefore determine

$$\lim_{t \uparrow \infty} \frac{N(t)}{t} = \lambda \quad (12.1)$$

the arrival rate, a reciprocal time. For (ii) and (iii) the arrival rate might have some periodicities (daily, weekly, yearly, etc.) i.e. λ , the arrival rate might itself be time dependent, but the waiting times are still random variables. Formally it is convenient to renormalize time so that

$$\tau = \lambda t \quad (12.2)$$

a dimensionless time in which terms we have a unit arrival rate. From the independence of arrival times it follows that

$$P(\tau_1 + \tau_2) = P(\tau_1)P(\tau_2). \quad (12.3)$$

The only function that satisfies this relationship is the exponential $P \propto e^{-c\tau}$ where c is constant. For example if (12.3) is differentiated with respect to τ_1 and τ_2 then it follows that

¹ This concept conveys the notion that there is no distinguished time origin. Thus the process is the same, independent of when we begin our observations.

$$\frac{P'(\sigma)}{P(\sigma)} = \frac{P'(\tau)}{P(\tau)} \quad (12.4)$$

and hence P'/P must be a constant. Therefore

$$P(\tau) = ce^{-c\tau}, \quad (12.5)$$

since

$$\int_0^{\infty} ce^{-c\tau} d\tau = 1. \quad (12.6)$$

But

$$\mu = \langle \tau \rangle = c \int_0^{\infty} e^{-c\tau} \tau d\tau = c^{-1} = 1 \quad (12.7)$$

and therefore

$$P(\tau) = e^{-\tau} \quad (12.8)$$

or in dimensional terms

$$P(t) = \lambda e^{-\lambda t}. \quad (12.9)$$

Obviously

$$\langle t \rangle = 1/\lambda, \quad (12.10)$$

where λ is the measured, (12.1), rate of arrivals. (12.8) is the probability of waiting times, τ (12.9) is referred to as a *Poisson process*, not to be confused with Poisson distributions. In fact (12.8) is just the gamma distribution $G_o(t; \lambda)$, (11.20), and is a pdf over $0 \leq t \leq \infty$.

Within a biological framework, we point out that in the mammalian cortex many, if not most, neurons receive inputs from large numbers of inputs, as much as $O(10^4)$. In such cases the assumption of Poisson arrivals is well founded. However, there are other neurons that are driven by as few as a single pre-synaptic neuron, in which case the Poisson assumption clearly does not apply.

Exercise 12.1. Show that for (12.8)

$$\sigma^2 = \langle (t - \langle t \rangle)^2 \rangle = 1/\lambda^2. \quad (12.11)$$

Therefore the standard deviation $\sigma = \langle (t - \langle t \rangle)^2 \rangle^{1/2}$ and the mean, inter-arrival time $1/\lambda$, are equal, and their ratio, the coefficient of variation, c_v , is unity,

$$c_v = \sigma/\mu = \frac{1/\lambda}{1/\lambda} = 1. \quad (12.12)$$

Poisson Distributions

This takes care of problem of waiting times. To deal with multiple arrivals observe that the probability of an arrival before a time t_1 is given by

$$\int_0^{t_1} \lambda e^{-\lambda t} dt = 1 - e^{-\lambda t_1}, \quad (12.13)$$

and therefore the probability of no arrivals before time t_1 is

$$P_0(t_1) = e^{-\lambda t_1}. \quad (12.14)$$

which is just (11.35) for $k = 0$, as indicated by the notation.

Clearly, the probability for an arrival in an increment dt is λdt , and therefore the probability of a non-arrival is $(1 - \lambda dt)$. Therefore, in general the probability of $k + 1$ arrivals in a time t is determined by

$$P_{k+1}(t + dt) = (1 - \lambda dt)P_{k+1}(t) + \lambda dt P_k(t). \quad (12.15)$$

This is said to be a Chapman-Kolmogorov relation. It follows from (12.5) that

$$\frac{d}{dt} P_{k+1}(t) = -\lambda P_{k+1}(t) + \lambda P_k(t), \quad (12.16)$$

and as implied by the notation this is satisfied by (11.35).

Another way to view (12.16) is that the first term on right hand is loss rate of P_{k+1} (to P_{k+2}), and second term is the gain rate to P_{k+1} from $P_k(t)$ arrivals. These are sometimes referred to as *death* and *birth* terms, respectively. It follows from (12.13) that

$$P_k(0) = 0, \quad k \neq 0 \quad (12.17)$$

and

$$P_0(0) = 1. \quad (12.18)$$

Exercise 12.2 (Optional). One can recursively determine the $P_k(t)$ from (12.16). Show

$$P_1(t) = \lambda t e^{-\lambda t}. \quad (12.19)$$

Also, obtain $P_2(t)$ and then $P_3(t)$ in this way.

We can also get all of them at once. Consider the z -transform

$$G(z, t) = \sum_{n=0}^{\infty} z^n P_n(t) \quad (12.20)$$

where z is the complex variable $z = x + iy$. It then follows that

$$\begin{aligned} \frac{\partial G}{\partial t} &= \sum_{n=0}^{\infty} z^n \frac{dP_n(t)}{dt} \\ &= \sum_{n=0}^{\infty} z^n \lambda (P_{n-1} - P_n) \\ &= -\lambda G + \lambda z G = \lambda(z-1)G. \end{aligned} \quad (12.21)$$

Clearly from (12.20) and (12.21) $G(z, 0) = 1$ and therefore

$$G(z, t) = e^{\lambda(z-1)t} = e^{-\lambda t} \sum_{n=0}^{\infty} \frac{(\lambda t)^n z^n}{n!} \quad (12.22)$$

which implies

$$P_n(t) = \frac{(\lambda t)^n}{n!} e^{-\lambda t} \quad (12.23)$$

and as promised we got them all at once, and is just (11.35)²

Attention: $P_n(t)$ is the probability of n arrivals within some **fixed** time t . It is not a probability in t , but a probability in n , and is referred to as the Poisson distribution (in n).

Exercise 12.3. Show that the variance is

$$\sigma^2 = \langle (n - \lambda t)^2 \rangle = \lambda t \quad (12.24)$$

Therefore the Poisson distribution, P_n has equal mean and variance.

Applications

In the following applications the Poisson distribution is considered for t fixed, and all n . To make this more explicit, we set $\lambda t = a$ and therefore for n large, using Stirling's formula, (11.33),

$$P_n(a) = \frac{a^n e^{-a}}{n!} \sim \left(\frac{1}{2\pi n} \right)^{\frac{1}{2}} e^{(n-a)} \left(\frac{a}{n} \right)^n. \quad (12.25)$$

or equivalently

$$P_n \approx \frac{e^{n-a+n(\ln a - \ln n)}}{\sqrt{2\pi n}}, \quad (12.26)$$

which has a maximum at $n = a$ and if expanded in the neighborhood of $n = a$ gives the Gaussian,

$$P_n = \frac{e^{-\frac{(n-a)^2}{2a}}}{\sqrt{2\pi a}}, \quad (12.27)$$

² Note that if we take $z = e^{-ixt}$ there is analogy with the characteristic function (11.41).

Example 1: Hecht, S., Shlaer, S. & Pirenne, M.H. "Energy, Quanta and Vision", J. Gen. Phys., 25, 819-840 (1942).

In the cited paper the authors sought to establish what is the threshold number of quanta captured by the rods (night vision) of the human retina needed for detection. The experiment was psychophysical and as you will see the authors were their own subjects. As emphasized in the paper it would be an error to suppose that the threshold for detection is sharp, i.e., *now you see it, now you don't*. This threshold has a range of values which depends on the subjects internal state, amongst other things. In other words the psychophysical boundary is a blurred one.

The assumption was that there was a threshold number of quanta in a flash for likelihood for detection. With the measured number of quanta in a flash, of duration t , is $a = \lambda t$, see (12.25), it is plausible that photon arrivals are a Poisson process, and therefore the probability of n or more photons detected in a flash is,

$$\sum_{k=n}^{\infty} P_k(a) = 1 - \sum_{k=0}^{n-1} P_k(a) \quad (12.28)$$

and a plot of this versus $\log_{10}(a)$ over a range of a is plotted in Figure 12.1. Recall that $P_n(a)$ is a pdf in n and therefore $\sum_{k=0}^{n-1} P_n(a)$ is a cumulative pdf. $\sum_{k=0}^{n-1} P_k$ is **poisscdf** in Matlab.

Exercise 12.4. Prove

$$\sum_{k=0}^n P_k(a) = \frac{1}{n!} \int_a^{\infty} t^n e^{-t} dt \quad (12.29)$$

which is called the incomplete gamma function (parts integration does the trick.)

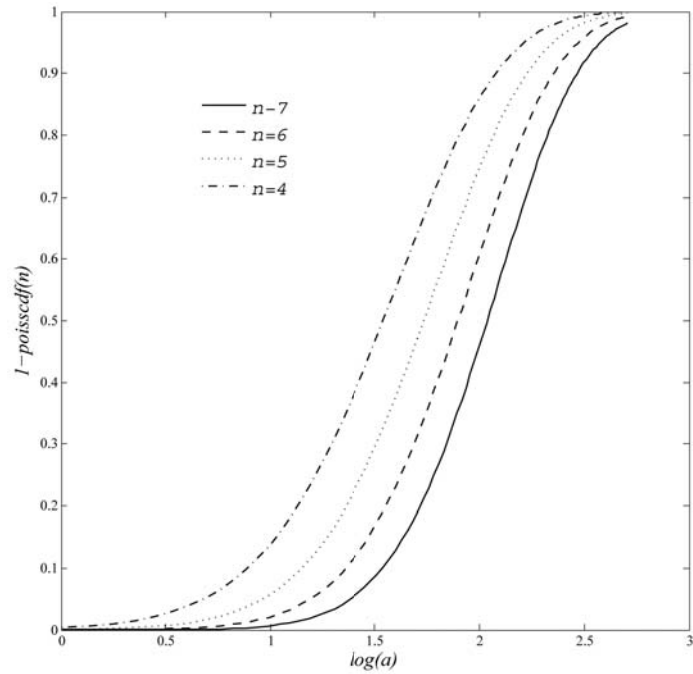


Fig. 12.1: Plot of (12.28) for various n . The abscissa is the logarithm of a , see text.

it is clear that the curves are well distinguished from each other.

In Figure 12.2 you see the result of the psychophysical experiments on the three authors, note the initials. It was concluded that the threshold for detection is about 5-8 photons

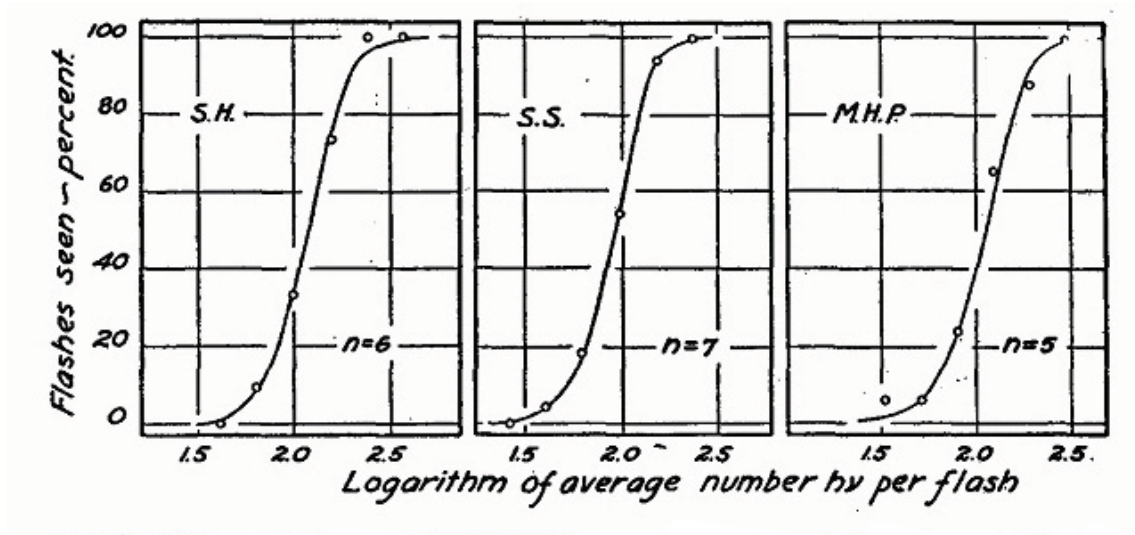


Fig. 12.2: Relation between the average energy content of a flash of light (in number of $h\nu$) and the frequency with which it is seen by three observers. Each point represents 50 flashes, except for S.H. where the number is 35. Taken from Hecht et al., 1942. The abscissa is $\log a$. The curves are Poisson distributions as shown in Figure 12.1.

The human visual system is a pretty remarkable piece of apparatus which operates over at least ten orders of magnitude in illumination. Incidentally, using direct electrophysiology it has been shown that in rabbit a single photon can be detected.

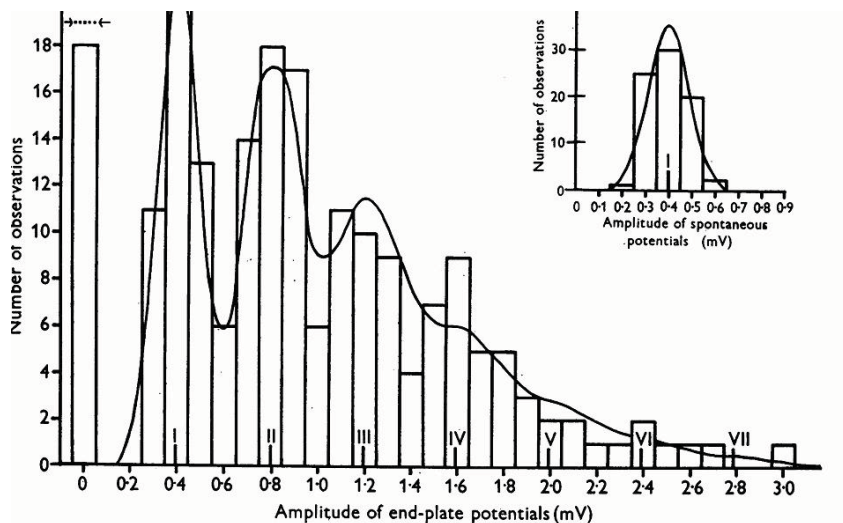
Example 2: del Castillo, J. & Katz, B. Quantal components of the end-plate potential. *J. Physiol.*, 124,560-573 (1954).

Katz et al. recorded from postsynaptic (heart) muscle fibers receiving impulses of acetylcholine, a neural transmitter, at the end plate. It must be assumed that prior investigation had noticed the "bumpiness" of the recordings and regarded this as *noise*. Katz et al. investigated this *noise*, and took as a hypothesis that synaptic release of acetylcholine took the form of vesicles of fixed size, but that the number of vesicles released, m , was a random variable which could be fitted by the Poisson density

$$p_k = \frac{m^k e^{-m}}{k!}, \quad (12.30)$$

where $m = \lambda t$, see (12.25).

Data from Boyd, I.A. and Martin, A.R. The end-plate potential in mammalian muscle. *J. Physiol.* (London), 132,74-91 (1956) for 198 trials, in which a single impulse was fired in the pre-synaptic nerve cell, is shown in the following histogram.



ig. 8. Histograms of e.p.p. and spontaneous potential amplitude distributions in a fibre in which neuromuscular transmission was blocked by increasing the magnesium concentration of the Krebs's solution to 12.5 mm. Peaks in e.p.p. amplitude distribution occur at 1, 2, 3 and 4 times the mean amplitude of the spontaneous miniature potentials. Gaussian curve is fitted to spon-

Fig. 12.3: Histogram of end-plate potentials. See above figure caption.

Inset is the histogram of spontaneous activity which implies a single vesicle leads to a membrane jump
 $h = 0.4mv$

The mean over $N_0 = 198$ trials of one presynaptic impulse was .933 mv and hence

$$m = \frac{.933}{0.4} = 2.33 \quad (12.31)$$

The probability of failure, $k = 0$, is

$$N_0 p_0 = N_0 e^{-m} = 19 \text{ vs } 18 \text{ (experiment)} \quad (12.32)$$

(Alternately, this offers another way by which to determine m .)

$$k = 1 : N_0 p_1 = N_0 \frac{m e^{-m}}{1!} = 44 \text{ vs } 44 \text{ (experiment)}$$

$$k = 2 : N_0 p_2 = N_0 \frac{m^2}{2} e^{-m} = 52 \text{ vs } 55$$

$$k = 3 : N_0 p_3 = 40 \text{ vs } 36$$

$$k = 4 : N_0 p_4 = 24 \text{ vs } 25$$

$$k = 5 : N_0 p_5 = 11 \text{ vs } 12$$

$$k = 6 : N_0 p_6 = 5 \text{ vs } 5$$

$$k = 7 : N_0 p_7 = 2 \text{ vs } 2$$

$$k = 8 : N_0 p_8 = 1 \text{ vs } 1$$

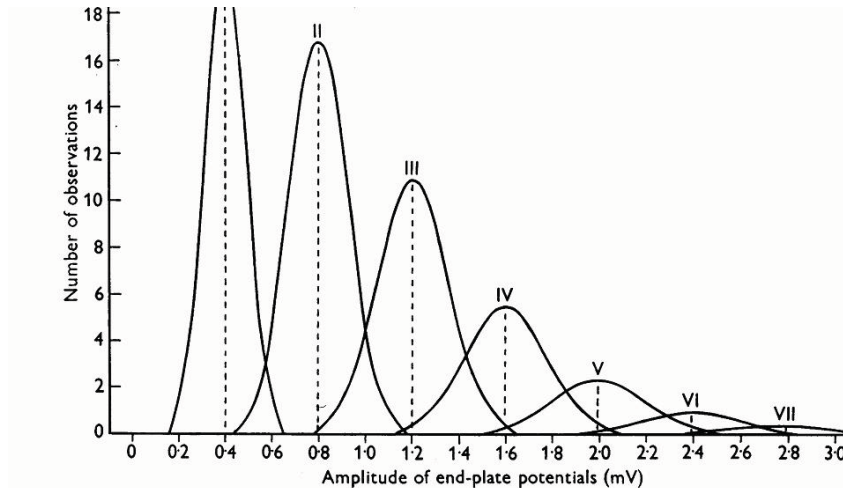


Fig. 9. Method of obtaining theoretical distribution of e.p.p. amplitudes illustrated in Fig. Number of e.p.p.'s (n) in each group is calculated from the Poisson equation $n = N e^{-m} m^x / x!$, where N is the total number of observations, x is the group number and m mean quantum content, obtained by dividing the mean e.p.p. amplitude by the mean amplitude of the spontaneous potentials. Gaussian curves are then drawn for each group about a mean amplitude xv and with a variance $x\sigma^2$, where v and σ^2 are the mean and variance of the spontaneous potentials.

Fig. 12.4: See above figure caption.

The continuous curve plotted on the histogram uses gaussians with appropriate means and variances. Bernard Katz received the Nobel prize for this work.

Statistical Mechanics

Another example of probabilistic reasoning comes from the 19th century effort to provide Thermodynamics with a mechanistic foundation. As a reference I mention the little book by Erwin Schrödinger entitled "Statistical Thermodynamics", which is a gem of scientific exposition. Schrödinger says "There is essentially only one problem in statistical thermodynamics: the distribution of a given amount of energy E over N identical systems". It is then assumed that the most likely distribution is the one observed in the *laboratory*.

The problem was largely solved by the great American physicist Josiah Willard Gibbs (after whom Gibbs's phenomenon, Lecture 6, is also named). He imagined a large number of identical systems, in loose contact, meaning at the same temperature, but in every other sense all the systems are independent. To fix things in your mind imagine a very dilute suspension of uniformly sized, small spheres, uniformly distributed in a solvent. The spheres are too far from each other to significantly interact with each other, but do interact with the solvent molecules, which are in constant agitated motion, based on their temperature. I.e., the spheres are at the same temperature, T , as the solvent – which might be referred to as a heat bath. Suppose the number of spheres is N , an extremely large number; and each sphere moves in its own *box*.

Suppose a and b refer to two boxes, and suppose $P_a(x)$ is the probability that the sphere in box a is at energy x , and $P_b(y)$ the probability that y is the energy of the sphere in box b . (The subscripts on P only identify a box, while the probability function P is the same in all instances.) Then consider

$$P_{a+b}(x+y) = P_a(x)P_b(y), \quad (12.33)$$

i.e., that the union of boxes a & b in the sense that they might be in contact and viewed together have energy $x+y$. The right hand side of (12.33) is a statement of the probability independence of boxes a & b , and as demonstrated in the previous lecture it follows that

$$P \propto e^{-\mu\epsilon} \quad (12.34)$$

where ϵ is the energy. To turn (12.34) into a probability, set

$$Z = \sum_{\epsilon} e^{-\mu\epsilon} \quad (12.35)$$

and

$$P(\epsilon) = e^{-\mu\epsilon}/Z. \quad (12.36)$$

The ‘constant’ μ is the same whether we look at one or both boxes. The only quantity that can reasonably be regarded as being the same for ‘boxes’ in thermal contact is Kelvin temperature T , which is expressed in degrees. Boltzman’s constant k converts degree to energy, i.e., kT has the units of energy, and therefore we take

$$\mu = \frac{1}{kT} \quad (12.37)$$

and therefore since there is only kinetic energy and three degrees of freedom for the single sphere of mass m

$$\epsilon = \frac{m}{2}(v_1^2 + v_2^2 + v_3^2) \quad (12.38)$$

and hence

$$P(\mathbf{v}) = \frac{e^{-m(v_1^2+v_2^2+v_3^2)/2kT}}{\left(\frac{2\pi kT}{m}\right)^{3/2}} \quad (12.39)$$

The denominator is calculated so that

$$\int_{-\infty}^{\infty} P(\mathbf{v})d\mathbf{v} = 1. \quad (12.40)$$

An immediate extension of (12.39) is obtained by supposing that there are n spheres per unit volume. Therefore the number density in (\mathbf{x}, \mathbf{v}) space is $\mathcal{P} = nP(\mathbf{v})$.

For our purposes (12.39), known as the Maxwell-Boltzmann distribution, is all that is needed. It is worth mentioning in passing that more complexity can be easily incorporated. Then all of Thermodynamics follows from these simple deliberations.

Brownian Motion

Einstein's Analysis

Compelling reasons can be given that probabilistic or "stochastic" modeling begins with the famous paper by Albert Einstein in 1905, in which he solves the problem of Brownian motion, another gem of scientific exposition which is easily read. (A reference for the present material, as well other illustrations, is "Handbook of Stochastic Methods" by Gardiner.) Recall that the origin of this problem were observations by Robert Brown, 1827, on the erratic motion of pollen suspended in water, as well as other substances. Brown and subsequent observers were able to convincingly rule out an "organic" origin to the movement of the pollen particles. Einstein assumed that the erratic motion of the particles was due to: (1) high frequency impacts from water molecules, due to fluctuations; (2) that a satisfactory description would result from a probabilistic rather than a deterministic description.

The pollen particles (gravity is ignored) suspended in solution constitute a *dilute gas*, in equilibrium with its environment the solvent at temperature T . Thus if m is the mass of a pollen particle, then particles have a velocity probability distribution given by (12.39) If particle mass m is large then $R = k/m \approx 0$, and $f(\mathbf{v}) \propto \delta(v_1)\delta(v_2)\delta(v_3)$, which says the particle sits still. But, if m is small enough, we expect the pollen particles, based on our coin tossing experience to migrate in time.

Einstein treats a one dimensional model problem, and asserts: (1) particles are independent; (2) there is a time interval τ , small compared observational times, such that at successive τ , the displacements, Δ , are independent; (3) there exists a stationary probability of displacement $\phi(\Delta)$ ³

$$\int \phi(\Delta)d\Delta = 1 \quad (12.41)$$

and that displacements, $-\Delta$ and Δ are equally likely,

$$\phi(-\Delta) = \phi(\Delta). \quad (12.42)$$

He then considers a one-dimensional model, and sets

$$f = f(x, t) \quad (12.43)$$

³ Note that this is different than (12.39), but based on (12.39) we can suppose a probability distribution of displacement, Δ .

to be the number density of particles per unit length at time t , so that

$$dn = f(x, t)dx \quad (12.44)$$

is the number in dx . It then follows that

$$f(x, t + \tau)dx = dx \int_{-\infty}^{\infty} f(x - \Delta, t)\phi(\Delta)d\Delta \quad (12.45)$$

where the left hand side is the number of particles in (x, dx) at $t + \tau$, and the right hand side calculates cell particles that jump to x in the next interval τ .

Since τ and Δ are *small*,

$$\begin{aligned} f(x, t + \tau) &\approx f(x, t) + \tau \frac{\partial f(x, t)}{\partial t} \\ f(x + \Delta, t) &\approx f(x, t) + \Delta \frac{\partial f(x, t)}{\partial x} + \frac{\Delta^2}{2} \frac{\partial^2 f(x, t)}{\partial x^2} \end{aligned} \quad (12.46)$$

If these are substituted into (12.45) it then follows that

$$\frac{\partial f}{\partial t} = D \frac{\partial^2 f}{\partial x^2} \quad (12.47)$$

with

$$D = \frac{1}{\tau} \int \frac{\Delta^2}{2} \phi(\Delta) d\Delta. \quad (12.48)$$

Clearly, (12.47) is what emerged from Fick's law, (3.80), earlier. For a particle starting at the origin we obtain the solution to (12.47) in the form

$$f = \frac{ne^{-x^2/4Dt}}{\sqrt{4\pi Dt}}, \quad (12.49)$$

where n is the number of pollen particles,

$$\int_{-\infty}^{\infty} f(x, t)dx = n. \quad (12.50)$$

$$\text{Expectation } \langle x^2 \rangle = \langle x^2 \rangle = 2Dt \quad (12.51)$$

which confirms the *random walk* of the pollen particle. ⁴

⁴ Note the similarity to coin tossing, (11.47).

Equation (12.45) is said to be a Chapman-Kolmogorov equation and in addition to properly accounting for all particles that jump to x , it states that the condition of the system at time t only depends on the state at the previous time, $t - \tau$. Recall that this is *Markov postulate*. It says that the system has amnesia about events before the last instant τ . A very important and pervasive assumption in modeling.

Equation (12.47), which is based on an expansion of the small quantity, Δ , is an example of a Fokker-Planck equation.

Another approach to the same phenomena was later given by Langevin.

Langevin's (Stochastic) Equation

It follows from (12.39) that for a pollen particle

$$\left\langle \frac{1}{2}mv^2 \right\rangle = \frac{1}{2}kT, \quad (12.52)$$

and since the pollen particle is extremely small, it experiences resistive viscous force in the fluid in which it is suspended given by the Stoke's force

$$-6\pi\eta av \quad (12.53)$$

where η is the viscosity, a the particle radius and v the (spherical) particle velocity $v = \frac{dx}{dt}$.

If X denotes the fluctuating force due to molecular bombardments then Newton's law is

$$m \frac{d^2x}{dt^2} = -6\pi\eta a \frac{dx}{dt} + X. \quad (12.54)$$

Multiply (12.54) by x to obtain

$$\frac{m}{2} \frac{d^2x^2}{dt^2} - mv^2 = -3\pi\eta a \frac{dx^2}{dt} + Xx \quad (12.55)$$

In the same spirit as statistical mechanics we image many laboratories performing the Brownian experiment and ensemble average over all experiments, then from (12.52)

$$\frac{m}{2} \frac{d^2}{dt^2} \langle x^2 \rangle - kT = -3\pi\eta a \frac{d}{dt} \langle x^2 \rangle \quad (12.56)$$

$$\langle xX \rangle = 0, \quad (12.57)$$

based on since X and $-X$ are equally likely. If (12.56) is integrated we obtain

$$\frac{d}{dt} \langle x^2 \rangle = \frac{kT}{3\pi\eta a} + ce^{-6\pi\eta at/m}, \quad (12.58)$$

with c an integration constant. But $m = 0(a^3)$ and a is small and hence the exponential can be taken as negligible. Note that the molecular force, X , is like a ‘will-o’-the-wisp’ in the analysis. Molecular consideration only enter through $\langle mv^2 \rangle = kT$.

Therefore

$$\langle x^2 \rangle - \langle x_0^2 \rangle = \frac{kT}{3\pi\eta a} t, \quad (12.59)$$

which is the same as Einstein’s result, (12.51) with

$$D = \frac{kT}{6\pi a\eta} \quad (12.60)$$

for the diffusion coefficient, a result also obtained by Einstein. Einstein’s and Langevin’s developments are the pioneering stochastic treatments of physics.

Population Equations

Preliminary Remarks

We have already considered diffusion, in Lecture 2, with the result that a one dimensional suspension of number density $n(x, t)$ is governed by,

$$\frac{\partial n}{\partial t} = -\frac{\partial Q}{\partial x}, \quad (12.61)$$

where Q is the flux of suspended particles. In higher dimensions

$$\frac{\partial n}{\partial t} = -\nabla Q. \quad (12.62)$$

Fick’s law (3.80) says that to lowest order we expect a concentration to run down its gradient

$$Q = -\kappa \nabla n, \quad (12.63)$$

which if substituted into (12.62) yields the diffusion equation.

Suppose aside from diffusion there is an active mechanism driving each particle of the suspension so that a particle at x_i moves with a velocity $V(x, t)$

$$\frac{dx_i}{dx} = V(x_i, t), \quad (12.64)$$

then in this case there is the convective flux

$$Q_0 = V(x, t)\rho, \quad (12.65)$$

in addition to Q , and therefore to include this term, the above equation (12.61), should be modified to read

$$\frac{\partial n}{\partial t} = -\frac{\partial}{\partial x}(Q_0 + Q) = -\frac{\partial}{\partial x}(V(x, t)\rho + -\kappa \frac{\partial n}{\partial x}). \quad (12.66)$$

It is a general feature of such formulations that the number of particles in the suspension be conserved, so if x_0 and x_1 are impenetrable boundaries, then $Q_0 + Q_1 = 0$ at x_0 and x_1 and thus if N is the total number of suspended particles,

$$\int_{x_0}^{x_1} n(x, t) dx = \frac{\partial N}{\partial t} = 0. \quad (12.67)$$

Statistical Mechanics of Cortical Population Dynamics

Sensory pathways in the cortex have $O(10^9)$ neurons, and the visual pathway is an example. Not only is this number daunting, but the fact that a typical neuron receives inputs from $O(10^4)$ other neurons further underlines the inherent complexity in attempting to model such a system. Redundancy is a recurring theme of the cortex, large numbers of neurons appear to be engaged in like activity, and this is a tool in the modeling described below. More specifically for vision early in the visual pathway (primary visual cortex, V1) a form of fourier analysis is performed. Small populations, say $10^2 - 10^3$, are then found to be tuned to specific local orientations, and others to a specific local spatial frequency.

We take advantage of this by considering the density $\rho(v, t)$ of neurons for some population of like neurons. The critical variable in the dynamics of a neuron is its membrane potential denoted here by v . The Hodgkin-Huxley equations are the gold standard for describing the electric activity of neurons, however, it has been shown that a very serviceable approximation is given by the dynamics of the simple RC circuit, see Figure (9.6). Within the framework of this model

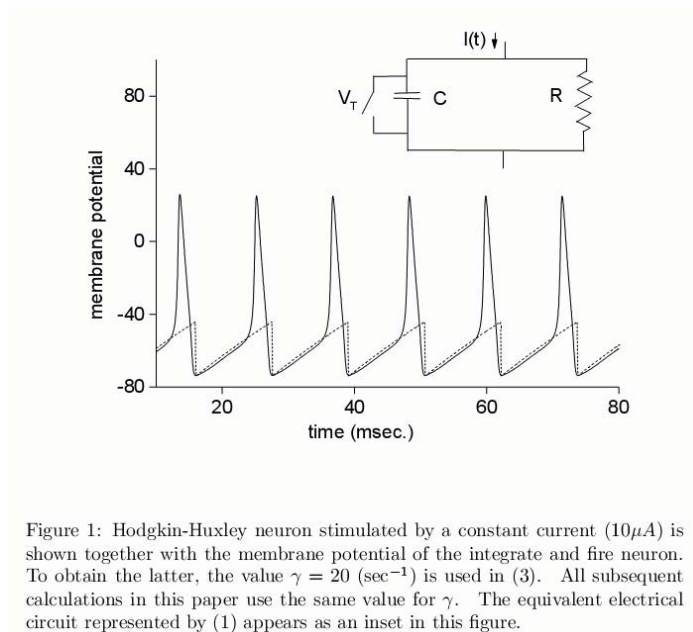


Fig. 12.5: Taken from Sirovich, L., Omurtag, A., Knight, B.W. *Dynamics of neuronal populations: The equilibrium solution. SIAM J. Appl. Math.*, 60, 2009-2028 (2000).

the membrane voltage is driven by a current until it reaches threshold, at which time the neuron fires an action potential, and the membrane potential is reset to its resting state. The normalized form for this integrate-and-fire neuron is

$$\frac{dv}{dt} = -\gamma v + h \sum_j \delta(t - t_j) \quad 0 \leq v \leq 1, \quad (12.68)$$

with $v = 0$, resting, and $v = 1$, threshold. γ is referred to as the leakage, and is related to membrane conductance. Note that $\{t_j\}$ denote arrival times of presynaptic arrivals, each of which elevates the membrane potential by h . (Going back to Katz's "end-plate potentials" analysis, we could allow for a distribution of h jumps.) Equation (12.68) appears to be linear, but the threshold condition renders it non-linear.

Since there are $O(10^4)$ pre-synaptic neurons dropping spikes on a neuron it is reasonable to assume that arrivals follow a Poisson process. Further

$$\sigma(t) = \left\langle \sum_j \delta(t - t_j) \right\rangle_{ensemble} \quad (12.69)$$

is the arrival rate and we allow for this to be time dependent.

The equation for the membrane voltage has two contributions, one from leakage, γ , and one from the jumps h . Each produces a *flux* of neurons across the unit interval, $0 \leq v \leq 1$.

Accumulation of neurons in dv in a time dt is

$$\begin{aligned} & \rho(v, t + dt)dv - \rho(v, t)dv = \\ & \gamma(v + dv, t)\rho(v + dv, t)dt - \gamma v\rho(v, t)dt + \sigma dt(\rho(v - h, t)dv - \rho(v, t)dv) \end{aligned} \quad (12.70)$$

which once again is a Chapman-Kolmogorov relation. Doing what comes naturally one gets

$$\frac{\partial}{\partial t}\rho(v, t) = \frac{\partial}{\partial v}(\gamma v\rho) + \sigma\rho(v - h, t) - \sigma\rho(v, t) \quad (12.71)$$

on

$$\frac{\partial \rho}{\partial t} = \frac{\partial}{\partial v}(\gamma v\rho) - \sigma \frac{\partial}{\partial v} \int_{v-h}^v \rho(v', t)dv' = -\frac{\partial}{\partial v}Q. \quad (12.72)$$

The first term of the right hand side of (12.71) is the contribution of convective flux due to leakage, the second is the *birth term* due to jumping from the left, and the third is the *death term*, due to jumping to the right. The net flux of neurons is given by

$$Q = -\gamma v\rho + \sigma \int_{v-h}^h \rho(v', t)dv'. \quad (12.73)$$

One boundary condition is

$$\rho(1, t) = 0 \quad (12.74)$$

called the *absorbing* boundary condition.

It follows that

$$Q(v = 1, t) = \sigma(t) \int_{1-h}^1 \rho(v', t)dv' = r(t) \quad (12.75)$$

is the firing rate and since we must conserve neurons,

$$Q(v = 0, t) = r(t). \quad (12.76)$$

is a second boundary condition. Therefore

$$\frac{\partial}{\partial t} \int_0^1 \rho(v, t)dv = - \int_0^1 \frac{\partial Q}{\partial v} dv = Q(v = 0, t) - Q(v = 1, t) \quad (12.77)$$

so that the number of neurons is conserved.

In Figure 12.6 you can see the result of the direct simulation of $n = 900, 9000,$ and $90,000$ individual neurons each satisfying (12.68) and receiving Poisson arrivals. These solutions converge to the solution of (12.77). Note that the error goes as $1/\sqrt{N}$, in keeping with the result of *coin-tossing* discussed in the previous lecture.

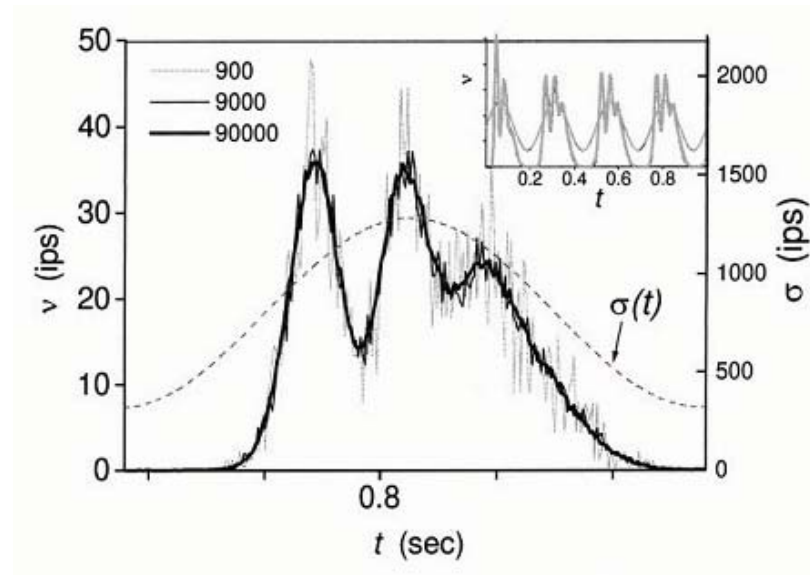


Fig. 12.6: The firing rates ν , of three populations consisting of 900, 9,000, and 90,000 neurons. They are driven by a sinusoidally modulated input with mean frequency σ , shown as the dashed curve. Neuron firings have been averaged over each millisecond. Main figure shows the last of the four periodic oscillations shown in the inset. As the number of neurons is increased, the random fluctuations in the firing rate diminish as the square root of population size. The populations receive no feedback.

If we allow $h \downarrow 0$ in (12.71) we obtain the Fokker-Planck approximation.

$$\frac{\partial \rho}{\partial t} = \frac{\partial}{\partial v} \left((\gamma v - s) \rho + \mu \frac{\partial \rho}{\partial v} \right) = \frac{\partial}{\partial v} Q \quad (12.78)$$

with $\mu = \frac{1}{2} \sigma h^2$ & $s = \sigma h$. This last equation goes under the name of Ornstein-Uhlenbeck equation, although it more appropriately should be attributed to Schrodinger.

Steady State

As an application we consider steady conditions $\frac{\partial}{\partial t} = 0, s = s_o$. In this case (12.78) has the first integral,

$$(s_o - \gamma v) \rho - \mu \frac{\partial \rho}{\partial v} = -\mu \frac{\partial \rho}{\partial v} \Big|_{v=1} = J_o \quad (12.79)$$

where J_o is the firing rate.

For reference purposes consider (12.68), the non-stochastic case under steady conditions

$$\frac{dv}{dt} = -\gamma v + s_o \quad (12.80)$$

which for $v(t=0) = 0$ has the solution

$$v = (1 - e^{-\gamma t}) \frac{s_o}{\gamma} \quad (12.81)$$

the neuron will fire when $v = 1$ or at time τ , such that

$$1 - \frac{\gamma}{s_o} = e^{-\gamma \tau} \quad (12.82)$$

$$\tau = \frac{1}{\gamma} \ln\left(1 - \frac{\gamma}{s_o}\right) \quad (12.83)$$

so that

$$\nu = \frac{1}{\tau} = \frac{-\gamma}{\ln(1 - \gamma/s_o)} \sim s_o, \quad (12.84)$$

and for $s_o < \gamma$ it never fires.

Equation (12.79) may be integrated to determine ρ . Recall, we still have the boundary condition, $\rho(v = 1) = 0$. Then if the condition that ρ be a probability

$$\int_0^1 \rho(v) dv = 1 \quad (12.85)$$

is imposed, we obtain

$$J_o = J_o(\gamma, s_o) \quad (12.86)$$

which is plotted along with $\nu(s_o)$ in the following plot.

We see from this plot that there is a range of currents for which the neuron governed by (12.78) fires but the deterministic neuron (12.80) does not fire. Equations (12.78) and (12.71) have stochasticity built into the model, and therefore allow for improbable events. Even for $s = \sigma h < \gamma$ we still can have improbable excursions so that arrivals overcome the leakage, and a neuron fires.

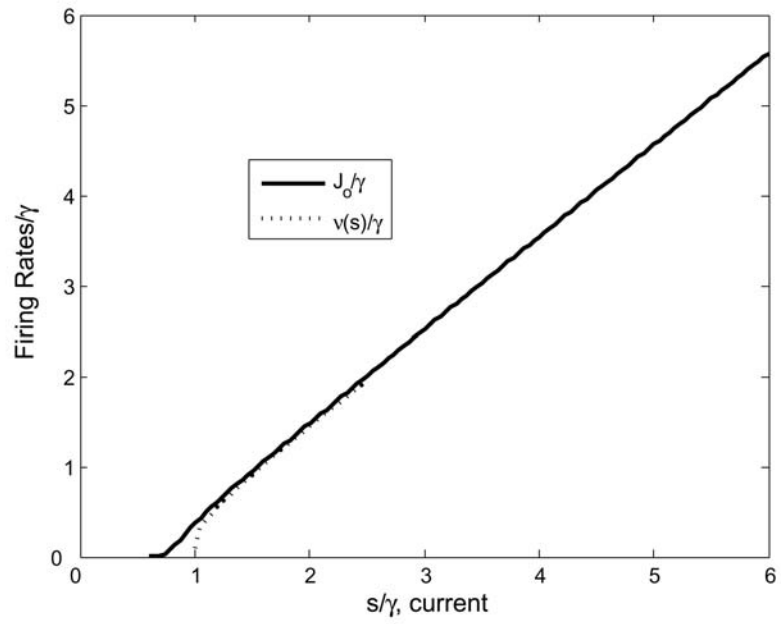


Fig. 12.7: The firing rate J_0/γ , from (12.86), and a function of current, s/γ . The faint dotted curve shows the results of integrating (12.80).