

Peripatetic

(A random walk
in random walks)

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Our general topics: ←

- ⊙ Some random (variable) background
- ⊙ What is a random walk?
- ⊙ Some Intuitive Derivations
- ⊙ Financial Modeling
- ⊙ Diffusion and Flux
- ⊙ Biology: Limits of Growth
- ⊙ Biology: Receptors, Channels, and Flow

Some random (variable) background ←

This is a brief tour (peripatetic – wandering about) of some topics in random walks. It mostly consists of a few interesting ideas to start exploration of the general topic. We'll start with a bit on random variables.

- A random variable is a view into a set of possible values. Associated with each possible value is a probability. For a discrete random variable, there is a finite or countably infinite set of possible values and probabilities $\{(a_i, p_i)\}$, with the condition that $\sum_i p_i = 1$. Thus, for example, we could talk about the random variable ξ drawing values from the set of possible values $\{(1, 1/2), (-1, 1/2)\}$. When we evaluate the random variable ξ , we get either 1 or -1, each with probability 1/2.

- We can build new random variables. For example, if ξ_1 and ξ_2 are random variables over $\{(1, 1/2), (-1, 1/2)\}$, then $\xi_1 + \xi_2$ is a random variable (but over the set $\{(2, 1/4), (0, 1/2), (-2, 1/4)\}$). We must be a bit careful sometimes – for example, $\xi_1 + \xi_1$ is also a random variable (but this time over $\{(2, 1/2), (-2, 1/2)\}$).
- Given a random variable X over $\{(a_i, p_i)\}$, we define the *expectation* (or *expected value*) of X by:

$$\langle X \rangle = \sum_i p_i a_i.$$

Note that the expectation is a linear operator:

$$\langle \alpha X + \beta Y \rangle = \alpha \langle X \rangle + \beta \langle Y \rangle$$

for α, β real numbers, and X, Y random variables.

- Note that the expectation of a constant α is that constant (a constant can be thought of as a random variable over $\{(\alpha, 1)\}$):

$$\langle \alpha \rangle = \alpha.$$

- Example: if ξ_1 and ξ_2 are random variables over $\{(1, 1/2), (-1, 1/2)\}$, then

$$\begin{aligned}\langle \xi_1 \rangle &= \frac{1}{2} * 1 + \frac{1}{2} * (-1) = 0 = \langle \xi_2 \rangle, \\ \langle \xi_1 + \xi_2 \rangle &= \langle \xi_1 \rangle + \langle \xi_2 \rangle = 0 + 0 = 0, \\ \langle \xi_1 \xi_2 \rangle &= \frac{1}{2} * 1 + \frac{1}{2} * (-1) = 0,\end{aligned}$$

but

$$\langle \xi_1^2 \rangle = \frac{1}{2} * 1^2 + \frac{1}{2} * (-1)^2 = 1,$$

and

$$\begin{aligned}\langle (\xi_1 + \xi_2)^2 \rangle &= \langle \xi_1^2 + 2 * \xi_1 \xi_2 + \xi_2^2 \rangle \\ &= \langle \xi_1^2 \rangle + 2 * \langle \xi_1 \xi_2 \rangle + \langle \xi_2^2 \rangle \\ &= 1 + 0 + 1 \\ &= 2.\end{aligned}$$

- Given a random variable X , we define the *variance* of X by:

$$V(X) = \langle (X - \langle X \rangle)^2 \rangle.$$

We can also calculate this as:

$$\begin{aligned} V(X) &= \langle (X - \langle X \rangle)^2 \rangle \\ &= \langle X^2 - 2X\langle X \rangle + \langle X \rangle^2 \rangle \\ &= \langle X^2 \rangle - 2\langle X\langle X \rangle \rangle + \langle \langle X \rangle^2 \rangle \\ &= \langle X^2 \rangle - 2\langle X \rangle^2 + \langle X \rangle^2 \\ &= \langle X^2 \rangle - \langle X \rangle^2. \end{aligned}$$

- The *standard deviation* of a random variable X is given by:

$$\sigma(X) = V(X)^{1/2}.$$

What is a random walk? ←

There are a variety of ways to define a random walk. Here we start with a relatively simple version, which will allow us to develop some classical results on random walks. Later, we can generalize.

- Let $\{\xi_i | i = 1, 2, 3, \dots\}$ be a set of (independent) random variables over $\{(1, \frac{1}{2}), (-1, \frac{1}{2})\}$ (in particular, 'observing' one of the random variables has no effect on observations of any of the rest of them). Then a *simple random walk* is a sequence (S_n) where

$$S_0 = 0,$$

$$S_n = \xi_1 + \xi_2 + \dots + \xi_n.$$

- It is easy to see that

$$-n \leq S_n \leq n.$$

- We have that

$$\langle S_0 \rangle = 0,$$

and thus

$$\begin{aligned} \langle S_n \rangle &= \langle S_{n-1} + \xi_n \rangle \\ &= \langle S_{n-1} \rangle + \langle \xi_n \rangle \\ &= \langle S_{n-1} \rangle + 0 \\ &= \langle S_{n-1} \rangle \\ &= \langle S_{n-2} \rangle \\ &\vdots \\ &= \langle S_0 \rangle \\ &= 0. \end{aligned}$$

- We also have

$$\begin{aligned}
\langle S_n^2 \rangle &= \langle (S_{n-1} + \xi_n)^2 \rangle \\
&= \langle S_{n-1}^2 + 2 * S_{n-1} \xi_n + \xi_n^2 \rangle \\
&= \langle S_{n-1}^2 \rangle + 2 * \langle S_{n-1} \xi_n \rangle + \langle \xi_n^2 \rangle \\
&= \langle S_{n-1}^2 \rangle + 2 * \sum_{i=1}^{n-1} \langle \xi_i \xi_n \rangle + 1 \\
&= \langle S_{n-1}^2 \rangle + 2 * \sum_{i=1}^{n-1} 0 + 1 \\
&= \langle S_{n-1}^2 \rangle + 1 \\
&= \langle S_{n-2}^2 \rangle + 2 \\
&\vdots \\
&= \langle S_0^2 \rangle + n \\
&= n,
\end{aligned}$$

and thus

$$\begin{aligned}
V(S_n) &= \langle S_n^2 \rangle - \langle S_n \rangle^2 \\
&= n - 0 \\
&= n.
\end{aligned}$$

In other words, the variance of S_n is n , and the standard deviation of S_n is \sqrt{n} .

- We know that S_n ranges between $-n$ and n . But how is it distributed across that range? In other words, if $-n \leq k \leq n$, what is the probability that $S_n = k$ (i.e., $P(S_n = k)$)? We can make a couple of observations. First, by symmetry, $P(S_n = k) = P(S_n = -k)$, since each of the ξ_i is over $\{(1, \frac{1}{2}), (-1, \frac{1}{2})\}$. Second, by a parity argument, if n is even and k is odd, or if n is odd and k is even, then $P(S_n = k) = 0$. Let us look, then, at the case n is even and $k \geq 0$ is also even.

We know that $S_n = \sum_i \xi_i$, and that each of the ξ_i is either -1 or 1 . Thus, $S_n = k$ when exactly $(\frac{n}{2} + \frac{k}{2})$ of the ξ_i are $+1$ and the rest (i.e., $n - (\frac{n}{2} + \frac{k}{2}) = (\frac{n}{2} - \frac{k}{2})$) are -1 . This can happen in $\binom{n}{\frac{n}{2} + \frac{k}{2}}$ different ways. Each of these is equally likely, and there are 2^n total possibilities.

Thus, we have that

$$\begin{aligned}
 P(S_n = k) &= \binom{n}{\frac{n}{2} + \frac{k}{2}} \frac{1}{2^n} \\
 &= \frac{n!}{\left(\frac{n}{2} + \frac{k}{2}\right)! \left(n - \left(\frac{n}{2} + \frac{k}{2}\right)\right)! 2^n} \\
 &= \frac{n!}{\left(\frac{n+k}{2}\right)! \left(\frac{n-k}{2}\right)! 2^n}
 \end{aligned}$$

We can also do the quick consistency check:

$$\begin{aligned}
 &\sum_{k=-n}^n P(S_n = k) \\
 &= P(S_n = 0) + 2 \sum_{k=1}^n P(S_n = k) \\
 &= P(S_n = 0) + 2 \sum_{k=1}^{n/2} P(S_n = 2k) \\
 &= P(S_n = 0) + 2 \sum_{k=1}^{n/2} \binom{n}{\frac{n}{2} + \frac{2k}{2}} \frac{1}{2^n}
 \end{aligned}$$

$$\begin{aligned}
&= P(S_n = 0) + \frac{1}{2^n} 2 \sum_{k=1}^{n/2} \binom{n}{\frac{n}{2} + k} \\
&= \frac{1}{2^n} \binom{n}{\frac{n}{2}} + \frac{1}{2^n} 2 \sum_{k=1}^{n/2} \binom{n}{\frac{n}{2} + k} \\
&= \frac{1}{2^n} \left(\binom{n}{\frac{n}{2}} + \sum_{k=1}^{n/2} \binom{n}{\frac{n}{2} + k} + \sum_{k=1}^{n/2} \binom{n}{\frac{n}{2} + k} \right) \\
&= \frac{1}{2^n} \left(\binom{n}{\frac{n}{2}} + \sum_{k=1}^{n/2} \binom{n}{n - (\frac{n}{2} + k)} + \sum_{k=1}^{n/2} \binom{n}{\frac{n}{2} + k} \right) \\
&= \frac{1}{2^n} \left(\binom{n}{\frac{n}{2}} + \sum_{k=0}^{n/2-1} \binom{n}{k} + \sum_{k=n/2+1}^n \binom{n}{k} \right) \\
&= \frac{1}{2^n} \left(\sum_{k=0}^n \binom{n}{k} \right) \\
&= \frac{1}{2^n} * 2^n \\
&= 1.
\end{aligned}$$

(ugh . . . :-)

- Let's generalize slightly, and suppose that our random walk may have unequal probabilities of moving in the two directions. In other words, suppose our random variables ξ_i are over $\{(1, p), (-1, q)\}$, with $q = 1 - p$.

In this case, given two such random variables ξ_1 and ξ_2 , we have:

$$\begin{aligned}
 \langle \xi_1 \rangle &= p * 1 + q * (-1) = p - q \\
 &= 2p - 1 = \langle \xi_2 \rangle, \\
 \langle \xi_1 + \xi_2 \rangle &= \langle \xi_1 \rangle + \langle \xi_2 \rangle = 2 * (2p - 1) \\
 &= 4p - 2, \\
 \langle \xi_1 \xi_2 \rangle &= (p^2 + q^2) * 1 + 2pq * (-1) \\
 &= p^2 - 2pq + q^2 = (p - q)^2 \\
 &= (2p - 1)^2 = 4p^2 - 4p + 1.
 \end{aligned}$$

We also have:

$$\langle \xi_1^2 \rangle = p * 1^2 + q * (-1)^2 = p + q = 1,$$

and

$$\begin{aligned} \langle (\xi_1 + \xi_2)^2 \rangle &= \langle \xi_1^2 + 2 * \xi_1 \xi_2 + \xi_2^2 \rangle \\ &= \langle \xi_1^2 \rangle + 2 * \langle \xi_1 \xi_2 \rangle + \langle \xi_2^2 \rangle \\ &= 1 + 2 * (p - q)^2 + 1 \\ &= 2 + 2 * (p - q)^2 \\ &= 2 + 2 * (4p^2 - 4p + 1) \\ &= 2 + 8p^2 - 8p + 2 \\ &= 4 + 8p^2 - 8p. \end{aligned}$$

- If we again let $S_0 = 0$ and $S_n = S_0 + \xi_1 + \dots + \xi_n$, we have that

$$\langle S_0 \rangle = 0,$$

and in general

$$\begin{aligned} \langle S_n \rangle &= \langle S_{n-1} + \xi_n \rangle \\ &= \langle S_{n-1} \rangle + \langle \xi_n \rangle \\ &= \langle S_{n-1} \rangle + p - q \\ &= \langle S_{n-2} \rangle + \langle \xi_{n-1} \rangle + p - q \\ &= \langle S_{n-2} \rangle + 2 * (p - q) \\ &\vdots \\ &= \langle S_0 \rangle + n * (p - q) \\ &= n * (p - q). \end{aligned}$$

- We also have

$$\begin{aligned}
\langle S_n^2 \rangle &= \langle (S_{n-1} + \xi_n)^2 \rangle \\
&= \langle S_{n-1}^2 + 2 * S_{n-1} \xi_n + \xi_n^2 \rangle \\
&= \langle S_{n-1}^2 \rangle + 2 * \langle S_{n-1} \xi_n \rangle + \langle \xi_n^2 \rangle \\
&= \langle S_{n-1}^2 \rangle + 2 * \sum_{i=1}^{n-1} \langle \xi_i \xi_n \rangle + 1 \\
&= \langle S_{n-1}^2 \rangle + 2 * \sum_{i=1}^{n-1} (p - q)^2 + 1 \\
&= \langle S_{n-1}^2 \rangle + 2(n - 1)(p - q)^2 + 1 \\
&= \langle S_{n-2}^2 \rangle + 2((n - 1) + (n - 2))(p - q)^2 + 2 \\
&\quad \vdots \\
&= \langle S_0^2 \rangle + 2 \left(\sum_{i=1}^{n-1} i \right) (p - q)^2 + n \\
&= 0 + n(n - 1)(p - q)^2 + n \\
&= n + n(n - 1)(p - q)^2,
\end{aligned}$$

and thus

$$\begin{aligned}V(S_n) &= \langle S_n^2 \rangle - \langle S_n \rangle^2 \\&= n + n(n-1)(p-q)^2 - n^2 * (p-q)^2 \\&= n - n(p-q)^2 \\&= n(p+q)^2 - n(p-q)^2 \\&= n((p+q)^2 - (p-q)^2) \\&= n(4pq) \\&= 4npq.\end{aligned}$$

In other words, the variance of S_n is $4npq$, and the standard deviation of S_n is $2\sqrt{npq}$.

Some Intuitive Derivations



Every so often, I like to be a physicist (or biologist) and cavalier about error bounds.

- Suppose $S_n = \sum_i \xi_i$ is a random walk, with ξ_i random variables over $\{(1, \frac{1}{2}), (-1, \frac{1}{2})\}$. Let us write $P(S_n = k)$ as $P(k, n)$.

We can observe that

$$P(k, n + 1) = \frac{1}{2}P(k - 1, n) + \frac{1}{2}P(k + 1, n).$$

Now assume that n and k are large, let δ and τ be (small) real numbers, and then let $x = \delta k$ and $t = \tau n$.

We then have $P(x, t) = P(\delta k, \tau n)$, and so

$$\begin{aligned} P(x, t + \tau) &= P(\delta k, \tau(n + 1)) \\ &= \frac{1}{2}P(\delta(k - 1), \tau n) + \frac{1}{2}P(\delta(k + 1), \tau n) \\ &= \frac{1}{2}P(x - \delta, t) + \frac{1}{2}P(x + \delta, t). \end{aligned}$$

From this, we get

$$\begin{aligned} P(x, t + \tau) - P(x, t) \\ = \frac{1}{2}(P(x - \delta, t) + P(x + \delta, t) - 2P(x, t)). \end{aligned}$$

Now consider two approximations. First, for small (infinitesimal) τ , we have

$$P(x, t + \tau) = P(x, t) + \tau * \frac{\partial P(x, t)}{\partial t},$$

and for small (infinitesimal) δ , we have

$$\begin{aligned} P(x + \delta, t) + P(x - \delta, t) \\ = 2P(x, t) + \delta^2 * \frac{\partial^2 P(x, t)}{\partial x^2}. \end{aligned}$$

Putting pieces together, we have:

$$\begin{aligned} \frac{\partial P(x, t)}{\partial t} &= \frac{\delta^2}{2\tau} \frac{\partial^2 P(x, t)}{\partial x^2} \\ &= D * \frac{\partial^2 P(x, t)}{\partial x^2} \end{aligned}$$

(i.e., the diffusion equation, with $D = \frac{\delta^2}{2\tau}$ the diffusion coefficient ...).

More generally, if we have a biased random walk (over $\{(1, p), (-1, q)\}$), then

$$P(x, t + \tau) = p * P(x - \delta, t) + q * P(x + \delta, t),$$

and, using the approximations, we have

$$\begin{aligned} & \tau * \frac{\partial P(x, t)}{\partial t} \\ = & P(x, t + \tau) - P(x, t) \\ = & p * P(x - \delta, t) + q * P(x + \delta, t) - P(x, t) \\ = & p * \left(P(x, t) - \delta * \frac{\partial P(x, t)}{\partial x} + \frac{\delta^2}{2} * \frac{\partial^2 P(x, t)}{\partial x^2} \right) \\ & + q * \left(P(x, t) + \delta * \frac{\partial P(x, t)}{\partial x} + \frac{\delta^2}{2} * \frac{\partial^2 P(x, t)}{\partial x^2} \right) \\ & - P(x, t) \\ = & (p + q - 1)P(x, t) + (q - p) * \delta * \frac{\partial P(x, t)}{\partial x} \\ & + \frac{(p + q)\delta^2}{2} * \frac{\partial^2 P(x, t)}{\partial x^2} \\ = & (q - p) * \delta * \frac{\partial P(x, t)}{\partial x} + \frac{\delta^2}{2} * \frac{\partial^2 P(x, t)}{\partial x^2}. \end{aligned}$$

Writing this in a slightly different form,
we have

$$\frac{\partial P(x, t)}{\partial t} = D * \frac{\partial^2 P(x, t)}{\partial x^2} + D * \beta * \frac{\partial P(x, t)}{\partial x},$$

where

$$D = \frac{\delta^2}{2\tau} \text{ and } \beta = \frac{2(1 - 2p)}{\delta}$$

(i.e., diffusion with drift ...).

- Let's look at another approach to continuous versions of these issues. Instead of looking at random variables over a discrete set, let the random variables draw their values from a probability distribution. In particular, let

$$w : \mathbb{R} \rightarrow [0, 1]$$

be an integrable (measurable) function, with

$$\int_{-\infty}^{\infty} w(s) ds = 1.$$

Then a random variable ξ over $w(s)$ gives the value s with probability $w(s)$ (i.e., $P(\xi = s) = w(s)$).

Note that we can use the Dirac delta function $\delta(x - x_0)$ to recover the discrete examples if we want to.

Recall that the Dirac delta function has the properties

$$\delta(x - x_0)dx = 0 \quad \text{if } |x - x_0| > \frac{dx}{2}$$

$$\delta(x - x_0)dx = 1 \quad \text{if } |x - x_0| \leq \frac{dx}{2}$$

and

$$\int_{-\infty}^{\infty} \delta(x - x_0)dx = 1.$$

Then, if we let

$$w(x) = \sum_i p_i * \delta(x - a_i),$$

we are back in the discrete case.

Let's mention here also that the delta function has the property:

$$\delta(x - x_0) = \frac{1}{2\pi} \int_{-\infty}^{\infty} e^{it(x_0-x)} dt.$$

Given a random variable ξ over a probability distribution $w(s)$, we can look at the expected value of the random variable

$$\langle \xi \rangle = \int_{-\infty}^{\infty} s * w(s) ds,$$

the mean square

$$\langle \xi^2 \rangle = \int_{-\infty}^{\infty} s^2 * w(s) ds,$$

the variance

$$V(\xi) = \langle \xi^2 \rangle - \langle \xi \rangle^2,$$

and so on.

Now suppose we have a probability distribution $w(s)$ with mean μ and standard deviation σ (i.e., if ξ is a random variable over $w(s)$, then $\mu = \langle \xi \rangle$, and $\sigma^2 = V(\xi)$). Note that there is no guarantee for a given distribution $w(s)$ that either the mean μ or standard deviation σ exist – the integrals could diverge. In this example, we are assuming they do exist.

Let $\{\xi_i\}$ be a collection of (independent) random variables over the distribution $w(s)$, and let $S_n = S_0 + \sum_1^n \xi_i$ (with $S_0 = 0$) be a random walk. What can we say about the distribution of the values of $\frac{1}{n}S_n$? In other words, what can we say about the distribution of the average of n (identically distributed) random variables?

We want to find the probability that $\frac{1}{n}S_n = x$ (let's write this as $P_n(x)$). We will have $\frac{1}{n}S_n = x$ if $\xi_i = s_i$ and $\frac{1}{n} \sum_i s_i = x$. The probability of this happening is $\prod_i w(s_i)$, since the ξ_i are independent of each other. We need to add up the probabilities over all possible ways that $\frac{1}{n} \sum_i s_i = x$ (as we did in the discrete case). In other words, we will have

$$P_n(x) = \int \int \cdots \int_{\frac{1}{n} \sum_i s_i = x} w(s_1) \cdots w(s_n) ds_1 \cdots ds_n.$$

The limits of integration are fairly messy, so we will use the Dirac delta function.

We will then have

$$P_n(x) = \int_{-\infty}^{\infty} \cdots \int_{-\infty}^{\infty} \delta\left(x - \frac{1}{n} \sum_j s_j\right) w(s_1) \cdots w(s_n) ds_1 \cdots ds_n.$$

Using the (fourier transform) property of the delta function, we have

$$\begin{aligned} 2\pi P_n(x) &= \int_{-\infty}^{\infty} \cdots \int_{-\infty}^{\infty} e^{it\left(\frac{1}{n} \sum_j s_j - x\right)} w(s_1) \cdots w(s_n) dt ds_1 \cdots ds_n \\ &= \int_{-\infty}^{\infty} \cdots \int_{-\infty}^{\infty} e^{-itx} \prod_j \left(e^{it\frac{s_j}{n}} w(s_j)\right) dt ds_1 \cdots ds_n \\ &= \int_{-\infty}^{\infty} e^{-itx} \left(\prod_j \int_{-\infty}^{\infty} \left(e^{it\frac{s_j}{n}} w(s_j)\right) ds_j \right) dt. \end{aligned}$$

If we now let $Q(t) = \int_{-\infty}^{\infty} e^{\frac{its}{n}} w(s) ds$, we have

$$P_n(x) = \frac{1}{2\pi} \int_{-\infty}^{\infty} e^{-itx} Q^n(t) dt.$$

Now let's look at $Q(t)$. We can expand the exponential to get

$$\begin{aligned}
 Q(t) &= \int_{-\infty}^{\infty} e^{\frac{its}{n}} w(s) ds \\
 &= \int_{-\infty}^{\infty} w(s) \left(1 + \frac{its}{n} - \frac{1}{2} \frac{t^2 s^2}{n^2} \dots\right) ds \\
 &= \int_{-\infty}^{\infty} w(s) ds + \frac{it}{n} \int_{-\infty}^{\infty} s * w(s) ds \\
 &\quad - \frac{t^2}{2n^2} \int_{-\infty}^{\infty} s^2 w(s) ds + \dots \\
 &= 1 + \frac{it}{n} \langle s \rangle - \frac{1}{2n^2} t^2 \langle s^2 \rangle + \dots
 \end{aligned}$$

Now we take the log, and use the expansion $\ln(1 + y) = y - \frac{1}{2}y^2 + \dots$ to get

$$\begin{aligned}
 \ln(Q^n(t)) &= n \ln\left(1 + \frac{it}{n} \langle s \rangle - \frac{t^2}{2n^2} \langle s^2 \rangle + \dots\right) \\
 &= n * \left(\frac{it}{n} \langle s \rangle - \frac{1}{2n^2} t^2 \langle s^2 \rangle - \frac{1}{2} \left(\frac{it}{n} \langle s \rangle\right)^2 + \dots\right) \\
 &= \left(it \langle s \rangle - \frac{1}{2n} t^2 (\langle s^2 \rangle - \langle s \rangle^2) + \dots\right) \\
 &= \left(it \mu - \frac{1}{2n} t^2 \sigma^2 + \dots\right)
 \end{aligned}$$

where μ and σ are the mean and standard deviation of the distribution $w(s)$.

Discarding all the higher order terms, and taking antilogs, we get

$$Q^n(t) = e^{it\mu - \frac{1}{2n}t^2\sigma^2},$$

and then that

$$P_n(x) = \frac{1}{2\pi} \int_{-\infty}^{\infty} e^{it(\mu-x) - \frac{1}{2n}t^2\sigma^2} dt.$$

Now we use the formula

$$\int_{-\infty}^{\infty} e^{at-bt^2} dt = \sqrt{\frac{\pi}{b}} * e^{\left(\frac{a^2}{4b}\right)}$$

with $a = i(\mu - x)$, $b = \frac{1}{2n}\sigma^2$, to finally get

$$\begin{aligned} P_n(x) &= \frac{1}{2\pi} \int_{-\infty}^{\infty} e^{it(\mu-x) - \frac{1}{2n}t^2\sigma^2} dt \\ &= \frac{1}{2\pi} \sqrt{\frac{\pi}{\frac{1}{2n}\sigma^2}} * e^{\left(-\frac{(\mu-x)^2}{4 * \frac{1}{2n}\sigma^2}\right)} \\ &= \frac{1}{\frac{\sigma}{\sqrt{n}} \sqrt{2\pi}} * e^{\left(-\frac{(x-\mu)^2}{2\left(\frac{\sigma^2}{n}\right)}\right)}. \end{aligned}$$

In other words, it is a normal distribution with mean μ and standard deviation $\frac{\sigma}{\sqrt{n}}$.

Note that we made no assumptions about the distribution $w(s)$ except that it actually has a mean (μ) and a standard deviation (σ) (and, of course, that it goes to zero fast enough for large $|s|$ that the approximations work out right . . .).

What this says is that if we average a bunch of identically distributed independent random variables, the result is a normal distribution, whether or not the original distribution was normal.

This is usually called the *Central Limit Theorem*.

Financial Modeling ←

Let's use some of these ideas to do some financial modeling. As an example, let's develop the (in)famous Black-Scholes model for options pricing.

- We can start with the simplest financial instrument, the fixed rate bond. If we “buy” amount V_0 of a rate r bond at time $t = 0$, then at time $t = 1$ we can redeem the for value $V_0(1 + r)$. If we wait longer to redeem the bond, then at some time in the future we can redeem the bond for

$$V(n, r) = V_0(1 + r)^n$$

One can also think of this as a “savings account” with interest rate r . In this case, we can ask the more general question, what is $V(t, r)$ for real values of t , rather than just integral values of t ?

This will depend on the specifics of the bond (savings account). In its simplest form, the bond will have “coupons” that can be redeemed at specific times in the future, or in the case of a savings account, interest will be “compounded” on specific dates.

Let’s look at various possibilities for compounding. Suppose the bond has (annual) interest rate r . If interest is compounded k times during the year (k would be 4 for quarterly compounding, 12 for monthly compounding, etc.), then the value at time t would be

$$V(t, r, k) = V_0 \left(1 + \frac{r}{k}\right)^{kt}$$

If we smooth this out, and let k go to infinity (i.e., “continuous compounding”), then we will have

$$V(t, r) = V_0 \lim_{k \rightarrow \infty} \left(1 + \frac{r}{k}\right)^{kt} = V_0 e^{rt}.$$

We thus know how to set a price for a bond to be redeemed at some time t in the future.

- Now let's generalize. Suppose that the interest rate r , instead of being fixed, varied over time. What price should we be willing to pay for such a financial instrument? We can think of this financial instrument as a stock (share) in a corporation. Our "return on investment" will be uncertain, and will depend on the performance of the corporation (and also on the change in price of the stock). We have the potential to make a large profit (if the price of the stock goes up), but we now also have the potential to lose money (if the price of the stock goes down).

There is a difficulty here in that we don't really have the flexibility to buy the stock at whatever price we want today (depending on our calculation of the future value of the stock), but can only buy at today's price.

One thing we can do (at least potentially, assuming there are sellers willing), is to

purchase an “option” to buy the stock at some fixed price at some specific time in the future. Let’s simplify things a bit, and assume that over the time period in question, the stock will not pay any dividends (in other words, our profit/loss will only depend on changes in the price of the stock).

Once a market in “options” is developed, a variety of things become possible. Not only can we purchase options to buy a stock at a given price at a given time in the future (a “call” option), but we can also purchase an option to sell a stock at a given price at a given time in the future (a “put” option). Note that an option protects us against an adverse change in the price of the stock. For example, if we purchase a “call” option, and the price of the stock goes down, we let the option expire, and we lose only the amount we paid for the option (the premium). We

are thus protected against large losses. More generally, if we buy both “put” and “call” options, we can “hedge” our bets, and (we believe) protect ourselves against large losses, at the price of limiting the amount of gain we might make.

Our task, then, is to develop a model that will allow us to determine (estimate?) the price we should be willing to pay for an option.

In order to develop our model, we will have to make a variety of assumptions, many of them “simplifying” assumptions. It is possible (likely?) that at least some of our assumptions will be unrealistic, but at least will allow us to do computations. This presents us with an interesting dilemma – if our model is unrealistic, we may make very bad decisions if we depend on the model, but, if we make the model “realistic,” it may be useless to us because we can’t do the computations. Apparently, such is life . . .

- For this example, we're going to develop (a version of) the Black-Scholes option pricing model.

We'll have to make a variety of assumptions. These will include:

1. There is a completely safe (e.g., "FDIC insured savings account") fixed rate asset available.
2. There are "frictionless" markets (i.e., we can buy or sell any instrument at any time in any amount).
3. There are no transaction costs.
4. No "arbitrage" (there are no financial instruments that provide "risk free" profits above the fixed rate asset).

The most critical assumptions we will have to make concern the form of variability of the “price” of the stock on which we will be buying our options.

1. Variability is continuous (and possibly even smooth?). This will allow us to work in continuous time.
2. The distribution is “stable” (i.e., the distribution of the variability does not change over time).
3. Increments are independent (i.e., variability does not depend on history – there is no “memory” in the distribution).
4. The distribution has a finite mean and finite variance.
5. Variability is “independent of price” (i.e., the “value” of a change in price does not depend on the specific current price).

Putting all of this together, we will assume that the stock price $x(t)$ gives us a continuous random variable

$$R(x, t) = \ln \left(\frac{x(t)}{x(0)} \right).$$

This random variable $R(x, t)$ will be the return on the stock at time t , associated with stock price $x(t)$. More specifically, we will assume that the price $x(t)$ satisfies the stochastic differential equation

$$dx(t) = \mu x(t) dt + \sigma x(t) dB_t$$

where B_t is Brownian motion, μ is the “drift,” and σ is the volatility. This is generally called *geometric Brownian motion*. This equation has the solution

$$x(t) = x(0) e^{\left(\left(\mu - \frac{\sigma^2}{2} \right) t + \sigma B_t \right)},$$

which is a log-normally distributed random variable with expected value $\langle x(t) \rangle = x(0) e^{\mu t}$, and variance $\text{Var}(x(t)) = x(0)^2 e^{2\mu t} (e^{\sigma^2 t} - 1)$.

The random variable $R(x, t)$ is normally distributed, with mean $(\mu - \sigma^2/2)t$ and variance $\sigma^2 t$.

We are interested in determining the current value of a financial instrument that will have a value in the future that depends on the price $x(t)$ (or return $R(x(t), t)$) of the underlying asset (stock). Let us call the value of this derived instrument $w(x, t)$. In the Black-Scholes case, $w(x, t)$ will be the value of a “call” option.

To understand this better, we will study “portfolios” of various financial instruments. So, suppose we form a portfolio by putting one unit of our money into the secure interest bearing asset, and an amount $-1/w_1$ (where $w_1 = (\partial w / \partial x)$) in a “call” option with strike price K at time T (i.e., at time T we can buy the stock a price K). Then the value of the portfolio will be $p = x - w/w_1$.

During a short period of time Δt , the value of the portfolio will change by $\Delta p = \Delta x - \Delta w/w_1$. We want to expand this formula, and fortunately there is a nice method (part of the *Ito calculus*) that allows us to write

$$\Delta w = \frac{\partial w}{\partial x} \Delta x + \frac{1}{2} \sigma^2 x^2 \frac{\partial^2 w}{\partial x \partial t} \Delta t + \frac{\partial w}{\partial t} \Delta t$$

(this is essentially the *chain rule* for *stochastic differentials*).

We then have

$$\Delta p = -\frac{1}{w_1} \left(\frac{1}{2} \sigma^2 x^2 w_{11} + w_2 \right) \Delta t$$

(where w_1, w_{11} , and w_2 are the appropriate partial derivatives, and σ^2 is a constant depending on w , essentially its variance or volatility).

Now we will use the “no arbitrage” assumption. Since Δp is an assured return, it must be that

$$\Delta p = r p \Delta t = r \left(x - \frac{w}{w_1} \right) \Delta t.$$

If we equate these two expressions for Δp , we get

$$-\frac{1}{w_1} \left(\frac{1}{2} \sigma^2 x^2 w_{11} + w_2 \right) \Delta t = r \left(x - \frac{w}{w_1} \right) \Delta t.$$

Dividing through by Δt , we can simplify to

$$w_2 + rxw_1 + \frac{1}{2} \sigma^2 x^2 w_{11} - rw = 0.$$

This is the Black-Scholes differential equation (B-S PDE) for $w(x, t)$. It has boundary conditions:

1. $w(0, t) = 0$ for all t .
2. $w(x, t) \sim x$ as $t \rightarrow \infty$.
3. $w(x, T) = \max(x - K, 0)$ (recall K is the strike price at time T).

- Our next task is to develop a solution to the B-S equation. We'll start by making some changes of variables. We'll reverse the order of time (with some normalization), since the “no arbitrage” rule allows us to use $t = T$ for a boundary condition. We'll also move into a “logarithmic” mode (since the riskless asset grows exponentially), and normalize with respect to K (the strike price) – we shouldn't worry about the units of the price (e.g., dollars or pounds):

$$\begin{aligned}\tau &= \frac{\sigma^2}{2}(T - t) \\ z &= \ln(x/K) \\ v &= \frac{w}{K}\end{aligned}$$

Now we do some calculations:

$$\frac{\partial t}{\partial \tau} = -\frac{2}{\sigma^2}$$

and

$$\frac{\partial x}{\partial z} = x.$$

Then we have

$$\begin{aligned}\frac{\partial v}{\partial \tau} &= \frac{1}{K} \frac{\partial w}{\partial \tau} = \frac{1}{K} \left(\frac{\partial w}{\partial x} \frac{\partial x}{\partial \tau} + \frac{\partial w}{\partial t} \frac{\partial t}{\partial \tau} \right) \\ &= \frac{1}{K} \left(-\frac{2}{\sigma^2} \right) w_2\end{aligned}$$

and

$$\begin{aligned}\frac{\partial v}{\partial z} &= \frac{1}{K} \frac{\partial w}{\partial z} = \frac{1}{K} \left(\frac{\partial w}{\partial x} \frac{\partial x}{\partial z} + \frac{\partial w}{\partial t} \frac{\partial t}{\partial z} \right) \\ &= \frac{1}{K} x w_1.\end{aligned}$$

Using this, we get

$$\begin{aligned}\frac{\partial^2 v}{\partial z^2} &= \frac{1}{K} \frac{\partial x w_1}{\partial z} = \frac{1}{K} \left(\frac{\partial w_1}{\partial z} x + w_1 \frac{\partial x}{\partial z} \right) \\ &= \frac{1}{K} \left(\frac{\partial w_1}{\partial x} \frac{\partial x}{\partial z} x + \frac{\partial w_1}{\partial t} \frac{\partial t}{\partial z} x + x w_1 \right) \\ &= \frac{1}{K} (x^2 w_{11} + x w_1).\end{aligned}$$

Now we'll do some rearranging of the B-S equation, and then put in what we have gotten from the change of variables. Starting from

$$w_2 + rxw_1 + \frac{1}{2}\sigma^2 x^2 w_{11} - rw = 0.$$

we multiply by $\frac{-2}{K\sigma^2}$

$$\frac{-2w_2}{K\sigma^2} + \frac{-2}{K\sigma^2}rxw_1 - \frac{1}{K}x^2 w_{11} + \frac{2}{K\sigma^2}rw = 0.$$

We rearrange, and add/subtract appropriate terms:

$$\begin{aligned} \frac{-2w_2}{K\sigma^2} &= \frac{x^2 w_{11}}{K} + \frac{2rxw_1}{K\sigma^2} - \frac{2rw}{K\sigma^2} \\ \frac{-2w_2}{K\sigma^2} &= \frac{x^2 w_{11}}{K} + \frac{w_1 x}{K} + \frac{2rxw_1}{K\sigma^2} + \frac{w_1 x}{K} - \frac{2rw}{K\sigma^2} \end{aligned}$$

or,

$$\begin{aligned} \frac{-2w_2}{K\sigma^2} &= \frac{1}{K}(x^2 w_{11} + xw_1) \\ &\quad + \left(\frac{2r}{\sigma^2} - 1\right) \frac{xw_1}{K} - \frac{2rw}{K\sigma^2} \end{aligned}$$

Then, putting in the change of variables, we have:

$$\frac{\partial v}{\partial \tau} = \frac{\partial^2 v}{\partial z^2} + (k - 1) \frac{\partial v}{\partial z} - kv$$

where $k = \frac{2r}{\sigma^2}$, and we have the boundary condition $v(z, 0) = \max(e^z - 1, 0)$.

This is close to a heat equation, but we need one more change of variables. If we let, for some constants α, β ,

$$u(z, \tau) = e^{\alpha z + \beta \tau} v(z, \tau)$$

we will have

$$\begin{aligned} \beta u + \frac{\partial u}{\partial \tau} &= \alpha^2 u + 2\alpha \frac{\partial u}{\partial z} + \frac{\partial^2 u}{\partial z^2} \\ &\quad + (k - 1) \left(\alpha u + \frac{\partial u}{\partial z} \right) - ku \end{aligned}$$

If we choose

$$\alpha = -\frac{1}{2}(k - 1)$$

and

$$\beta = \alpha^2 + (k - 1)\alpha - k = -\frac{1}{4}(k + 1)^2,$$

then we are left with the heat equation:

$$\frac{\partial u}{\partial \tau} = \frac{\partial^2 u}{\partial z^2} .$$

At this point we'll just appeal to standard methods for solving the heat equation (e.g., Fourier series methods). The general solution will be of the form:

$$u(z, \tau) = \frac{1}{\sigma\sqrt{2\pi\tau}} \int_{-\infty}^{\infty} u_0(y) e^{-(z-y)^2/(2\sigma^2\tau)} dy.$$

Undoing the changes of variable, we get:

$$w(x, t; K, T, r) = x\Phi(d_1) - Ke^{-r(T-t)}\Phi(d_2) ,$$

where Φ is the standard normal cumulative distribution function

$$\Phi(x) = \frac{1}{\sqrt{2\pi}} \int_{-\infty}^x e^{(-\frac{u^2}{2})} du$$

and

$$d_1 = \frac{\ln(x/K) + (r + \frac{1}{2}\sigma^2)(T - t)}{\sigma\sqrt{T - t}}$$
$$d_2 = \frac{\ln(x/K) + (r - \frac{1}{2}\sigma^2)(T - t)}{\sigma\sqrt{T - t}}$$

càdlàg

Diffusion and Flux ←

- Now let's suppose we have many "random walkers" in some environment, and we observe the behavior of the collection of walkers. If the walkers are tiny particles in a fluid, being buffeted about by the molecules of the fluid, this process is often called *brownian motion* (after the Scottish botanist Robert Brown, who observed the jittery motion of pollen grains and moss spores in water). If the density distribution of the walkers is non-uniform, we can expect to observe flows in the density distribution over time.

As observed above, in the continuous limit, we have the "heat equation" as the PDE governing the (probability) density distribution of the walkers. In one dimension, this is:

$$\frac{\partial P(x, t)}{\partial t} = D * \frac{\partial^2 P(x, t)}{\partial x^2}$$

More generally, in higher dimensions we will have:

$$\begin{aligned}\frac{\partial P(\vec{r}, t)}{\partial t} &= D * \Delta P(\vec{r}, t) \\ &= D * \nabla^2 P(\vec{r}, t)\end{aligned}$$

where

$$\Delta = \nabla^2 = \nabla \cdot \nabla = \sum_{k=1}^n \frac{\partial^2}{\partial x_k^2}$$

is the Laplacian operator.

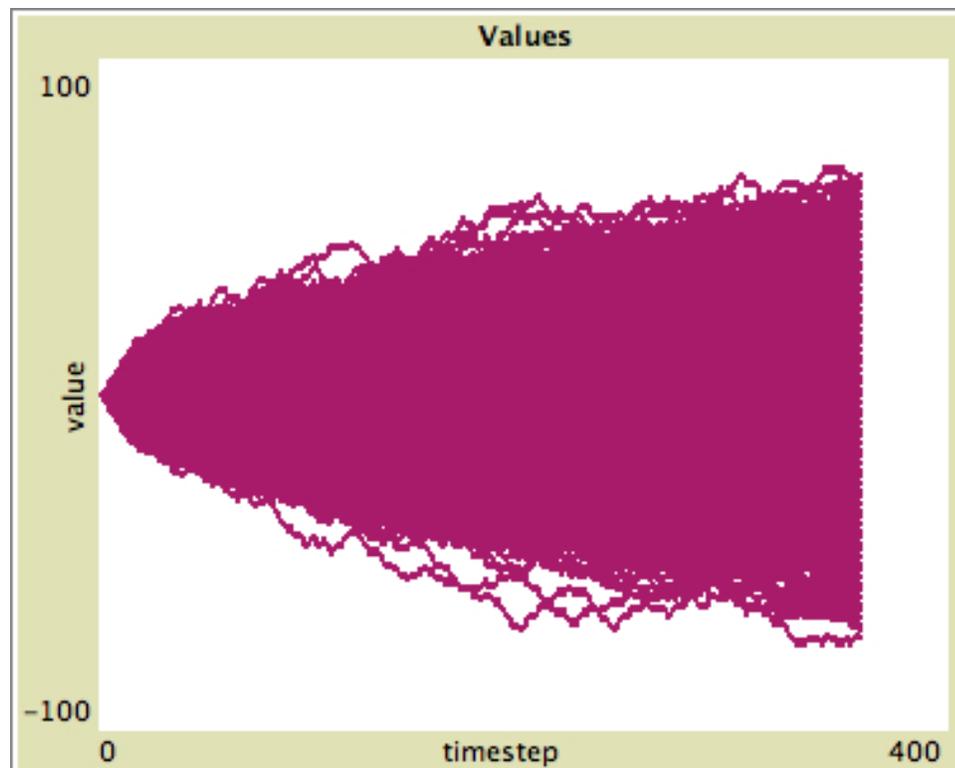
If the diffusion coefficient depends on the position and/or density, we have:

$$\frac{\partial P(\vec{r}, t)}{\partial t} = \nabla \cdot \left(D(P, \vec{r}) \nabla P(\vec{r}, t) \right).$$

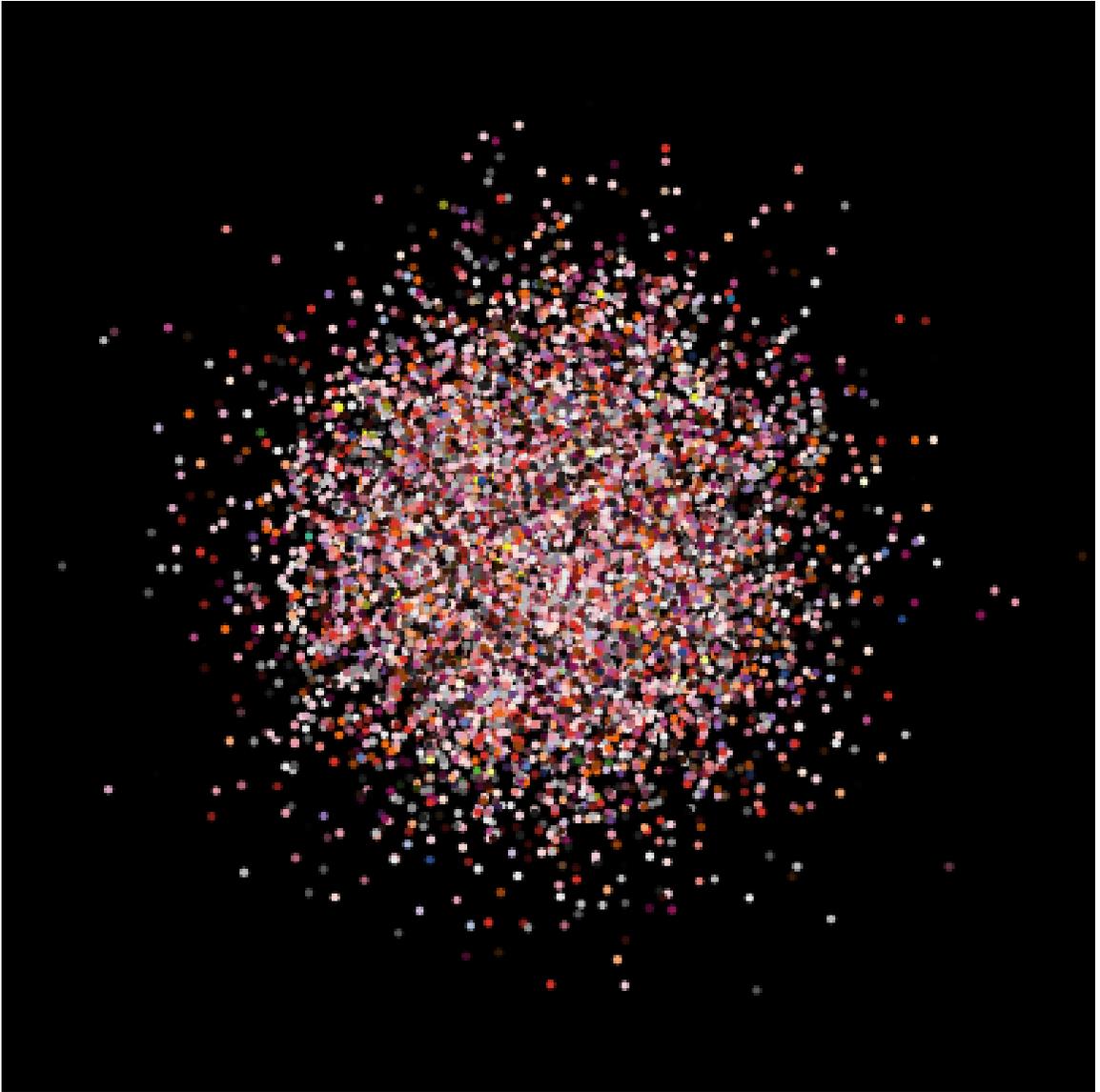
In the case of constant diffusion coefficient (D), this is a linear PDE. In the more general case, we are working with a nonlinear PDE.

Given this framework, we can explore various boundary conditions and special cases.

For example, if the walkers all start at location $\vec{0}$, over time they will map out a sample of a normal distribution with mean position $\vec{0}$ and mean square displacement $\langle |\vec{r}|^2 \rangle = q_i Dt$, where q_i depends on the dimension ($q_i = 2, 4, 6$ in dimensions 1, 2, 3). In 1 dimension, it is easy to see the \sqrt{t} mean displacement:

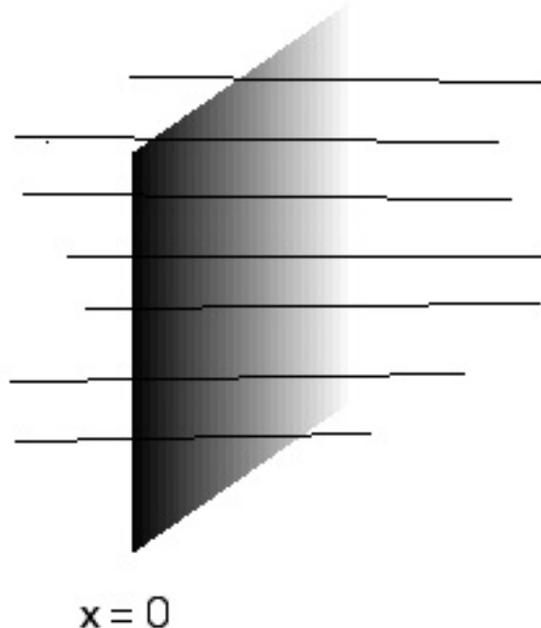


Here is a 2-dimensional example:



- Now, suppose that there are variations in the distribution of the walkers. Over time, we will see a “flow” in the distribution. We can call the rate of this flow the “flux” of the distribution.

Consider a 1-dimensional example. Suppose that the walkers live in three dimensions, but are constrained to walk along lines parallel to the x axis. We would like to calculate the flux through the plane $x = 0$.



Assume that the walkers move left or right a distance δ with probability $1/2$ in each time step τ . Then between time t and $t + \tau$, some walkers will cross the plane $x = 0$ from left to right, and some from right to left. Only those walkers within distance δ of $x = 0$ can cross $x = 0$ during one time step. If $N(l)$ and $N(r)$ are the number of walkers within δ to the left/right of $x = 0$, then the expected net number of particles crossing $x = 0$ to the right will be $1/2N(l) - 1/2N(r)$.

Doing some manipulations, the flux through $x = 0$ will be

$$J_x = -\frac{\delta^2}{2\tau} \frac{1}{\delta} \left[\frac{N(r)}{A\delta} - \frac{N(l)}{A\delta} \right]$$

where A is an area. Taking continuous limits, this boils down to

$$J_x = -D \frac{\partial P}{\partial x}$$

(the negative means the flow is from higher to lower concentrations). This is usually called *Fick's first law of diffusion*.

We will have, in general,

$$J_x = -D \frac{\partial P}{\partial x}$$

$$J_y = -D \frac{\partial P}{\partial y}$$

$$J_z = -D \frac{\partial P}{\partial z}$$

and, for radial flow from a central point,

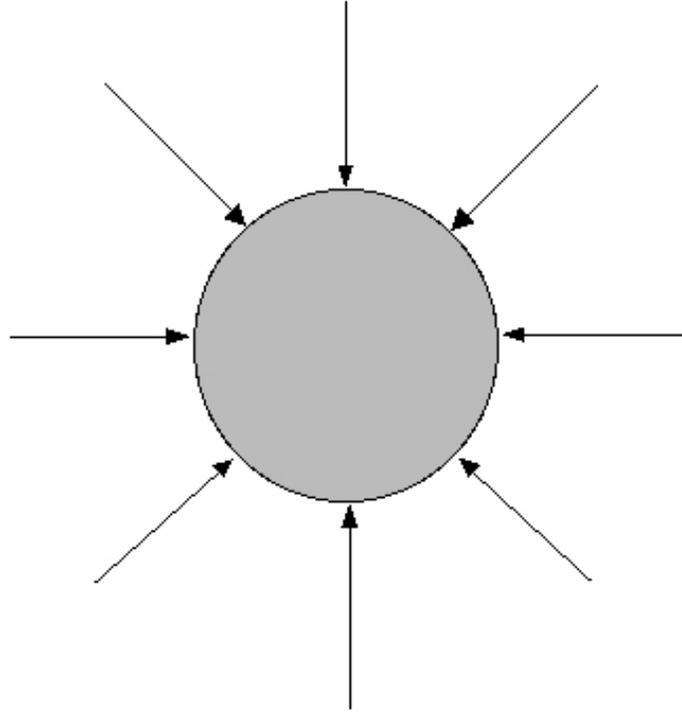
$$J_r = -D \frac{\partial P}{\partial r}.$$

Biology: Limits of Growth



- Let's look at an application of Fick's First Law to limits to growth. We will consider an immobile cell that acquires its nutrients through absorption of nearby diffusing resources. For simplicity, we will assume that the cell is spherical, that we only need to consider a single resource, which is (initially) uniformly distributed through the medium in which the cell lives, and that the cell's membrane is completely effective in removing the resource from the medium at its surface. We will also assume that the pool in which the cell is living is so large that the concentration of nutrient far from the cell is essentially constant. We will assume that everything else is "simple" also, as needed . . .

Here's a general picture of the situation:



Let the radius of the cell be r_c , the concentration of nutrient far from the cell is P_∞ , and the cell is at the origin. At the steady state (after the cell has been in the pool for a long time), we will have $\frac{d(P)}{dt} = 0$, and therefore, outside the cell, we will have

$$\begin{aligned} 0 &= \nabla^2 P \\ &= \frac{1}{r^2} \frac{d}{dr} \left(r^2 \frac{d(P)}{dr} \right) \end{aligned}$$

We have the boundary conditions that $P(r_c) = 0$, and $P(\infty) = P_\infty$. With these conditions, the steady state concentration will be

$$P(r) = P_\infty * \left(1 - \frac{r_c}{r}\right),$$

and the (radial) flux will be

$$J_r = -D * P_\infty * \frac{r_c}{r^2}.$$

The total rate of flow of resource into the cell (the *current*) will be

$$\begin{aligned} I &= Area * (-Flux) \\ &= 4\pi r_c^2 (-J_r) \\ &= 4\pi r_c^2 D P_\infty \frac{r_c}{r_c^2} \\ &= 4\pi D P_\infty r_c. \end{aligned}$$

The inflow thus will increase linearly with increase in radius of the cell. This may at first seem somewhat counter intuitive – while the surface area of the cell grows as the square of the radius, the inflow of resources only grows linearly with the radius.

The linear increase in inflow will impose limits on the possible growth of a cell.

As a first approximation, we can estimate that the metabolic needs of a cell depend on its total mass, hence on its volume, and hence on r_c^3 . We can write the metabolic need of the cell as

$$\text{Metabolic need} = \frac{4\pi r_c^3 M}{3}$$

where M expresses the metabolic resource consumption rate in moles per second per cubic meter. The maximum size the cell can attain will be reached when the resource inflow is equal to the metabolic need, i.e., when

$$4\pi DP_\infty r_c = \frac{4\pi r_c^3 M}{3}.$$

We can solve this equation for r_c :

$$r_c = \sqrt{\frac{3DP_\infty}{M}}.$$

A particular example of this phenomenon is phytoplankton, which use bicarbonate ions (HCO_3^-) as a source of carbon for photosynthesis. The metabolic need is about one mole of bicarbonate per second per cubic meter of cell cytoplasm, the concentration of bicarbonate in seawater is about 1.5 moles per cubic meter, and the diffusion coefficient for bicarbonate in water is about $1.5 * 10^{-9} m^2 s^{-1}$. Putting these numbers into the equation, we get

$$\begin{aligned}
 r_c &= \sqrt{\frac{3DP_\infty}{M}} \\
 &= \sqrt{\frac{3 * 1.5 * 10^{-9} m^2 s^{-1} * 1.5 \text{ mole} * m^{-3}}{1 \text{ mole} s^{-1} m^{-3}}} \\
 &= \sqrt{3 * 1.5 * 1.5 * 10^{-9} m^2} \\
 &= \sqrt{6.75 * 10^{-9} m^2} \\
 &= \sqrt{6,750 * 10^{-12} m^2} \\
 &\approx 80 \mu m.
 \end{aligned}$$

This is a fairly typical size for phytoplankton. Note that an individual

cell could be larger than this, but its photosynthesis rate would be constrained.

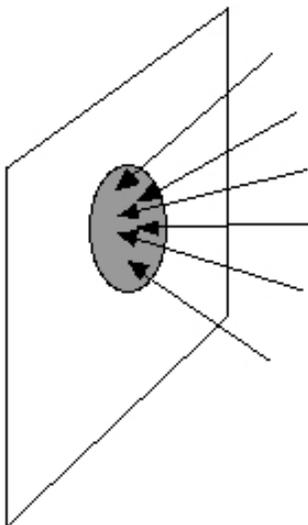
The increase in metabolic need generally does not increase quite as fast as the increase in mass (volume). Evidence points to the increase being more like $M^{3/4}$. This will make some minor differences in the details, but the general principle of limits to growth will still hold . . .

This example, and the next one on receptor/channels, are explored more fully in the books *Random Walks in Biology* by Berg, and *Chance in Biology* by Denny and Gaines.

Biology: Receptors, Channels, and Flow ←

- For our next example, we'll look at more restricted flows into a cell. This might be flow into a receptor, or through a channel.

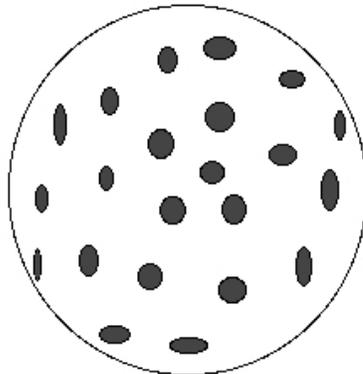
We start by looking at diffusive flow into a circular disk of radius r . We assume that the disk is in the plane boundary of a semi-infinite medium. The medium contains a (diffusing) resource, absorbed by/through the disk.



Assuming that the concentration of the resource far away from the disk is P_∞ , the diffusion coefficient of the resource in the medium is D , and the radius of the disk is r_d , then the current into the disk will be given by:

$$I_d = 4Dr_dP_\infty.$$

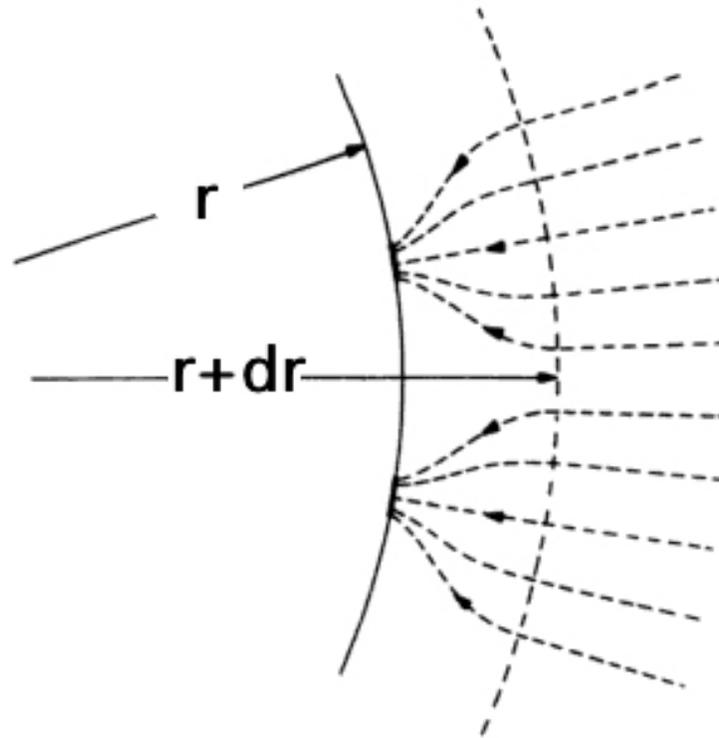
We are actually thinking of the bounding plane as being the cell membrane, with the radius of the disk small in comparison with that of the cell. Our goal now is to understand the behavior of the system if there are many disk-like patches on the surface of the cell.



The simple assumption that the total absorption of many patches is just the sum of the absorptions of the individual patches can't be right. For example, if the radius of the sphere is 1,000 times the radius of a disk/patch (i.e., $r_c = 10^3 r_d$), and we cover the surface of the sphere with patches, we would use approximately 4,000,000 patches. The naive estimate, using our formula for the flow through a patch, would be that the total flow through the $4 * 10^6$ patches would be $4 * 10^6 * 4DP_\infty r_d$. But, from the previous section, we know that we should expect the flow to be more like $4\pi DP_\infty 10^3 r_d$, so we are off by a factor of more than 1,000.

We'll have to look a little more carefully at what is happening.

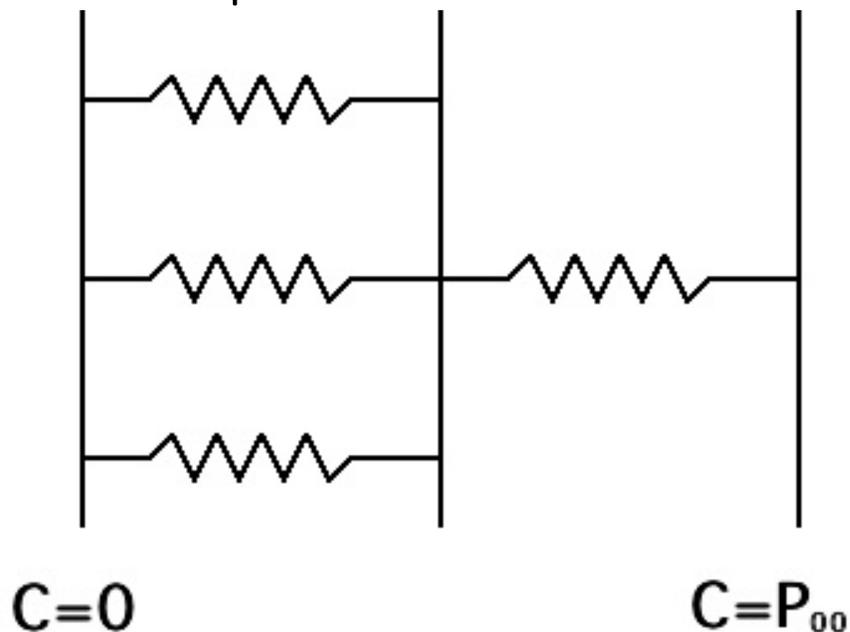
Let's consider the situation if we had a couple of the disks near each other on the surface of a sphere:



The lines of flux are radial outside $r + dr$. The concentration of resource is 0 at the surface of the sphere, P_∞ outside the larger sphere of radius $r + dr$, and some intermediate value in between.

We can analyze the system through analogy with electrical potential. It is

equivalent to a system in which electricity flows through a resistive medium to conductive patches on the sphere, with the resistive medium at potential P_∞ and the patches at potential 0. By Ohm's Law, the current through a resistor is equal to the potential drop between its terminals divided by its resistance. In our situation, at steady state diffusion we have $I = C/R$ where I is the diffusion current, C is the concentration difference, and R is the diffusion resistance. The patches will share the inflowing resource, like resistors in parallel:



The resistance for the sphere will be $R_c = \frac{1}{4\pi D r_c}$. The resistances for the disks will be $R_d = \frac{1}{4D r_d}$. The total resistance of the circuit (with N disks on the surface of the sphere) will be

$$\begin{aligned} R &= R_{r_c+dr_c} + \frac{R_d}{N} \\ &= \frac{1}{4\pi(r_c + dr_c)} + \frac{1}{4DNr_d}. \end{aligned}$$

Since $dr_c \ll r_c$, we get the reasonable approximation that

$$\begin{aligned} R &\approx \frac{1}{4\pi r_c} + \frac{1}{4DNr_d} \\ &= \frac{1}{4\pi r_c} \left(1 + \frac{\pi r_c}{Nr_d} \right) \\ &= R_{r_c} \left(1 + \frac{\pi r_c}{Nr_d} \right) \end{aligned}$$

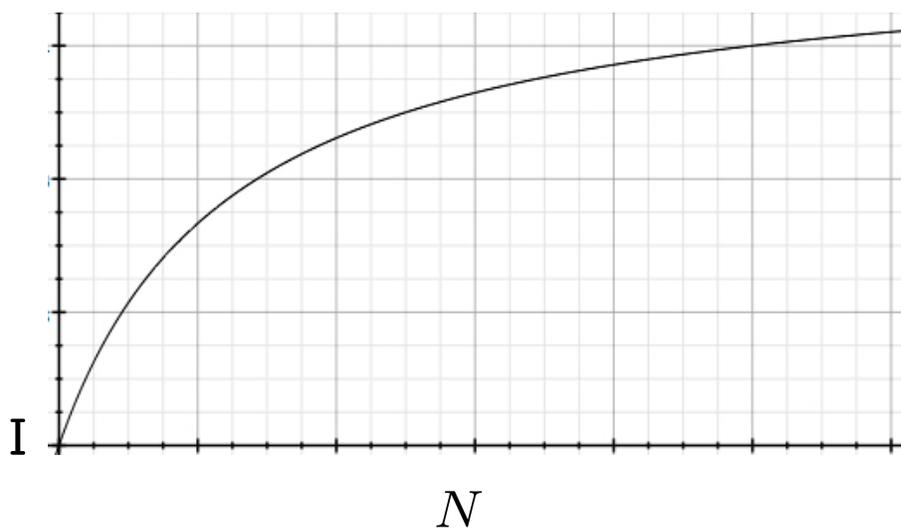
The diffusion resistance for a sphere with N disks on it will be greater than the resistance of a sphere by a factor of $1 + \frac{\pi r_c}{Nr_d}$.

The current through the patches into the cell will be smaller than the current into a sphere completely covered with patches by the same factor:

$$I = \frac{4\pi D r_c P_\infty}{1 + \frac{\pi r_c}{N r_d}}.$$

For small N , with the patches widely separated from each other, the current will increase as $4N D r_d P_\infty$. For large N (the cell nearly covered with patches), the current will be (asymptotically) $4\pi D r_c P_\infty$.

Here is a general picture of the growth of the current with increasing N :



- Given this relationship, we can see that the diffusion current through the patches will reach $\frac{1}{2}$ its maximum when $N = \frac{\pi r_c}{r_d}$. This number can be surprisingly small.

As an example, suppose the cell has radius $r_c = 5\mu\text{m}$, and the receptor “disks” are proteins with binding sites with radius $r_d \approx 10\text{\AA}$. This cell can absorb the corresponding resource at $\frac{1}{2}$ its maximum when $N \approx 15,700$. Only a small fraction of the surface area of the cell is covered with receptors, that is

$$\frac{N\pi r_d^2}{4\pi r_c^2} = 1.6 * 10^{-4}.$$

The typical distance between receptors will be roughly

$$\left(\frac{4\pi r_c^2}{N}\right)^{1/2} = 0.14\mu\text{m},$$

or approximately 140 times the binding site radius.

A consequence of this is that a cell can have many varieties of receptors or channels, each working at 1/2 their maximum, as long as the receptors are specific to their particular resource and don't interfere with each other.

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