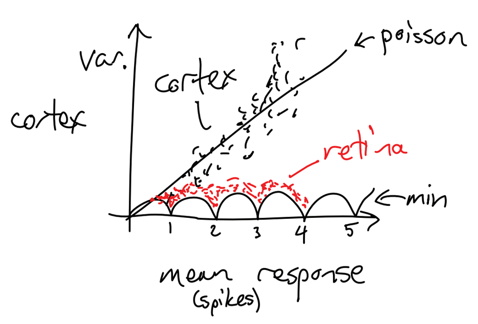
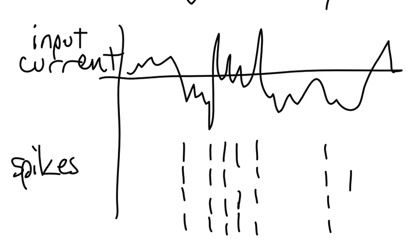
Stochastic Linear Networks

Neurons are noisy.

"Fano factor" $= \frac{\sigma^2}{\mu} \sim 1$ in cortex



Neurons are reliable: if you inject the same current many times, you get nearly the same spikes



How to reconcile? "Noisy" responses come from other neural responses. Let's develop tools for analyzing this.

Linear stochastic networks

$$\tau \dot{r}_i = -r_i + \sum_j W_{ij} r_j + h_i(t)$$

h_i is white noise

$\langle h_i \rangle = 0$

$\langle h_i(t) h_j(t') \rangle = c\,\delta_{ij}\,\delta(t-t')$

In diagonal basis of A, $A = U \Lambda U^{-1}$:

$$\tau \dot{\tilde{r}}_k = -\tilde{r}_k + \lambda_k \tilde{r}_k + \tilde{h}_k \qquad \lambda_k: \text{eigenvalue}, \quad \tilde{r}: U^{-1} r$$

$$\dot{\tilde{r}}_k = -\underbrace{\left(\frac{1-\lambda_k}{\tau}\right)}_{1/\tau_k}\tilde{r}_k + \tilde{h}_k$$

$1/\tau_k$: effective time constant for mode k

$$\tilde{r}_k(t) = e^{-t/\tau_k}\,\tilde{r}_k(0) + \int e^{-\frac{t-t'}{\tau_k}}\,\tilde{h}_k(t')\,dt'$$

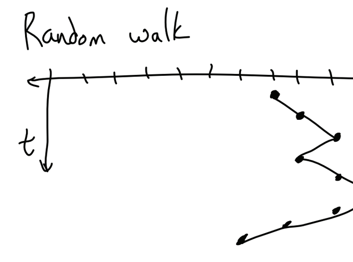
Recall solution to linear network:

$$r(t) = e^{At} r(0) + \int_{-\infty}^{t} e^{A(t-\tau)} h(\tau)\,d\tau$$

Easier in discrete time

1D

Random walk



$x_{t+1} = x_t + a_t$

$a_t = \pm 1$

$\langle a_t \rangle = \mu$

$\langle \delta a_t^2 \rangle = \langle a_t^2 \rangle - \langle a_t \rangle^2 = \mu - \mu^2$

$\langle x_{t+1} - x_t \rangle = \mu \Rightarrow \langle x_t \rangle = \mu t$

$\langle x_{t+1}^2 \rangle - \mu^2 t^2 = \langle x_t^2 \rangle - \mu^2 t^2 + \langle a_t^2 \rangle =$

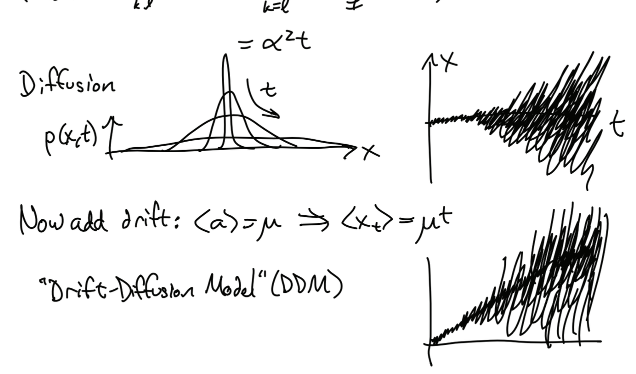
$x_{t+1} = x_t + a_t = \sum_{t'}^{t} a_{t'} \qquad \langle a_t \rangle = 0, \quad \langle a_t^2 \rangle = \alpha^2$

Take statistics:

$\langle x_{t+1} \rangle = \sum \langle a \rangle = 0$

$\langle x_{t+1}^2 \rangle = \sum_{k\ell}^{t,t} \langle a_k a_\ell \rangle = \sum_{k=\ell}^{t} \langle a_k^2 \rangle + \sum_{\neq}^{t,t} \langle a_k \rangle \langle a_\ell \rangle = \alpha^2 t$

Diffusion



Now add drift: $\langle a \rangle = \mu \Rightarrow \langle x_t \rangle = \mu t$

"Drift-Diffusion Model" (DDM)

Now add decay:

$x_{t+1} = b x_t + a_t$

$\langle x_{t+1} \rangle = b \langle x_t \rangle + \langle a_t \rangle$

Assume stationary: $p(x_{t+1}) = p(x_t)$

Find mean and variance

$\langle x_{t+1} \rangle = \langle x_t \rangle = \bar{x}$

$\bar{x} = b\bar{x} + \mu \rightarrow \boxed{\bar{x} = \frac{\mu}{1-b}}$

$\langle x_{t+1}^2 \rangle = \langle (b x_t + a_t)^2 \rangle$

$= b^2 \langle x_t^2 \rangle + 2b \langle a_t x_t \rangle + \langle a_t^2 \rangle$

$\langle x^2 \rangle = b^2 \langle x^2 \rangle + 2b\mu \frac{\mu}{1-b} + \alpha^2 + \mu^2$

$\langle x^2 \rangle (1-b^2) = \alpha^2 + \mu^2 \left(1 + \frac{2b}{1-b}\right)$

$\frac{1-\cancel{b}+\cancel{2}b}{1-b} = \frac{1+b}{1-b}$

$\langle x^2 \rangle = \frac{\alpha^2}{1-b^2} + \mu^2 \frac{\cancel{1+b}}{(1-b)(1-b)\cancel{(1+b)}}$

$\langle x^2 \rangle - \bar{x}^2 = \boxed{\langle \delta x^2 \rangle = \frac{\alpha^2}{1-b^2}}$

$\left(\frac{\mu}{1-b}\right)^2$

Independent of μ

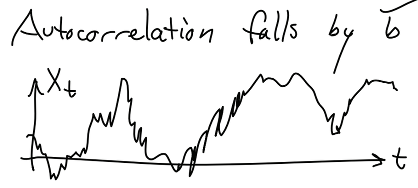
Compute Autocorrelation

$\langle x_{t+1} x_t \rangle = b \langle x_t^2 \rangle + \langle a_t x_t \rangle$

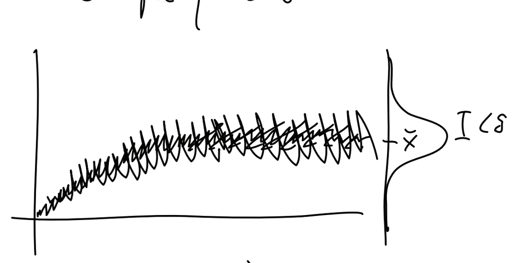
$\langle \delta x_{t+1} \delta x_t \rangle = b\left(\frac{\alpha^2}{1-b^2} + \frac{\mu^2}{(1-b)^2}\right) + \mu \frac{\mu}{1-b} - \frac{\mu^2}{(1-b)^2}$

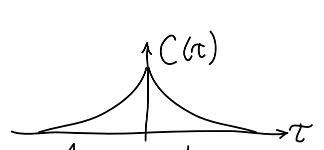
$= b\frac{\alpha^2}{1-b^2} + \mu^2 \cancel{\frac{b(1+b) + (1+b)(1-b) - (1+b)}{(1-b)^2(1+b)}}^{\,0}$

Autocorrelation falls by b each time step



Sample process





Autocorrelation

$C(\tau) = \langle x_t x_{t+\tau} \rangle - \bar{x}^2$

Now in continuous time

$x_{t+1} = b x_t + a_t$

$x_{t+1} - x_t = (b-1) x_t + a_t$

$dx_t = -(1-b) x_t + (\mu + \sigma\, dW_t)$

$dx_t = \frac{dt}{\tau}(\bar{x} - x_t) + \sigma\, \underbrace{dW_t}$

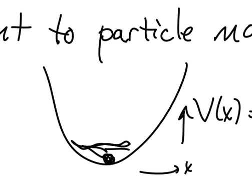
$\tau \dot{x} = -x + h$

technical: W_t is a 'Wiener process' aka Brownian motion

Delicacy with limit $\lim_{dt \to 0}$ required

"Ornstein-Uhlenbeck Process" (OU process)

Equivalent to particle moving in a harmonic well



$V(x) = \frac{x^2}{2}$ so $F = -V' = -x$

decay = restoring force

When we track only the probability distribution instead of one stochastic realization, we obtain the Fokker-Planck equation:

$$\frac{\partial p}{\partial t} = \theta \frac{\partial}{\partial x}\left[(x-\mu)p\right] + D\frac{\partial^2 p}{\partial x^2} \quad \text{for } p(x,t)$$

$1/\tau$ Drift Diffusion

This is a deterministic partial differential eqn that describes a stochastic ordinary diff eqn.

Can solve by taking moments. Take $\mu = 0$:

$$\int dx\, x \frac{\partial p}{\partial t} = \frac{\partial}{\partial t}\langle x \rangle = \theta \int \underbrace{x}_{u} \underbrace{\frac{\partial}{\partial x} xp\, dx}_{dv} + D \int x \frac{\partial^2 p}{\partial x^2} dx$$

$$= \theta\left[uv\Big|_{-\infty}^{\infty} - \int v\, du\right] + \cdots \nearrow 0$$

$$= \theta\left[\cancel{x^2 p\Big|_{-\infty}^{\infty}}^{\,0} - \int xp\, dx\right]$$

$$\frac{\partial}{\partial t}\langle x \rangle = -\theta \langle x \rangle \Longrightarrow \langle x \rangle = x_0 e^{-\theta t}$$

Similarly: $\frac{\partial \langle x^2 \rangle}{\partial t} = -2\theta \langle x^2 \rangle + 2D \Rightarrow \langle x^2 \rangle = \frac{D}{\theta}\left(1 - e^{-2\theta t}\right)$

Short time: Consider $x_0 = 0$, $t \ll \frac{1}{\theta}$. Then $\langle x \rangle = 0$, $\langle x^2 \rangle \approx 2Dt \longrightarrow$ unrestricted random walk

long time: Equilibrium distribution

$p(x,t) \propto e^{-\frac{2\theta}{2\sigma^2}(x-\mu)^2}$ Gaussian

all time: Starting from $p(x,0) = \delta(x - x_0)$

$$p(x,t) \propto \exp\left[-\frac{\theta}{2D}\frac{(x - x_0 e^{-\theta t})^2}{1 - 2e^{-2\theta t}}\right]$$

Multivariate

Same dynamics apply for each mode.

But in general, modes will be correlated.

$$dX_t = AX_t + B + C\,dW_t \qquad \left(\Sigma_w = CC^T \text{ "cholesky decomposition"}\right)$$

cannot always diagonalize both simultaneously!

Try to express using independent dW_t:

$C^{-1} dX_t = C^{-1} A C C^{-1} X_t + C^{-1} B + dW_t$

$dX_t' = A' X_t' + B' + dW_t$

But now we try to solve for dynamics,

$U^{-1} dX' = U^{-1} U \Lambda U^{-1} X' + U^{-1} B' + U^{-1} dW$

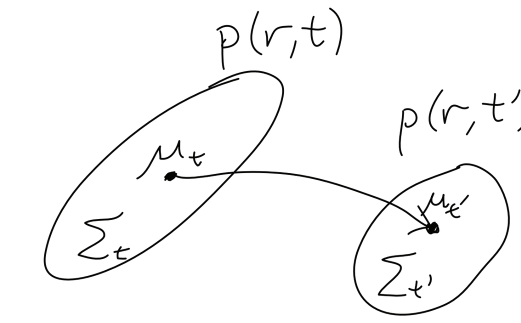
$d\tilde{X} = \Lambda \tilde{X} + \tilde{B} + d\tilde{W}$

correlated again!

Dynamic of mean are easy: $\dot{\bar{r}} = A\bar{r} + B$

Dynamics of Covariance are hard (not solvable analytically): $\dot{\Sigma}_r = A \Sigma_r A^T + CC^T$

Intuition



What if we don't measure r directly, but only via a meavurement matrix with additive noise?

Then we can use a Kalman filter, which assumes Linear dynamics, Gaussian signal + noise

Nonlinear networks

$\tau \dot{r} = -r + f(Wr + I)$

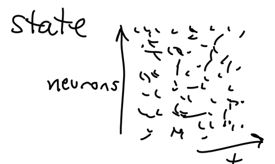
Clearly $r = 0$ is a fixed point, but it may be unstable.

Consider $r \neq 0$.

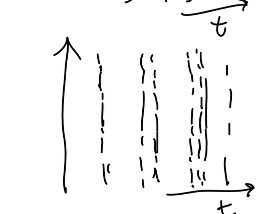
If f is sufficiently nonlinear then r will be non-gaussian.

However, for some W, the central limit theorem ensures that Wr is gaussian — even uncorrelated!

for example, the Asynchronous state when neurons act independently



versus the Synchronous state when neurons are correlated — epilepsy!



We can then use methods of stochastic nets to understand the behavior of such nonlinear networks.