Population Density Models.

* Nykamp + Tranchina, JCNS *
2000

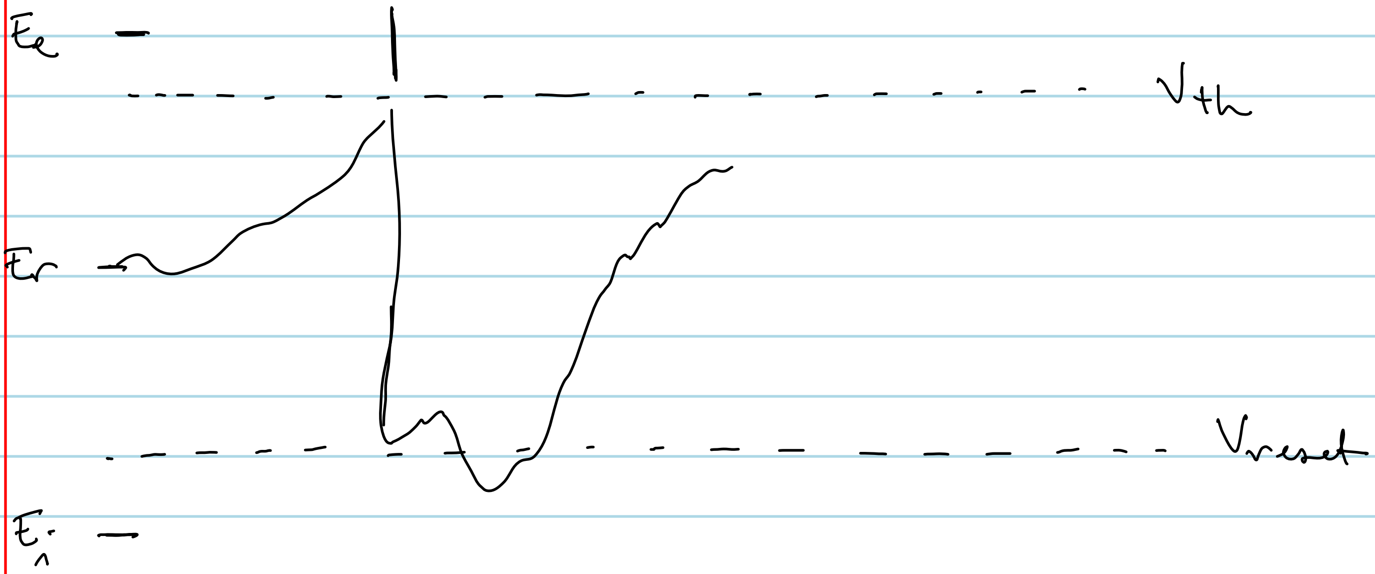
Gerstner et al, Ch. 13.

- Leaky Integrate + Fire Neuron with...
  - leak conductance g_r, leak reversal potential E_r
  - Excitatory syn. inputs $g_e(t)$, " " E_e
  - Inhibitory " " $g_i(t)$, " " E_i

$$C\dot{V} = g_r(E_r - V) + g_e(t)(E_e - V) + g_i(t)(E_i - V)$$

$\div$ by g_r, let $\tau = \frac{C}{g_r}$, $G_e(t) = \frac{g_e}{g_r}$, $G_i = \frac{g_i}{g_r}$

$$\tau\dot{V} = (E_r - V) + G_e(t)(E_e - V) + G_i(t)(E_i - V)$$



- Fast (δ-fn) E, I synaptic inputs

Consider 1 input, $G_e(t) = A_e^k \, \delta(t - T_e^k)$

Solve LIF equation, $v(T_e^{k+}) - V(T_e^{k-}) = \Delta V$

$$= \left(1 - e^{-\Gamma_e^k}\right)\left[E_e - V(T_e^{k-})\right],$$ where

$$\Gamma_e^k = A_e^k/\tau.$$

In limit $A_e^k \to \infty$, (strong-synapse), $\Delta V = E_e - V(T_e^{k-})$,

ie jump all the way → E_e reversal potential:
Makes sense!

- FACT! Synapses have stochastic amplitudes. Define VIA complementary CDFs...

$$\Pr\left(\Gamma^*_{e/i} > x\right) = \tilde{F}_{\Gamma^*_{e/i}}(x)$$

where $\Gamma^*_{e/i} = 1 - \exp\left(-\Gamma^k_{e/i}\right)$

And... $T^k_{e/i}$ are Poisson processes w/ rates ν_i

• POPULATION DENSITY: •

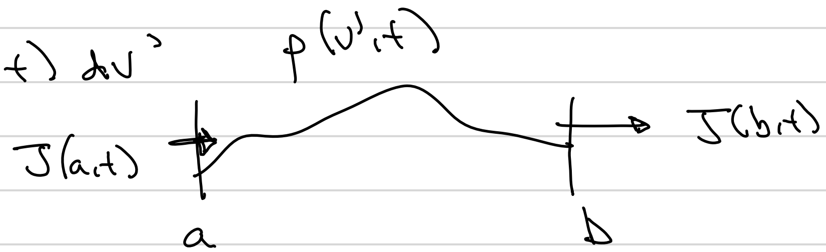
Consider one neuron evolving w/ above ...

$Pr(V(t) \in (v, v+dv)) = p(v,t)\,dv$

(OR ... for Population of identical, indep. neurons ... $= Pr(V(t) \in (v, v+dv))$, for neuron chosen at random.

$=$ Fraction of neurons with $V(t) \in (v, v+dv)$)

· $Pr(V(t) \in (a,b)) = \int_a^b p(v',t)\,dv'$



PROBABILITY

· Flux $J(a,t)$: proba. $V(t)$ is below a at time t + above a at $t+dt$

− " " " above " " " " + below " " "

= $J(a,t)\,dt$.

(can be + or −)

$$\frac{\partial}{\partial t}\int_a^b p(v',t)\,dv' = J(a,t) - J(b,t)$$, if $v_{reset} \notin (a,b)$

$$\frac{\partial}{\partial t}\int_a^v p(v',t)\,dv' = J(a,t) - J(v,t)$$; Take $\frac{\partial}{\partial v}$

$$\frac{\partial}{\partial t} p(v,t) = -\frac{\partial}{\partial v} J(v,t)$$

What's missing? Still need to ...

Incorpoate neural firing and reset:

- FIRING RATE $r(t) = J(V_{th}, t)$

- Reset: if $V_{reset} \in (a,b)$

$$\frac{\partial}{\partial t}\int_a^b \rho(v',t)\,dv' = r(t) + J(a,t) - J(b,t)$$

$\uparrow$ rate enter (a,b) due to reset

so, in general: (assume here $a < V_{reset}$)

$$\frac{\partial}{\partial t}\int_a^{v} \rho(v',t)\,dv' = r(t)\cdot \underbrace{H(v-V_{reset})}_{\text{(only include if } v > V_{reset})} + J(a,t) - J(v,t)$$

Take $\frac{\partial}{\partial V}$ $\longrightarrow$

$$\boxed{\frac{\partial}{\partial t}\rho(v,t) = r(t)\,\delta(v - V_{reset}) - \frac{\partial}{\partial v} J(v,t)} \qquad (1)$$

Divide : $J = J_\ell + J_e + J_i$

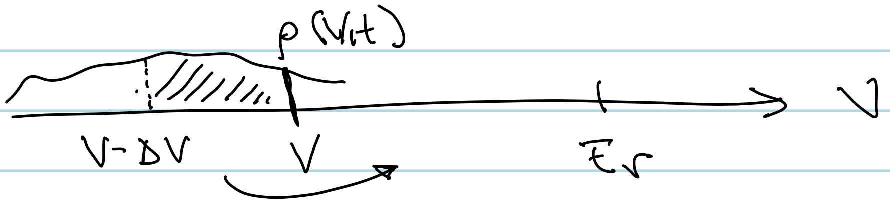
LEAK FLUX . EXC. FLUX INH. FLUX

- $J_\ell(v,t)\,dt$ = proba ($V(t)$ below V and $V(t+dt)$ above V) −
  " " above " " below V)

... due to drift

$$\frac{dV}{dt} = \frac{1}{\tau}(E_r - V)$$

Say:



Trajectories in $[V-\Delta V, V]$ will cross V. $\Delta V \approx \frac{dV}{dt}\cdot dt$

$$J_\ell(v,t)\cdot dt = p(V,t)\cdot \Delta V \approx p(V,t)\cdot \frac{dV}{dt}\cdot dt$$

$$\rightarrow J_\ell(v,t) = p(v,t)\cdot \frac{dV}{dt}(V,t)$$

Excitatory flux

- $J_e(t)$ = proba $V(t)$ below V and $V(t+dt)$ above V, due to exc. flux

$$= \Pr\left[T_e^k \in (t, t+dt)\right] \cdot$$

$$\underbrace{\int dV' \rho(V', t)}_{\Pr[V \in (V', V'+dV')]} \cdot \Pr\Big[\underbrace{\Gamma_e^{*k}(E_e - V')}_{\Pr(\text{kick lg. enough!})} > (V - V')\Big]$$

limits of integral: $\displaystyle\int_{E_i}^{V} dV' \ldots$

$V \leftarrow$ JUMPING UP past V

$E_i \leftarrow$ lower bound on $V(t)$

$$= dt \cdot \nu_e(t) \int_{E_i}^{V} dV' \rho(V', t) \, \tilde{F}_{\Gamma_e^*}\left(\frac{V - V'}{E_e - V'}\right)$$

- Inhibitory flux. LIKEWISE:

$$J_i(t) = -\nu_i(t) \int_{V}^{V_{th}} dV' \rho(V', t) \, \tilde{F}_{\Gamma_i^*}\left(\frac{V - V'}{E_i - V'}\right)$$

$V_{th} \leftarrow$ upper bound

$V \leftarrow$ jumping DOWN past V

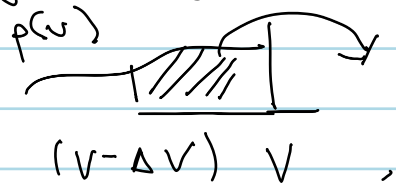
ASIDE:

Why could we simply **ADD** leak + synaptic fluxes above?

Concern: DOUBLE-COUNTING trajectories that move past V, e.g. due to **BOTH** leak and excitation

Consider time interval before spike T_e^k, $[T_e^k - dt, T_e^k]$

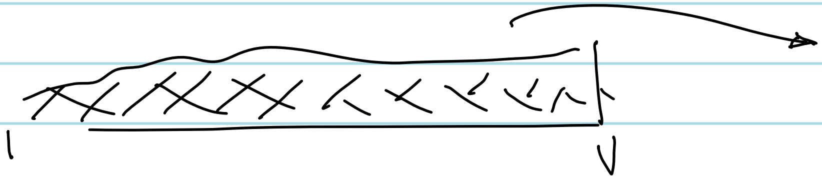
□ Traj. crossing due to drift:



,

where $\Delta V = [E_r - V] \cdot dt$
$\rightarrow 0$ as $dt \rightarrow 0$.

□ Traj. crossing due to synaptic event T_e^k



$V - \underbrace{\Gamma_e^* [E_e - V]}_{\delta V_{jump}}$

Point: $\Delta V_{jump} \not\rightarrow 0$ as $dt = 0$!

The "double counted" trajectories are a fraction:

$$\sim \frac{\Delta V}{\Delta V_{jump}} \rightarrow 0 \quad \text{as } dt \rightarrow 0.$$

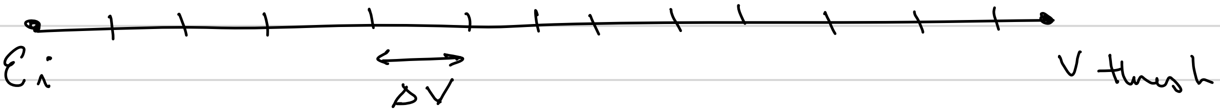
SUMMARY (JUST SAY ...)

... an interesting difference in "type" of events...
gradual finite velocity due to drift, from dt
vs.
∞-velocity, 0-time jumps from $q_{t_e}(t)$ ...

allowing our derivation.

(i) Together w/ def^{n} of $J = J_{\ell} + J_e + J_i$ ... defines full Population density model.

- Direct numerical approach:
  - Discretize voltage



Compute $\frac{\partial J_{e,i,\ell}}{\partial V}$ on grid. (Evaluate $J(v,t)$ on grid, then finite-difference)

Discretize $\delta(V - V_{reset})$ (see details in Nykamp + Tranchina)

Solve resulting ODE^{s} numerically (trap. rule).

Details: Appendix JCNS... ensure stability, etc.

Fig^{s} $\underline{8}$ of ppr ... Accompanying handout.

Why BOTHER?

- Speedup of ~100x over direct LIF sims w/ 1000 neurons per pop.

Faster still w/...: More neurons

· diffusion approx. below.

· Cain lecture: Modern diPDE methods

· Eigenfunction Expansion (Knight 2000)
or
PCA approach (Knight/Omurtag 1999):

Project → ~10-D space, almost instant solutions in Low-D approx.

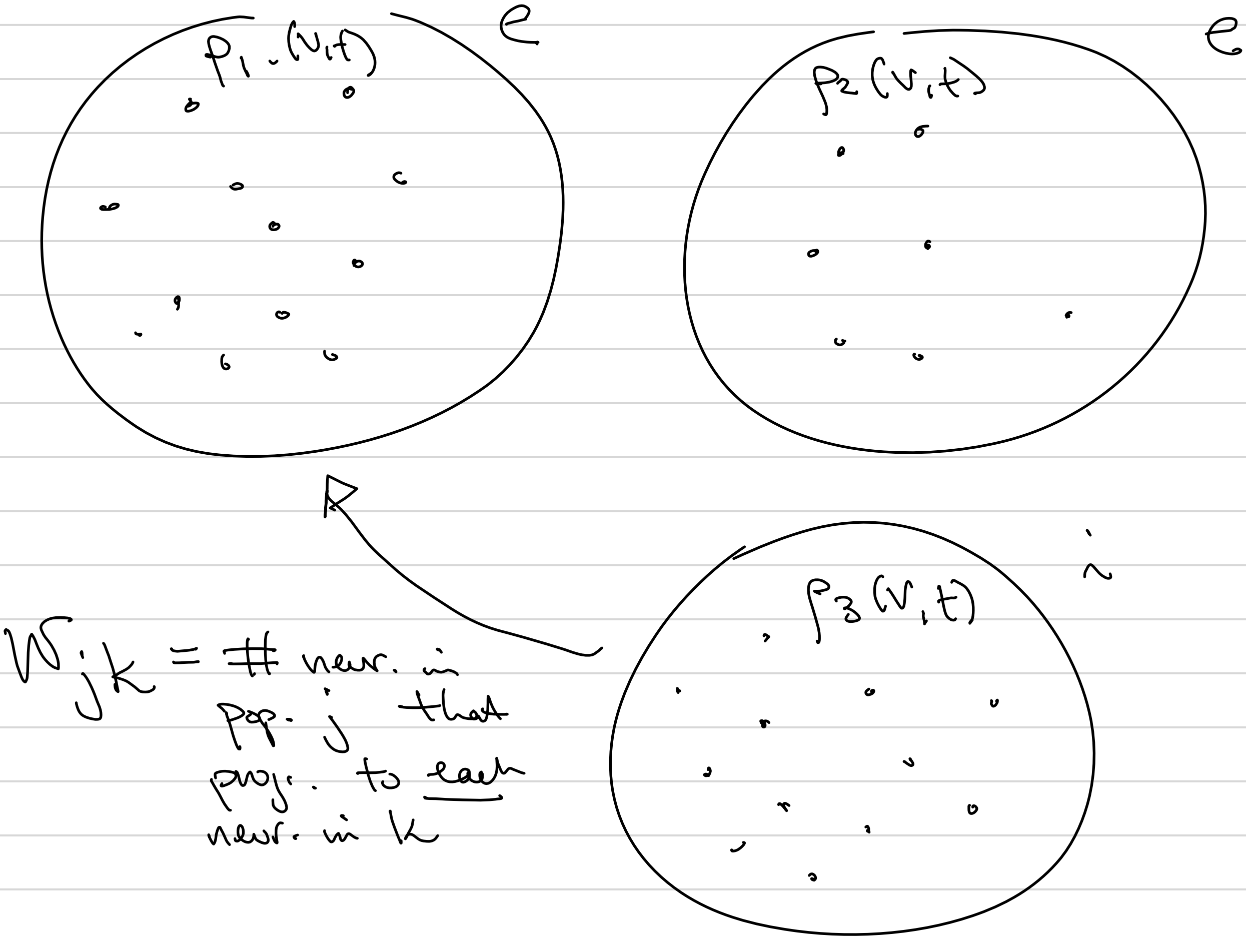
· Theory: ● "Dimension" of Pop. Dynamics

●· Explicit expression's for firing rates as $f^{\underline{ns}}$ of input "drive" + "background"

Chance Abbott Reyes Neuron 2003
"Gain and background inputs..."

· Extend → Theory of interacting neural populations
(or "self-consistent" coupling within a given population)

- Dynamics of INTERACTING population's.



e : Each pop either exc or inh.

W_{jk} = # neur. in pop. j that proj. to each neur. in k

- Other pop^s set input RATE :

$$\nu_e^k = \underbrace{\nu_{e,0}^k(t)}_{\text{“Background” rate}} + \sum_{j \in \text{exc. pops}} W_{jk} \int_0^\infty \underbrace{\alpha_{jk}(t')}_{\text{Temporal kinetics of pop-pop coupling}} r^j(t-t')\,dt'$$

→ Coupled Pop. density eq^ns.

DIFFUSION APPROXIMATION.

Consider, e.g.

$$J_e(v,t) = \nu_e(t) \int_{E_i}^{v} \tilde{F}_{\Gamma_e^*}\left(\frac{v-v'}{E_e-v'}\right) \rho(v',t)\, dv'$$

T-Series of $\rho(v',t)$ around v:

$$\rho(v',t) \approx \rho(v,t) + (v'-v)\,\frac{\partial \rho}{\partial v}(v,t) \longrightarrow$$

$$J_e(v,t) \approx \nu_e(t) \Big[\underbrace{\int_{E_i}^{v} \tilde{F}_{\Gamma_e^*}\left(\frac{v-v'}{E_e-v}\right) dv'}_{c_{1e}(v)} \cdot \rho(v,t) \; +$$

$$\underbrace{\int_{E_i}^{v} \tilde{F}_{\Gamma_e^*}\left(\frac{v-v'}{E_e-v}\right) (v'-v)\, dv'}_{-c_{2e}(v)} \cdot \frac{\partial}{\partial v}\rho(v,t)$$

$$= \nu_e(t)\left[c_{1e}(v)\,\rho(v,t) - c_{2,e}\,\frac{\partial}{\partial v}\rho(v,t) \right]$$

With similar approx. of $J_i(t)$, find:

$$\frac{\partial \rho}{\partial t} = -\frac{\partial}{\partial v}\left[\left(\nu_e(t)\, c_{1e}(v) - \nu_i(t)\, c_{1i}(v) + \frac{E_r - v}{\tau} \right) \rho(v,t) \right]$$

$$-\frac{\partial}{\partial v}\left[\left(\nu_e(t)\, c_{2e}(v) + \nu_i(t)\, c_{2i}(v) \right) \frac{\partial \rho(v,t)}{\partial v} \right]$$

$$+ \delta(v - v_{reset})\, r(t) \quad ;$$

$$r(t) = -\nu_e(t)\, c_{2e}(v_{th}) \frac{\partial \rho}{\partial v}(v_{th}, t)$$

B.C. $\rho(v_{th}, t) \equiv 0$; $\rho(-\infty, t) = 0$.

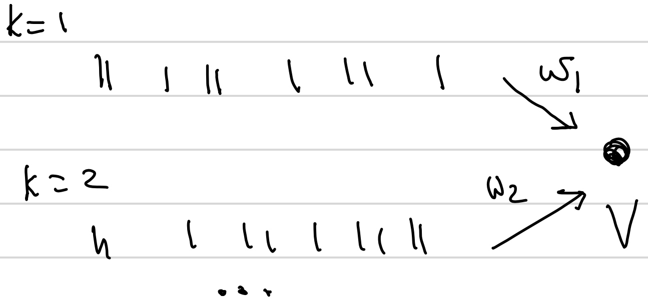
- Good approx. when $\frac{\partial^2 \rho}{\partial v^2}$ is small compared with essential support of $\tilde{F}_{\Gamma^*_{e,i}}(\cdot)$ ...

i.e., limit of small synaptic events.

· For simpler, <u>current - based</u> LIF, (8.41, Text)

do similar derivation.

$$\frac{dV}{dt} = -\frac{V}{\tau} + \frac{1}{C} I^{ext} + \sum_k \sum_{t_k^f} w_k \, \delta(t - t_k^f) \qquad \left(\begin{matrix} 8.20 \\ \text{Gerstner} \end{matrix} \right)$$



Incoming poisson trains, rates ν_k, δ-fn CURRENT PULSES, weights w_k

Multiple "types" k
IMPORTANT CASE: $w_1 > 0$, EXCITATORY
$w_2 < 0$, INHIBITORY

· Sec. 8.4 takes similar diffusion limit ⟶

$$\tau \frac{\partial}{\partial t} p(v,t) = -\frac{\partial}{\partial v}\left[\left(-v + \tau \sum_k \nu_k w_k \quad \right) p(v,t)\right]$$
$$+ \frac{1}{2}\left[\tau \sum_k \nu_k w_k^2\right] \frac{\partial^2}{\partial v^2} p(v,t)$$
$$+ \tau \, r(t) \, \delta(V - V_{reset})$$

<u>where</u> $r(t) = \frac{1}{2}\left(\tau \sum_k \nu_k w_k^2\right) \frac{\partial p}{\partial v}(v,t) \Big|_{v_{th}}$

DEFINE: $\mu = \tau \sum_k \nu_k w_k$: "Mean input"

$\sigma^2 = \tau \sum_k \nu_k w_k^2$: "Variance of input"

(STRICTLY: $\mu = \left\langle \frac{1}{T} \int_0^T \sum_k \sum_{t_k^f} \delta(t - t_k^f) \right\rangle$

Mean of Mean input over time interval

$\sigma^2 = \mathrm{var}($ " $)$)

$$\rightarrow \tau \frac{\partial}{\partial t} p(v,t) = -\frac{\partial}{\partial v}\left[(-v+\mu)\right] p(v,t) + \frac{1}{2}\sigma^2 \frac{\partial^2}{\partial v^2} p(v,t)$$

$$+ r(t)\,\delta(v - v_{reset})$$

where $r(t) = \frac{1}{2}\sigma^2 \frac{\partial p}{\partial v}(v,t)\Big|_{v_{th}}$ (13.16, Text)

· FACT: equivalent to STOCHASTIC DIFFERENTIAL EQUATION

$$dV = \frac{1}{\tau}\left[-V+\mu\right]dt + \frac{1}{2}\frac{\sigma}{\sqrt{\tau}}\,dW_t$$

See: Both μ and σ impact rate.

· What do we expect to see biologically?

Say... $k = e, i$: excit. + inhib. pops.

$$\nu_e = \underset{\substack{\uparrow \\ \#\text{ pre-syn} \\ e\text{ cells...}}}{N_e}\, r_e \leftarrow \text{firing at rate } r_e \qquad ; \quad \nu_i = N_i r_i$$

Large $N_{e,i}$ limit $(\approx 1{,}000)$

How should weights w_e, w_i scale?

CASE 1:

$$w_e = \frac{\overline{w}_e}{N_e} r_e \quad , \quad w_i = \frac{\overline{w}_i}{N_i} r_i$$

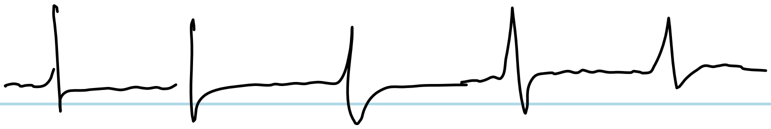
Keeps... $\frac{\mu}{\tau} = \overline{w}_e r_e + \overline{w}_i r_i$, constant. But...

BUT $$\frac{\sigma^2}{\tau} = N_e r_e \left(\frac{\overline{w}_e}{N_e}\right)^2 + N_i r_i \left(\frac{\overline{w}_i}{N_i}\right)^2 \longrightarrow 0 \ !$$

Drift-Dominated regime.

Need: (Take $\tau = 1$ here + below)

$\mu > V_{th}$. to fire. Then, firing close to oscillatory:



w/ Fano Factor << 1.

EMPIRICALLY: Many cells have Fano ≈ 1

CASE 2: $w_e = \frac{\overline{w_e}}{\sqrt{N_e}}$, $w_i = \frac{\overline{w_i}}{\sqrt{N_i}}$

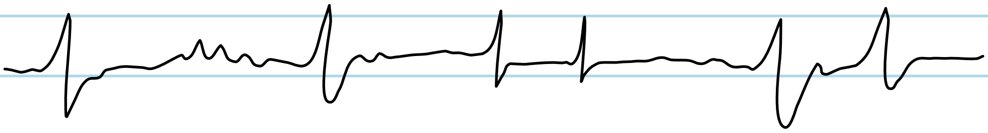
$\sigma^2 = r_e w_e^2 + r_i w_i^2$, const. ... BUT

$\mu = \overline{w_e}\sqrt{N_e}\, r_e + \overline{w_i}\sqrt{N_i}\, r_i \longrightarrow \pm\infty$, UNLESS

$\overline{W_e}\, r_e \sqrt{N_e} = -\overline{w_i}\, r_i \sqrt{N_i}$ so $\mu = 0$.

THAT is BALANCED REGIME.

Average exc. + inh. cancel. Only fluctuations drive activity.



FANO ≈ 1 !

Softky + Koch 1993
Shadlen + Newsome J. Nsci 94
van Vreeswijk + Sompolinsky, Science 1996

What happens empirically? Cardin et al Neuron 2008:

(slide...) BOTH μ and σ^2 vary w/ stim, during changes in firing rate $r(t)$.

- Intracellular recordings from CAT V1 during pres. of two types of visual stim.

- Measure intracellularly, record Mean $(V(t))$
  Std $(V(t))$ (w/ spikes deleted).

Application to GAIN of neural populations . . .

ABBOTT / CHANCE . . . 2000 NEURON

R. PANG PRESENTATION !

→ Application to <u>Linear Response</u> input-output dynamics.

Richardson, Phys. Rev. E, 2007. ; Sec. 13.5.2, Gerstner et al

"general" integrate + fire, eg EIF

$$\frac{\partial \rho}{\partial t} = -\frac{\partial}{\partial V}\left[f(V)+\mu\right]\rho + \frac{\sigma^2}{2}\frac{\partial^2}{\partial V^2}\rho + r(t)\,\delta(V-V_{reset})$$

$$r(t) = \frac{1}{2}\sigma^2 \frac{\partial^2 \rho}{\partial V^2}\Big|_{V_{thresh}}$$

$$= -\frac{\partial}{\partial V} J(V) + r(t)\,\delta(V-V_{reset})$$

Say: $\mu = \mu_0$, $\sigma = \sigma_0^2$, constant.

Consider: STEADY STATE $\rho(V,t) = \rho_0(V)$

$r(t) = r_0$

$J(V) = J_0(V)$

STEADY STATE

$$\rightarrow \quad 0 = -\frac{\partial}{\partial V} J_0(V) + r_0\,\delta(V-V_{reset}) \qquad (1)$$

$$J_0(V) = \left[f(V)+\mu_0\right]\rho_0(V) - \frac{1}{2}\sigma^2\frac{\partial}{\partial V}\rho_0(V) \qquad (2)$$

Two FIRST-ORDER ODE!

(1). Let $j_0 = \frac{1}{r_0} J_0$, treating r_0 as unknown const.

Then $j_0(V_{th}) = 1$. (1) says

$$\frac{\partial}{\partial V} j_0(V) = \delta(V - V_{reset}) \quad ; \quad \int_V^{V_{th}} dV'$$

$$-j_0(V) = \int_V^{V_{th}} dV'\,\delta(j' - V_{reset}) - 1$$

$$-j_0(V) = (1 - H(V - V_{reset}) - 1$$

$$j_0(V) = H(V - V_{reset})$$

(2) $\left([f(V) + \mu_0] p_0(V) \right) - \frac{\sigma^2}{2} \frac{\partial p_0(V)}{\partial V} = r_0 j_0(V)$, $\underline{p_0(V_{th}) = 0}$

__LET__ ... $r_0 \tilde{p}_0(V) = p_0(V)$ [Note $p_0(V) \sim r_0$], rearrange →

$$\frac{d\tilde{p}_0(V)}{dV} = \frac{2}{\sigma^2} \left[(f(V) + \mu_0) \tilde{p}_0(V) - H(V - V_{reset}) \right]$$

Solve via (BACKWARD) numerical integration (ie, Euler Method) V_{th}; I.C. $p_0(V) = 0$

Integrate until V^* s.t. $p_0(V^*) = 0$
(Expect b/c $f(V^*) > 0$ for $V^* << 0$,
and integrating BACKWARDS.

· Determine CONSTANT... via normalization,

$$\int_{V^*}^{V_{th}} dV' \, p_0(V') = 1.$$

· __For__... $f(V) = -V$, leaky integrate + fire, can carry out integration __explicitly__. __GET__:

$$r_0 = \sqrt{\pi} \int_{\frac{V_{reset} - \mu_0}{\sigma_0}}^{\frac{V_{thresh} - \mu_0}{\sigma_0}} dx \, \exp(x^2) \left[1 + \exp(x) \right]$$

Consider small perturbation to ONE of parameters μ or σ^2.
Do case where μ perturbed here.

$$\mu \to \mu_0 + \varepsilon\left[\cos(\omega t) + i\sin(\omega t)\right] \qquad ; \sigma^2 \equiv \sigma_0$$

$$= \mu_0 + \varepsilon e^{i\omega t}$$

$$p(t) = p_0(V) + \varepsilon p_1(V,t) \quad ; \quad r(t) = r_0 + \varepsilon r_1(t)$$

· $p_0(V)$, r_0 solved above. And, at $O(\varepsilon^1)$:

(1') $$\frac{\partial}{\partial t} p_1(V,t) = -\frac{\partial}{\partial V} J_1(V) + r_1(t)\,\delta(V - V_{reset})$$

(2') $$J_1(V) = \left[f(V) + \mu_0\right] p_1(V,t) - \frac{\sigma^2}{2}\frac{\partial}{\partial V} p_1(V,t) - e^{i\omega t} p_0(V)$$

$$\equiv J_0\, p_1 - F_1$$

F. Transform...

(1') $$i\omega\, p_1(V,\omega) = -\frac{\partial}{\partial V} J_1(V,\omega) + \hat{r}_1(\omega)\,\delta(V - V_{reset})$$

(2') $$J_1(V,\omega) = J_0\, p_1(V,\omega) - p_0(V)$$

(1') Is 1^{st}-order ODE for $J_1(V,\omega)$ in terms of p_1

(2') Is 1^{st} order ODE for $p_1(V,\omega)$ in terms of $J_1(V,\omega)$

Solve COUPLED system backwards from Vthresh, again via numerical integration.

→ Frequency response

$$G(\omega) = \frac{\hat{r}_1(\omega)}{e^{i\omega t}} \quad ; \quad \text{Write } G(\omega) = \underset{\substack{\uparrow \\ \underline{\text{Gain}}}}{A_1}(\omega)\, e^{i \underset{\substack{\uparrow \\ \text{Phase} \\ \underline{\text{Shift}}}}{\phi_A(\omega)}}$$

Key results:

Fig. 13.9 [Slide...] EIF cells

For... Modulation via $\mu(t)$

- Resonance in $A_1(\omega)$ near $\frac{1}{r_0}$ disappears with more background noise σ_0^2
- Low frequencies NOT phase shifted... But
  - low noise → -45° shift for high freq.
  - high noise → -90° " " " ".

For... Modulation via $\sigma(t)$

- Similar resonance
- Phase shifts always → -90°.

POINT... "Background" σ_0^2 impacts temporal processing.

$\boxed{\text{Re - Entry}}$

$$I(t) \longrightarrow \boxed{p(v,t)} \xrightarrow{r(t) \,=} r_0 + \underbrace{G} * I(t)$$

Input current

$$\begin{array}{cc} \uparrow & \uparrow \\ \mu & \sigma \frac{dW}{dt} \end{array}$$

Noisy "background" input

Linear Response filter $G(t)$
(Depends on μ, σ)
Computed in last class, ala
Gerstner et al 13.5.2.

- **AND...** (See Ostojic + Brunel, PLOS CB 2011)...

$G_s(\omega)$ is critical in linking noisy neural populations $\longrightarrow$ GLM spiking models.

SETUP: $\tau \frac{dV}{dt} = -V + \psi(V) + I(t)$,

$\begin{cases} I(t) = I_{\text{background}} + I_{\text{signal}} \\ = \mu_0 + \sigma_0 \eta(t) + s(t) \end{cases}$

$\uparrow$ EIF

OUR TARGET: what we seek to fit.

$\rightarrow$ "GLM:" or "cascade" rate $r(t) = F\left(D * s(t) \right)$; around a $\quad (*)$

baseline r_0, $r(t) \approx r_0 + F'(0)\, D * s(t)$

LIMIT 1: WEAK SIGNAL ($|s(t)|$ small)

$= r_0 + G_s(t) * s(t)$

From linear response methods, via above: $G_s(\omega)$

$\longrightarrow D = G_s(t) / F'(0)$

—— · ——

LIMIT 2: Slow signal $s(t)$

- Now, consider STEADY STATE RESPONSE to stimulus $s(t) \equiv \bar{s}$.

$\bar{r} = F(D * \bar{s}) = F(D_0 \bar{s})$, where $D_0 = \int_0^t D(t')\,dt'$

ALSO $\bar{r} = r_0(\mu_0 + \bar{s}) \longrightarrow$

$r_0(\mu_0 + \bar{s}, \sigma_0)$

FROM SOLVING STEADY STATE DENSITY EQUATION. NONLINEAR FUNCTION!

$F(D_0 \bar{s}) = r_0(\mu_0 + \bar{s})$

$F(\bar{s}) = r_0(\mu_0 + \bar{s}/D_0)$

Say: Also true for *dynamic* stimuli $\longrightarrow$

$(*)$, above: $r(t) = F(D * s(t)) =$

So Model is... $r(t) = r_0\left(\mu_0 + \frac{D * s(t)}{D_0} \right)$

$$= r_0\left(\mu_0 + \frac{G_s * s(t)}{F'(0)\, D_0} \right)$$

[SLIDE]

Fig. 1 of Ostojic + Brunel: Good approximation of stochastically spiking EIF system.

THUS...

Have derived link b/w (noisy) LIF-type model and...

GLM type model.

Useful "FORWARDS" (Theory of coupled GLM,

- with linearized Φ →

  Hawkes Processes, explicit expressions for correlations + collective response in networks.).

- with nonlinear Φ : Fluctuation Expansion... Buice.)

A second major USE: "Rate" (MEAN FIELD) "approximation... Average over many indep. copies → deterministic expression for rates.

· Connection to firing rate equations:

Say $G(t) = A e^{-t/\tau_{eff}}$ ... Reasonable approx. for EIF system, Fig. 4 Ostojic + Brunel. PLoS CB 2011.

Then $G * s(t) = x(t)$, where

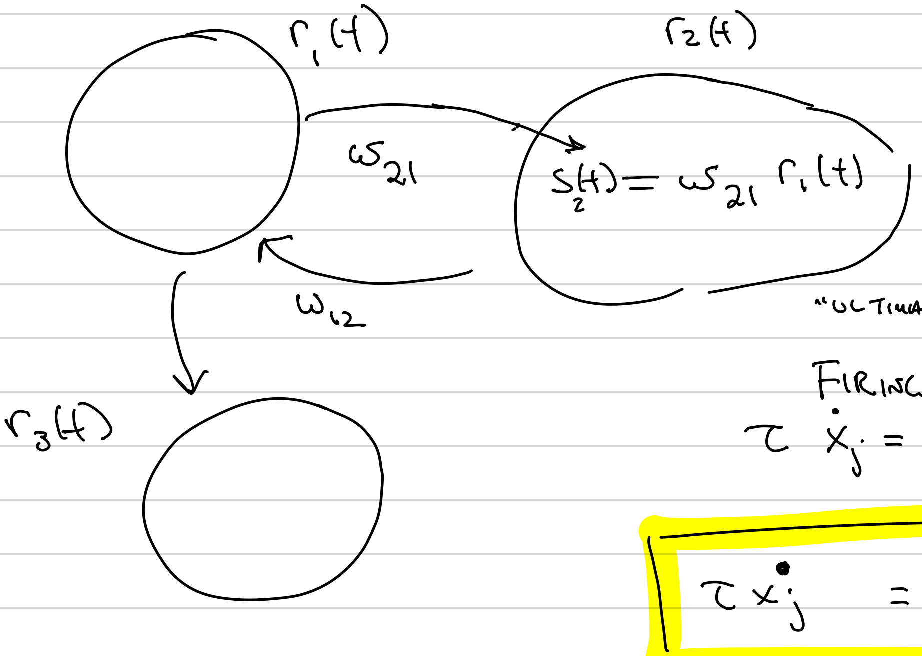
$$\tau_{eff} \dot{x} = -x + A s(t) \qquad (x(0)=0)$$

Have RATE DYNAMICS:

$$\tau \dot{x} = -x + A(s(t)), \qquad r = r_0\left(I_0 + \frac{x}{D_0}\right)$$

$$\equiv f(x), \text{ sigmoid.}$$

Coupled rate equations... [ASIDE BELOW on coupling via rates]



INPUT... depends on other pop. rates...

"ULTIMATE, POWERFUL SIMPLIFICATION:"

FIRING RATE EQUATIONS

$$\tau \dot{x}_j = -x_j + A \sum_k w_{jk} r_k(t)$$

$$\boxed{\tau \dot{x}_j = -x_j + A \sum_k w_{jk} f(x_k)}$$

ASIDE ON COUPLING VIA rates r :

Poisson process w/ rate r.

mean # spikes in $\Delta t = r \Delta t$

std. dev " " " $= \sqrt{r \Delta t}$

So... if $r >> 1$, mean >> std. dev... approx pop output as $r(t)$.

("Complete" way to couple populations... via coupled pop. density equations, $\nu_e(t) = \sum_k W_{ik} r_k(t)$, as covered previously)

- Do not cover the below, 2016.... Would need some careful attention!

Also * IMPORTANT * ... cover this <u>BEFORE</u> get to the rate eq^n simplification above, which has totally mean-driven dynamics.

<u>RATHER</u>... need a theory like Ostojic N Nsci 2014, probably Brunel 2000 / Brunel-Amit 1997, that has rates $r(\mu, \underline{\underline{\sigma}})$!

- USING A RATE MODEL TO EXPLAIN EXISTENCE + STABILITY OF THE BALANCED STATE

"Balanced" : $W_E \nu_E + W_I \nu_I = 0$
E and I

Softky + Koch
1993
Shadlen + Newsome 1998
8.2.2, Text

Why do we expect such a state to be STABLE? van Vreeswijk + Sampolinsky, Neural Comp. 2008.

Goal: ($\overset{\text{ESB}}{\text{to}}$ work through):

- Let $w_{EE} = J_{EE}\sqrt{N}$
  $w_{II} = -J_{II}\sqrt{N}$.
  $w_{IE} = J_{IE}\sqrt{N}$, ...

Write down, study stability of the corresponding 2-D rate eq^n ...

Get $\overset{\text{eq. +}}{\text{ineq.}}$ constraints (J_{EE}, J_{EI}, etc...)

a la VV / Samp.

Setting $\tau = 1$,

$$\dot{x}_E = -x_E + J_{EE}\sqrt{N}\, f(x_E) - J_{EI}\sqrt{N}\, f(x_I)$$

$$\dot{x}_I = -x_I + J_{IE}\sqrt{N}\, f(x_E) - J_{II}\sqrt{N}\, f(x_I)$$

At large N:

"Balanced" Fixed point:

$$J_{EE} \cdot f(x_E) = J_{EI} \, f(x_I)$$

$$J_{IE} \, f(x_E) = J_{II} \, f(x_I)$$

(Exists: 2 eq^{ns} in 2 unknowns.
Need inequality constraints for positive
solutions for $f(x)$.

Stability: Guaranteed! 2-D linearization,
eigenvalues.