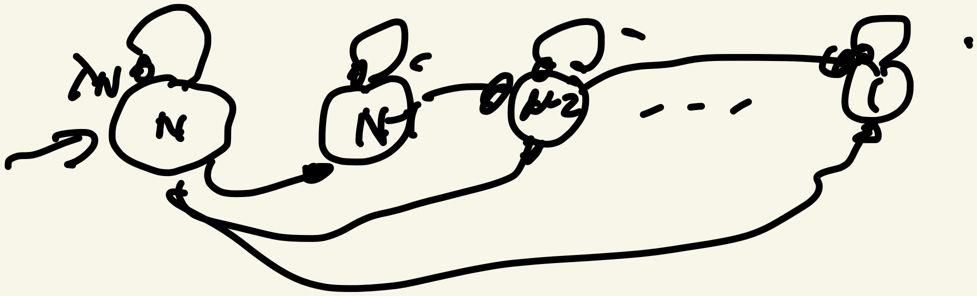
Review: non normal

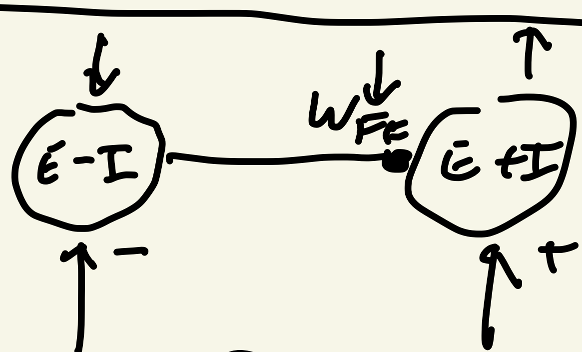


$$\tau \frac{dr_i}{dt} = -r_i + \underbrace{i \text{ (external ε ff)}}$$

$$r_i(t) = \underbrace{r_i(0)\, e^{-\frac{t}{\tau}(1-\lambda_i)}} + \frac{1}{\tau}\int_0^t dt'\, e^{-\frac{1-\lambda_i}{\tau}(t-t')}\, i(t')$$

$$\frac{1}{\tau}\int_0^t dt'\, e^{-\frac{(1-\lambda_{N-1})}{\tau}(t-t')}\, e^{-\frac{(1-\lambda_N)}{\tau}t'}$$

$$\frac{e^{-(1-\lambda_{N-1})\frac{t}{\tau}} - e^{-(1-\lambda_N)\frac{t}{\tau}}}{\lambda_{N-1} - \lambda_N}$$



⊣I

$$\underline{r} = \begin{pmatrix} E \\ I \end{pmatrix}$$

$$\cancel{\tau \frac{d\underline{r}}{dt}}^{\,0} = -\underline{r} + W\underline{r} + \underline{h}$$

$$= -(1-W)\underline{r} + \underline{h}$$

$$(1-W)\, r = h$$

$$\underline{r = (1-W)^{-1} h}$$

$$r = (1-W)^{-1} h \qquad h = \begin{pmatrix} h_E \\ h_I \end{pmatrix} = \boxed{\begin{pmatrix} 0 \\ 1 \end{pmatrix}}$$

$$W = \begin{pmatrix} w_{EE} & -w_{EI} \\ w_{IE} & -w_{II} \end{pmatrix}$$

$$\underbrace{\begin{pmatrix} a & b \\ c & d \end{pmatrix}}_{M}^{-1} = \frac{1}{\det M} \begin{pmatrix} d & -b \\ -c & a \end{pmatrix}$$

$$(1-W)^{-1} = \frac{1}{\underline{\det(1-W)}} \begin{pmatrix} 1+w_{II} & -w_{EI} \\ w_{IE} & 1-w_{EE} \end{pmatrix}$$

>0 stable fixed point

Response of $I \downarrow \iff 1-w_{EE}<0$

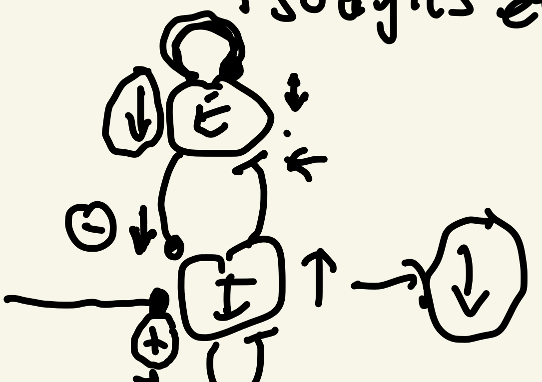
$w_{EE}>1$

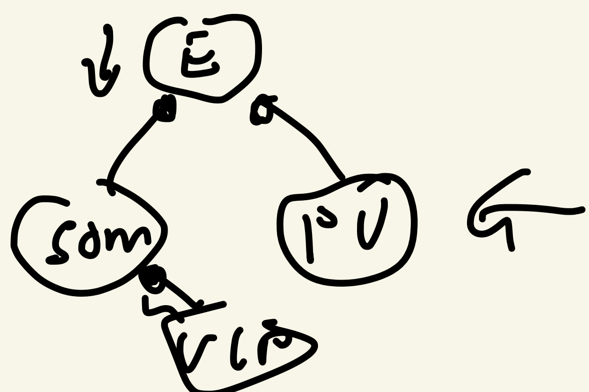
$$\frac{d\underline{r}}{dt} = (W-1)\underline{r} + \underline{h}$$

$$\frac{dr_E}{dt} = \underline{(w_{EE}-1)}\, r_E - \underbrace{w_{EI} r_I}_{\text{froze}} + h_E$$

Inhibition-stabilized network (ISN)

Tsodyks et al 1997 Ozeki et al 2009





$(1-\underline{W})r = h$ $\qquad h = \begin{bmatrix} \cancel{h_{E}} \to 0 \\ h_{I1} \\ h_{I2} \\ \vdots \\ h_{IN} \end{bmatrix}$ $\qquad \underline{W_{EI_i}}$

$r_E: (1-W_{EE})r_E - \sum_i W_{EI_i} r_{I_i} = 0$

$$\underline{(1-W_{EE})} r_E = \underbrace{\sum_{i \in I} W_{EI_i} r_{I_i}}_{\text{total inhib received by E}}$$

$W_{EE} > 1$ $\qquad$ total inhib received by E

a negative #

$r_E \downarrow \to$ total inhib $\downarrow$ $\uparrow$

Ozeki et al 2009
Adesnik 2017
Isaacson-Al 2017

Surround suppression

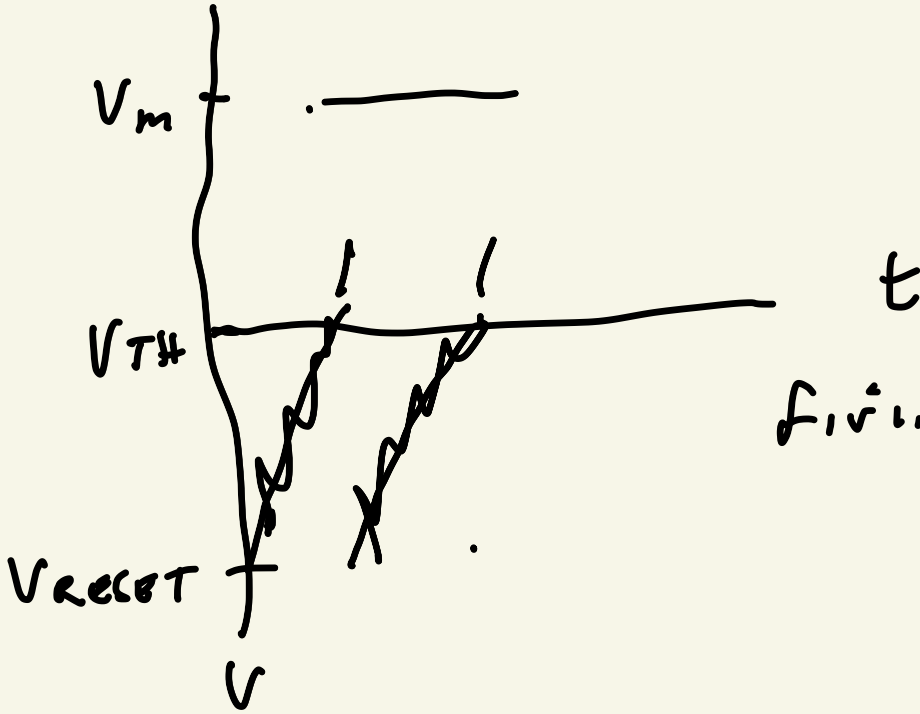
Hirsted 2019
Svoboda 2019

BALANCED NETWORKS

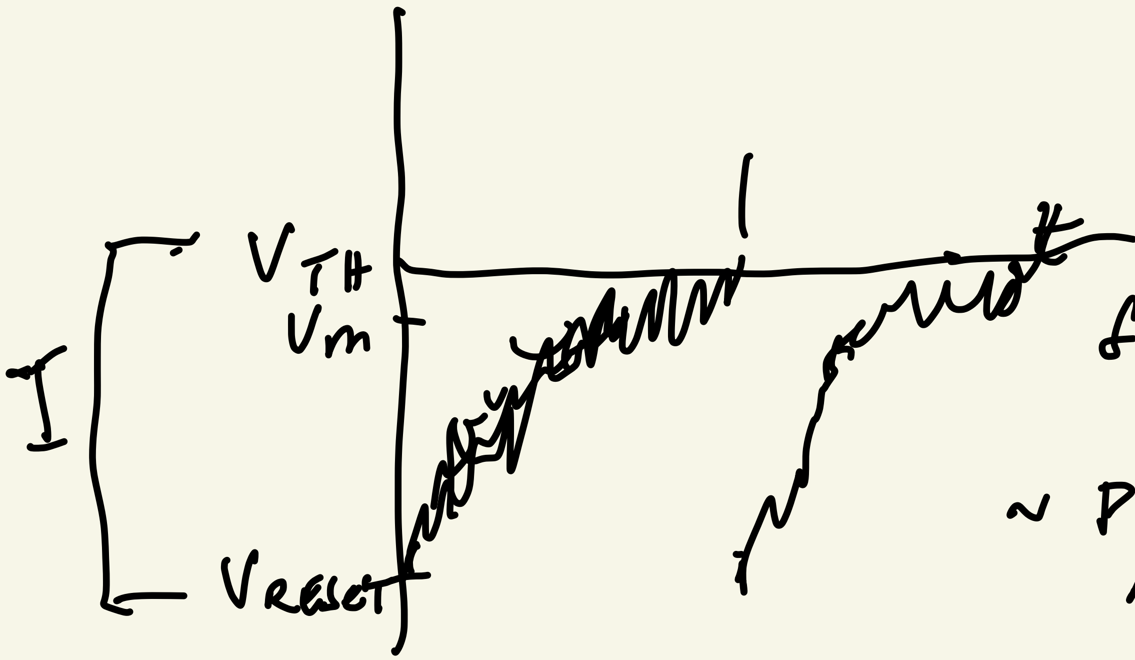
irregular $\qquad$ | | | | | | $\quad$ clock

| || | || | $\quad$ Poisson

- intrinsic stochasticity
  - Na^+ channels
  - synaptic release ?
- corr input ?
- fluctuation-driven firing



firing on mean



firing on fluctuations

~ Poisson w/ a refractory period

irregular

Requirements

$V_{mean} \sim O(Th) \sim O(1)$

$V_\sigma \sim O(1)$

Cell receives K input K big

mean $\propto K$ uncorrelated variance $\propto K$ $\sigma_V \propto \sqrt{K}$

μ = mean ~ K $\sigma_v \sim \sqrt{K}$

Van Vreeswijk & Sompolinsky 1996
1998

$E \sim K$ $I \sim K$

cancel dynamics

net $\sim \sqrt{K}$

$\mu = J K$ (# of spikes in integration time)

J: mean syn weight of inputs

K: # inputs

# of spikes in integration time $= r\tau$

r: mean rate

τ: integration time ~ EPSP time constant

$\sigma^2 = J^2 K \underbrace{\mathrm{var}(r\tau)}_{r\tau} = J^2 K r \tau$

$$\boxed{\sigma = J\sqrt{K r \tau} + \text{corrs} \;\Big|\; \mu = J K r \tau}$$

Random connectivity

"Mean field" dynamics $\left.\begin{matrix} r_E \\ r_I \end{matrix}\right]$ average of pop

$r = \begin{pmatrix} r_E \\ r_I \end{pmatrix}$ $\frac{d\underline{r}}{dt} = -\underline{r} + f(W\underline{r} + \underline{h})$

W satisfies simple conditions $\det W > 0$

$J \sim \frac{1}{\sqrt{K}}$ mean ~ $\sqrt{K}$ var ~ $O(1)$

W: $KJ \sim \sqrt{K}$

$$\tau \frac{d\underline{r}}{dt} = -\underline{r} + f\Big(\underset{\sqrt{K}}{\underset{\uparrow}{W}}\,\underline{r} + \underset{\sqrt{K}}{\underset{\uparrow}{\underline{h}}}\Big)$$

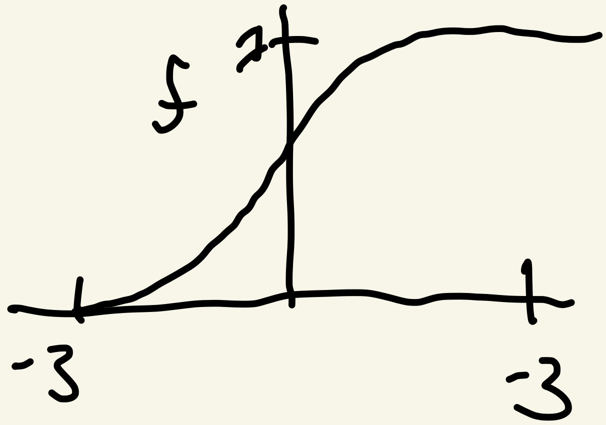
$$W\underline{r} + \underline{h} \sim O(1)$$

$$\underline{r} = \underset{O(1)}{\underline{r}_0} + \overset{O(1)}{\frac{r_1}{\sqrt{K}}} + \frac{1}{K} r_2 + \dots$$

$$\underline{r}_0 = -W^{-1} h$$

$$W r_0 = -h$$

$$\sqrt{K} \rightarrow \frac{W r_1}{\sqrt{K}} \sim O(1)$$



$J \sim \frac{1}{\sqrt{K}}$

$W \sim \sqrt{K}$

$h \sim K$

$m \sim O(\sqrt{K}) \xrightarrow{\text{bal}} O(1)$

$\sigma \sim O(1)$

But:

(1) Only get linear response

$$r_0 = -W^{-1} h = \text{linear}(h)$$

$$\frac{r_1}{\sqrt{K}} << r_0$$

$\longrightarrow$ synaptic nonlinearity

(2) Predicts external input $\underset{\sqrt{K}}{}$ >> net input $\underset{O(1)}{}$

Silence ctx $\rightarrow$ voltage response $\downarrow$

Where is cortex really?

Ahmadian & Miller arXiv

rest → thresh ~ 20 mV

After balancing

μ mean ~ 10–20 mV

σ ~ 1–5 mV

$\frac{\sigma}{\mu} \sim \frac{1}{2} \to \frac{1}{20}$

Before balancing

$\mu \sim J K r \tau \qquad \sigma \sim J \sqrt{K r \tau}$

$\frac{\sigma}{\mu} \sim \frac{1}{\sqrt{K r \tau}} \sim \frac{1}{\sqrt{K}}$

$\tau = 10\,ms \sim \frac{1}{100}\,Hz$

$\frac{\sqrt{K r \tau}}{K}$

$\frac{\mu}{\sigma} \sim \sqrt{K r \tau}$

$\sim 2 \to 20$

		500	1000	2000	4000
r	0.1 Hz	.7	1	1.4	2
	1 Hz	2.2	3.2	4.5	6.3
	10 Hz	7.1	10	14.2	20

$r_0 = -W^{-1} h + \frac{1}{\sqrt{K r \tau}}$

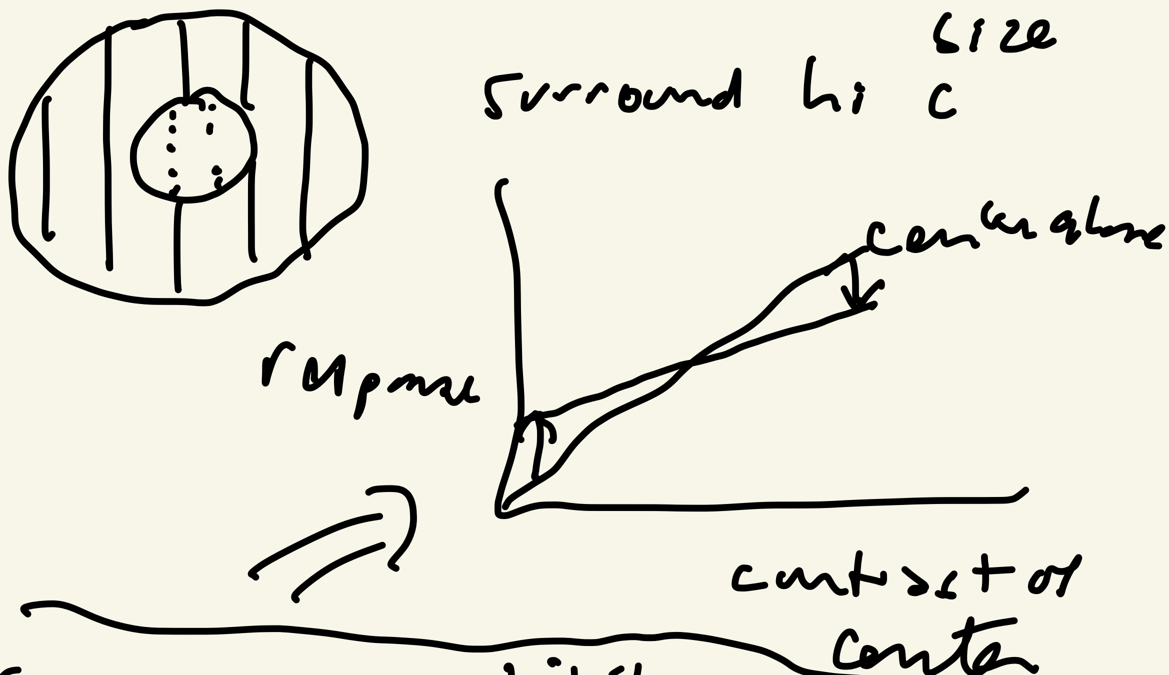
$O(1) \quad O(1) \quad O(1)$

Sensory Cortical nonlinearities

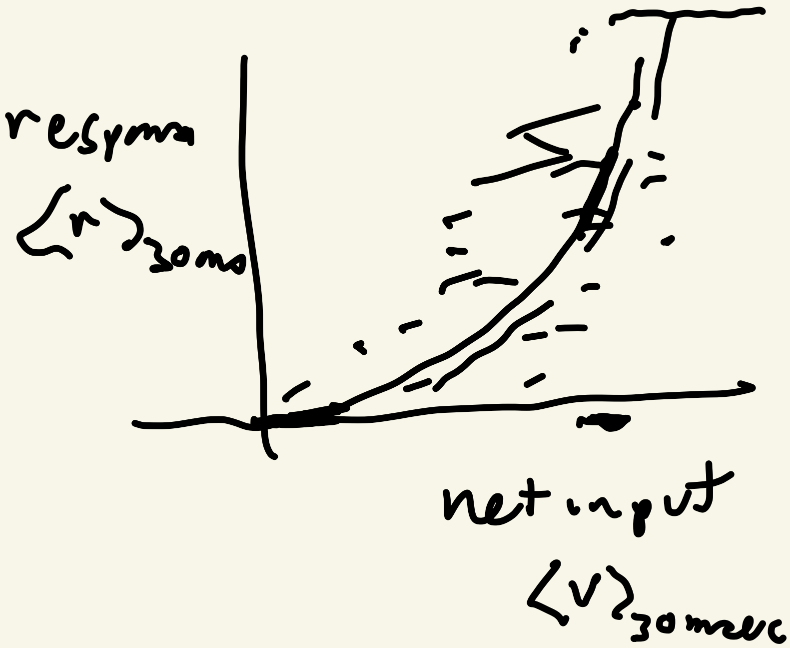
(1) Add two stimuli → sublinear
~ average of two individual

except if they're weak
→ linear

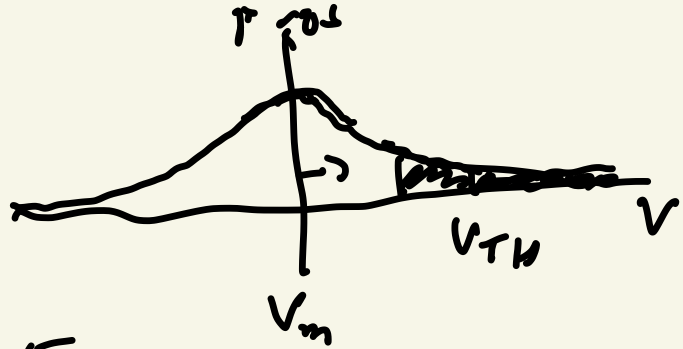
(2) Increasing strength → shrinkage of summation field size
(contrast
→ ↑ thalamic firing rate



(3) response variability decreases with adding stimulus



Expect this spiking model firing on the fluctuations



$$\langle r \rangle \sim \langle v \rangle^n \quad n \sim 2-5$$

$$\underline{r} = f(W\underline{r} + \underline{h}) = k(W\underline{r} + \underline{h})_+^n$$

k: $\frac{Hz}{(mV)^n}$ $\quad W$: $\frac{mV}{Hz}$ $\quad \underline{r}$: Hz $\quad \underline{h}$: mV

$$\Rightarrow (W\underline{r} + \underline{h})_+^n$$

$$\tau \frac{d\underline{r}}{dt} = -\underline{r} + (W\underline{r} + c\underline{g})_+^n$$

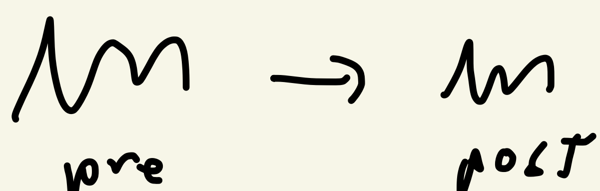
$$\underline{r} = (W\underline{r} + c\underline{g})_+^n$$

$|\underline{h}| = c$

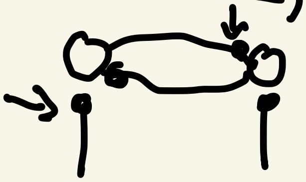
$\underline{g} = \underline{h}/c$

Effective synaptic strength

$\boxed{c \ll 1}$



syn strength ⊗ gain (post)



$$\underline{r} = (c\underline{g} + \underbrace{W(c\underline{g}}_{} + W(\ldots)_+^n)_+^n)_+^n$$

$$= (c\underline{g})_+^n + h.o.t.(c)$$

$x \ll 1$

$x^n \ll x$

$c << 1$ loosely (sn) coupled
weak eff syn strengths
Feedforward (monosynaptic) dominates
$\Rightarrow$ Supralinear response summation

$c >> 1$ $\Rightarrow$ more strongly coupled
$\alpha >> 1$ recurrence dominates over ff
$\beta << 1$

$$\underline{r} = (W\underline{r} + c\underline{g})_+^n$$

$[Wr] = [c]$
$\|W\| = \psi$
$J = W/\psi$
$y = \dfrac{r\psi}{c}$

$$\frac{cy}{\psi} = \left(\cancel{\psi} J \frac{cy}{\cancel{\psi}} + cg\right)_+^n$$

$$= c^n \left(\underline{Jy + g}\right)_+^n$$

$r = \dfrac{cy}{\psi}$

$$y = \underbrace{\psi c^{n-1}}_{\alpha} (Jy + g)_+^n$$

$W = \psi J$

$c << 1 \Leftrightarrow \alpha << 1$
$c >> 1 \Leftrightarrow \alpha >> 1$

$\begin{pmatrix} r_E \\ r_I \end{pmatrix}$

$$-g + \left(\frac{y}{\alpha}\right)^{\frac{1}{n}} = Jy$$

$$y = -J^{-1} g + \beta y^{\frac{1}{n}} \qquad \beta \doteq \frac{1}{\alpha^{\frac{1}{n}}}$$

$$= \underbrace{-J^{-1} g}_{y_0} + \underbrace{\beta\left(-J^{-1} g + \beta (\ldots)^{\frac{1}{n}}\right)^{\frac{1}{n}}}$$

$Jy_0 = -g$

$\alpha = \psi c^{n-1}$

$\alpha \ll 1$ weakly coupled

$\alpha \sim O(1)$

$\alpha \gg 1$ strongly coupled

$\beta \sim O(1)$ $\qquad \alpha^{\frac{1}{n}} \sim O(1)$

$$\alpha = \psi c^{n-1} \sim K^{\frac{n}{2}}$$

$\psi \uparrow \sqrt{K}$, $c \uparrow \sqrt{K}$

$$\beta \sim \frac{1}{\left(K^{\frac{n}{2}}\right)^{\frac{1}{n}}} = \frac{1}{\sqrt{K}}$$