Probabilistic inference in networks of spiking neurons

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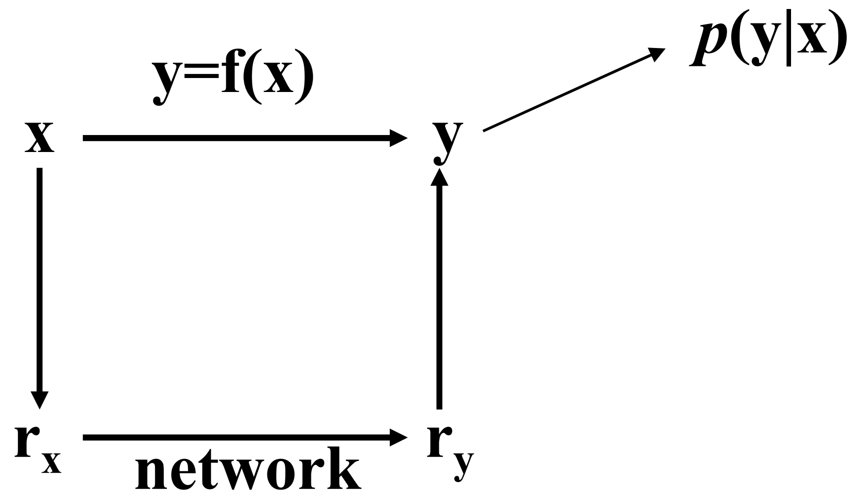
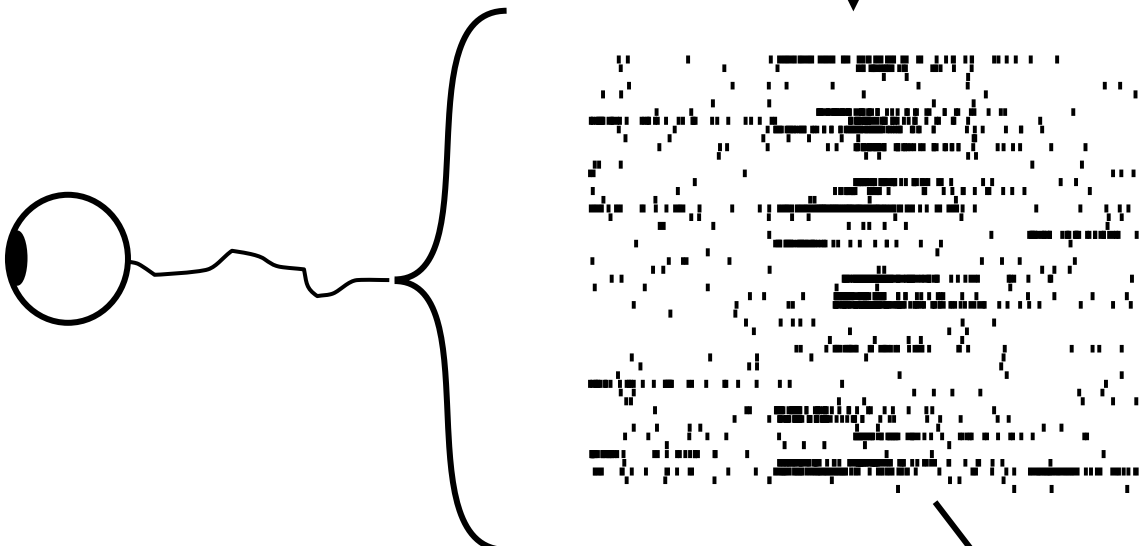
learn to

Goal: understand how networks of neurons compute.



$\mathbf{r_x}$

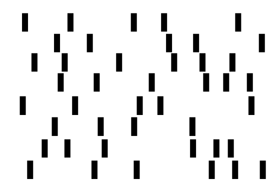
x = image



y = sunset

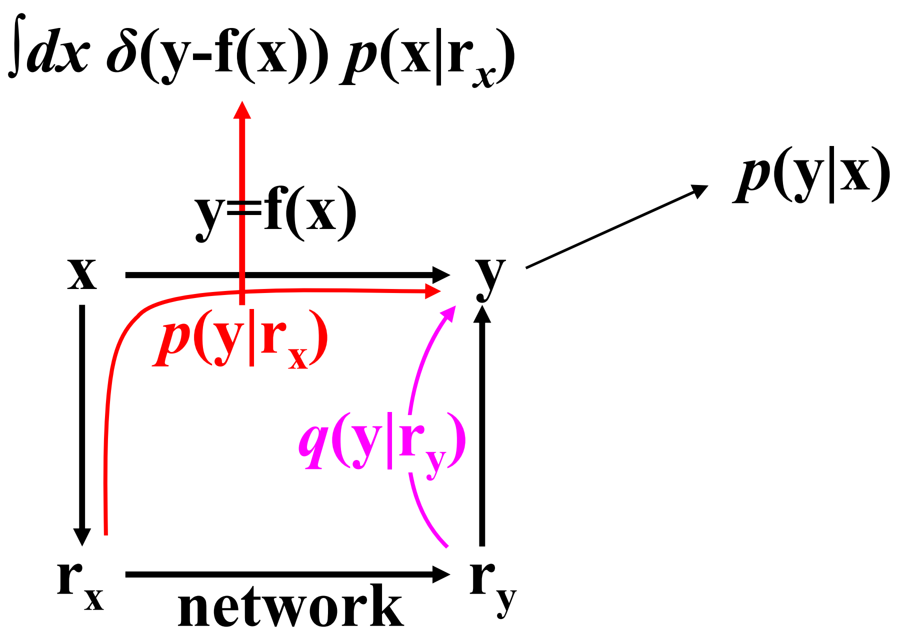
network

true probability: $p(y|\mathbf{r_x})$



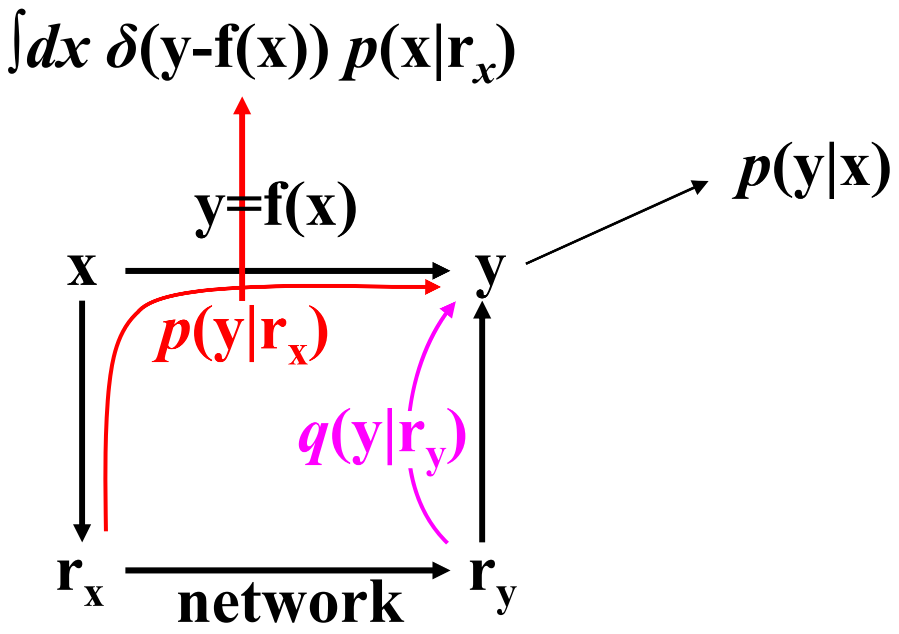
$q(y|\mathbf{r}_y)$ ← $\mathbf{r}_y$ →

goal: choose the network so these are as close as possible, and $\mathbf{r}_y$ codes only for sunsets.



Goal: choose network so that $p(y|r_x)$ is close to $q(y|r_y)$ and r_y is a "pure code" for y.

Quantitatively: minimize $D_{KL}(p(y|r_x)||q(y|r_y))$



minimize $D_{KL}(p(y|r_x)||q(y|r_y))$ with respect to:

1. **Parameters of the encoding model (e.g., $p(r_x|x)$, $q(r_y|y)$).**
2. **Parameters of the <u>biologically plausible</u> network.**

Three examples:

- **multisensory integration**
- $z = f(x, y)$
- **a hard problem**

minimize $D_{KL}(p(y|r_x)||q(y|r_y))$ **with respect to:**

1. **Parameters of the encoding model (e.g.,** $p(r_x|x)$, $q(r_y|y)$**).**
2. **Parameters of the biologically plausible network.**

Take home message

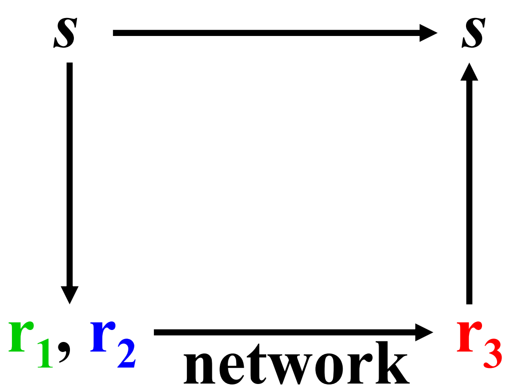
In some ways this talk is largely technical – I'm going to tell you how biologically plausible networks could perform some (relatively) simple computations.

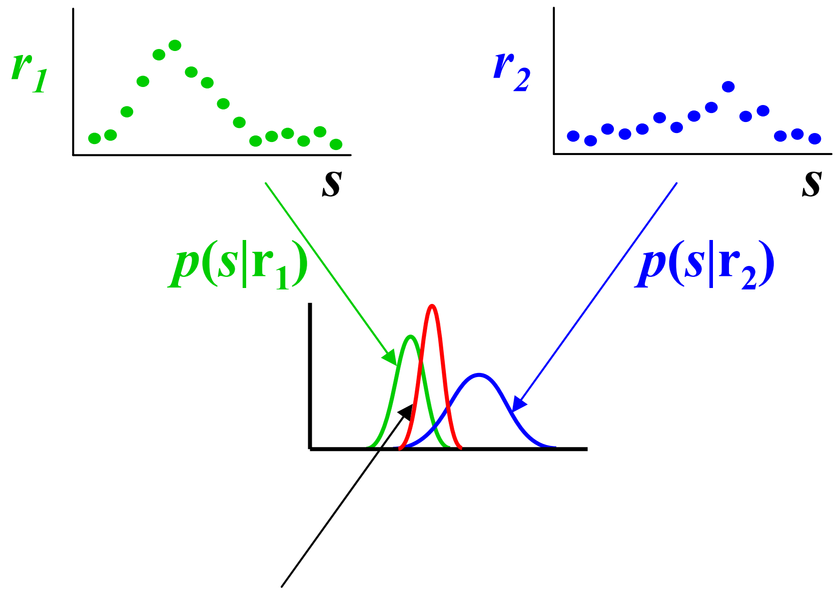
There are no deep insights into how the brain works.

Two things to pay attention to:

1. our methodology,
2. the problems we don't solve.

1. multisensory integration





$$p(s|r_1, r_2) \propto p(s|r_1)p(s|r_2)$$

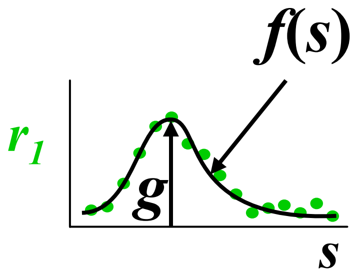
$$\text{minimize } D_{KL}(p(s|r_1, r_2)||q(s|r_3))$$

encoding model: exponential family with linear sufficient statistics

independent Poisson:

$$p(\mathbf{r}|s, g) = \prod_i \frac{1}{r_i!} [g f_i(s)]^{r_i} \exp[-g f_i(s)]$$

$$= \varphi(\mathbf{r}, g) \exp[\mathbf{h}(s) \cdot \mathbf{r}]$$



$$h_i(s) = \log f_i(s)$$

$$\varphi(\mathbf{r}, g) = \exp\left[-\sum_i \log r_i! + r_i \log g - g f_i(s)\right]$$

$$\exp[r_i \log g + r_i \log f_i(s)]$$

encoding model: <u>exponential family with linear sufficient statistics</u>

$$p(\mathbf{r}|s, g) = \varphi(\mathbf{r}, g) \exp[\mathbf{h}(s)\cdot\mathbf{r}]$$

$$p(s|\mathbf{r}) \propto \exp[\mathbf{h}(s)\cdot\mathbf{r}]$$

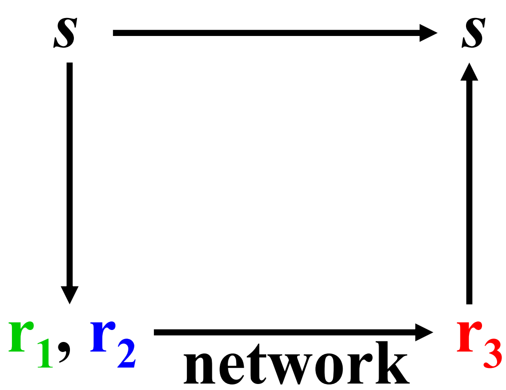
the gain parameter doesn't appear in the posterior!!!!

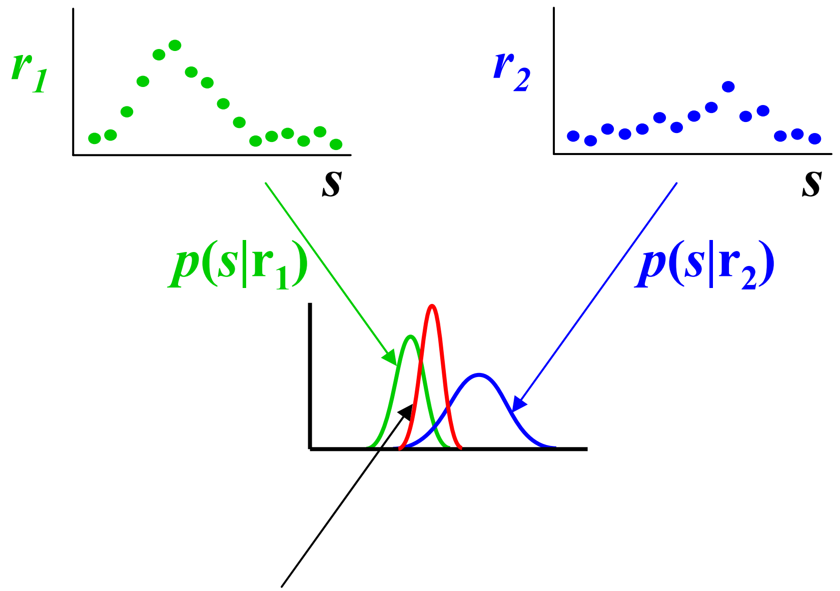
encoding model: linear PPC

$$p(\mathbf{r}|s, g) = \varphi(\mathbf{r}, g) \exp[\mathbf{h}(s)\cdot\mathbf{r}]$$

$$p(s|\mathbf{r}) \propto \exp[\mathbf{h}(s)\cdot\mathbf{r}]$$

the gain parameter doesn't appear in the posterior!!!!





$$p(s|\mathrm{r}_1, \mathrm{r}_2) \propto p(s|\mathrm{r}_1)p(s|\mathrm{r}_2)$$

$$\text{minimize } D_{KL}(p(s|\mathrm{r}_1, r_2)||q(s|\mathrm{r}_3))$$

minimize $D_{KL}(p(s|r_1, r_2)||q(s|r_3))$

$p(s|r_1, r_2) \propto p(s|r_1)p(s|r_2)$

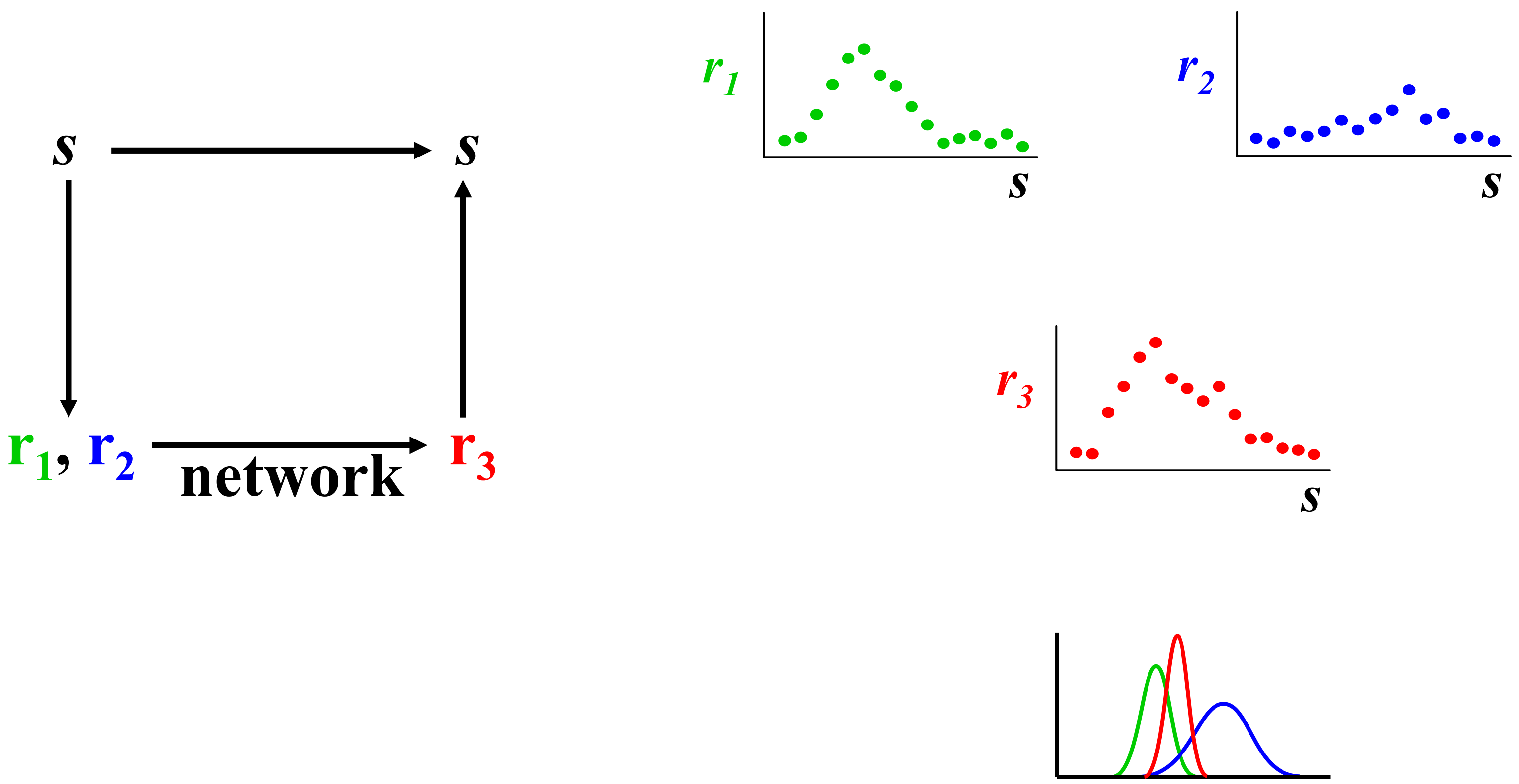
$p(s|r_1) \propto \exp[h(s)\cdot r_1]$

$p(s|r_2) \propto \exp[h(s)\cdot r_2]$

$q(s|r_3) \propto \exp[h(s)\cdot r_3]$

$p(s|r_1, r_2) \propto p(s|r_1)p(s|r_2) \propto \exp[h(s)\cdot(r_1+r_2)]$

network: $r_3 = r_1+r_2$



Ma et al., *Nature Neurosci.* (2006)

The encoding model matters!

Gaussian encoding model:

$$p(r_1|s) \propto \exp[-(f(s)-r_1)^2/2\sigma_1^2]$$
$$p(r_2|s) \propto \exp[-(f(s)-r_2)^2/2\sigma_2^2]$$

these will vary from trial to trial

$$p(s|r_1, r_2) \propto p(s|r_1)p(s|r_2) \propto \exp[-(f(s)-ar_1-br_2)^2/2\sigma^2]$$

$$1/\sigma^2 = 1/\sigma_1^2 + 1/\sigma_2^2$$
$$a = \sigma^2/\sigma_1^2$$
$$b = \sigma^2/\sigma_2^2$$

network: $r_3 = ar_1 + br_2$

depend on σ_1 and σ_2, which depend, probabilistically, on r_1 and r_2.

The encoding model matters!

linear PPC encoding:

$$p(\mathbf{r}_1|s) \propto \varphi(\mathbf{r}_1, \mathbf{g}_1) \exp[\mathbf{h}(s)\cdot\mathbf{r}_1]$$
$$p(\mathbf{r}_2|s) \propto \varphi(\mathbf{r}_2, \mathbf{g}_2) \exp[\mathbf{h}(s)\cdot\mathbf{r}_2]$$

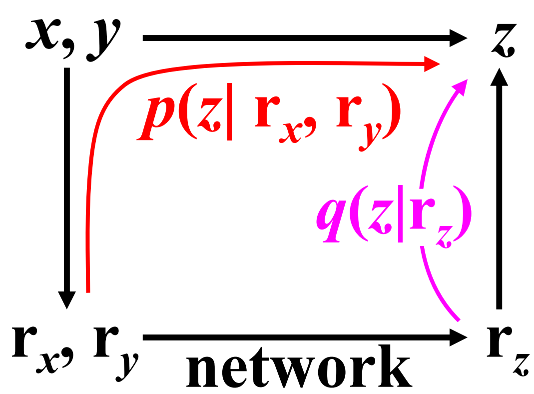
these will vary from trial to trial

network: $\mathbf{r}_3 = \mathbf{r}_1 + \mathbf{r}_2$

This was a simple example, but it has the main ingredients:

1. **The encoding model matters.**
2. **Once you specify the encoding model, the network follows.**

2. computing functions $z=f(x, y)$



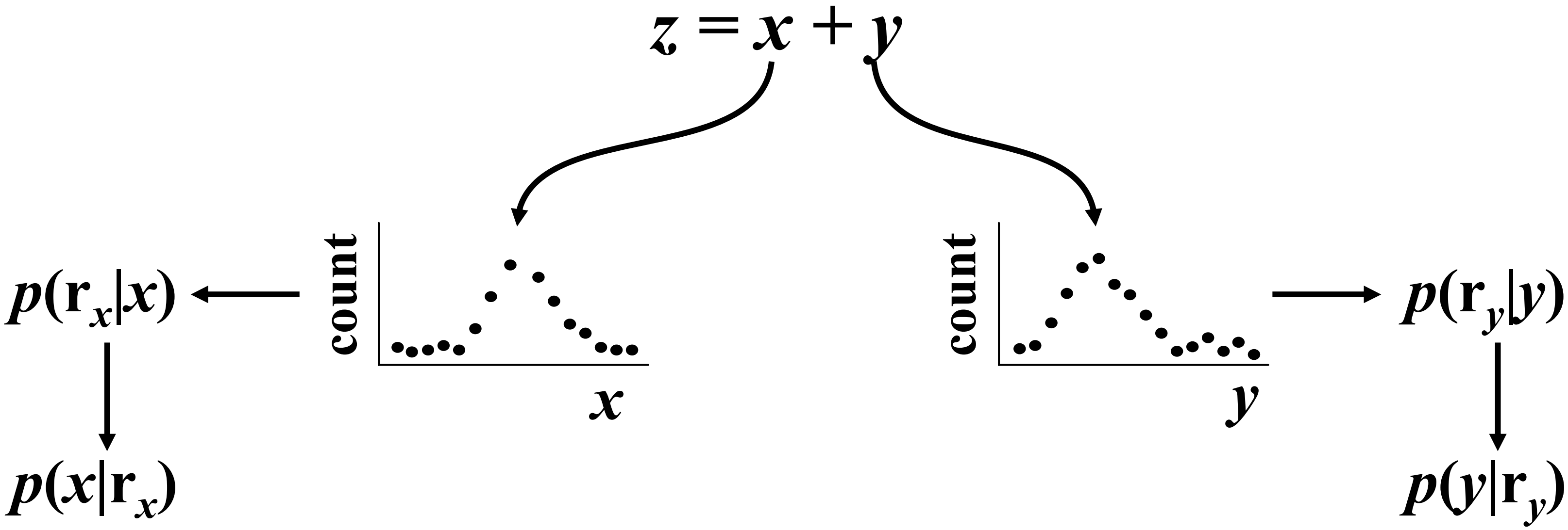
minimize $D_{KL}(p(z|r_x, r_y)||q(z|r_z))$ with respect to:

1. **Parameters of the encoding model.**
2. **Parameters of the network.**

typically, we can't find the optimal network

Find the optimal network for linear transformations and Gaussian posterior distributions;

use that network architecture for nonlinear transformation and non-Gaussian posteriors.



$$p(z|\mathrm{r}_x, \mathrm{r}_y) = \int dx dy\ \delta(z-(x+y))\ p(x|\mathrm{r}_x)\ p(y|\mathrm{r}_y)$$

hard integral!

$$z = x + y$$

The Gaussian case

$$p(z|\mathbf{r}_x, \mathbf{r}_y) = \int dxdy\, \delta(z-(x+y))\, p(x|\mathbf{r}_x)\, p(y|\mathbf{r}_y)$$

$p(z|\mathbf{r}_x, \mathbf{r}_y)$: $N(\mu_x+\mu_y, \sigma_x^2 + \sigma_y^2)$

$p(x|\mathbf{r}_x)$: $N(\mu_x,\sigma_x^2)$

$p(y|\mathbf{r}_y)$: $N(\mu_y,\sigma_y^2)$

Easier problem:

1. parameterize the mean and variance in a linear PPC;
2. find a network such that

$$\mu_z = \mu_x + \mu_y$$
$$\sigma_z^2 = \sigma_x^2 + \sigma_y^2$$

An (important) aside: representation matters Suppose

$p(r_x|x) \sim \exp[-(x-a \cdot r_x)^2/2b \cdot r_x] \sim p(x|r_x)$

$p(r_y|y) \sim \exp[-(y-a \cdot r_y)^2/2b \cdot r_y] \sim p(y|r_y)$

$p(r_z|z) \sim \exp[-(z-a \cdot r_z)^2/2b \cdot r_z] \sim p(z|r_z)$

$\mu_x = a \cdot r_x$
$\sigma_x^2 = b \cdot r_x$

$\mu_y = a \cdot r_y$
$\sigma_y^2 = b \cdot r_y$

$\mu_z = a \cdot r_z$
$\sigma_z^2 = b \cdot r_z$

An (important) aside: representation matters Suppose

$$p(\mathrm{r}_x|x) \sim \exp[-(x-\mathrm{a}\cdot\mathrm{r}_x)^2/2\mathrm{b}\cdot\mathrm{r}_x] \sim p(x|\mathrm{r}_x)$$

$$p(\mathrm{r}_y|y) \sim \exp[-(y-\mathrm{a}\cdot\mathrm{r}_y)^2/2\mathrm{b}\cdot\mathrm{r}_y] \sim p(y|\mathrm{r}_y)$$

$$p(\mathrm{r}_z|z) \sim \exp[-(z-\mathrm{a}\cdot\mathrm{r}_z)^2/2\mathrm{b}\cdot\mathrm{r}_z] \sim p(z|\mathrm{r}_z)$$

$$\mu_x = \mathrm{a}\cdot\mathrm{r}_x$$
$$\sigma_x^2 = \mathrm{b}\cdot\mathrm{r}_x$$

$$\mu_y = \mathrm{a}\cdot\mathrm{r}_y$$
$$\sigma_y^2 = \mathrm{b}\cdot\mathrm{r}_y$$

$$\mu_z = \mathrm{a}\cdot\mathrm{r}_z = \mu_x + \mu_y$$
$$\sigma_z^2 = \mathrm{b}\cdot\mathrm{r}_z = \sigma_x^2 + \sigma_y^2$$

goal

An (important) aside: representation matters. Suppose

$$p(r_x|x) \sim \exp[-(x - a \cdot r_x)^2/2b \cdot r_x] \sim p(x|r_x)$$

$$p(r_y|y) \sim \exp[-(y - a \cdot r_y)^2/2b \cdot r_y] \sim p(y|r_y)$$

$$p(r_z|z) \sim \exp[-(z - a \cdot r_z)^2/2b \cdot r_z] \sim p(z|r_z)$$

$$\mu_x = a \cdot r_x$$
$$\sigma_x^2 = b \cdot r_x$$

$$\mu_y = a \cdot r_y$$
$$\sigma_y^2 = b \cdot r_y$$

$$\mu_z = a \cdot r_z = \mu_x + \mu_y = a \cdot r_x + a \cdot r_y$$
$$\sigma_z^2 = b \cdot r_z = \sigma_x^2 + \sigma_y^2 = b \cdot r_x + b \cdot r_y$$

goal

optimal network:

$$r_z = r_x + r_y$$

If brains had evolved to perform linear transformations ($z=ax+by$), and noise was Gaussian, then encoding probably would have looked like

$$p(\mathbf{r}_x|x) \sim \exp[-(x-\mathbf{a}\cdot\mathbf{r}_x)^2/2\mathbf{b}\cdot\mathbf{r}_x].$$

The fact that the encoding model does not look like this is probably a clue to what the brain has evolved to compute.

So far this is just a clue – we haven't made sense of it.

An (important) aside: representation matters! Suppose

$$p(\mathbf{r}_x|x) \sim \exp[-(x-\mathbf{a}\cdot\mathbf{r}_x)^2/2\mathbf{b}\cdot\mathbf{r}_x] \sim p(x|\mathbf{r}_x)$$

$$p(\mathbf{r}_y|y) \sim \exp[-(y-\mathbf{a}\cdot\mathbf{r}_y)^2/2\mathbf{b}\cdot\mathbf{r}_y] \sim p(y|\mathbf{r}_y)$$

$$p(\mathbf{r}_z|z) \sim \exp[-(z-\mathbf{a}\cdot\mathbf{r}_z)^2/2\mathbf{b}\cdot\mathbf{r}_z] \sim p(z|\mathbf{r}_z)$$

$$\mu_x = \mathbf{a}\cdot\mathbf{r}_x$$
$$\sigma_x^2 = \mathbf{b}\cdot\mathbf{r}_x$$

$$\mu_y = \mathbf{a}\cdot\mathbf{r}_y$$
$$\sigma_y^2 = \mathbf{b}\cdot\mathbf{r}_y$$

$$\mu_z = \mathbf{a}\cdot\mathbf{r}_z = \mu_x + \mu_y = \mathbf{a}\cdot\mathbf{r}_x + \mathbf{a}\cdot\mathbf{r}_y$$
$$\sigma_z^2 = \mathbf{b}\cdot\mathbf{r}_z = \sigma_x^2 + \sigma_y^2 = \mathbf{b}\cdot\mathbf{r}_x + \mathbf{b}\cdot\mathbf{r}_y$$

goal

optimal network:

$$\mathbf{r}_z = \mathbf{r}_x + \mathbf{r}_y$$

The real thing: a linear PPC

$$p(\mathbf{r}_x|x) \sim \exp[-\mathbf{a}\cdot\mathbf{r}_x(x - \mathbf{b}\cdot\mathbf{r}_x/\mathbf{a}\cdot\mathbf{r}_x)^2/2]$$

$$p(\mathbf{r}_y|y) \sim \exp[-\mathbf{a}\cdot\mathbf{r}_y(x - \mathbf{b}\cdot\mathbf{r}_y/\mathbf{a}\cdot\mathbf{r}_y)^2/2]$$

$$p(\mathbf{r}_z|z) \sim \exp[-\mathbf{a}\cdot\mathbf{r}_z(x - \mathbf{b}\cdot\mathbf{r}_z/\mathbf{a}\cdot\mathbf{r}_z)^2/2]$$

this is a linear PPC:

$$= \exp[-\mathbf{a}\cdot\mathbf{r}_x x^2/2 + \mathbf{b}\cdot\mathbf{r}_x x + (\mathbf{b}\cdot\mathbf{r}_x)^2/2\mathbf{a}\cdot\mathbf{r}_x]$$

$$= \varphi(\mathbf{r}_x) \exp[(-(x^2/2)\mathbf{a} + x\mathbf{b}) \cdot\mathbf{r}_x]$$

$\mathbf{h}(x)$

The real thing: a linear PPC

$$p(\mathbf{r}_x|x) \sim \exp[-\mathbf{a}\cdot\mathbf{r}_x(x - \mathbf{b}\cdot\mathbf{r}_x/\mathbf{a}\cdot\mathbf{r}_x)^2/2] \sim p(x|\mathbf{r}_x)$$

$$p(\mathbf{r}_y|y) \sim \exp[-\mathbf{a}\cdot\mathbf{r}_y(x - \mathbf{b}\cdot\mathbf{r}_y/\mathbf{a}\cdot\mathbf{r}_y)^2/2] \sim p(y|\mathbf{r}_y)$$

$$p(\mathbf{r}_z|z) \sim \exp[-\mathbf{a}\cdot\mathbf{r}_z(x - \mathbf{b}\cdot\mathbf{r}_z/\mathbf{a}\cdot\mathbf{r}_z)^2/2] \sim p(z|\mathbf{r}_z)$$

$$\mu_x = \mathbf{b}\cdot\mathbf{r}_x/\mathbf{a}\cdot\mathbf{r}_x$$
$$\sigma_x^2 = 1/\mathbf{a}\cdot\mathbf{r}_x$$

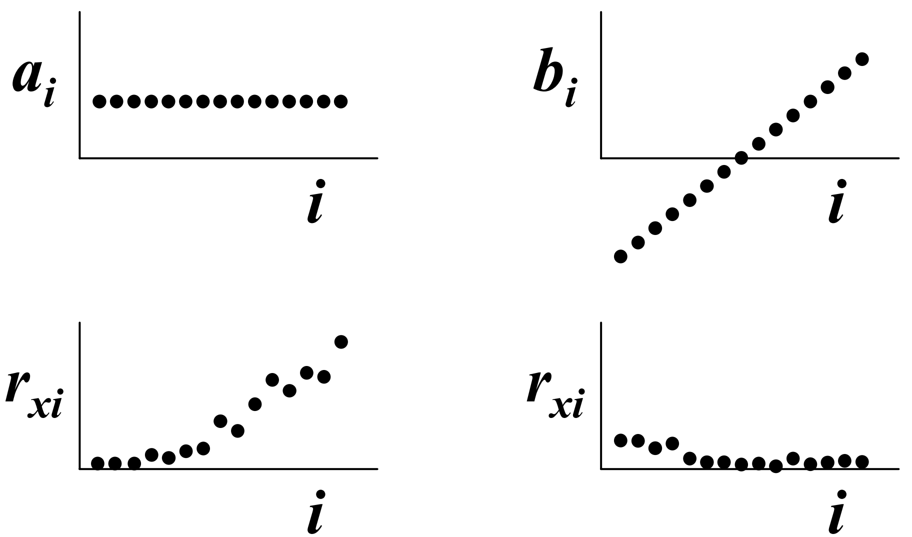
The real thing: a linear PPC

$$p(\mathbf{r}_x|x) \sim \exp[-\mathbf{a}\cdot\mathbf{r}_x(x - \mathbf{b}\cdot\mathbf{r}_x/\mathbf{a}\cdot\mathbf{r}_x)^2/2] \sim p(x|\mathbf{r}_x)$$

$$p(\mathbf{r}_y|y) \sim \exp[-\mathbf{a}\cdot\mathbf{r}_y(x - \mathbf{b}\cdot\mathbf{r}_y/\mathbf{a}\cdot\mathbf{r}_y)^2/2] \sim p(y|\mathbf{r}_y)$$

$$p(\mathbf{r}_z|z) \sim \exp[-\mathbf{a}\cdot\mathbf{r}_z(x - \mathbf{b}\cdot\mathbf{r}_z/\mathbf{a}\cdot\mathbf{r}_z)^2/2] \sim p(z|\mathbf{r}_z)$$

$$\mu_x = \mathbf{b}\cdot\mathbf{r}_x/\mathbf{a}\cdot\mathbf{r}_x$$
$$\sigma_x^2 = 1/\mathbf{a}\cdot\mathbf{r}_x$$



positive mean,
low variance

negative mean,
high variance

The real thing: a linear PPC

$$p(\mathbf{r}_x|x) \sim \exp[-\mathbf{a}\cdot\mathbf{r}_x(x - \mathbf{b}\cdot\mathbf{r}_x/\mathbf{a}\cdot\mathbf{r}_x)^2/2] \sim p(x|\mathbf{r}_x)$$

$$p(\mathbf{r}_y|y) \sim \exp[-\mathbf{a}\cdot\mathbf{r}_y(x - \mathbf{b}\cdot\mathbf{r}_y/\mathbf{a}\cdot\mathbf{r}_y)^2/2] \sim p(y|\mathbf{r}_y)$$

$$p(\mathbf{r}_z|z) \sim \exp[-\mathbf{a}\cdot\mathbf{r}_z(x - \mathbf{b}\cdot\mathbf{r}_z/\mathbf{a}\cdot\mathbf{r}_z)^2/2] \sim p(z|\mathbf{r}_z)$$

$$\mu_x = \mathbf{b}\cdot\mathbf{r}_x/\mathbf{a}\cdot\mathbf{r}_x$$
$$\sigma_x^2 = 1/\mathbf{a}\cdot\mathbf{r}_x$$

$$\mu_y = \mathbf{b}\cdot\mathbf{r}_y/\mathbf{a}\cdot\mathbf{r}_y$$
$$\sigma_y^2 = 1/\mathbf{a}\cdot\mathbf{r}_y$$

$$\mu_z = \mathbf{b}\cdot\mathbf{r}_z/\mathbf{a}\cdot\mathbf{r}_z$$
$$\sigma_z^2 = 1/\mathbf{a}\cdot\mathbf{r}_z$$

The real thing: a linear PPC

$$p(\mathbf{r}_x|x) \sim \exp[-\mathbf{a}\cdot\mathbf{r}_x(x - \mathbf{b}\cdot\mathbf{r}_x/\mathbf{a}\cdot\mathbf{r}_x)^2/2] \sim p(x|\mathbf{r}_x)$$

$$p(\mathbf{r}_y|y) \sim \exp[-\mathbf{a}\cdot\mathbf{r}_y(x - \mathbf{b}\cdot\mathbf{r}_y/\mathbf{a}\cdot\mathbf{r}_y)^2/2] \sim p(y|\mathbf{r}_y)$$

$$p(\mathbf{r}_z|z) \sim \exp[-\mathbf{a}\cdot\mathbf{r}_z(x - \mathbf{b}\cdot\mathbf{r}_z/\mathbf{a}\cdot\mathbf{r}_z)^2/2] \sim p(z|\mathbf{r}_z)$$

$$\mu_x = \mathbf{b}\cdot\mathbf{r}_x/\mathbf{a}\cdot\mathbf{r}_x$$
$$\sigma_x^2 = 1/\mathbf{a}\cdot\mathbf{r}_x$$

$$\mu_y = \mathbf{b}\cdot\mathbf{r}_y/\mathbf{a}\cdot\mathbf{r}_y$$
$$\sigma_y^2 = 1/\mathbf{a}\cdot\mathbf{r}_y$$

$$\mu_z = \mathbf{b}\cdot\mathbf{r}_z/\mathbf{a}\cdot\mathbf{r}_z = \mu_x + \mu_y$$
$$\sigma_z^2 = 1/\mathbf{a}\cdot\mathbf{r}_z = \sigma_x^2 + \sigma_y^2$$

goal

The real thing: a linear PPC

$$p(\mathbf{r}_x|x) \sim \exp[-\mathbf{a}\cdot\mathbf{r}_x(x - \mathbf{b}\cdot\mathbf{r}_x/\mathbf{a}\cdot\mathbf{r}_x)^2/2] \sim p(x|\mathbf{r}_x)$$

$$p(\mathbf{r}_y|y) \sim \exp[-\mathbf{a}\cdot\mathbf{r}_y(x - \mathbf{b}\cdot\mathbf{r}_y/\mathbf{a}\cdot\mathbf{r}_y)^2/2] \sim p(y|\mathbf{r}_y)$$

$$p(\mathbf{r}_z|z) \sim \exp[-\mathbf{a}\cdot\mathbf{r}_z(x - \mathbf{b}\cdot\mathbf{r}_z/\mathbf{a}\cdot\mathbf{r}_z)^2/2] \sim p(z|\mathbf{r}_z)$$

$$\mu_x = \mathbf{b}\cdot\mathbf{r}_x/\mathbf{a}\cdot\mathbf{r}_x$$
$$\sigma_x^2 = 1/\mathbf{a}\cdot\mathbf{r}_x$$

$$\mu_y = \mathbf{b}\cdot\mathbf{r}_y/\mathbf{a}\cdot\mathbf{r}_y$$
$$\sigma_y^2 = 1/\mathbf{a}\cdot\mathbf{r}_y$$

$$\mu_z = \mathbf{b}\cdot\mathbf{r}_z/\mathbf{a}\cdot\mathbf{r}_z = \mu_x + \mu_y = \mathbf{b}\cdot\mathbf{r}_x/\mathbf{a}\cdot\mathbf{r}_x + \mathbf{b}\cdot\mathbf{r}_y/\mathbf{a}\cdot\mathbf{r}_y$$
$$\sigma_z^2 = 1/\mathbf{a}\cdot\mathbf{r}_z = \sigma_x^2 + \sigma_y^2 = 1/\mathbf{a}\cdot\mathbf{r}_x + 1/\mathbf{a}\cdot\mathbf{r}_y$$

goal

$$\mathbf{r}_z = \frac{\mathbf{a}}{\mathbf{a}\cdot\mathbf{a}}\,\frac{\mathbf{a}\cdot\mathbf{r}_x\ \mathbf{a}\cdot\mathbf{r}_y}{\mathbf{a}\cdot\mathbf{r}_x + \mathbf{a}\cdot\mathbf{r}_y} + \frac{\mathbf{b}}{\mathbf{b}\cdot\mathbf{b}}\,\frac{\mathbf{a}\cdot\mathbf{r}_x\ \mathbf{b}\cdot\mathbf{r}_y + \mathbf{a}\cdot\mathbf{r}_y\ \mathbf{b}\cdot\mathbf{r}_x}{\mathbf{a}\cdot\mathbf{r}_x + \mathbf{a}\cdot\mathbf{r}_y} + \mathbf{c}\ f(\mathbf{r}_x, \mathbf{r}_y)$$

$\mathbf{a}\cdot\mathbf{b} = 0$

$\mathbf{a}\cdot\mathbf{c} = \mathbf{b}\cdot\mathbf{c} = 0$

$$\mathbf{a}\cdot\mathbf{r}_z = \frac{\mathbf{a}\cdot\mathbf{r}_x\ \mathbf{a}\cdot\mathbf{r}_y}{\mathbf{a}\cdot\mathbf{r}_x + \mathbf{a}\cdot\mathbf{r}_y}$$

$$\mathbf{b}\cdot\mathbf{r}_z = \frac{\mathbf{a}\cdot\mathbf{r}_x\ \mathbf{b}\cdot\mathbf{r}_y + \mathbf{a}\cdot\mathbf{r}_x\ \mathbf{b}\cdot\mathbf{r}_y}{\mathbf{a}\cdot\mathbf{r}_x + \mathbf{a}\cdot\mathbf{r}_y}$$

$$\mathbf{b}\cdot\mathbf{r}_z/\mathbf{a}\cdot\mathbf{r}_z = \mathbf{b}\cdot\mathbf{r}_x/\mathbf{a}\cdot\mathbf{r}_x + \mathbf{b}\cdot\mathbf{r}_y/\mathbf{a}\cdot\mathbf{r}_y$$

$$1/\mathbf{a}\cdot\mathbf{r}_z = 1/\mathbf{a}\cdot\mathbf{r}_x + 1/\mathbf{a}\cdot\mathbf{r}_y$$

goal

$$\mathbf{r}_z = \frac{\mathbf{a}}{\mathbf{a}\cdot\mathbf{a}} \frac{\mathbf{a}\cdot\mathbf{r}_x \; \mathbf{a}\cdot\mathbf{r}_y}{\mathbf{a}\cdot\mathbf{r}_x + \mathbf{a}\cdot\mathbf{r}_y} + \frac{\mathbf{b}}{\mathbf{b}\cdot\mathbf{b}} \frac{\mathbf{a}\cdot\mathbf{r}_x \; \mathbf{b}\cdot\mathbf{r}_y + \mathbf{a}\cdot\mathbf{r}_y \; \mathbf{b}\cdot\mathbf{r}_x}{\mathbf{a}\cdot\mathbf{r}_x + \mathbf{a}\cdot\mathbf{r}_y} + \mathbf{c}\, \mathbf{f}(\mathbf{r}_x, \mathbf{r}_y)$$

quadratic nonlinearity: $\sum_{jk} w_{ijk}\, r_{xj}\, r_{yk}$

$$\mathbf{r}_z = \frac{\mathbf{a}}{\mathbf{a}\cdot\mathbf{a}} \frac{\mathbf{a}\cdot\mathbf{r}_x\,\mathbf{a}\cdot\mathbf{r}_y}{\mathbf{a}\cdot\mathbf{r}_x + \mathbf{a}\cdot\mathbf{r}_y} + \frac{\mathbf{b}}{\mathbf{b}\cdot\mathbf{b}} \frac{\mathbf{a}\cdot\mathbf{r}_x\,\mathbf{b}\cdot\mathbf{r}_y + \mathbf{a}\cdot\mathbf{r}_y\,\mathbf{b}\cdot\mathbf{r}_x}{\mathbf{a}\cdot\mathbf{r}_x + \mathbf{a}\cdot\mathbf{r}_y} + \mathbf{c}\, \mathbf{f}(\mathbf{r}_x, \mathbf{r}_y)$$

quadratic nonlinearity: $\sum_{jk} w_{ijk}\, r_{xj}\, r_{yk}$

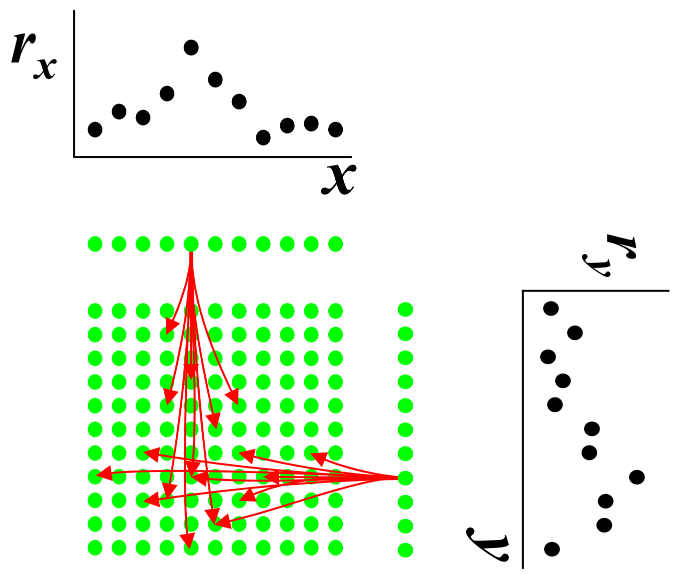
divisive normalization

$$\mathbf{r}_z = \frac{\mathbf{a}}{\mathbf{a}\cdot\mathbf{a}}\,\frac{\mathbf{a}\cdot\mathbf{r}_x\;\mathbf{a}\cdot\mathbf{r}_y}{\mathbf{a}\cdot\mathbf{r}_x + \mathbf{a}\cdot\mathbf{r}_y} + \frac{\mathbf{b}}{\mathbf{b}\cdot\mathbf{b}}\,\frac{\mathbf{a}\cdot\mathbf{r}_x\;\mathbf{b}\cdot\mathbf{r}_y + \mathbf{a}\cdot\mathbf{r}_y\;\mathbf{b}\cdot\mathbf{r}_x}{\mathbf{a}\cdot\mathbf{r}_x + \mathbf{a}\cdot\mathbf{r}_y} + c\,\mathbf{f}(\mathbf{r}_x, \mathbf{r}_y)$$

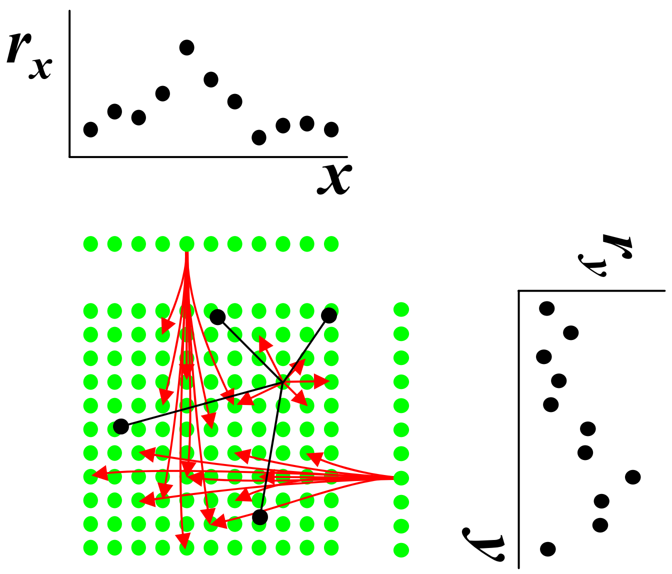
quadratic nonlinearity: $\sum_{jk} w_{ijk}\, r_{xj}\, r_{yk}$

divisive normalization

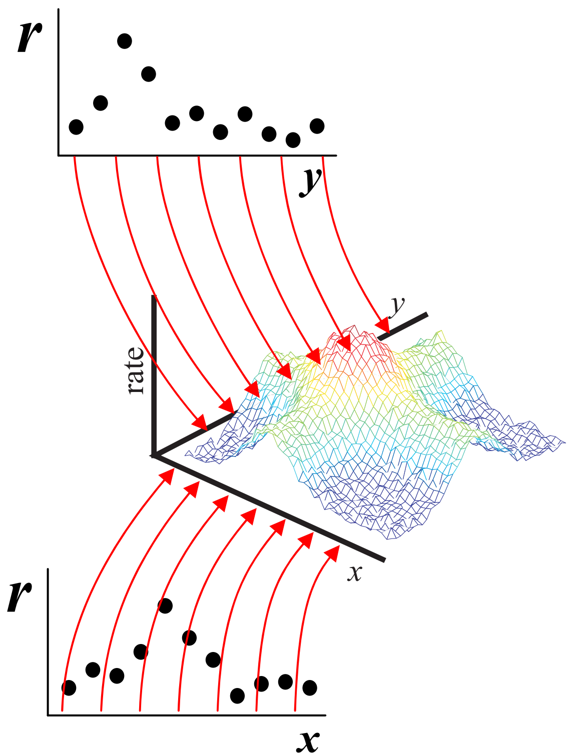
The optimal network has a quadratic nonlinearity and divisive normalization.

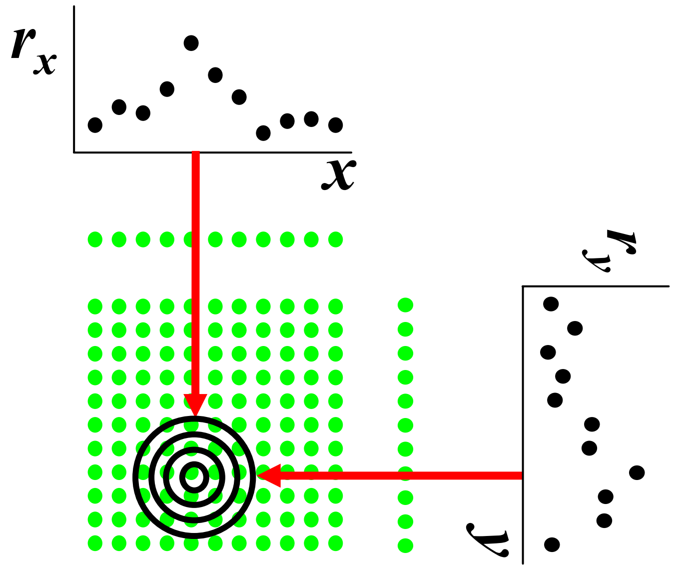


r_x
x
r_y
y

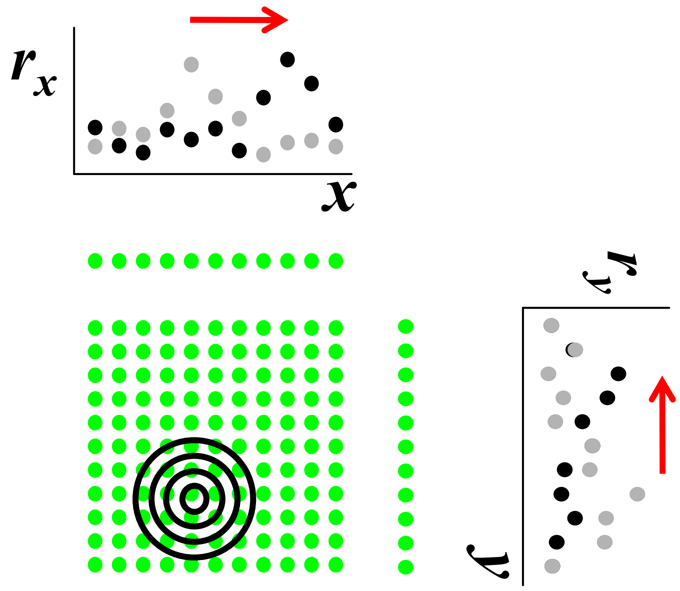


r_x
x
r_y
y

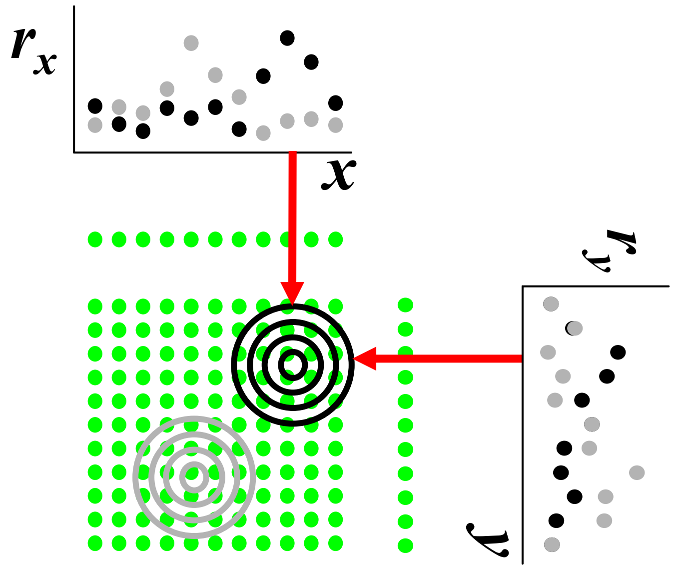

r
y
rate
y
x
r
x



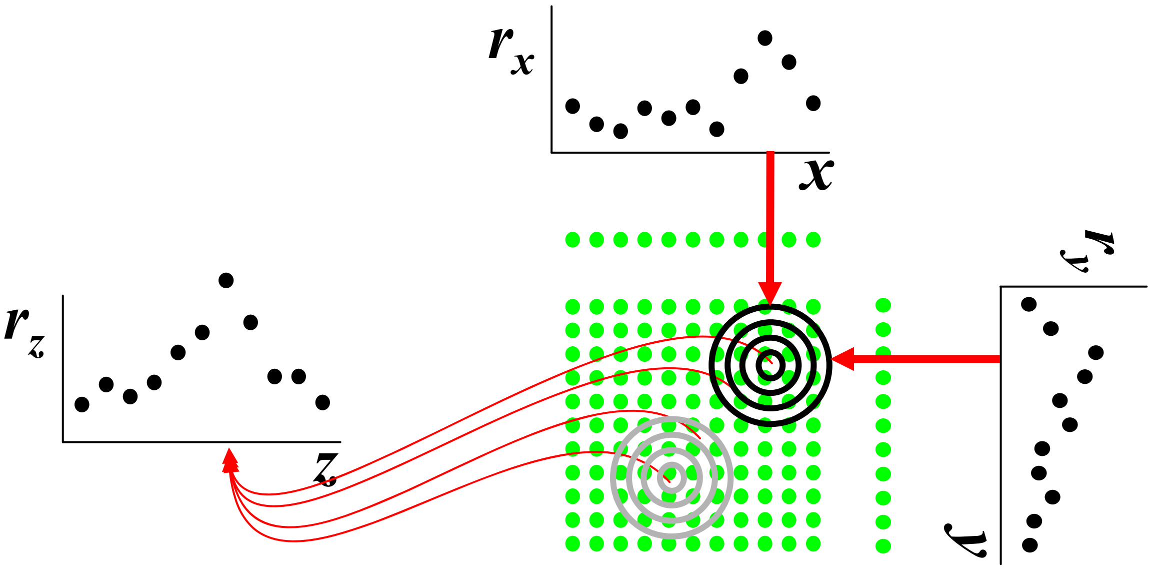
r_x
x
r_y
y



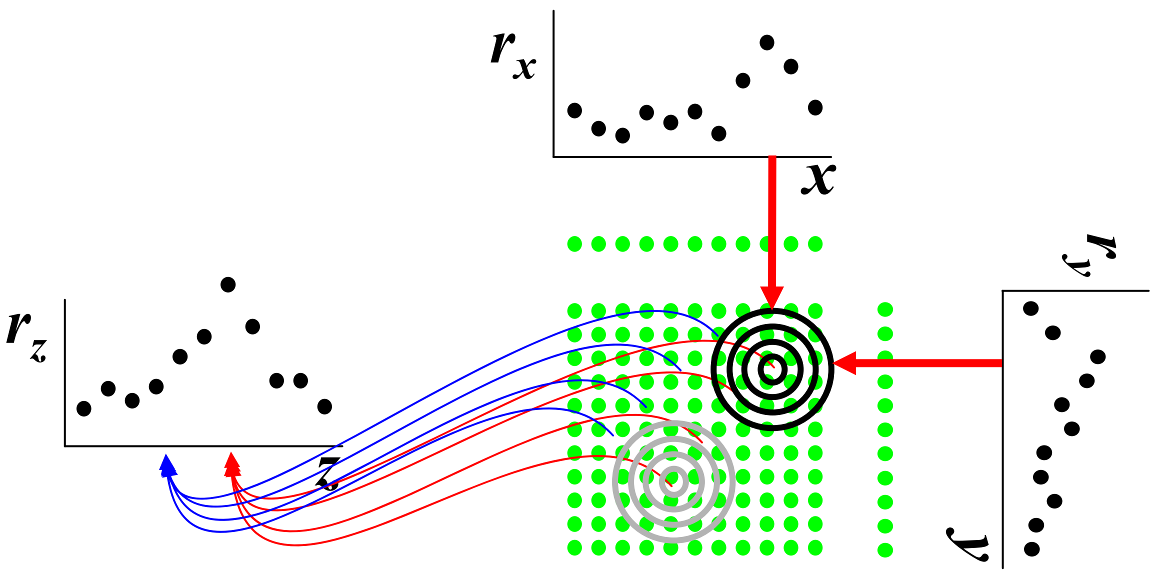
r_x
x
r_y
y



r_x
x
r_y
y



r_x
x
r_y
y
r_z
z

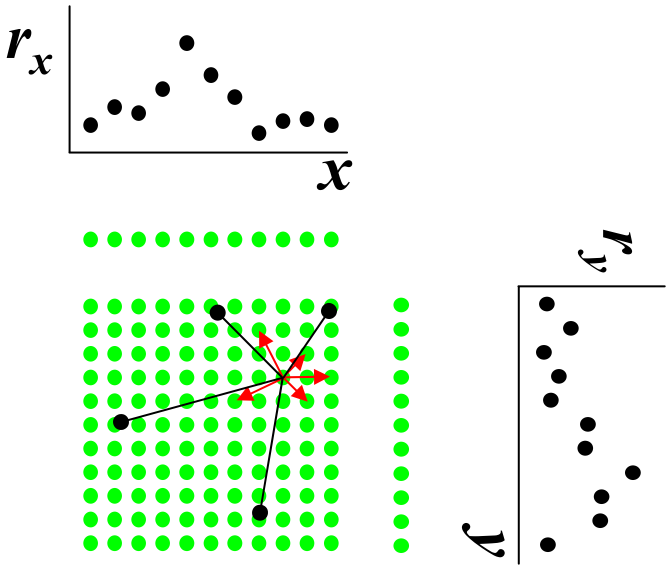


Deneve et al., *Nature Neurosci.* (2001)

the new analysis tells us exactly what the recurrent connections need to do:

they need to produce a hill of activity whose amplitude scales as

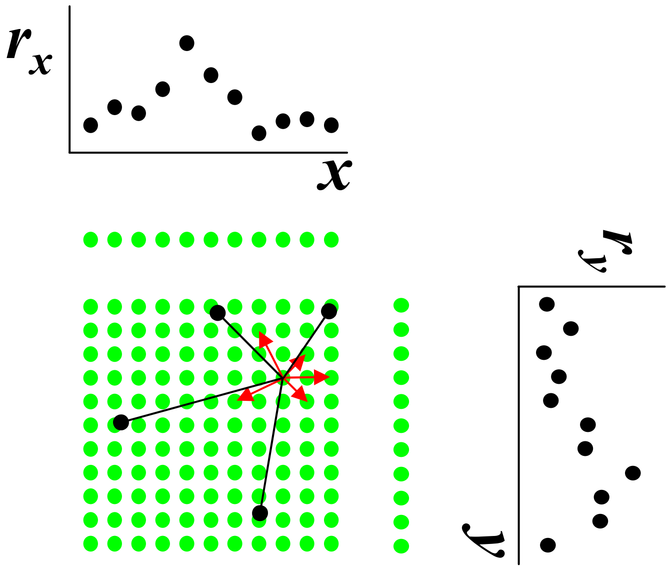
$$\frac{\mathbf{r}_{xi}\,\mathbf{r}_{yj}}{\sum_i \mathbf{a}_i\,\mathbf{r}_{xi} + \mathbf{a}_i\,\mathbf{r}_{yi}}$$

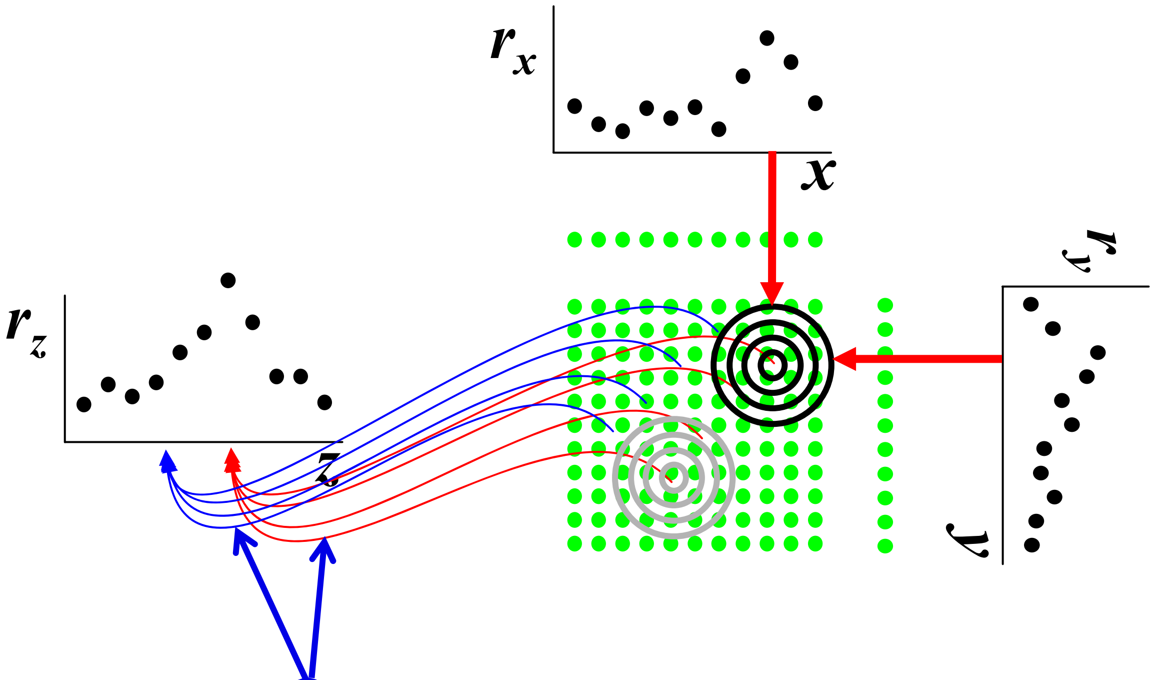


the new analysis tells us exactly what the recurrent connections need to do:

they need to produce a hill of activity whose amplitude scales as

$$\frac{\alpha r_{xi} + \beta r_{yi} + \gamma r_{xi}\, r_{yj}}{\sum_i a_i\, r_{xi} + a_i\, r_{yi}}$$





$$\frac{\sum_{jk} w_{ijk}\, r_{xj}\, r_{yk}}{\sum_i \mathbf{a}_i\, \mathbf{r}_{xi} + \mathbf{a}_i\, \mathbf{r}_{yi}}$$

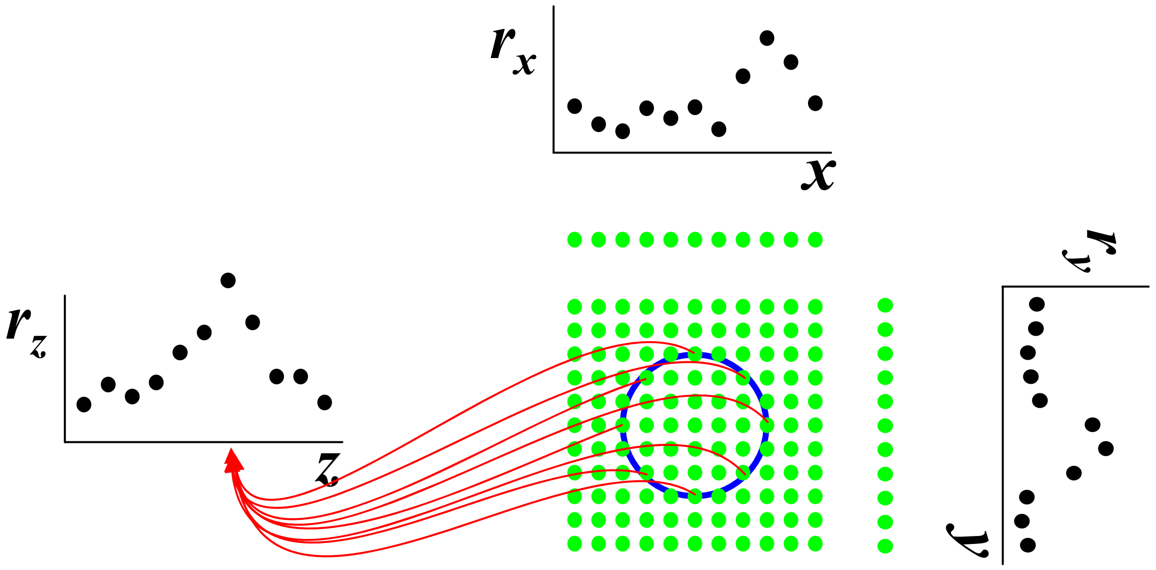
An aside: our network is deterministic,

$$\mathbf{r}_z = \frac{\mathbf{a}}{\mathbf{a}\cdot\mathbf{a}} \frac{\mathbf{a}\cdot\mathbf{r}_x\ \mathbf{a}\cdot\mathbf{r}_y}{\mathbf{a}\cdot\mathbf{r}_x + \mathbf{a}\cdot\mathbf{r}_y} + \frac{\mathbf{b}}{\mathbf{b}\cdot\mathbf{b}} \frac{\mathbf{a}\cdot\mathbf{r}_x\ \mathbf{b}\cdot\mathbf{r}_y + \mathbf{a}\cdot\mathbf{r}_y\ \mathbf{b}\cdot\mathbf{r}_x}{\mathbf{a}\cdot\mathbf{r}_x + \mathbf{a}\cdot\mathbf{r}_y} + \mathbf{c}\ \mathbf{f}(\mathbf{r}_x, \mathbf{r}_y)$$

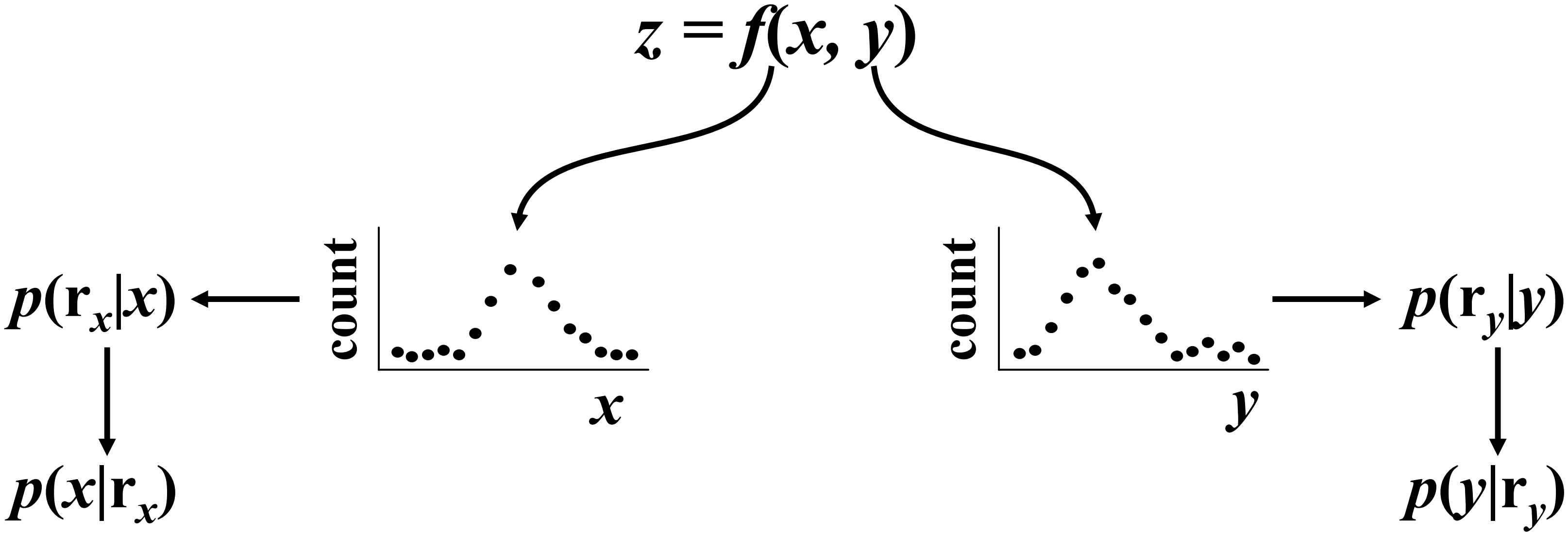
If neurons are sufficiently uncorrelated, we can replace rates with spikes, and the information loss will scale as 1/*N*.

This information loss is negligible compared to the loss associated with approximate computations.

can handle nonlinear functions (e.g., $z=x^2+y^2$)



the hard part is choosing the recurrent connectivity properly.



$$p(z|\mathrm{r}_x, \mathrm{r}_y) = \int dxdy\ \delta(z - f(x, y))\ p(x|\mathrm{r}_x)\ p(y|\mathrm{r}_y)$$

hard integral!

$$p(z|\mathbf{r}_x, \mathbf{r}_y) = \int dx\,dy\; \delta(z - f(x, y))\; p(x|\mathbf{r}_x)\; p(y|\mathbf{r}_y)$$

hard integral!

$$\mathbf{r}_z = \mathbf{F}(\mathbf{r}_x, \mathbf{r}_y) \leftarrow \textbf{network}$$

$$p(z|\mathbf{r}_z) = p(z|\mathbf{F}(\mathbf{r}_x, \mathbf{r}_y)) = p(z|\mathbf{r}_x, \mathbf{r}_y)$$

goal

approach: minimize

$$D_{KL}\left(p(z|\mathbf{r}_x, \mathbf{r}_y) \| p(z|\mathbf{r}_z)\right)$$

$$\mathbf{r}_z = \mathbf{F}(\mathbf{r}_x, \mathbf{r}_y)$$

network

network: $\mathbf{r}_z = \mathrm{F}(\mathbf{r}_x, \mathbf{r}_y; \Theta)$

minimize: $\mathrm{D}_{\mathrm{KL}}\left(p(z|\mathbf{r}_x, \mathbf{r}_y) \,||\, q(z|\mathbf{r}_z)\right)$

with respect to network parameters and parameters of encoding model

problem #1: there's a trivial solution,

$$\mathbf{r}_z = (\mathbf{r}_x, \mathbf{r}_y)$$

solution: demand that

$$p(z|\mathbf{r}_z) \sim \exp[\mathbf{h}(z)\cdot\mathbf{r}_z]$$

pure code!

minimize

$$D_{KL}\left(p(z|\mathbf{r}_x, \mathbf{r}_y)\,||\,\exp[\mathbf{h}(z)\cdot\mathbf{r}_z]/Z\right)$$

problem #2: what class of networks do we consider?

$$r_{zi} = \frac{\sum_j w_{ij}^x r_{xj} + \sum_j w_{ij}^y r_{yj} + \sum_{jk} w_{ijk} r_{xj} r_{yk}}{\alpha_i + w_i \sum_j \mathbf{a}_j \mathbf{r}_{xj} + \mathbf{a}_j \mathbf{r}_{yj}}$$

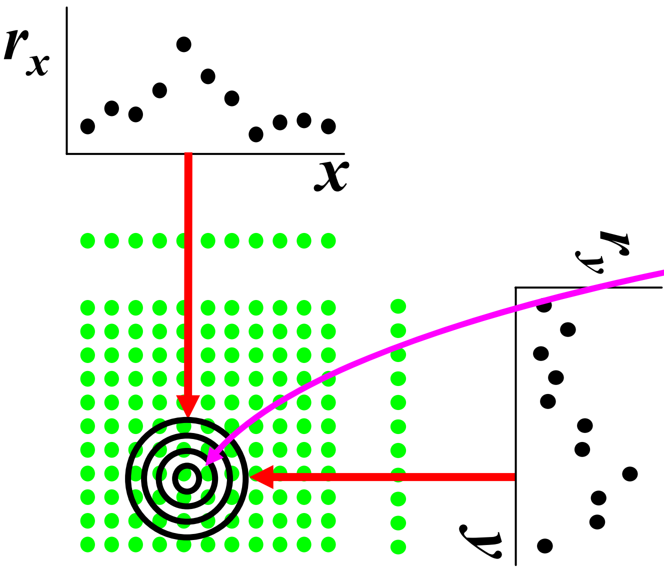
minimize

$$D_{KL}\left(p(z|\mathbf{r}_x, \mathbf{r}_y) \,||\, \exp[\mathbf{h}(z)\cdot\mathbf{r}_z]/Z\right)$$

with respect to h(z) and the parameters of the network,

$$r_{zi} = \frac{\sum_j w_{ij}^x r_{xj} + \sum_j w_{ij}^y r_{yj} + \sum_{jk} w_{ijk} r_{xj} r_{yk}}{\alpha_i + w_i \sum_j \mathbf{a}_j \mathbf{r}_{xj} + \mathbf{a}_j \mathbf{r}_{yj}}$$

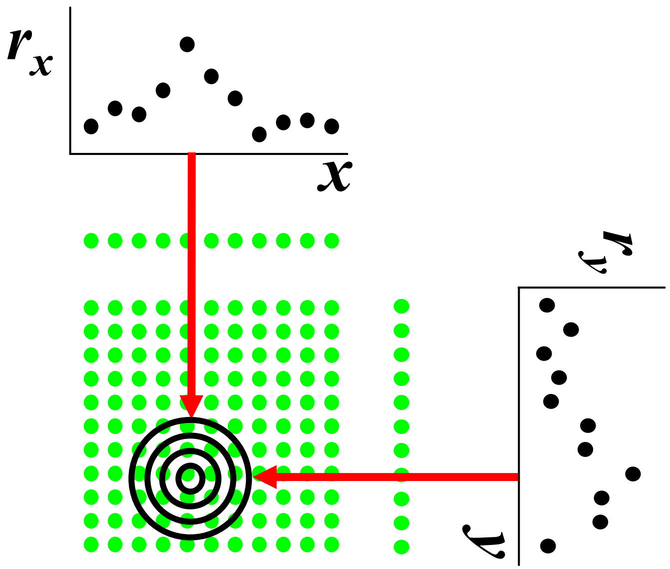
intuition



$$r_{zi} = \frac{\sum_j w^{x}_{ij}\, r_{xj} + \sum_j w^{y}_{ij}\, r_{yj} + \sum_{jk} w_{ijk}\, r_{xj}\, r_{yk}}{\alpha_i + w_i \sum_j \mathbf{a}_j\, \mathbf{r}_{xj} + \mathbf{a}_j\, \mathbf{r}_{yj}}$$

- quadratic nonlinearity produces a hill of activity
- divisive normalization corrects for it

intuition



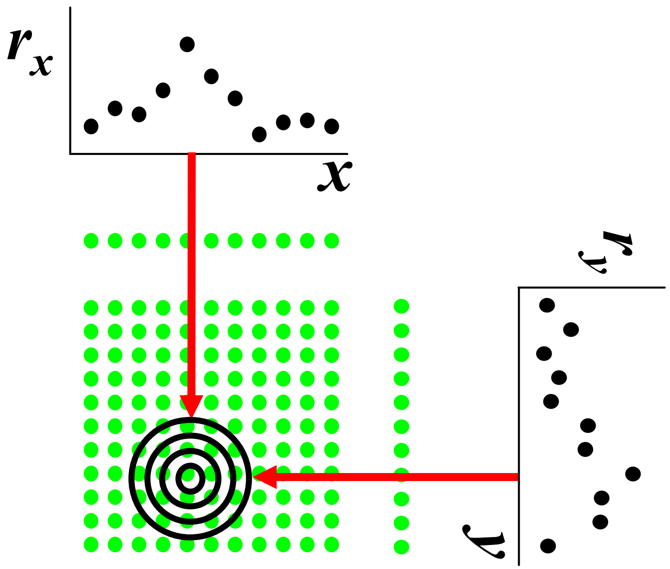
$$r_z = \frac{r_x r_y}{r_x + r_y}$$

$$1/r_z = 1/r_x + 1/r_x$$

$$\sigma_z^2 \sim 1/r_z$$

$$z = f(x, y) \Rightarrow \sigma_z^2 = \alpha\sigma_x^2 + \beta\sigma_y^2$$

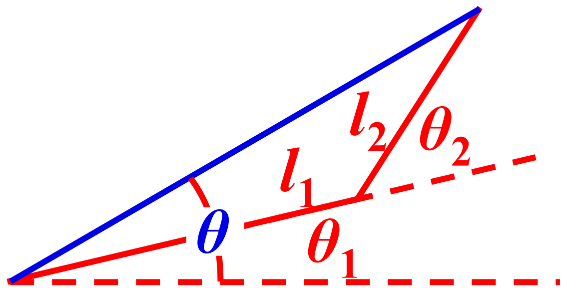
intuition



$$r_{zi} = \frac{\sum_j w^x_{ij}\, r_{xj} + \sum_j w^y_{ij}\, r_{yj} + \sum_{jk} w_{ijk}\, r_{xj}\, r_{yk}}{\alpha_i + w_i \sum_j \mathbf{a}_j\, \mathbf{r}_{xj} + \mathbf{a}_j\, \mathbf{r}_{yj}}$$

$z = f(x, y)$ => $\sigma_z^2 = \alpha\sigma_x^2 + \beta\sigma_y^2$

2-joint arm



$$\theta = \tan^{-1} \frac{l_1 \sin(\theta_1) + l_2 \sin(\theta_1 + \theta_2)}{l_1 \cos(\theta_1) + l_2 \cos(\theta_1 + \theta_2)}$$

$$p(\mathrm{r}|\theta) \sim \exp[\, \textstyle\sum_i \cos(\theta - \varphi_i)\, r_i \,]$$

minimize

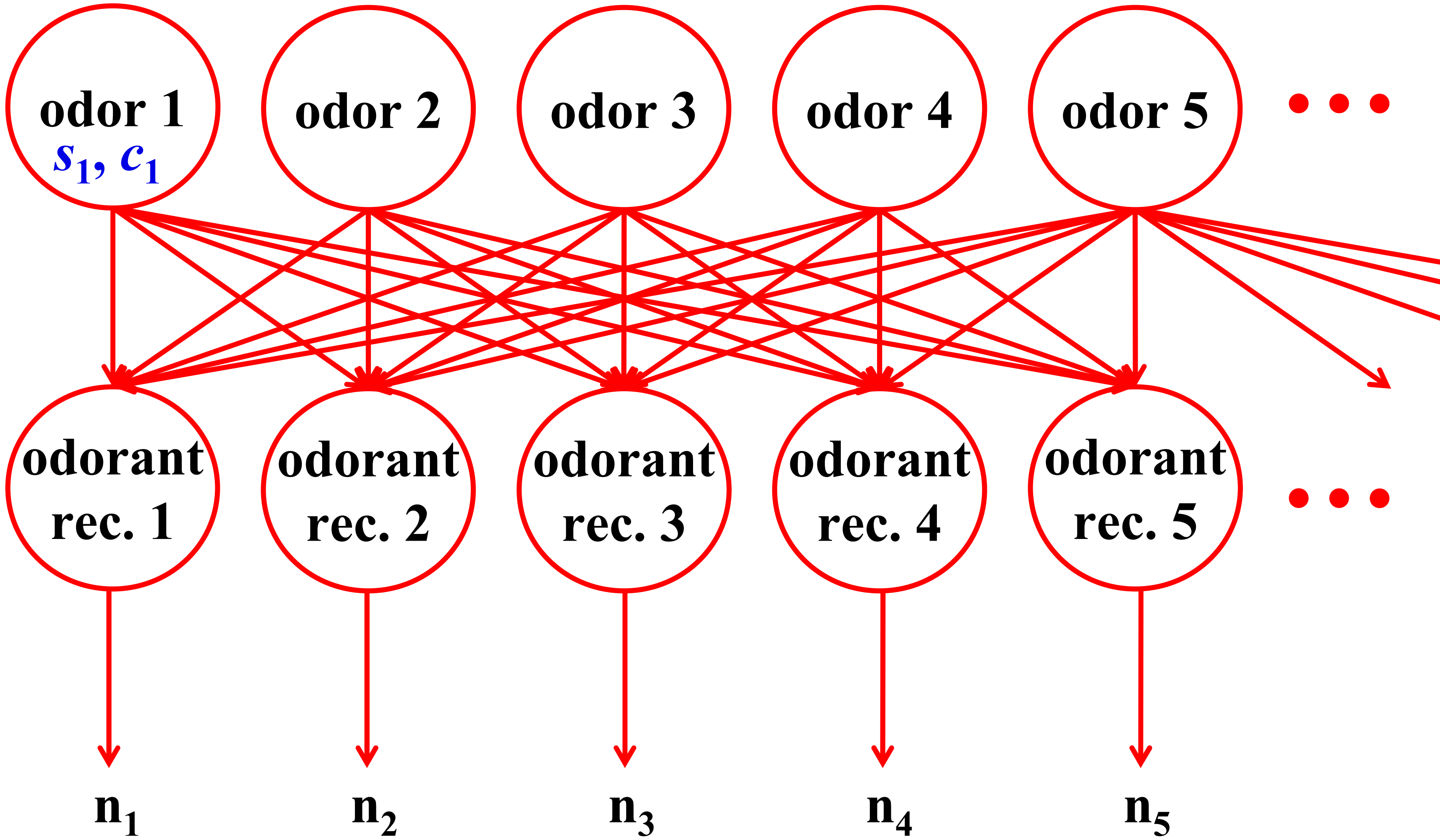
$$D_{KL}\left(p(\theta|\mathbf{r}_1, \mathbf{r}_2)\,\middle\|\,\exp[\mathbf{h}(\theta)\cdot\mathbf{r}]/Z\right)$$

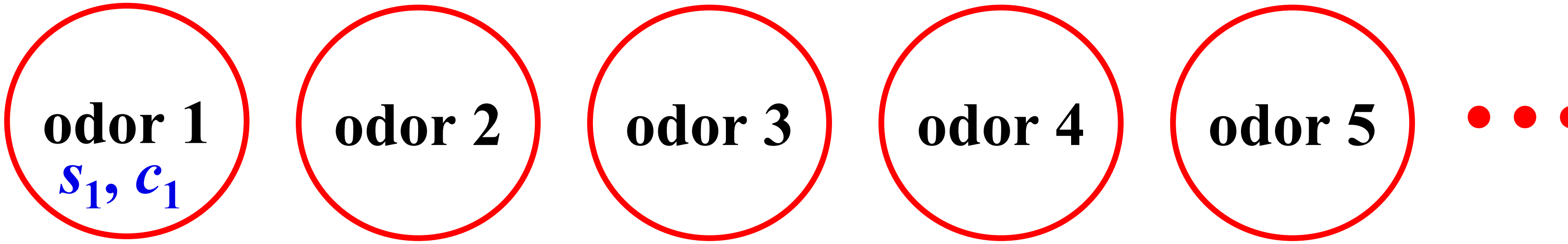
with respect to the parameters of the network

$$r_i = \frac{\sum_j w_{ij}^1 r_{1j} + \sum_j w_{ij}^2 r_{2j} + \sum_{jk} w_{ijk} r_{1j} r_{2k}}{\alpha_i + w_i \sum_j \mathbf{a}_j \mathbf{r}_{1j} + \mathbf{a}_j \mathbf{r}_{2j}}$$

$$\frac{D_{KL}\left(p(\theta|\mathbf{r}_1, \mathbf{r}_2)\,\middle\|\,p(\theta|\mathbf{r})\right)}{I(\theta; \mathbf{r}_1, \mathbf{r}_2)} \approx 0.05 \text{ (5\% information loss)}$$

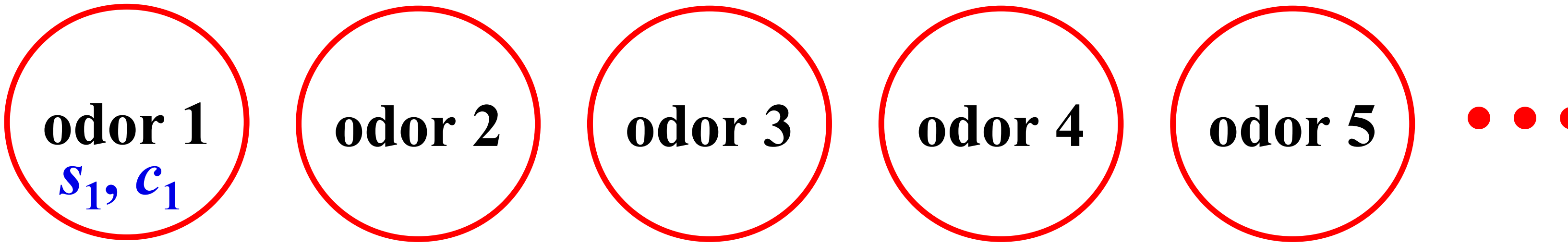
3: a hard problem (simplified olfaction)





s: 0=absent
1=present

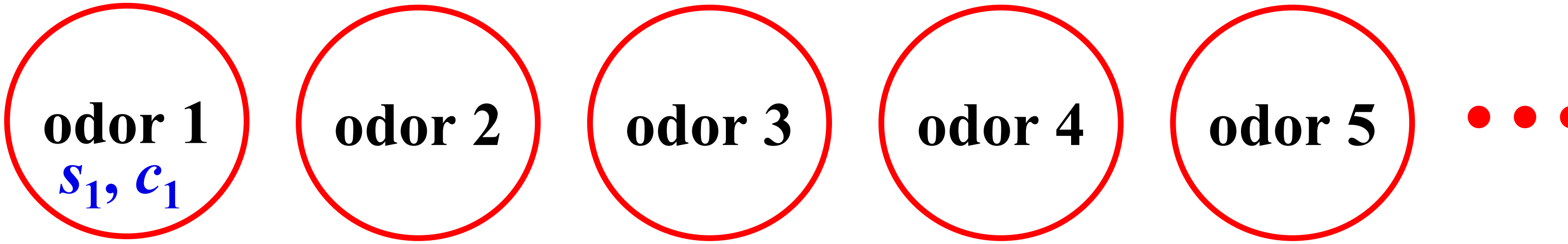
c: concentration



$$o_i = \sum_j W_{ij}\, s_j c_j$$

$$p(\mathbf{n}_i \,|\, o_i) \sim \exp[\mathbf{h}(o_i)\cdot\mathbf{n}_i]$$

goal: compute $p(s_i |\, \mathbf{n}_1, \mathbf{n}_2, \mathbf{n}_3, \ldots)$

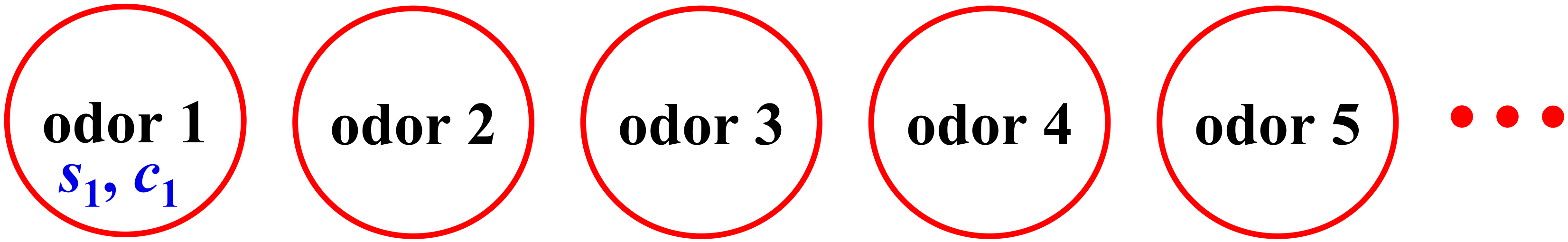


find a network

$$n_i^{\text{out}} = F(n_1, n_2, \ldots)$$

such that

$$p(s_i | n_i^{\text{out}}) = p(s_i | n_1, n_2, \ldots)$$



Intractible:

$$p(s_i|\mathrm{n}_1, \mathrm{n}_2, \ldots) = \sum_{\{s_i,\, j \neq i\}} \int \mathrm{dc}\; p(s_1, c_1, s_2, c_2, \ldots|\mathrm{n}_1, \mathrm{n}_2, \ldots)$$

***k* odors:**

2^{k-1} terms in the sum

***k*-dimensional integral**

minimize

$$\mathrm{D_{KL}}\Big(p(s_i|\mathrm{n}_1, \mathrm{n}_2, \ldots)\Big|\Big|\exp[\mathrm{h}(s_i)\cdot \mathrm{n}_i^{\mathrm{out}}]/Z\Big)$$

with respect to the parameters of the network

$$n_i^{\mathrm{out}} = \frac{\sum_{jk} w_{ij}^{k} n_{kj} + \sum_{jk} w_{ijk}^{km} n_{lj} n_{mk}}{\alpha_i + w_i \sum_{jk} \mathrm{a}_j^{k} n_{kj}}$$

$$\frac{\mathrm{D_{KL}}\Big(p(s_i|\mathrm{n}_1, \mathrm{n}_2, \mathrm{n}_3, \mathrm{n}_4)\Big|\Big|p(s_i|\mathrm{n}_i^{\mathrm{out}})\Big)}{I(s_i; \mathrm{n}_1, \mathrm{n}_2, \mathrm{n}_3, \mathrm{n}_4)} \approx 0.02 \text{ (2\% information loss)}$$

4 odors:

$$\frac{\mathrm{D_{KL}}\left(p(s_i|\mathrm{n}_1, \mathrm{n}_2, \mathrm{n}_3, \mathrm{n}_4)\,\middle\|\,p(s_i|\mathrm{n}_i^{\mathrm{out}})\right)}{I(s_i; \mathrm{n}_1, \mathrm{n}_2, \mathrm{n}_3, \mathrm{n}_4)} \approx 0.02 \text{ (2\% information loss)}$$

100s of odors:

work in progress

Summary

Our approach: minimize

$$D_{KL}\left(p(\xi|\mathbf{r}^{in})\,\|\,\exp[\mathbf{h}(\xi)\cdot\mathbf{r}^{out}]/Z\right)$$

$(x, y, z, \ldots)$

$\xi = f(x, y, z, \ldots)$

with respect to the parameters of the network

$$r_i^{\text{out}} = \frac{\sum_j w_{ij}\, r_j^{\text{in}} + \sum_{jk} w_{ijk}\, r_j^{\text{in}}\, r_k^{\text{in}}}{\alpha_i + w_i \sum_j \mathrm{a}_j\, \mathrm{r}_j^{\text{in}}}$$

Summary

Our approach: minimize

$$D_{KL}\left(p(\xi|\mathbf{r}^{in})\,\|\,\exp[\mathbf{h}(\xi)\cdot\mathbf{r}^{out}]/Z\right)$$

$q(\xi|x, y, z, \ldots)$

$(x, y, z, \ldots)$

with respect to the parameters of the network

$$r_i^{\text{out}} = \frac{\sum_j w_{ij}\, r_j^{\text{in}} + \sum_{jk} w_{ijk}\, r_j^{\text{in}}\, r_k^{\text{in}}}{\alpha_i + w_i \sum_j a_j\, r_j^{\text{in}}}$$

Summary

Our approach: minimize

$$D_{KL}\left(p(\xi|\mathrm{r}^{in})\,\middle\|\,\exp[\mathrm{h}(\xi)\cdot\mathrm{r}^{out}]/Z\right)$$

$p(\xi|\mathrm{r}^{in}) \rightarrow (x, y, z, \ldots)$

$\exp[\mathrm{h}(\xi)\cdot\mathrm{r}^{out}]/Z \rightarrow q(\xi|x, y, z, \ldots)$

Just finding $p(\xi|\mathrm{r}^{in})$ is a hard inference problem,

$$p(\xi|\mathrm{r}^{in}) = \int dx\, dy\, dz\, \ldots\, \delta(\xi - \mathrm{f}(x, y, z, \ldots))\, p(x, y, z, \ldots\, |\mathrm{r}^{in})$$

implementing it in a network is even harder.

$$p(\xi|\mathbf{r}^{in}) = \int dx\, dy\, dz\, \ldots\, \delta(\xi - f(x, y, z, \ldots))\, p(x, y, z, \ldots\, |\mathbf{r}^{in})$$

We have to do approximate inference.

- **parameterized probability distributions.**

- **approximate networks, chosen by minimizing a cost function.**

I talked about one parameterization and one class of networks. The big open questions:

what is the appropriate parameterization for the brain?
what is the appropriate class of networks?
how is all this learned?

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