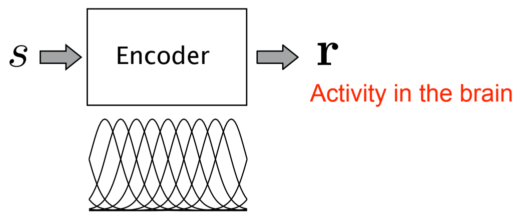
1. Encoding (continued)

readings: encoding D&A ch.1

Encoding problem: $P[\mathbf{r}|s]$

What is the relationship between stimuli in the world and the activity of the brain?



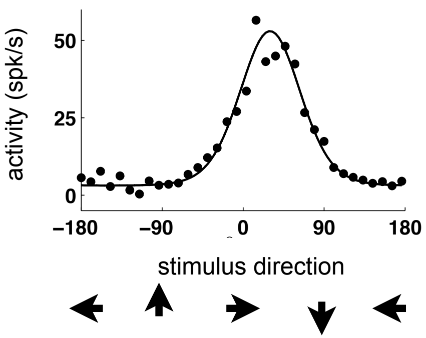
properties of neurons

Single cell tuning curves vs population response

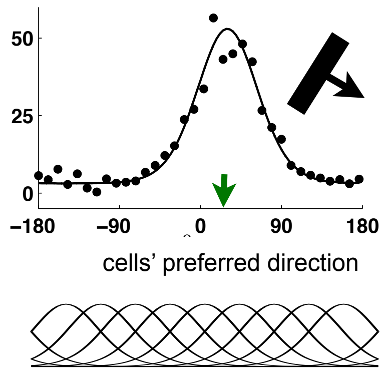
Single cell tuning curve: change stimulus, record spike count for every stimulus

Population response: keep stimulus fixed, record spike count of every neuron in the population

one cell -- many stimuli



many cells -- one stimulus

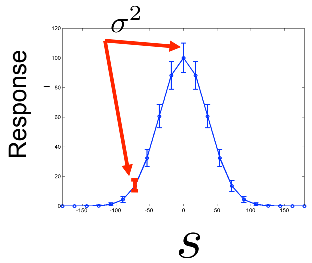


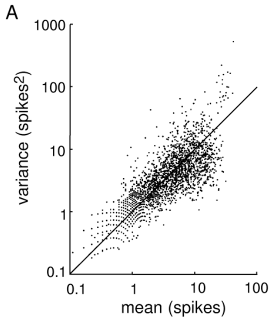
2. Describing 'the noise'

- Beyond describing only the mean spike count ...
- To model the statistics of the response (one trial), we can use tools from probability theory: stochastic (random) processes.
- The spike count *r* on one trial is considered as a random variable.
- The probability of getting each outcome (n=1,2 .., 10, 50 spikes) is given by a probability distribution for which we want to find a suitable model.
- To do that, we use known statistics of *n*: the mean $<n>=f(s)$ and 2d order statistics (variance, correlations).

Describing the variance of the spike count

- Measure the variance of the spike count, for a number of repetitions with the same stimulus.
- Experiments show that the variance of the spike count is linearly related to the mean spike count (with prop. const ~1).
- Noise is often described as Poisson, or Gaussian with a variance proportional to the mean.





$$var(n) = F * mean(n)$$

F: Fano Factor

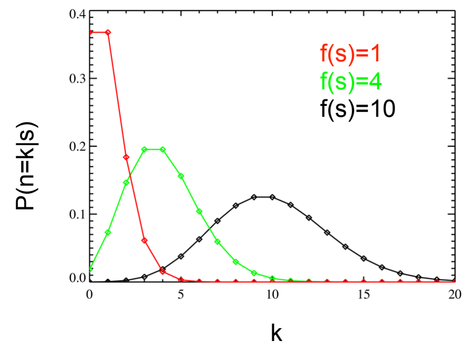
[O Keefe, 1997 - MT cortex]

a) Poisson Distribution

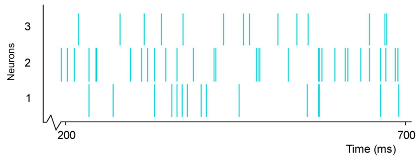
- Probability of a spike count (positive integer -- discrete probability distribution) occurring in a fixed period of time, knowing average spike count f(s)
- The assumption is that the generation of each spike (and its stochasticity) is independent of all other spikes

$$P(n = k|s) = \frac{e^{-f(s)} f(s)^k}{k!}$$

e.g. if f(s)=10, P(n=10|s)=0.125
P(n=7|s)=0.09
P(n=3|s)=0.007



a) Poisson Distribution



How to construct a Poisson Spike train

- Divide time window T into N bins. p=probability of spiking in each bin.
- In each bin, toss a coin with probability P(head)=p, if you get a head, record a spike.
- For small p, the number of spikes in T follows a Poisson distribution.

Properties

- variance(spike count) = mean(spike count). (~data)
- Inter-spike intervals (ISI) follow an exponential distribution (~data, except for very short intervals(refractory period) and for bursting neurons).

- Poisson model can be made to include a refractory period
- Homogeneous: mean spike count is fixed in time window f(s) / Inhomogeneous -- changing in time window :f(s,t).

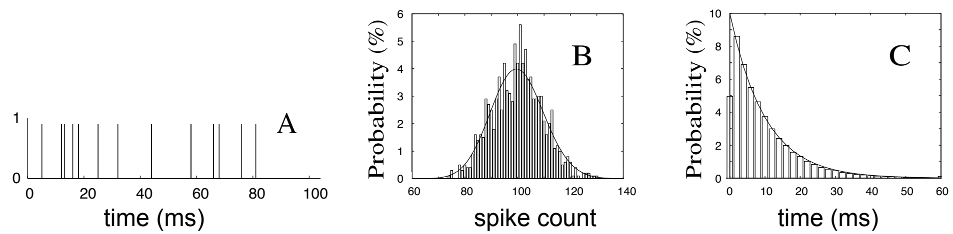
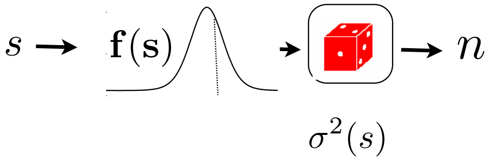


Figure 1: **A.** Snippet of a Poisson spike train with $r = 100$ and $\delta t = 1$ msec. **B.** Spike count histogram calculated from many Poisson spike trains, each of 1 sec duration with $r = 100$, superimposed with the theoretical (Poisson) spike count density. **C.** Interspike interval histogram calculated from the simulated Poisson spike trains superimposed with the theoretical (exponential) interspike interval density.

b) Gaussian distribution



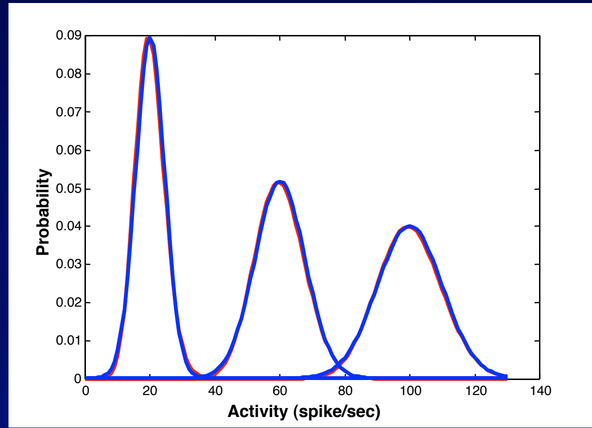
- Another model that is commonly used to describe the variability of the spike count is the Gaussian noise model.
- The activity of a neuron (number of spikes) can be described as:

$$n = f(s) + \eta(s)$$

$$\eta(s) \simeq N(0, \sigma^2(s))$$

- To mimic a Poisson process, we choose $\sigma^2(s) = f(s)$

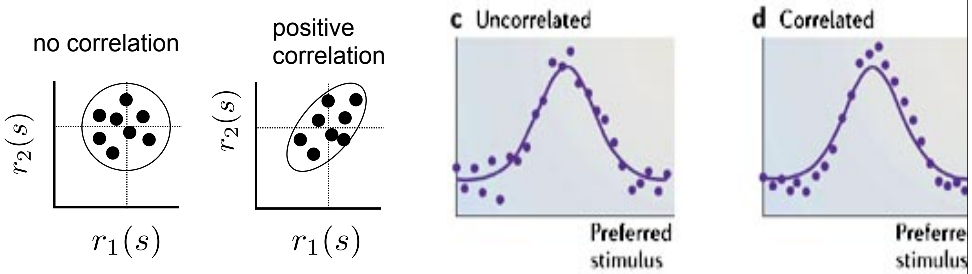
Comparison of Poisson vs Gaussian noise with variance equal to the mean



From one neuron to the population : Describing pair-wise noise correlations

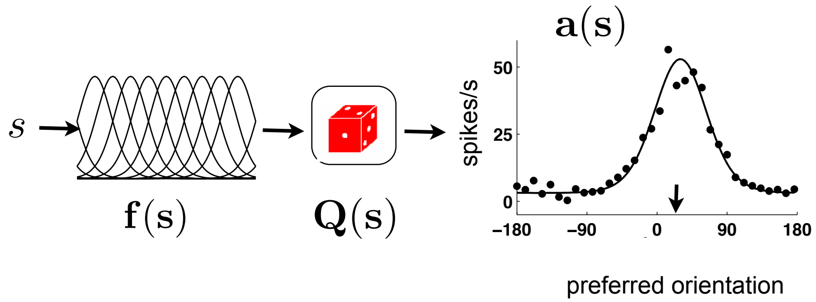
- An important question in neuroscience is to understand whether the noise is independent between neurons.
- Measure Trial-to-trial fluctuations of pairs of neurons, for same s.

When neuron 1 is above its mean, is neuron 2 also ? or are their fluctuations independent?



- Experimental data show weak positive correlations, which might be critical for the accuracy of the code.

"Tuning Curve + Noise" Population Model



The activity of a neuron (number of spikes) can be described as:

$$a_i = f_i(s) + \eta_i(s) \qquad \eta(\mathbf{s}) = N(0, \mathbf{Q}(\mathbf{s}))$$

$$P[\mathbf{r}|s] = \frac{1}{\sqrt{(2\pi)^N |\mathbf{Q}(\mathbf{s})|}} e^{-\frac{1}{2}(\mathbf{r}-\mathbf{f}(\mathbf{s}))^{\mathbf{T}}\mathbf{Q}^{-1}(\mathbf{s})(\mathbf{r}-\mathbf{f}(\mathbf{s})))}$$

Where does the noise come from?

• Is this ‘Poisson’ variability really noise? (unresolved, yet critical question)

• Where could it come from?
• Probably not in the sensory inputs (e.g. random arrival of photons)
• Probably not in the spike initiation mechanism (Mainen and Sejnowski 1995)
• Probably not in the stochastic nature of opening / closing of ion channels
• Probably not in the unreliable synapses (spontaneous AP, spontaneous release of vesicles, variability in size of PSPs).

Where does the noise come from?

• Neurons embedded in a recurrent network with sparse connectivity and balance between excitatory and inhibitory inputs tend to fire with Poisson statistics (Van vreeswijk and Sompolinksy, 1997)

• a consequence of using steady signals (Mainen and Sejnowski, 1995, Butts et al 2007).

• Variability could offer distinct advantages (eg. enhance weak signals, encoding and manipulating uncertainty (Alex Pouget) or emerge from deterministic Bayesian processes (Sophie Deneve))

• Large Spontaneous Activity (Tsodyks al 1999; Fizser et al . 2004)

Further reading: Neuronal variability: noise or part of the signal? Stein et al, Nature Rev Neuroscience, 2005.

Encoding: Summary

✤ Spikes are the important signals in the brain.
✤ What is still debated is the code: number of spikes, exact spike timing, temporal relationship between neurons’ activities?

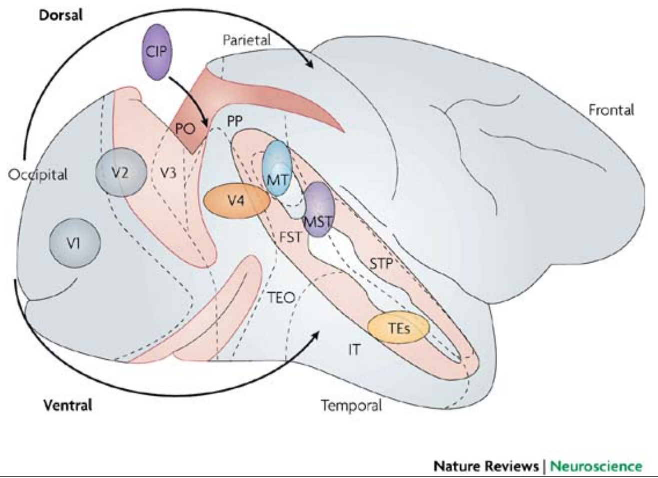
✤ Experimentalists have characterized the activity of neurons all over the brain and in particular in sensory cortex, motor cortex etc .., mainly in terms of tuning curves and response curves. A variety of well-specialized areas. Detailed wiring and mechanisms at the origins of these responses are largely unknown.

✤ Other techniques to predict activity (when stimulus is changing) : STA, reverse correlation.

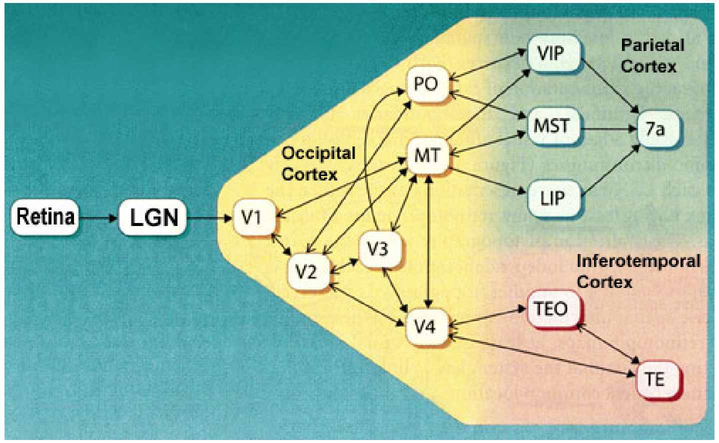
✤ The large variability (in ISI, number of spikes) is often well described by a Poisson or Gaussian model.

Overview of the visual cortex

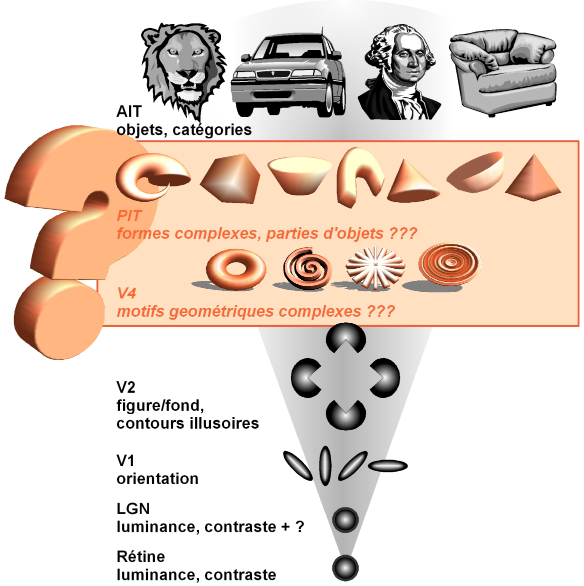
Two streams:
• **Ventral** ‘What’: V1,V2, V4, IT, form recognition and object representation
• **Dorsal** ‘Where’: V1,V2, MT, MST, LIP, VIP, 7a: motion, location, control of eyes and arms



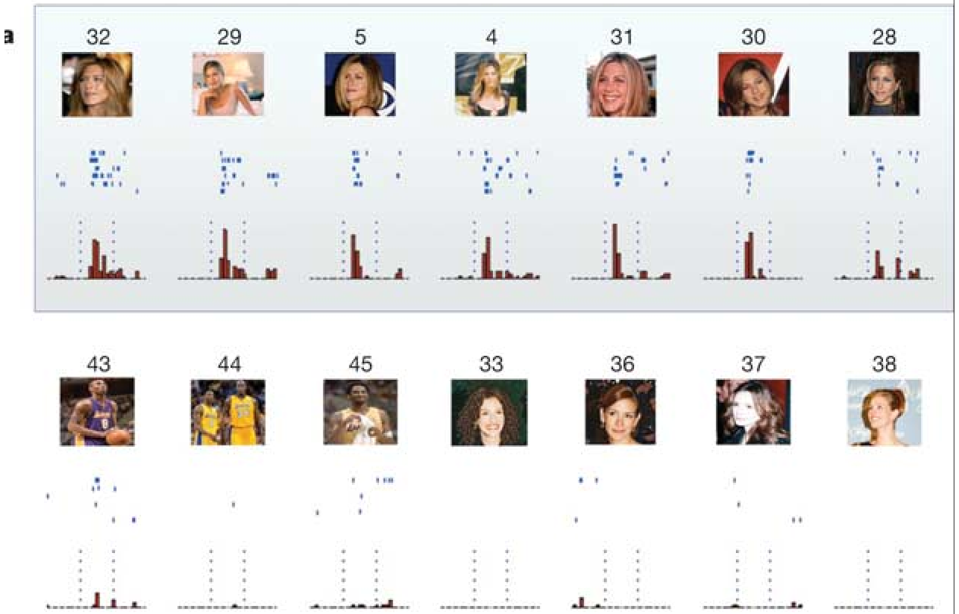
Overview of the visual cortex



Ventral pathway



Quiroga et al, *Nature*, 2005 -- Invariant visual representation by single neurons in the human brain (MTL), a.k.a the Jennifer Aniston Neuron.



Dorsal pathway

• **MT: MOTION.** stimulus of choice: random dot patterns.

Dorsal pathway

• **MST**: linear, radial, circular motion (flow field).

• **LIP**: spatial position in head-centered coordinates. spatial attention, spatial representation. saliency map -- used by oculo-motor system (the "saccade planning area"). spatial memory trace and anticipation of response before saccade.

• **VIP**: spatial position in head-centered coordinates, multi-sensory responses. speed, motion.

• **7a:** large receptive fields, encode both visual input and eye position.

Encoding applications: Cochlear implants ('bionic ears')

http://www.youtube.com/watch?v=4Avc3nNFxIA&feature=related

http://www.youtube.com/watch?v=-WA7-k_UcWY&feature=related

• surgically implanted electronic device that provides a sense of sound to a person who is profoundly deaf or severely hard of hearing.
• 188 000 people worldwide in 2009.
• a set of electrodes stimulating neurons in the cochlea.