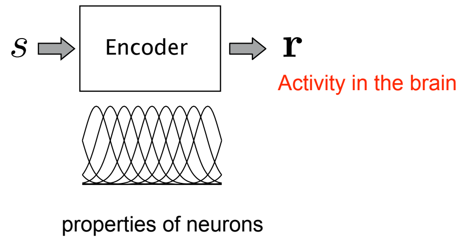
1. Encoding (continued)

Readings: encoding D&A ch.1

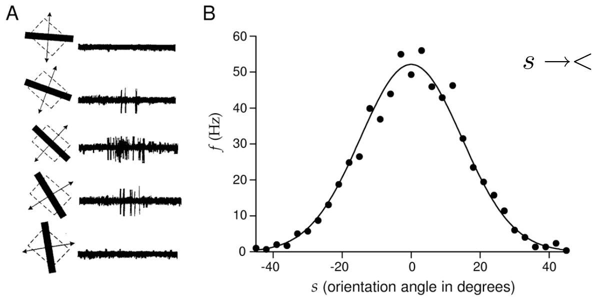
Encoding problem: $P[\mathbf{r}|s]$

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



1. Modeling the average firing rate <r(s)>

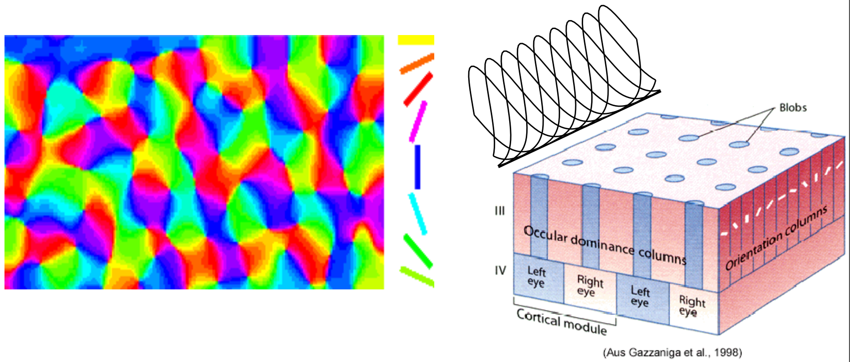
- Focus description on average firing rate <r(s)>.
- Tuning curves: modify an aspect *s* of the stimulus, and measure <r(s)>
- V1 neurons: highly selective to the orientation of the stimulus (e.g. bar) flashed in their receptive field.
- Such bell-shaped (Gaussian-like) tuning curves are very common in the cortex.



$$s \rightarrow < r(s) >$$

A Population Code

- in V1, neurons of every preferred orientation, direction, spatial freq. etc.. can be found: population code.
- Retinotopy, preferred orientations, directions are very precisely organized, forming columns and maps.

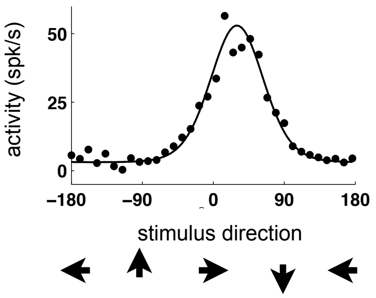


Single cell tuning curves vs population response

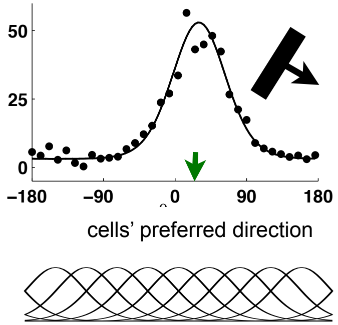
Single cell tuning curve: change stimulus, record spike count for every stimulus

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

one cell -- many stimuli



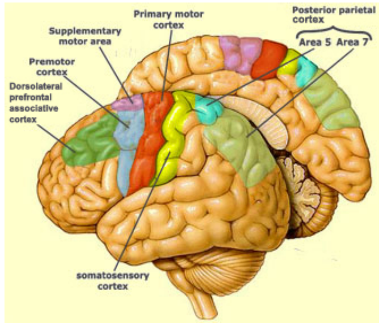
many cells -- one stimulus

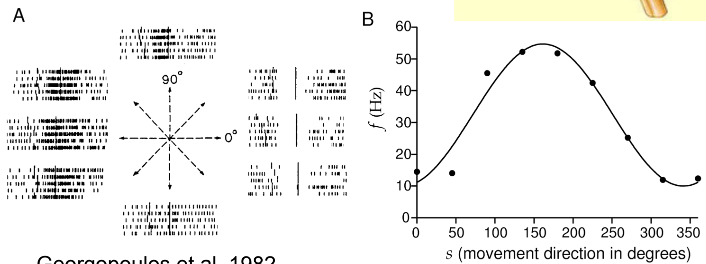


Tuning curves everywhere ...

- Primary motor cortex (M1) -- arm reaching task
- <r> as a function of the direction in which the monkey moved his arm
- Here described as a cosine

$$f(s) = r_0 + (r_{\max} - r_0)\cos(s - s_{\max})$$





Georgopoulos et al, 1982

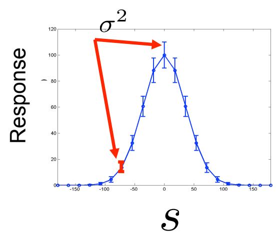
2. Describing 'the noise'

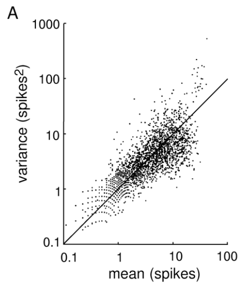
- Beyond describing only the mean spike count … the variability in the spike count.

- 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 P(nls) 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 - definition

• Poisson distribution, named after French mathematician Siméon Denis Poisson, is a discrete probability distribution that expresses the probability of a given number of events occurring in a fixed interval of time and/or space if these events occur with a known constant rate and independently of the time since the last event.

• if the average number of events in the interval/ rate is λ
The probability of observing k events in an interval is given by the equation:

$$P(k \text{ events in interval}) = e^{-\lambda}\frac{\lambda^k}{k!}$$

where

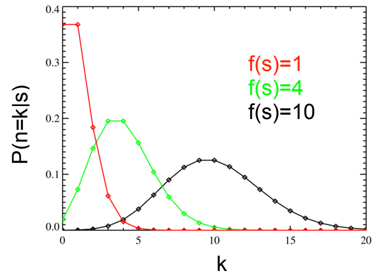
- e is the number 2.71828... (Euler's number) the base of the natural logarithms
- k takes values 0, 1, 2, …
- k! = k × (k − 1) × (k − 2) × … × 2 × 1 is the factorial of k.

a) Poisson Distribution - P(n|s)

• Poisson distribution is an appropriate model for describing the number of spikes in a time window.
• The rate / average number of spikes for a given stimulus s is also what is measured by the tuning curve f(s)

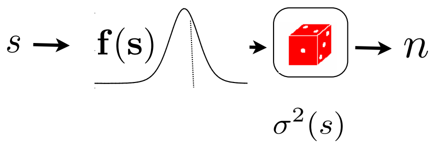
$$P(n=k|s) = \frac{e^{-f(s)}f(s)^k}{k!}$$

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



• It is a property of the Poisson distribution that var(n)=E(n)=f(s)

b) Gaussian Distribution

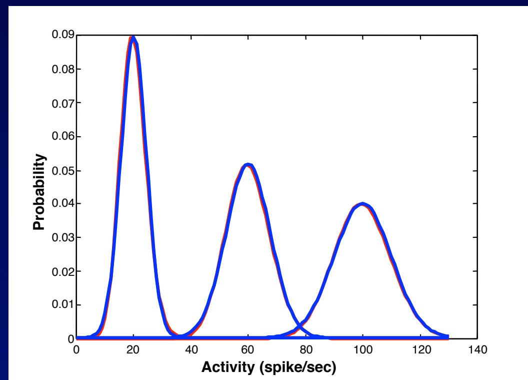


• Another model that is commonly used to describe the variability of the spike count is the Gaussian noise model.
• The activity of a neuron (number of spikes) can be described as:

$$n = f(s) + \eta(s)$$
$$\eta(s) \simeq N(0, \sigma^2(s))$$

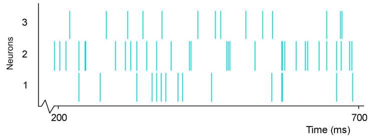
• To mimic a Poisson distribution, we choose $\sigma^2(s) = f(s)$

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



c) From Poisson Distribution to Poisson Process

• We can be interested to model not only the number of spikes (or any event), but the temporal sequence of such spikes.



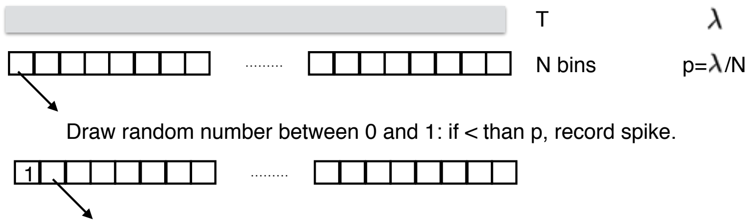
Such that the number of spikes will be described with a Poisson distribution.

We can use the model of the Poisson Process.

c) Poisson Processes - spike sequences

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.



c) Poisson Processes - spike sequences

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).

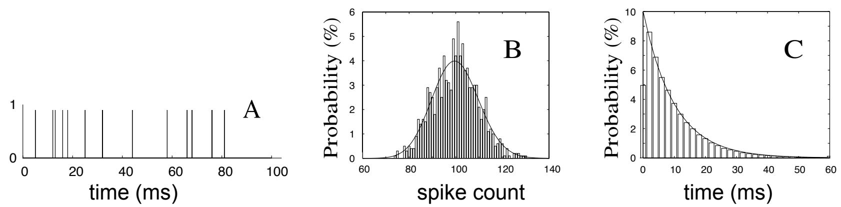
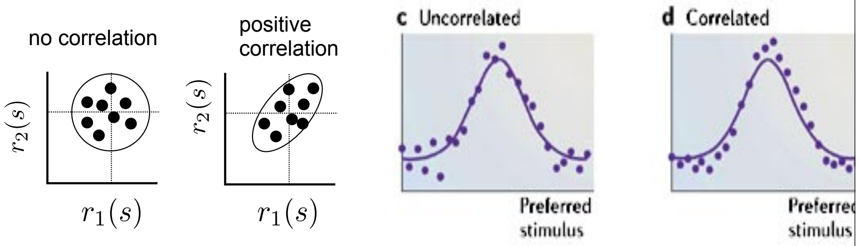


Figure 1: **A.** Snippet of a Poisson spike train with $r = 100$ and $\delta t = 1$ msec. **B.** Spike count histogram calculated from many Poisson spike trains, each of 1 sec duration with $r = 100$, superimposed with the theoretical (Poisson) spike count density. **C.** Interspike interval histogram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

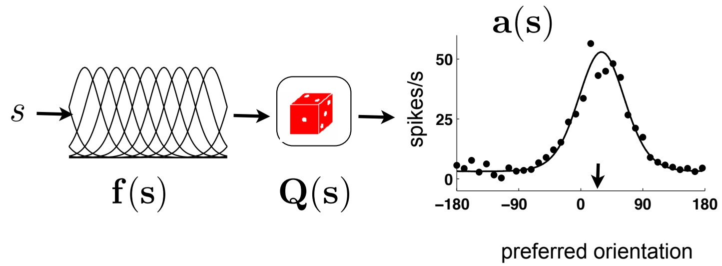
From one neuron to the population : Describing pair-wise noise correlations

• 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.

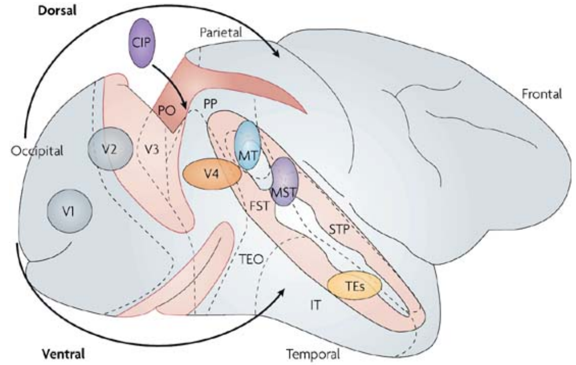
- ✤ Other techniques to predict activity (when stimulus is changing) : STA, reverse correlation.

- ✤ 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



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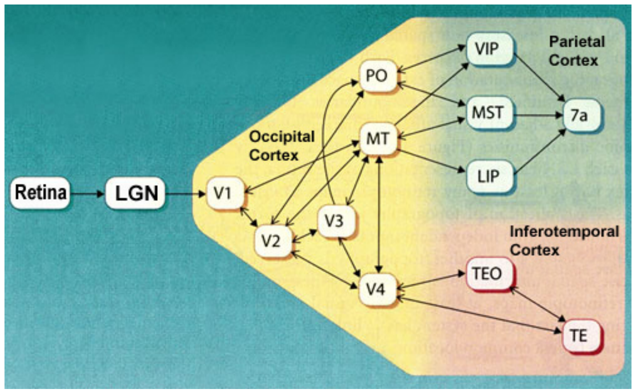
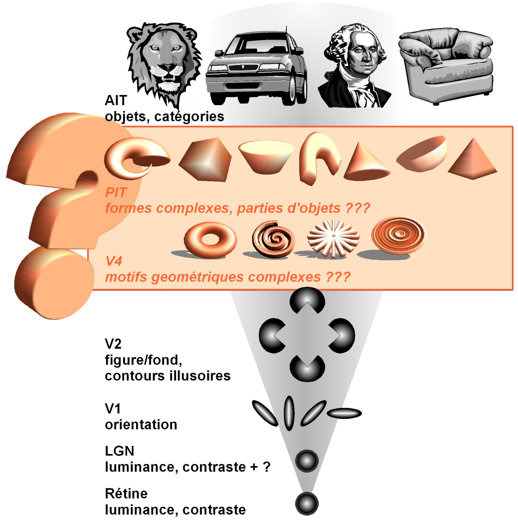
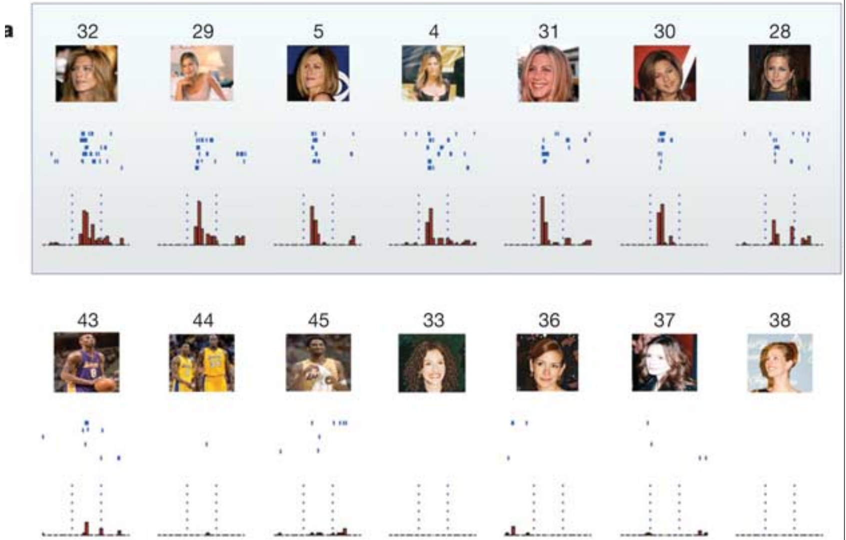
Overview of the visual cortex



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.



https://www.youtube.com/watch?v=635Ntur8K2s

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.