University of BRISTOL

Firing rates, tuning curves and neural receptive fields

Dr Amelia Burroughs

Learning Objectives

To understand that neurons may use different coding schemes

- these may depend upon firing rates (this lecture) or firing times (later lectures)

How do we measure firing rates?

What is rate coding and how can we model it?

Neurons tend to be tuned to respond to specific stimuli, or specific features of stimuli

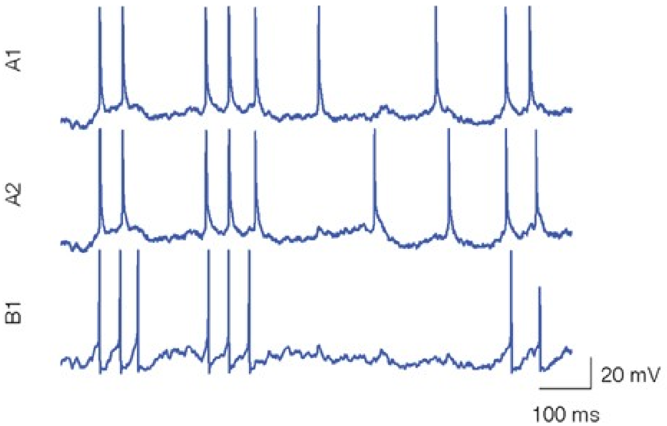
- understand what a neurons receptive field and what a tuning curve is

To understand what is meant by rate decoding

Neural Coding

If we record spikes from a single neuron, we tend to say we have a ‘spike train’

- this is the sequence of spikes



The spike train presumably tells us about how neurons code information.

We typically imagine this to be:

- **spike rate (rate coding)** or
- **spike timing (temporal coding)**

Characterising the relationship between a stimulus and a response is difficult

- Neuronal responses are complex and variable!
- what about other things like spike variability or neural state?

Rossant et al., 2011 Frontiers in Neuroscience

Neural Coding

How do neurons encode a stimulus?

The neural code is how neurons map a stimulus to a response.

Rate coding example: motor neurons
- motor neurons innervate (send axons to) muscles, how strongly a muscle contracts with the firing rate of the neuron.

Temporal coding example: Visual system
- information is encoded by the precise time of individual spikes. Spike times are locked to an external stimuli.

But it's not always that simple….
- what happens if the time scale for changes in a stimulus is of the same order as the average interval between spikes?

Neural Coding

We want to isolate features of a neural response that encode features of a stimulus

- neurons respond temporally to a stimulus, eg. by an increase in firing rate

Typically, many neurons respond, therefore stimuli are encoded by the activities of large numbers of neurons = **population coding**

- we must therefore not only examine the firing patterns of individual neurons, but also the relationship of these firing patterns to each other in the population of neurons

We are now going to look at coding using firing rates

Neural Responses are Probabilistic

The sequence of action potentials generated by a given stimulus varies from trial to trial, even for the exact same neuron

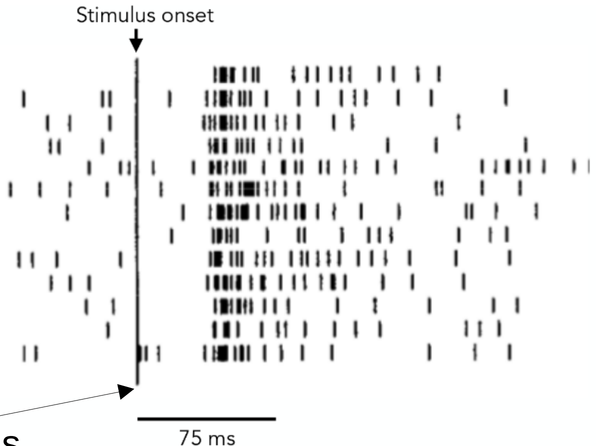
Neuronal responses are therefore often treated probabilistically
- responses are typically characterised as the probability of a spike occurring at a particular time during a trial

The firing rate is therefore often estimated by determining the fraction of trials during which a spike occurred between times t and $t + \Delta t$

Rate Coding

The average number of spikes per unit time (typically 100ms - 500ms)
- firing rates form a rate code (sometimes called ‘frequency code’)

You don’t want the time interval in which you calculate the rate to be too great because you would lose temporal resolution



Time = 0 ms

Raster plot of spikes from a single monkey visual cortex neuron from repeated presentations (each row) of a visual stimulus (oriented grating).

A raster plot:
because action potentials are so brief, we can characterise spike trains as a list of times that spikes occured

Properties of a rate

Non-negative: we can only have zero or positive firing rates

Continuous: You have to said a range within which the rate is calculated

Usually it is a latent variable rather than directly measurable: we have to infer the rate from the recorded activity

Properties of neural firing rates

1) Typically they are low on average (0.1 – 10 Hz (spikes per second))

2) Varies systematically across brain regions (pyramidal cells in the somatosensory cortex fire slowly at ~ 0.1 Hz whereas Purkinje cells in the cerebellum fire intrinsically at ~ 50 Hz)

3) Heterogeneous even within a population of neurons of the same type (typically follows a log-normal distribution)

Properties of a rate

Non-negative: we can only have zero or positive firing rates

Continuous: You have to said a range within which the rate is calculated

Usually it is a latent variable rather than directly measurable: we have to infer the rate from the recorded activity

Properties of neural firing rates

1) Typically they are low on average (0.1 – 10 Hz (spikes per second))

2) Varies systematically across brain regions (pyramidal cells in the somatosensory cortex fire slowly at ~ 0.1 Hz whereas Purkinje cells in the cerebellum fire intrinsically at ~ 50 Hz)

3) Heterogeneous even within a population of neurons of the same type (typically follows a log-normal distribution)

How do we measure firing rates?

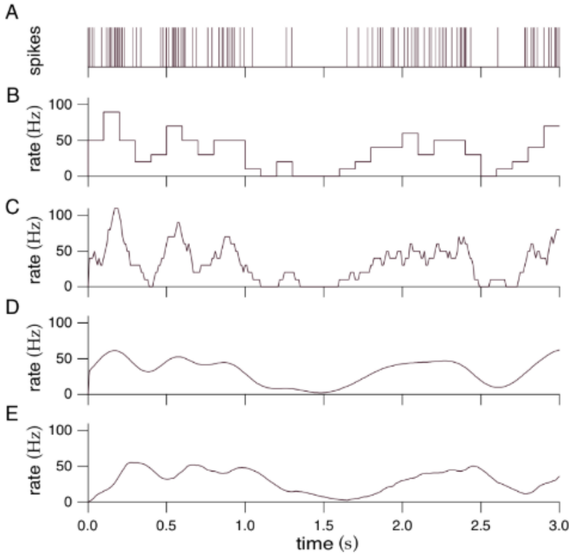


Figure 1.4: Firing rates approximated by different procedures. A) A spike train from a neuron in the inferior temporal cortex of a monkey recorded while that animal watched a video on a monitor under free viewing conditions. B) Discrete-time firing rate obtained by binning time and counting spikes with $\Delta t = 100$ ms. C) Approximate firing rate determined by sliding a rectangular window function along the spike train with $\Delta t = 100$ ms. D) Approximate firing rate computed using a Gaussian window function with $\sigma_t = 100$ ms. E) Approximate firing rate for an α function window with $1/\alpha = 100$ ms. (Data from Baddeley et al., 1997.)

A) Spike train

B) Discrete-time (100ms bins) firing rate

C) Approximate firing rate (rectangular window (100ms) function slides along spike train)

D) Approximate rate with Gaussian window

E) Approximate firing rate from an α function window

[Dayan & Abbott, 2001]

Why do we think that most information gets encoded as rate?

Neuron firing is often quite imprecise and signals sent out by the same neuron vary greatly in response to the repeated presentation of an identical stimulus

- therefore a coding scheme that relies on spike rate rather than specific timing of spikes could be more robust

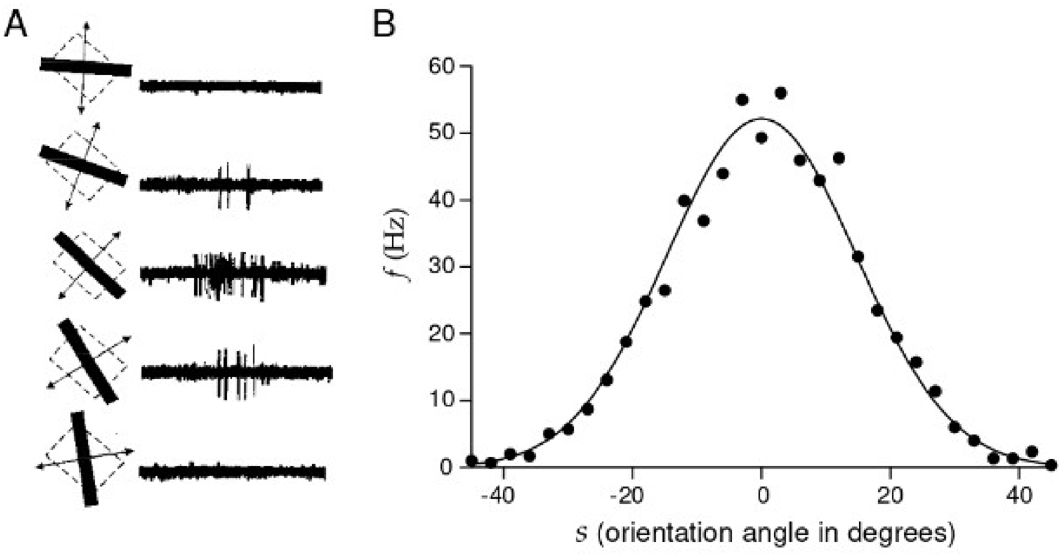
But rates are highly variable and change over time…

On top of this, neuronal responses typically depend on many different properties of a given stimulus, their rate may therefore be sensitive to multiple features of a single stimulus.

Modelling Rate Coding

A simple way of characterising the response of a neuron is to count the number of action potentials fired during the presentation of a stimulus.

If we average the number of AP fired over a trial and divide by trial duration, we get the average firing rate. If you write this as a function of the stimulus parameter, you get a response tuning curve.



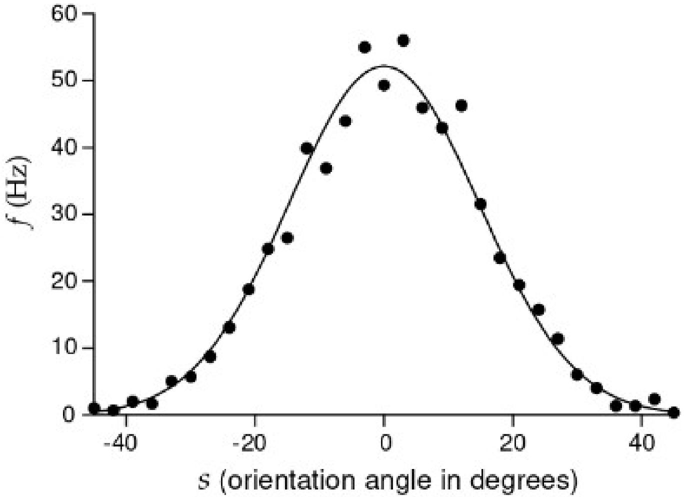
Guassian Tuning Curves

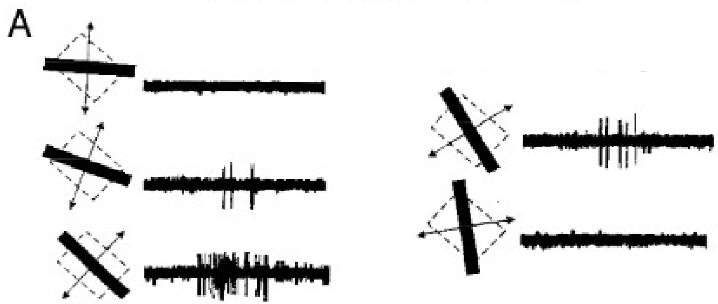
The data can be fitted with a response tuning curve of the form:

$$r(x) = \alpha e^{-\left(\frac{x-\mu}{\sigma}\right)^2}$$

where r(x) is the firing rate of the neuron in response to the orientation angle, x, of the bar. α represents the maximum average firing rate, μ is the orientation angle evoking the maximum response (0^o) and σ determines the width of the tuning curve.

Gaussian tuning curve





Other examples of Gaussian tuning curves

Tuning curves characterise the selectivities of neurons in visual and other sensory areas to a variety of stimulus parameters
- we just saw orientation tuning in V1

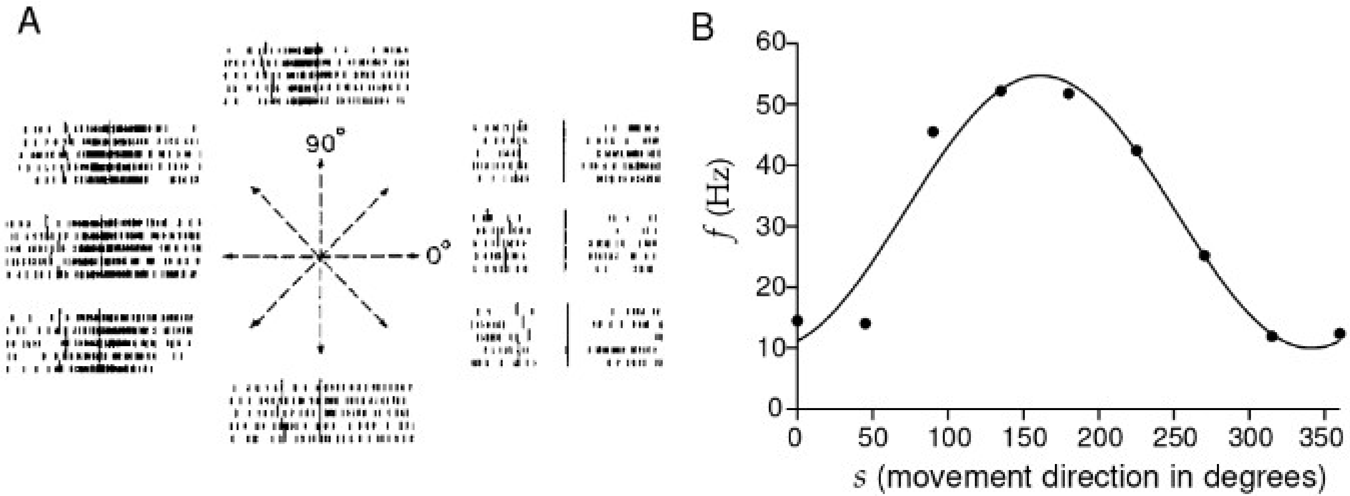
Another example would be place cell firing in the hippocampus in response to an animal’s location.

But not all neural responses are modelled with a Guassian.

You also get cosine response tuning curves, sigmoidal tuning curves,

Cosine tuning curves

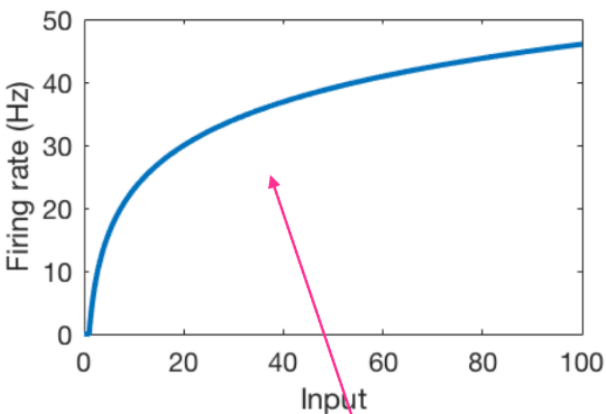
An example of a cosine response tuning curve is in the primary motor cortex M1 as a monkey reaches:



The firing pattern of the cell is correlated with the direction of the arm movement and therefore encodes information about this aspect of motor action.

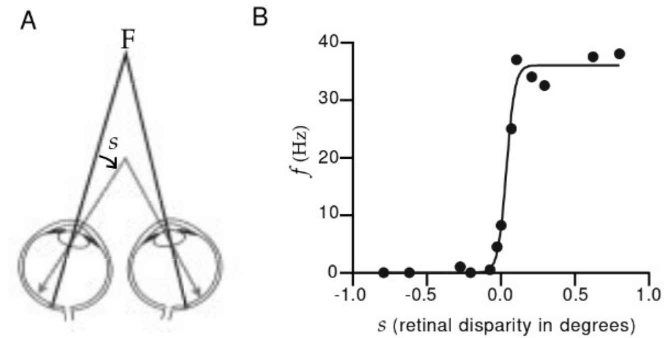
Other types of tuning curves

$$r(x) = \alpha \log(x)$$



e.g. mechanoreceptors,
visual image contrast

Accounts for the fact that humans are sensitive to absolute, rather than relative changes = Weber's law



V1 neurons depend on retinal disparity
- gives a sigmoidal tuning curve

Retinal disparity:
How far an object is (and whether it is to the left of right) from the fovea.

$$f(s) = \frac{r_{\max}}{1 + \exp\left((s_{1/2} - s)/\Delta_s\right)}$$

Tuning curves and receptive fields

Some neurons in the brain will only fire in response to a specific aspect of a perceived stimulus

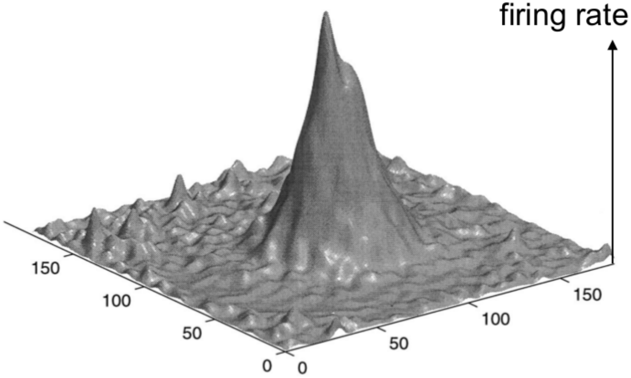
- eg. place cells are cells that typically only fire when an animal is found within a very specific location of its environment
- eg. some cells in the visual system are sensitive to the orientation of lines within a visual scene and will only fire in response to edges that are in a very specific orientation

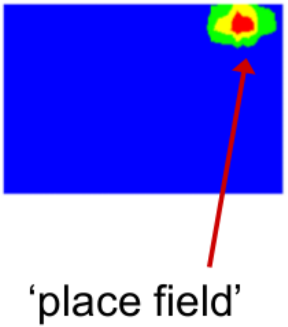
These patterns of activity (stimulus-response relationships) can be described using tuning curves and receptive fields

Tuning curve: A neuron's tuning curve is a description of its firing rate as a function of some property of the stimulus

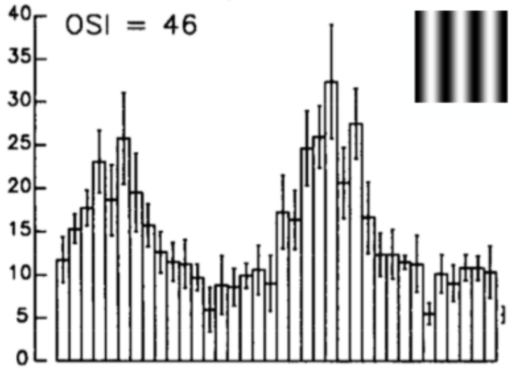
Receptive field: A neuron's receptive field is the subset of the stimulus space that the neuron responds to

Place cell tuning curve and receptive fields





Tuning curve and receptive field for a cell in the visual cortex

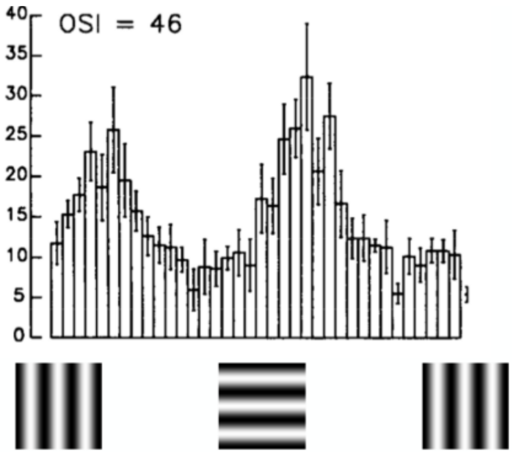


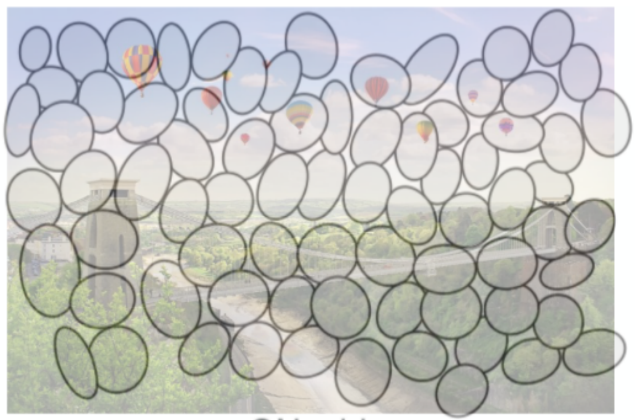
This cell is tuned to respond best to vertical bars.

It has a receptive field:

This cell would therefore respond pretty well to this image of the suspension bridge.

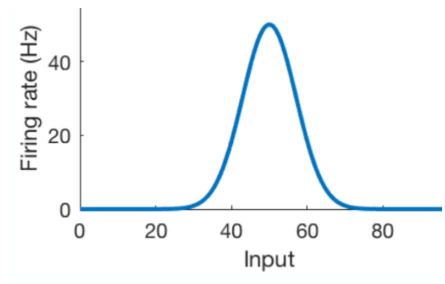
Tuning curve and receptive fields for populations of cell in the visual cortex

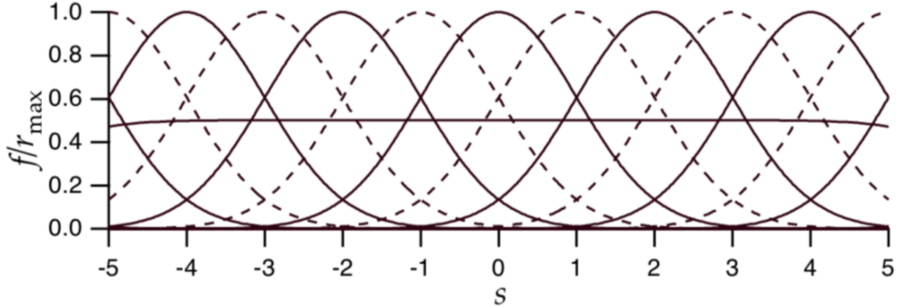




[Chapman & Stryker, *J Neurosci*, 1993] [Field & Chichilnisky, *Annu Rev Neurosci*, 2007]

Modelling rate coding in populations of neurons



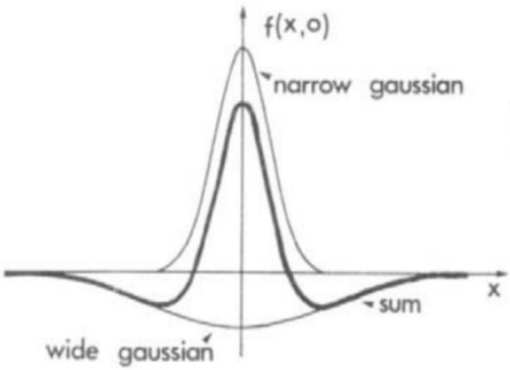


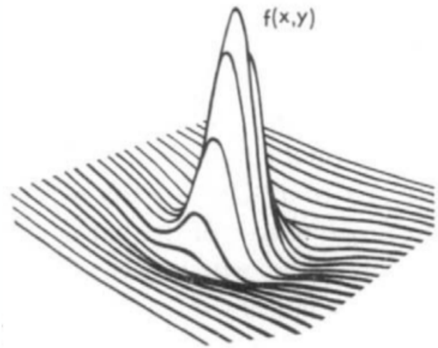
In the hippocampus, place cells fire collectively at ~7-12 Hz (theta rhythm)

The spike times of a particular place cell in relation to the phase of the theta rhythm gives additional information about the location of the animal not provided by place cells individually.

Knowing when individual spikes occur in relation to the theta rhythm allows us to distinguish two locations of opposite sides of the peak of the tuning curve.

Modelling receptive fields





$$f(x, y) = g_1\sigma_1{}^{-2}\pi^{-1}.\exp(-(x^2 + y^2)/\sigma_1{}^{-2}) - g_2\sigma_2{}^{-2}\pi^{-1}.\exp(-(x^2 + y^2)/\sigma_2{}^{-2})$$

Models ‘ON’ centre region and ‘OFF’ surround region, typical of retinal ganglion cells.

[Rodieck, *Vision Res*, 1965]

Problems with a rate code

Tuning curves allow us to make predictions about the average firing rate of a neuron, and to extend this prediction to populations of neurons, but:

They do not allow us to describe how the firing rate varies around the mean.

Often the increase in a neurons firing rate with increasing intensity of a stimulus is **non-linear**

- rate coding **ignores any temporal structure** within the spike train

The timing and duration of **non-spiking periods may be just as important,** especially in neurons that are highly active intrinsically (spontaneously active in the absence of external driving forces)

- for example we saw that Purkinje cells fire at ~40Hz even in the absence of any input to their dendrites

Temporal coding

Some studies have shown that individual spike timing may be critical to encoding information about properties of a stimulus

How precisely we are able to measure spike timing determines the resolution of our temporal code

Temporal coding can be:

- precise timing of individual spikes
- high-frequency firing rate fluctuations

The temporal structure of the spike train is determined by both the dynamics of the stimulus and the neural encoding process

- stimuli that change rapidly tend to generate precisely timed spikes

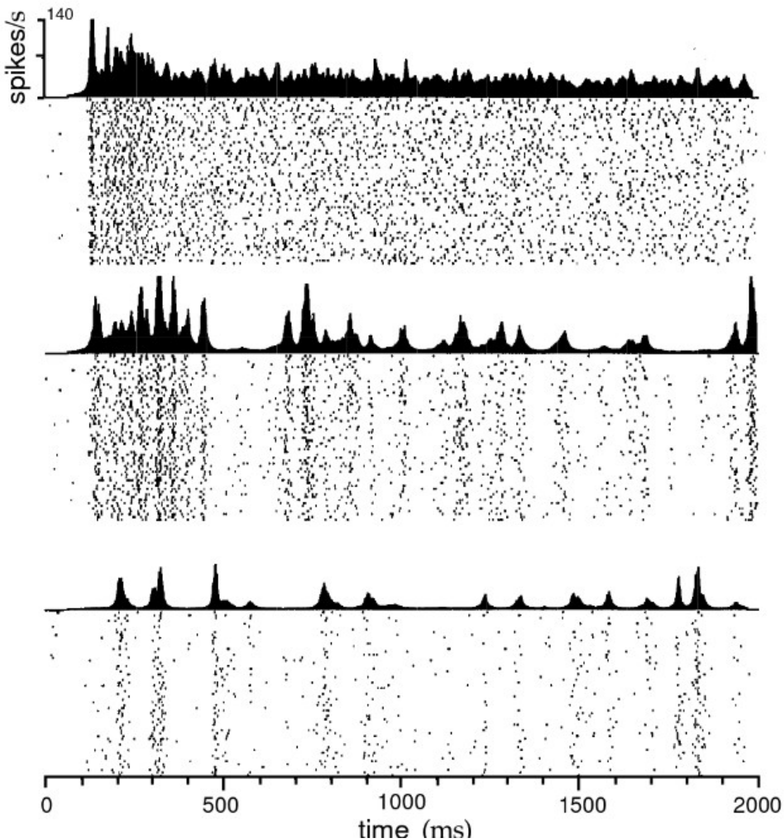
… BUT, temporal coding should refer only to temporal precision in the response that is not solely generated by the dynamics of the stimulus

Neural coding using rate an time

A recording of one neuron in response to moving dots stimuli.

There were three different stimuli of moving dots, with lots of trials for each condition.

The rasters are shown below and firing rates above.



The activity in this top panel would typically reflect a rate code

The activity in this bottom panel would typically reflect a temporal code

Neural decoding

Up until now we have considered neural encoding
- this describes the neural response to a given stimuli:

P(response|stimulus) = ?

Decoding is the opposite of encoding. It asks the question, given a neural response what is the probability of the stimulus?

Decoding involves trying to estimate the stimulus from the neural activity:

P(stimulus|response) = ?

We want to be able to reconstruct the sensory stimuli from neural activity.

Rate decoding

Various theories have been proposed for decoding neural activity:

1) Population vector

2) Optimal linear estimator

3) Maximum likelihood and Bayesian decoding

Conclusions

The average firing rate expressed as a function of a stimulus parameter is called the response tuning curve and we have seen:

- Guassian tuning curves
- cosine tuning curves
- sigmoidal tuning curves

Rate coding may not be the only way neurons encode information:

- they may also rely on the precise timing of individual spikes, or changes in high frequency firing

This represents a temporal code

The struggle now is to be able to decode neural information