Neural coding

Stefano Panzeri
IIT, Robotics, Brain and Cognitive Sciences Dept
Laboratory of Brain Signals Analysis
stefano.panzeri@iit.it

Lecture 2

Temporal codes (or: how the brain uses time to represent information)

Overview of lecture 2

• Single neuron coding
• How single neurons use time to represent information
• Ms-precise transients or patterns of spikes
• Slow Oscillations
• Multiplexing
The neuronal code is a sequence of spikes

- **Somatic electrode** – subthreshold membrane potential plus Action Potentials (spikes)
- **Extracellular electrode**
- **Axonal electrode** – subthreshold membrane potential are attenuated and only spikes propagate long distance

Single Neuron Variability

<table>
<thead>
<tr>
<th>Trial</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trial 1</td>
<td>I</td>
<td>I</td>
<td>I</td>
<td>I</td>
</tr>
<tr>
<td>Trial 2</td>
<td>I</td>
<td>I</td>
<td>I</td>
<td>I</td>
</tr>
<tr>
<td>Trial 3</td>
<td>I</td>
<td>I</td>
<td>I</td>
<td>I</td>
</tr>
<tr>
<td>Trial 4</td>
<td>I</td>
<td>I</td>
<td>I</td>
<td>I</td>
</tr>
</tbody>
</table>
Decoding brain activity

Decoding is difficult because of neural noise and must be performed probabilistically.

Measuring spike times with ms precision improves decoding of information.

Is the precise timing of spikes important to carry information about stimuli?
We say that there is temporal coding if the timing of spikes carries information about stimuli that cannot be possibly extracted from simply counting the spikes in the response time window.

**Whisking**

\[ \text{Whisking} \approx 125 \text{ ms} \]

**Temporal precision of neural codes**

What is the minimal temporal precision with which we need to register the spikes in order to obtain as much information as possible about the stimuli?
\[ \Delta T = \text{temporal precision in registering the spikes} \]
Somatosensory Cortex
Late stage of processing
Many neurons
Input from motor cortex

Ganglion
First spiking stage after whisker follicle
Few neurons

Effect of precision of spike timing with natural stimuli

100% correct

Ganglion
Cortex


Different sandpaper textures (P1200 vs P400) are represented by patterns of spike times but not by spike counts

Spike count info
Additional spike timing info

Spike counts encode big texture differences
Spike times encode finer texture differences

First-Spike Timing Neuron
Rat somatosensory cortex neuron
Responses to rapid deflection of different whiskers
In this neuron, the identity of the stimulated whisker is clearly coded only by the timing of the first spike emitted after whisker deflection

Spike Timing Coding - Human Neuron
Human tactile afferents responding to skin stimulation on a fingertip.
The curvature of the surface is represented by the timing of 1st spikes, and not by spike counts
The spike timing precision is high for faster stimuli (such as random noise in each frame) and lower for slower stimuli (such as natural movies).

Local Field Potentials

Field potentials measure the superposition of (dipole) fields generated by many neurons.

Synaptic Excitation

EEG and FPs rely on sources and sinks (current flows) rather than levels of depolarization.

During AP or synaptic potential, depolarization is seen at all points intracellularly.

Extracellularly, either positive or negative potentials are seen.

LFPs reflect synaptic inputs

LFPs recorded with a medium-impedance electrode placed near layer 5 of cortex reflect a weighted average of dendro-somatic components of synaptic signals and correlate typical pattern of subthreshold oscillations of pyramidal neurons.

They pick signals originating from neurons up to ~0.5 to 2 mm away.
LFPs and EEGs share similar generation mechanism and similar dynamics

Power spectra of LFPs show a very wide range of fluctuations over a very broad band of frequencies

Fluctuations at lower frequencies have higher power and are coherent over a larger distance on the skull
Fluctuations at lower frequencies have higher power and are coherent over a larger distance on the skull.

Working hypotheses on how to extract more information from neural signals:

- The different signals extracted from an extracellular electrode (LFPs, spikes) carry complementary information and thus must be decoded together.
- The rich temporal structure of brain signals carries information which is irretrievably lost if signals are temporally averaged.

Experiment 1 – auditory cortex

The model system: Macaque auditory cortex, Primary fields A1, R and caudal belt fields.

The signals: Local field potentials (LFP) and unit activity recorded during passive listening of natural sounds.
Spike patterns are informative when sampled with precision \( \Delta t \) of at least 4-8 ms. Spike patterns provide significantly more stimulus information than rates. For a 48 ms window, the information gain is about 100%.

\[
\Delta t = 8 \text{ ms} \\
T = 4 \times 8 = 32 \text{ msec}
\]


\[
P(\text{count } | s_i) = \sum_{c} P(c) P(\text{count } | c) \log \frac{P(c|\text{count } | s_i)}{P(c)}
\]

If the stimulus window is small then

Count values = 0, 1, ...
If the stimulus window is small then
Phase of firing values = 0, 1, 1, 1, ...
Robustness to sensory noise

<table>
<thead>
<tr>
<th>Noise Level</th>
<th>Information [bits/sec]</th>
</tr>
</thead>
<tbody>
<tr>
<td>No-Noise</td>
<td>0.32</td>
</tr>
<tr>
<td>Low-Noise</td>
<td>0.64</td>
</tr>
<tr>
<td>Medium-Noise</td>
<td>2.00</td>
</tr>
<tr>
<td>High-Noise</td>
<td>4.00</td>
</tr>
</tbody>
</table>

Information gain [%] for Low Noise:

- Rate: 200%
- Pattern: 600%
- Phase of rate: 0%
- Phase of pattern: 0%

All temporal codes provide considerable information gains with respect to the rate.

Can a phase of firing code be decoded?

The LFP phase is correlated over considerable distances (global).

Many afferent neurons will have access not only to the spiking activity of the efferent neuron, but also to its phase of firing.
Experiment 2 – visual cortex

The model system: Primary visual cortex of the opiate-anaesthetized macaque

The signals: Local field potentials (LFP) and single-unit spiking activity recorded during binocular presentation of Hollywood color movies

Montemurro, Rasch, Murayama, Logothetis and Panzeri (2008) Current Biology

The slow-LFP phase at which a spike rate is emitted conveys 55% more information about the movie than spike counts

Information in phase at which a spike rate is observed is novel w.r.t that of spike counts

Montemurro, Rasch, Murayama, Logothetis and Panzeri (2008) Current Biology
Information in spike patterns (16 ms resolution) is higher than that in spike count and is complementary to that carried by the delta (1-4 Hz)-range phase of firing.


**Hypothesis:** Slow LFP information reflects entrainment to slow regularities in the input.

These nested codes might help decoding spike timing information in absence of knowledge of stimulus timing.

Potential advantages of nested codes mixing fine spike times with slow phase:

- Carry information complementary to codes purely based on spikes.
- With respect to codes purely based on spike rates or spike times relative to stimulus timing:
  - They lead to much higher information rates
  - They may be potentially easier to decode
  - They are more robust to sensory noise

Temporal codes and behavior

The above results show that temporal codes carry more information than that carried by codes neglecting the temporal dimension.

Is this extra information available in the time domain actually used by the brain?

If so, it should have a measurable impact on behavior.
Jacobs et al., PNAS (2009)

Yang et al., Nature Neurosci (2009)

Engineer et al., Nature Neurosci (2008)
Summary

- Temporal codes are used by single neurons to carry information
- Ms-precise transients or patterns of spikes
- Slow Oscillations (freq. few Hz)
- Multiplexing
- Information in temporal codes is found at all stages of the nervous system and has an impact on behaviour