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Neural coding

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Lecture 2

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

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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

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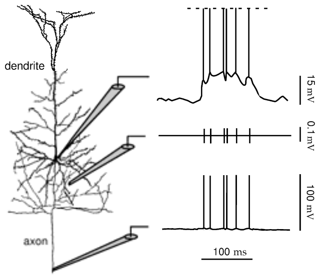
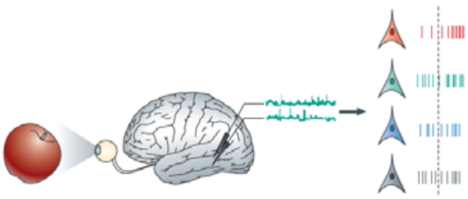
The neuronal code is a sequence of spikes



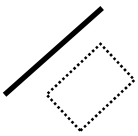
Somatic electrode – subthreshold membrane potential plus Action Potentials (spikes)

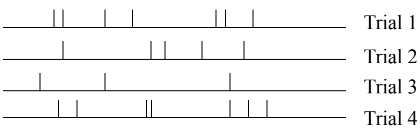
Extracellular electrode

Axonal electrode– subthreshold membrane potential are attenuated and only spikes propagate long distance

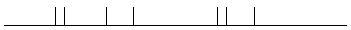


Single Neuron Variability





Decoding brain activity



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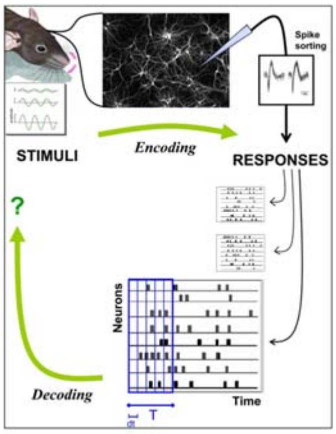
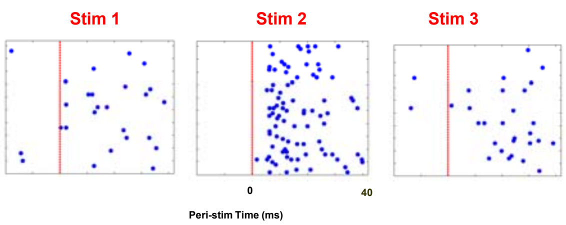
Decoding brain activity



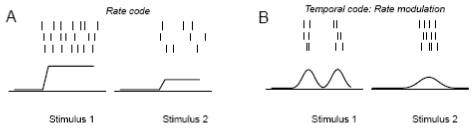
Decoding is difficult because of neural noise and must be performed probabilistically

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

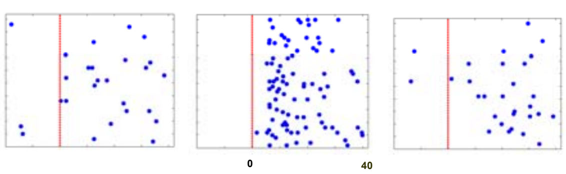


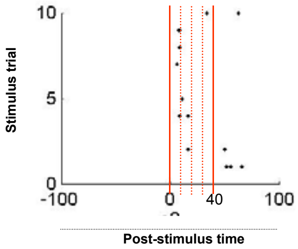
Whisking

≈ 125 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?

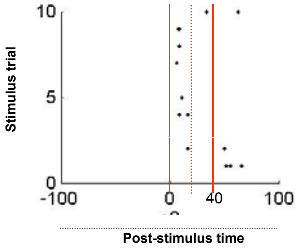




ΔT = 10 ms

Spike count	Spike timing
1	0001
1	1000
1	1000
1	1000
0	0000
1	0100
2	1100
0	0000
1	0100
0	0000
0	0000

ΔT = temporal precision in registering the spikes

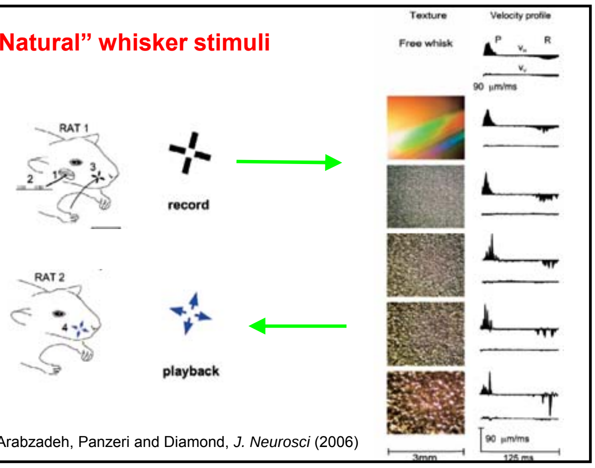


ΔT = 20 ms

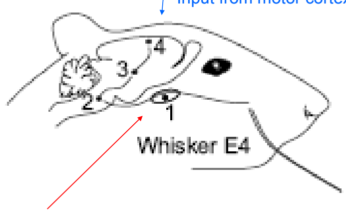
Spike count	Spike timing
1	01
1	10
1	10
1	10
0	00
1	01
2	20
0	00
1	10
0	00
0	00

ΔT = temporal precision in registering the spikes

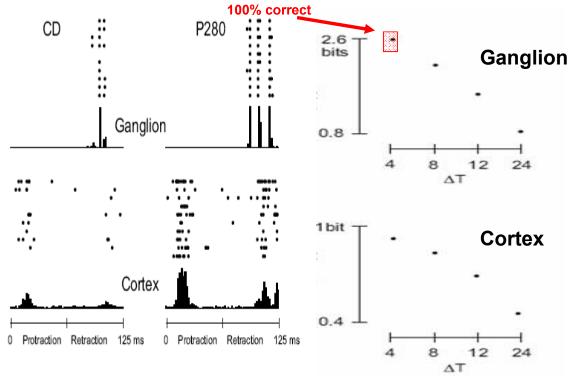
"Natural" whisker stimuli



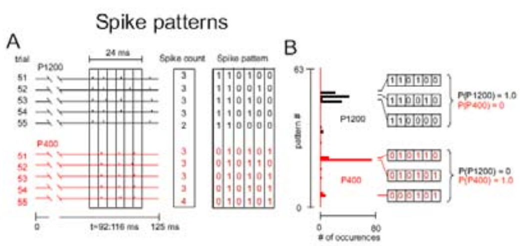
Arabzadeh, Panzeri and Diamond, *J. Neurosci* (2006)



Effect of precision of spike timing with natural stimuli



Arabzadeh, Panzeri and Diamond, *J. Neurosci* (2006)

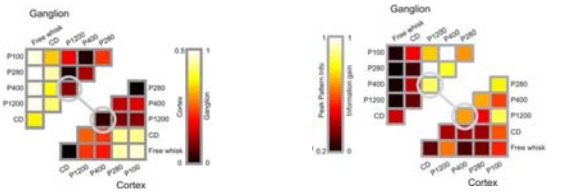


Different sandpaper textures (P1200 vs P400) are represented by patterns of spike times but not by spike counts

Arabzadeh, Panzeri and Diamond, J. Neurosci. (2006)

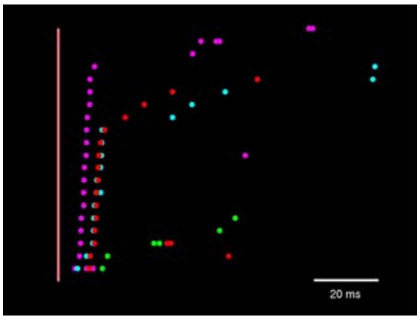
Spike count info

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

Panzeri, Petersen, Schultz, Lebedev & Diamond (2001) Neuron 29: 769.

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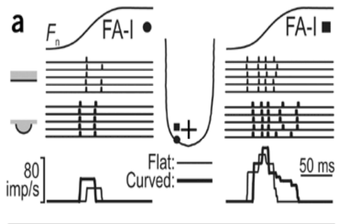
Spike Timing Coding - Human Neuron



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

Johansson and Birznieks (2004) Nature Neuroscience 7: 170.

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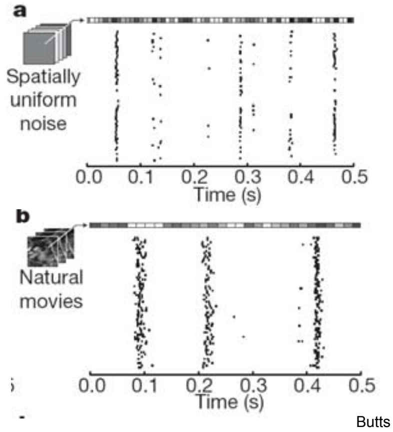
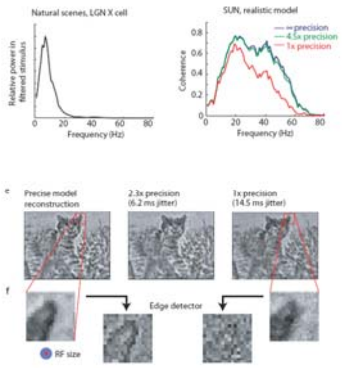
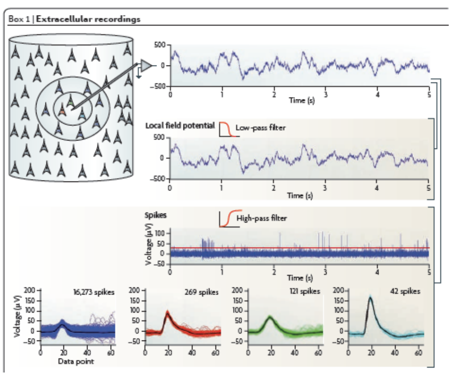


The spike timing precision is high for faster stimuli (such as random noise in each frame and lower for slower stimuli (such as natural movies)

Butts et al, Nature (2008)



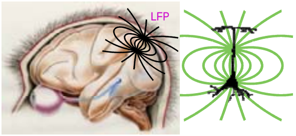
Butts et al, Nature (2008)

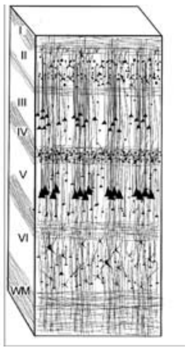


Quian Quiroga & Panzeri (2009) Nature Reviews Neuroscience

Local Field Potentials

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





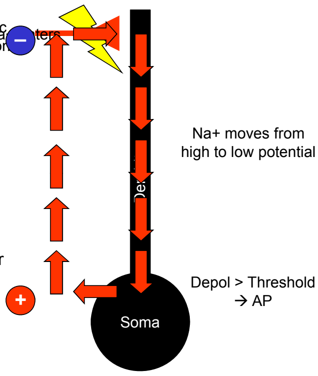
Synaptic Excitation

Synaptic Activation

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

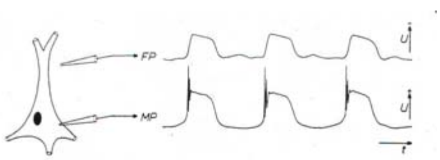
During AP or synaptic potential, depolarization is seen at all point *intracellularly*

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



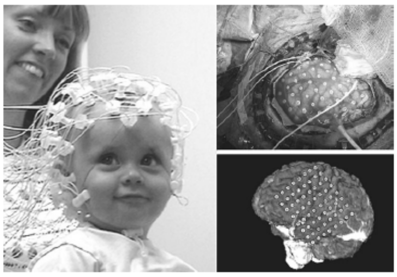
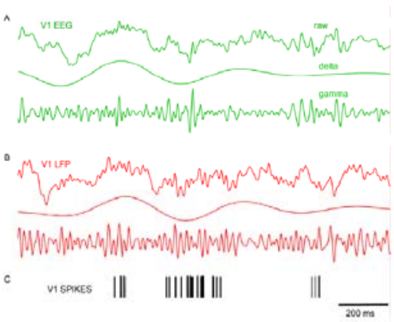
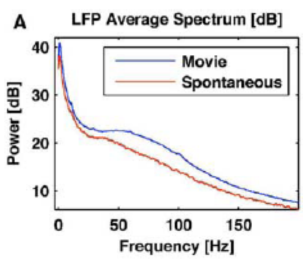


Figure 4.1. Electrical activity of the cerebral cortex can be monitored by multiple electrodes placed on the scalp ("geodesic" helmet, left). Better spatial resolution can be achieved by subdural "grid" electrodes: intraoperative placement of the subdural grid after craniotomy (top right) and the estimated electrode positions of the recording sites based on the patient's structural MRI (magnetic resonance imaging) scan acquired after the electrodes were implanted (bottom right). Infant photo is courtesy of A. Benasich, Infancy Studies Laboratory, Rutgers University; photo of grid electrodes is courtesy of R.T. Knight and R. Canolty, University of California–Berkeley.

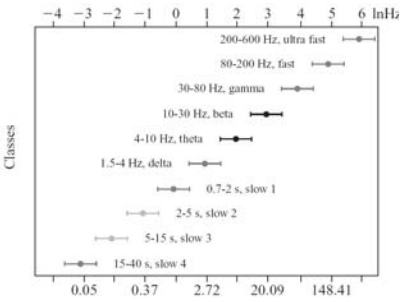


LFPs and EEGs share similar generation mechanism and similar dynamics



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

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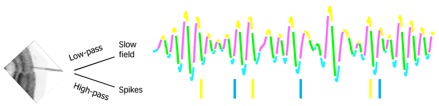
Working hypotheses on how to extract more information from neural signals



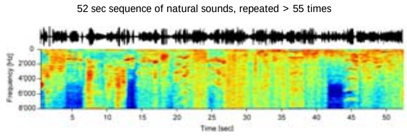
✓**The different signals extracted from an extracellular electrode (LFPs, spikes) carry complementary information and thus must be decoded together**

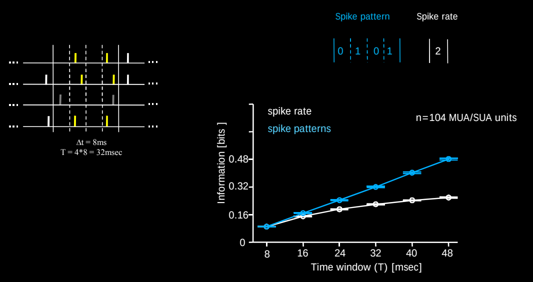
✓**The rich temporal structure of brain signals carries information which is irremediably lost if signals are temporally averaged**

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



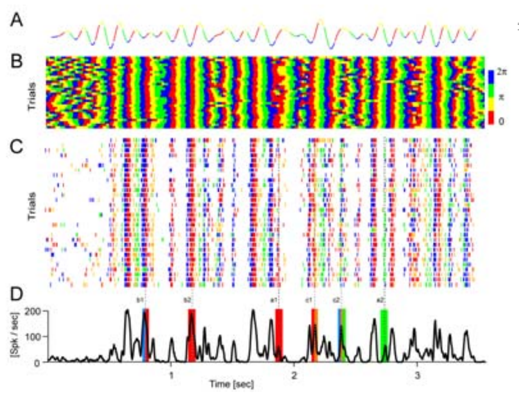


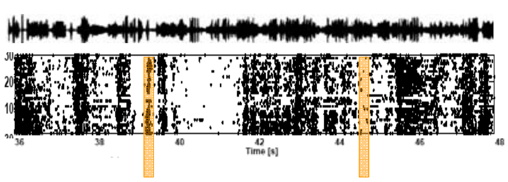
Spike patterns are informative when sampled with precision Δt of at least 4-8 ms

Spike patterns provide significantly more stimulus information than rates.

For a 48ms window, the information gain is about 80%

Kayser, Montemurro, Logothetis & Panzeri (2009) Neuron

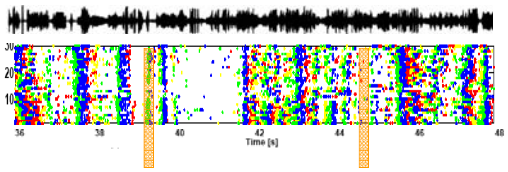




P(count |s_1) P(count |s_2)

$$I(S;Count) = \sum_{c,s} P(s)P(c\,|\,s)\log\frac{P(c\,|\,s)}{P(c)}$$

If the stimulus window is small then
Count values = 0,1,…

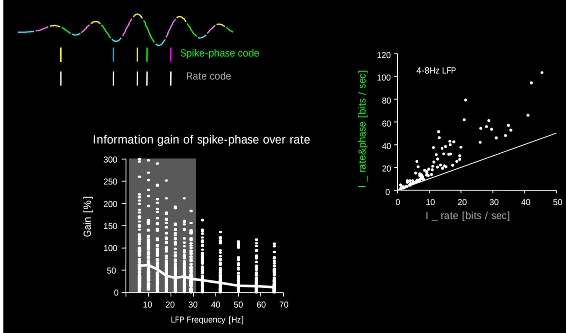


P(φof spikes | s_1)

P(count | s_2)

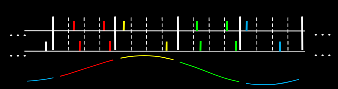
$$I(S;PhaseofSpikes)=\sum_{c,s}P(s)P(\varphi ofspikes\,|\,s)\log\frac{P(\varphi ofspikes\,|\,s)}{P(\varphi ofspikes)}$$

If the stimulus window is small then
Phase of firing values = 0,1,1,1,1…



The phase of rate provides significantly more and genuinely novel information than the firing rate, for frequencies < 30 Hz.

Spike-pattern and spike-phase

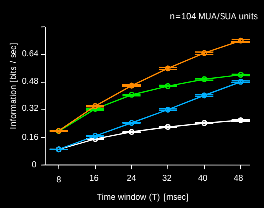


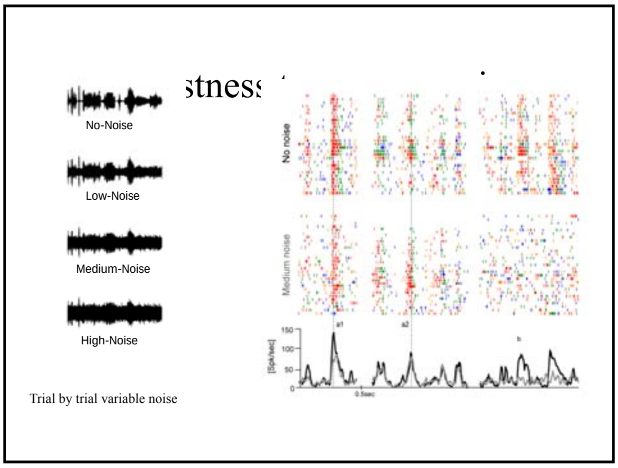
Information in spike patterns -> I_pattern

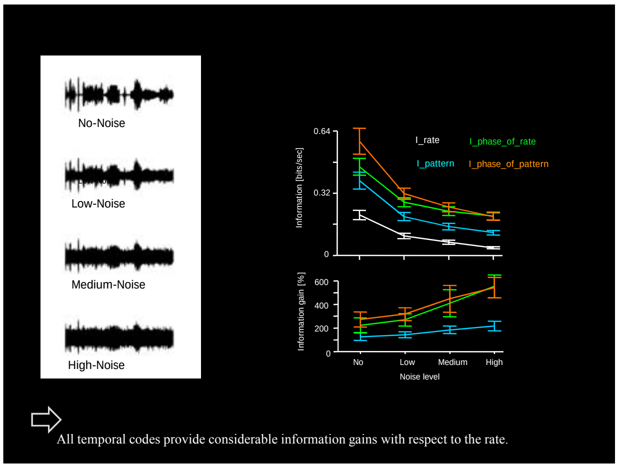
Information in spike patterns & relative timing to slow LFPs -> I_phase_of_pattern

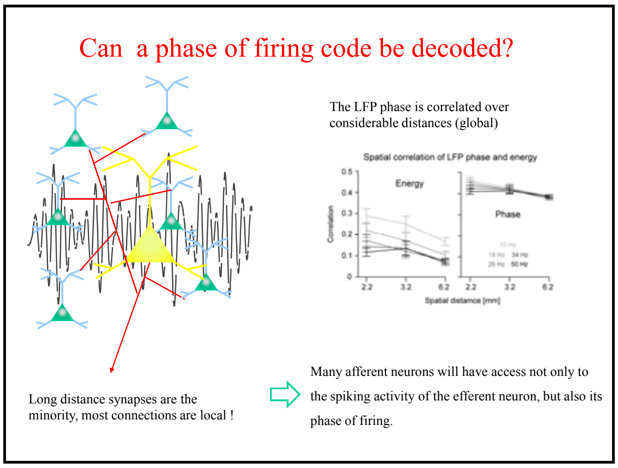
Firing rate -> I_rate

Information in firing rate & relative timing to slow LFPs -> I_phase_of_rate




No-Noise
Low-Noise
Medium-Noise
High-Noise
Trial by trial variable noise
No noise
Medium noise
150
100
50
0
[Spk/sec]
0.5sec

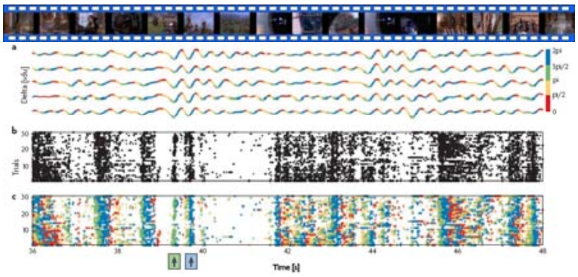

No-Noise
Low-Noise
Medium-Noise
High-Noise
I_rate
I_phase_of_rate
I_pattern
I_phase_of_pattern
0.64
0.32
0
Information [bits/sec]
600
400
200
0
Information gain [%]
No
Low
Medium
High
Noise level
All temporal codes provide considerable information gains with respect to the rate.


Can a phase of firing code be decoded?
The LFP phase is correlated over considerable distances (global)
Spatial correlation of LFP phase and energy
Energy
Phase
Correlation
Spatial distance [mm]
Long distance synapses are the minority, most connections are local !
Many afferent neurons will have access not only to the spiking activity of the efferent neuron, but also its phase of firing.

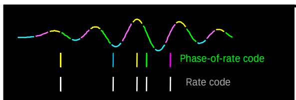
Experiment 2 – visual cortex

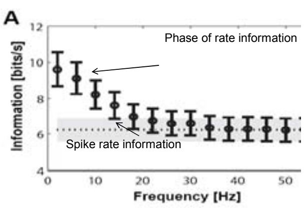
The model system: Primary visual cortex of the opiate-anaesthetized macaque

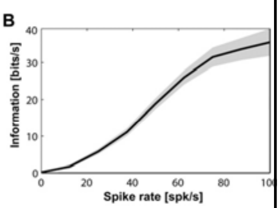
The signals: Local field potentials (LFP) and single-unit spiking activity recorded during binocular presentation of Hollywood color movies



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



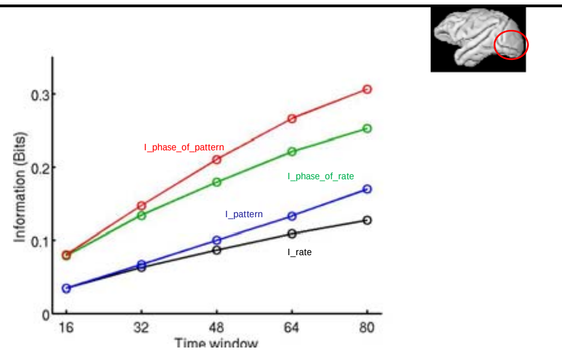




The slow-LFP phase at which a spike rate is emitted conveys 55% more information about the movie than spike counts

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

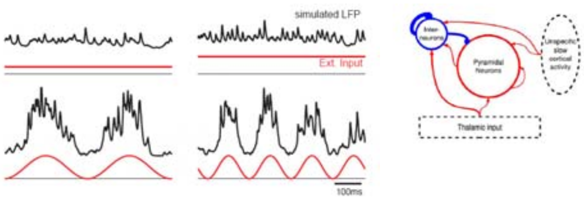


Information in spike patterns (16 ms resolution) is higher than that in spike count and is complementary to that carried by the delta (1-4 Hz)-range phase of firing

Mazzoni et al (2009) in preparation

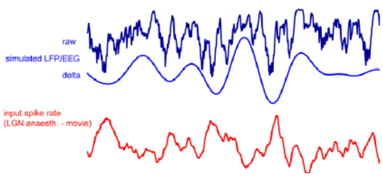
Two time scales

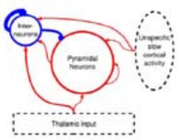
Hypothesis: Slow LFP information reflects entrainment to slow regularities in the input



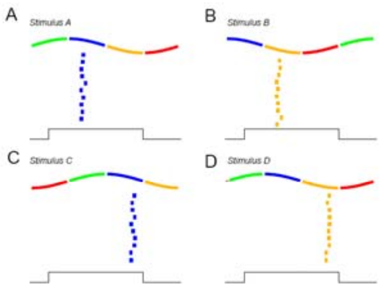
Mazzoni, Panzeri, Logothetis, Brunel – PLoS Comp Biol (2008)

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





Mazzoni, Panzeri, Logothetis, Brunel – PLoS Comp Biol (2008)



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:

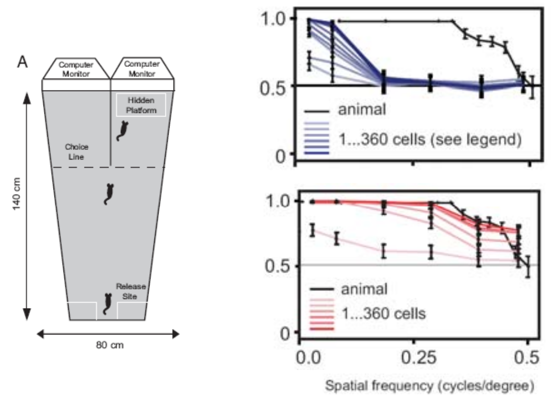
•They lead to much higher information rates
•They may be potentially easier to decode
•They are more robust to sensory noise

Temporal codes and behavior

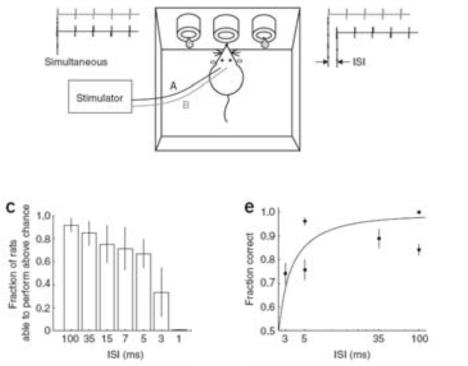
The above results show that temporal codes carry more information than that carried by codes neglecting the temporal dimension.

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

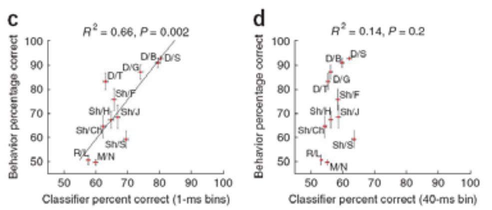
If so, it should have a measurable impact on behavior



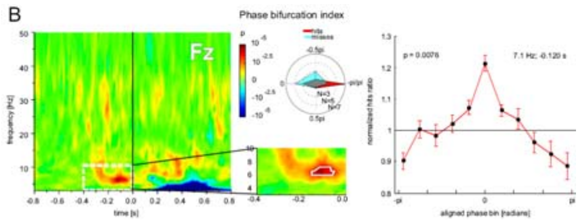
Jacobs et al , *PNAS* (2009)



Yang et al , *Nature Neurosci* (2009)



Engineer et al , *Nature Neurosci* (2008)



Busch et al , *J Neurosci* (2009)

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

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