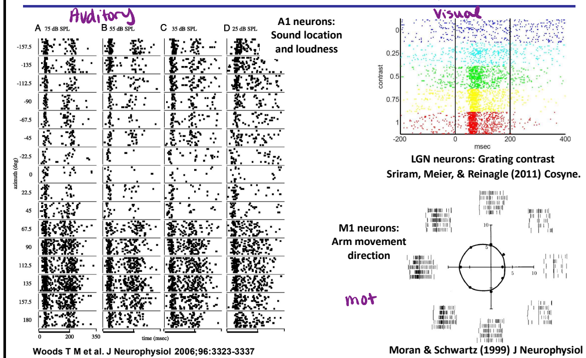

## Rate coding in the nervous system

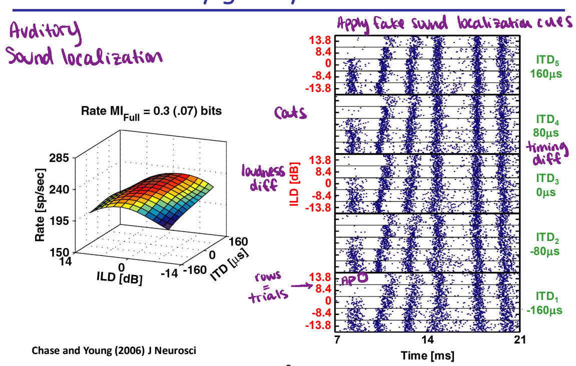





Folds filter sound waves by freq

Difference b/t ears:
1. Sound
2. Interaural timing
3. Frequency

## Why go beyond rate?






## What kinds of codes are possible?

Mutual Information:

$$MI(R;S) = \sum_{r \in R} \sum_{s \in S} p(r,s) \log_2 \left( \frac{p(r,s)}{p(r)p(s)} \right)$$

joint

assumes independence

**What should we choose for R?**



## What kinds of codes are possible?

Don't memorize this slide

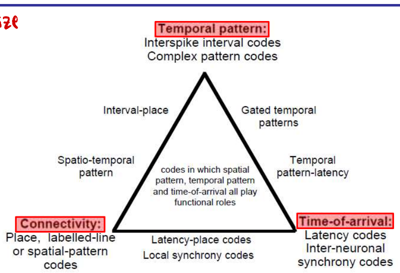



Figure 2. A space of possible neural codes

Cariani: As if time really mattered: Temporal strategies for neural coding of sensory information. Communication and Cognition - AI, Special issue on Self-Reference in Biological and Cognitive Systems, L. Rocha, ed., 1995; 12 (2-3): 157-219.



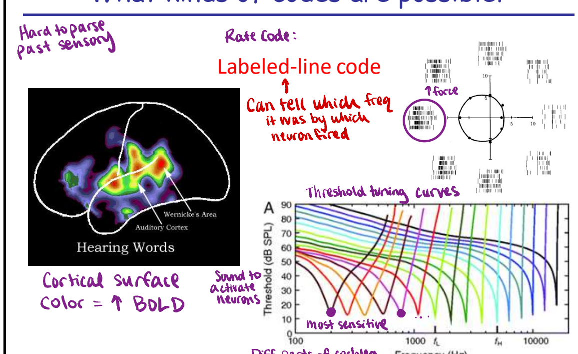
## What kinds of codes are possible?

Hard to parse past sensory

Rate Code:

Labeled-line code

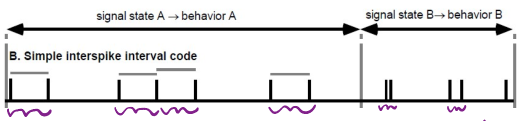
Can tell which freq it was by which neuron fired



## What kinds of codes are possible?

Δ stim = prob Δ

ISI code




Fairly consistent ISI

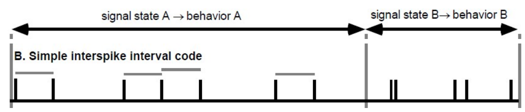
not consistent

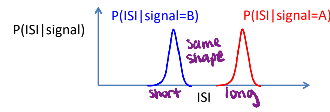
Cariani: As if time really mattered: Temporal strategies for neural coding of sensory information. Communication and Cognition - AI, Special issue on Self-Reference in Biological and Cognitive Systems, L. Rocha, ed., 1995; 12 (2-3): 157-219.



## What kinds of codes are possible?

ISI code




Response variable can convey info about the signal

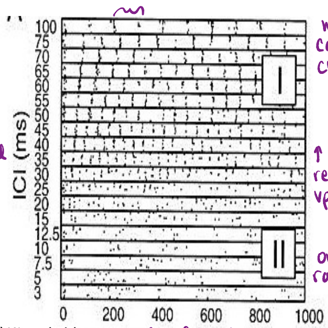
Cariani: As if time really mattered: Temporal strategies for neural coding of sensory information. Communication and Cognition - AI, Special issue on Self-Reference in Biological and Cognitive Systems, L. Rocha, ed., 1995; 12 (2-3): 157-219.



## Example of an ISI code

Auditory click trains

click interval




w/ interval you can decode the click frequency

↑ speed, still responds reliably up to a point

one pop encodes rate & other speed

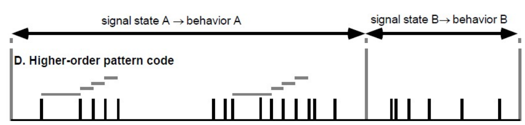
Lu and Wang (2000) J Neurophysiol

single neuron



## What kinds of codes are possible?

Higher-order pattern code




Can particular patterns of spikes convey information?

Cariani: As if time really mattered: Temporal strategies for neural coding of sensory information. Communication and Cognition - AI, Special issue on Self-Reference in Biological and Cognitive Systems, L. Rocha, ed., 1995; 12 (2-3): 157-219.

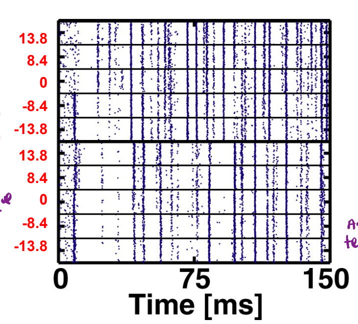


## Example of a temporal pattern code

Auditory

interaural level difference (ILD)

one ear relative to other ear




High freq SN

Spectral notch differences

Low freq SN

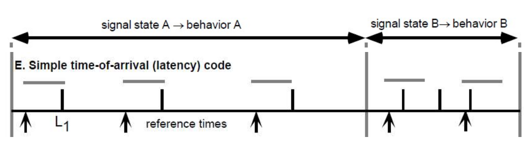
As you Δ SN, temporal pattern Δs



## What kinds of codes are possible?

external event, how long until neuron responds?

Latency code

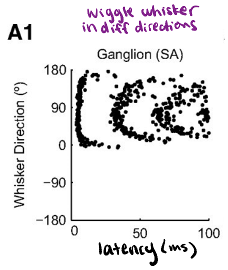



Cariani: As if time really mattered: Temporal strategies for neural coding of sensory information. Communication and Cognition - AI, Special issue on Self-Reference in Biological and Cognitive Systems, L. Rocha, ed., 1995; 12 (2-3): 157-219.

## Example of a latency code

Whisker direction system (mouse)

wiggle whisker in diff directions




latency (ms)

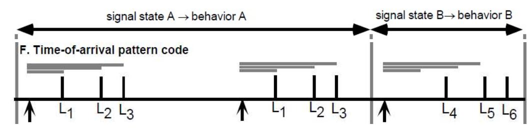
Ganglion cells can convey direction information by latency of spiking

Bale and Petersen (2009) J Neurophysiol



## What kinds of codes are possible?

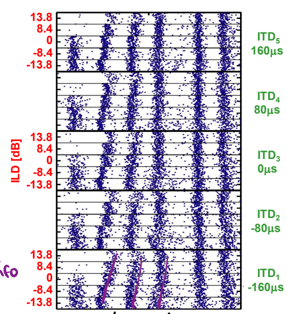
Time-of-arrival pattern code




Cariani: As if time really mattered: Temporal strategies for neural coding of sensory information. Communication and Cognition - AI, Special issue on Self-Reference in Biological and Cognitive Systems, L. Rocha, ed., 1995; 12 (2-3): 157-219.



## Example of a time of arrival pattern code




timing in 1st few time bins encodes info about ILD

time (ms)

Chase and Young (2006) J Neurosci



## What kinds of codes are possible?

Burst: Voltage spikes from Calcium (can violate refractory rules since no Na)

Burst length code

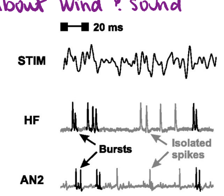

# of spikes in Calcium burst can convey info (burstiness)

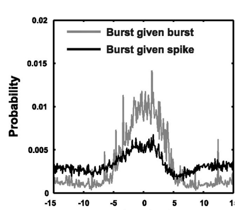
Cariani: As if time really mattered: Temporal strategies for neural coding of sensory information. Communication and Cognition - AI, Special issue on Self-Reference in Biological and Cognitive Systems, L. Rocha, ed., 1995; 12 (2-3): 157-219.



## Example of a burst code

Cricket cercal system
→ hairs on legs convey info about wind & sound




Play owl hoot, sensitive neurons

bursts conveyed preferentially

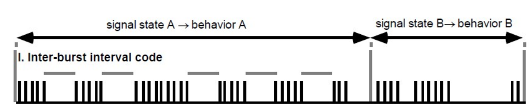
Sabourin and Pollack (2009) J Neurophysiol



## What kinds of codes are possible?

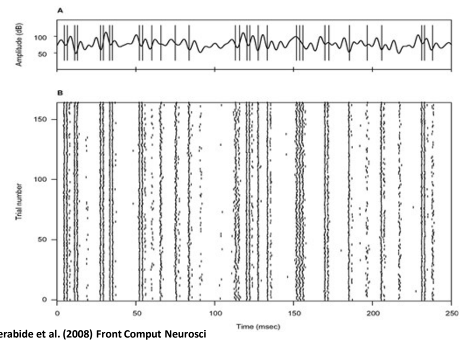
length of time in b/t bursts

IBI code




Cariani: As if time really mattered: Temporal strategies for neural coding of sensory information. Communication and Cognition - AI, Special issue on Self-Reference in Biological and Cognitive Systems, L. Rocha, ed., 1995; 12 (2-3): 157-219.

## Example of an IBI code?



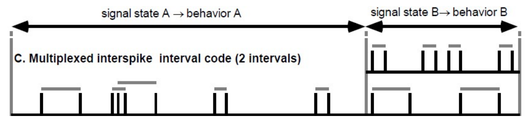

Eyherabide et al. (2008) Front Comput Neurosci



## Multiplexing: Mixing codes

single message (string of spikes) can convey more than one message depending on how its decoded

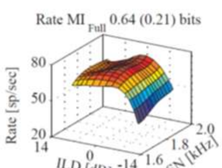
Multiplexed ISI code

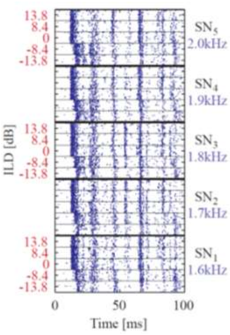



Cariani: As if time really mattered: Temporal strategies for neural coding of sensory information. Communication and Cognition - AI, Special issue on Self-Reference in Biological and Cognitive Systems, L. Rocha, ed., 1995; 12 (2-3): 157-219.



## Example of code multiplexing




Diff temporal patterns can convey independent info from firing rates

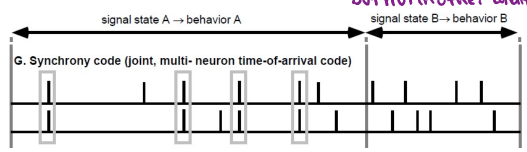


## Population codes

2 neurons, each Poisson, w/ same rate for 2 signal states (A & B)

Synchrony code

If you look across the 2 neurons, under one condition those spikes are aligned in time but not in other condition




Probability of firing doesn't depend on it being state A or B

Cariani: As if time really mattered: Temporal strategies for neural coding of sensory information. Communication and Cognition - AI, Special issue on Self-Reference in Biological and Cognitive Systems, L. Rocha, ed., 1995; 12 (2-3): 157-219.

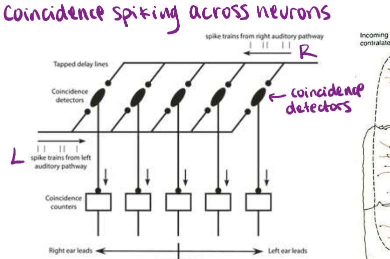
info encoded in joint activity of neurons

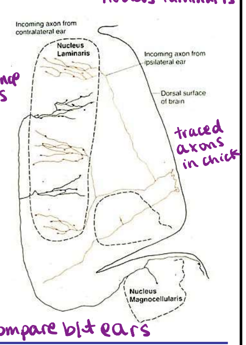


## Example of a synchrony code

Coincidence spiking across neurons

nucleus laminaris




Carr and Konishi (1988) PNAS

compare b/t ears



## How do we measure the info in each code?

$$MI(R;S) = \sum_{r \in R} \sum_{s \in S} p(r,s) \log\left(\frac{p(r,s)}{p(r)p(s)}\right)$$

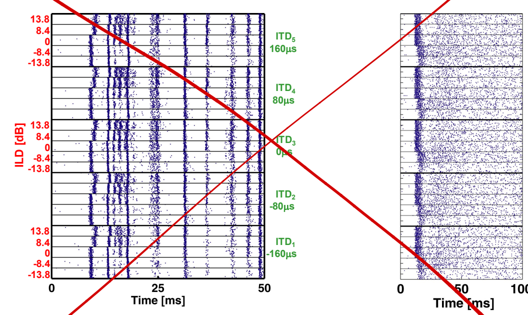
- Choosing the response variable, R, amounts to choosing a code!
- *It also amounts to ignoring the information carried by all other codes.*

## Measuring MI in timing codes

- First-spike latency codes ← not going to be on homework or exams!!
- *Temporal pattern codes*
  - *Direct*
  - *Decoded*



## First spikes are special






## Latency information comes in two forms

$$MI(F;S)=\sum_{r\in R}\sum_{s\in S} p(f,s)\log\left(\frac{p(f,s)}{p(f)p(s)}\right)$$

- F=[C,T]. C = did neuron spike? T = Time of spike.



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- Chain Rule of Information:
  MI(C,T;S)=MI(C;S)+MI(T;S|C).



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$MI_{FSL}$ $MI_{count}$



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  MI(C,T;S)=MI(C;S)+MI(T;S|C).

$MI_{FSL}$ $MI_{count}$

$$MI(T;S|C)=\sum_{c\in C} p(c)\sum_{t\in T}\sum_{s\in S} p(t,s|c)\log\left(\frac{p(t,s|c)}{p(t|c)p(s|c)}\right)$$

## Latency information comes in two forms

$$MI(F;S)=\sum_{r\in R}\sum_{s\in S} p(f,s)\log\left(\frac{p(f,s)}{p(f)p(s)}\right)$$

- F=[C,T]. C = did neuron spike? T = Time of spike.
- Chain Rule of Information:

$$\underbrace{MI(C,T;S)}_{MI_{FSL}}=\underbrace{MI(C;S)}_{MI_{count}}+\underbrace{MI(T;S|C)}_{(1-p_{spike})MI(T;S|C=0)\,+\,p_{spike}MI(T;S|C=1)}.$$



## Latency information comes in two forms

$$MI(F;S)=\sum_{r\in R}\sum_{s\in S} p(f,s)\log\left(\frac{p(f,s)}{p(f)p(s)}\right)$$

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$$\underbrace{MI(C,T;S)}_{MI_{FSL}}=\underbrace{MI(C;S)}_{MI_{count}}+MI(T;S|C).$$

$$\underbrace{(1-p_{spike})MI(T;S|C=0)}_{0} + p_{spike}\underbrace{MI(T;S|C=1)}_{MI_{timing}}$$



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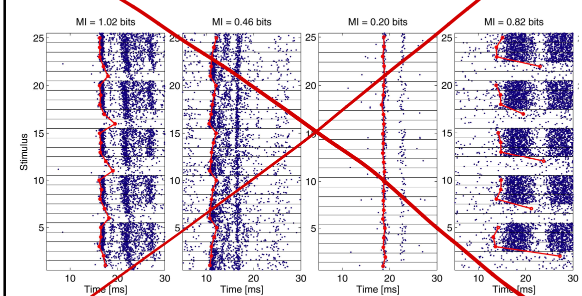
$$\underbrace{(1-p_{spike})MI(T;S|C=0)}_{0} + p_{spike}\underbrace{MI(T;S|C=1)}_{MI_{timing}}$$

$$MI_{FSL} = MI_{count} + p_{spike}\, MI_{timing}$$



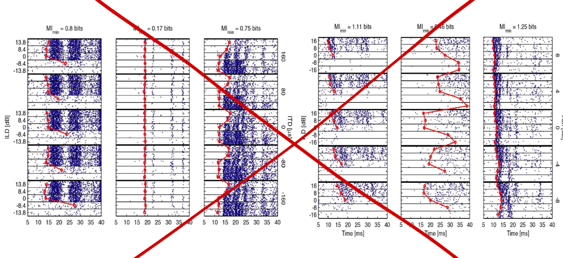
## First spike latency functions can be diverse




Chase and Young (2007) PNAS



## First spike latency functions can be diverse



Chase and Young (2007) PNAS



## Measuring MI in timing codes

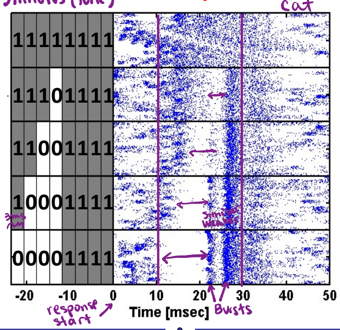
- *First-spike latency codes*
- Temporal pattern codes
  - Direct
  - *Decoded*

## How do we estimate MI in timing codes?

Stimulus (tone) ***Directly:*** anesthetized cat

0 = tone off
1 = tone on

auditory gap detection
(tinnitus)
↓
encoding sound not there

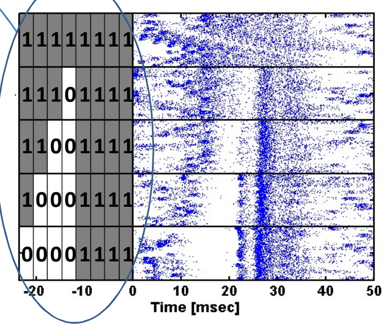





## An example

**Possible Stimuli**
Random variable describing the temporal sequence of tone amplitudes over a 24ms period. It is composed of $2^8$ equally probable values.

$p(s)=1/256 \; \forall \; s$



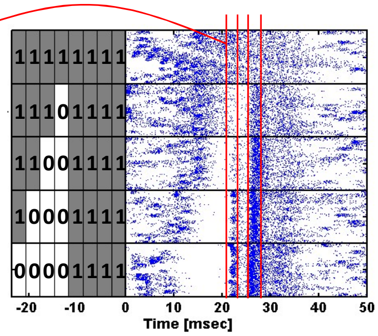



## An example

**Possible Responses**
Random variable describing the presence or absence of a spike in b consecutive bins.
($2^b$ possibilities)

$p(r|s)$ will need to be measured for each response/stimulus pair

*The curse of dimensionality*






## Measuring MI in timing codes

- *First-spike latency codes*
- Temporal pattern codes
  - *Direct* Response vs. stimulus
  - Decoded Decode (map response to estimated stimulus)



## How do we estimate MI in timing codes

***Through decoding:***

- Use the response to build an estimate of the stimulus, $\hat{s}=f(r)$.
- Compute $MI(\hat{S},S)$. (actual → $S$; estimated → $\hat{S}$)
- By the data processing inequality, $MI(R;S) \geq MI(\hat{S};S)$.

Upper-bounded by actual stimulus
good decoder → guess patterns



## What decoder should we use?

- Any decoder! The better the decoder, the more information you can prove is in the pattern.
- Also, it can be possible to use different decoders to help decipher what aspects of the spike train carry information.

## Summary

- Neurons can (and do!) transmit information in a variety of ways, including…
  - Rate/place codes (labeled lines)
  - First spike latency codes
  - Temporal patterns
  - Synchrony
- First spike latency is a combination of two response variables.
- The direct method for estimation MI in temporal patterns suffers from the curse of dimensionality.

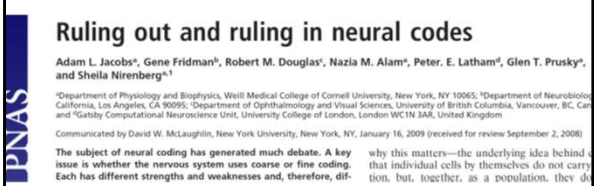


## Yes, but….

How do we know this information is relevant to the animal?

How do we know if the code is actually used?





# Ruling out and ruling in neural codes

Adam L. Jacobs[a], Gene Fridman[b], Robert M. Douglas[c], Nazia M. Alam[a], Peter. E. Latham[d], Glen T. Prusky[a], and Sheila Nirenberg[a,1]

[a]Department of Physiology and Biophysics, Weill Medical College of Cornell University, New York, NY 10065; [b]Department of Neurobiolog… California, Los Angeles, CA 90095; [c]Department of Ophthalmology and Visual Sciences, University of British Columbia, Vancouver, BC, Can… and [d]Gatsby Computational Neuroscience Unit, University College of London, London WC1N 3AR, United Kingdom

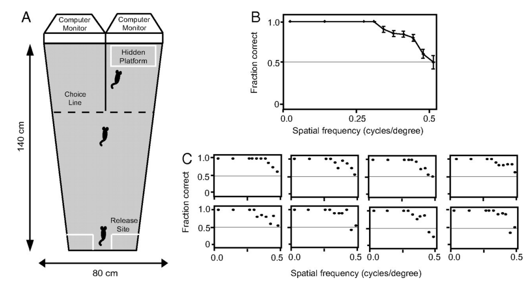
Communicated by David W. McLaughlin, New York University, New York, NY, January 16, 2009 (received for review September 2, 2008)

**The subject of neural coding has generated much debate. A key issue is whether the nervous system uses coarse or fine coding. Each has different strengths and weaknesses and, therefore, dif-**

why this matters—the underlying idea behind … that individual cells by themselves do not carry … tion, but, together, as a population, they do…



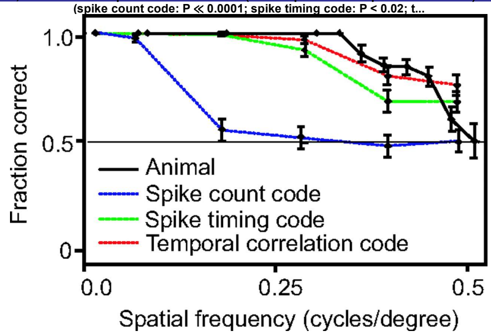
**Performance of the animal on a 2-alternative, forced choice visual discrimination task.**




Adam L. Jacobs et al. PNAS 2009;106:14:5936-5941




**The spike count code and spike timing (instantaneous rate) code performed worse than the animal, whereas the temporal correlation code (within spike train temporal correlations) did not (spike count code: P ≪ 0.0001; spike timing code: P < 0.02; t...**

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