Neural coding and adaptation

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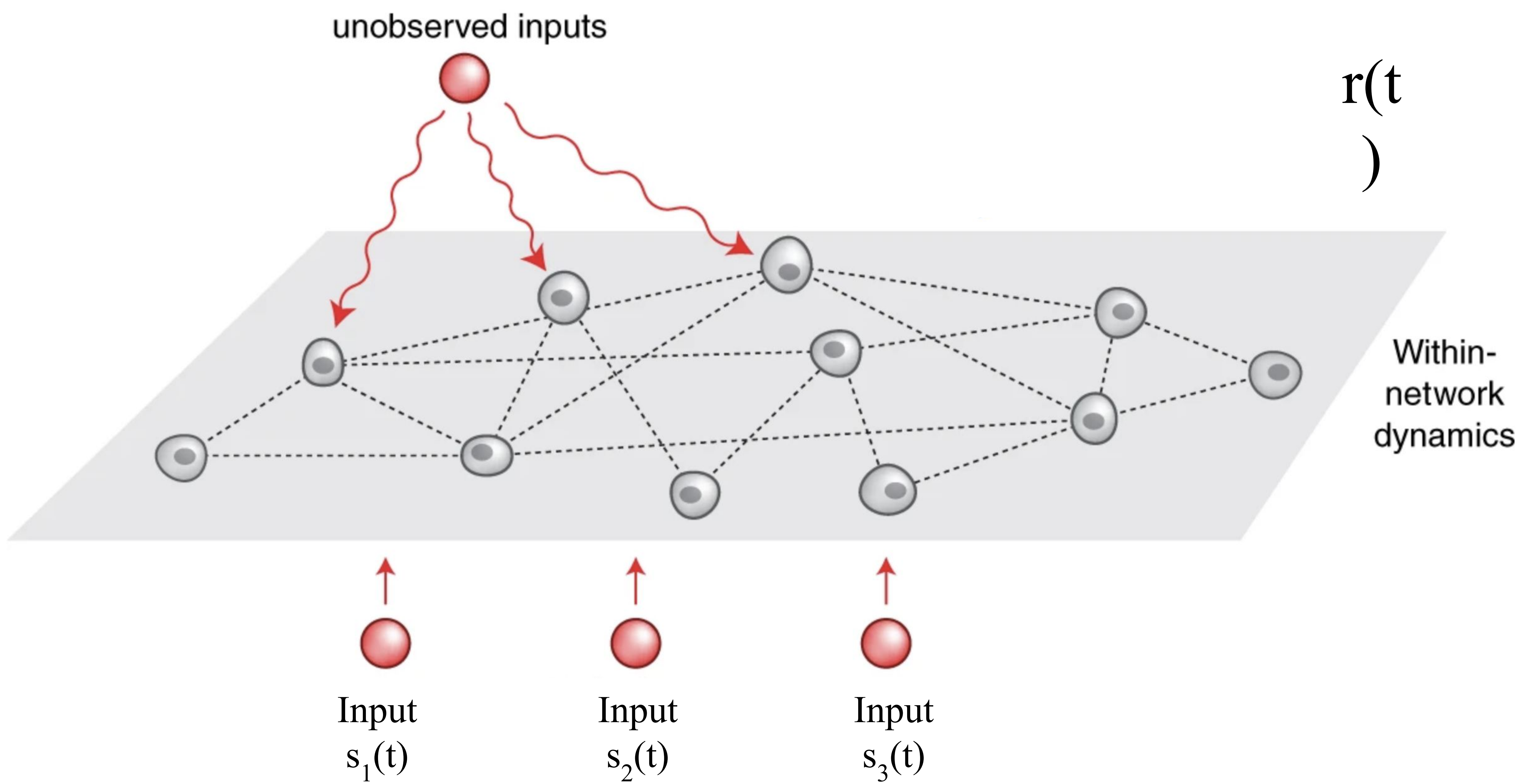
Plan

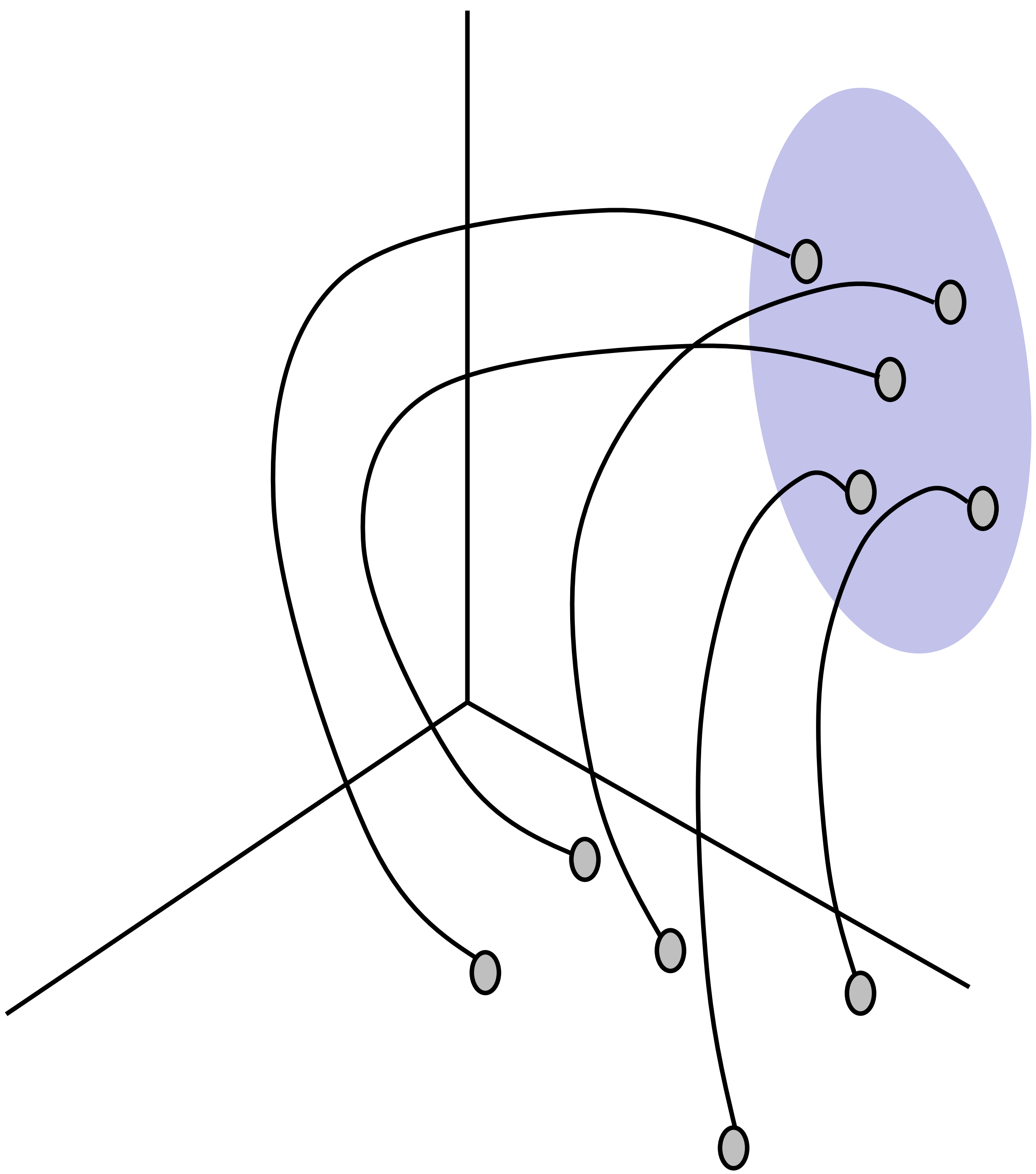
- Neural coding
- Some basic methods for exploring coding
- Coding is a moving target: adaptation
- Adaptation and its role in coding

What could neural coding mean?



r(t
)

The concept of *representation*



$$dr(t)/dt = F(r(t) + I(t))$$

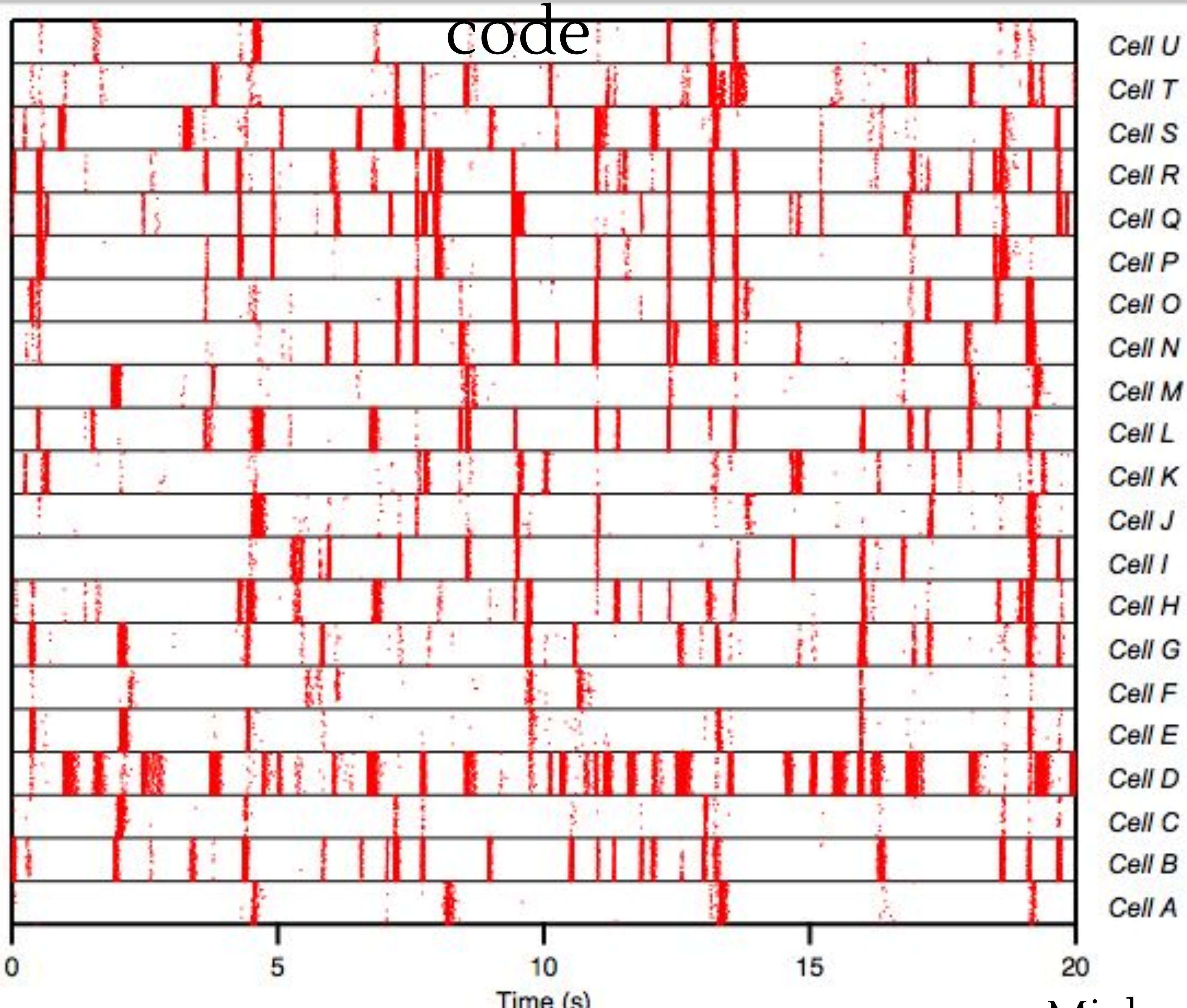
What is the relationship between external variables and r?

What can one infer about brain state from observing r?

Is r the right variable set?
What low dimensional structure do these response states have?

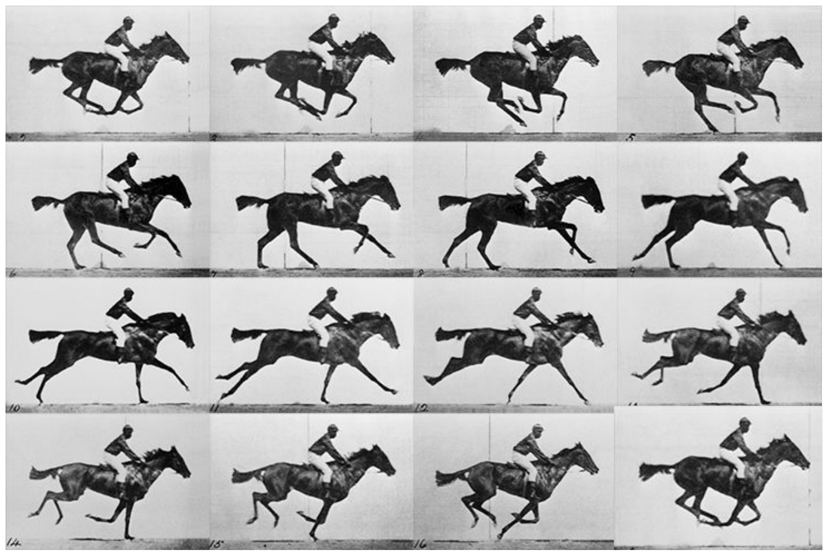
What dynamics does the network carry out and what computation does it embody?

At the sensory end, this definitely looks like a code

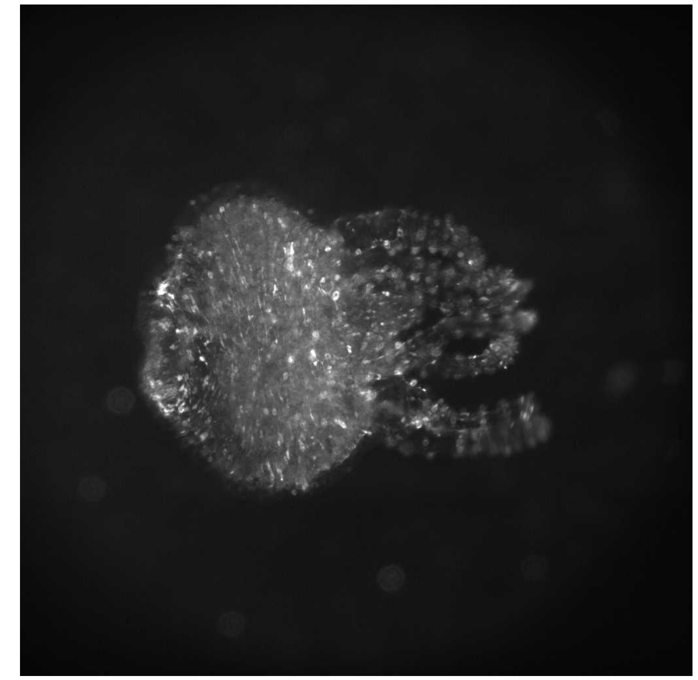


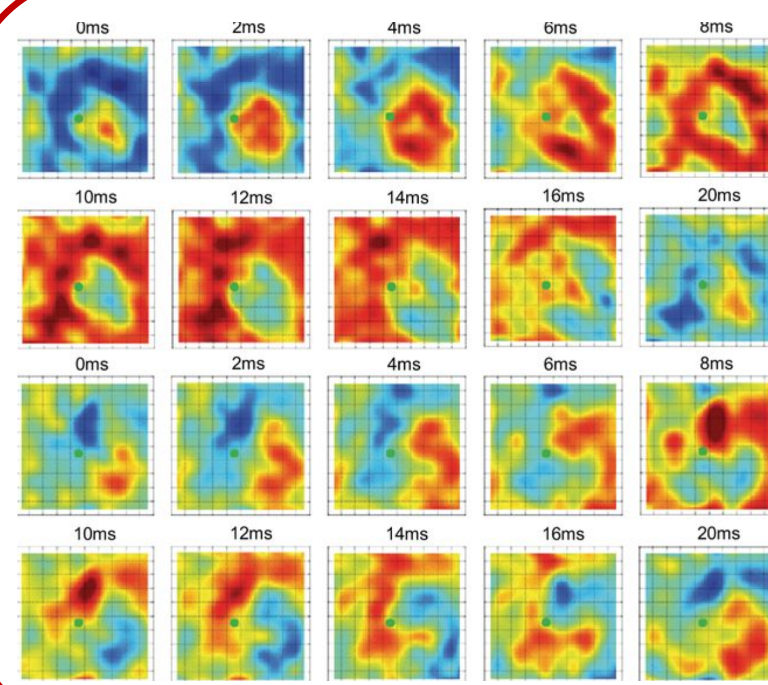
Michael J. Berry II

Neural coding

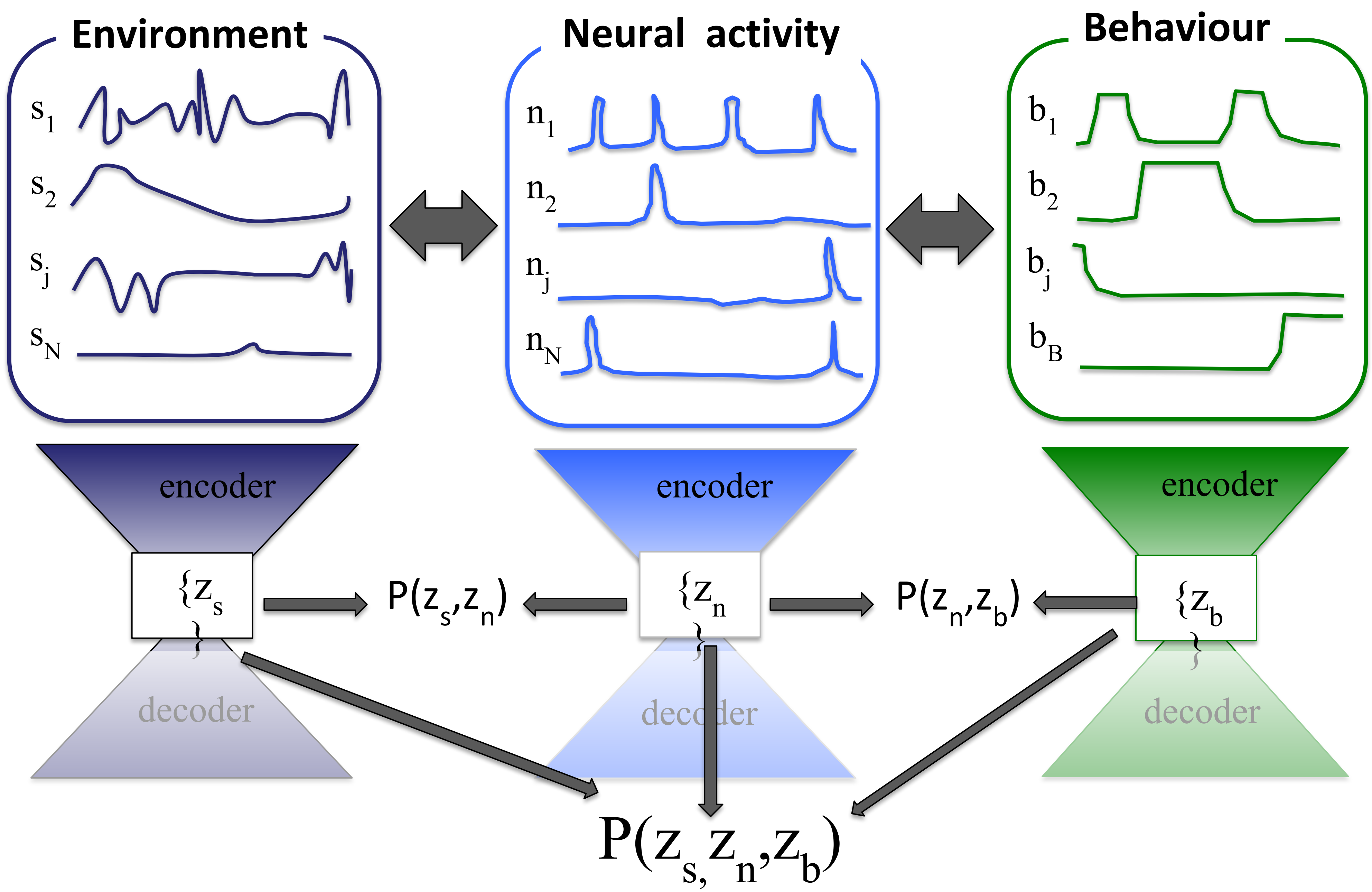


$$P(X|Y)$$

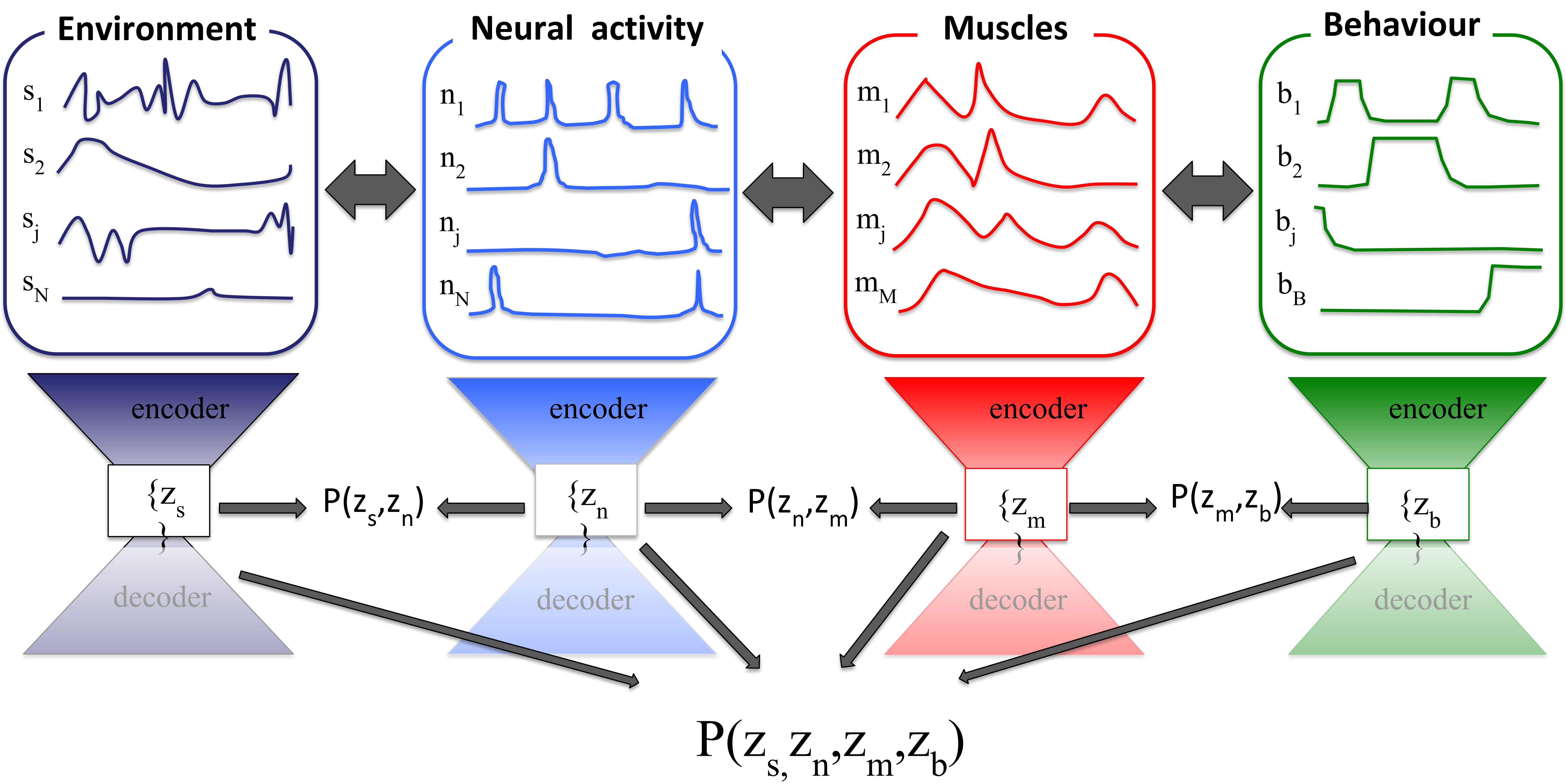




Statistical models in neuroscience



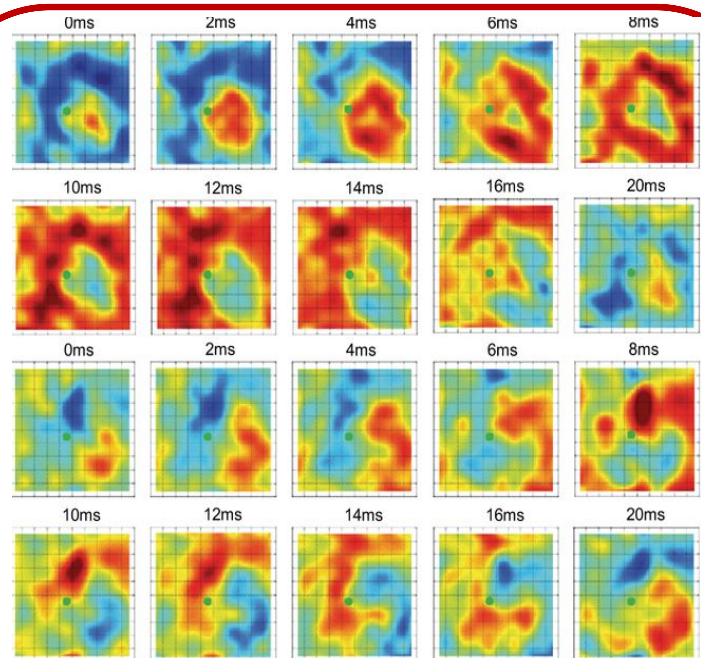
Statistical models in neuroscience

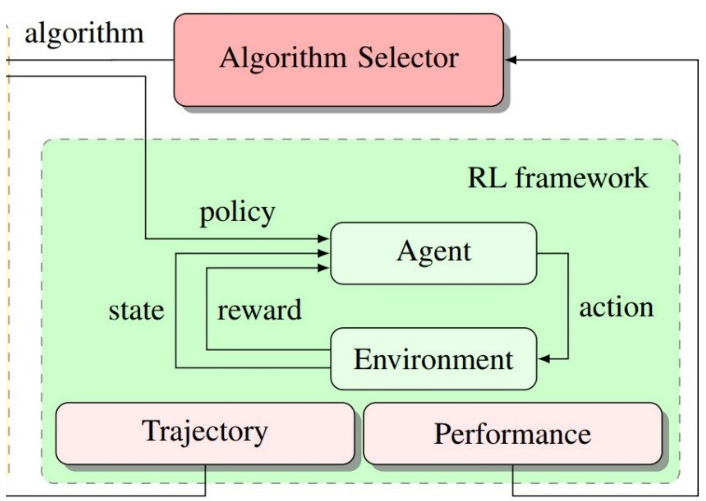


Finding representations is just a starting point

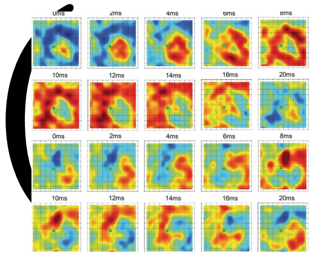
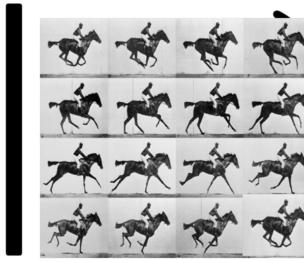
$$P(z_s, z_n, z_m, z_b)$$

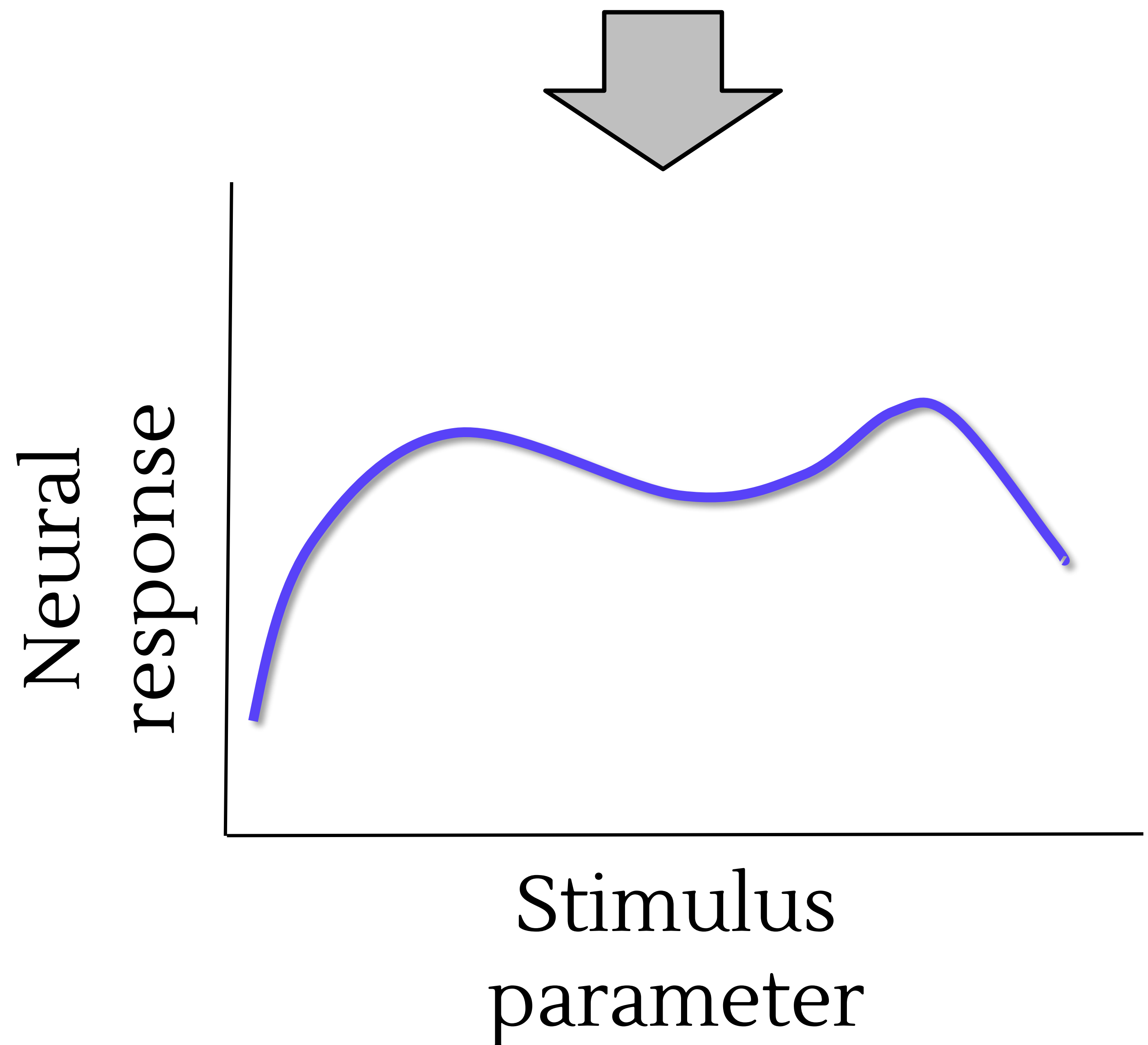
?





"Neural coding" is a quest to reduce dimensionality

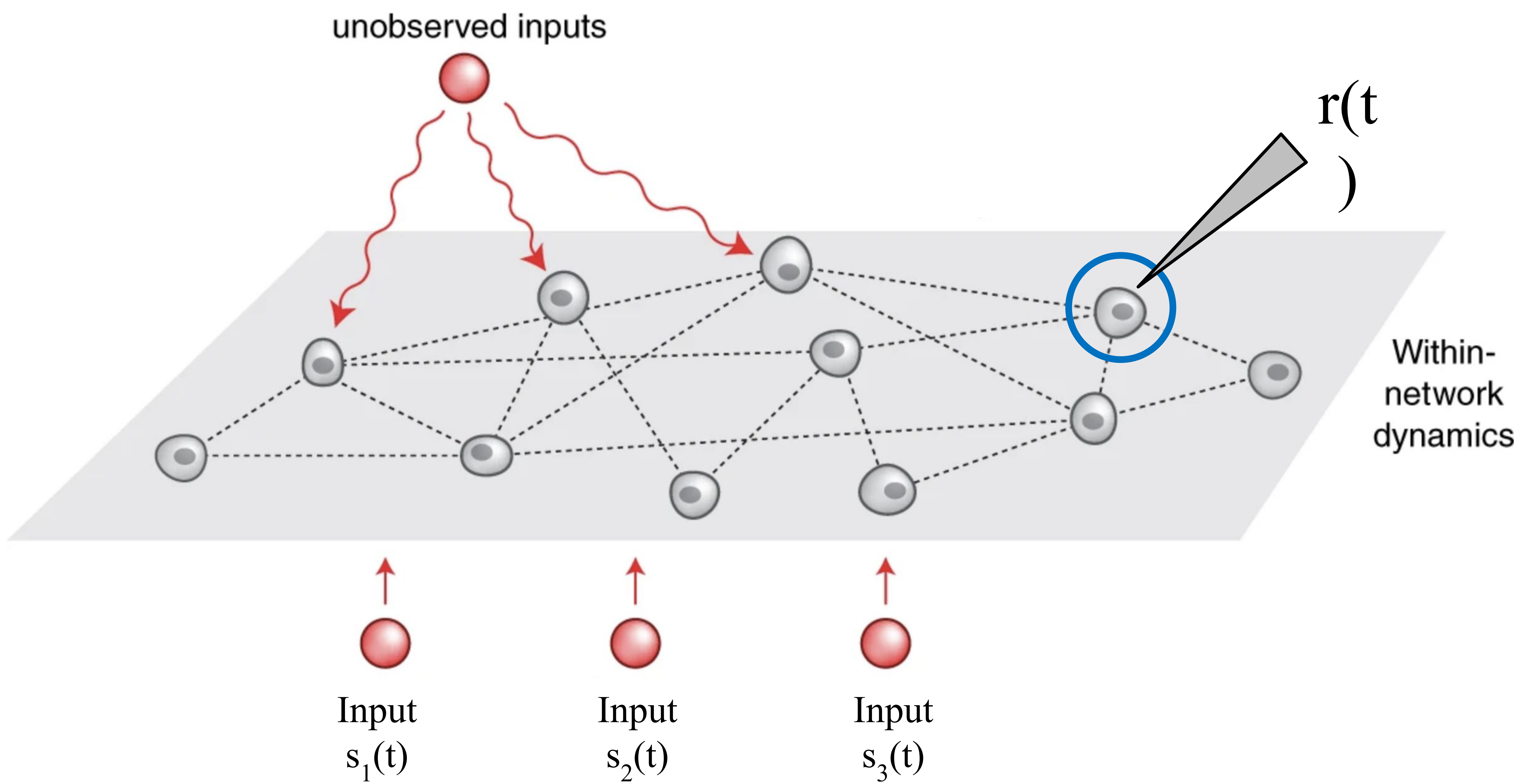
P( | )



Dimensionality reduction

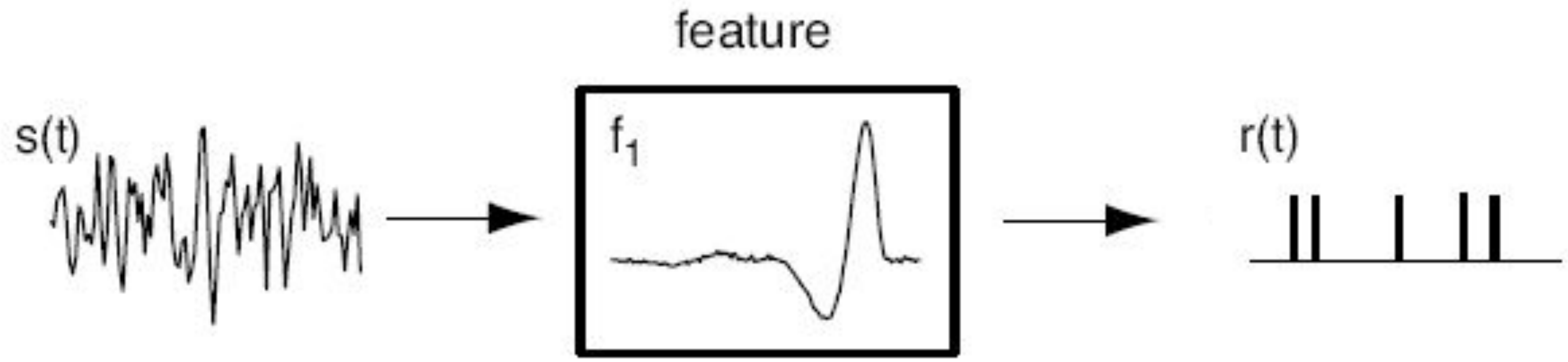
$$S(t) = \sum a_i(t)\varphi_i$$

Coding



unobserved inputs
r(t
)
Within-
network
dynamics
Input
s1(t)
Input
s2(t)
Input
s3(t)

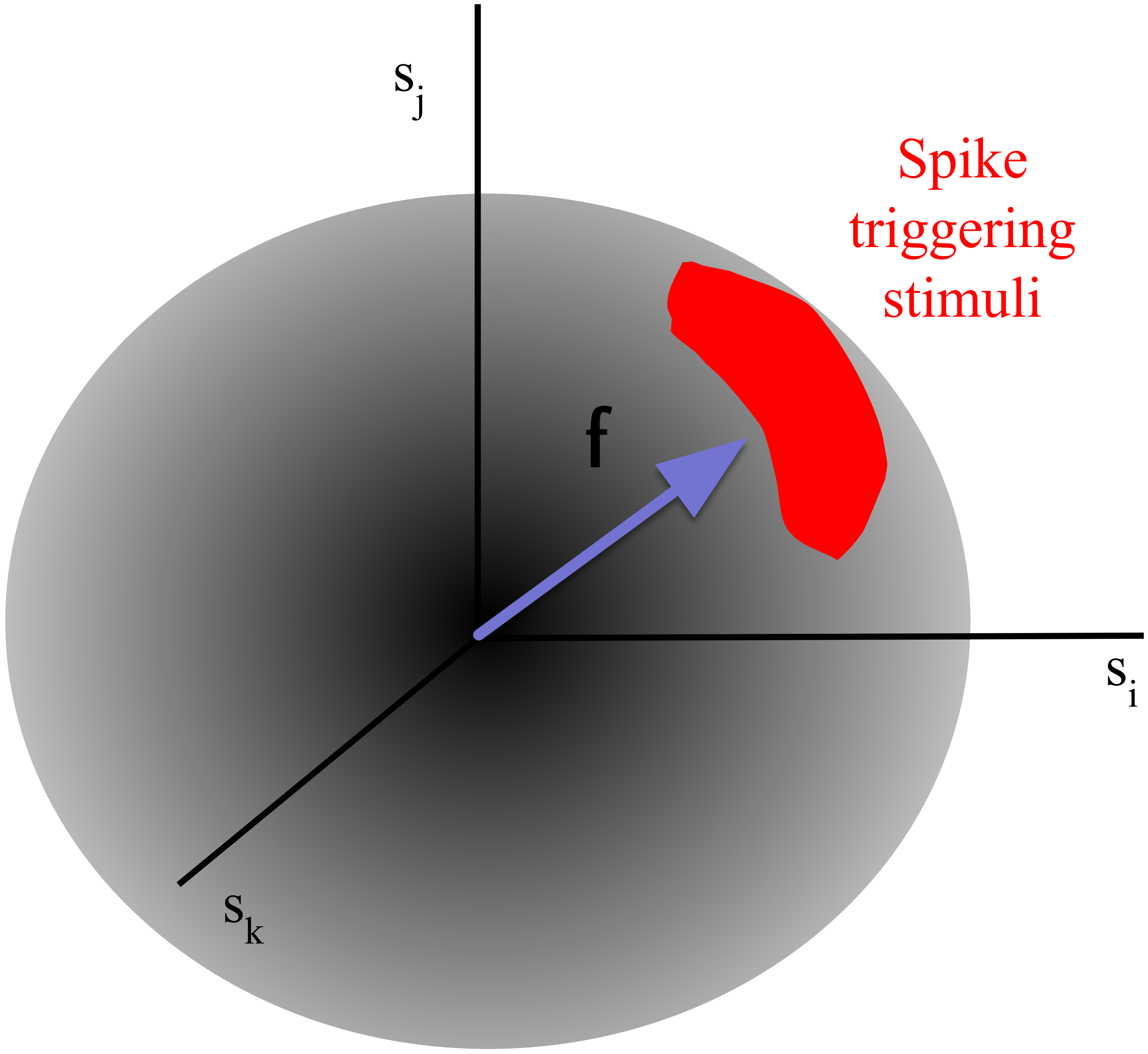
Build from linear coding model



Linear filter: $r(t) = \int f(\tau)\, s(t-\tau)\, d\tau$

The weights *f* are a linear filter

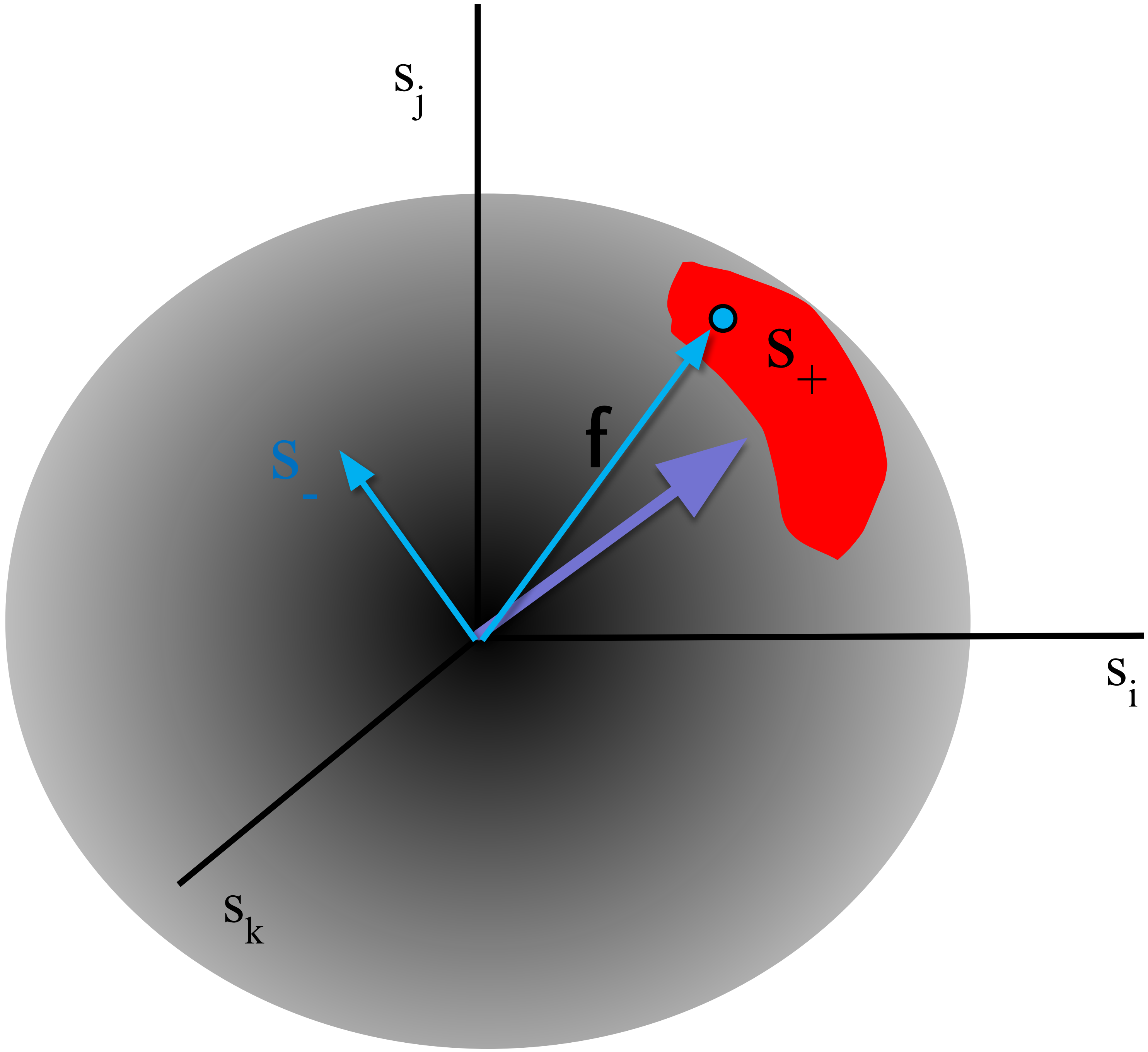
Linear filter: $r(t) = \int f(\tau)\, s(t-\tau)\, d\tau$



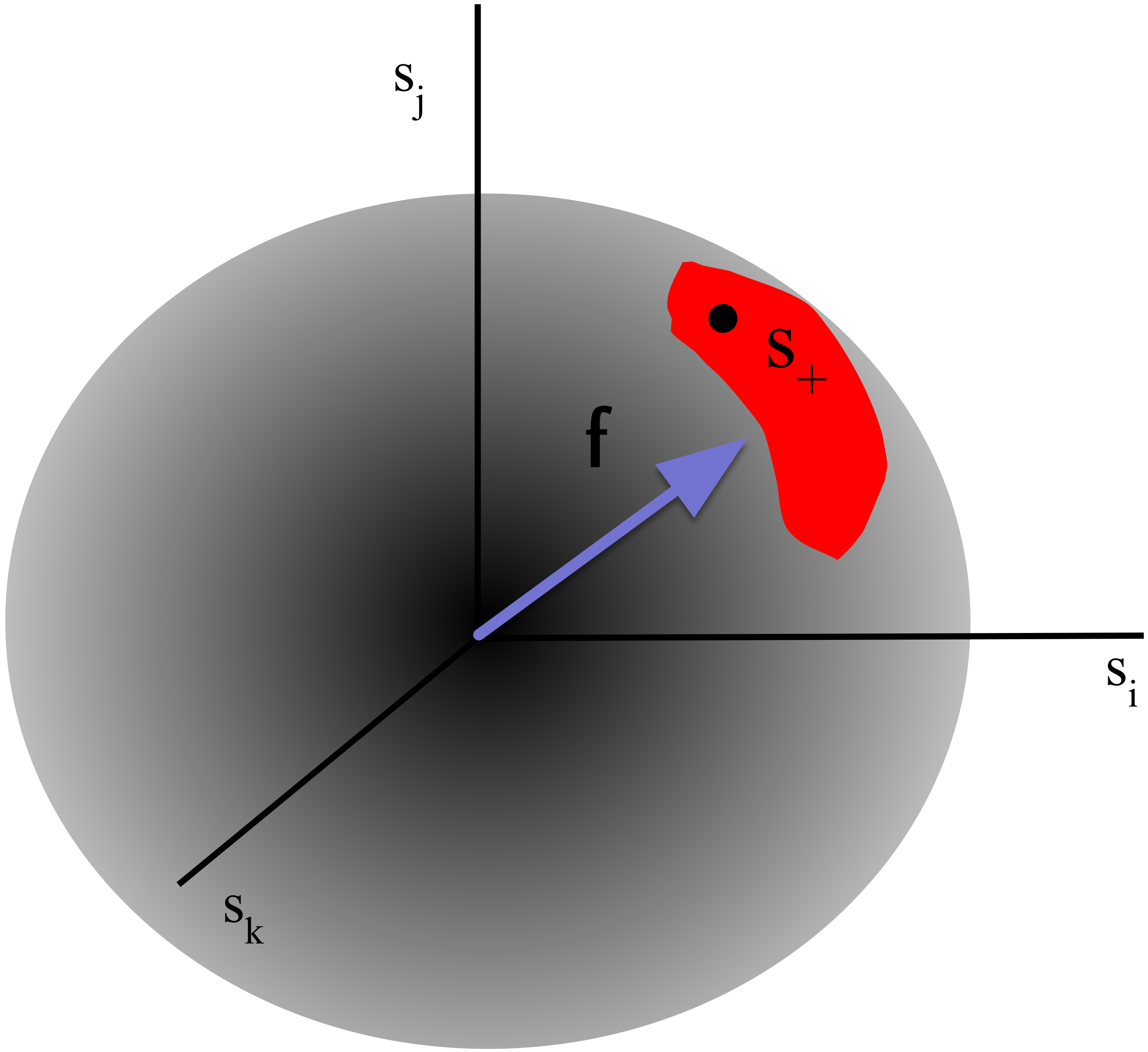
Filtering = convolution = projection = feature template

Linear filtering = convolution = projection

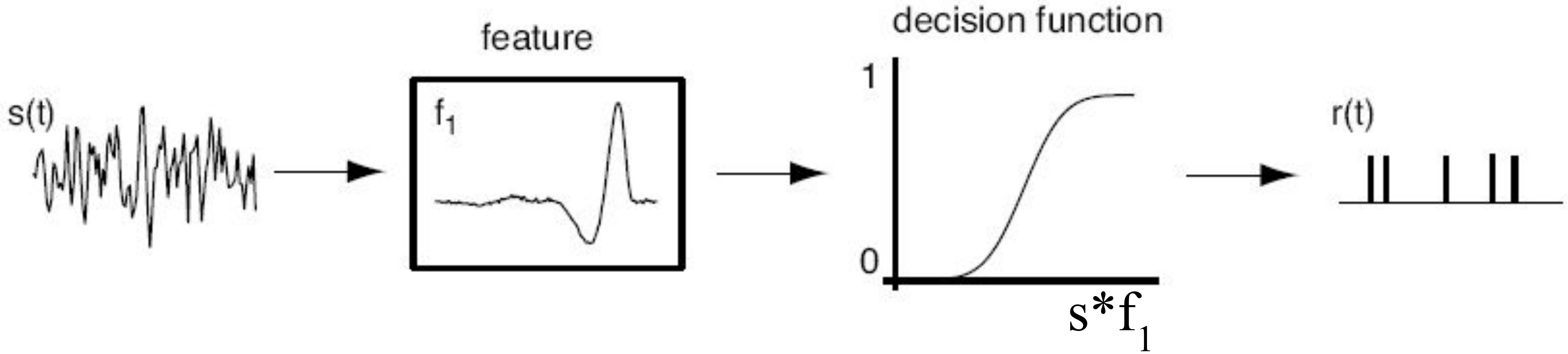
Linear filter: $r(t) = \int f(\tau)\, s(t-\tau)\, d\tau$



Need another step

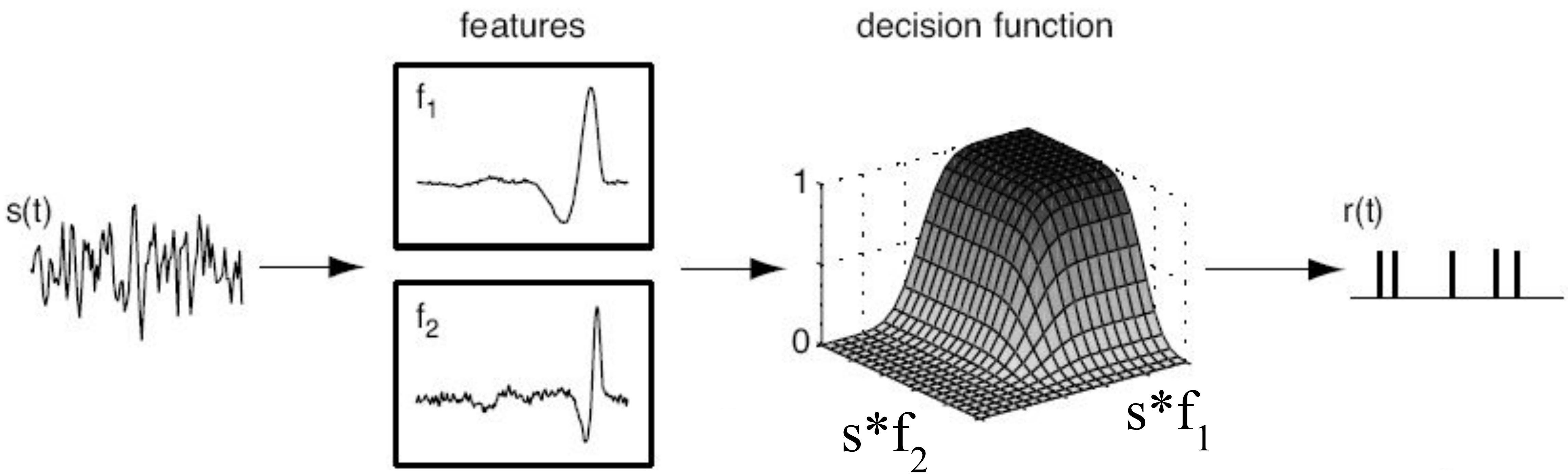


Next most basic coding model



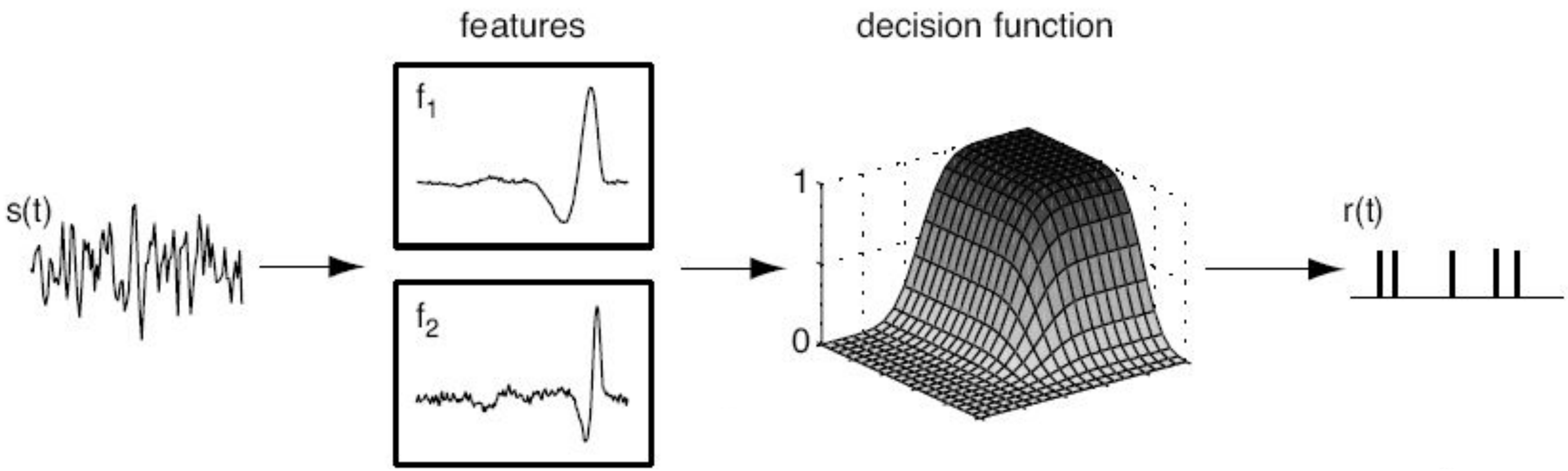
Linear filter & nonlinearity: $r(t) = g(\int f(\tau)\, s(t-\tau)\, d\tau)$

Why stop there: multidimensional



Linear filters & nonlinearity: $r(t) = g(s*f_1, s*f_2, ..., s*f_n)$

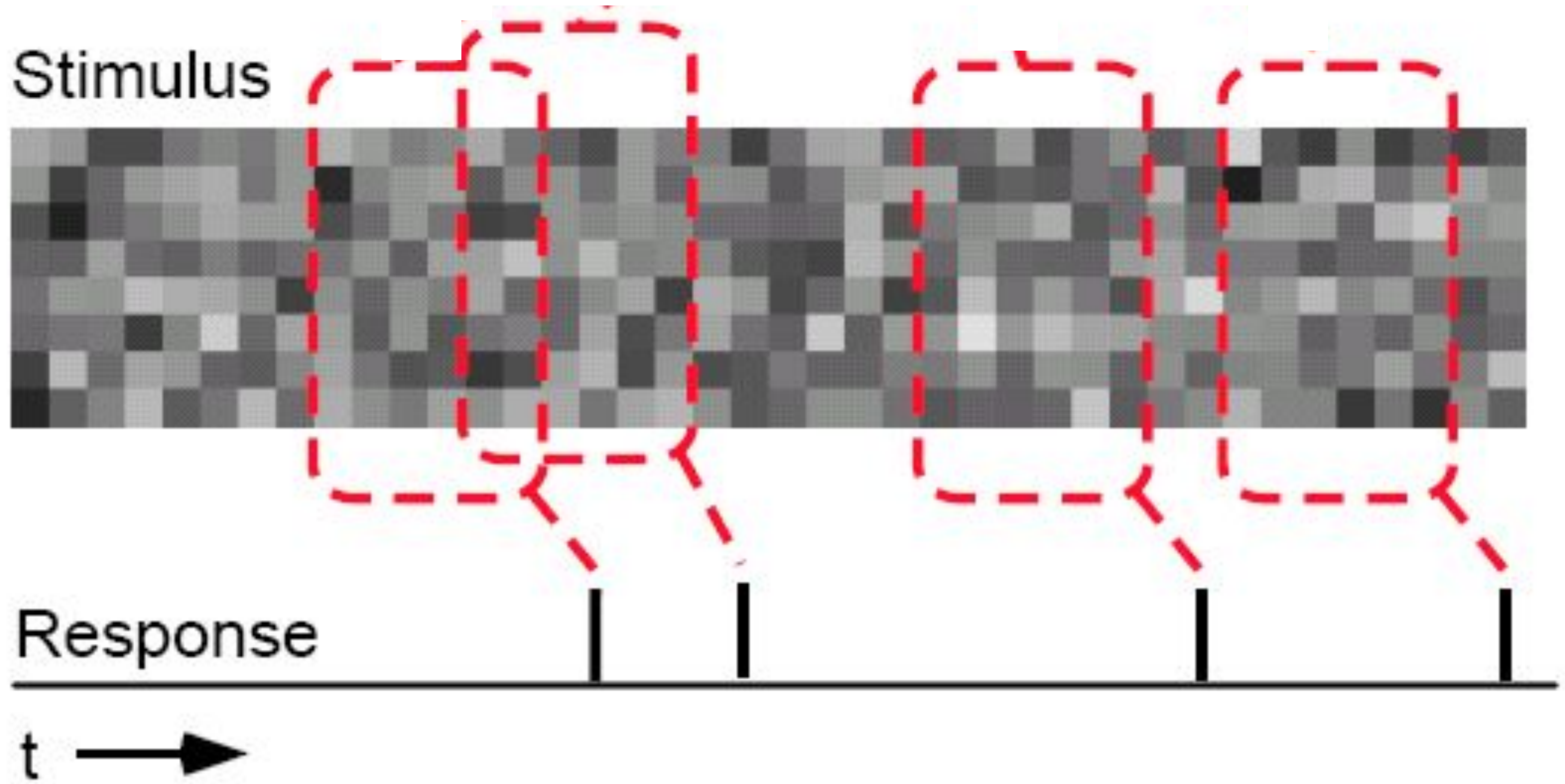
Coding



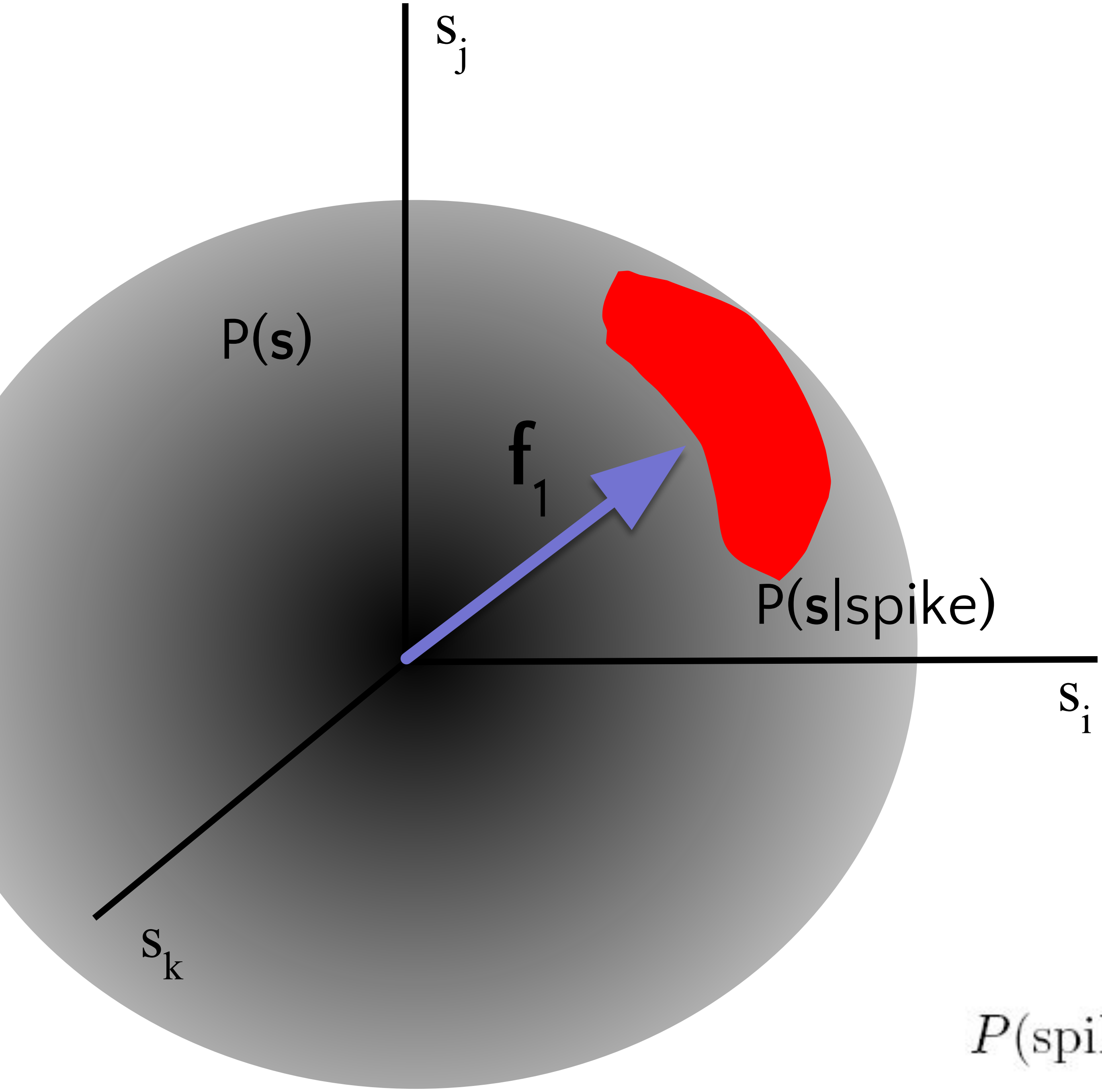
Generalizes the idea of representation to any arbitrary
stimulus feature and any arbitrary nonlinearity

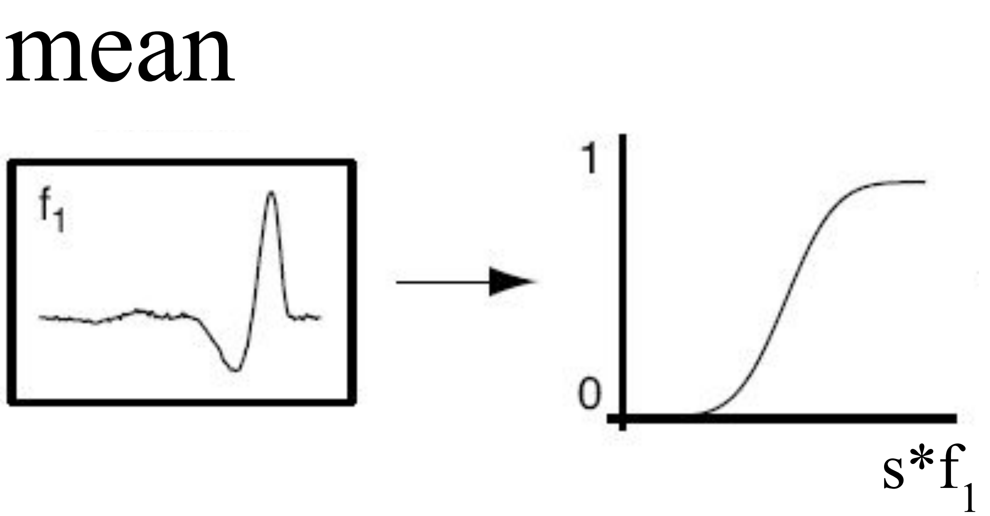
Allows us to quantify how neural representations change

Determining models from random stimuli



Determining models from Gaussian stimuli





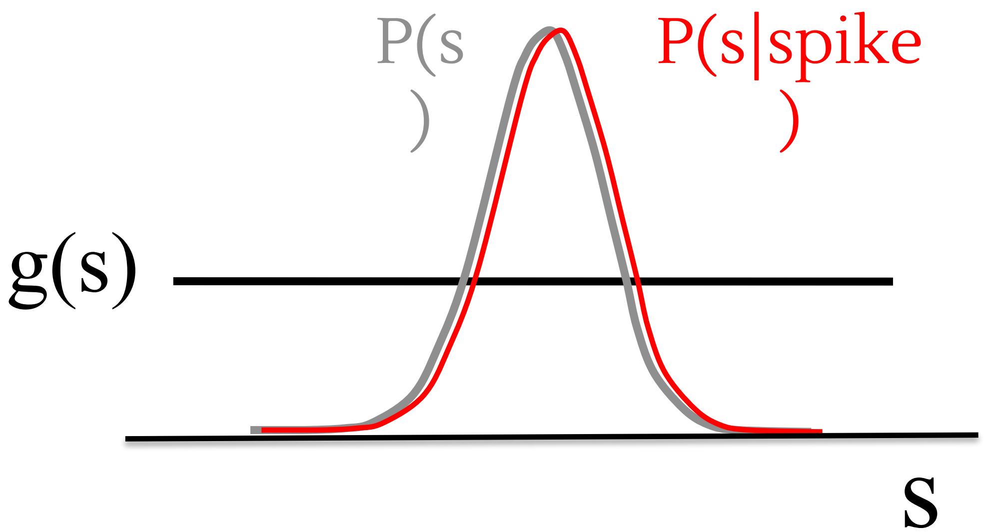
$$P(\text{spike}|\text{stimulus}) = \frac{P(\text{stimulus}|\text{spike})P(\text{spike})}{P(\text{stimulus})}$$

Finding the nonlinearity

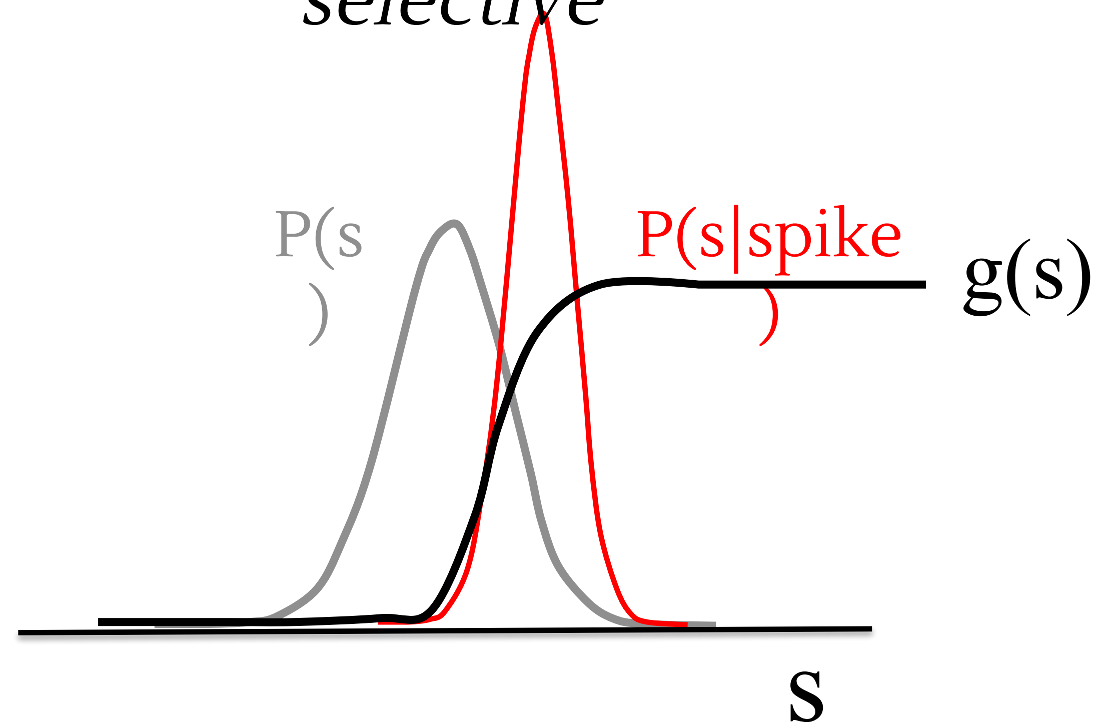
s = stimulus*f

Input/output: P(spike|s) = P(s|spike) P(spike) / P(s)

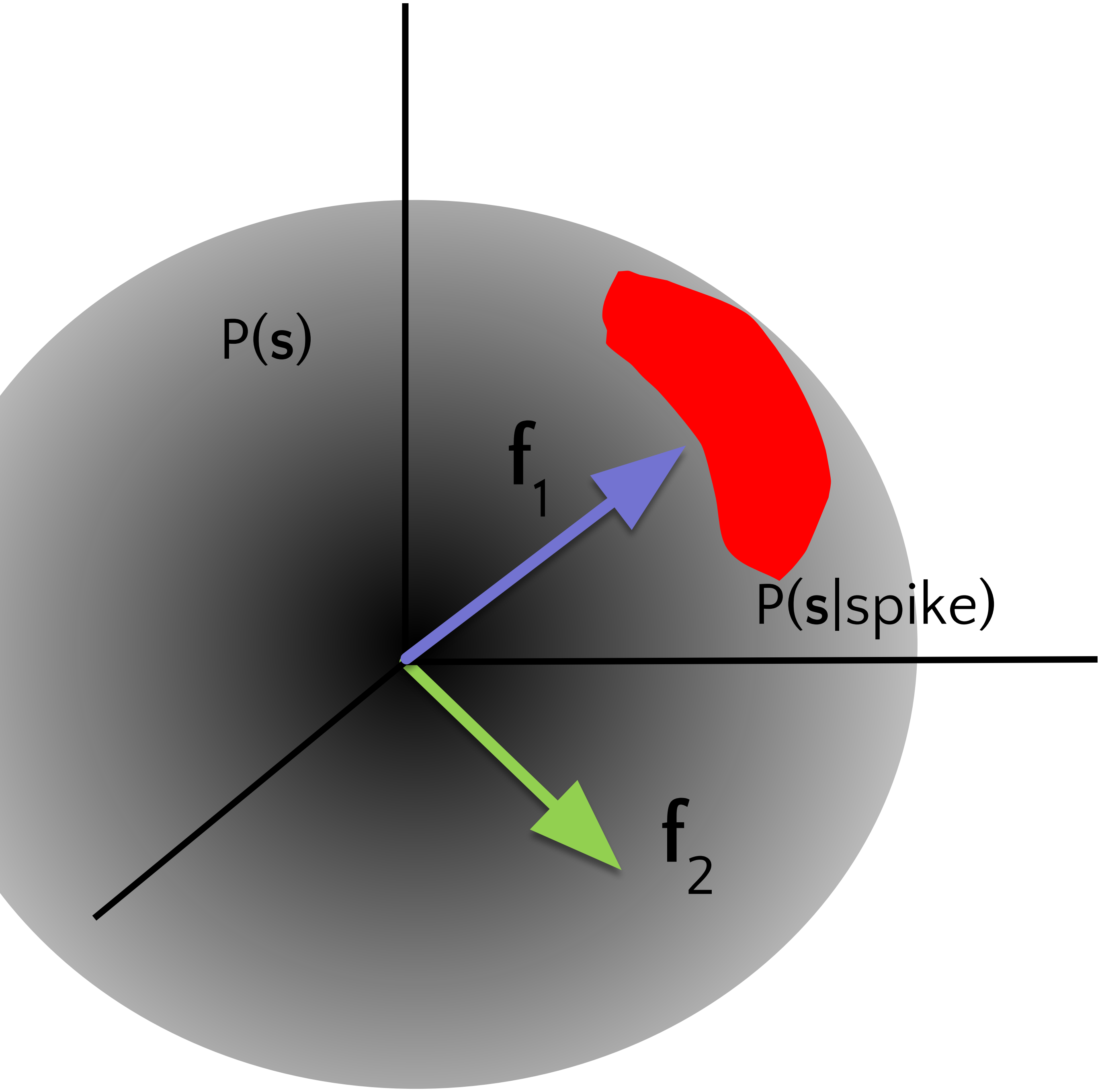
Fail: spikes *unrelated* to stimulus



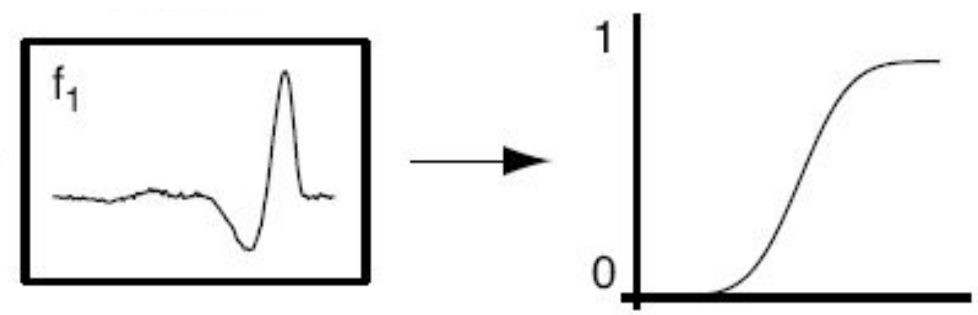
Interesting: spikes are *selective*



Determining models from random stimuli

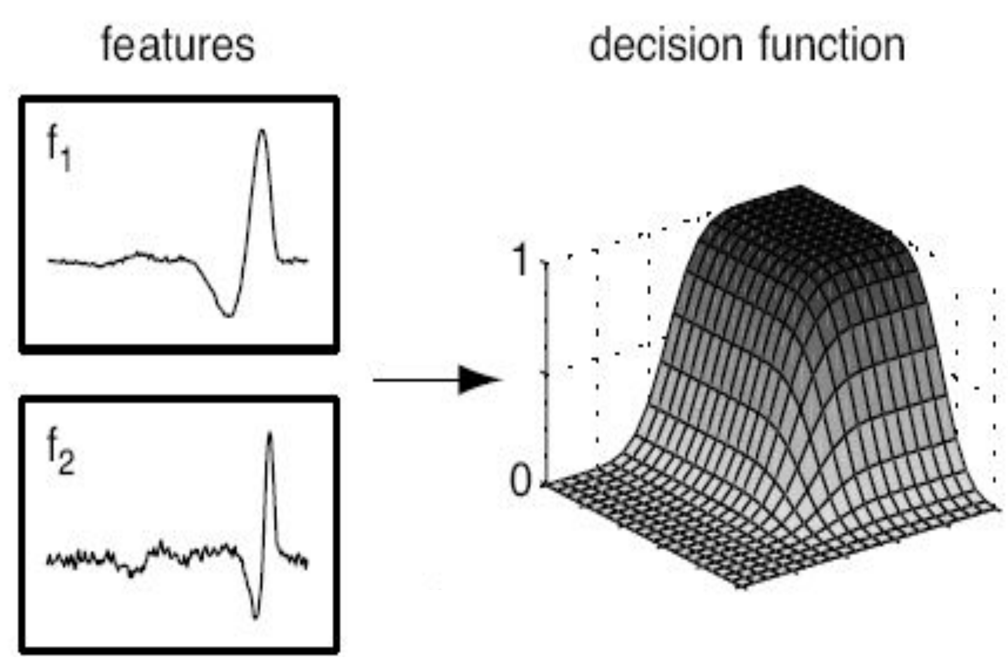


mean



$$f = \bar{s}$$

covariance

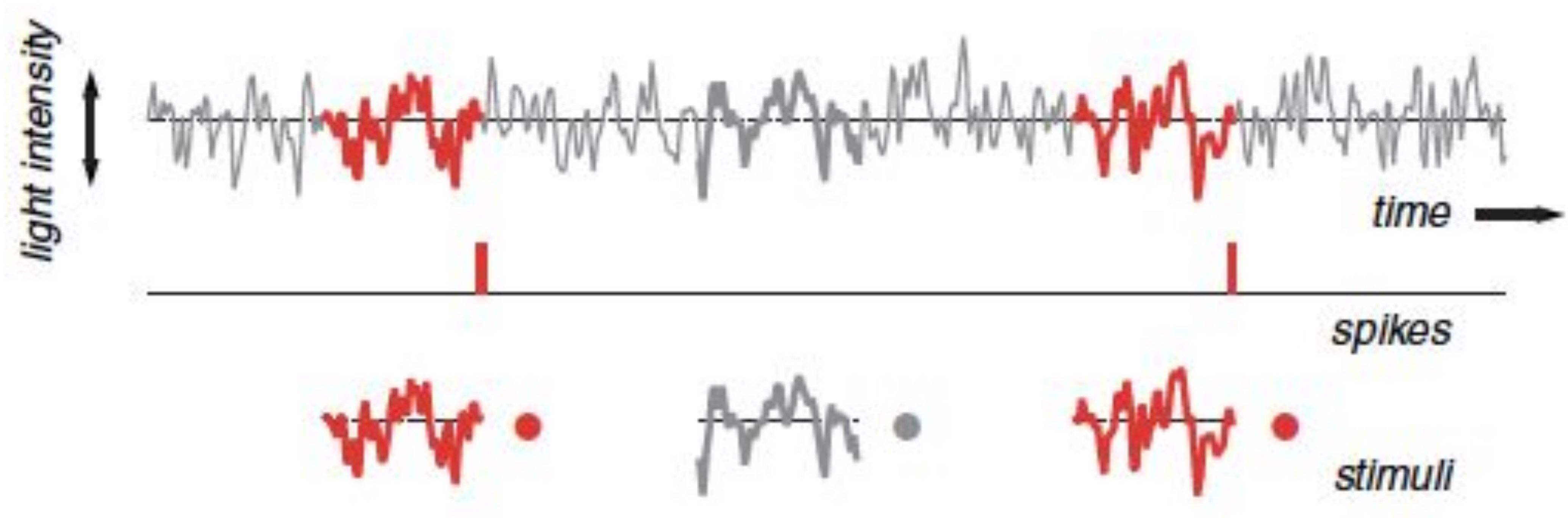


$f_i, f_j \rightarrow$ eigenmodes

Identifying multiple features

Compute the covariance matrix of spike-conditioned stimulus samples:

$$C_{ij} = \langle (s(t - i\tau) - \overline{s_i})(s(t - j\tau) - \overline{s_j}) \rangle$$



Bialek et al., 1988; Brenner et al., 2000; Bialek and de Ruyter, 2005

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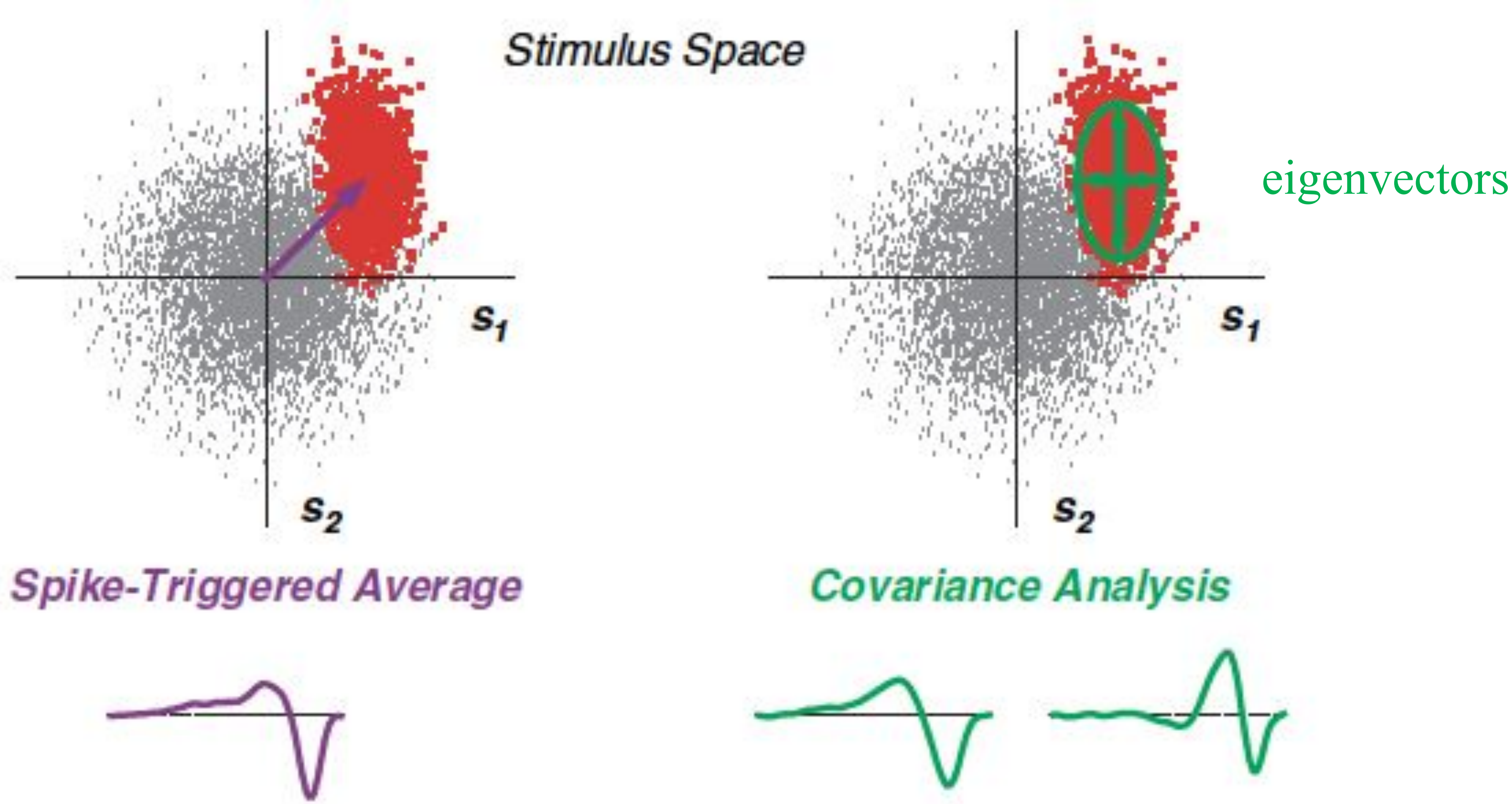

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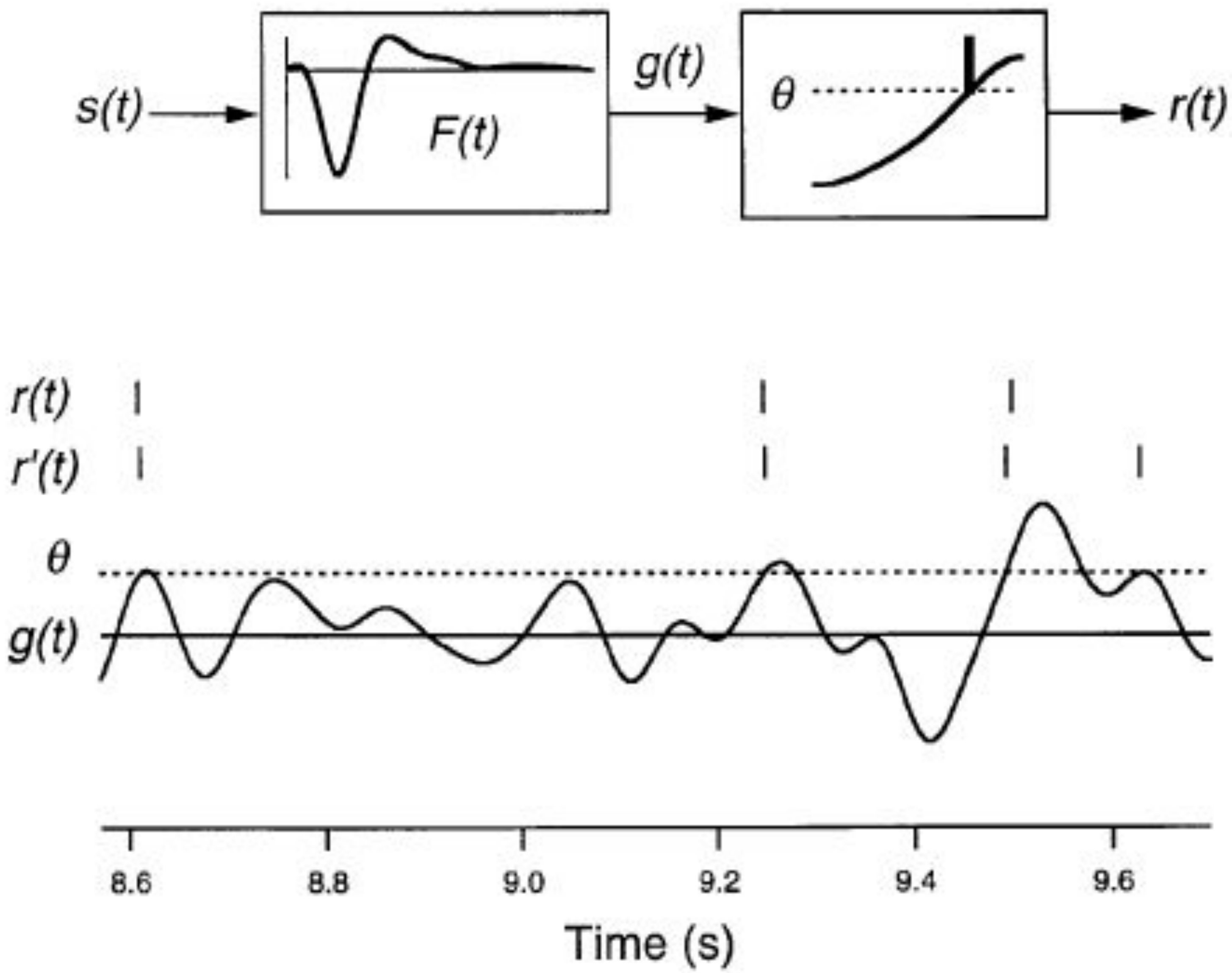
How does this work with simple models?



Modeling precise spike times from visual neurons, Keat et al, Neuron 2001

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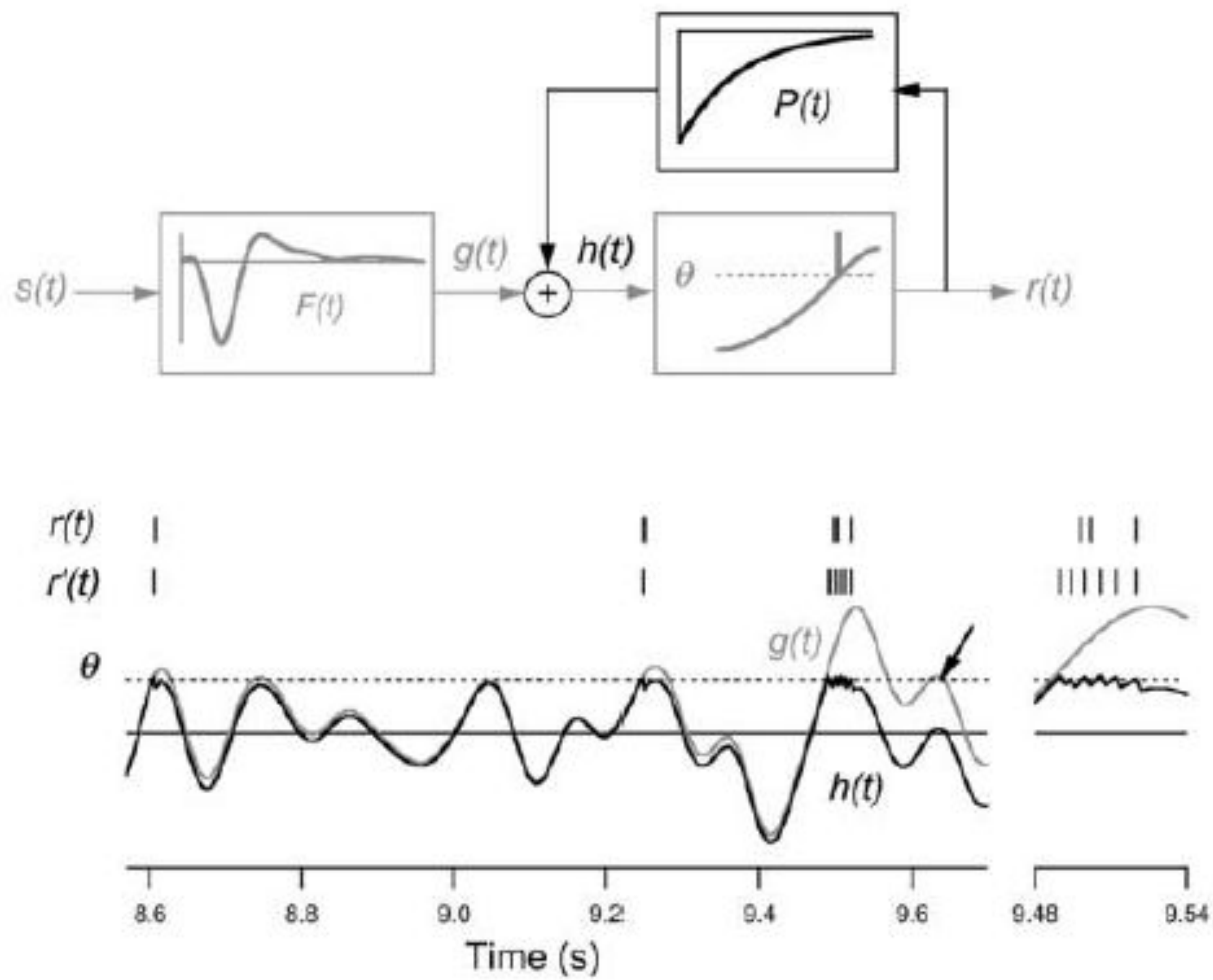
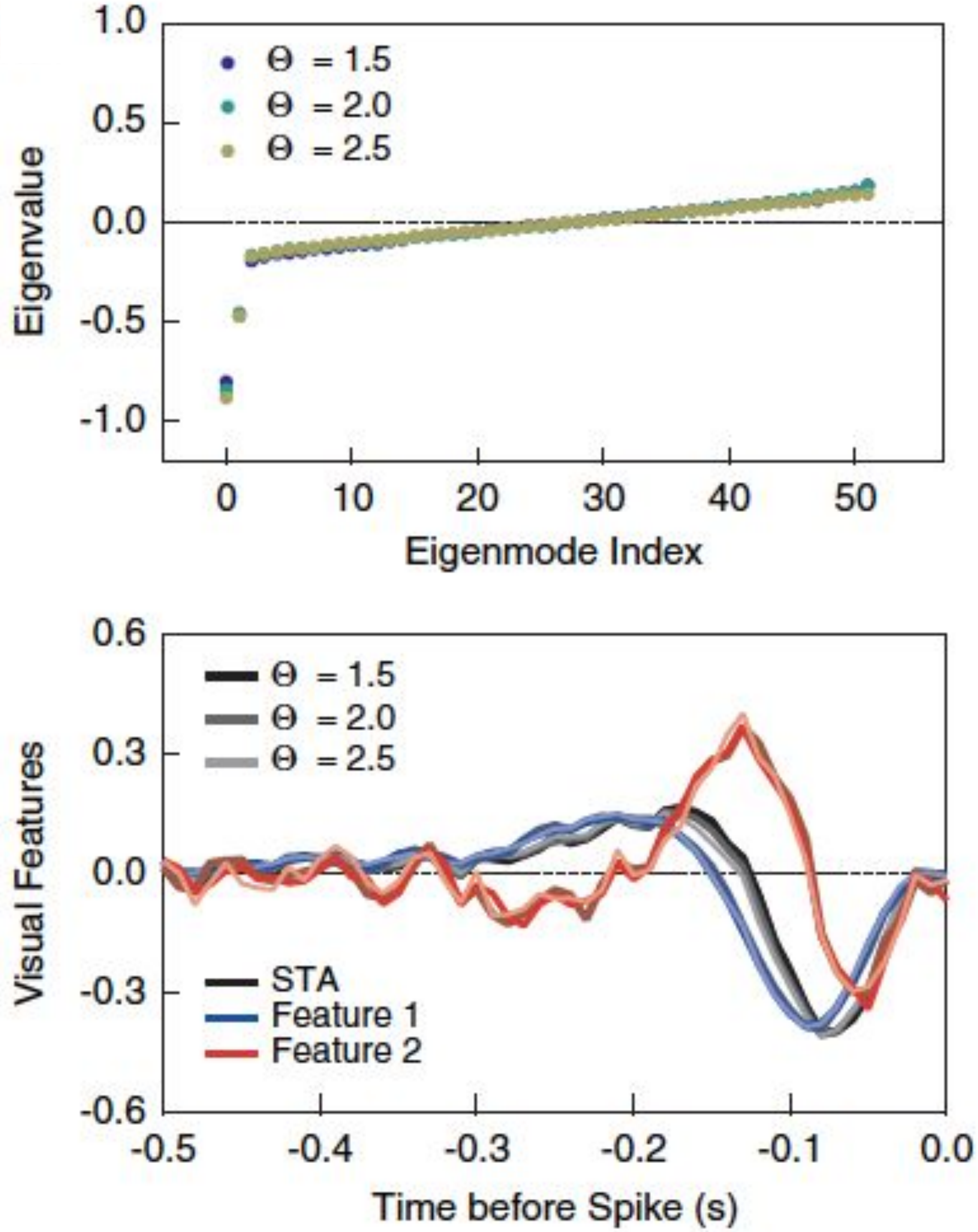
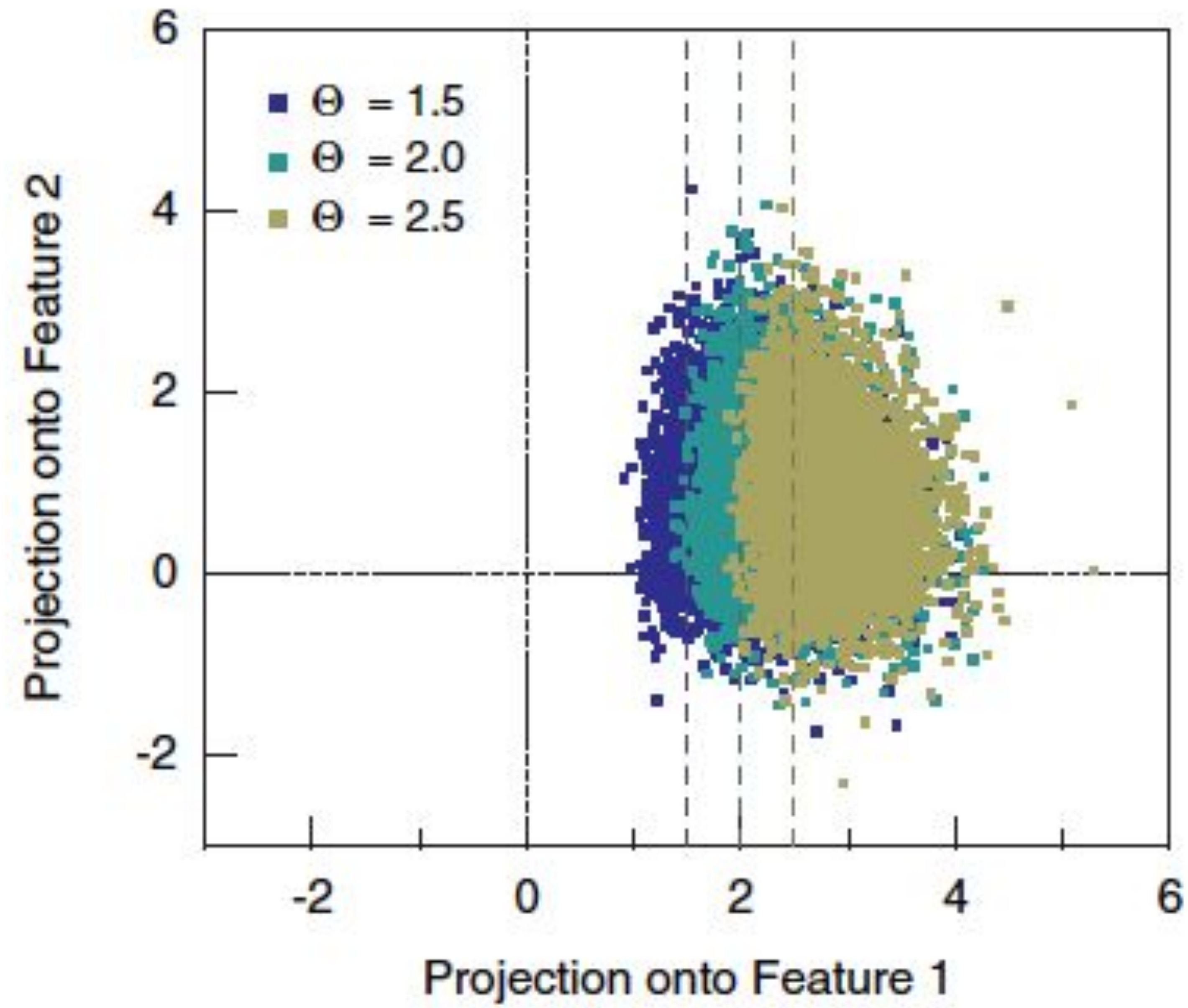


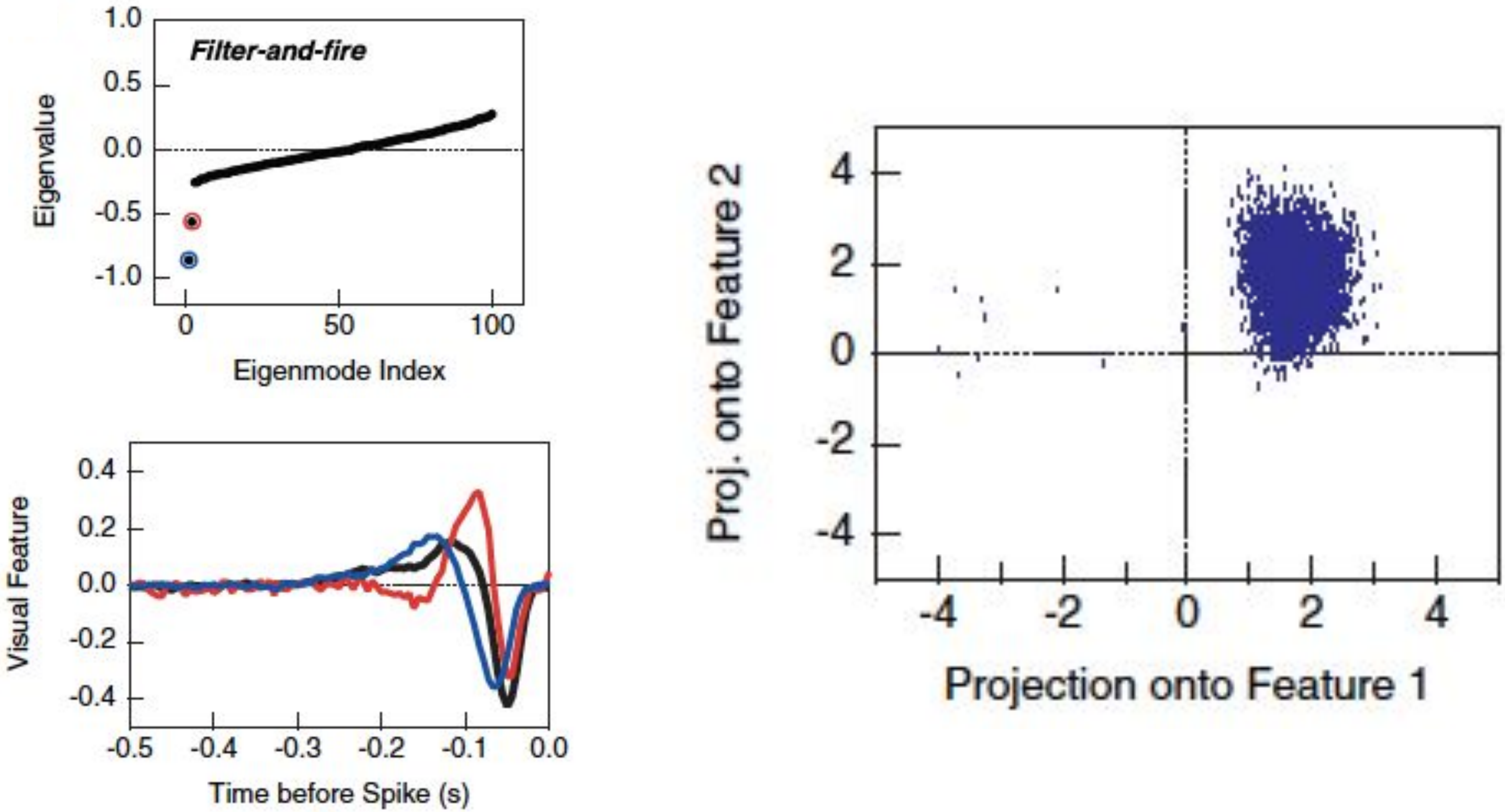
Modeling precise spike times from visual neurons, Keat et al, Neuron 2001

Filter and fire model

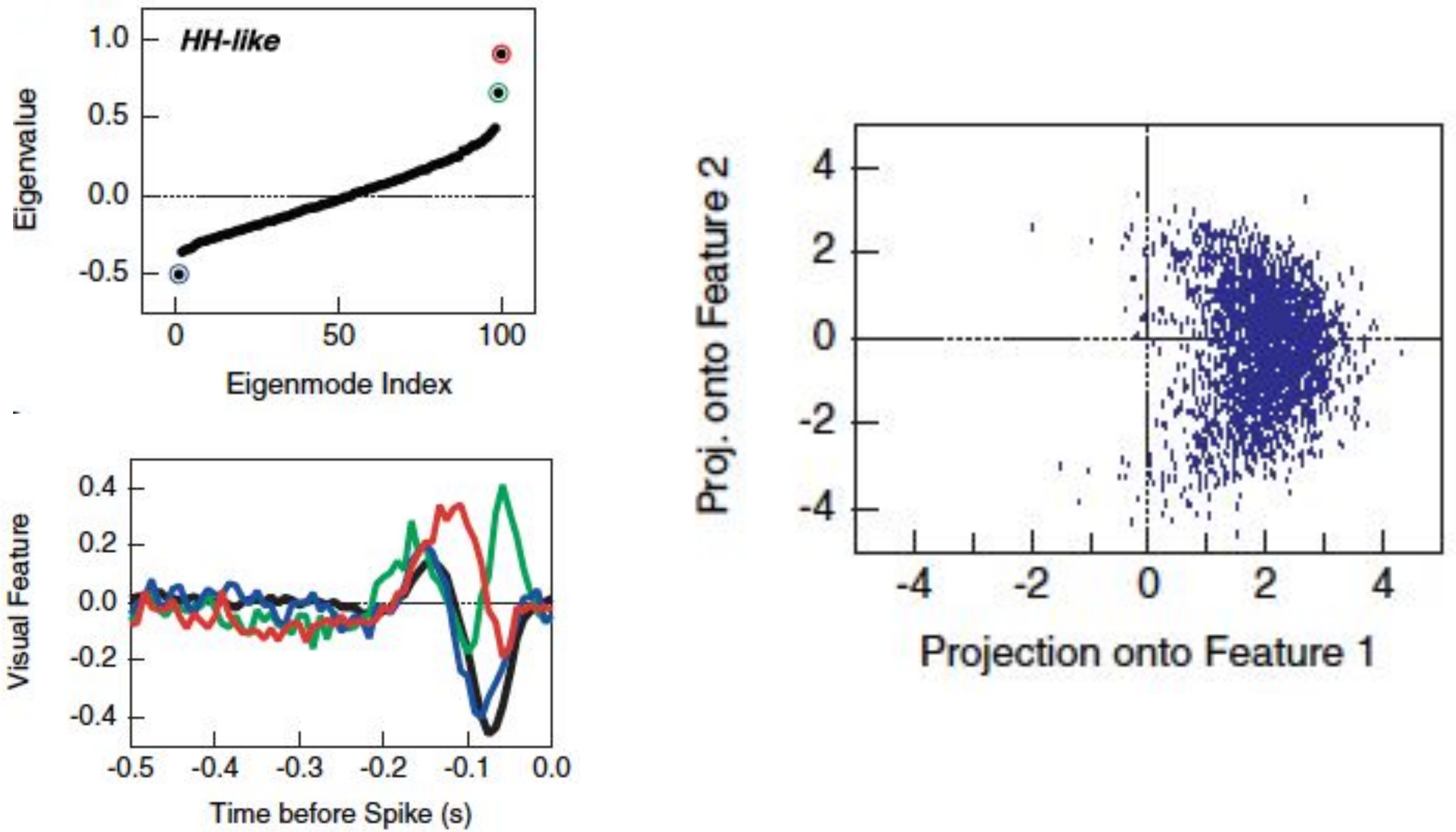




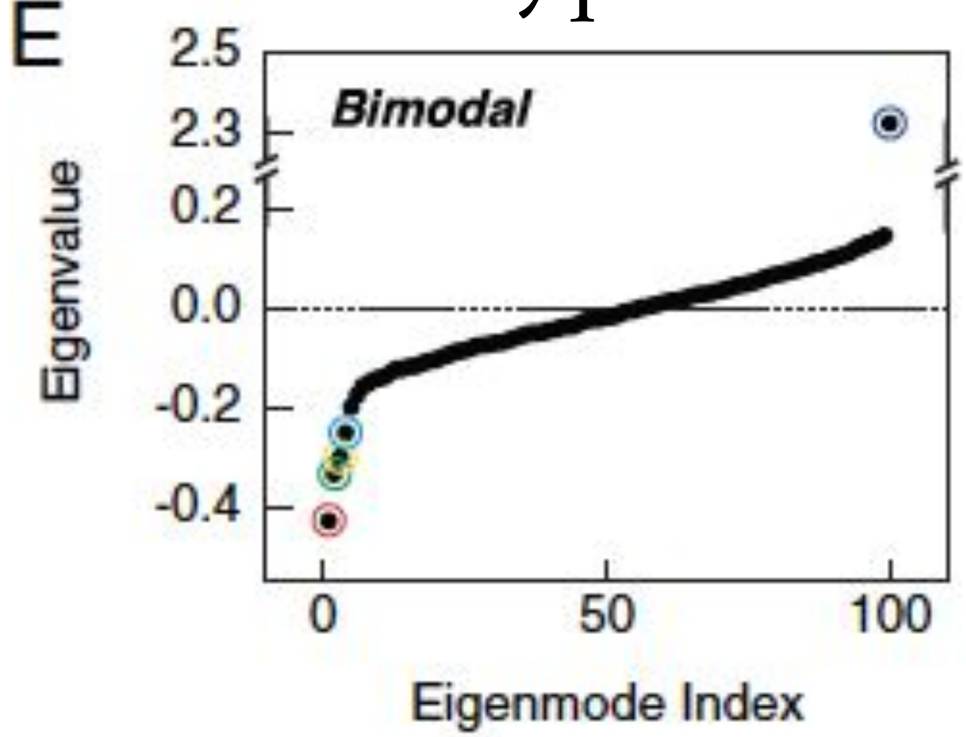
Retinal ganglion cell types

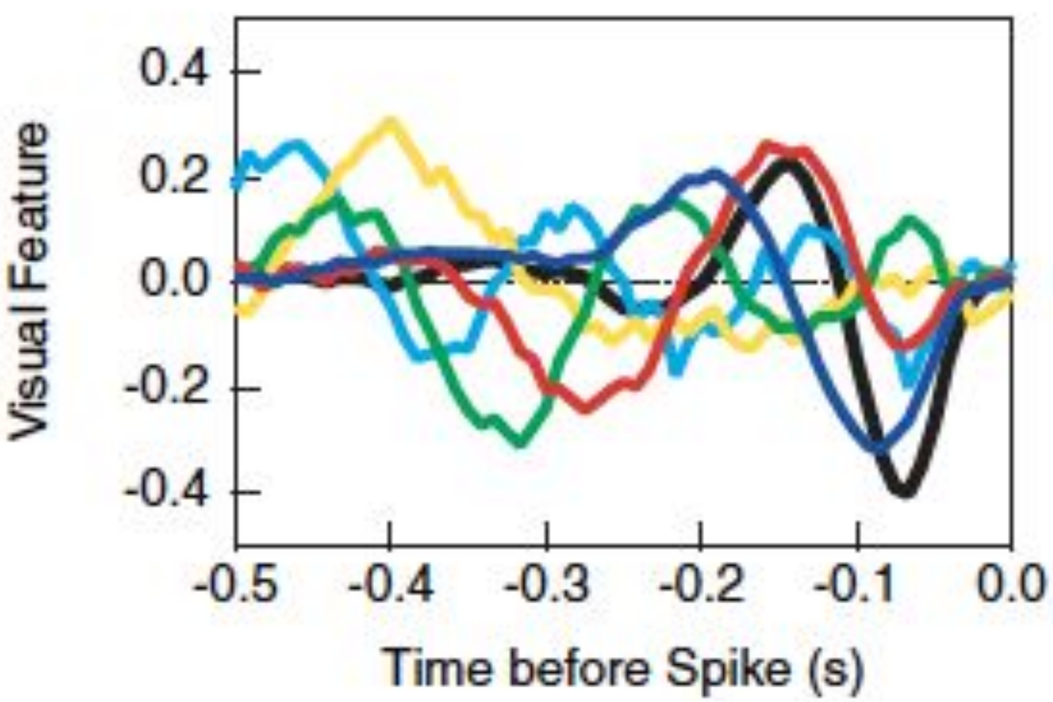


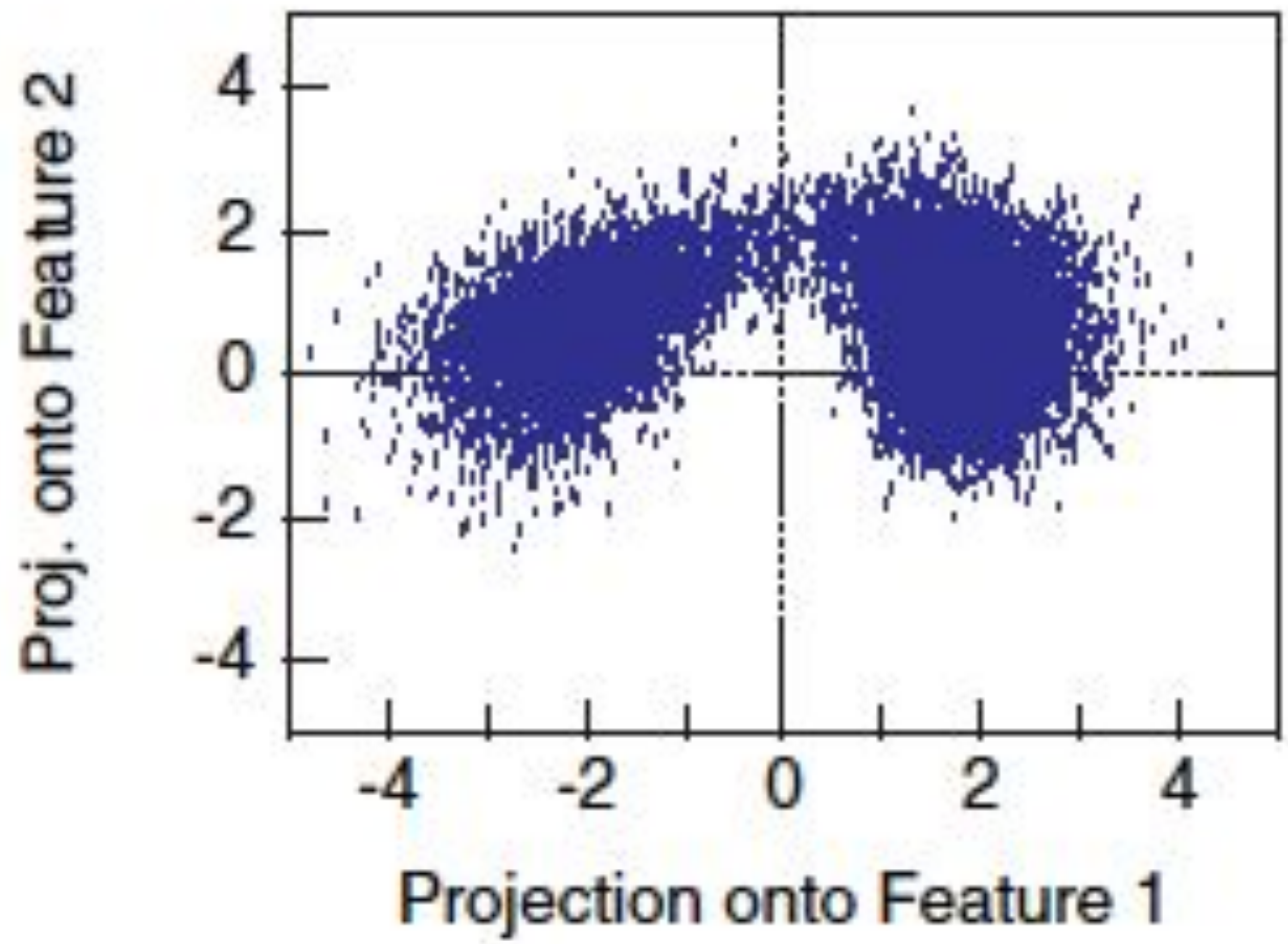
Retinal ganglion cell types



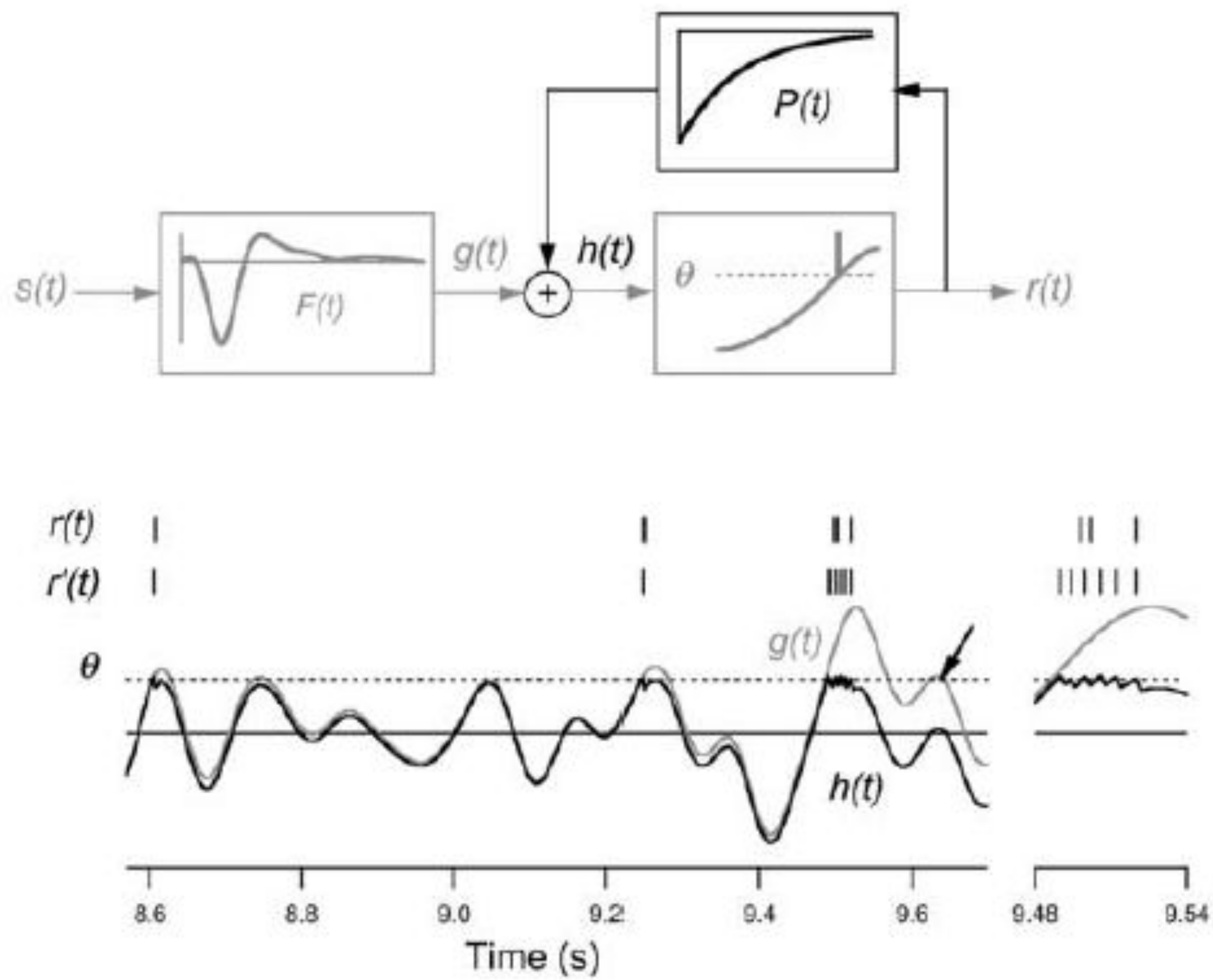
Retinal ganglion cell types





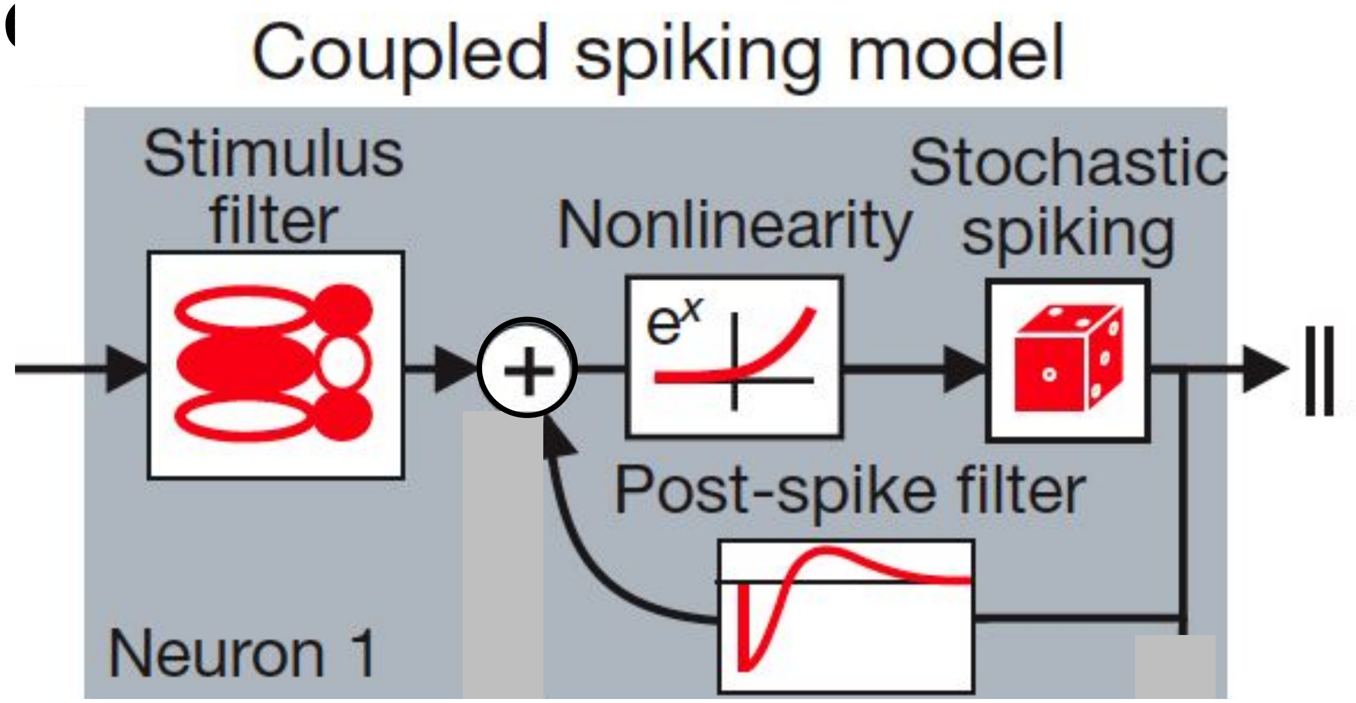


How might one deal with spike history effects?



Modeling precise spike times from visual neurons, Keat et al, Neuron 2001

Generalized linear model

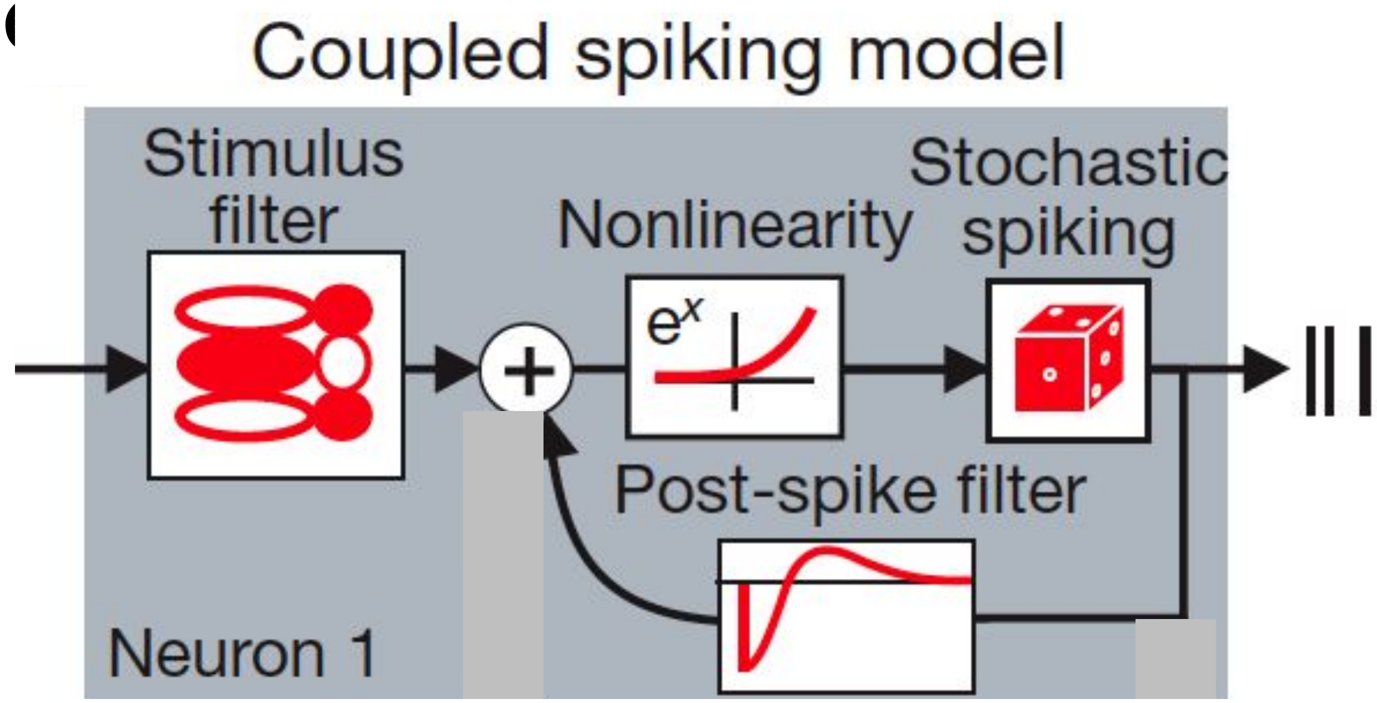


GLM: $r(t) = g(f*s + h*r + \ldots)$

Pillow et al., *Nature* 2008; Truccolo, .., Brown, *J. Neurophysiol.* 2005

Generalized linear model

stimulus



GLM: $r(t) = g(f*s + h*r + ...)$

Fit by writing down the *likelihood* of the spike data given
a choice of model, and maximizing over the free parameters of the model (g, f, h, ..)

Poisson $P_T(k) = (r(t)T)^k \exp(-r(t)T)/k!$

Pillow et al., *Nature* 2008; Truccolo, .., Brown, *J. Neurophysiol.*

Comparison for real-life data

Neuron

Primer

Analysis of Neuronal Spike Trains, Deconstructed

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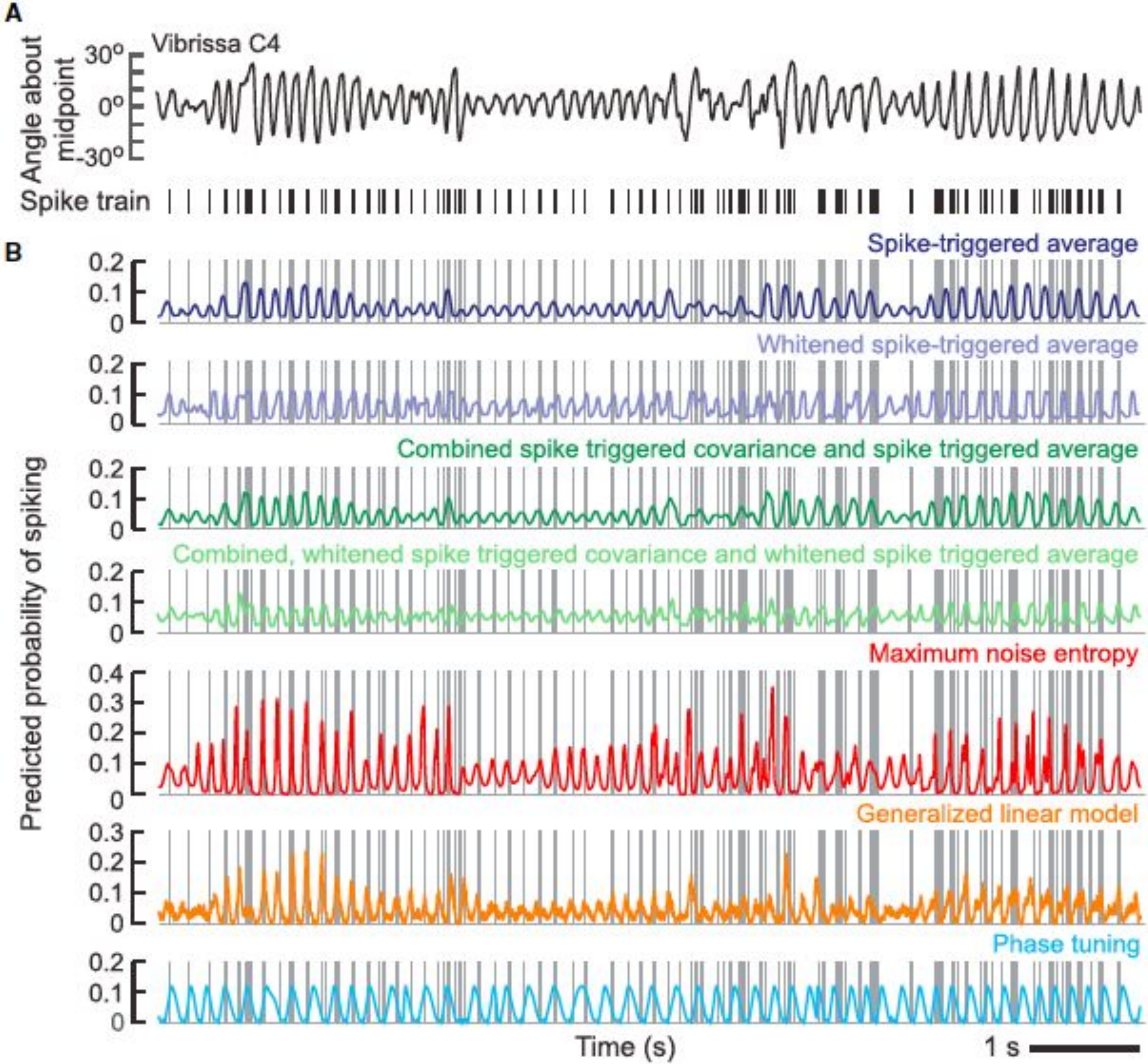
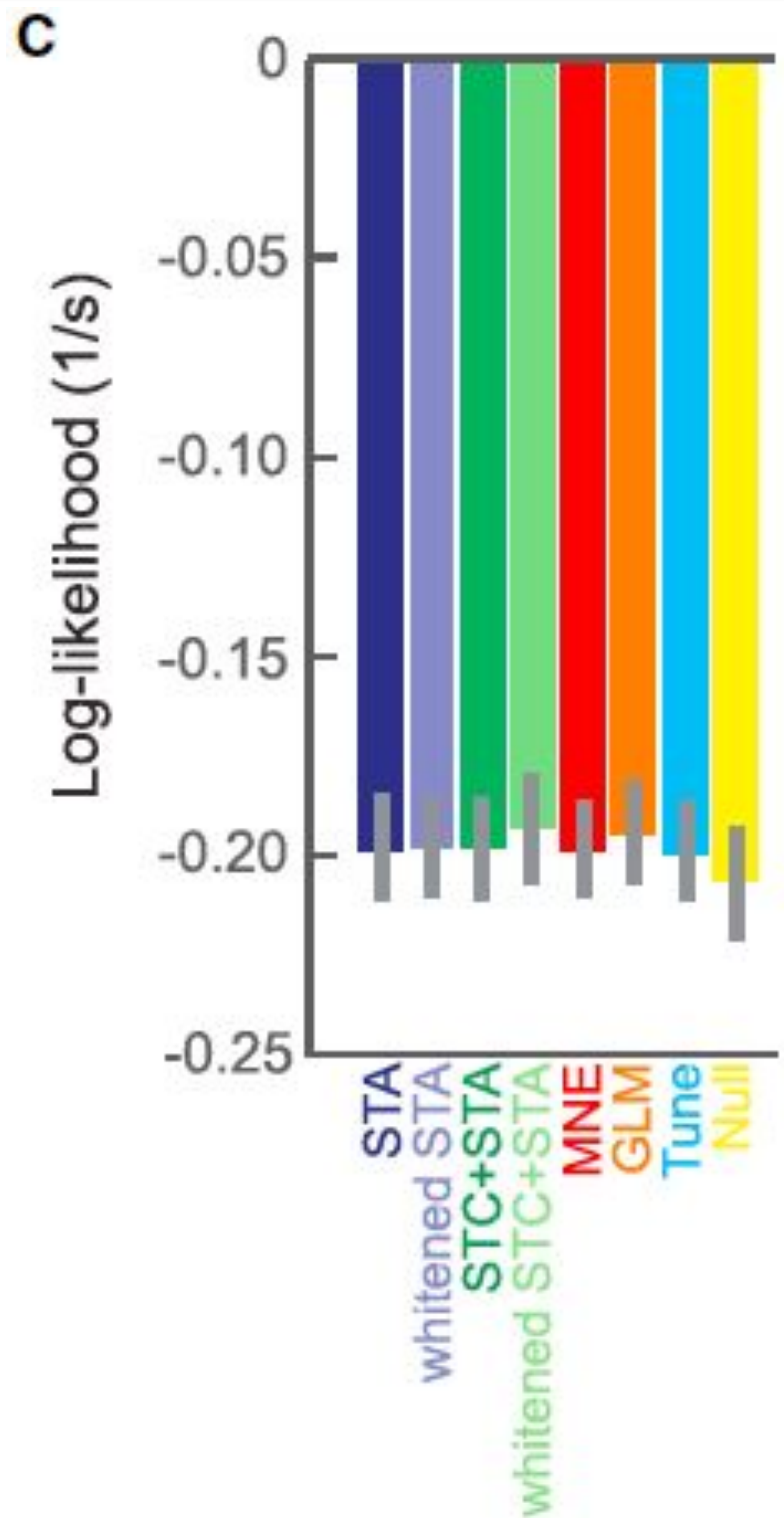
http://dx.doi.org/10.1016/j.neuron.2016.05.039

As information flows through the brain, neuronal firing progresses from encoding the world as sensed by the animal to driving the motor output of subsequent behavior. One of the more tractable goals of quantitative neuroscience is to develop predictive models that relate the sensory or motor streams with neuronal firing. Here we review and contrast analytical tools used to accomplish this task. We focus on classes of models in which the external variable is compared with one or more feature vectors to extract a low-dimensional representation, the history of spiking and other variables are potentially incorporated, and these factors are nonlinearly transformed to predict the occurrences of spikes. We illustrate these techniques in application to datasets of different degrees of complexity. In particular, we address the fitting of models in the presence of strong correlations in the external variable, as occurs in natural sensory stimuli and in movement. Spectral correlation between predicted and measured spike trains is introduced to contrast the relative success of different methods.

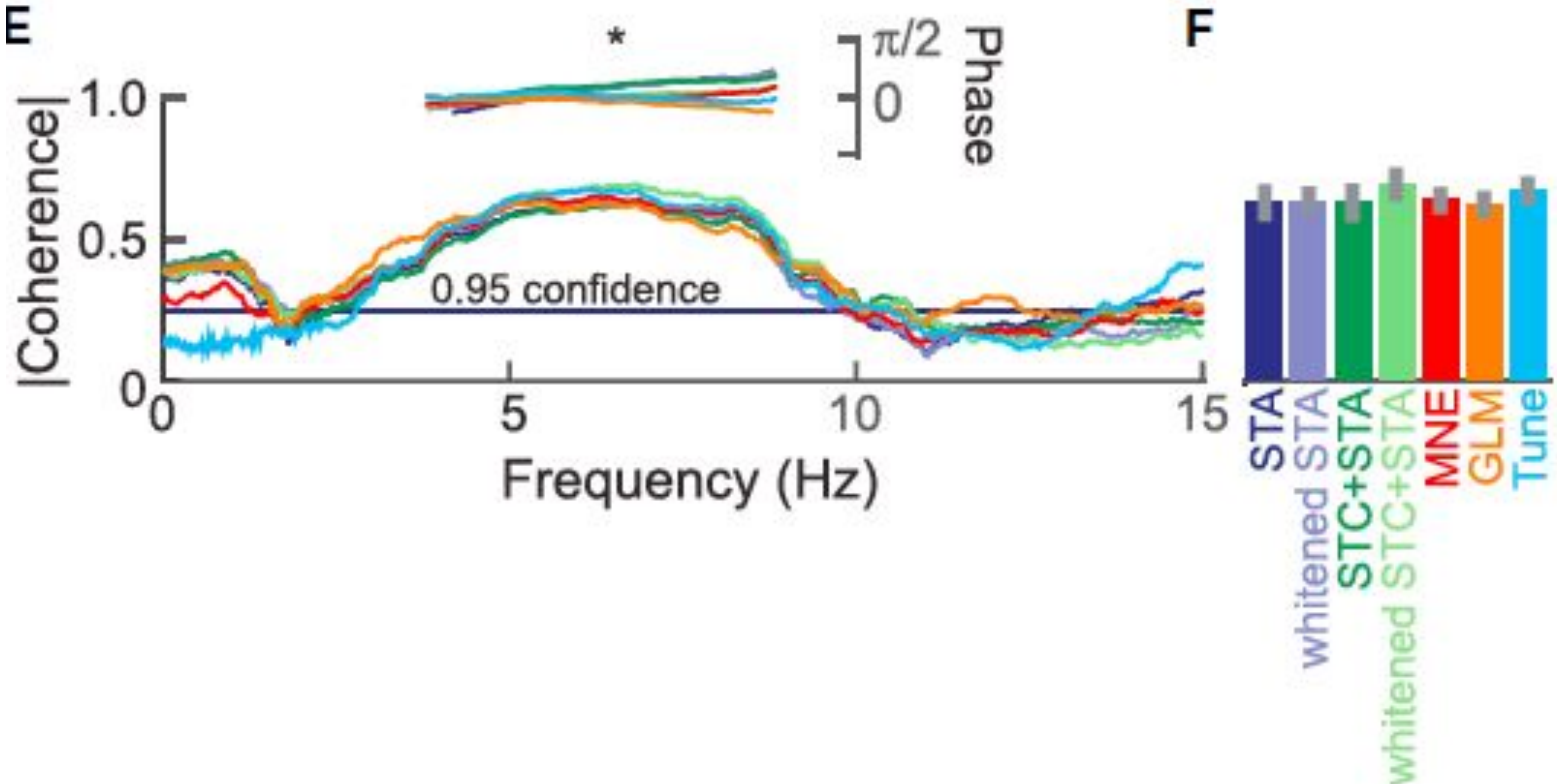

A
Vibrissa C4
Angle about midpoint
30°
0°
-30°
Spike train
B
Spike-triggered average
Whitened spike-triggered average
Combined spike triggered covariance and spike triggered average
Combined, whitened spike triggered covariance and whitened spike triggered average
Maximum noise entropy
Generalized linear model
Phase tuning
Predicted probability of spiking
0.4
0.3
0.2
0.1
0
Time (s)
1 s

Who wins?

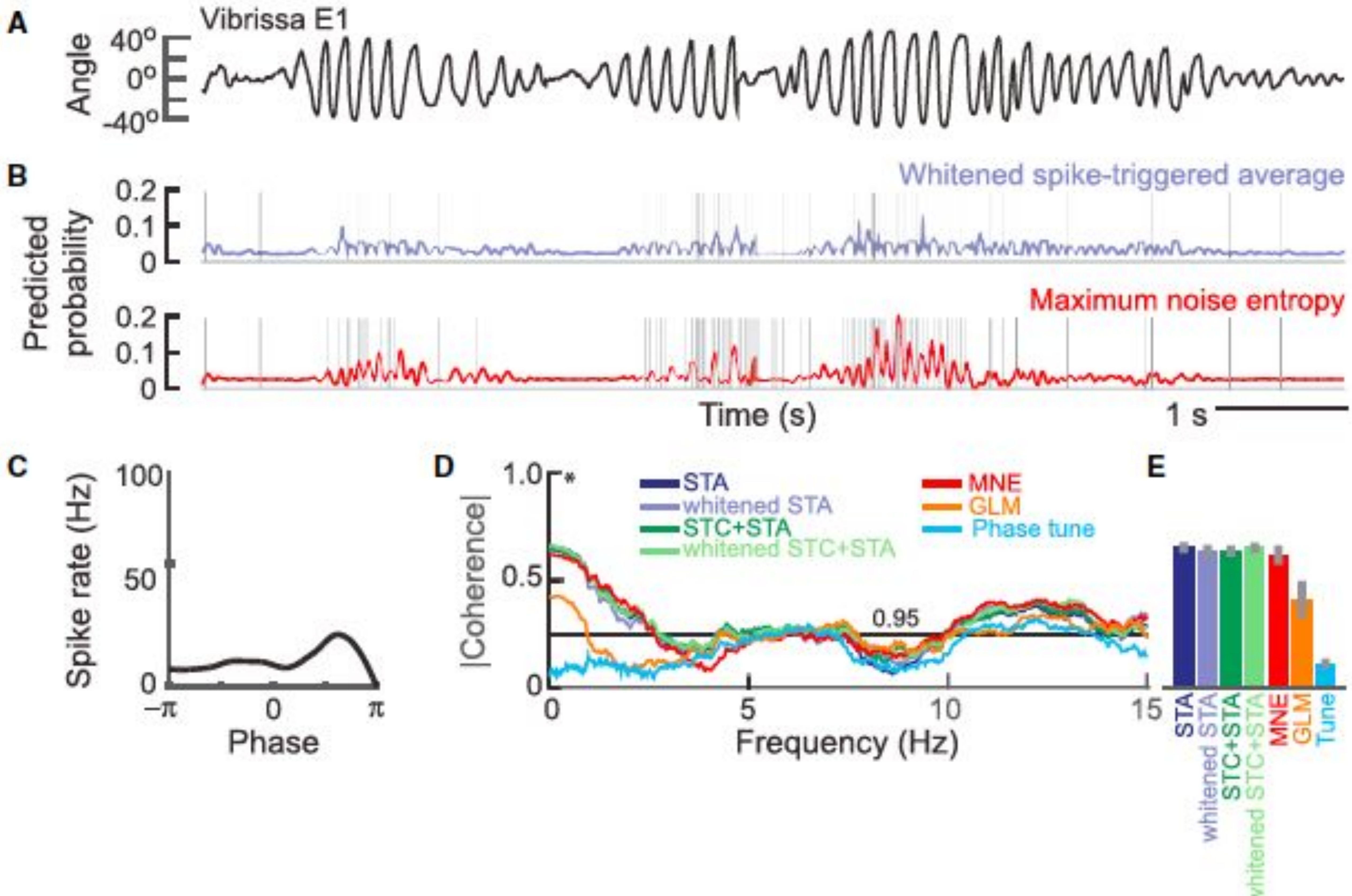


c
Log-likelihood (1/s)
0
-0.05
-0.10
-0.15
-0.20
-0.25
STA
whitened STA
STC+STA
whitened STC+STA
MNE
GLM
Tune
Null

Who wins?: coherence

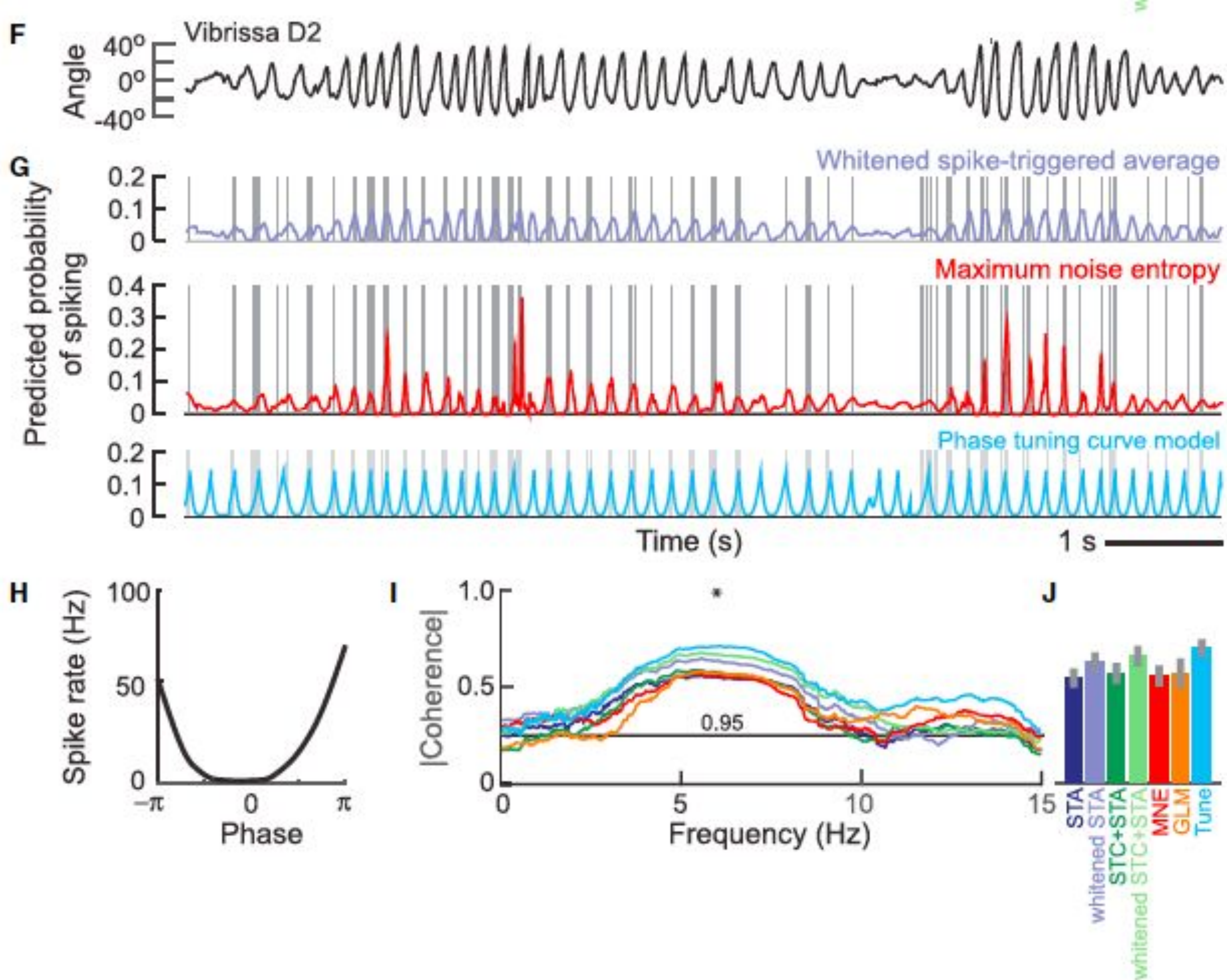


Who wins?

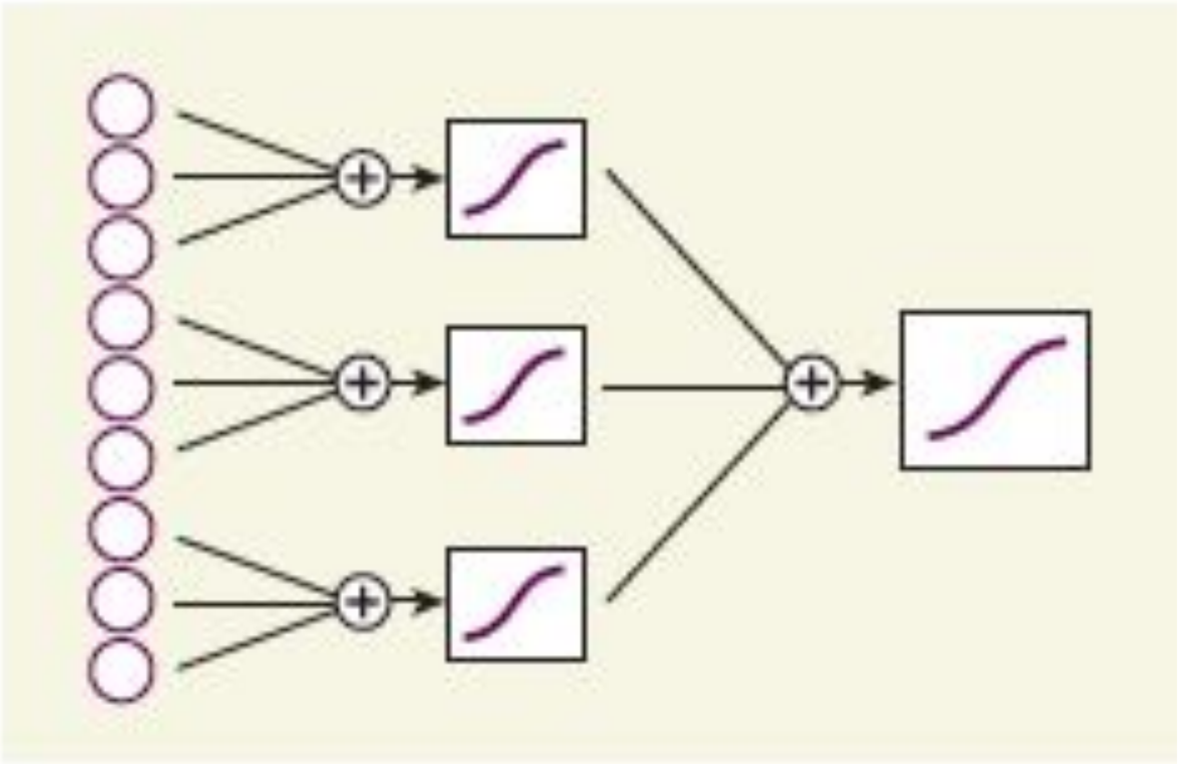


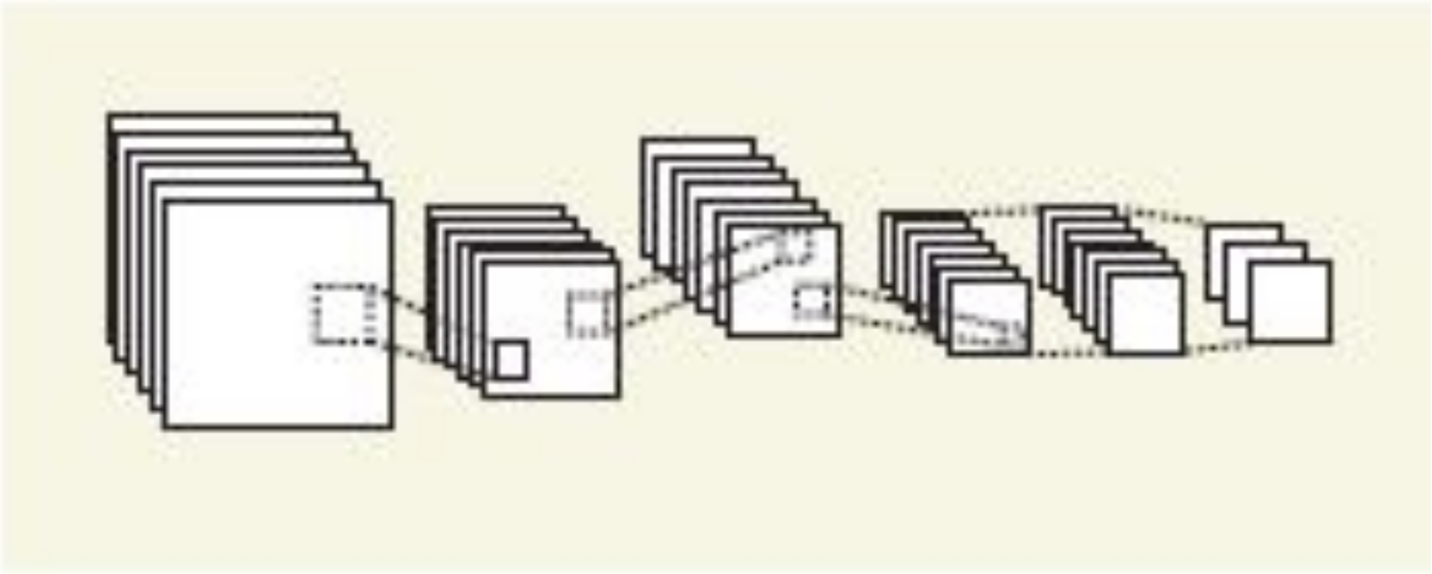
A
Vibrissa E1
Angle
40°
0°
-40°
B
Whitened spike-triggered average
Predicted probability
0.2
0.1
0
Maximum noise entropy
Time (s)
1 s
C
Spike rate (Hz)
100
50
0
−π
0
π
Phase
D
|Coherence|
1.0
0.5
0
STA
whitened STA
STC+STA
whitened STC+STA
MNE
GLM
Phase tune
0.95
0
5
10
15
Frequency (Hz)
E
STA
whitened STA
STC+STA
whitened STC+STA
MNE
GLM
Tune

Who

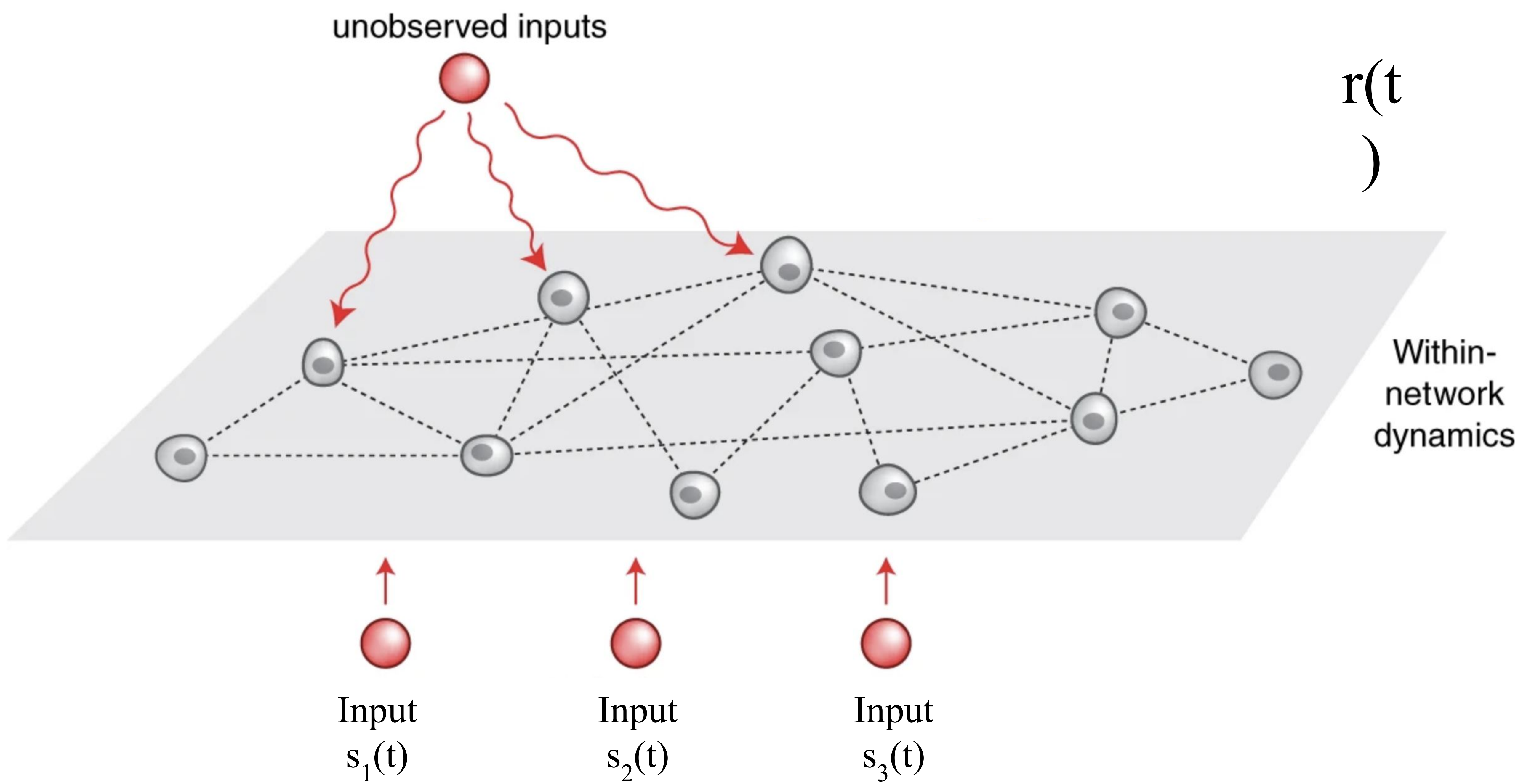

F
Vibrissa D2
Angle
40°
0°
-40°
G
Whitened spike-triggered average
Maximum noise entropy
Phase tuning curve model
Predicted probability of spiking
0.4
0.3
0.2
0.1
0
Time (s)
1 s
H
Spike rate (Hz)
100
50
0
−π
0
π
Phase
I
|Coherence|
1.0
0.5
0
0.95
*
0
5
10
15
Frequency (Hz)
J
STA
whitened STA
STC+STA
whitened STC+STA
MNE
GLM
Tune

Next gen models to fit input/output



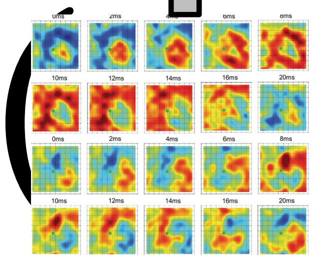
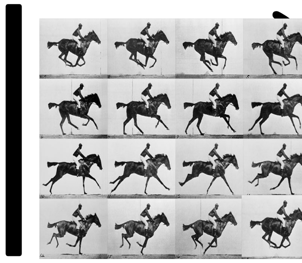


Complexities



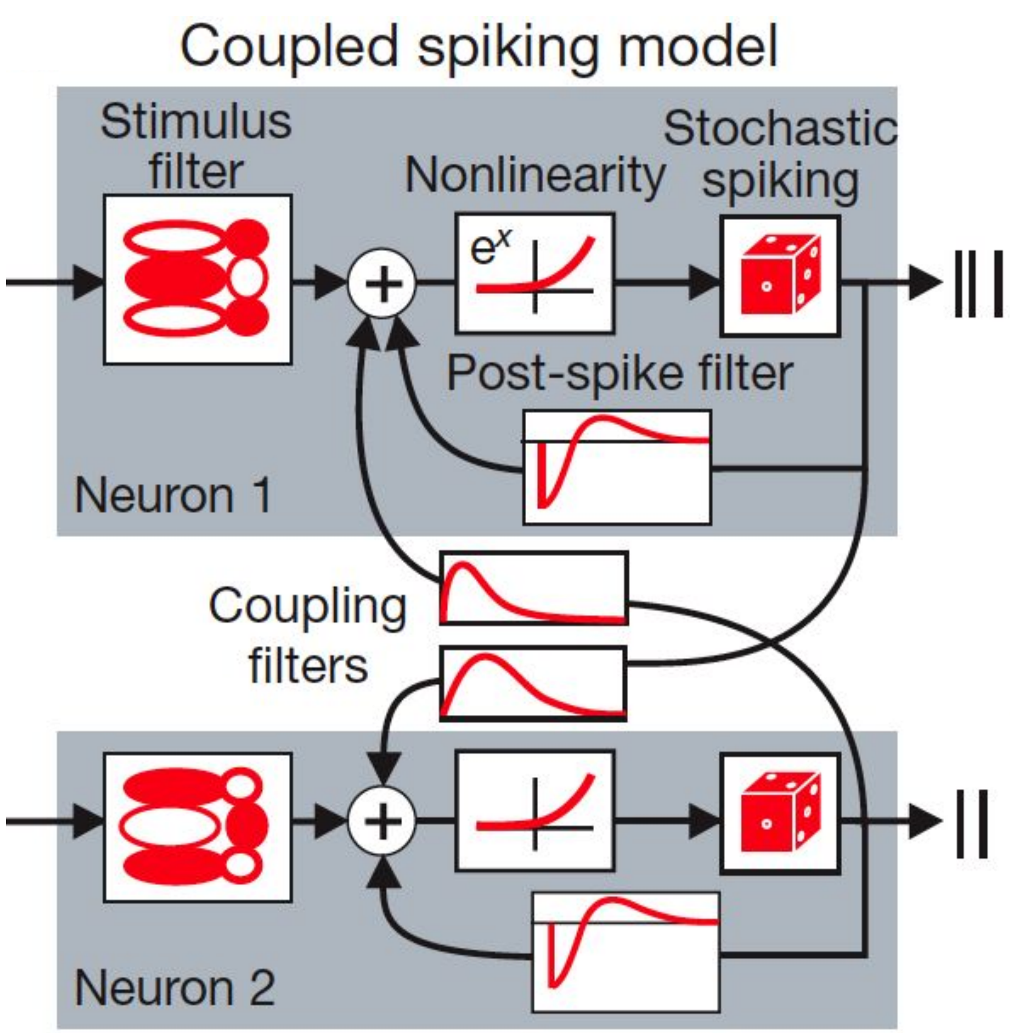
Neuronal populations

reduce this

P( | )

Generalize to networks

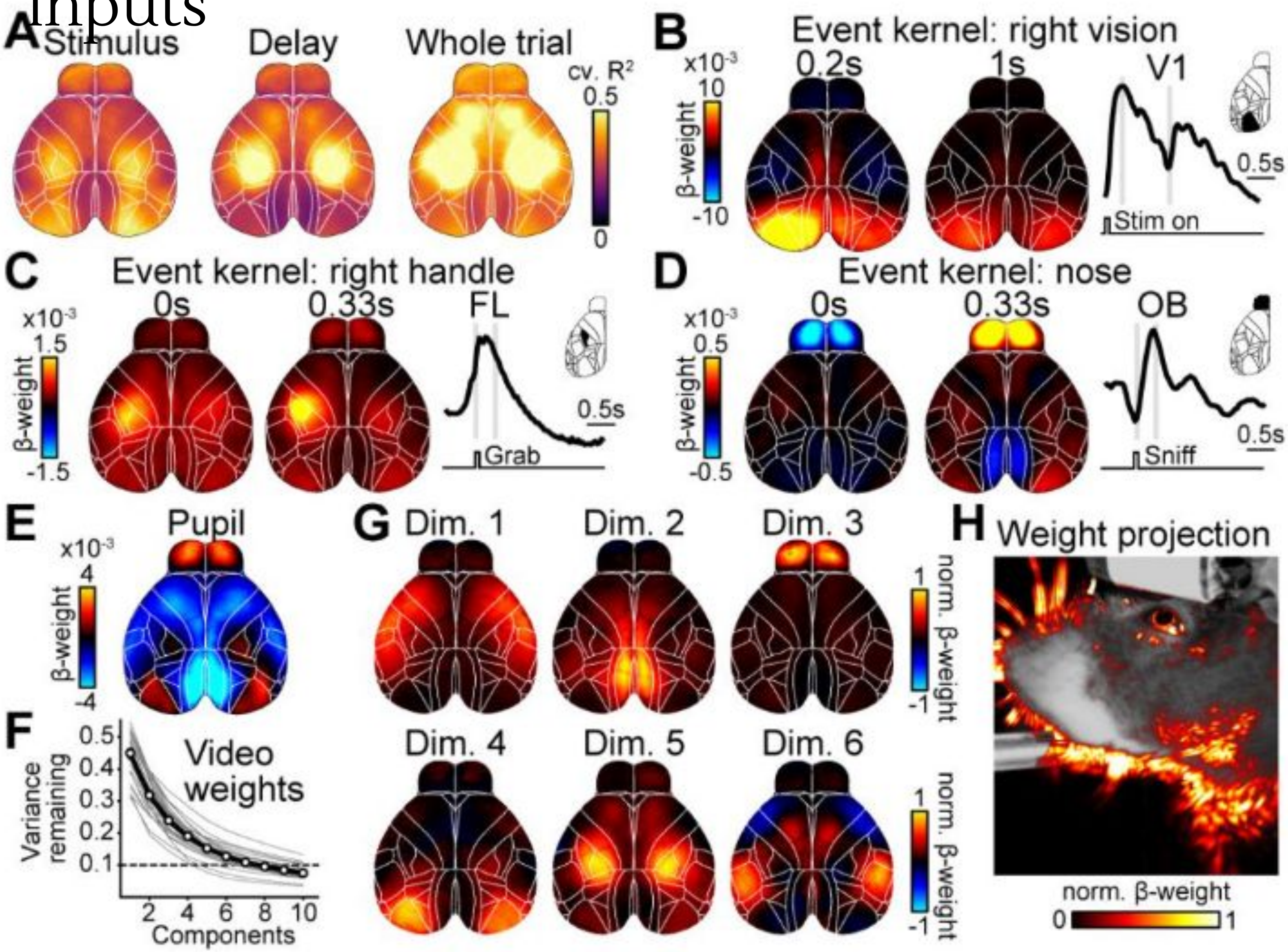
joint reductions



canonical correlation analysis

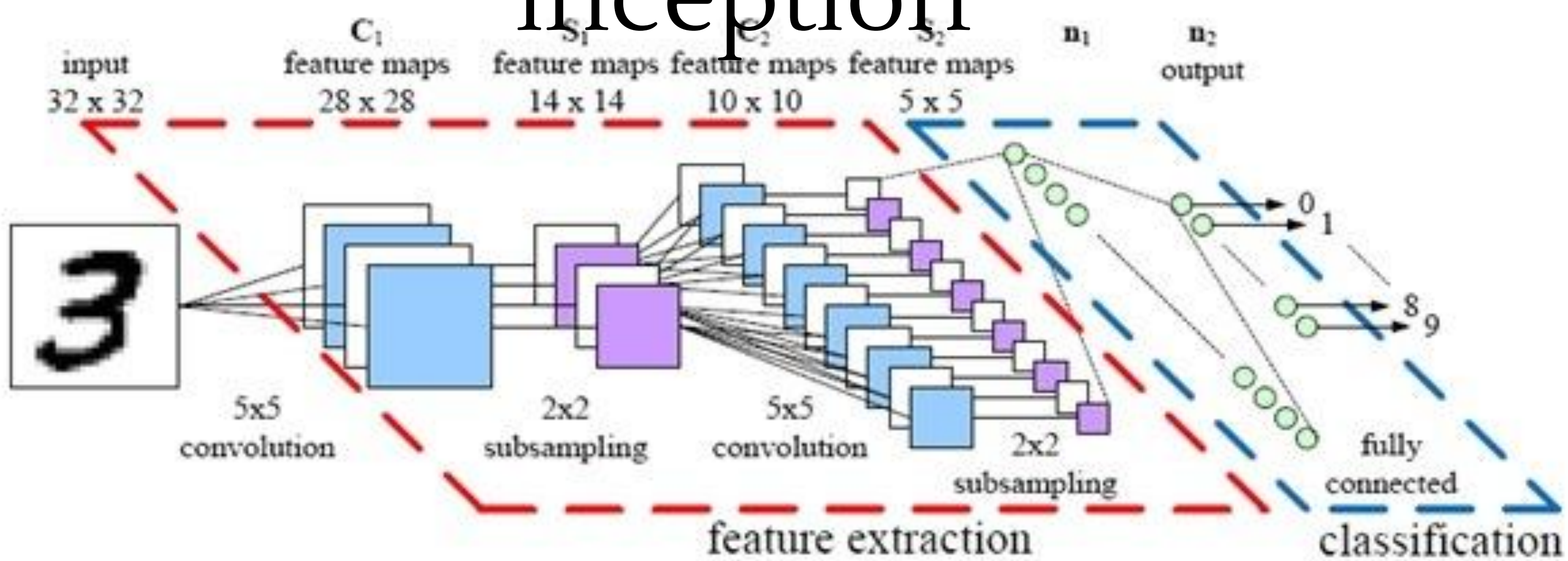
dPCA

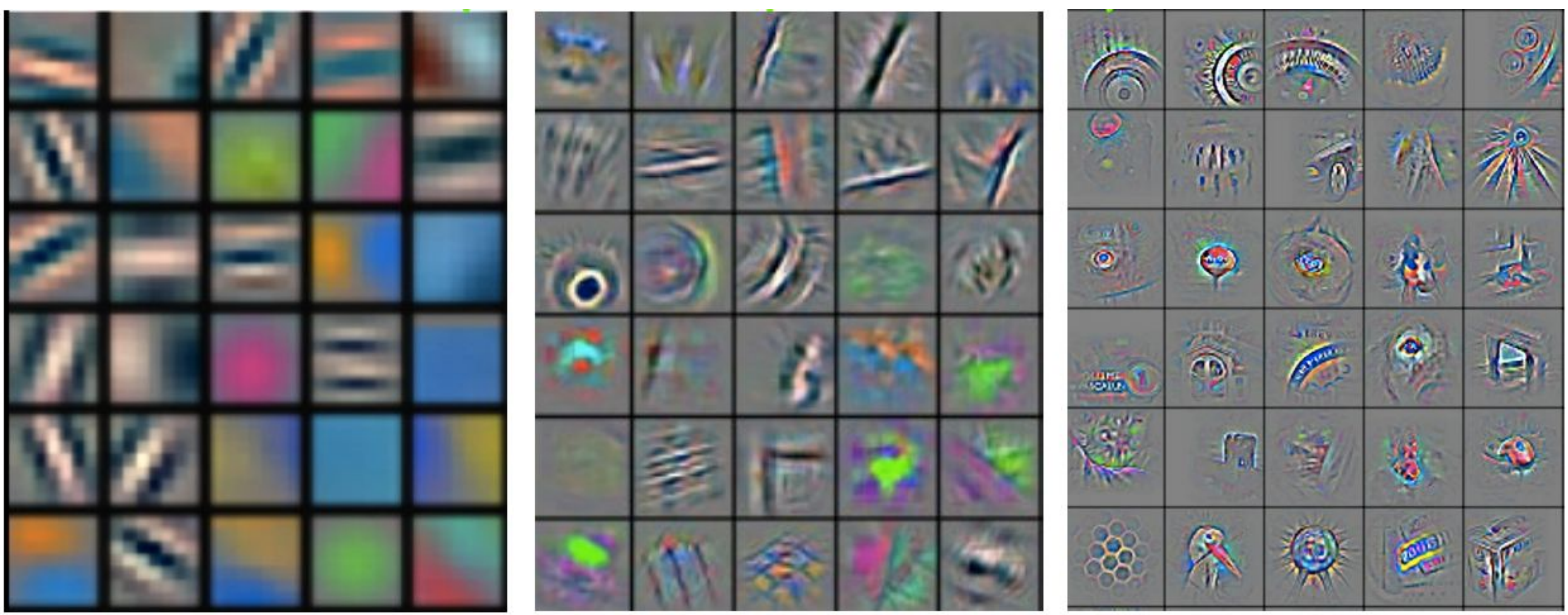
Unobserved inputs



Musall, Kaufman et al., 2018

Complex feature spaces: artiphysiology and inception



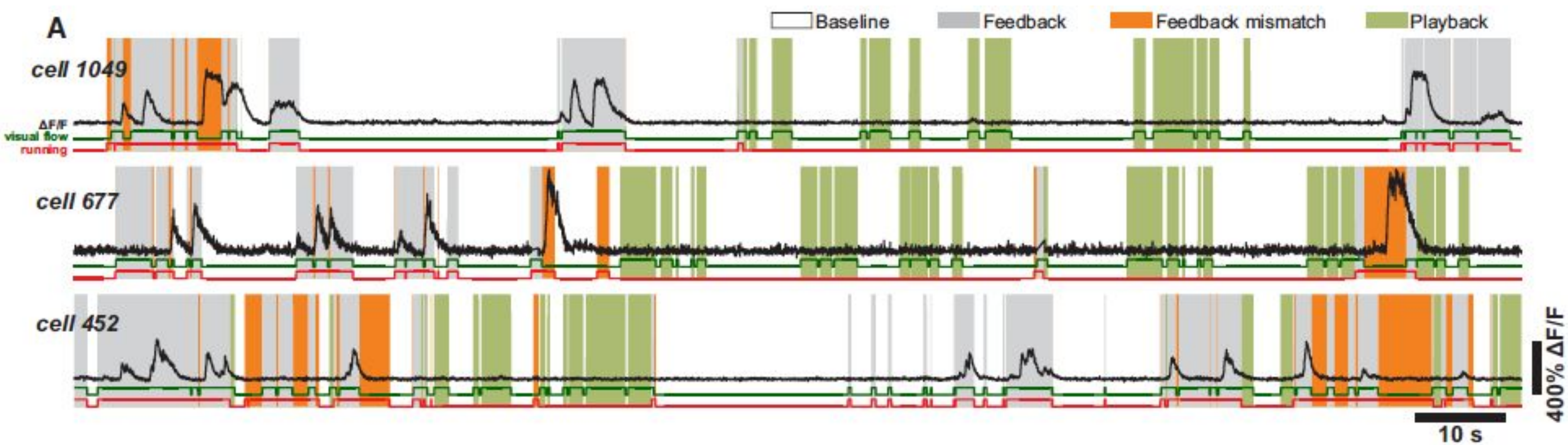


Feature visualization of convolutional net trained on ImageNet from [Zeiler & Fergus 2013]

Top-down effects: signatures of "internal models"

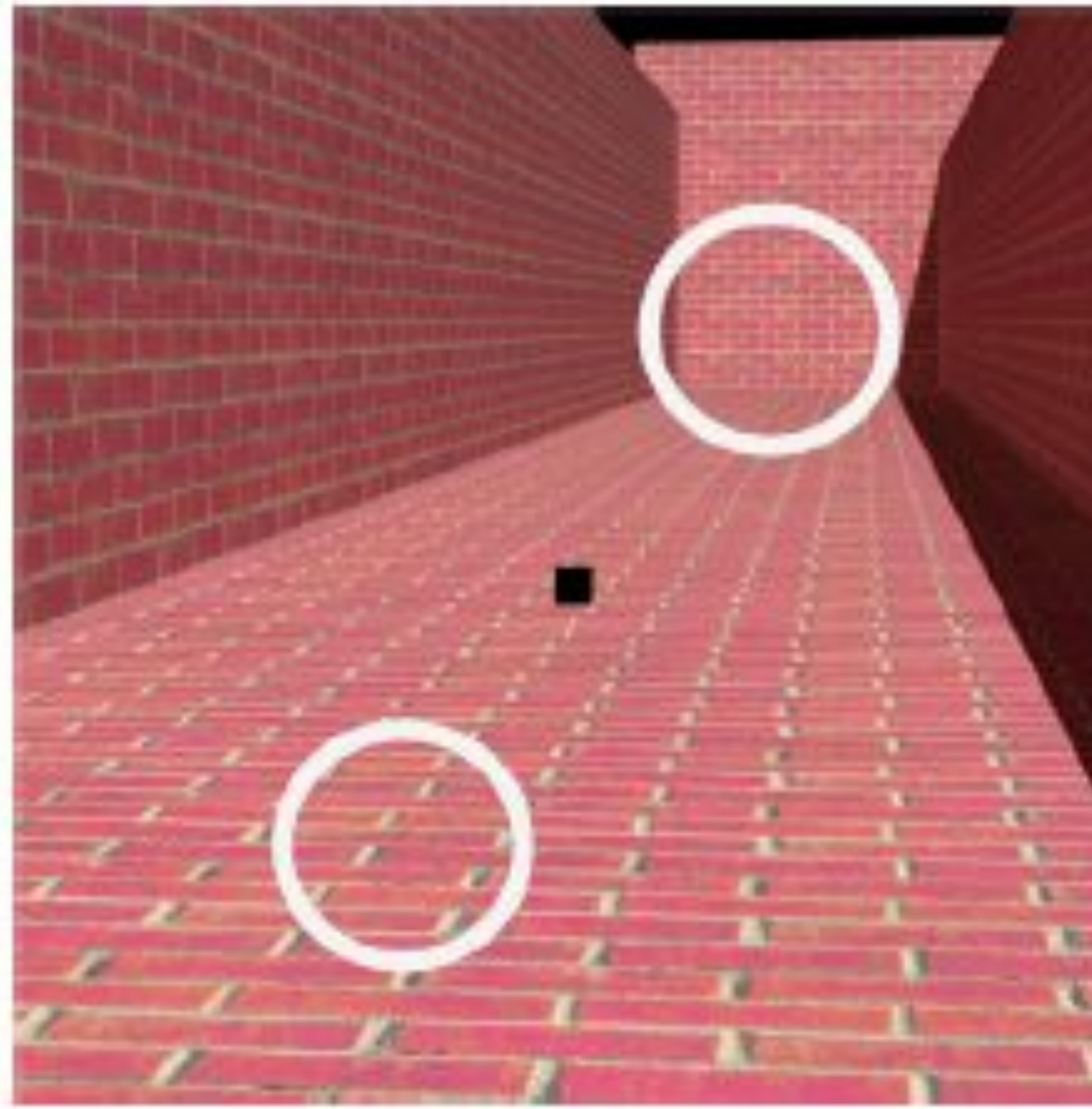
Sensorimotor Mismatch Signals in Primary Visual Cortex of the Behaving Mouse

Georg B. Keller,[1,2,*] Tobias Bonhoeffer,[1] and Mark Hübener[1,*]
[1]Max Planck Institute of Neurobiology, 82152 Munich-Martinsried, Germany
[2]Present address: Friedrich Miescher Institute for Biomedical Research, Maulbeerstrasse 66, CH-4058 Basel, Switzerland



Internal models: top-down effects

Scott Murray, Dan Kersten,
Greg Horwitz

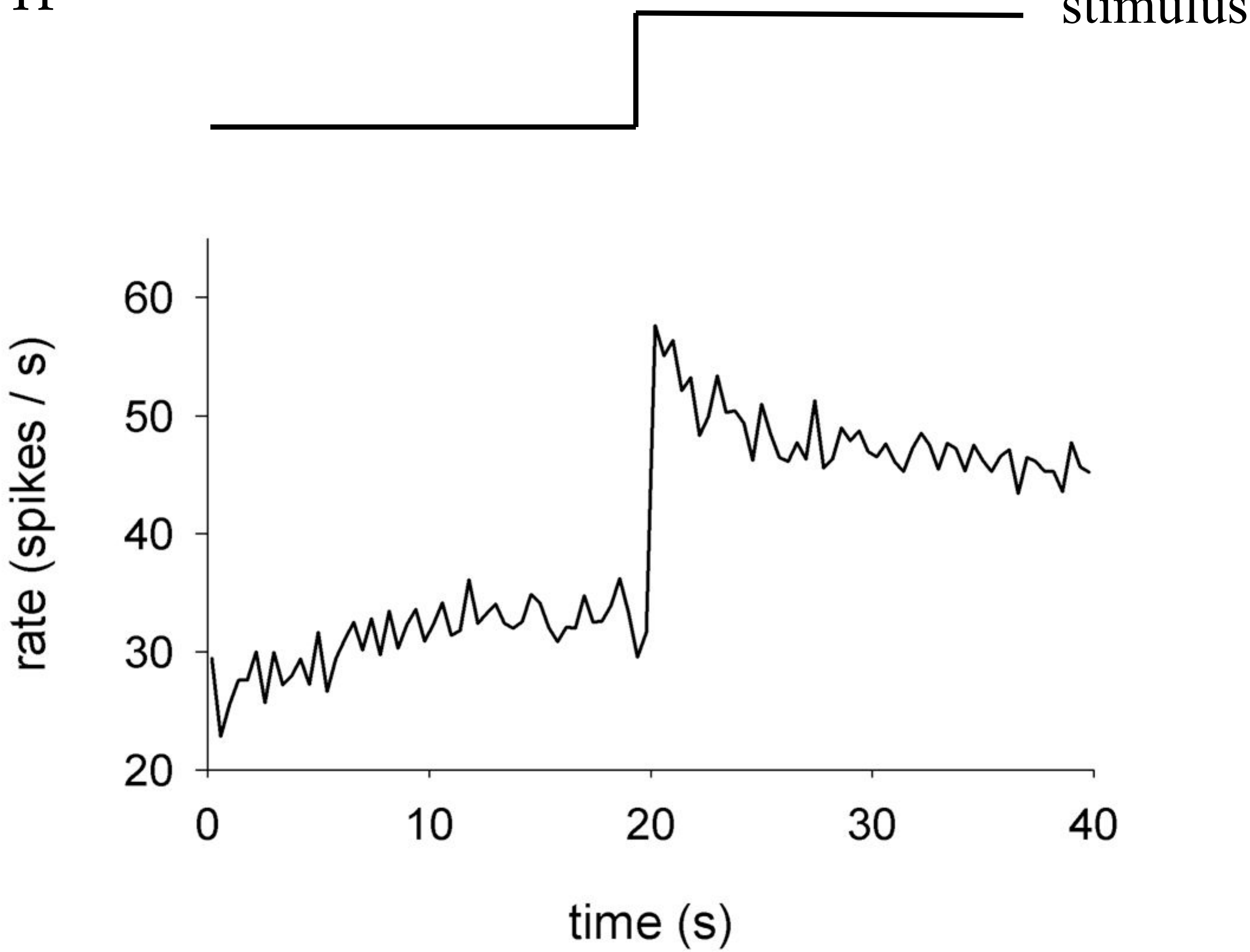


Ni et al., Curr. Biology,

Plan

- ✔ Neural coding
- ✔ Some basic methods for exploring coding
- Coding is a moving target: adaptation

Adaptation



History dependence

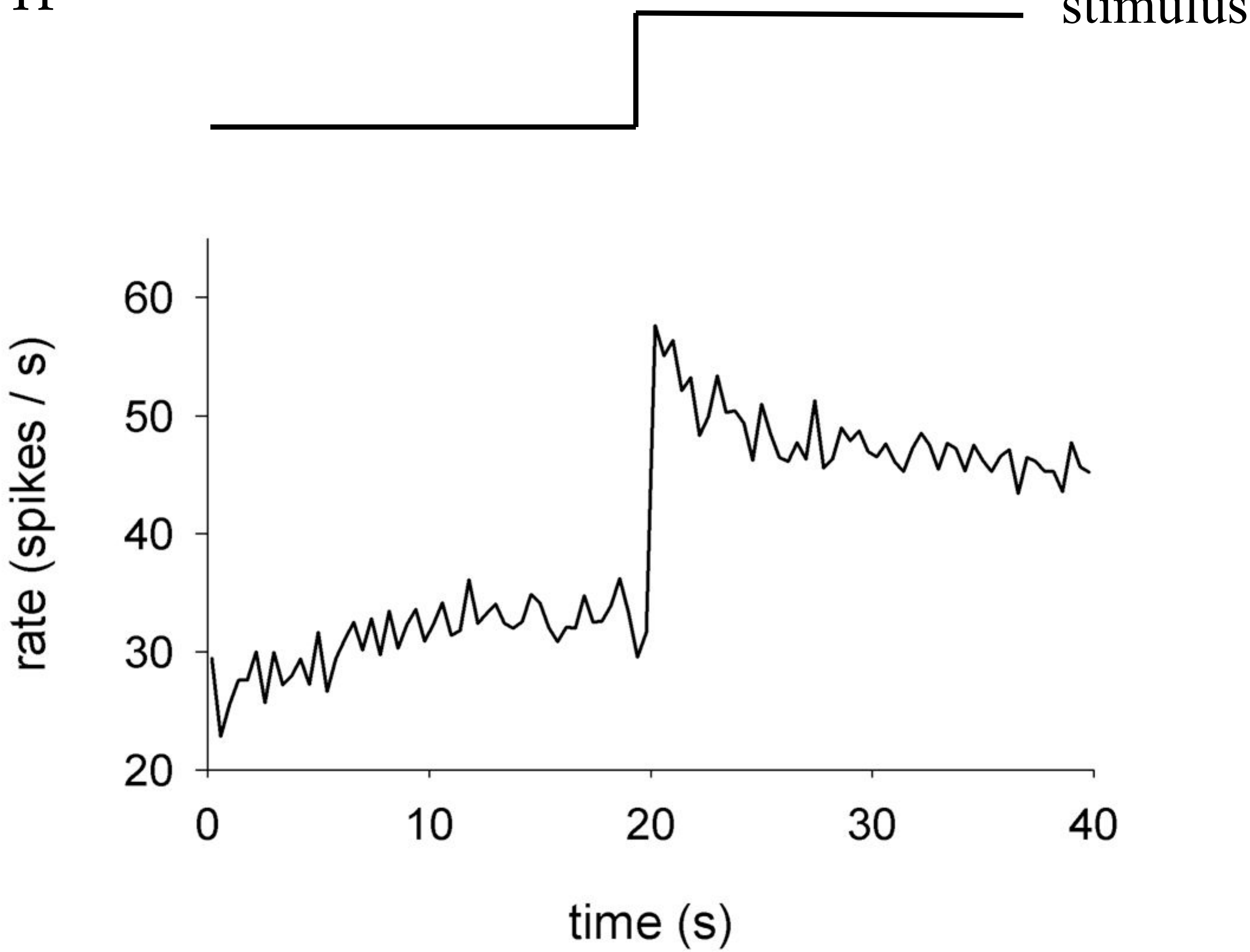
- Ion channel dynamics
- Synaptic dynamics
- Network dynamics

… forms of short term memory
… enrich computational properties of neurons

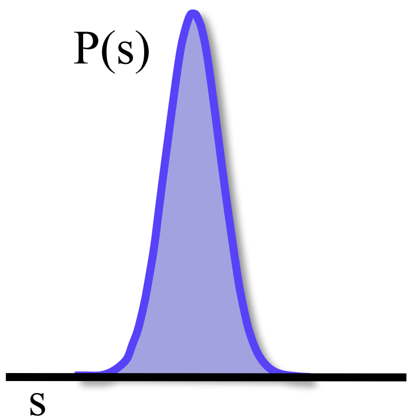
Encoding complex signals

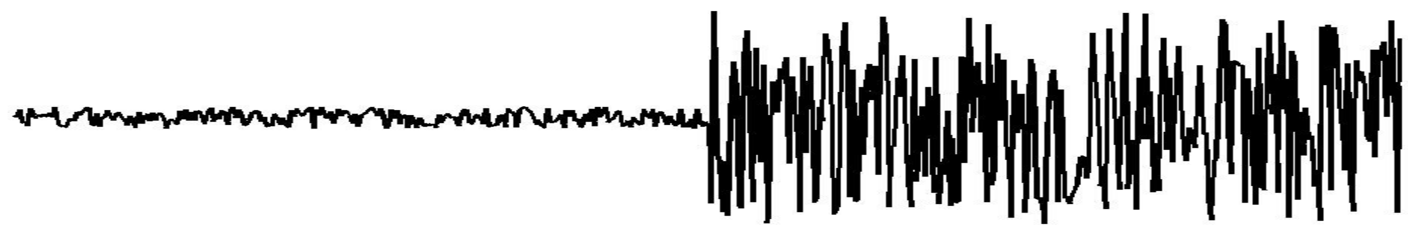
How do neural systems maintain high fidelity representations
of stimulus details in the face of fluctuating amplitudes?

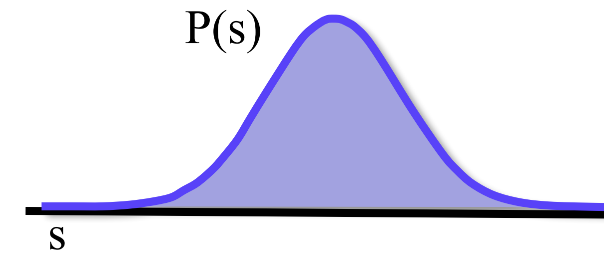
Adaptation

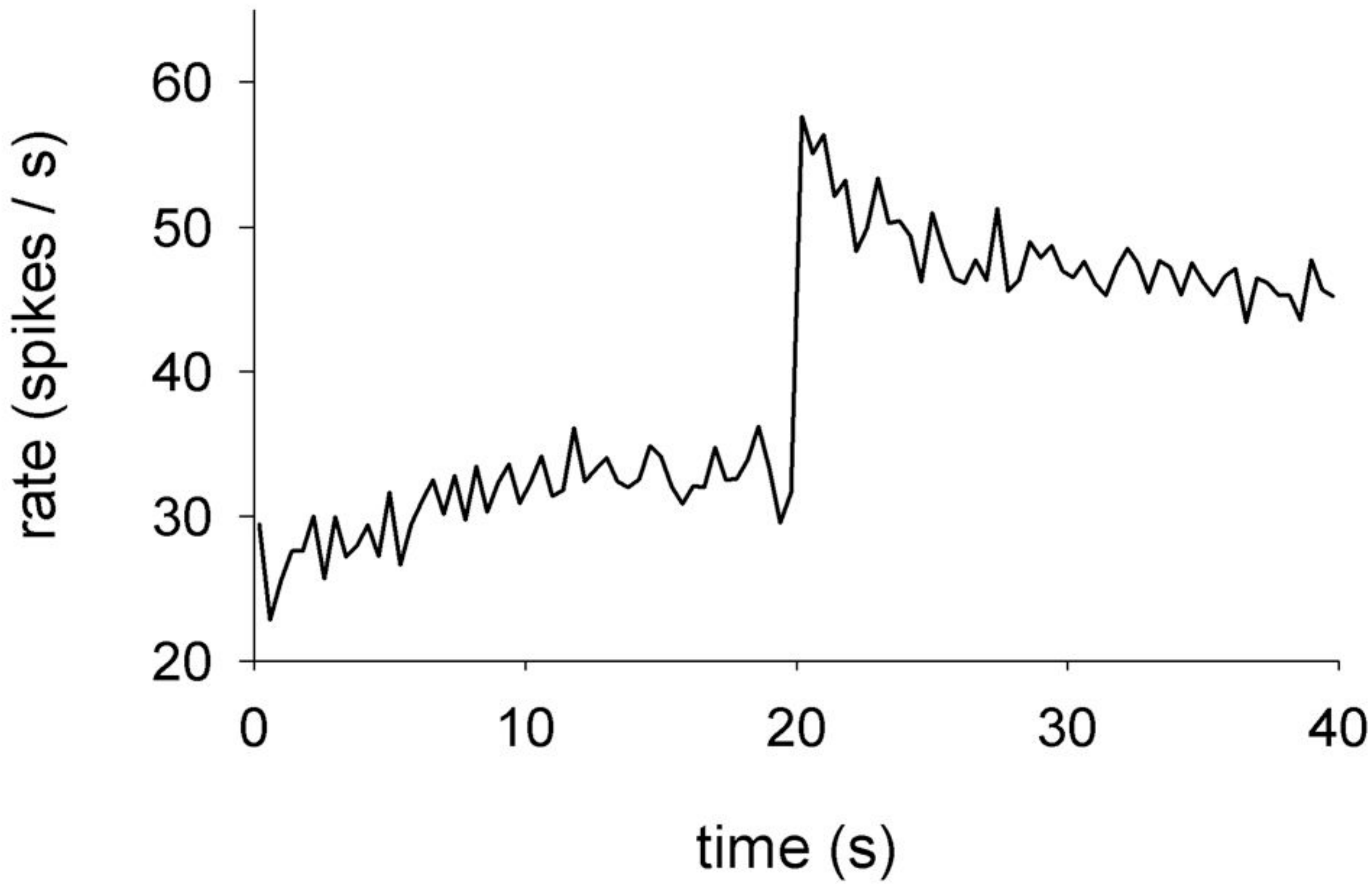


Adaptation to a change in stimulus distribution







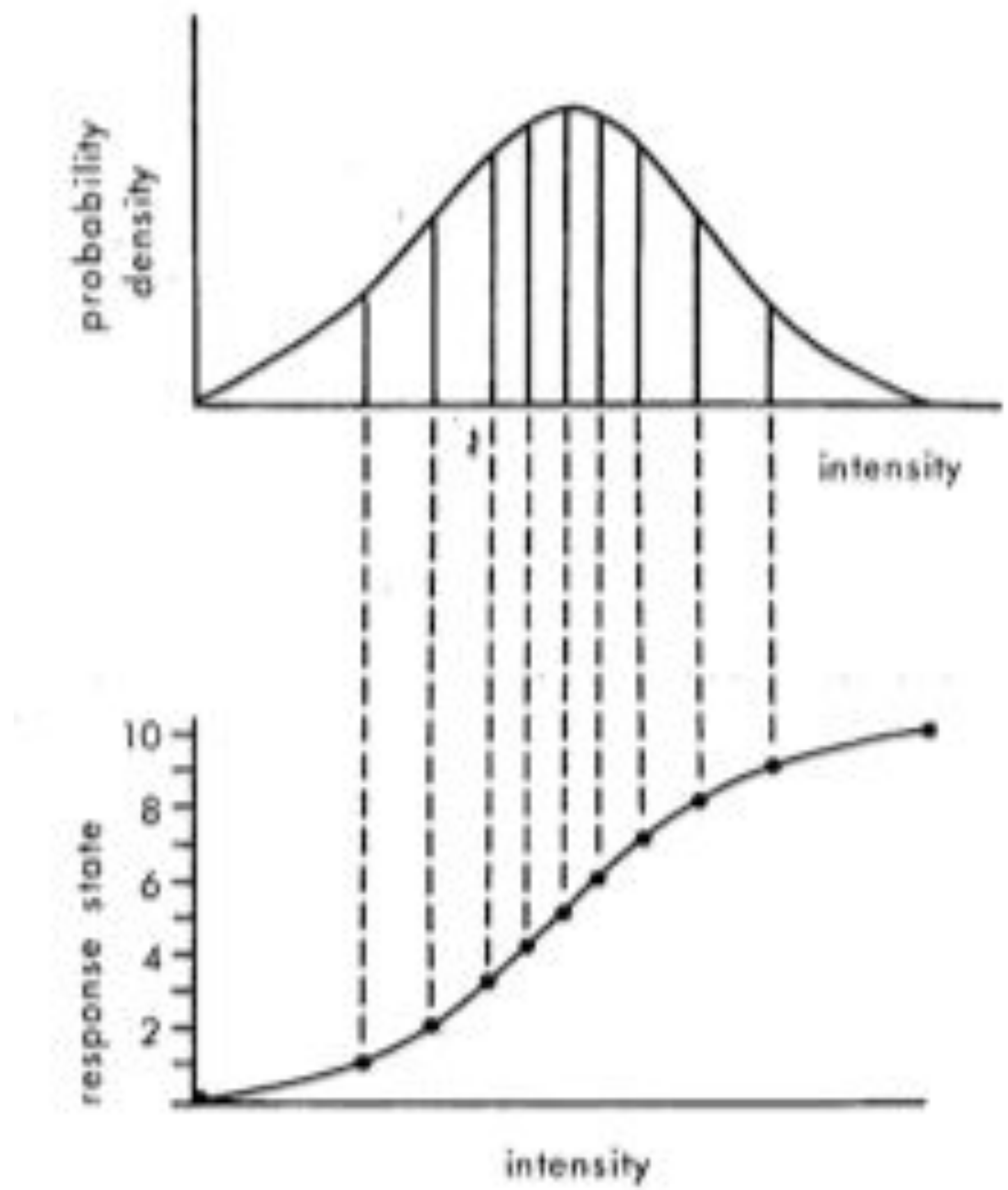


Input/output curves depend on the stimulus

- Optimal coding: sensory systems should maximize information transmission

- Goal: efficient use of available response bandwidth

- Predicts dependence of I/O curves on input distribution

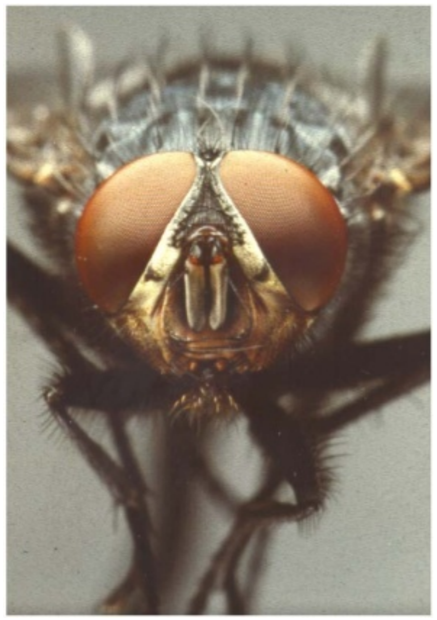


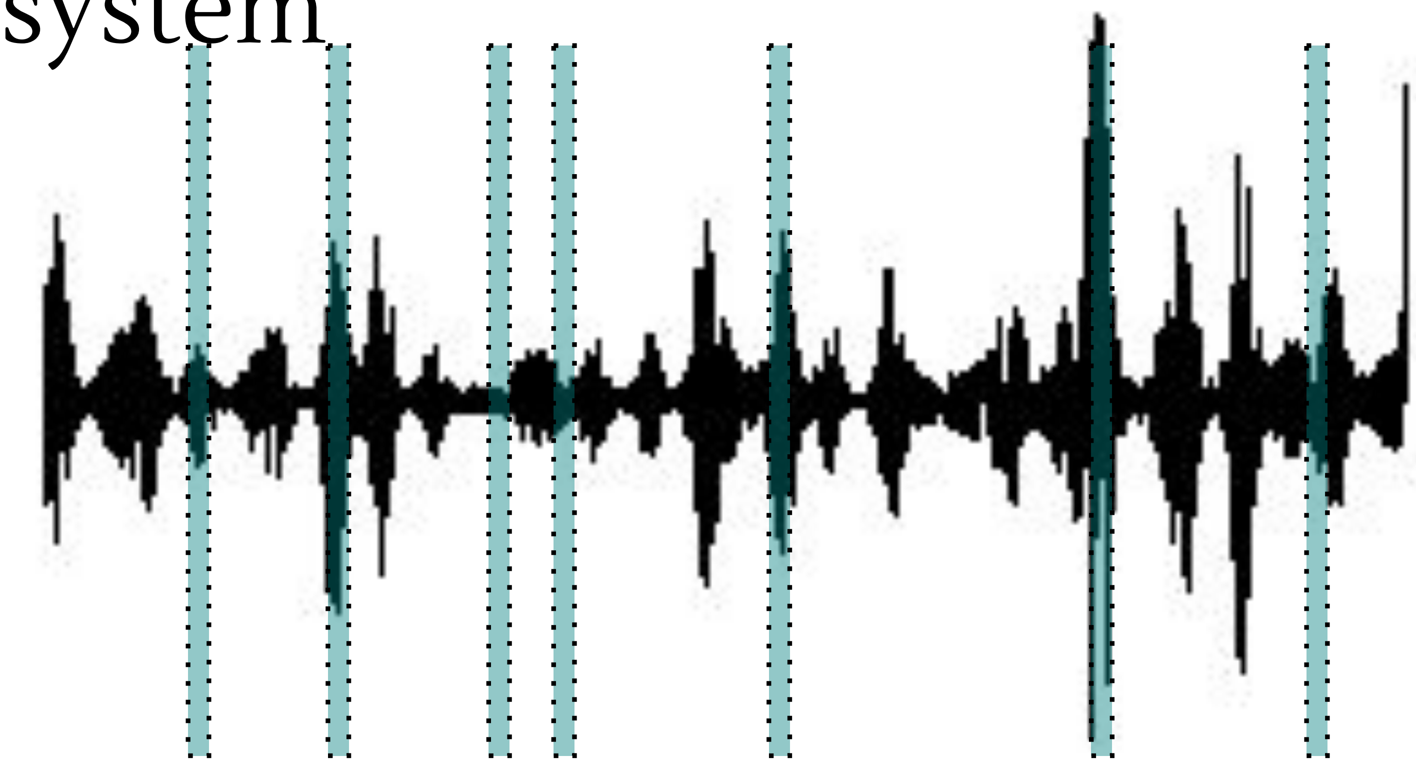
Laughlin, 1981

Dynamically optimal coding

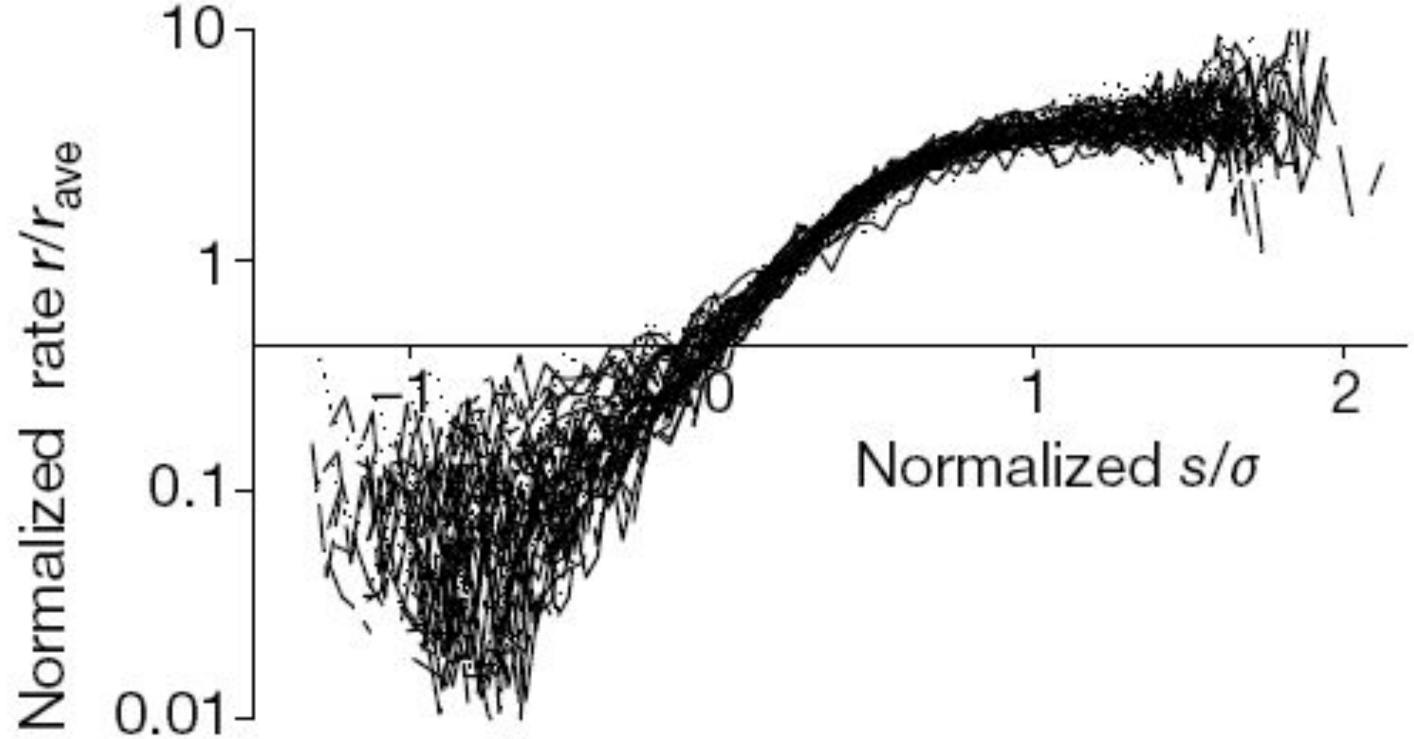
What would an optimal neuron do?

Normalized stimulus representation in the fly visual system



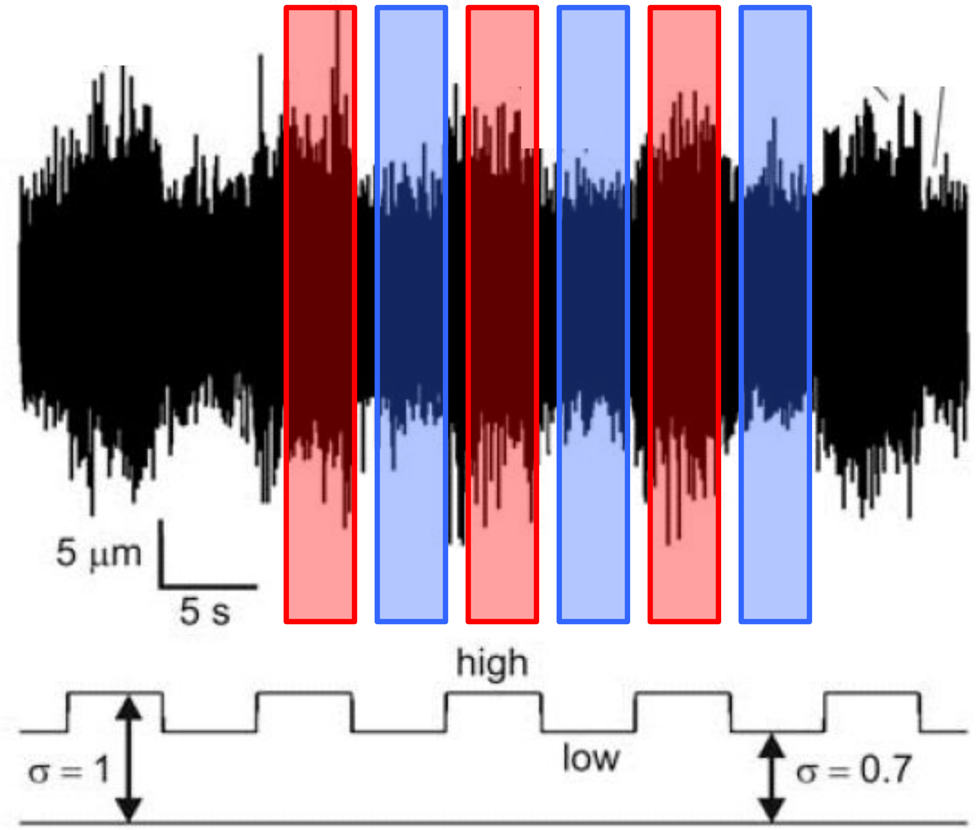


For fly neuron H1, determine the input/output relations throughout the stimulus presentation

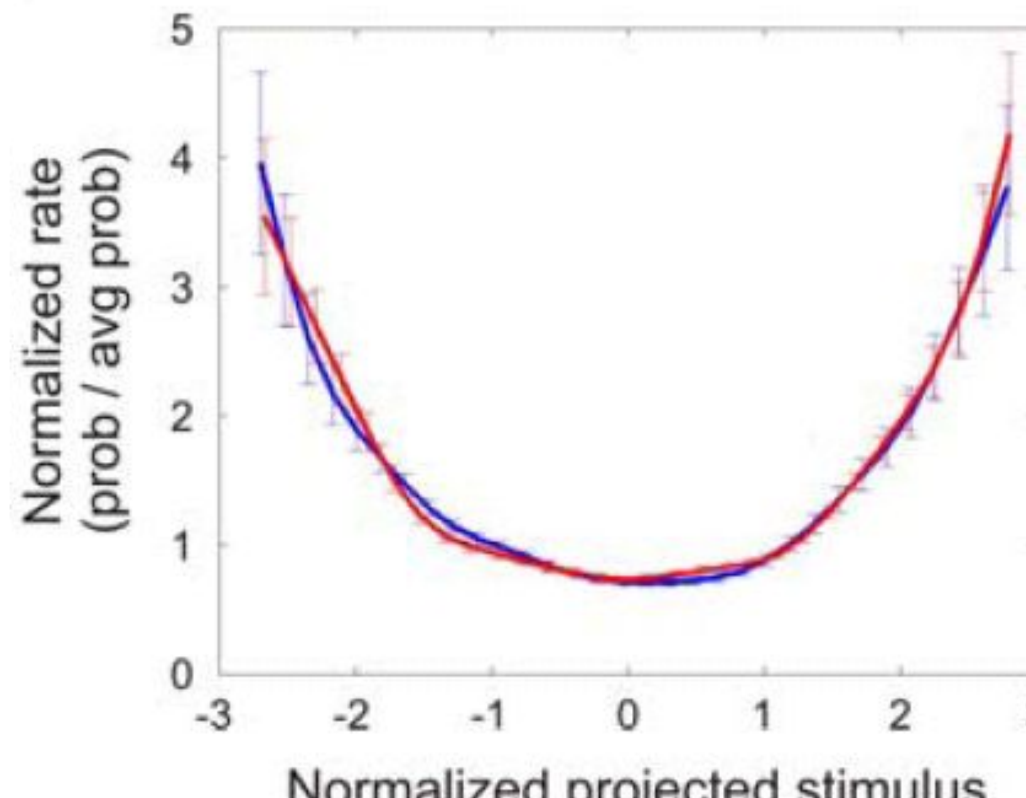


A. Fairhall, G. Lewen, R. R. de Ruyter and W. Bialek (2001)

Normalized stimulus representation in rat barrel cortex

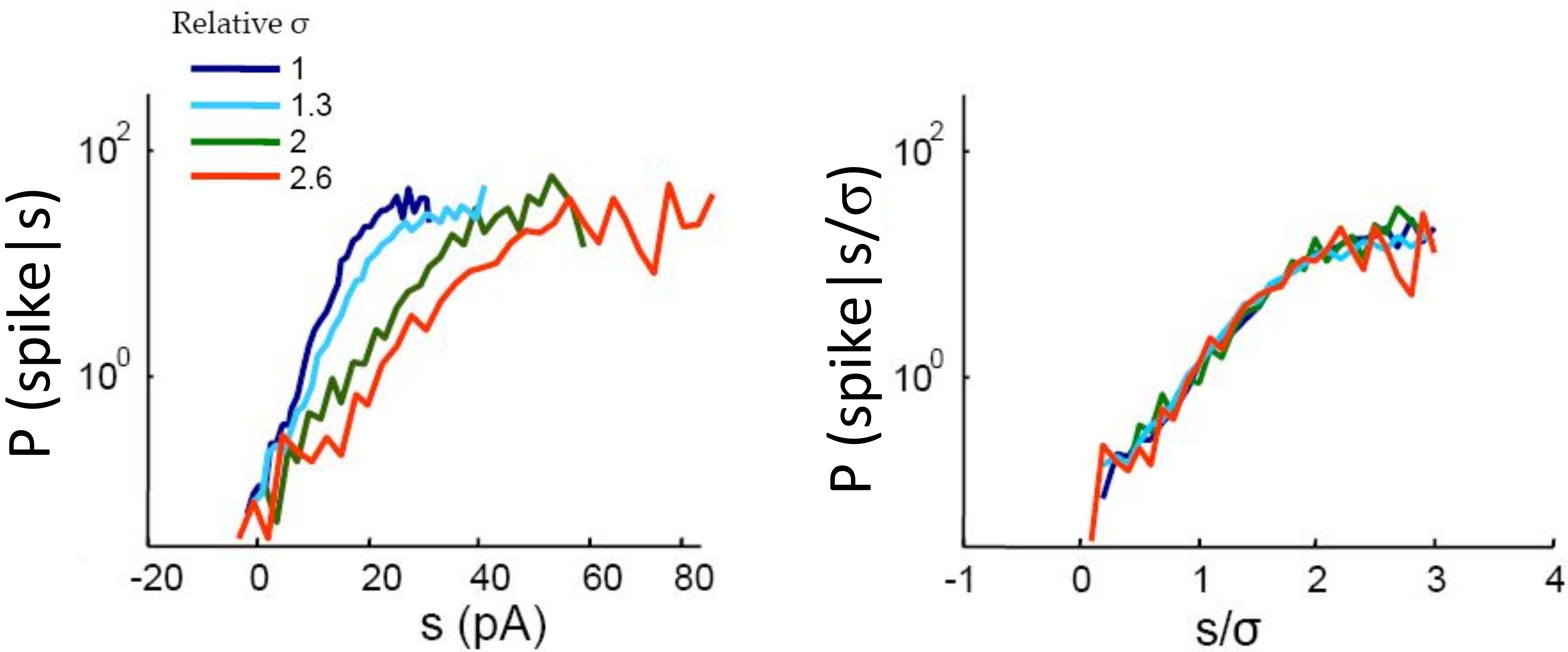


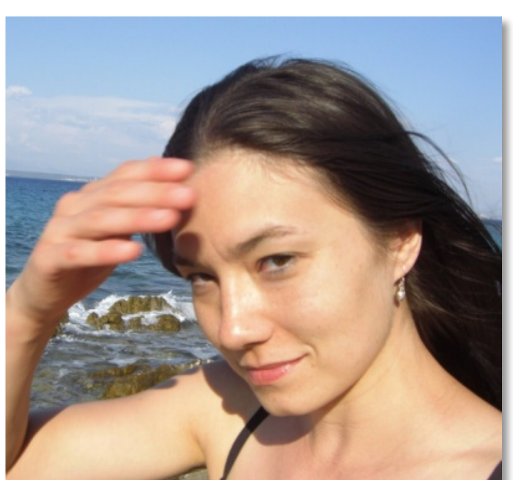
Extracellular *in vivo* recordings
of responses to whisker motion
S1 barrel cortex in the anesthetized rat



M. Maravall et al., PLoS Biology (2007)

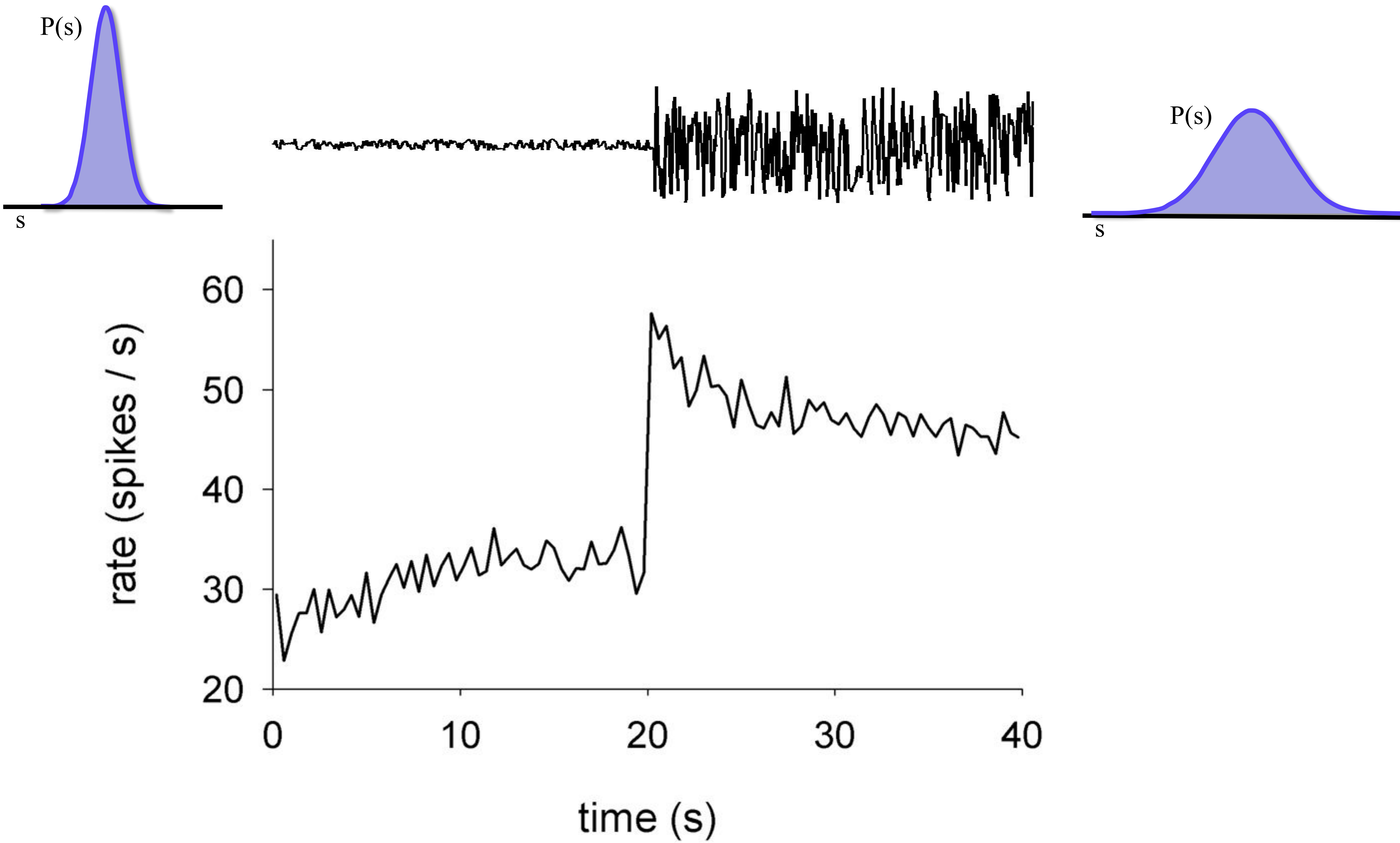
Normalized input representation in single cortical neurons



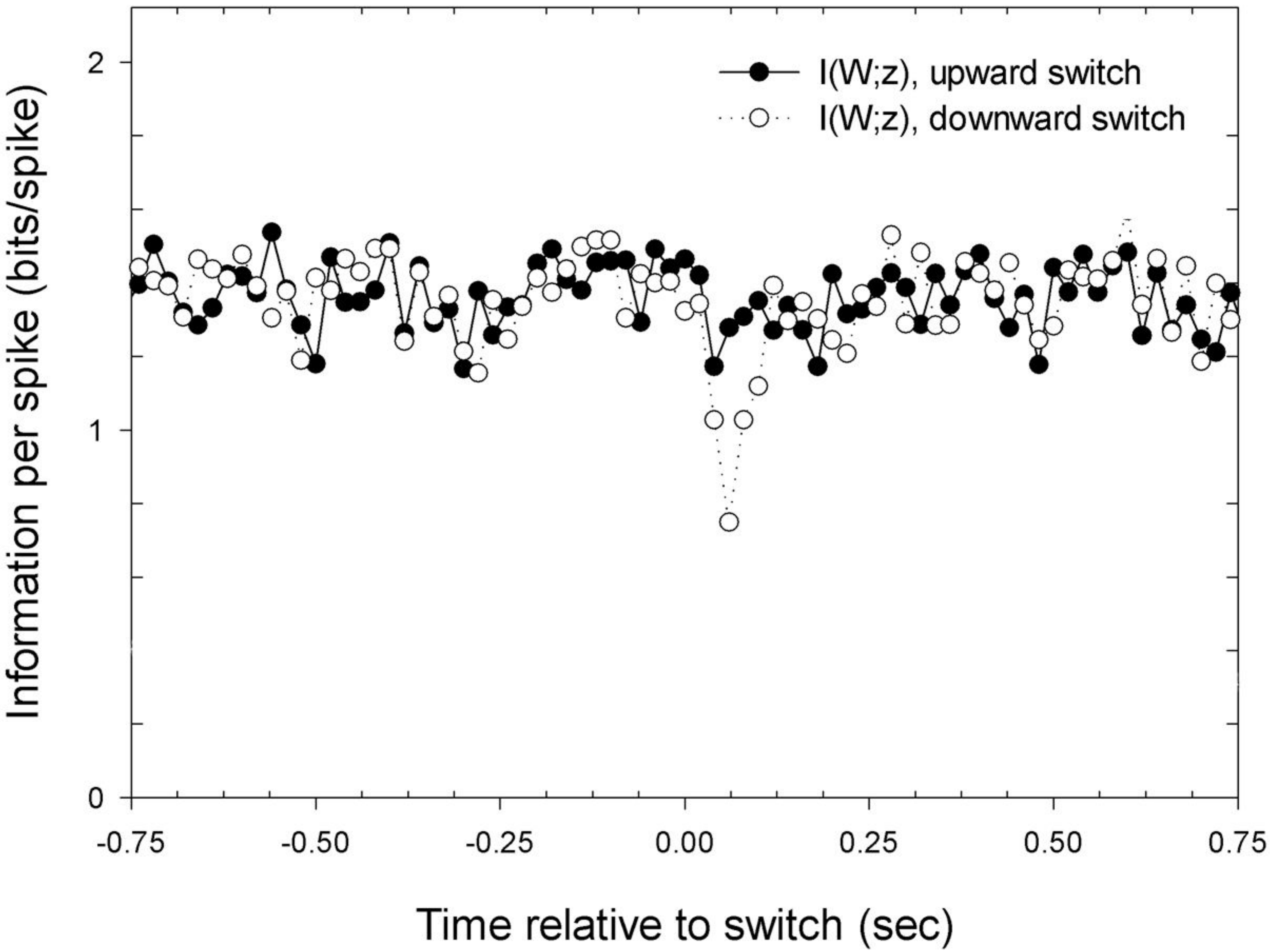


R. Mease, A. Fairhall and W. Moody

How rapidly is gain rescaling happening?

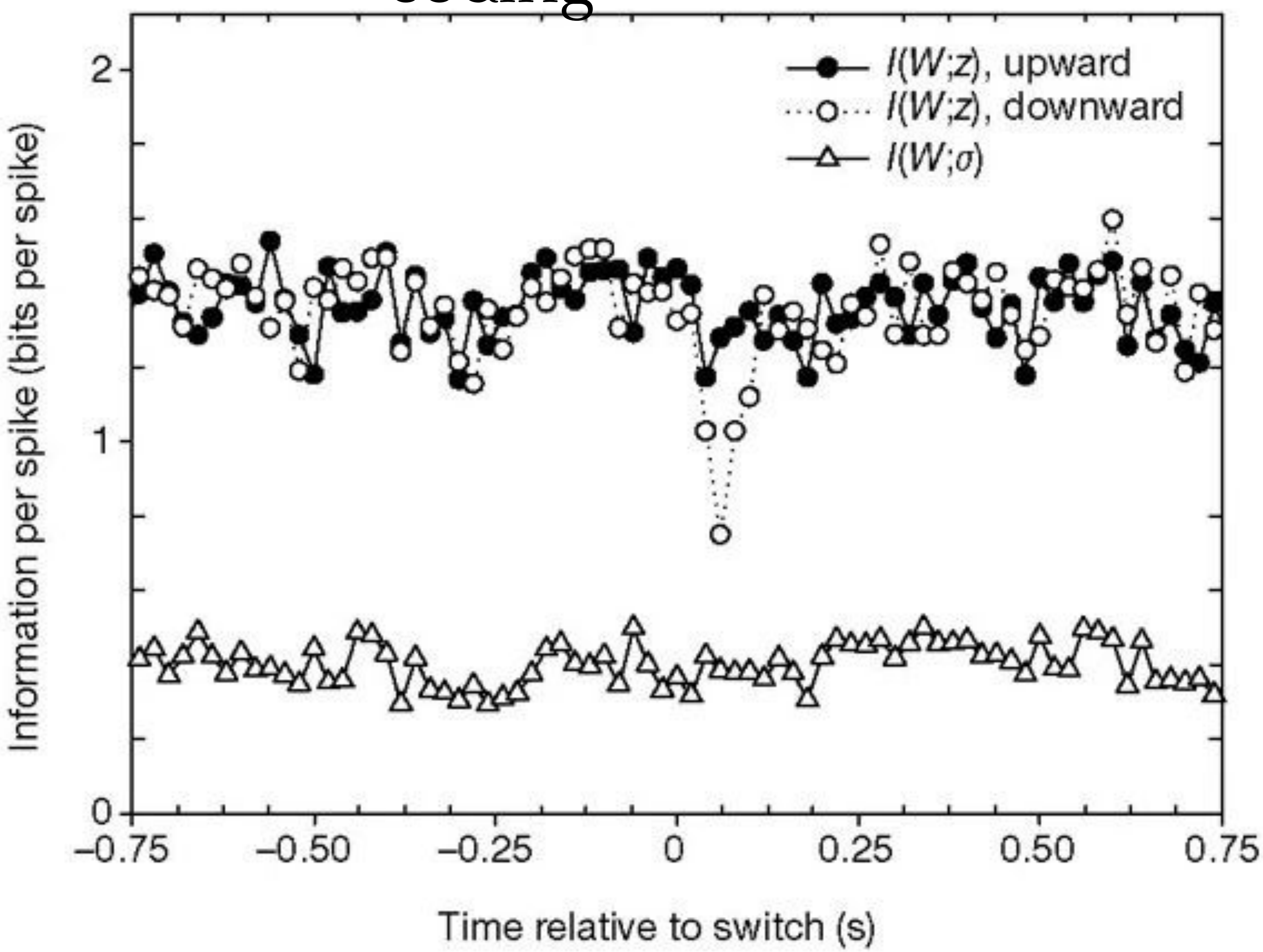


Using information to evaluate efficient coding

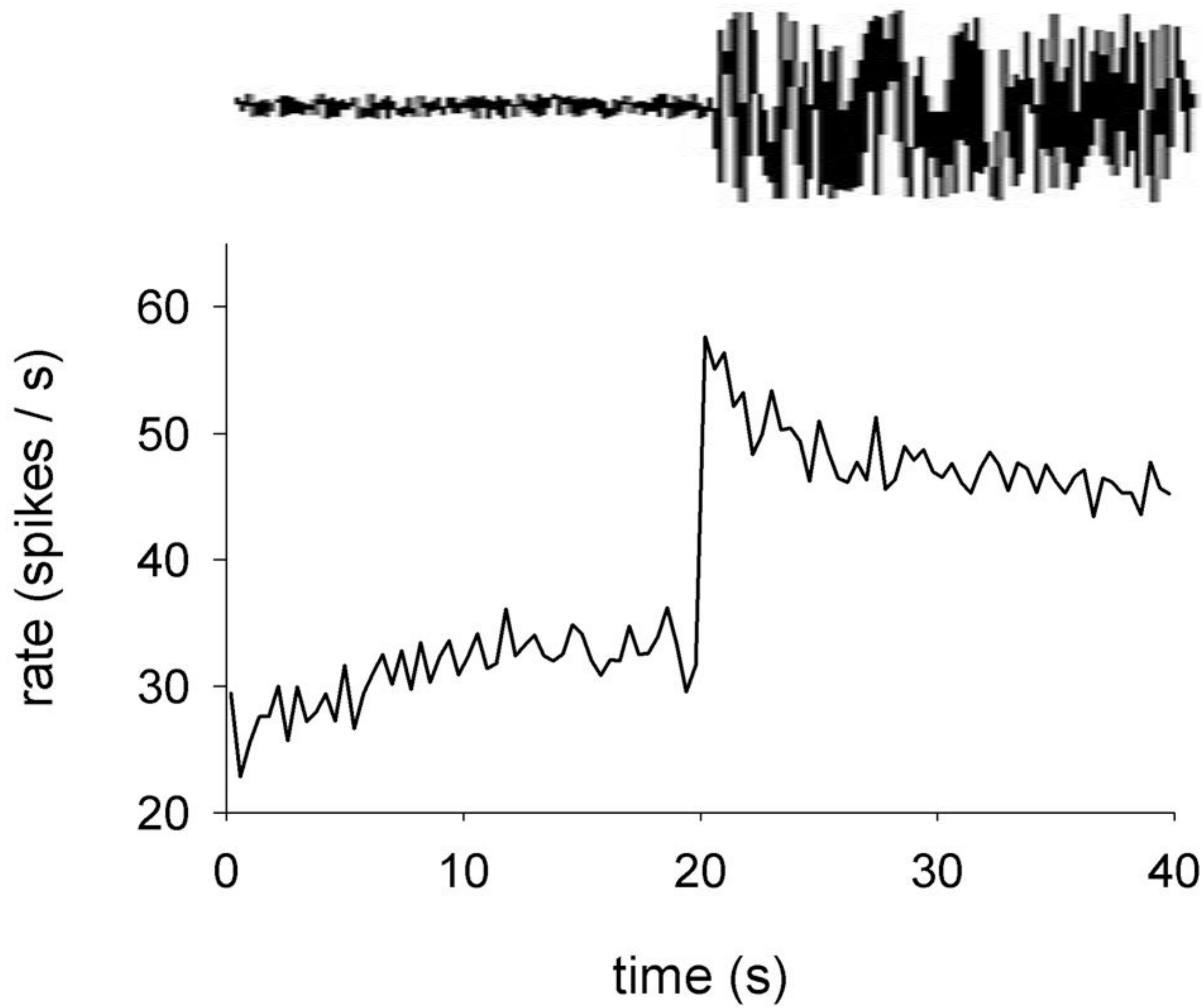


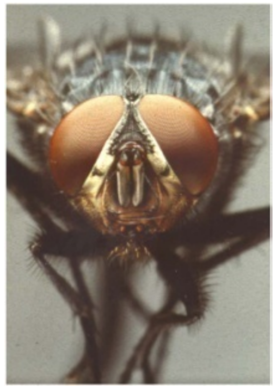
Does normalized coding lead to ambiguity?

Using information to evaluate *envelope* coding

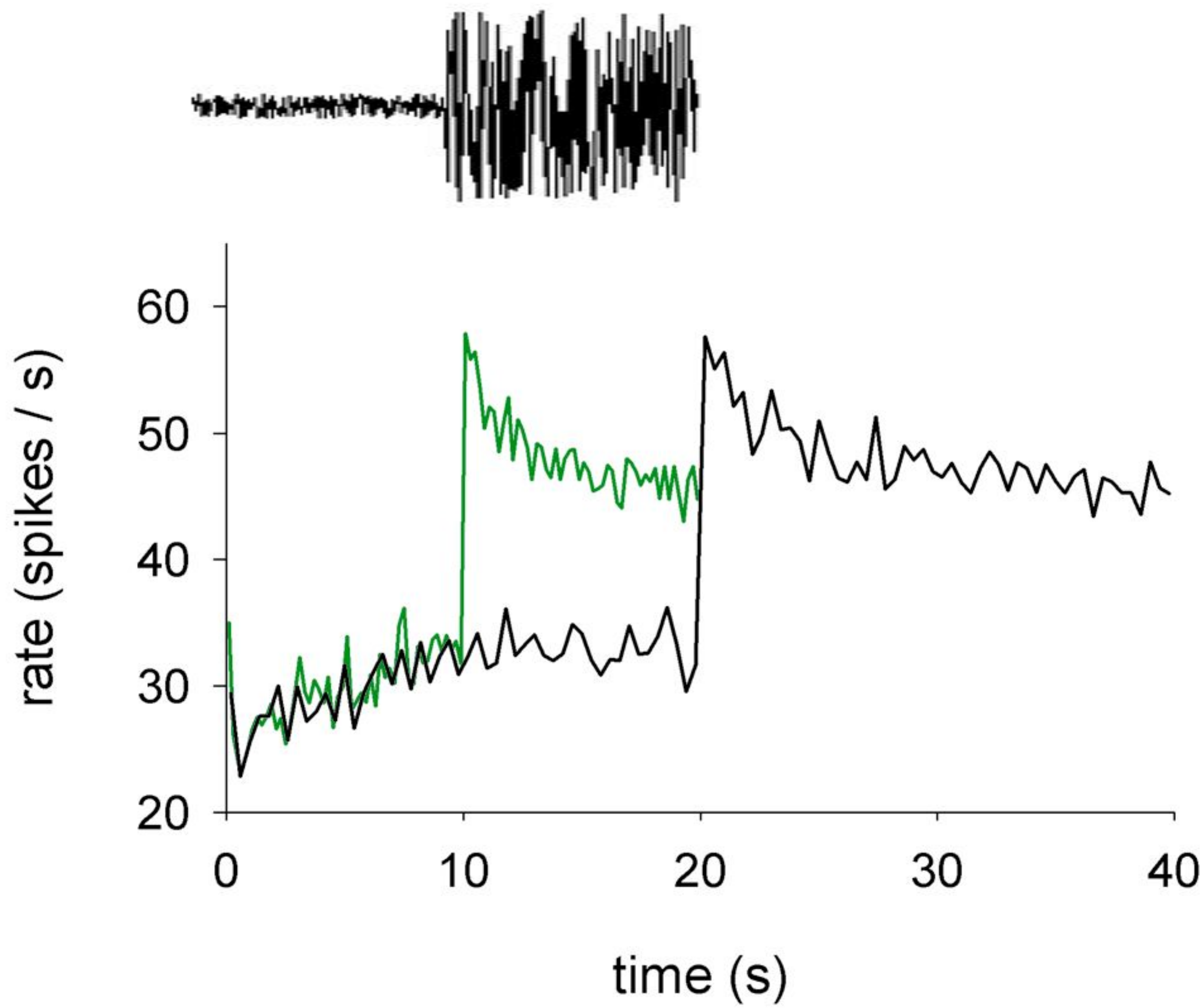


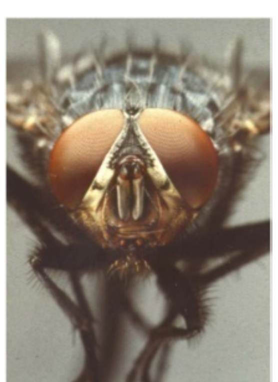
Firing rate adaptation to signal statistics



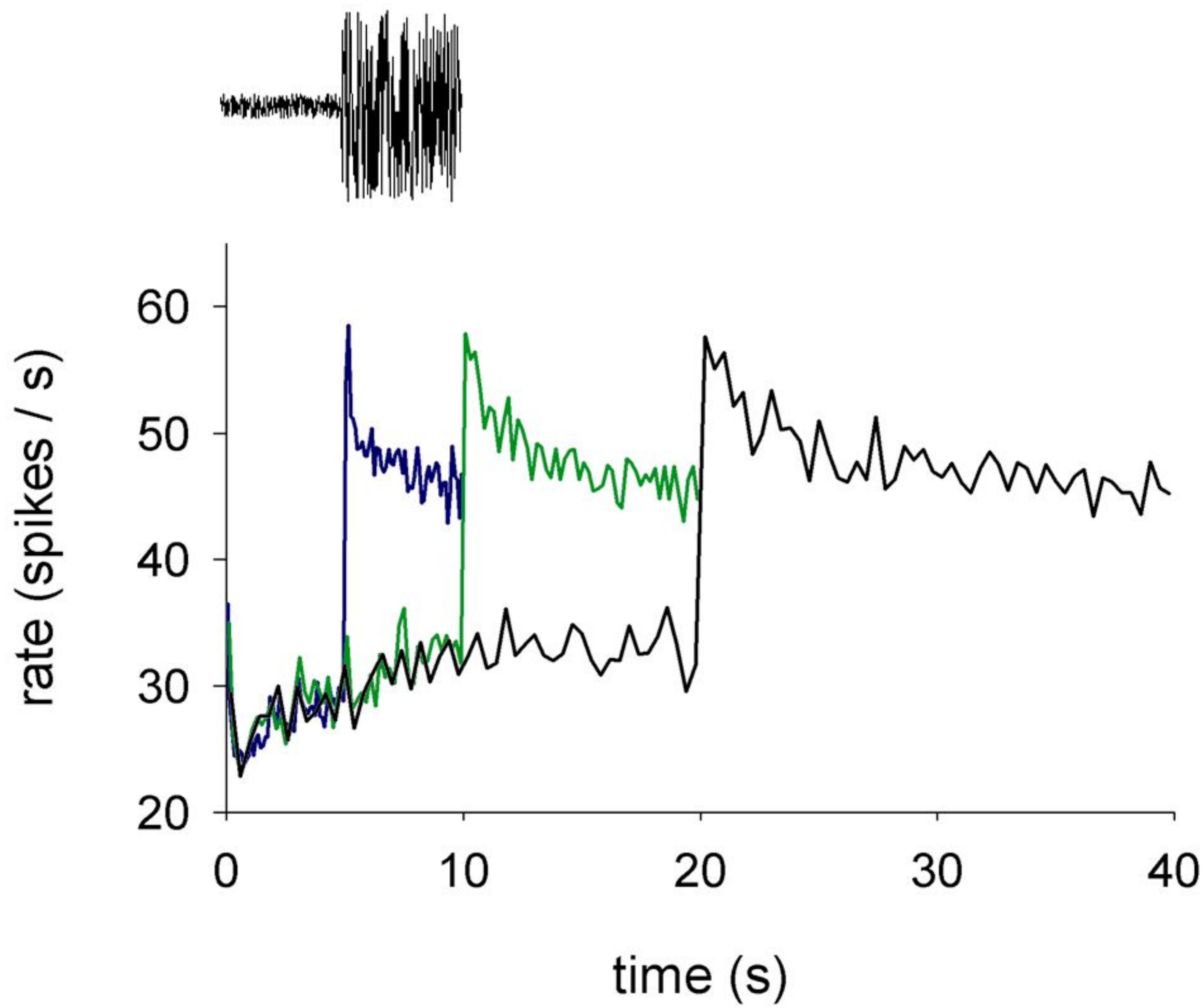


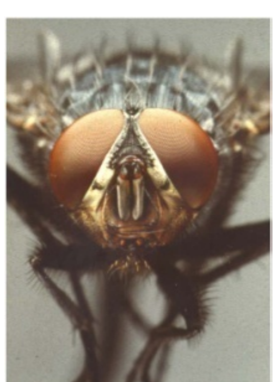
Firing rate adaptation to signal statistics



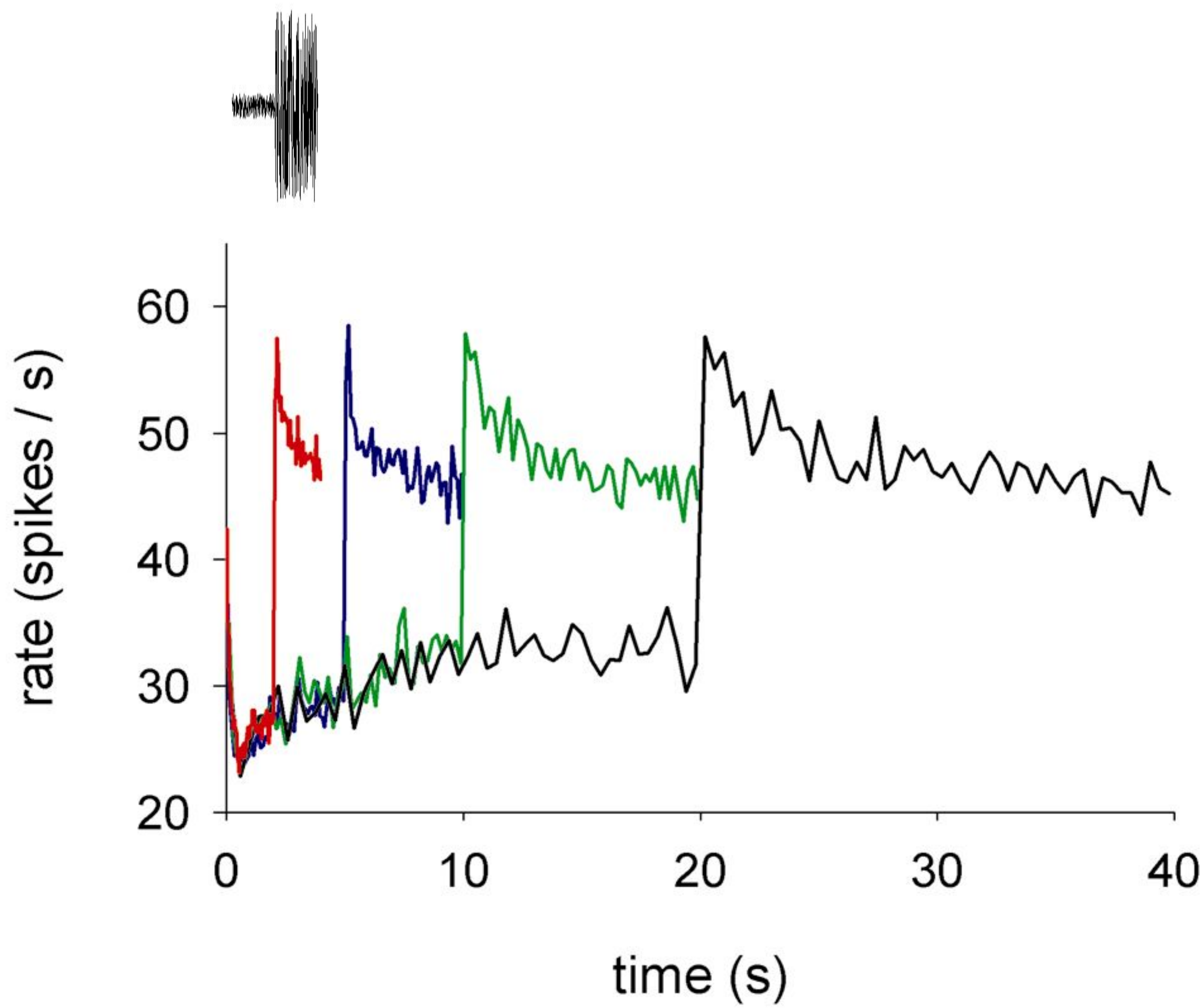


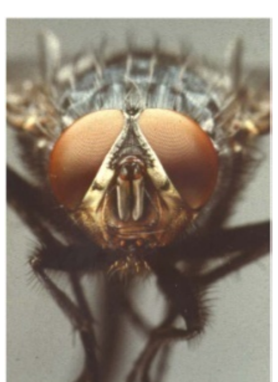
Firing rate adaptation to signal statistics





Firing rate adaptation to signal statistics

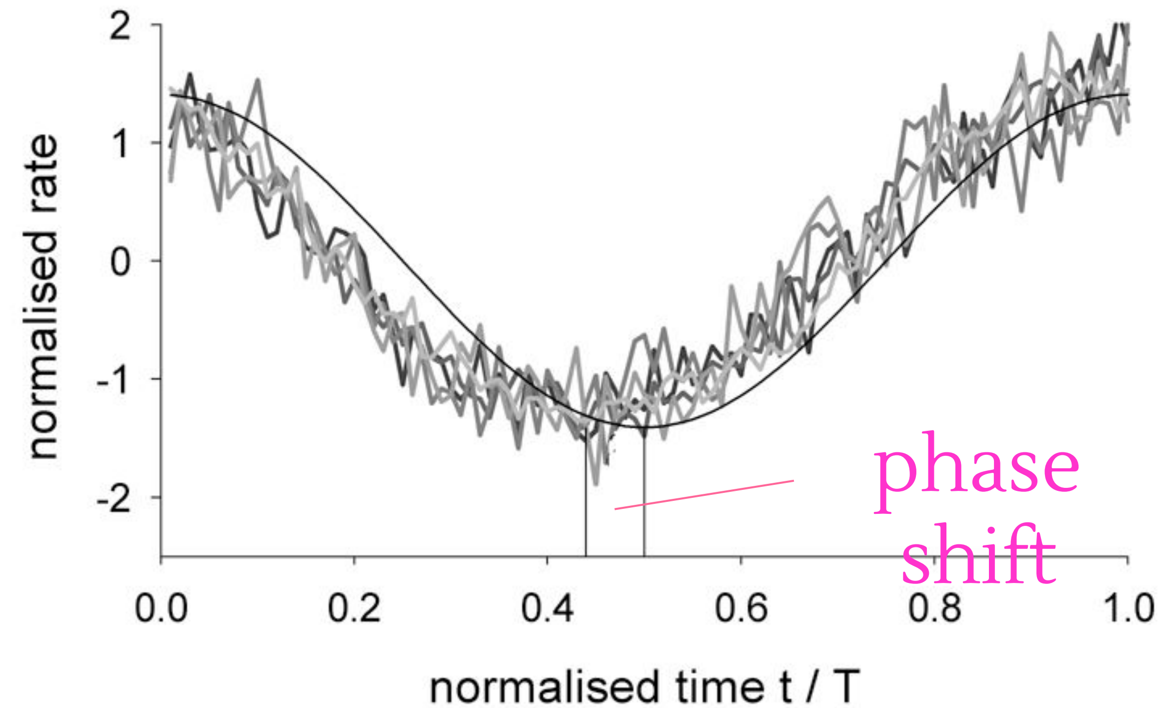


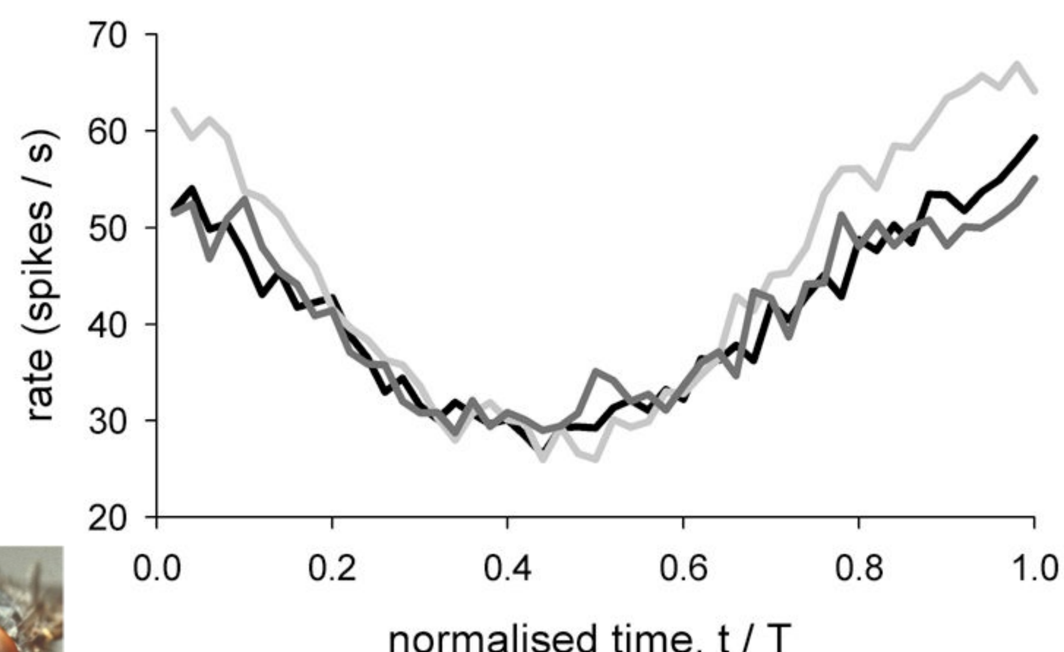


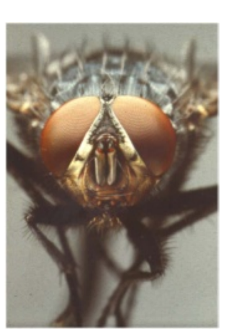
Fairhall, Bialek, Lewen and de Ruyter (2001)

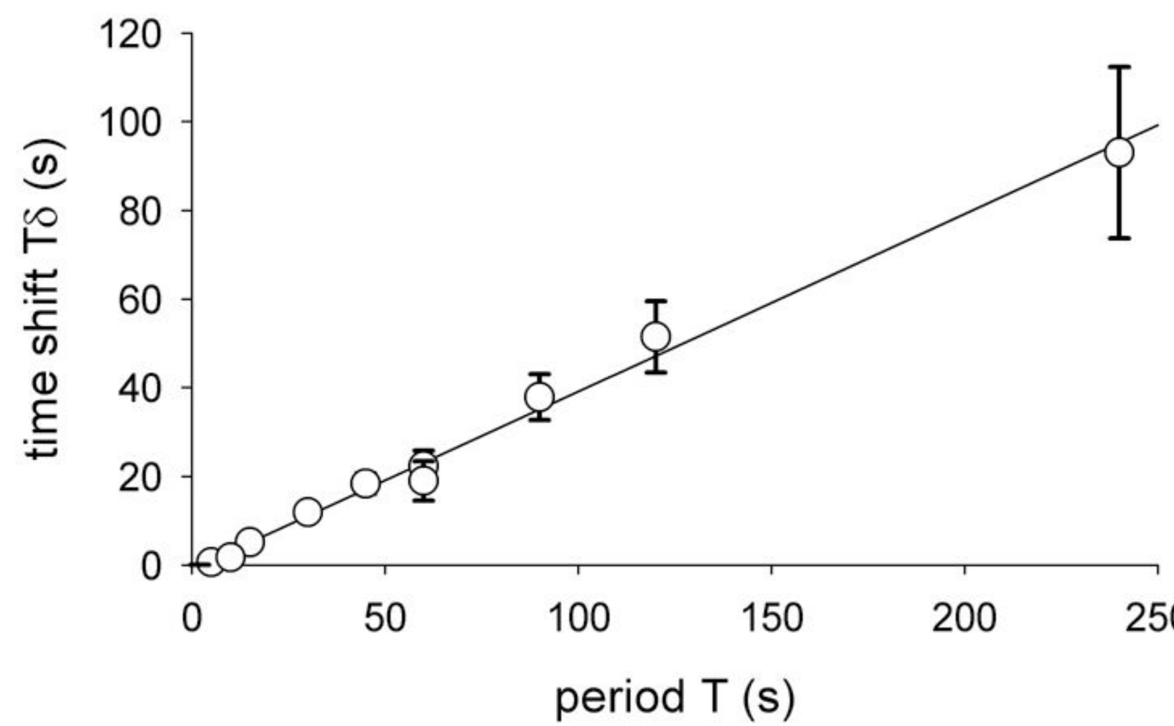
Finding the transfer function

- Stimulate with a set of sine waves at different frequencies
- Variance envelope ~ exp[sin t/T]









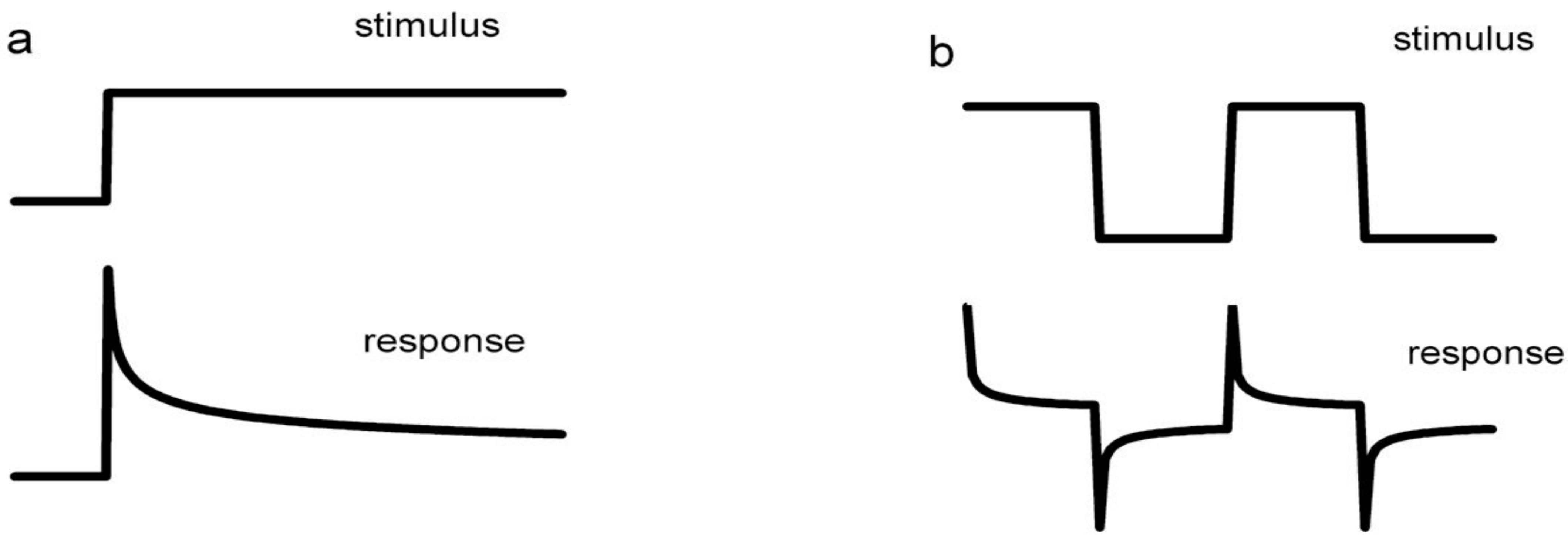
T = 30s, 60s, 90s

The transfer function: *fractional differentiation*

Fourier representation $(i\omega)^\alpha$:
each frequency component scaled by ω^α
and with phase shifted by a constant phase i^α $\alpha\pi/2$

power-law response

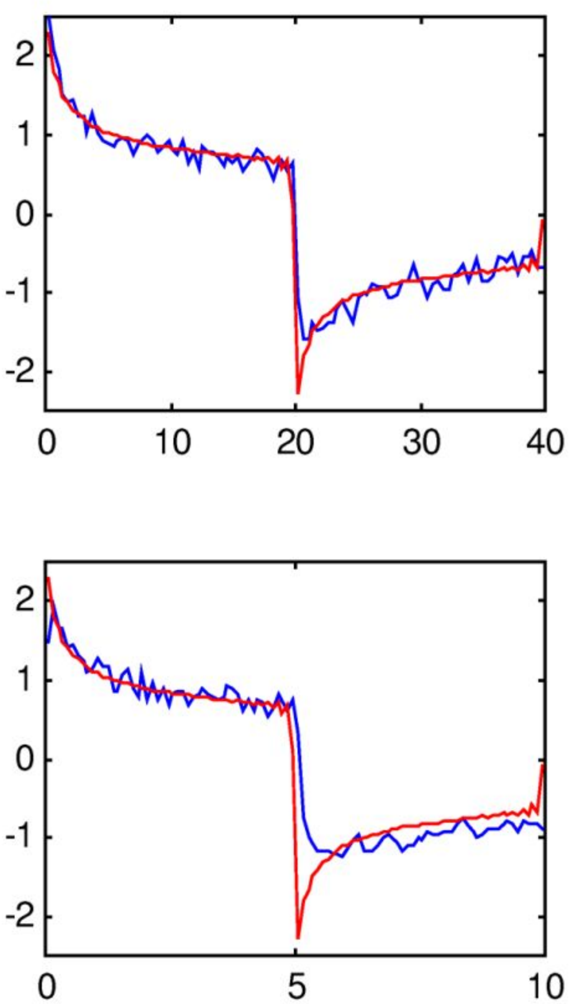
scaling response
to a square



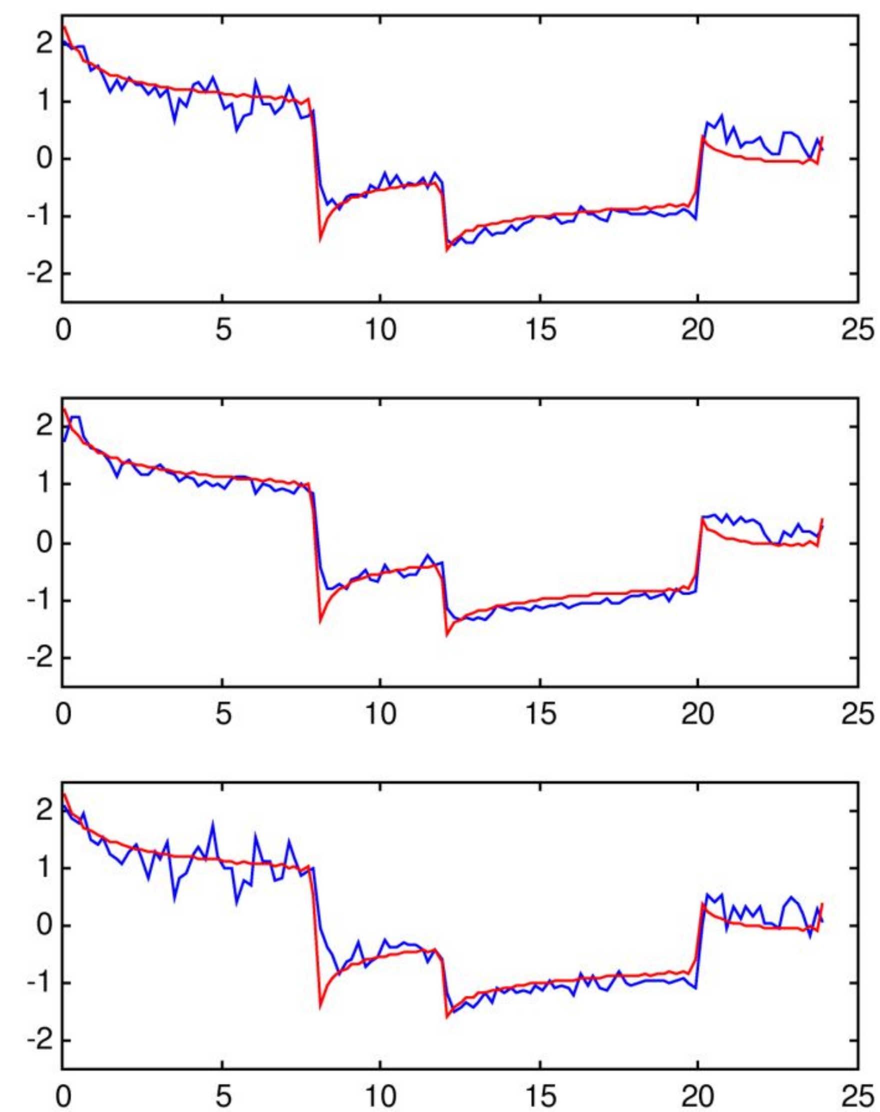
Fractional differentiation

From sinusoid experiments, find exponent $\alpha \sim 0.2$

Two-state switching



Three-state switching



Multiplexing

- **Spike timing** optimally encodes instantaneous fluctuations
- **Spike rate** encodes envelope (optimally?)

Common rules for temporal information processing in cortex?

S1 V1 A1

Ilan Lampl

Nicholas Priebe

Eli Nelken

Kenneth Latimer

HFSP

Common rules for information processing in cortex?

Common stimulus design: 20ms pulses

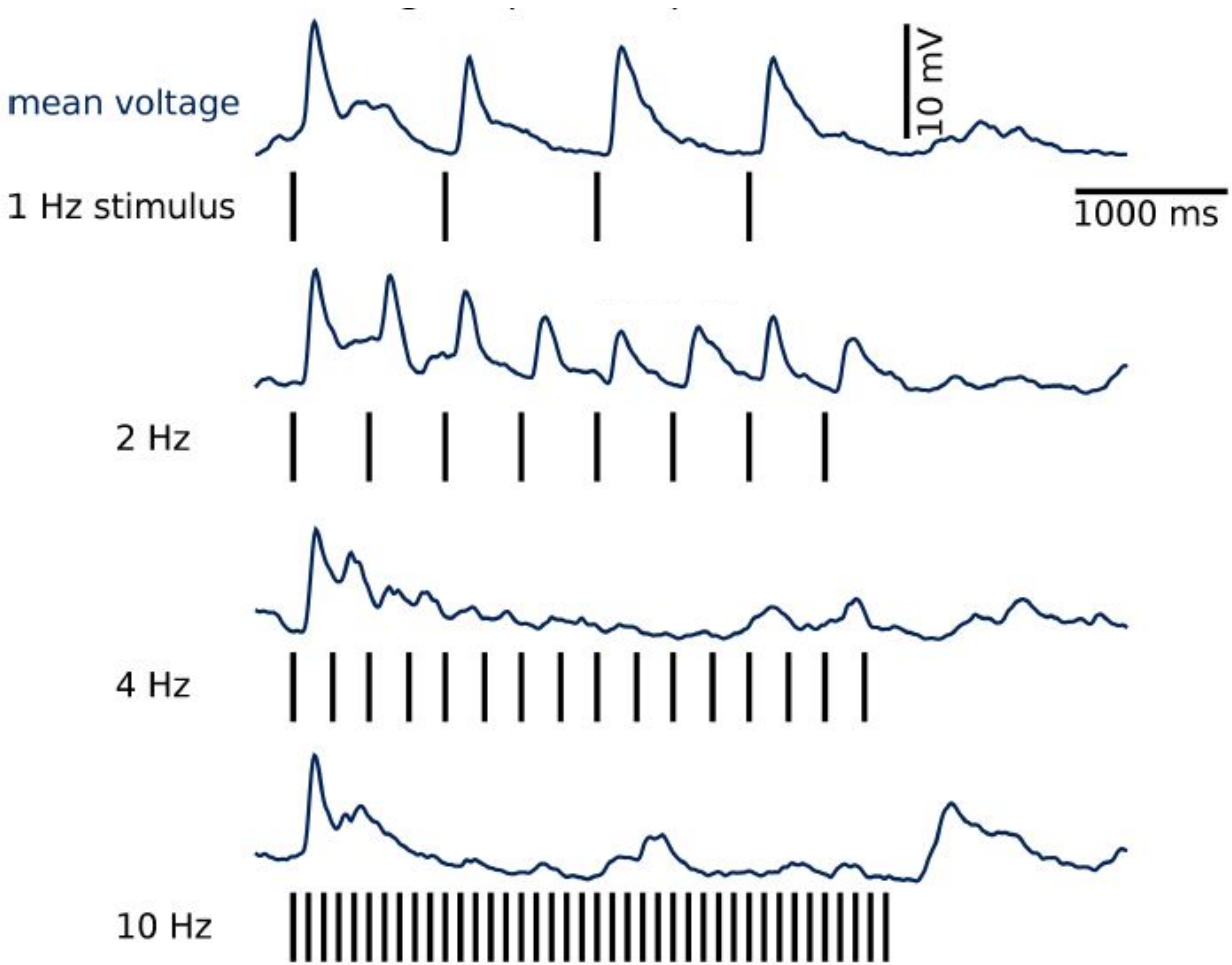
V1
Full-field flicker

S1
Whisker deflection

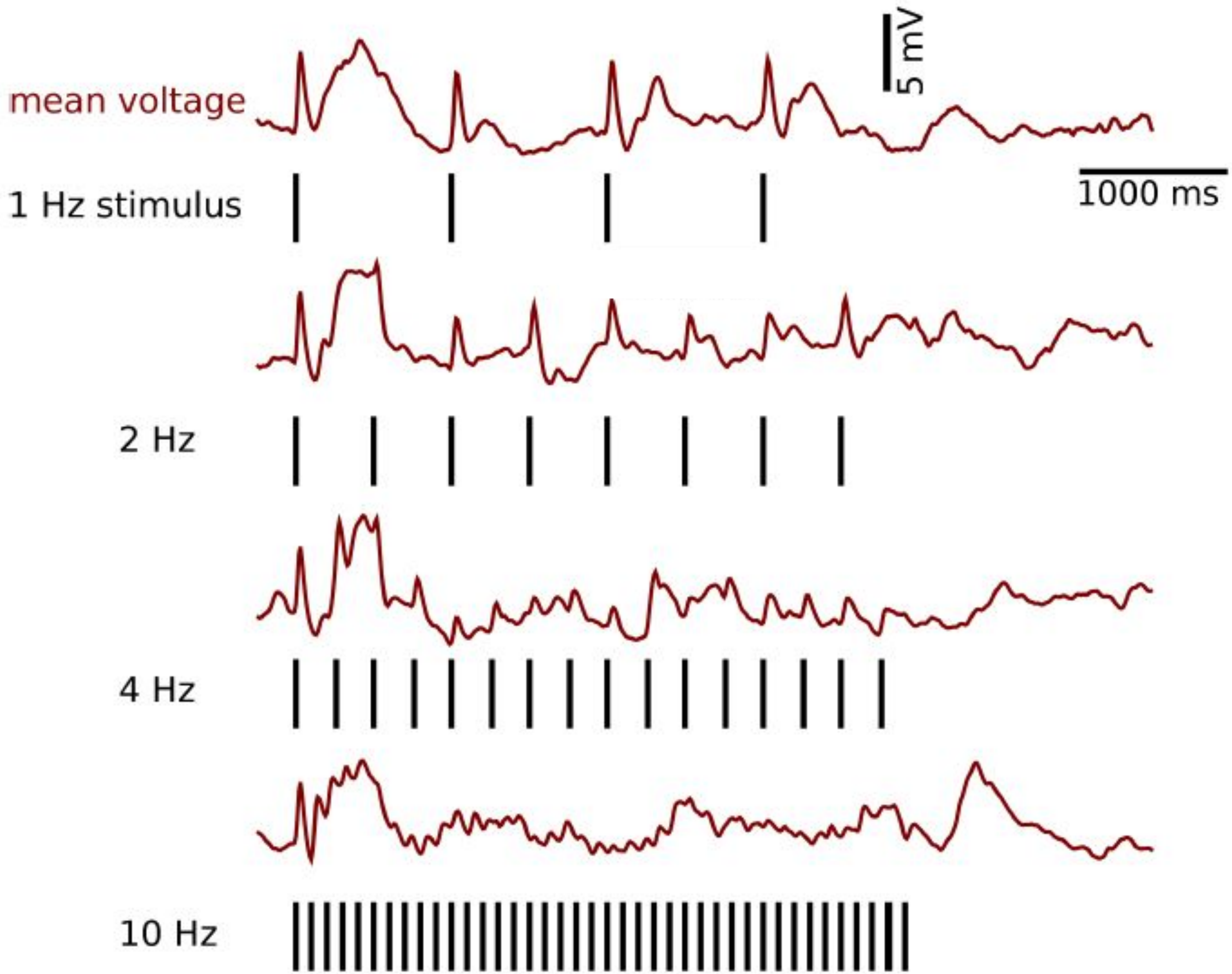
A1
Click

- Same mouse strain (C57BL/6)
- Same anaesthesia (urethane and chlorproxithene)
- Whole cell current clamp recording

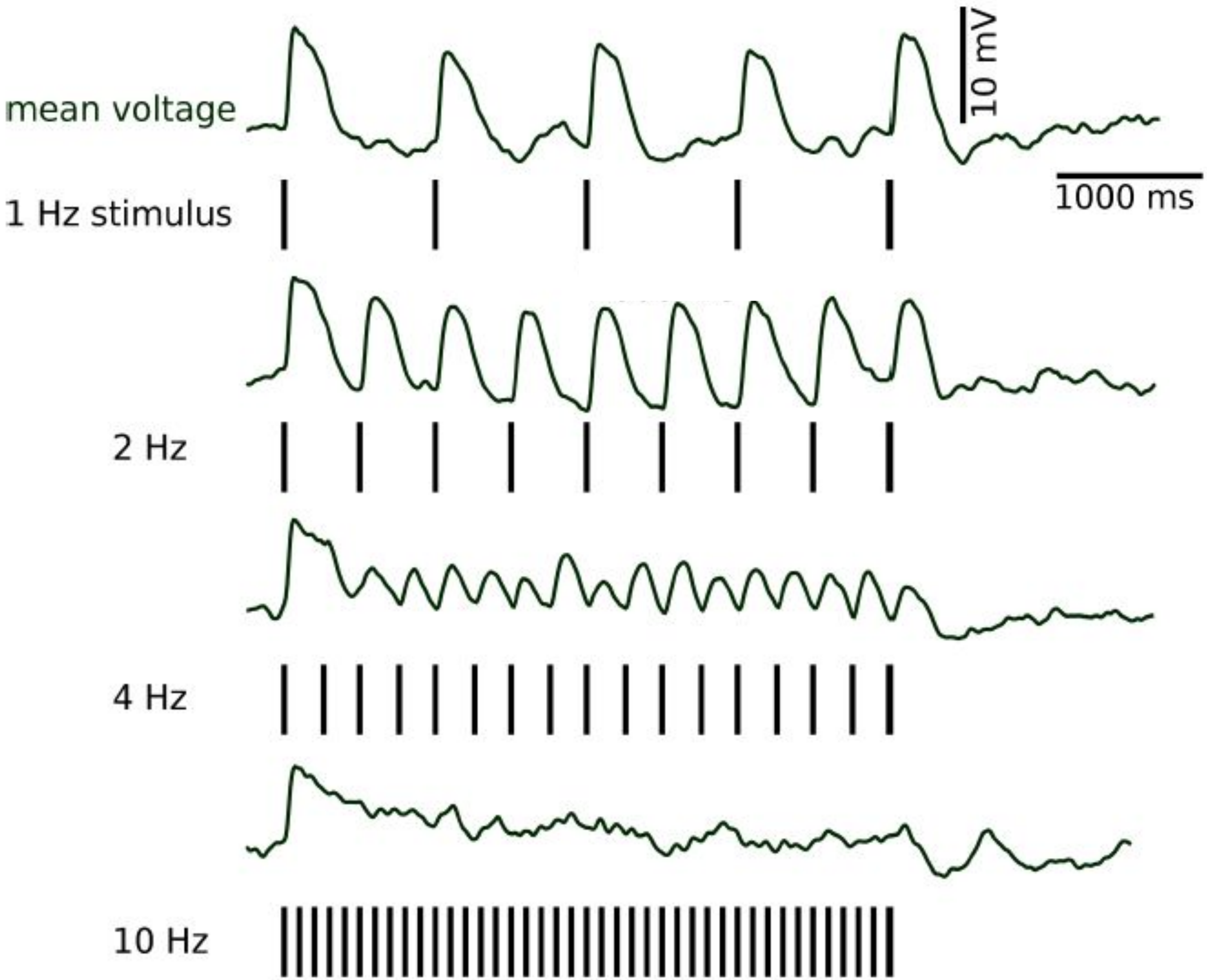
Pulse responses in V1



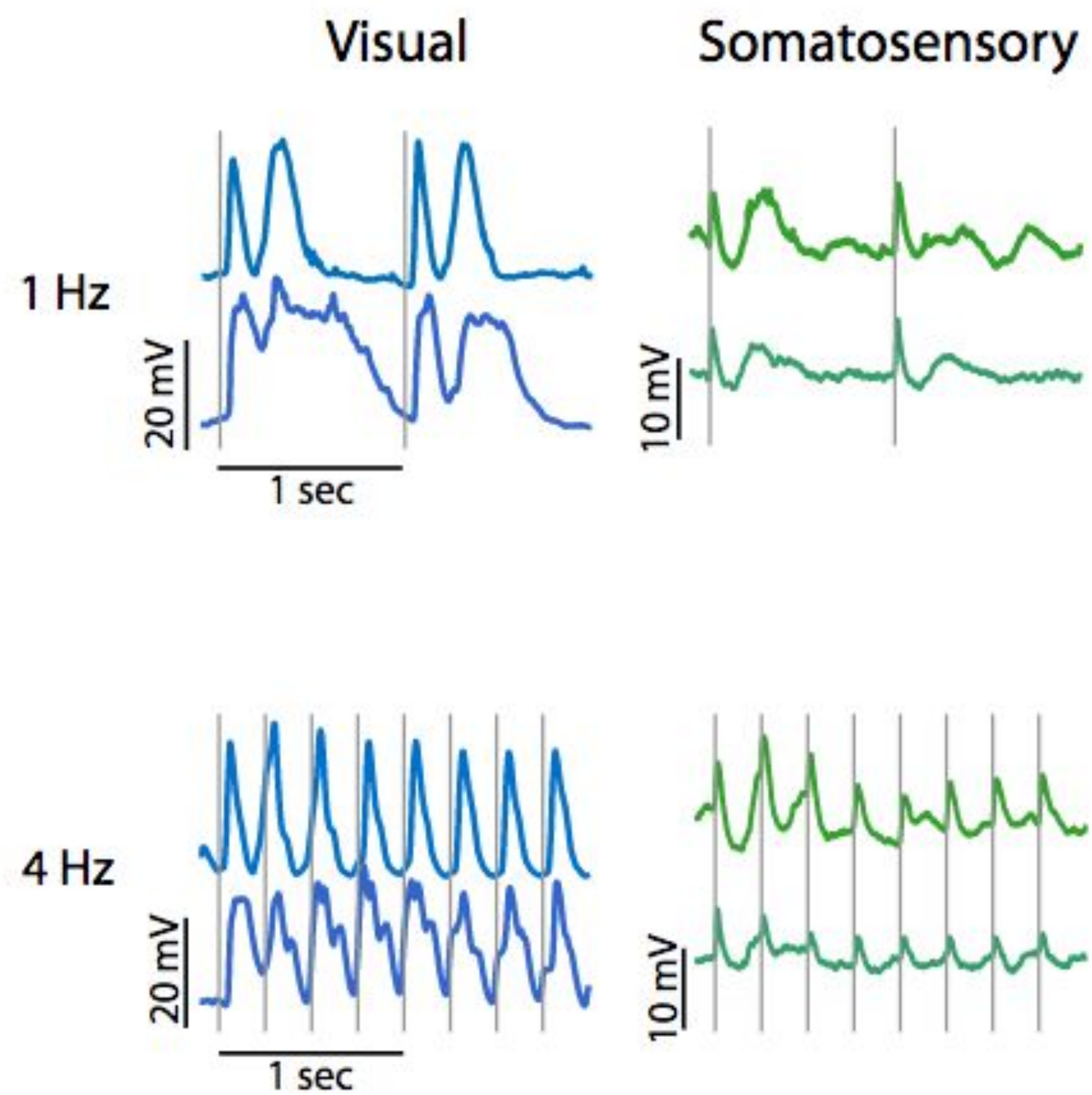
Pulse responses in S1



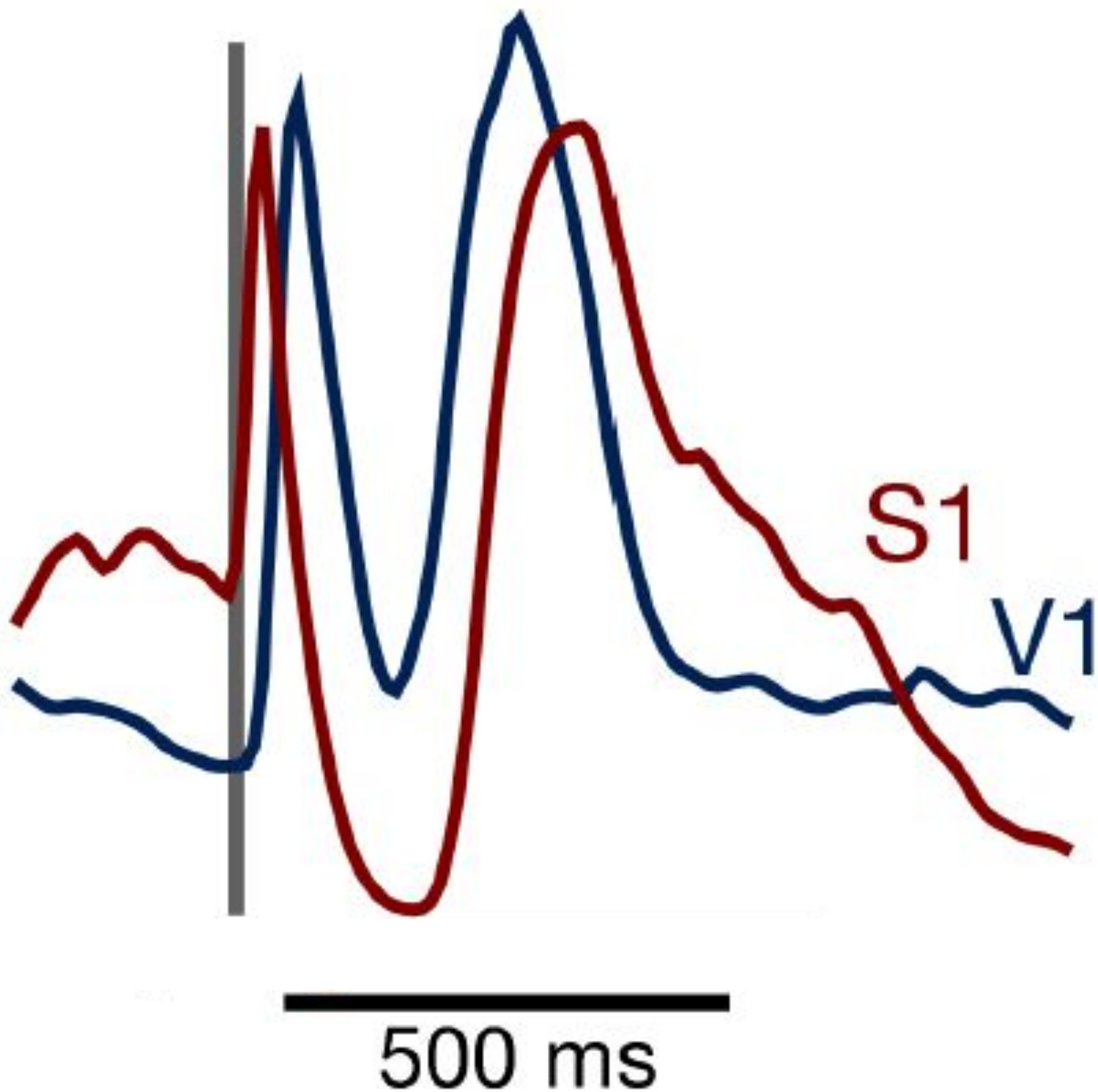
Pulse responses in A1



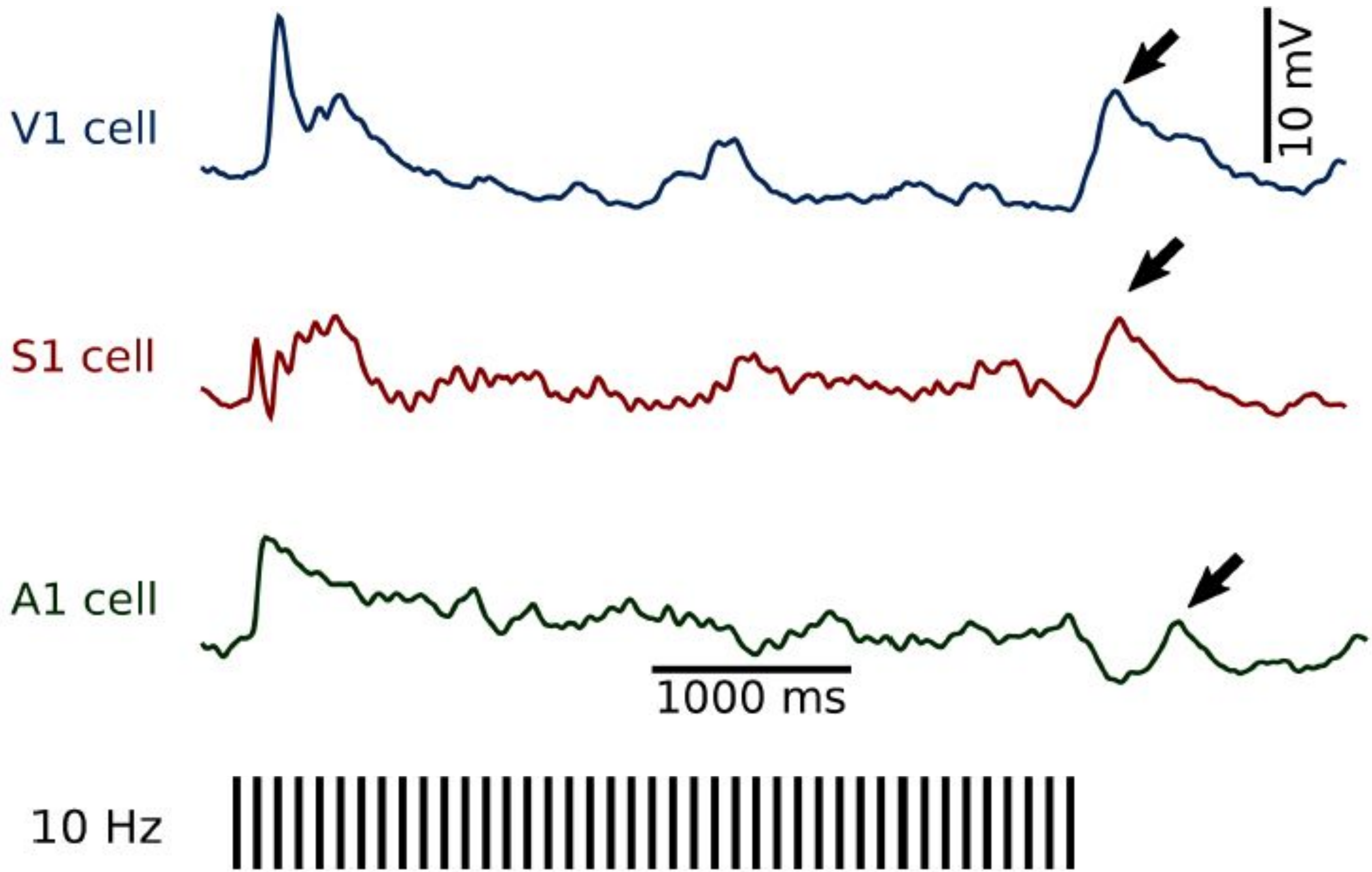
Complex single-pulse response in V1 and S1



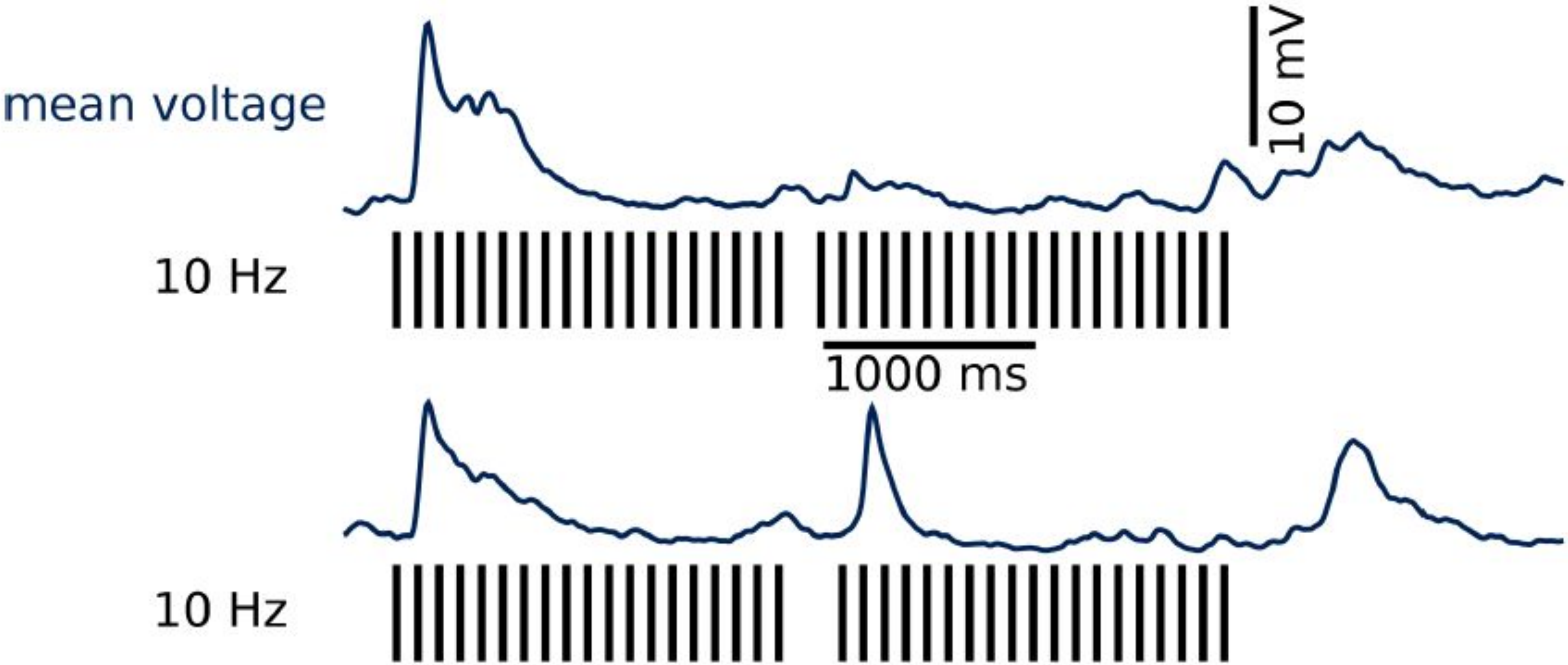
Complex single-pulse response in V1 and S1



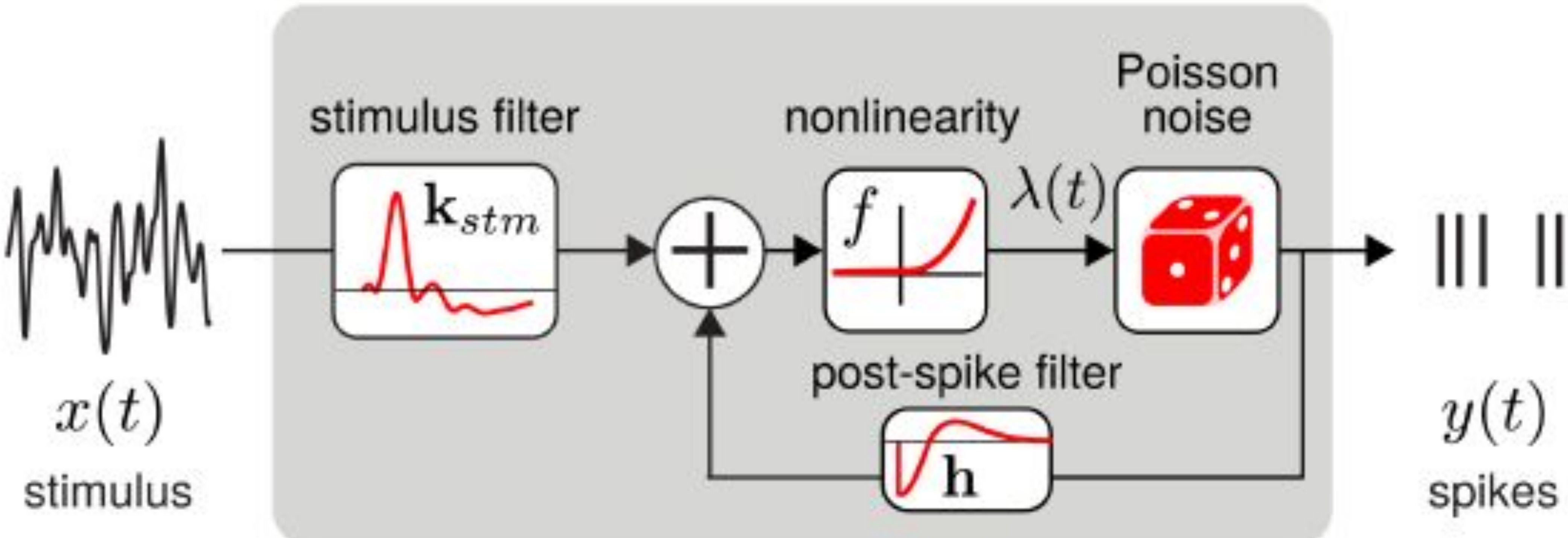
Temporal pattern detection: offset response



Omitted stimulus response

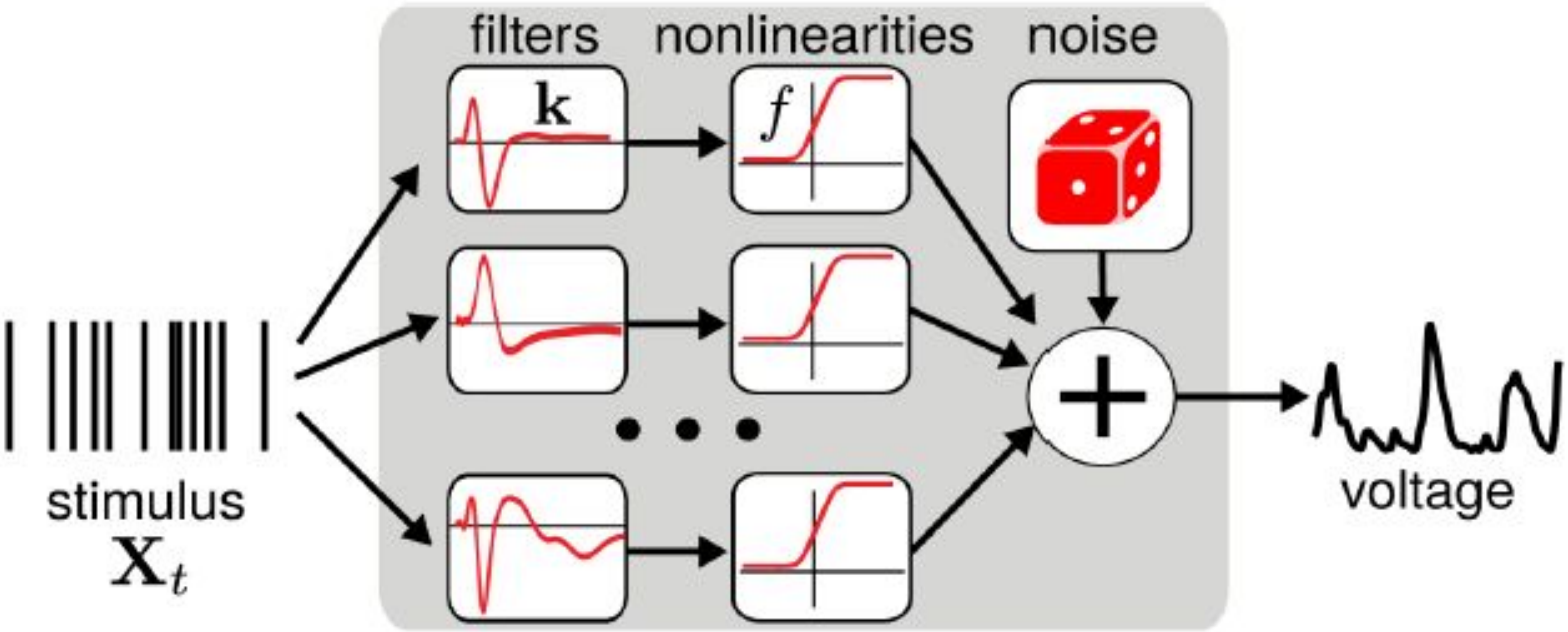


First pass approach: model



Fit model with Poisson inputs

Extended GLM models

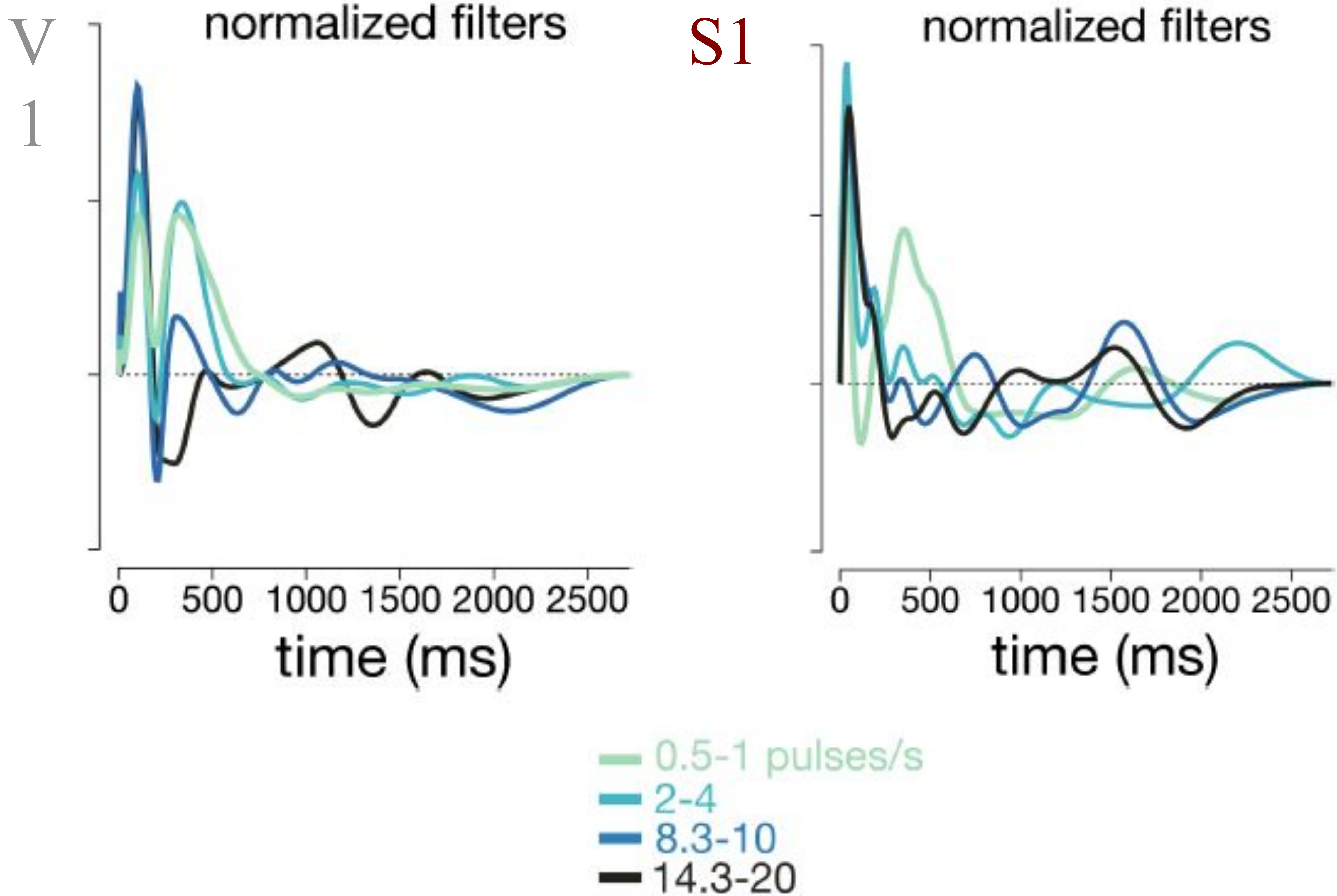


$$V_t = \sum_{i=1}^{N} f\left(\mathbf{X}_t^\top \mathbf{k}_i\right) + b + \epsilon_t, \qquad \epsilon_t \sim \mathcal{N}\left(0, \sigma^2\right)$$

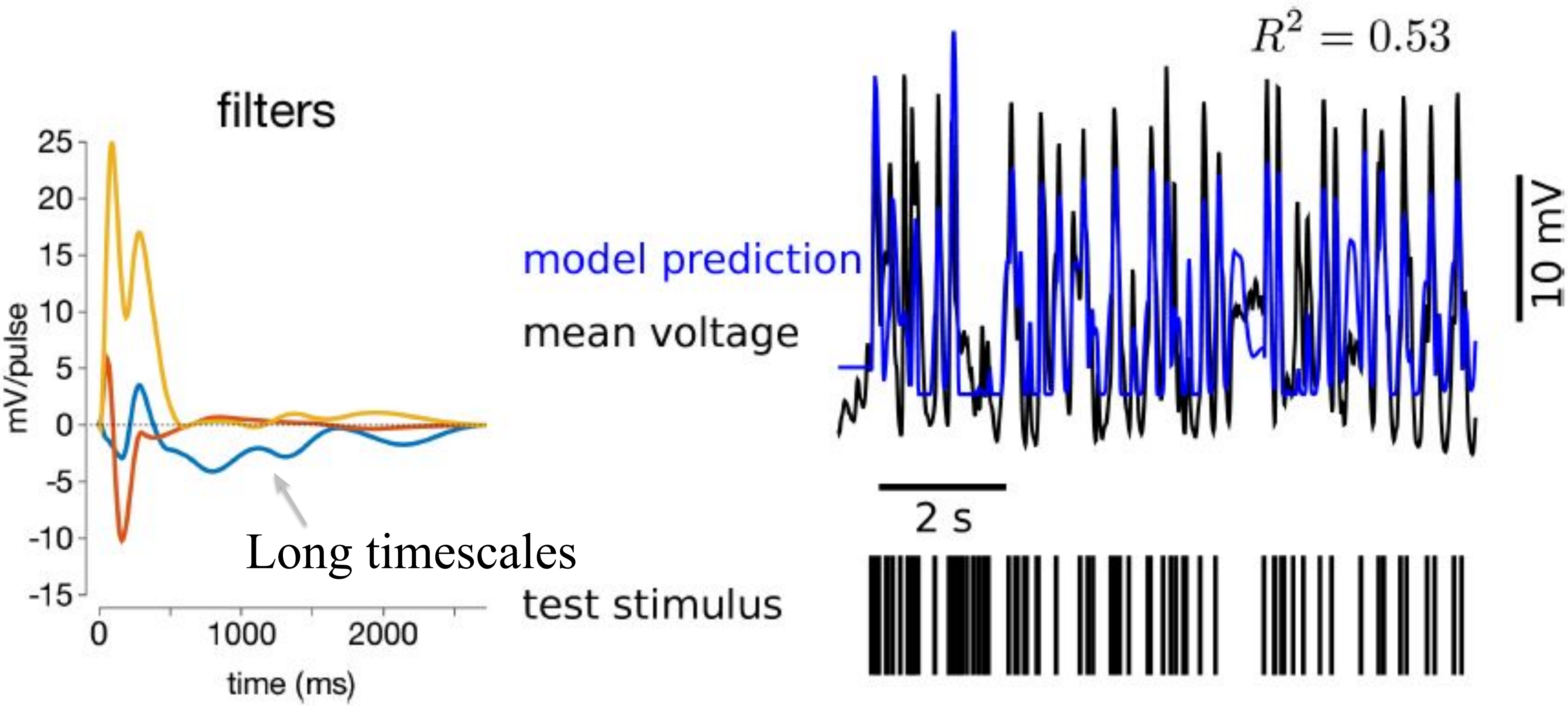
"subunits"

Latimer and Pillow, Butts

Filters depend on stimulus frequency



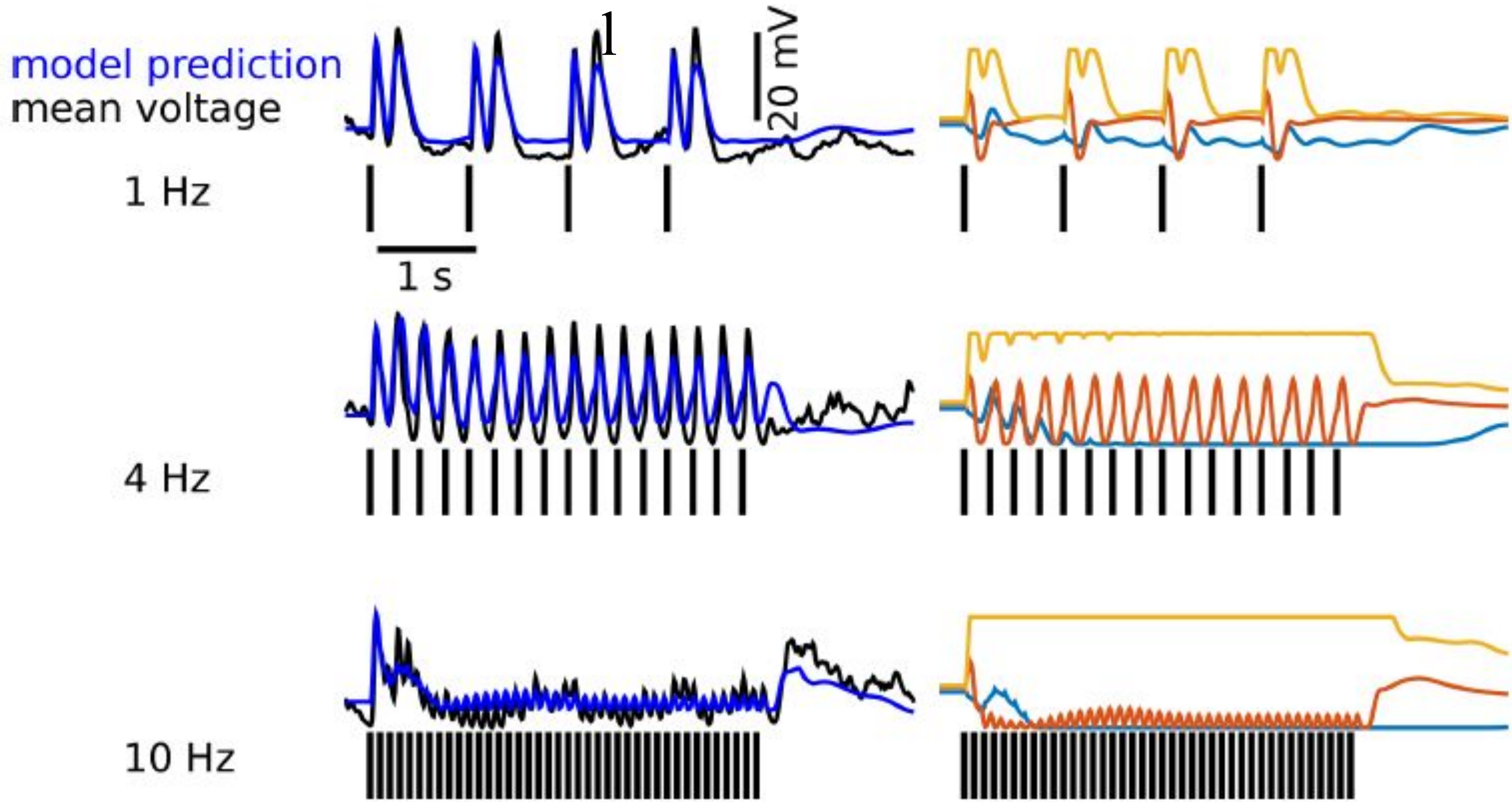
Fit using Poisson trains of multiple frequencies



Use model to predict response to periodic stimulus

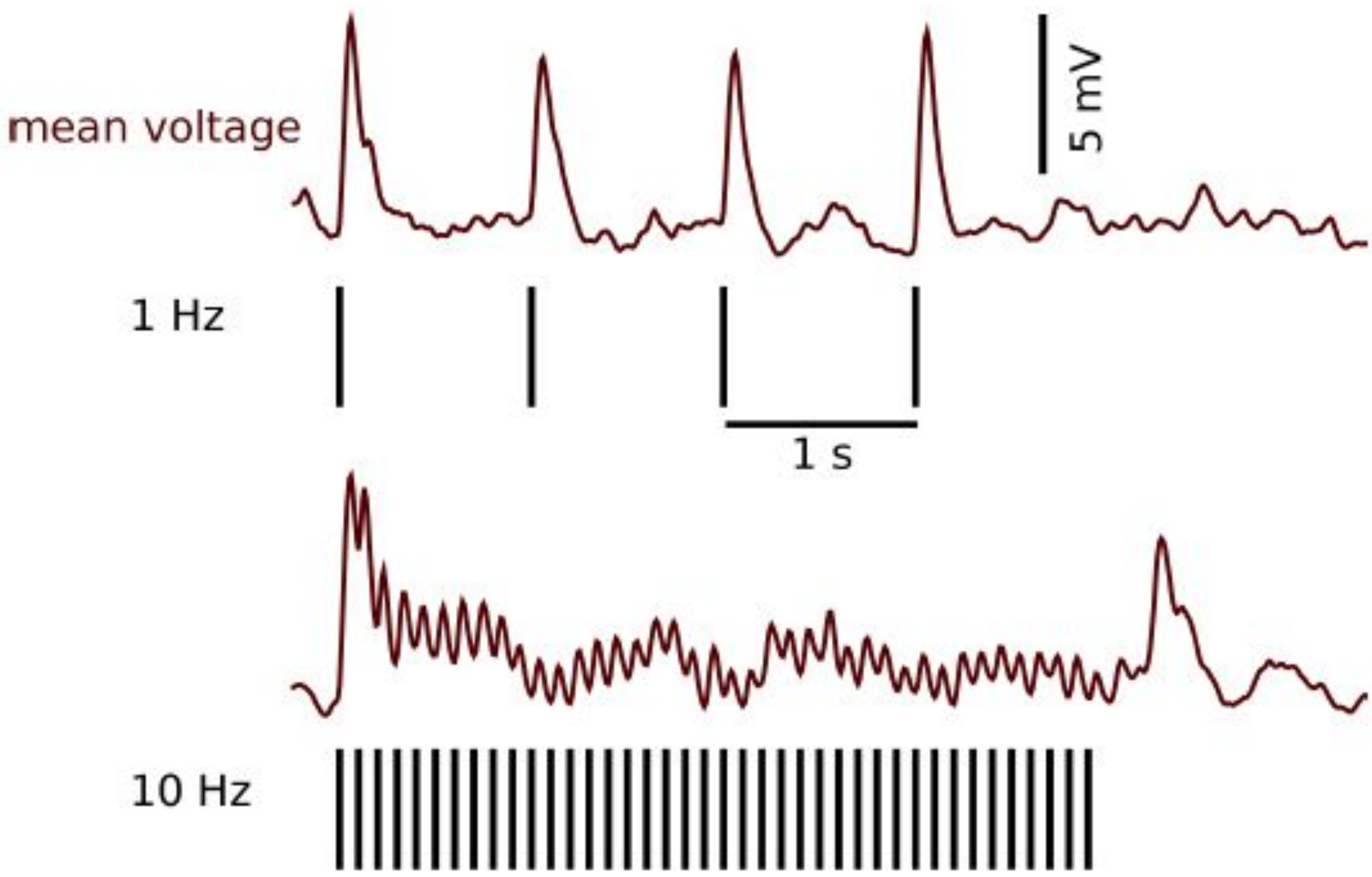
Total

By subunit



Different components responsible for biphasic pulse response and offset

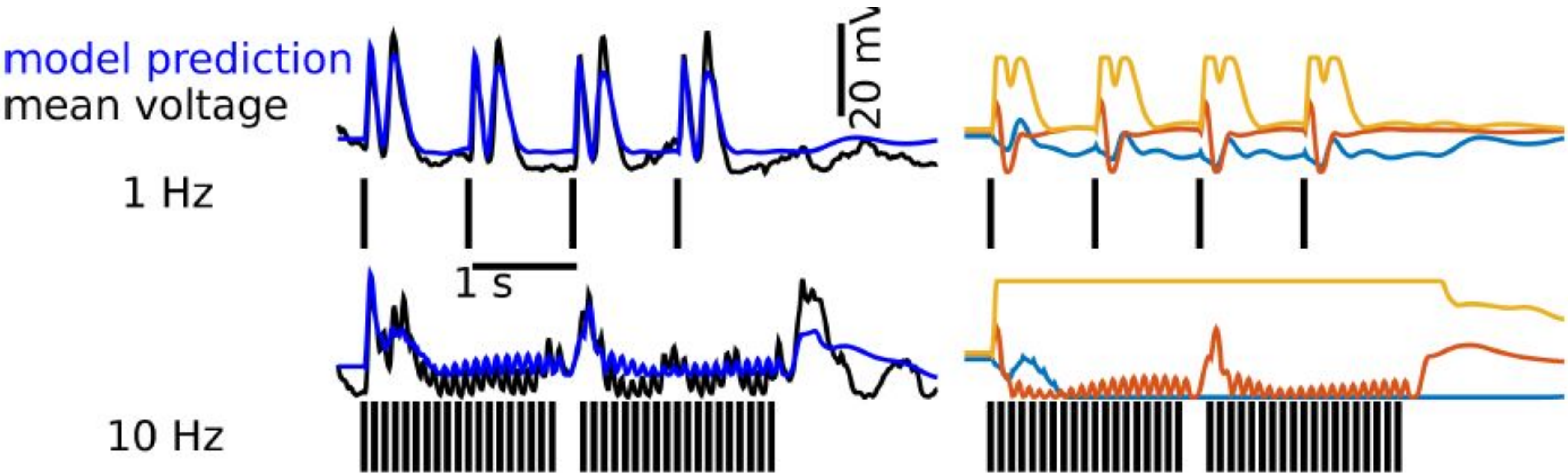
S1 example: can have simple pulse response and offset



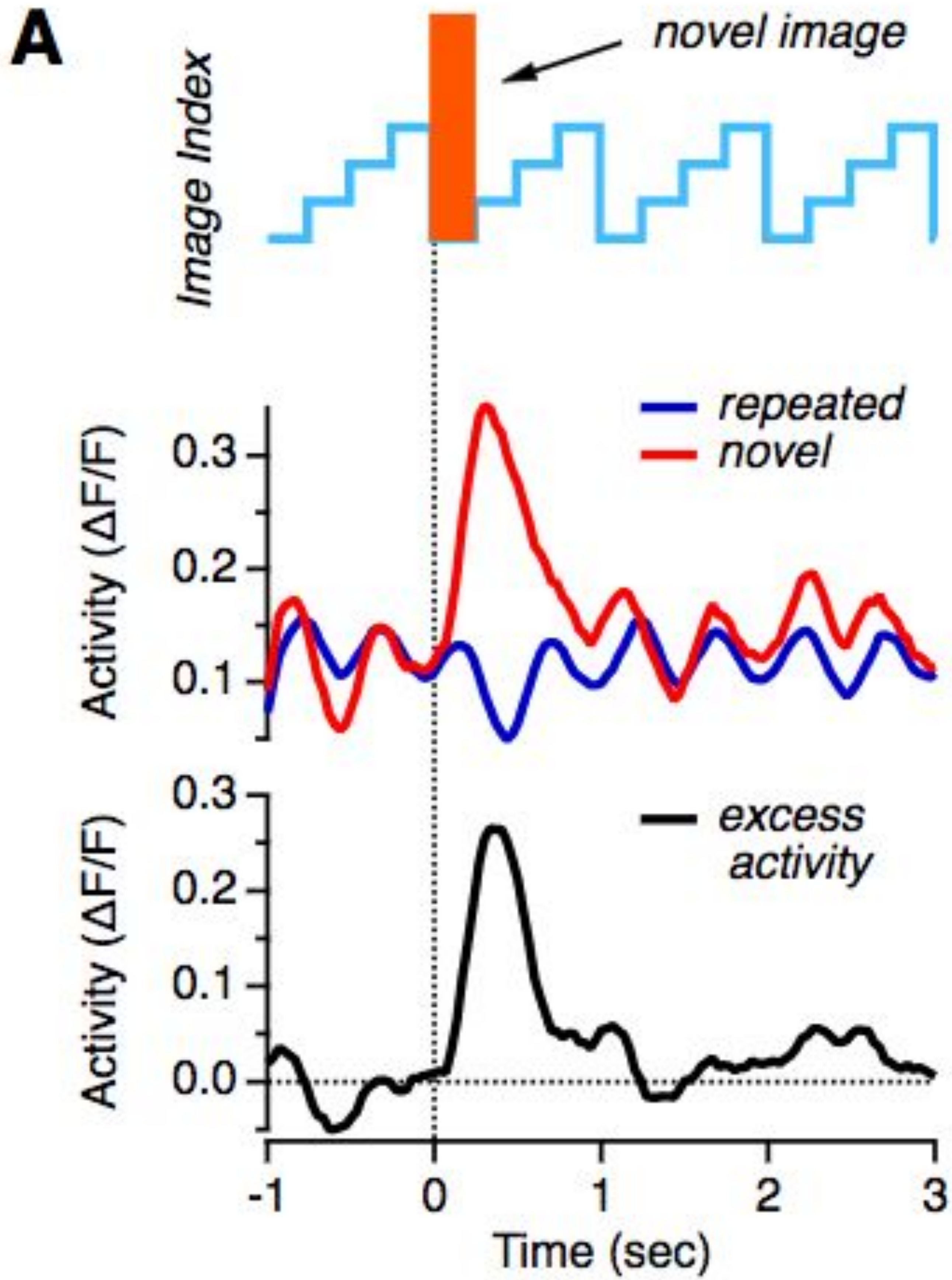
Offset subunit captures omitted response

Tota
l

By subunit



Novelty detection in sequences



Jomann, .., Tank, Berry, bioarxiv

Subsummary

- Complex multiple timescale dynamics: a substrate for pattern detection
- Captured by relatively simple filter model; requires several filters
- Timescale and some feature differences between different cortical areas
- Some responses may be inherited from thalamus; some thalamocortical
- Little differentiation in response by cell type: differences in circuit
- Caveat: all anaesthetized!

Capturing adaptation

$$\frac{d\boldsymbol{r}}{dt} = F(\boldsymbol{r}, \boldsymbol{s}) \longrightarrow \boldsymbol{r}(t) = f(\boldsymbol{s}_{\boldsymbol{\tau}}(t))$$

With adaptation, apply a separation of timescales:

$$\boldsymbol{r}(t) = f(\boldsymbol{s}_{\boldsymbol{\tau}}(t), \boldsymbol{\theta}_T(t)) \quad \text{where} \quad \boldsymbol{\theta}_T(t) = g(\boldsymbol{s}_{\boldsymbol{T}}(t))$$

E.g. in fly H1:

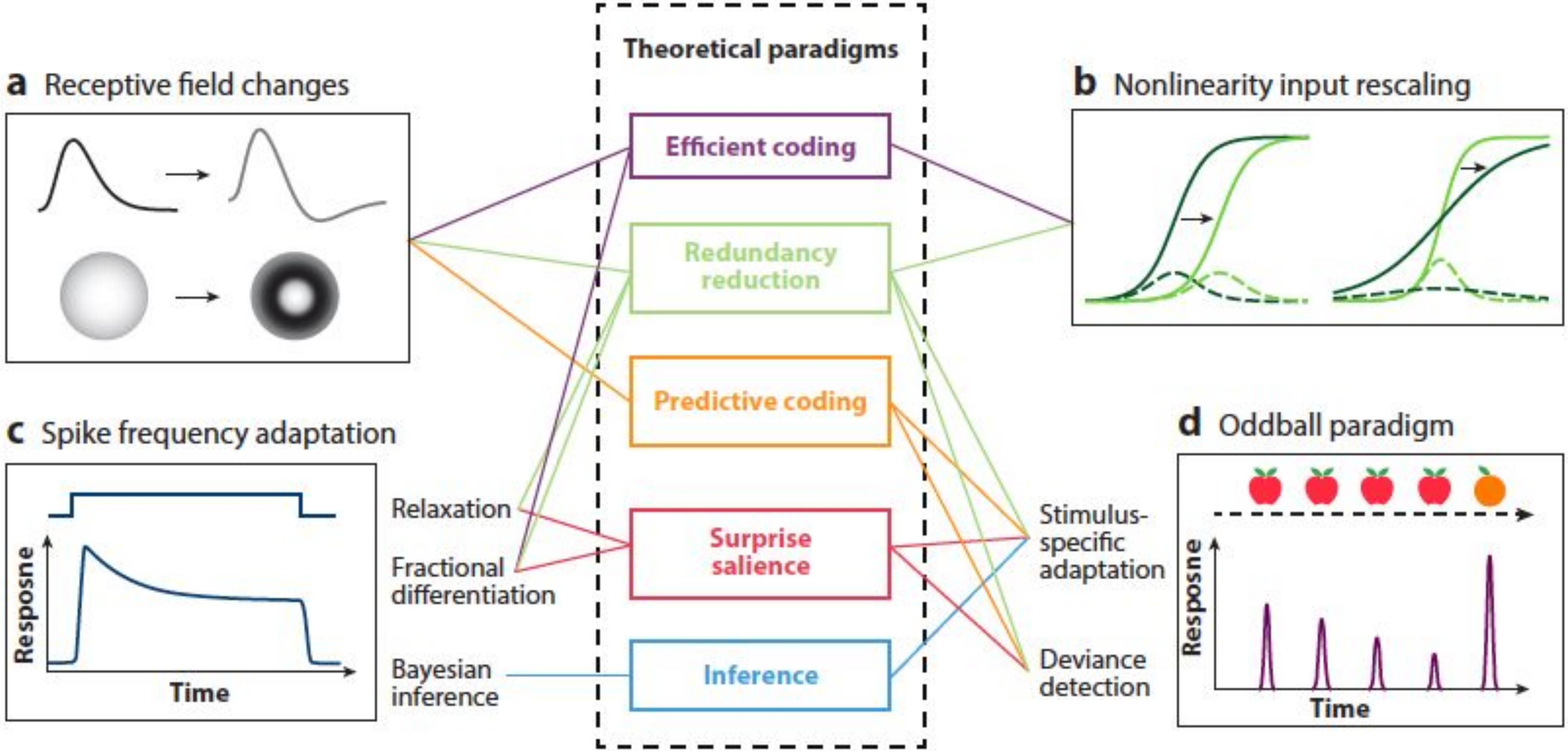
$$\boldsymbol{r}(t) = R(\sigma(t)) f(\boldsymbol{s}_{\boldsymbol{\tau}}(t)/\sigma(t))$$

However, likely need to consider:

$$\boldsymbol{r}(t) = h(\boldsymbol{s}_{\boldsymbol{T}}(t))$$

Weber and Fairhall, 2019

Theoretical paradigms for adaptation



Weber and Fairhall, 2019

Summary

- Sensory systems use common strategies to optimally represen
stimulus information in dynamically varying environments
- Can capture multiple timescales of responses in statistical models
- Adaptation can be thought of as encoding longer timescale temporal
properties
- Can resolve ambiguities by considering temporally multiplexed code
- Low-level biological properties confer computational richness