Neural population state and auditory encoding

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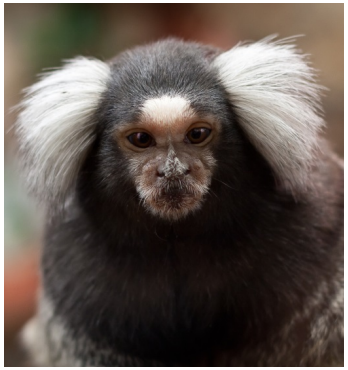
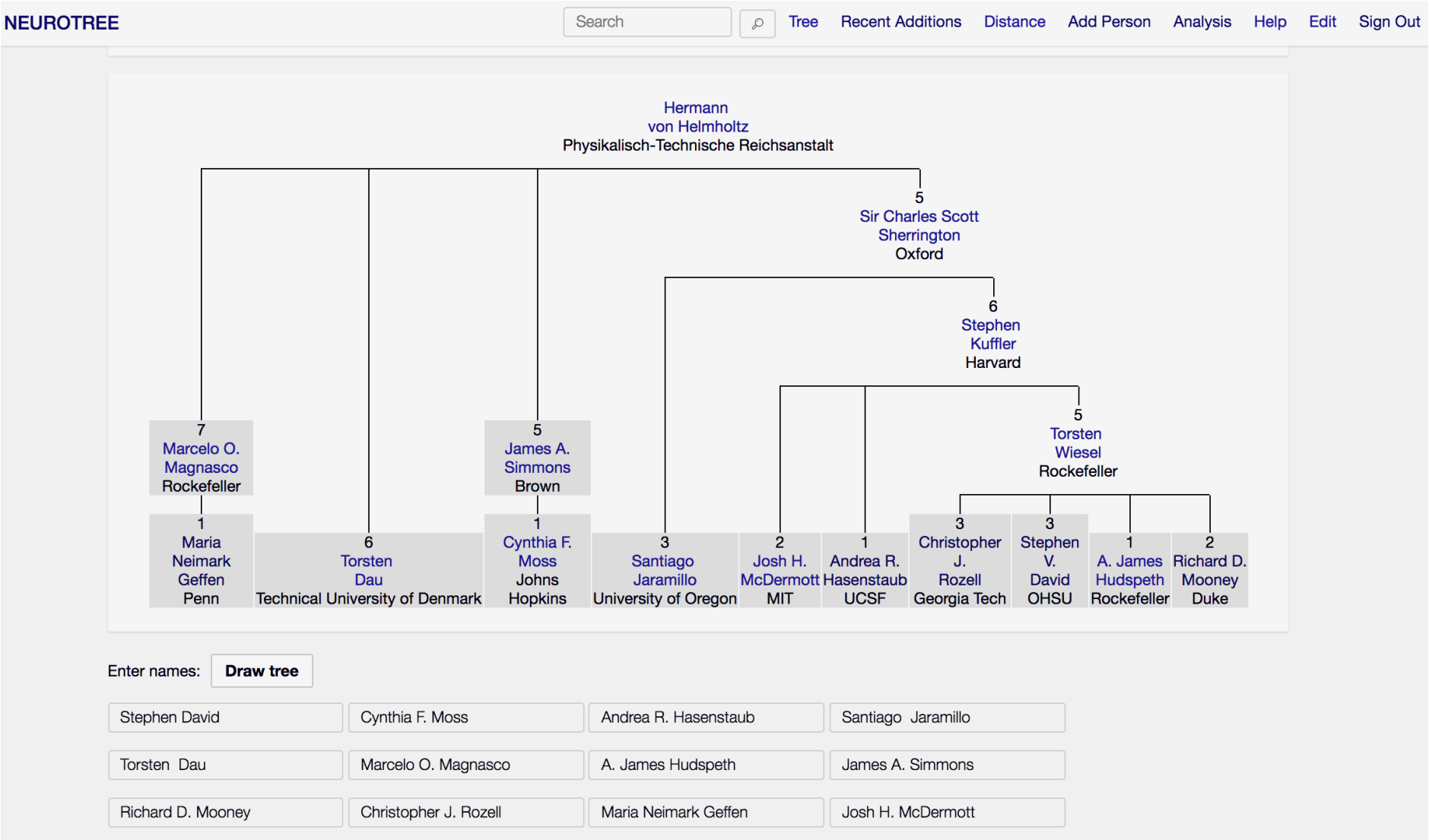
https://hearingbrain.org/

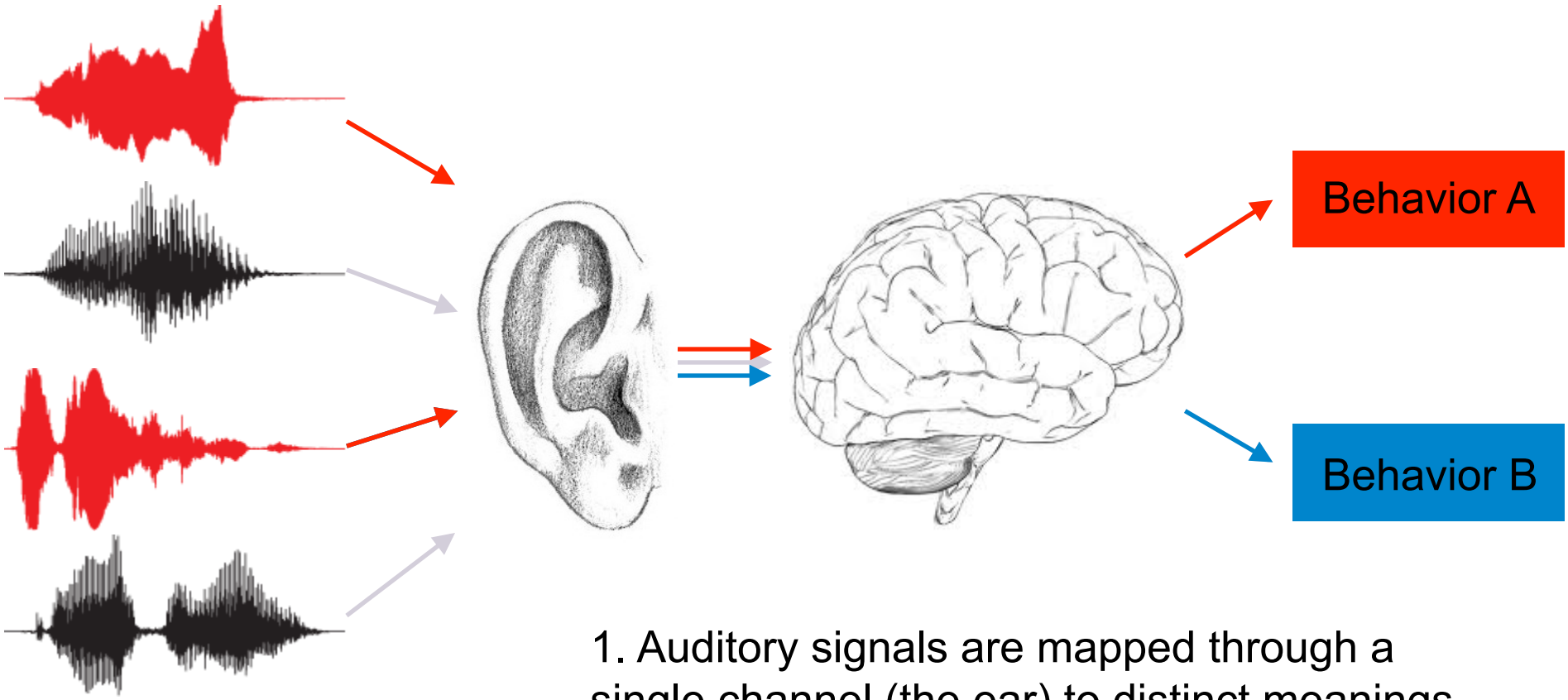


An aside on clustering...



http://neurotree.org/beta/grouptree.php

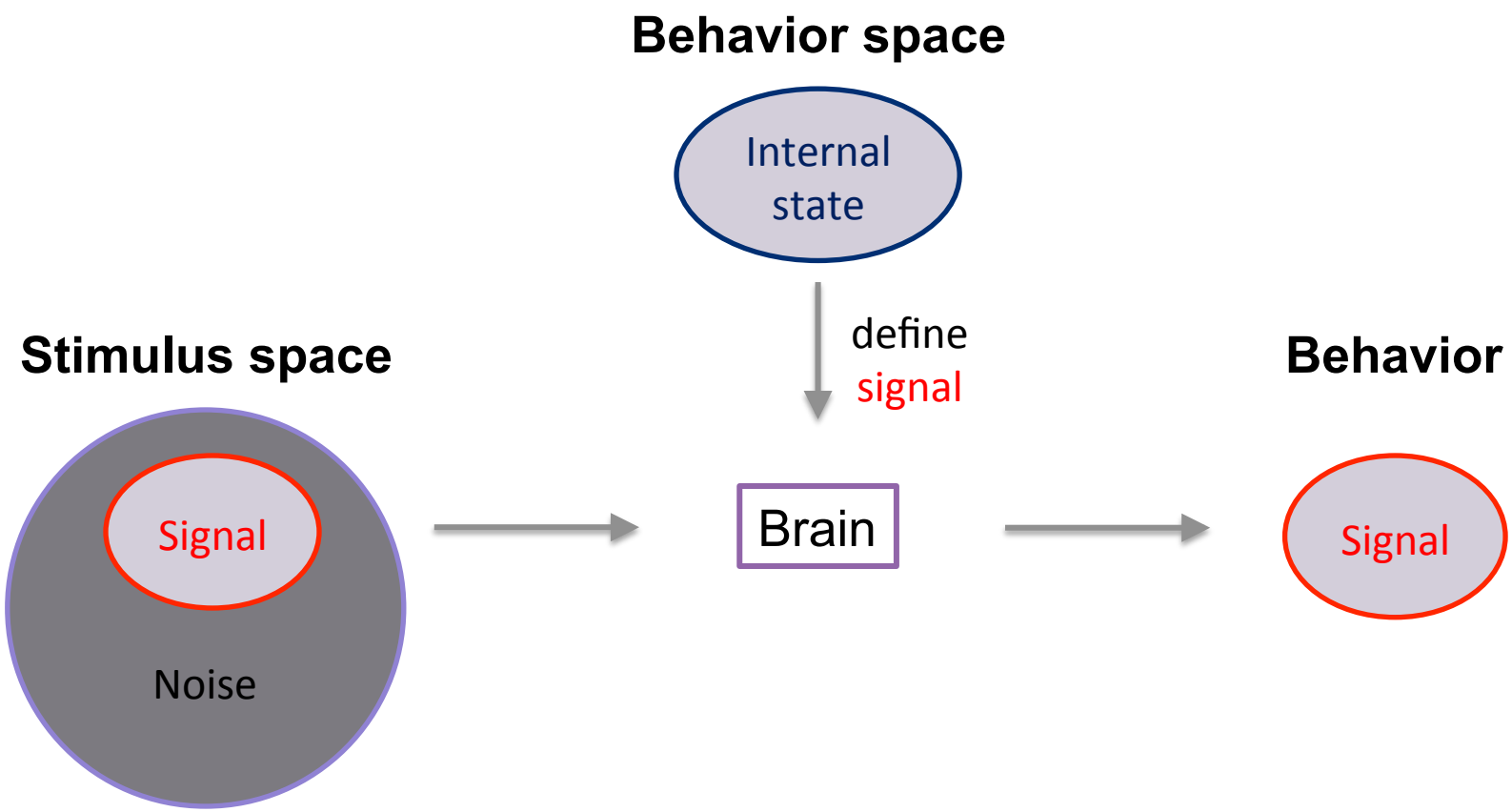
Hearing happens in context



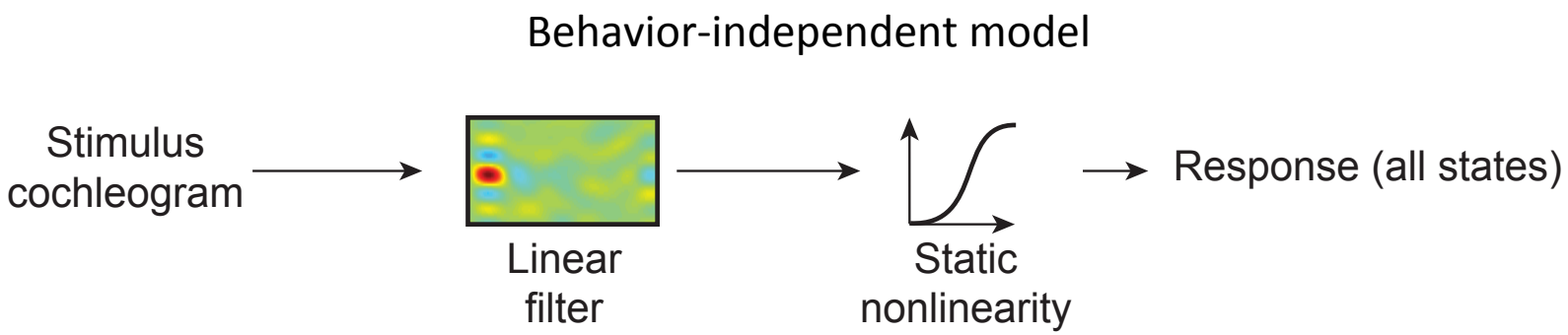
1. Auditory signals are mapped through a single channel (the ear) to distinct meanings and behaviors.

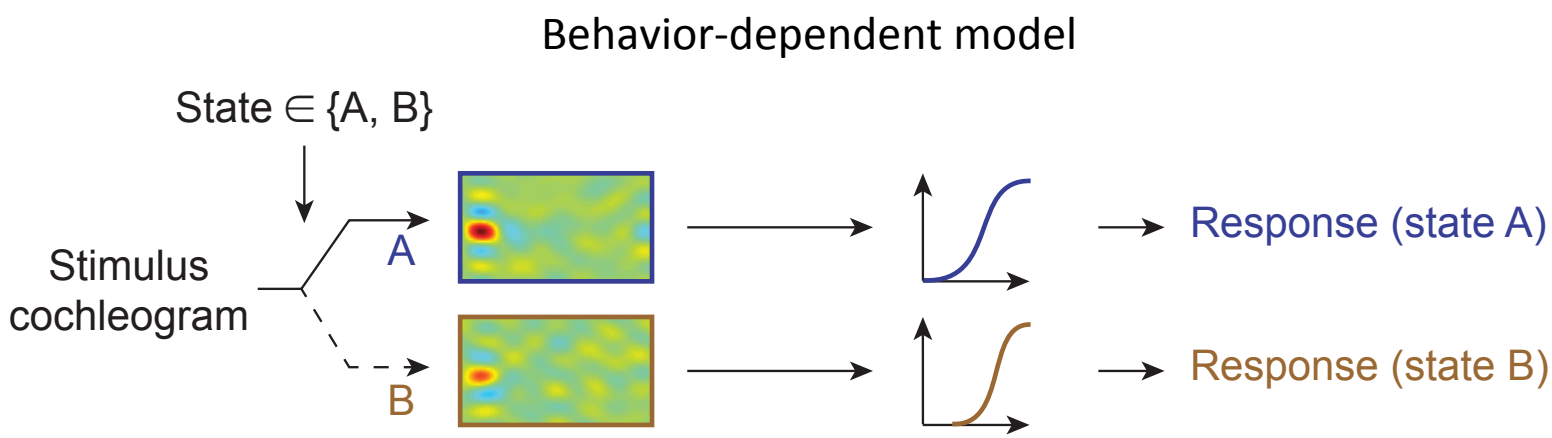
2. The mapping between stimulus and behavior changes with context.

Hearing happens in context



State-dependent encoding models

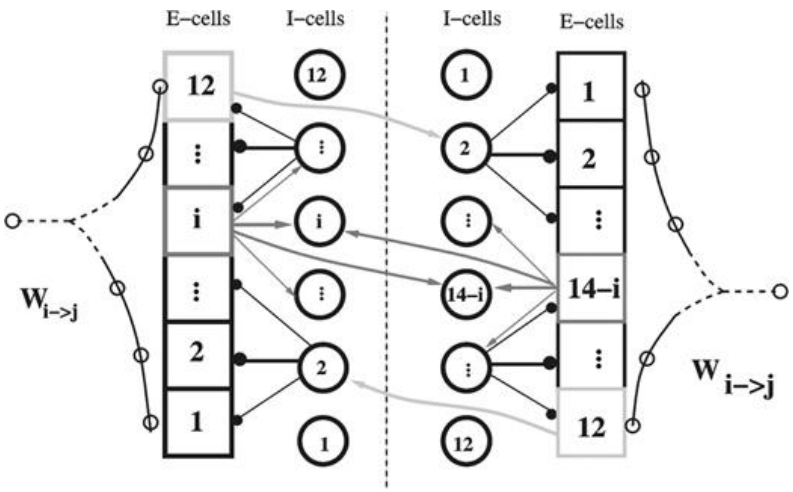




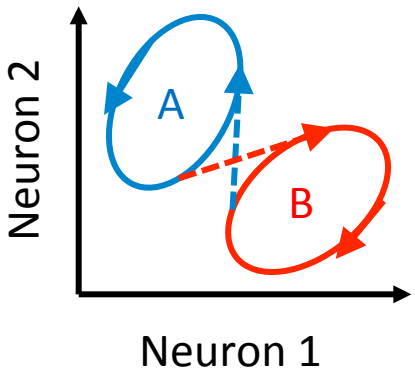
Integrating behavioral state into encoding models

- How accurately do behavior-dependent models describe neural activity?
- What does the pattern of behavioral effects reveal about neural algorithms?
- Can we link behavioral changes to physiological mechanisms?

What is a behavioral state?



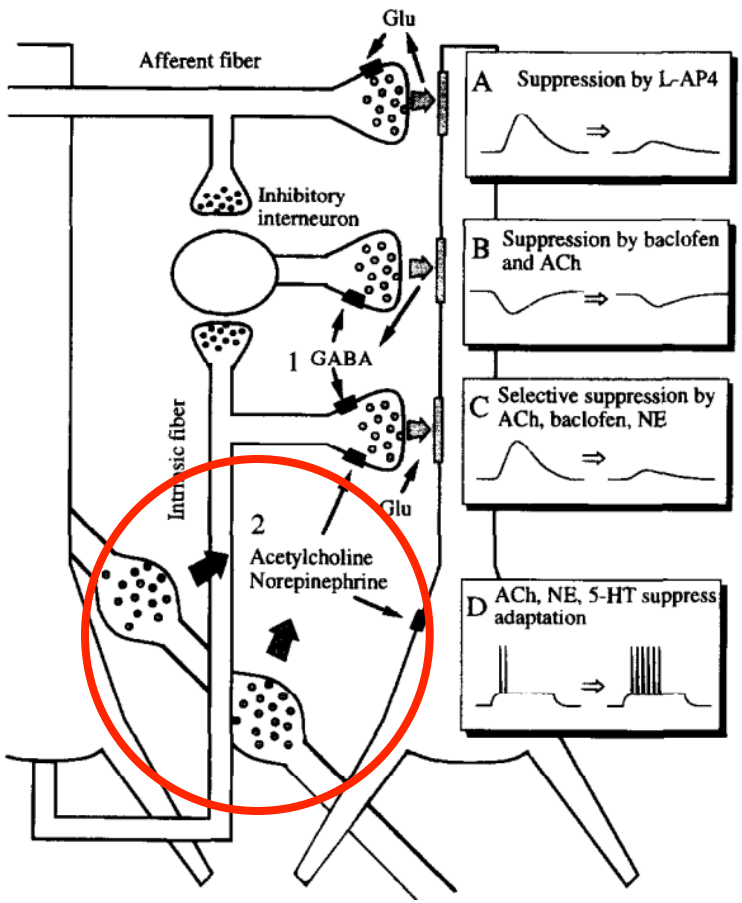
(Miller et al. 2003)



Option 1: Discrete changes in recurrent network activity

- State = switch between stable attractor by a modulatory trigger
- Classic psychology design
  - CS+/CS- (Bakin & Weinberger 1996)
  - Passive/active (Fritz et al. 2003)
  - Spatial vs. spectral (Rodgers & DeWeese 2014)
  - Moving/quiescent (Schneider et al. 2014)
  - Auditory/visual (Williamson et al. 2015)
  - Attend feature A vs. B (Downer et al. 2017)

What is a behavioral state?



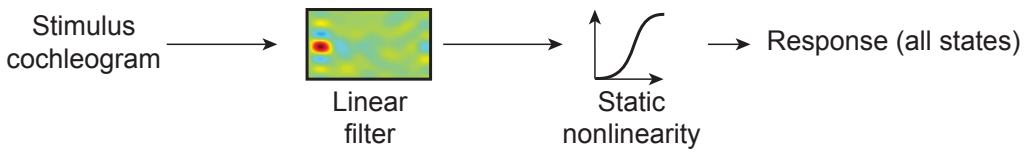
(Hasselmo 1995)

Option 2: Continuous changes in neuromodulatory tone

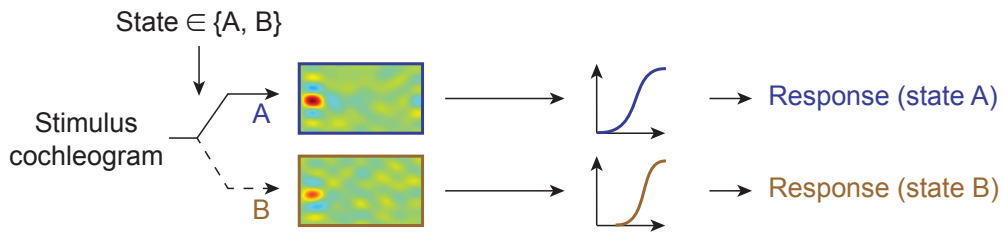
- State = Synaptic weights of auditory filters altered by transient neuromodulation
- Smooth changes in behavioral state
  - Arousal (McGinley et al. 2015)
  - Hippocampal state (Aranov et al. 2017)
- Sensory context
  - SNR of noise (Rabinowitz et al. 2013)
  - Degree of adaptation (Ulanovsky et al. 2003)

Models with discrete and continuous state

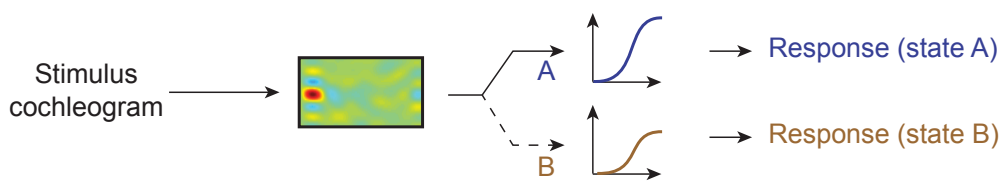
Behavior-independent model



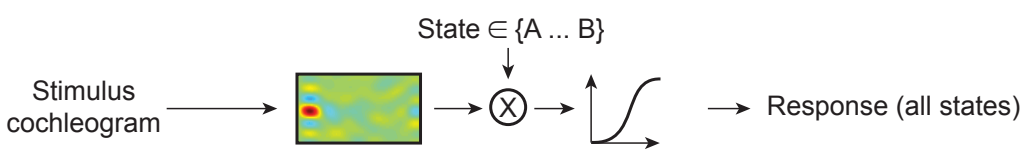
Full discrete model

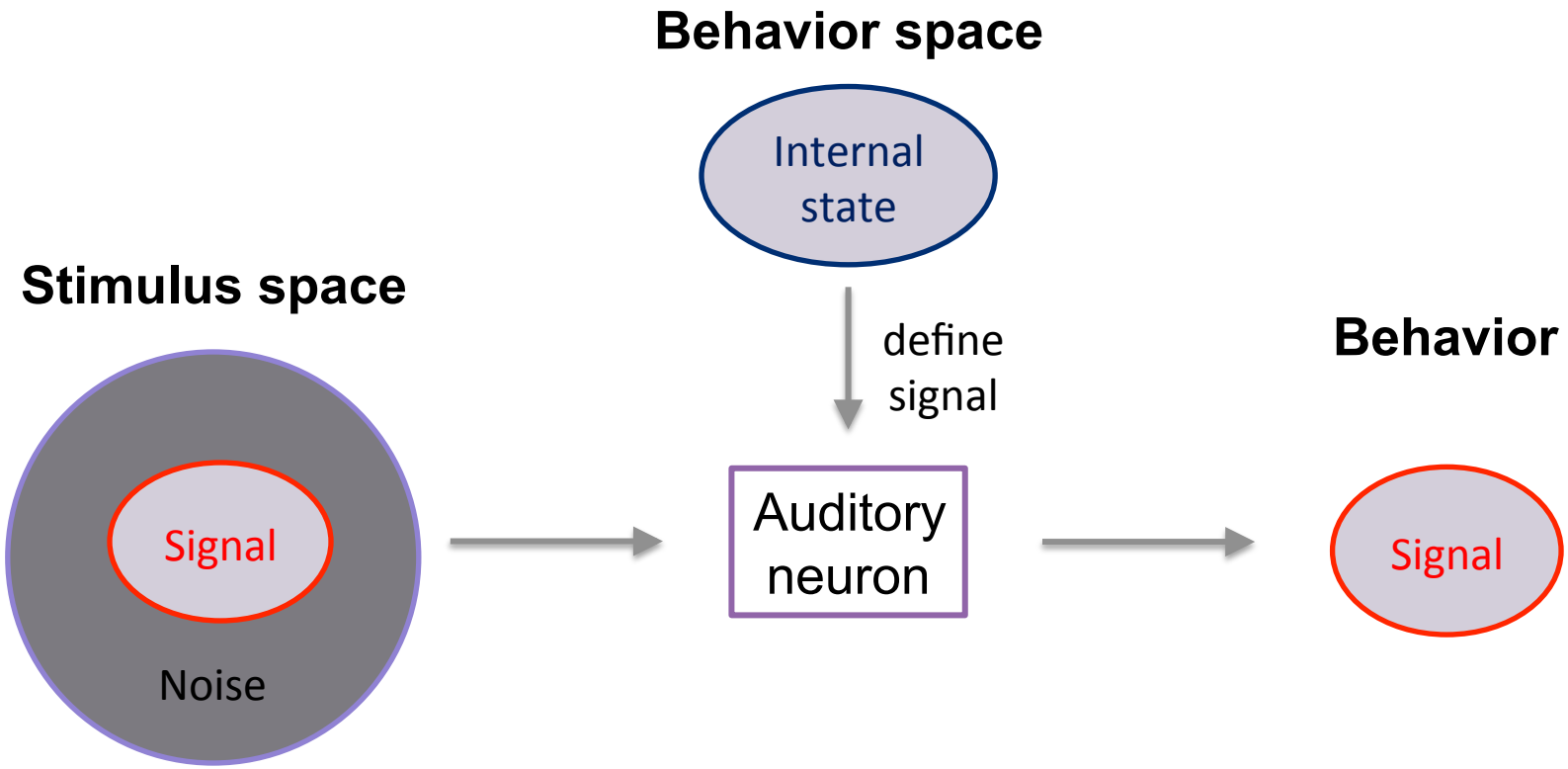


Partial discrete model



Partial continuous model



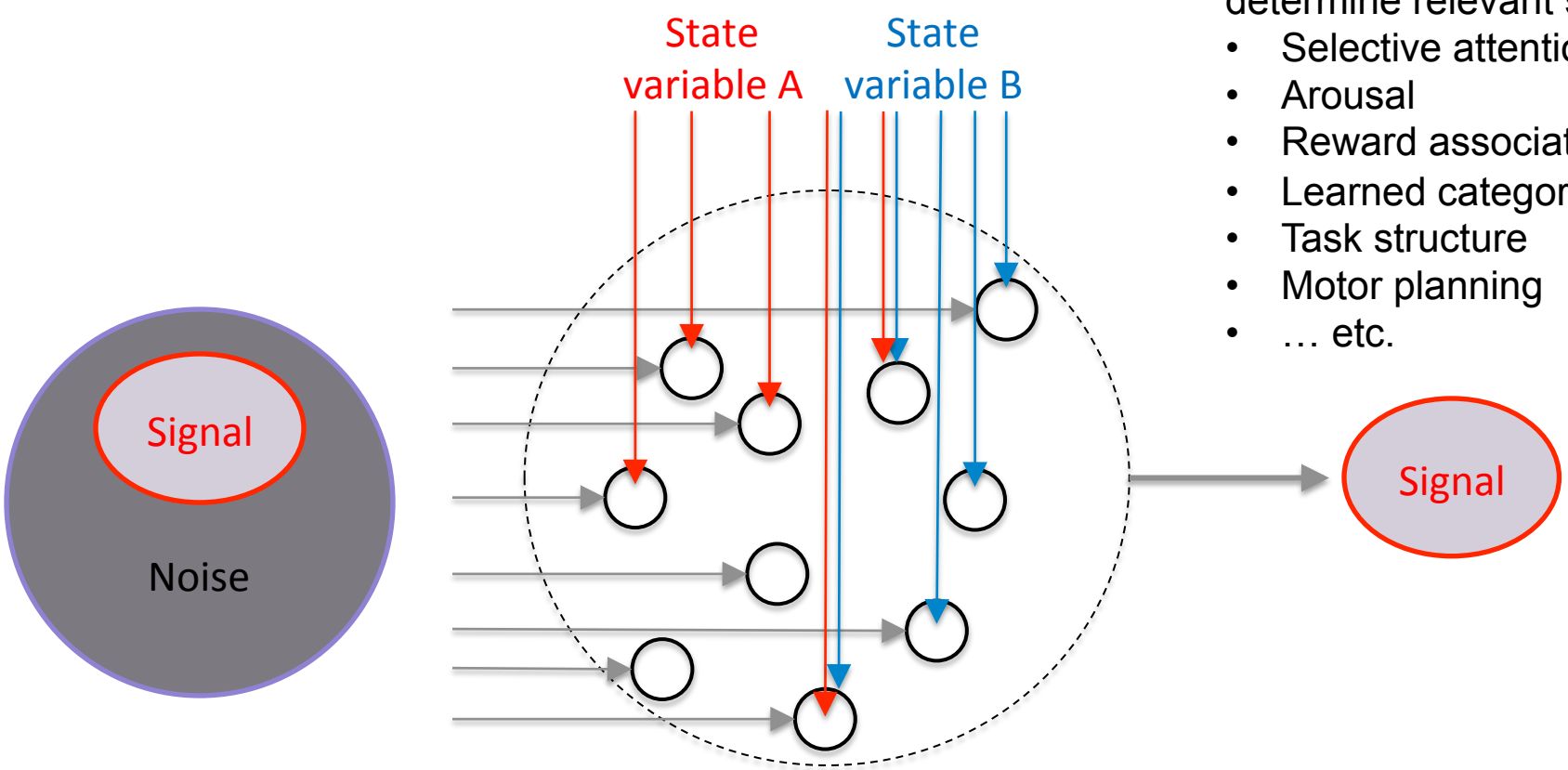


1. Use a systematic approach to develop and validate more accurate encoding models

2. Use discrete state-dependent models to study a processing hierarchy

3. **Integrate continuous state variables into a population coding model**

Internal state shapes sensory representations



Multiple aspects of state determine relevant signal:

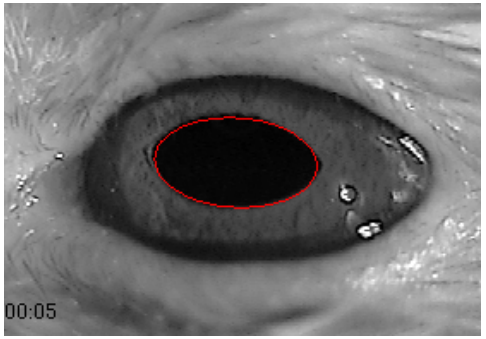
- Selective attention
- Arousal
- Reward associations
- Learned categories
- Task structure
- Motor planning
- … etc.

Pupil diameter as a continuous index of arousal

- The pupil regulates the luminance and focus of images on the retina. (Beatty and Lucero-Wagner 2000)

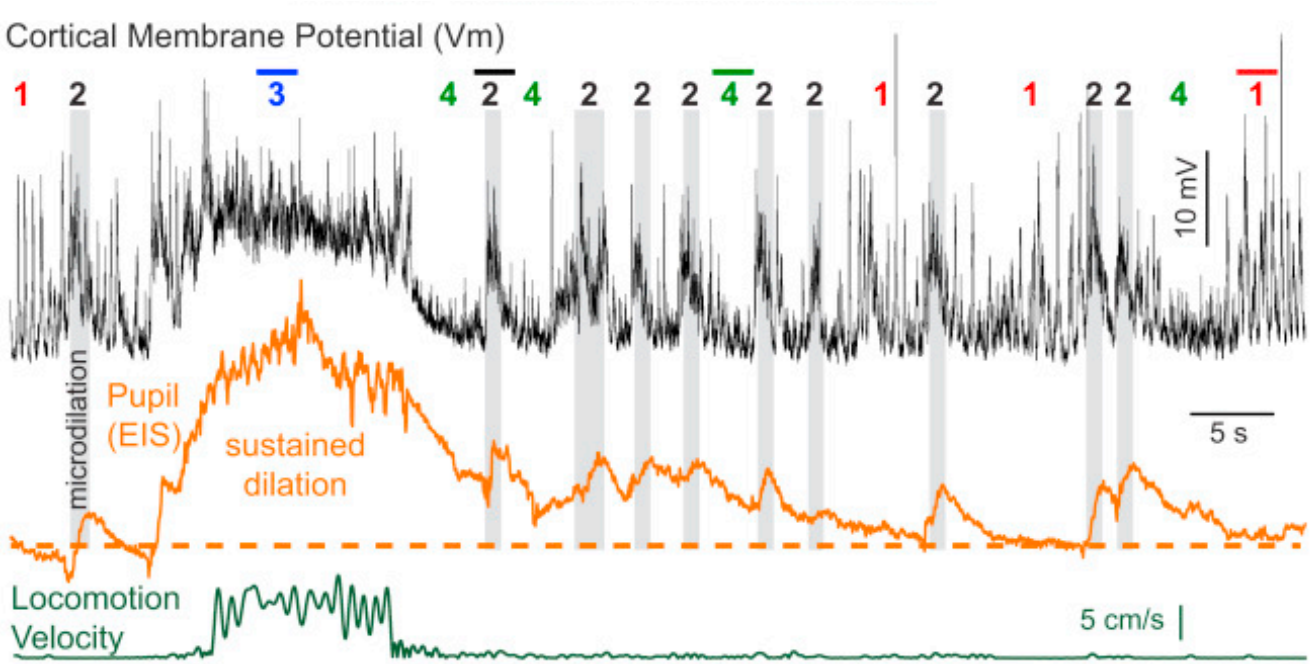
- In humans, pupil size also reflects cognitive processes such as emotional arousal and mental effort. (Hess and Polt Science 1960; Laeng et al Persp. Psych Sci. 2012)

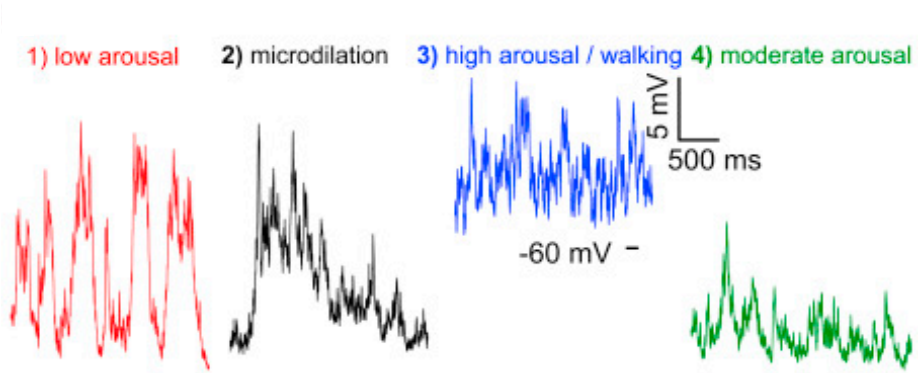
- Pupil size is correlated with changes in spontaneous and evoked activity in sensory cortex and thalamus, oscillatory activity in hippocampus, and behavioral performance. (Reimer, et al Neuron 2014; Vinck, et al Neuron 2015; McGinley, et al Neuron 2015)



Ferret pupil (constant light, ~20x speed)

Pupil diameter and waking state





Pupil size tracks spontaneous membrane potential dynamics in mouse auditory cortex.

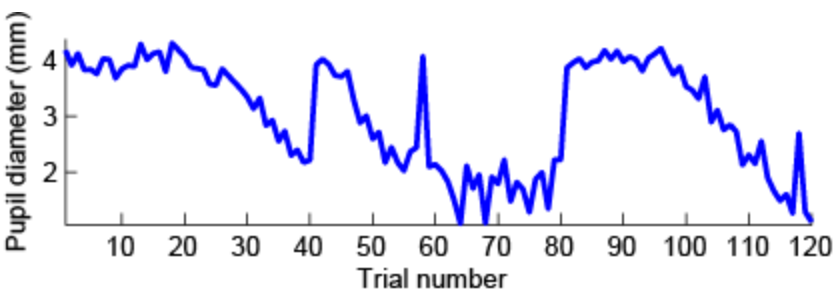
McGinley et al. 2015

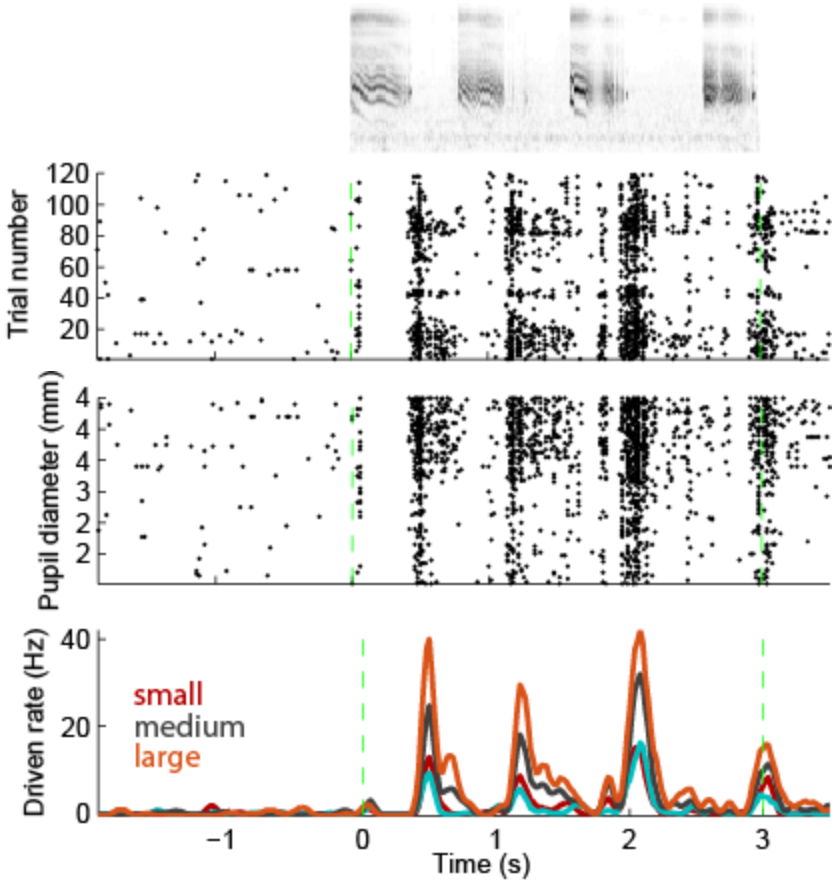
Pupil-indexed around modulates sound-evoked activity

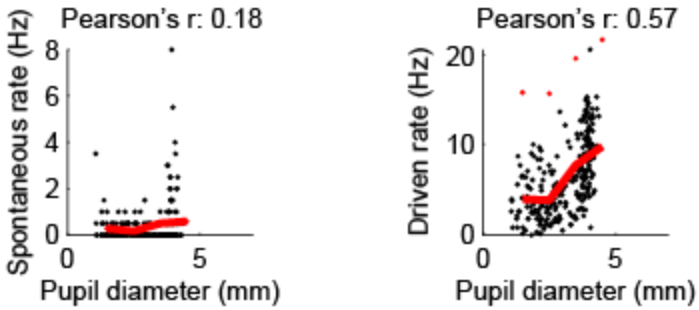
Spike raster sorted by time

Spike raster sorted by pupil size

PSTH per pupil size







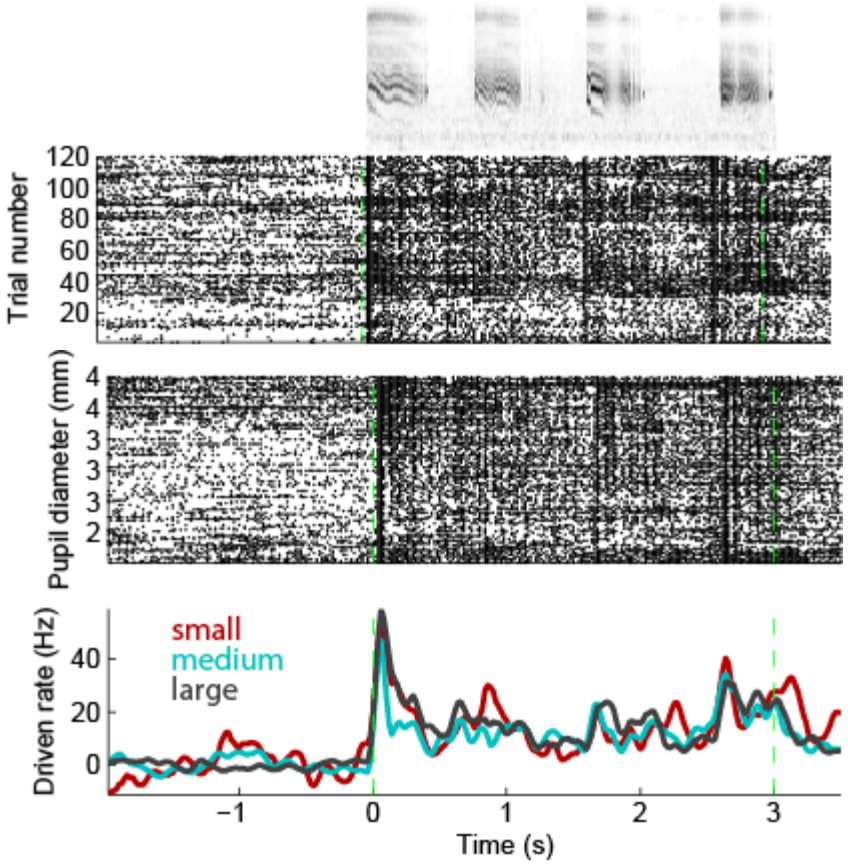
McGinley et al 2015

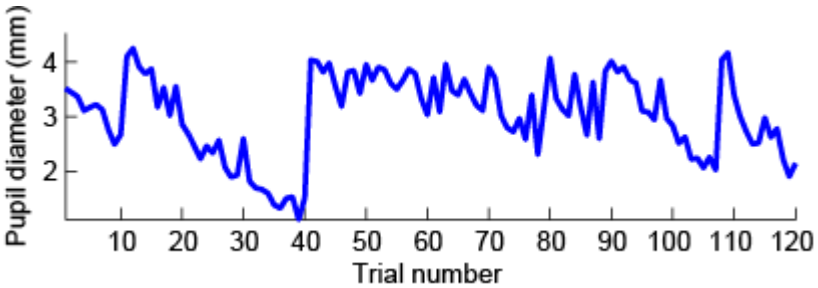
Some neurons show non-monotonic pupil effects

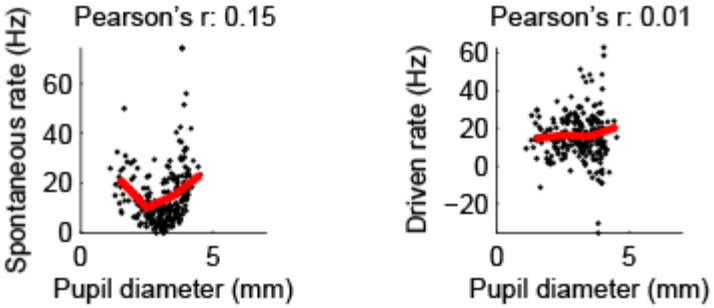
Spike raster sorted by time

Spike raster sorted by pupil size

PSTH per pupil size







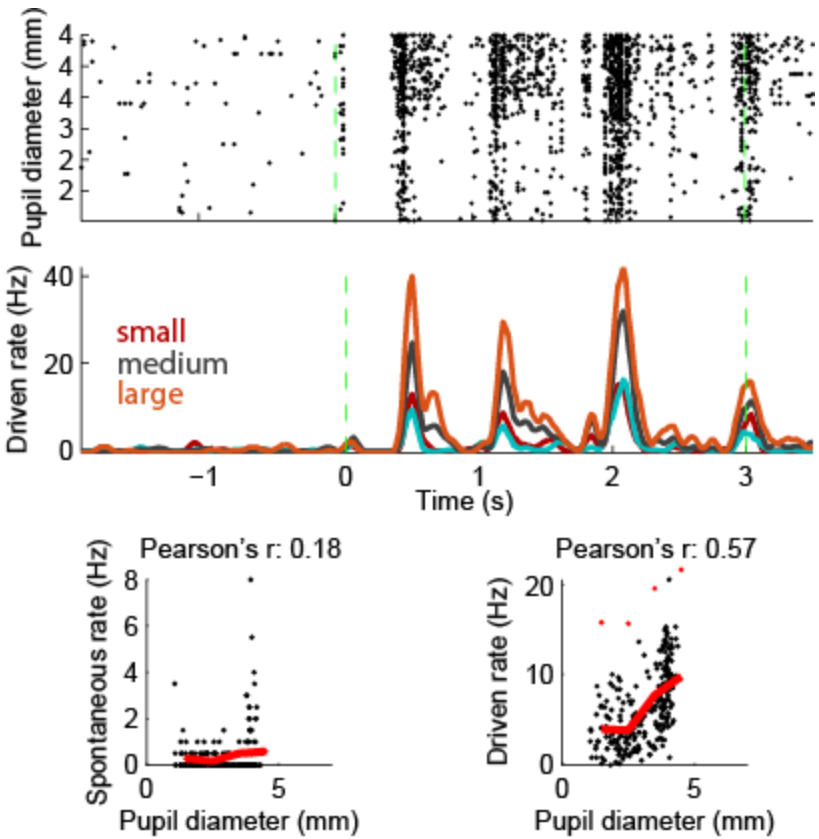
Linear regression model for pupil effects

$P(t)$: Pupil diameter, continuous variable

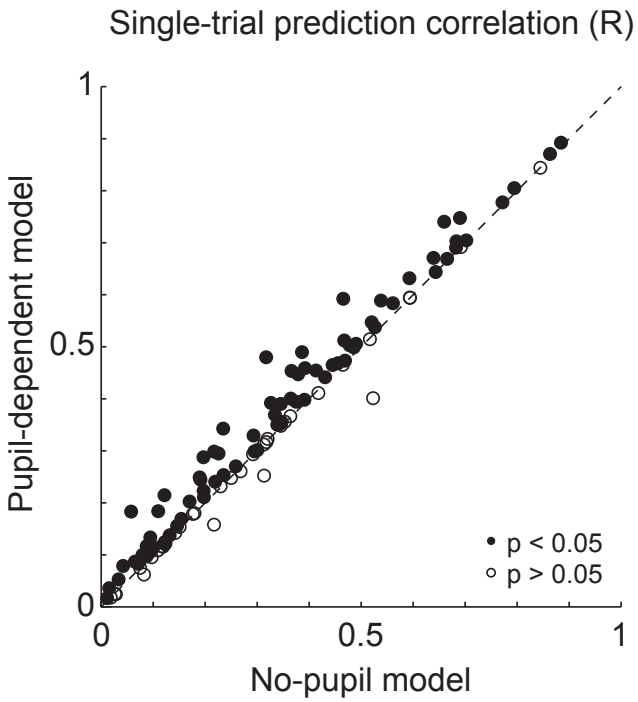
$$r(t) = r_0(t) + gP(t) + dP(t)$$

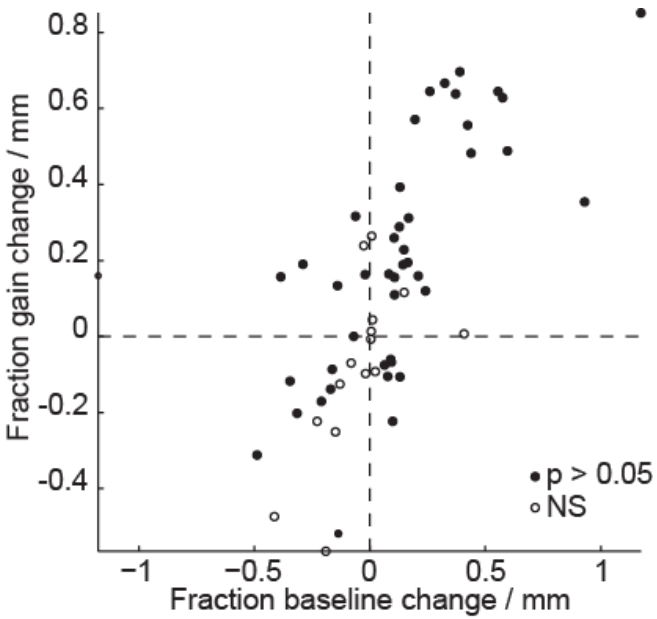
Gain: scales evoked response

Baseline: scales spontaneous activity



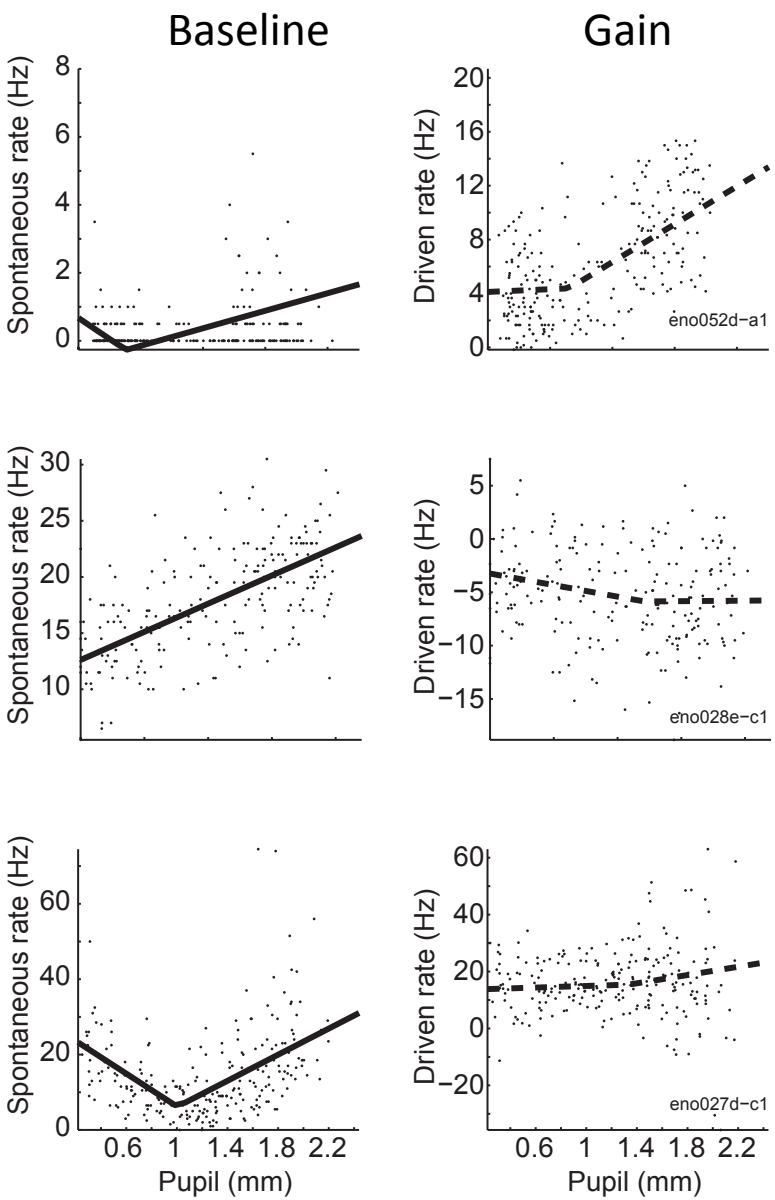
Linear regression model for pupil effects

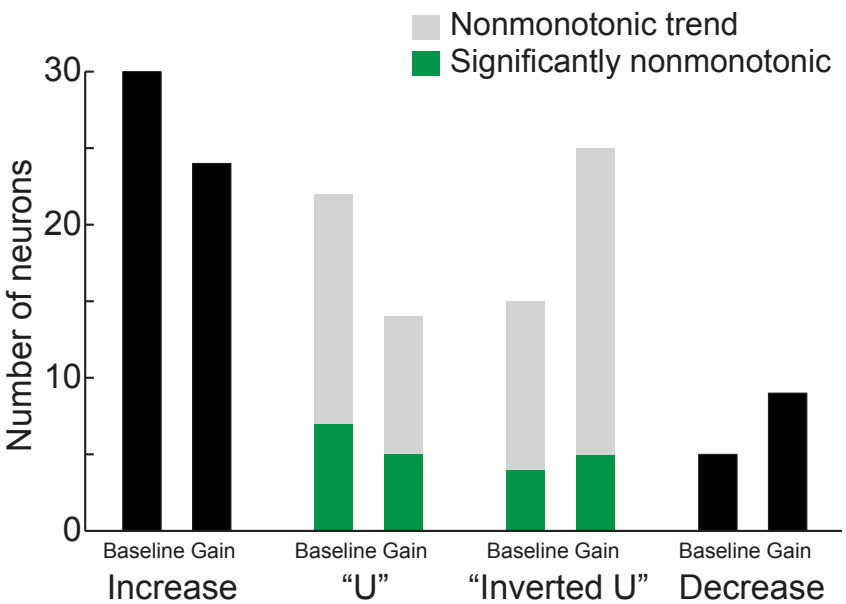




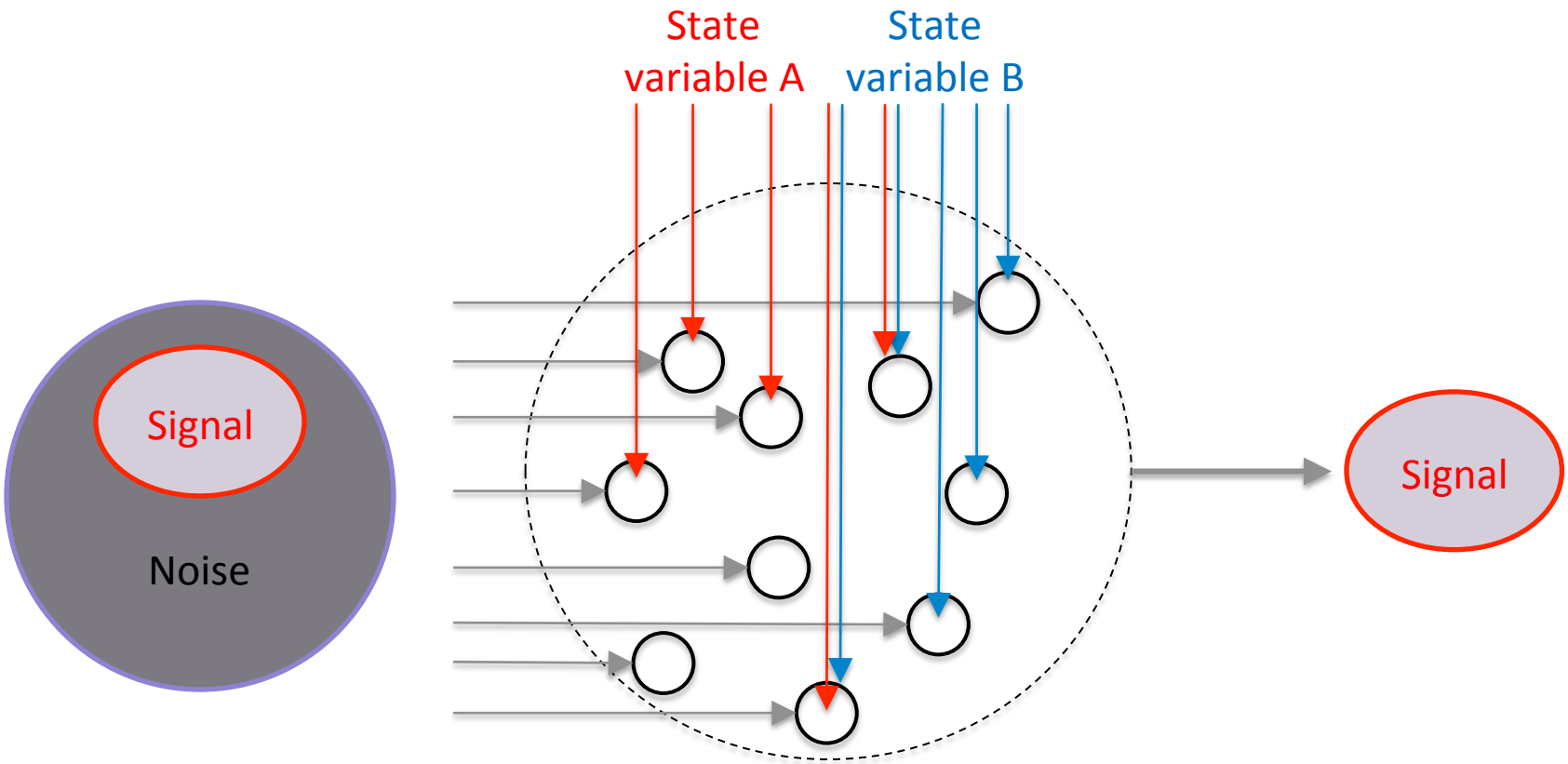
$$r(t)=r\downarrow 0\ (t)gP(t)+dP(t)$$

Diverse effects of pupil diameter on A1 activity



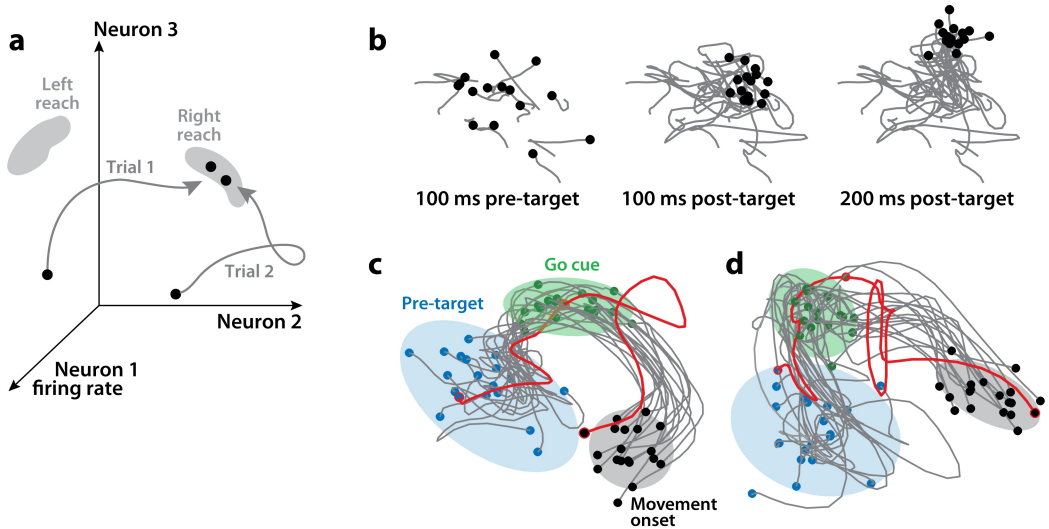


Internal state shapes sensory representations



State-space models

Dimensionality reduction reveals latent variables in motor cortex populations:

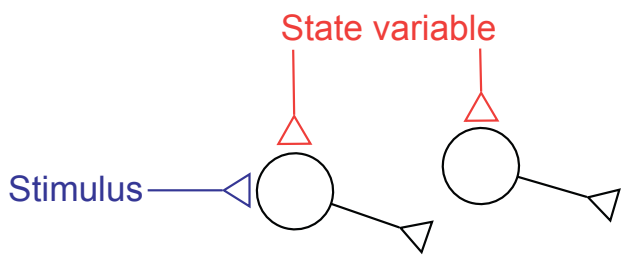


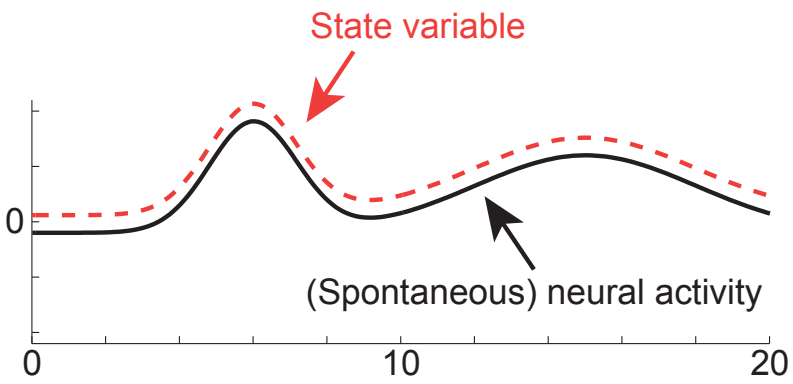
Shenoy et al 2013

See also Pachitariu et al 2013 for sensory cortex version.

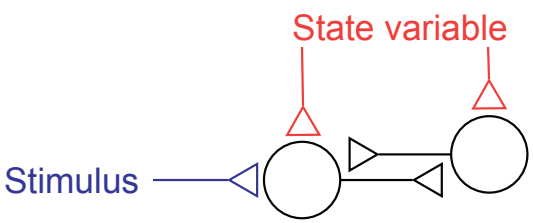
Timescales of modulation

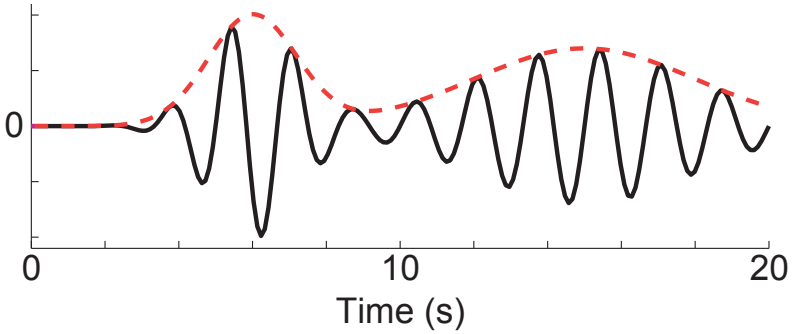
State-dependent **activation**





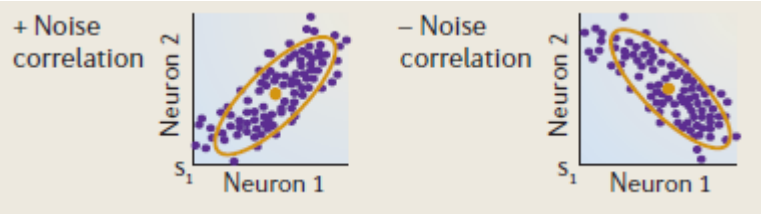
State-dependent **covariance**

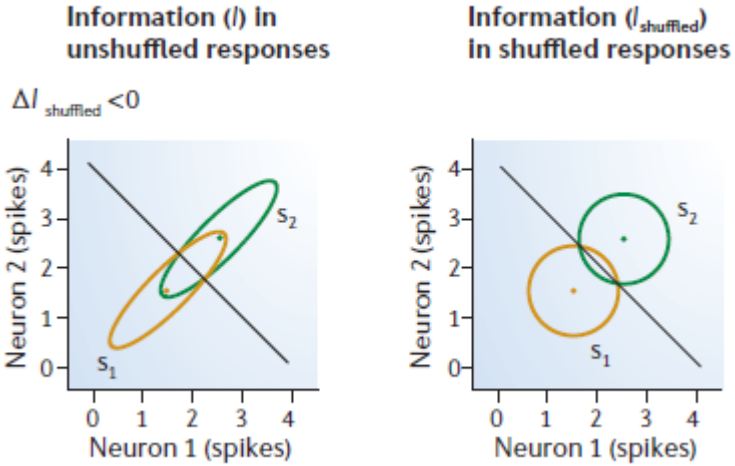




Correlated noise and population coding

- Correlated noise is co-activation of two or more neurons, independent of a stimulus.
- Noise correlations are typically thought to interfere with accurate population coding.
- Classically attributed to lateral coupling between neurons.
- … could these correlations fluctuate under the influence of a top-down signal?

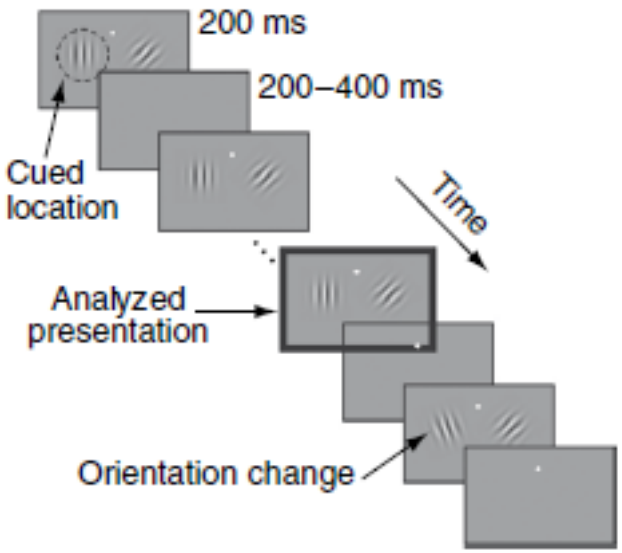




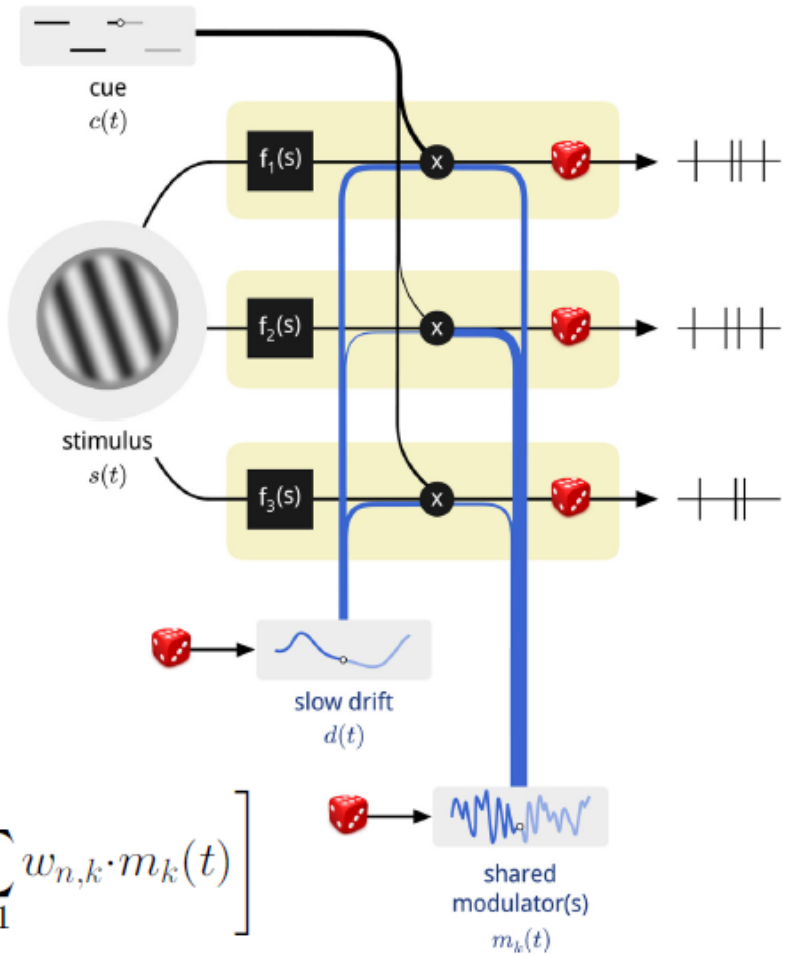
Averbeck et al. 2006

Internal state reflected by shared modulators?

Visual attention task



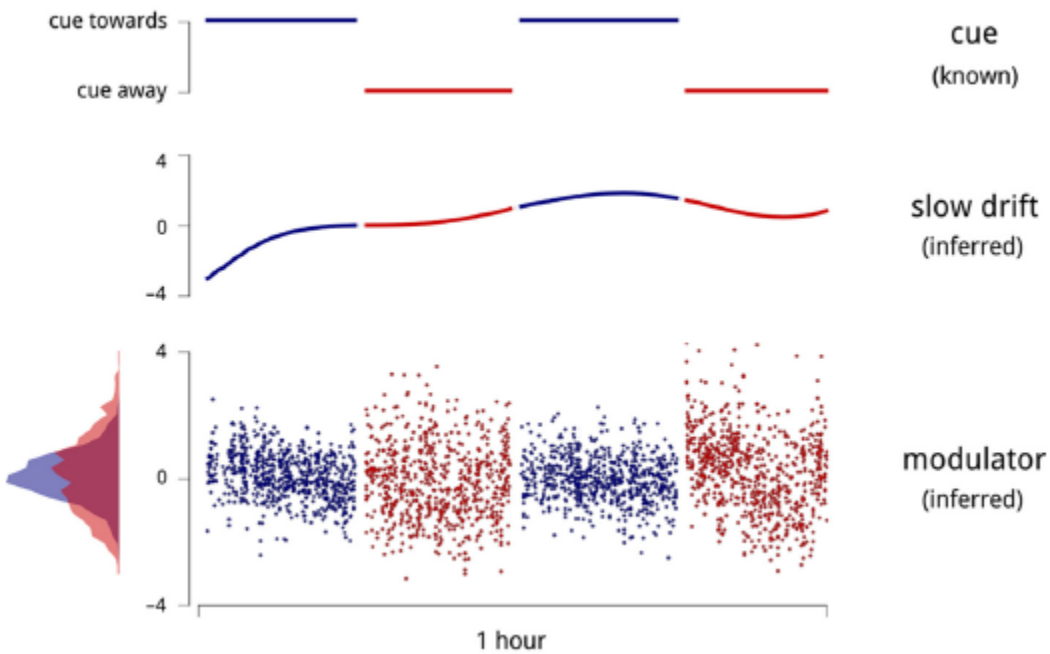
Model simultaneous V4 spiking



$$r_n(t) = f_n(s(t)) \cdot \exp\left[u_n \cdot c(t) + v_n \cdot d(t) + \sum_{k=1}^{K} w_{n,k} \cdot m_k(t)\right]$$

Cohen & Maunsell 2009; Rabinowitz et al. 2015

Visual selective attention impacts shared modulators

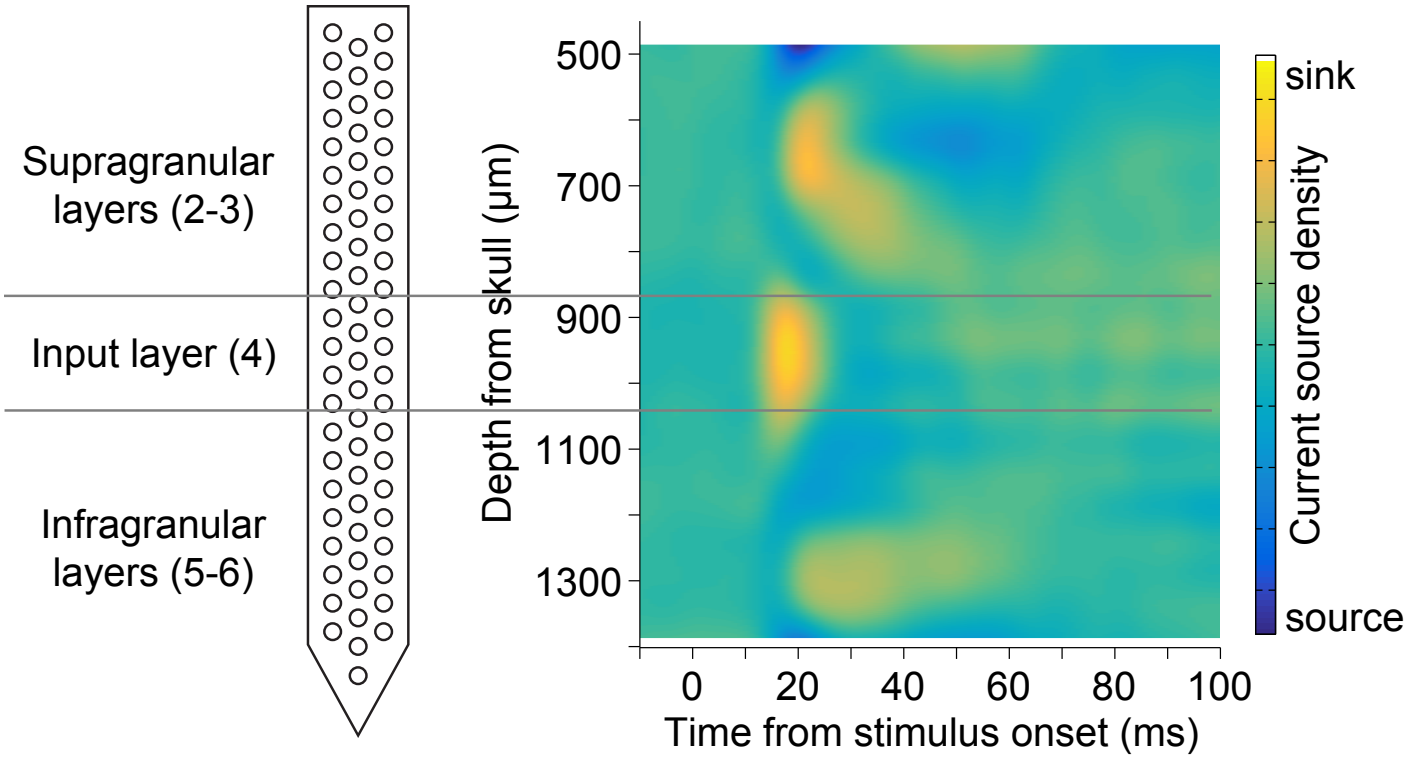


Global state (arousal?)

Task-modulated variance

Rabinowitz et al. 2015

Depth arrays record activity across cortical laminae

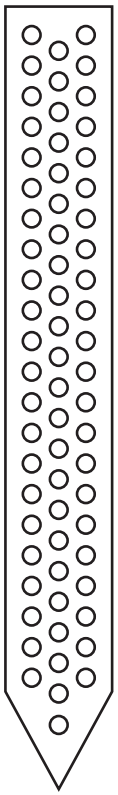


64- to 256-channel arrays (Masmanidis lab, UCLA) permit simultaneous recording of single-unit data across identified cortical laminae.

Lakatos et al. 2007; Shobe et al. 2015

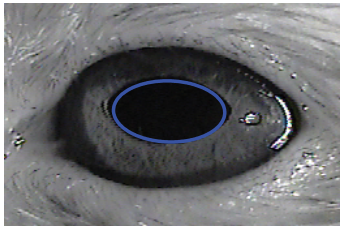
Depth array recordings

Record A1

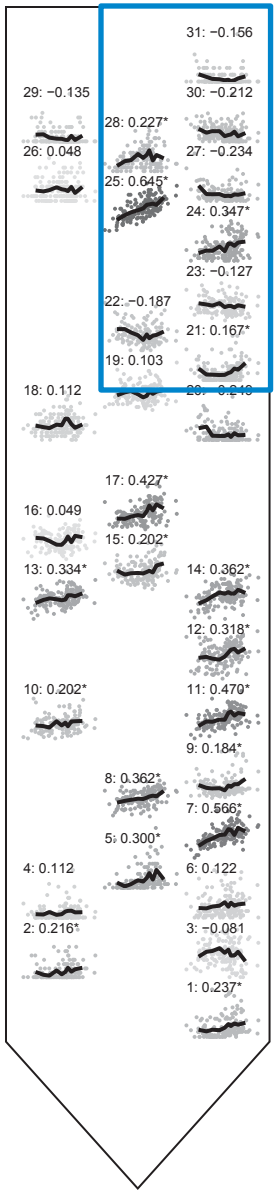


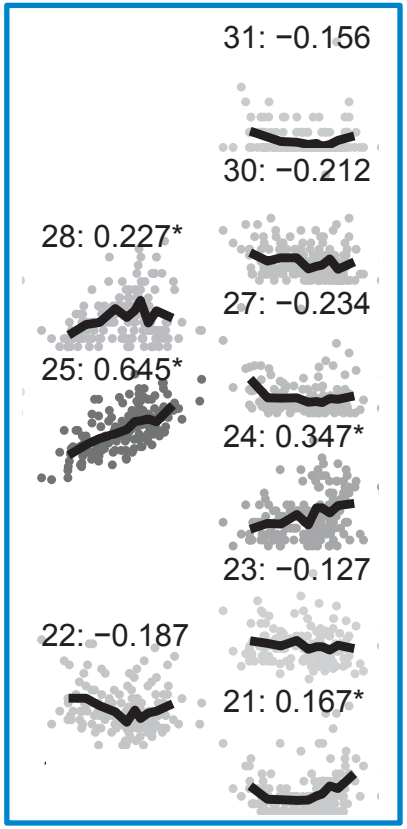
Present vocalizations

Measure pupil



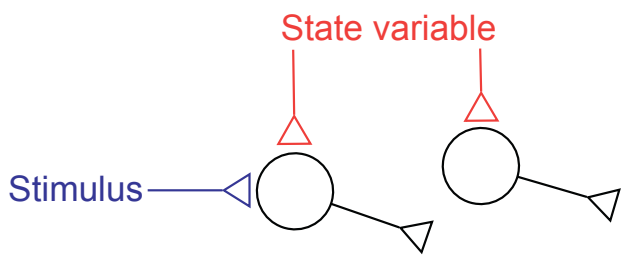
Pupil vs. spontaneous rate:

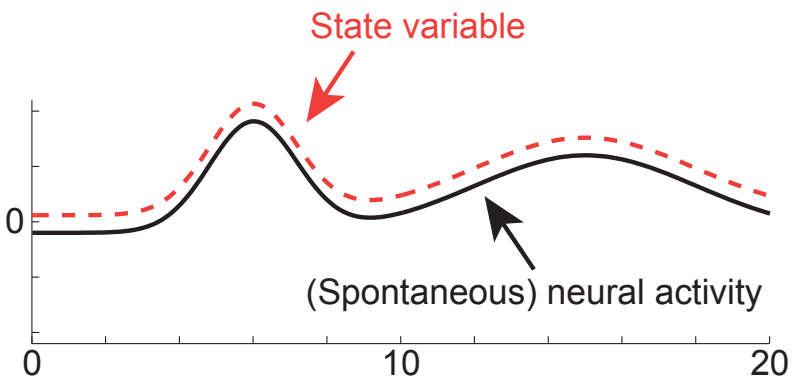




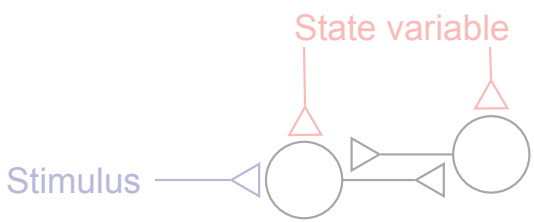
Timescales of modulation

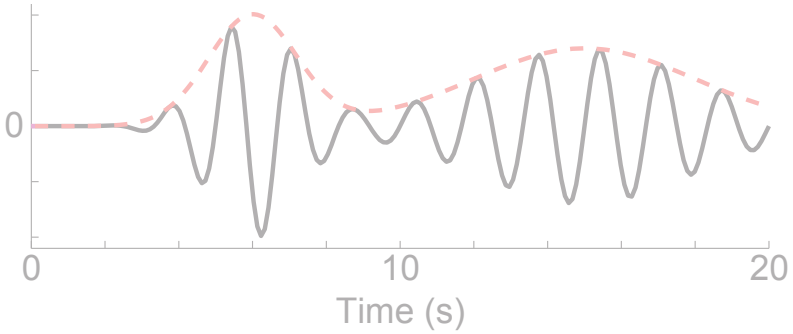
State-dependent **activation**



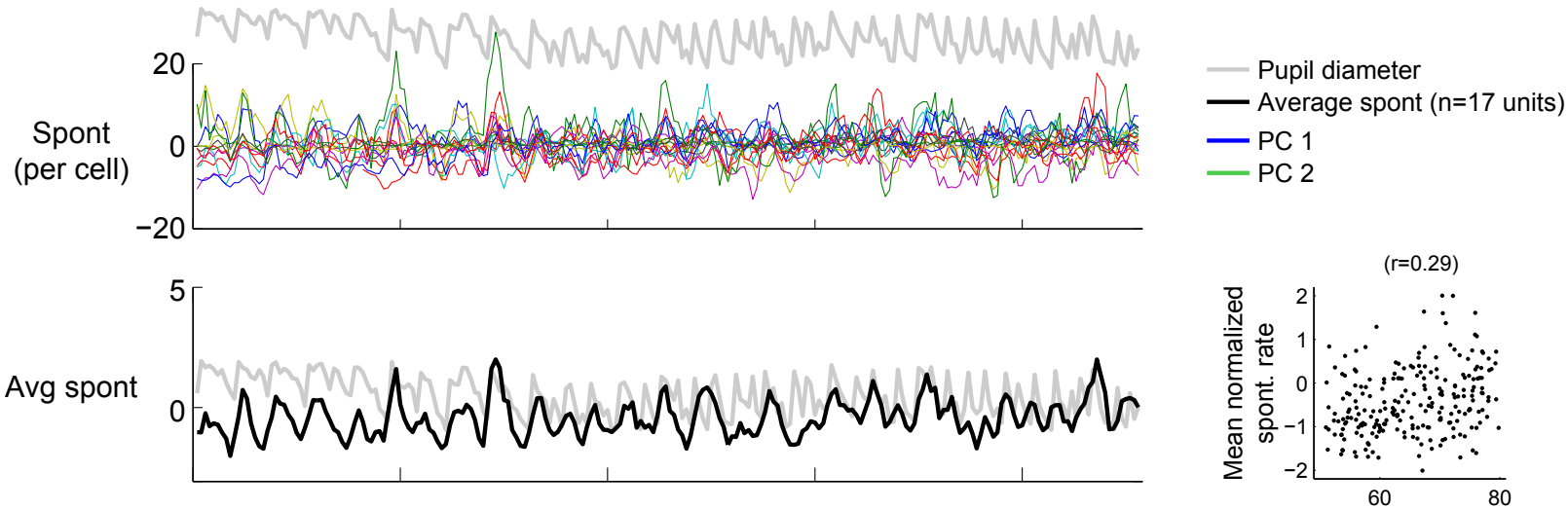


State-dependent **covariance**

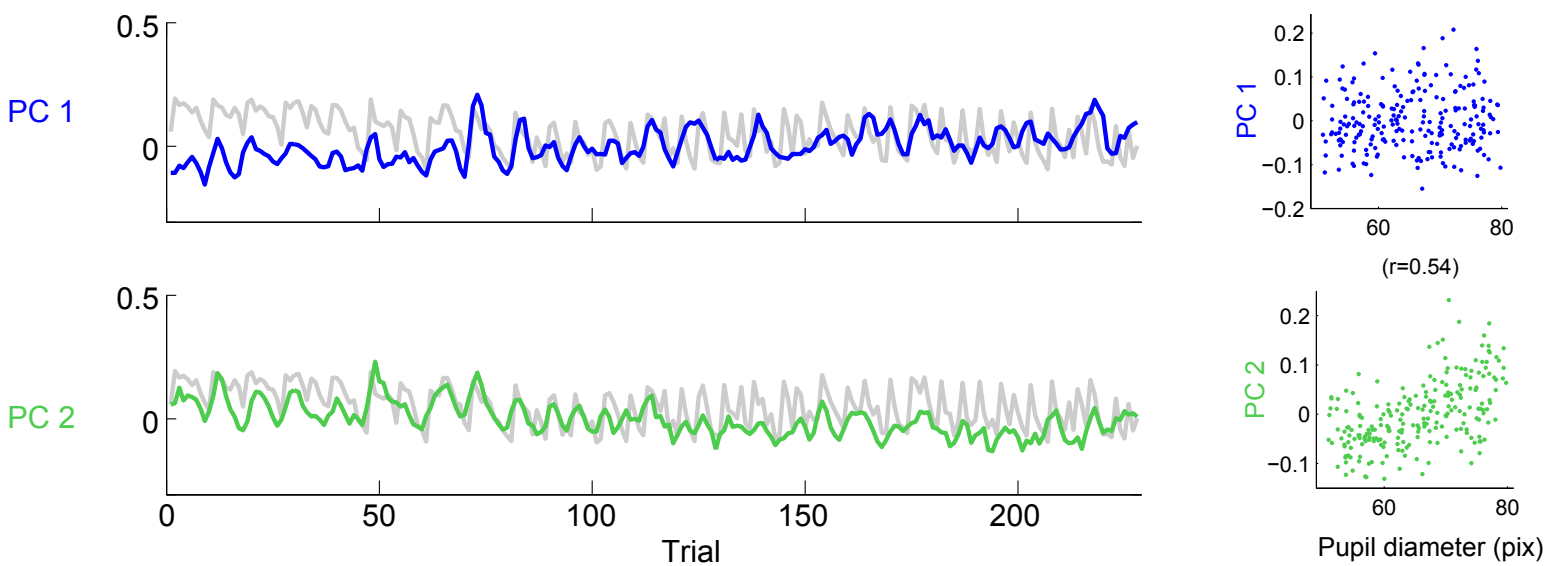




Pupil reflects a latent state variable

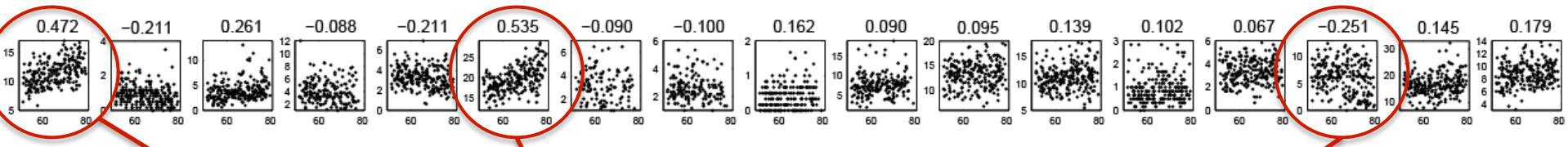


Principle components of population spontaneous activity (*independent* of pupil)

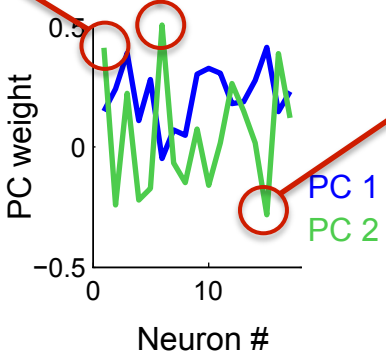


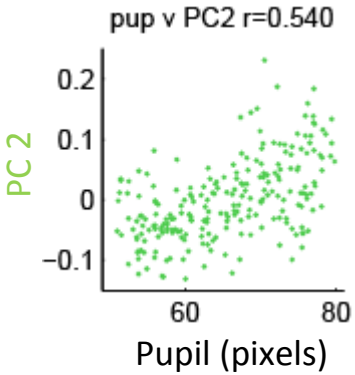
Individual neural contributions vary

Spontaneous rate vs. pupil diameter



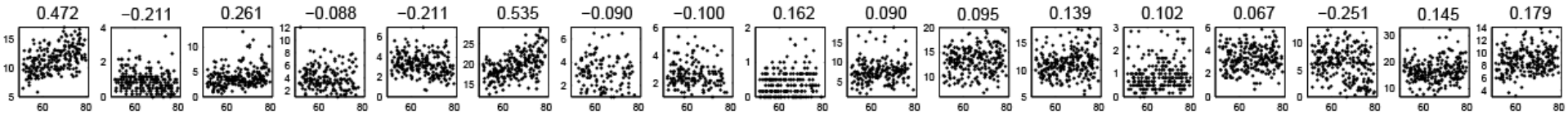
PCA of population spontaneous activity



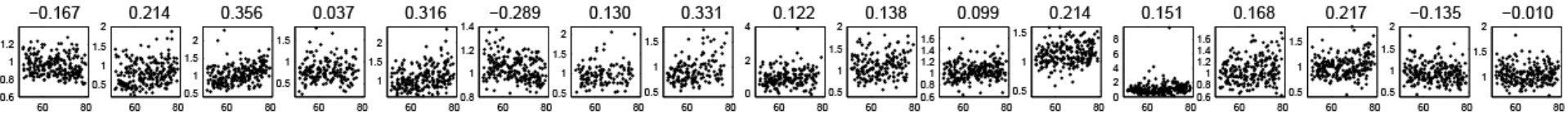


Gain versus spontaneous pupil effects differ

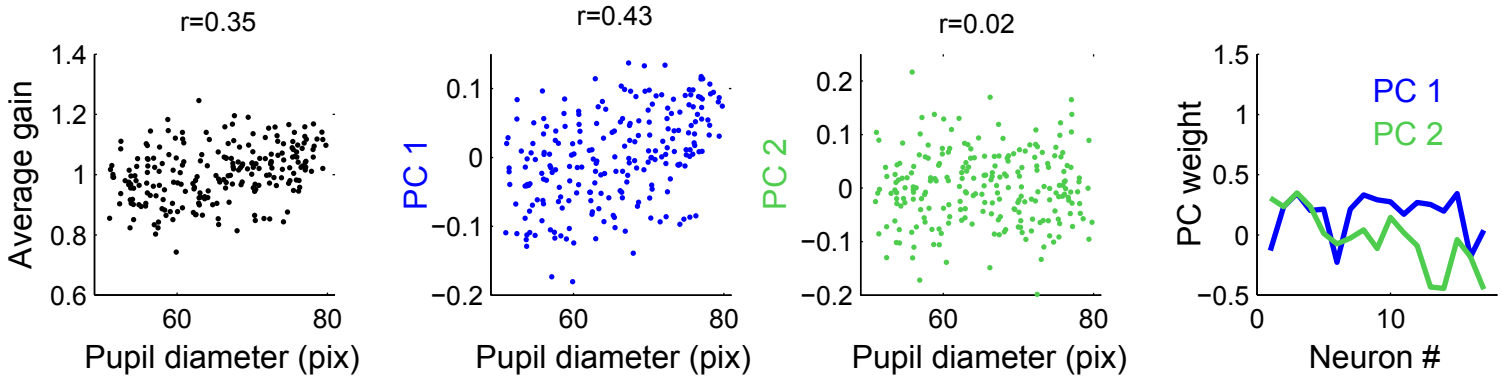
Spontaneous rate vs. pupil diameter



Response gain vs. pupil diameter

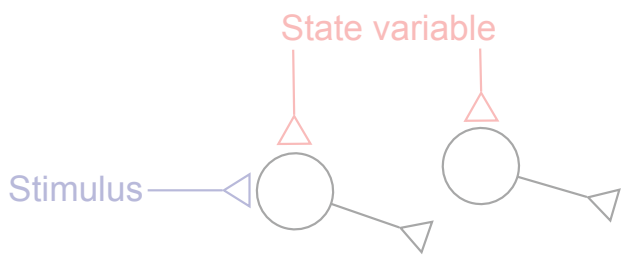


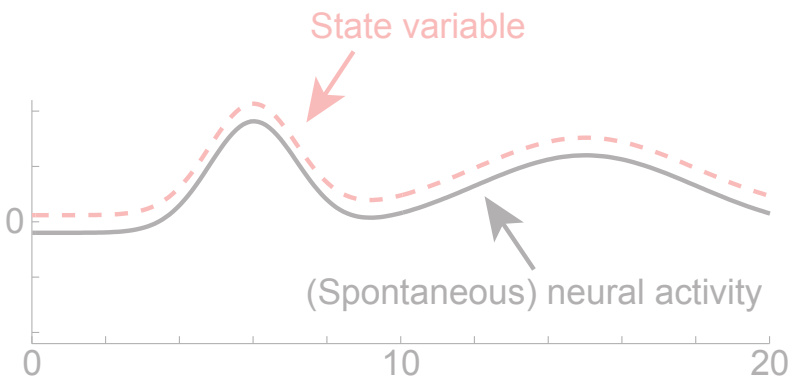
PCA of population gain



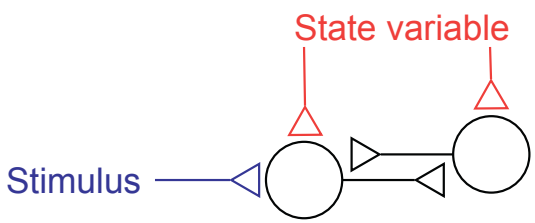
Timescales of modulation

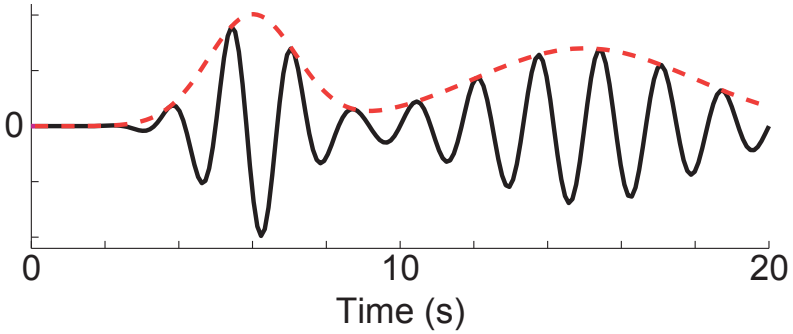
State-dependent **activation**



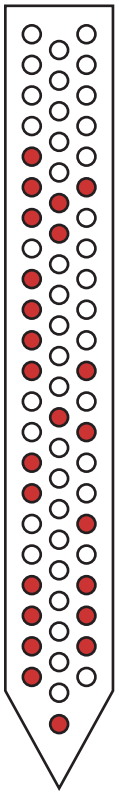


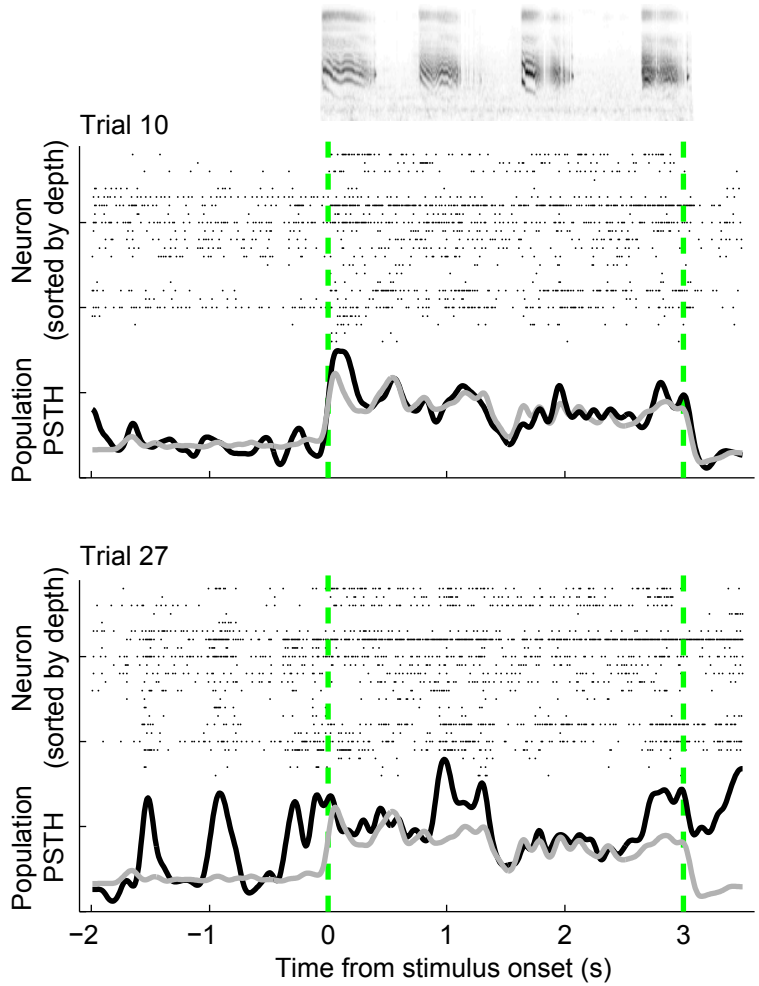
State-dependent **covariance**





Population responses vary across repeated stimuli





Average population PSTH

Single-trial population PSTH

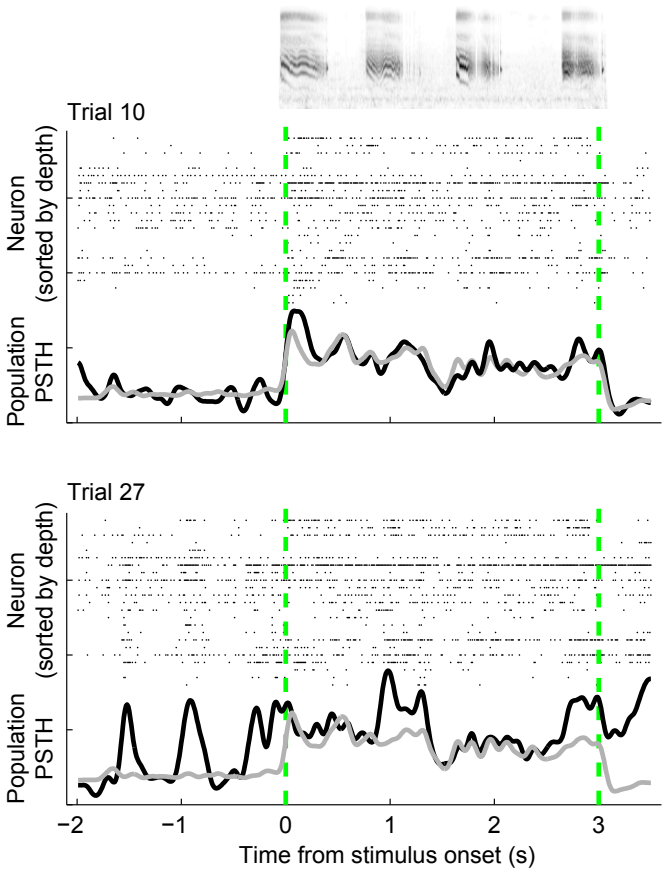
$$r_i(t) = r_i(t) + \sum_{k \neq i} g_i(k)$$

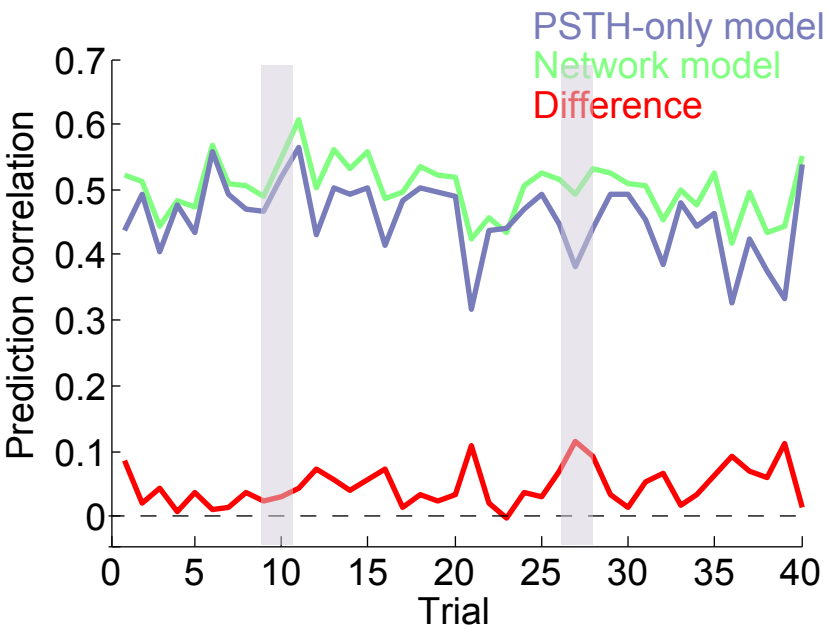
Average sound-evoked response, "optimal" encoding model

Network state model based on activity of neighboring neurons

Pillow et al. 2008; Stevenson et al. 2012

Coherent fluctuations explain trial-to-trial variability





cc(PSTH-only, difference) = −0.71

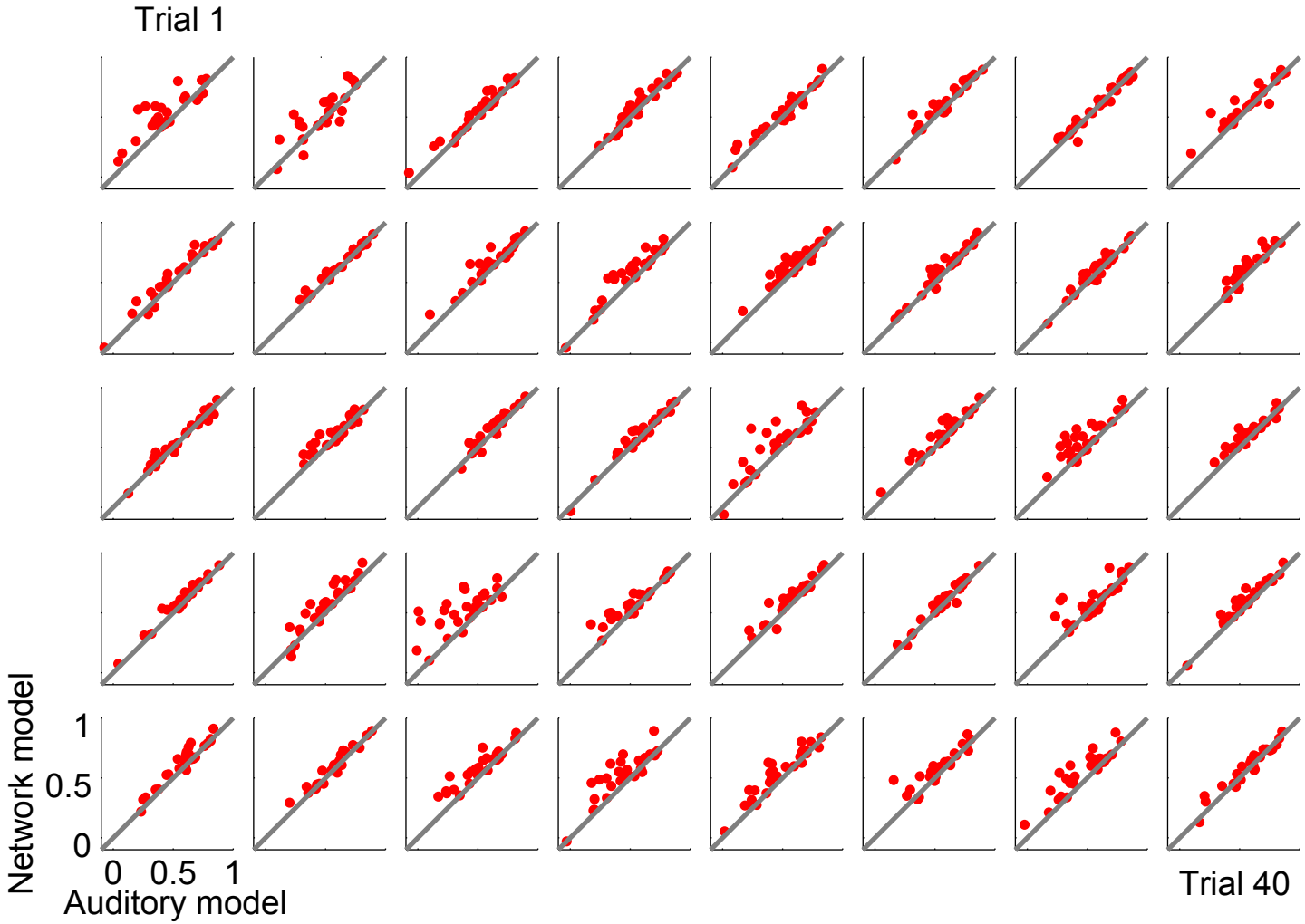
PSTH-only model

$r_i(t) = r_i(t)$

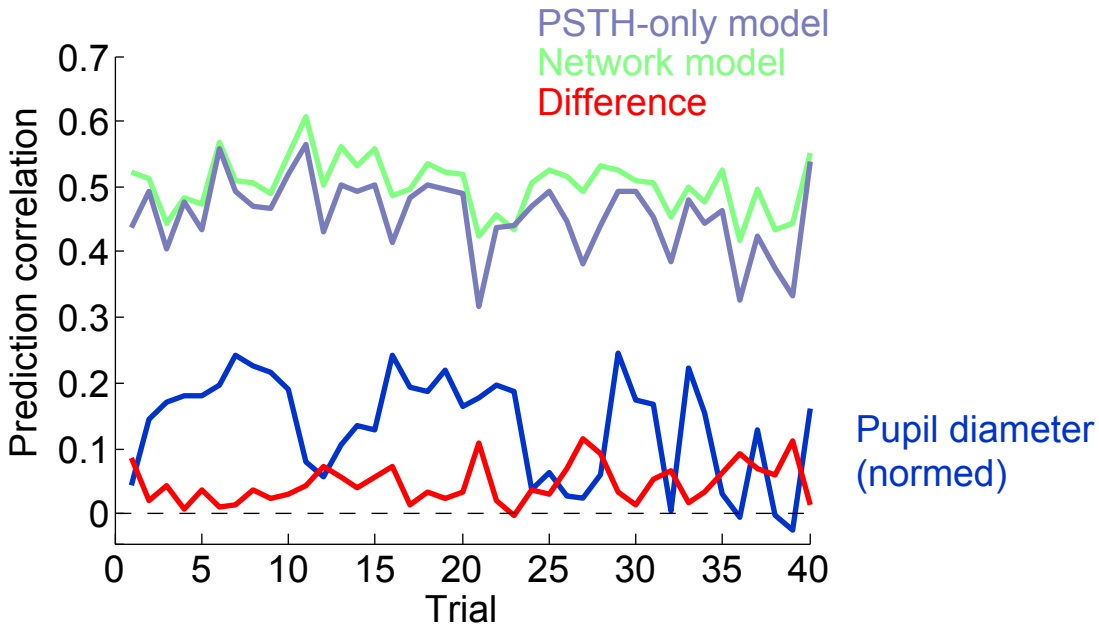
Network model

$r_i(t) = r_i(t) + \sum_{k \neq i} g_i($

Coherent fluctuations explain trial-to-trial variability



Network model performance correlated with arousal



cc(PSTH-only, difference) = −0.71

cc(pupil, difference) = −0.65

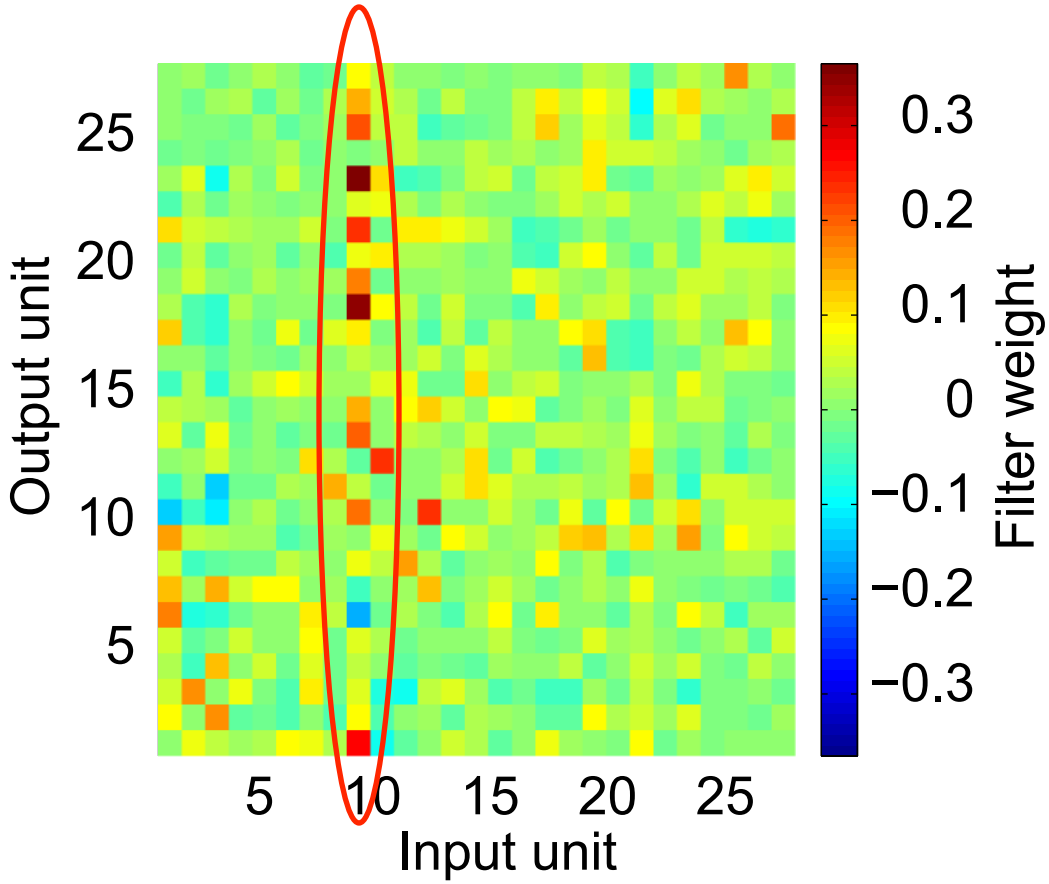
PSTH-only model

$r_i(t) = r_i(t)$

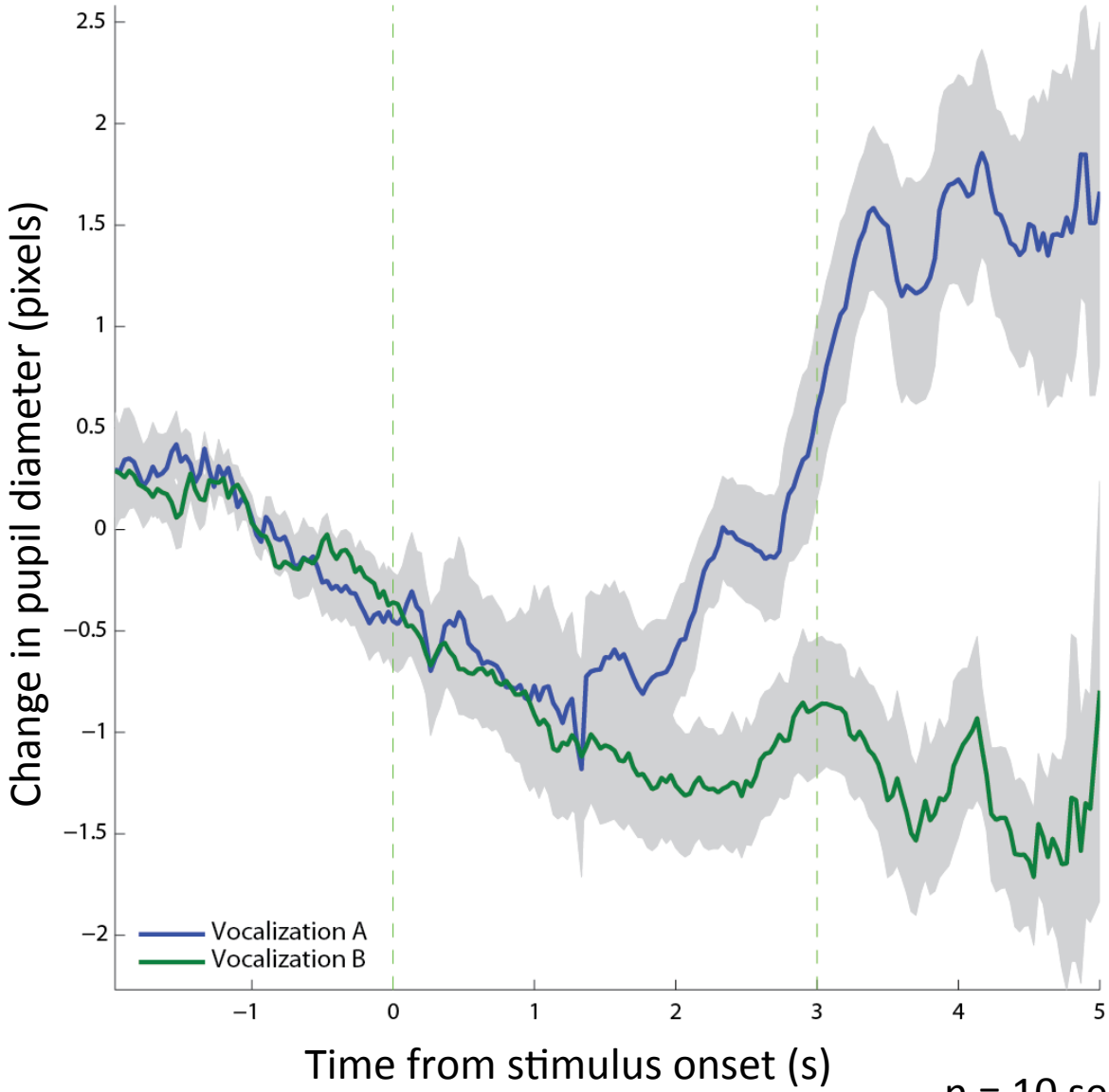
Network model

$r_i(t) = r_i(t) + \sum_{k \neq i} g_i($

Network model weights reveal master neurons?



Sound-evoked pupillary response

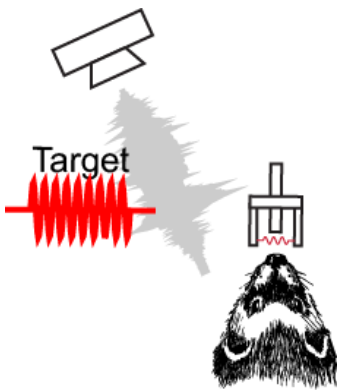


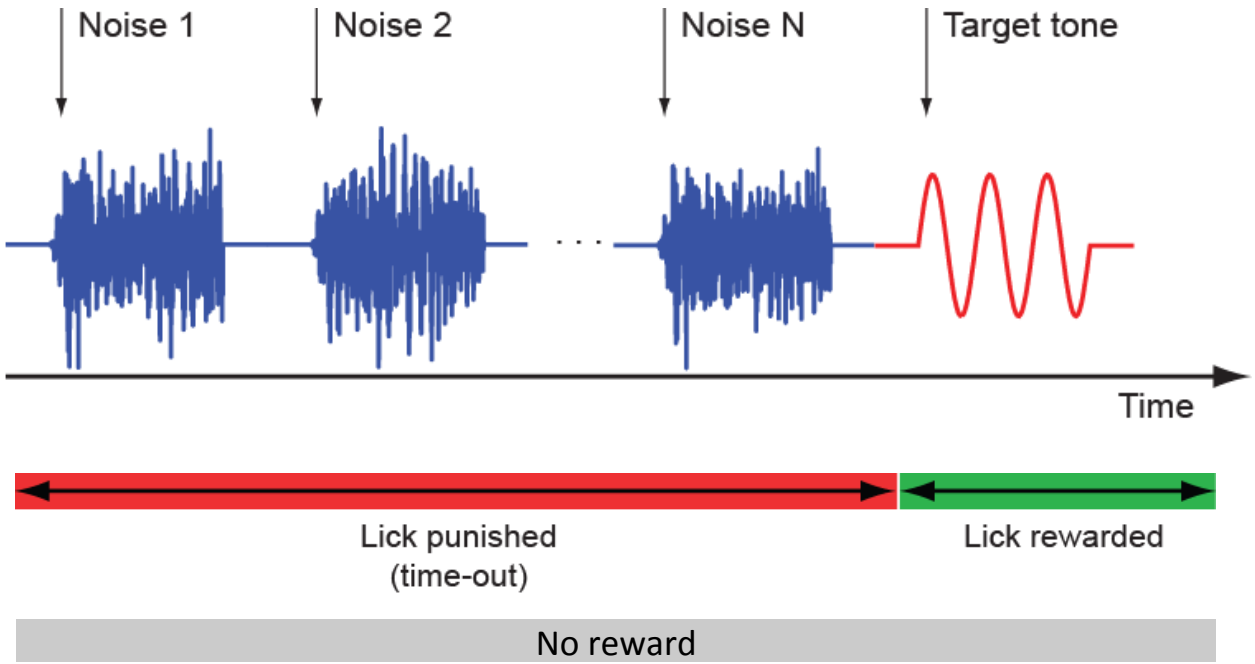
Vocalization A

Vocalization B

n = 10 sessions, ~1000 repetitions

Tone detection task





Two discrete states

Approach behavior

Passive listening

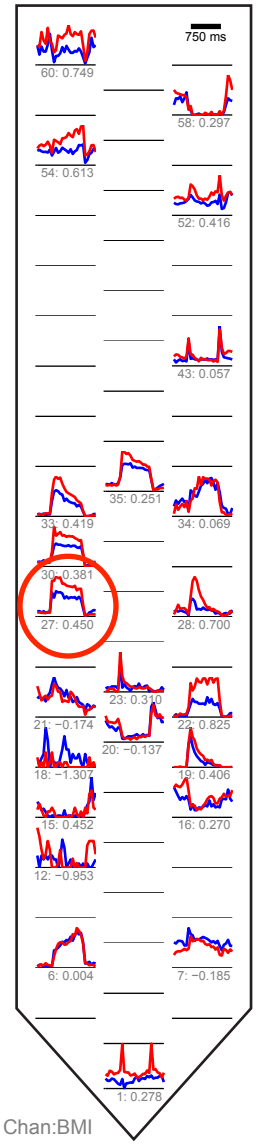
Methods: Go/no-go tone detection behavior. Record single-unit activity during behavior and during passive presentation of task stimuli. Compare evoked activity between behavior and passive listening.
Reference: Broadband noise (TORCs), 0.75-1.5 sec.
Target: Pure tone, level and duration matched to reference noise.

(David et al., 2012)

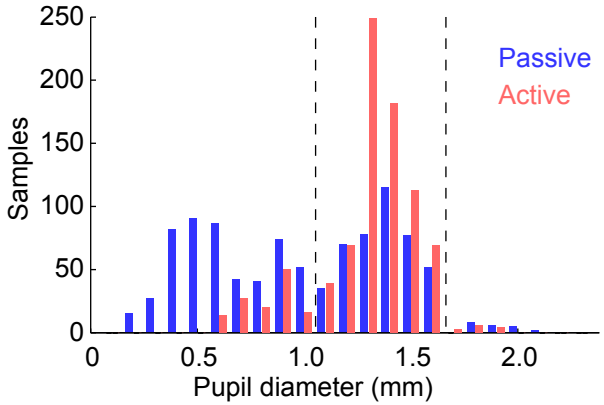
Array recordings during behavior

Noise PSTH response

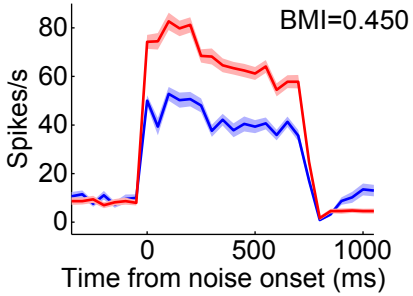
Active vs. passive



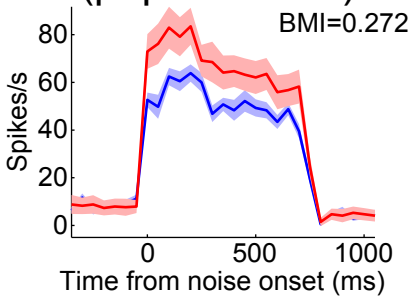
Pupil per behavior condition



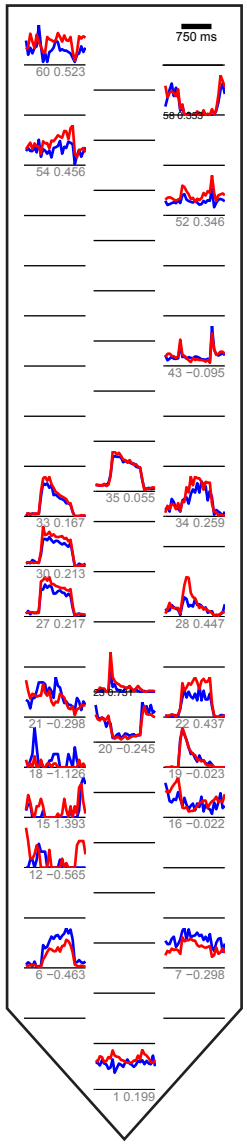
Active vs. passive



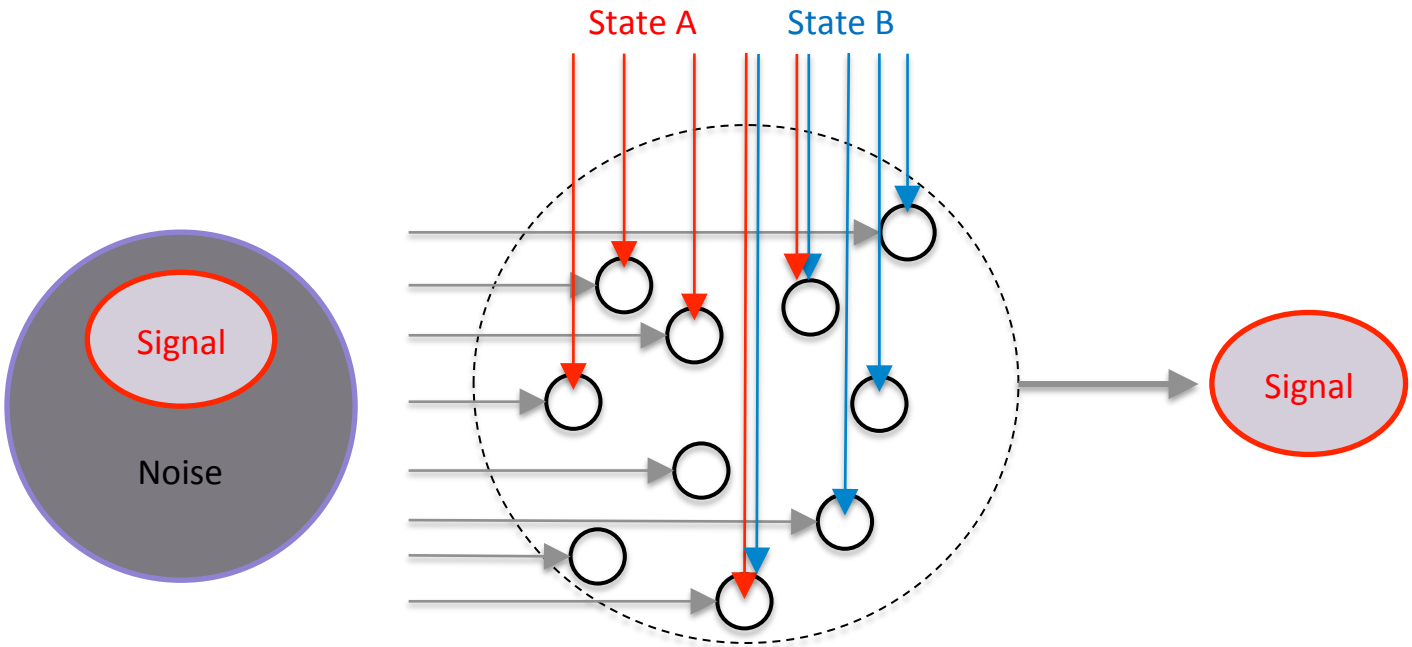
Active vs. passive
(pupil normed)



Active vs. passive
(pupil normed)



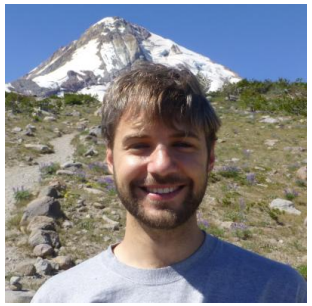
Internal state shapes sensory representations



- Activity of most neurons in A1 are modulated by pupil diameter but with varying sign and monotonicity.
- Slow state changes can modulate faster covariance between neurons.
- Interactions between state variables can reveal circuit properties within neural populations.

Thanks!

Ivar Thorson



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