Neural population state and auditory encoding

Stephen David
Oregon Health & Science University
July 12, 2017

davids@ohsu.edu
https://hearingbrain.org/
An aside on clustering...
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

**Stimulus space**

- Signal
- Noise

**Behavior space**

- Internal state
  - define signal

**Behavior**

- Signal
State-dependent encoding models

Behavior-independent model

Stimulus cochleogram → Linear filter → Static nonlinearity → Response (all states)

Behavior-dependent model

State ∈ \{A, B\}

Stimulus cochleogram → Response (state A)

Stimulus cochleogram → Response (state B)
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?

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?

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**

Stimulus cochleogram → Linear filter → Static nonlinearity → Response (all states)

**Full discrete model**

State ∈ \{A, B\}

Stimulus cochleogram → A → Response (state A)

Stimulus cochleogram → B → Response (state B)

**Partial discrete model**

Stimulus cochleogram → A → Response (state A)

Stimulus cochleogram → B → Response (state B)

**Partial continuous model**

State ∈ \{A ... B\}

Stimulus cochleogram → Response (all states)
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
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 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

\[ r(t) = r_{\downarrow 0}(t)g_P(t) + d_P(t) \]

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

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 variable A

State variable B

Signal

Noise

Signal
Dimensionality reduction reveals latent variables in motor cortex populations:

See also Pachitariu et al 2013 for sensory cortex version.
Timescales of modulation

State-dependent **activation**

State-dependent **covariance**

(Spontaneous) neural activity
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

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

Model simultaneous V4 spiking

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:

Depth array recordings

Present vocalizations

Measure pupil

Pupil vs. spontaneous rate:
Timescales of modulation

State-dependent **activation**

- Diagram showing the interaction between a stimulus and a state variable.
- Graph illustrating the state-dependent activation with a time (s) axis from 0 to 20.

State-dependent **covariance**

- Diagram showing the interaction between a stimulus and a state variable.
- Graph illustrating the state-dependent covariance with a time (s) axis from 0 to 20 and a y-axis representing the (spontaneous) neural activity.

Note: The text in the diagram indicates the terms 'State variable', 'Stimulus', and 'State-dependent activation' and '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

pup v PC2 r=0.540
Gain versus spontaneous pupil effects differ

Spontaneous rate vs. pupil diameter

Response gain vs. pupil diameter

PCA of population gain

<table>
<thead>
<tr>
<th>Pupil diameter (pix)</th>
<th>Average gain</th>
<th>PC 1</th>
<th>PC 2</th>
<th>PC weight</th>
</tr>
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<tbody>
<tr>
<td>60</td>
<td>0.472</td>
<td>-0.211</td>
<td>0.261</td>
<td>0.535</td>
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<tr>
<td>80</td>
<td>0.162</td>
<td>0.090</td>
<td>0.095</td>
<td>0.139</td>
</tr>
</tbody>
</table>

PCC: $r = 0.35$

PCC: $r = 0.43$

PCC: $r = 0.02$
Timescales of modulation

State-dependent **activation**

State-dependent **covariance**
Population responses vary across repeated stimuli

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

\[ r_{\downarrow i}(t) = r_{\downarrow i}(t) + \sum_{k \neq i} g_{\downarrow i}(t) \]

Prediction correlation
\[ cc(PSTH-only, difference) = -0.71 \]
Coherent fluctuations explain trial-to-trial variability
Network model performance correlated with arousal

\[ r_{ij}(t) = r_{ij}(t) + \sum_{k \neq i} g_{ij}(k) r_{kj}(t) \]

Prediction correlation
\[ \text{cc(PSTH-only, difference)} = -0.71 \]
\[ \text{cc(pupil, difference)} = -0.65 \]

PSTH-only model
Network model
Pupil diameter (normed)
Network model weights reveal master neurons?
Tone detection task

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

Active vs. passive (pupil normed)
• 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!

Laboratory of Brain, Hearing & Behavior:
Brad Buran, postdoc
**Luke Shaheen**, postdoc
Jean Liénard, postdoc
Jesyn Lai, postdoc
Daniela Saderi, graduate student
**Zachary Schwartz**, graduate student

Former members:
Sean Slee, postdoc (Biotronik)
**Ivar Thorson**, postdoc (Octopus Robotics)

Support:
NIDCD, DARPA, Metaknowledge Network, NSF

http://hearingbrain.org/