Arousal enhances discrimination of natural sounds in auditory cortex

Charles R. Heller, Daniela Saderi, Zachary P. Schwartz, Stephen V. David
Oregon Hearing Research Center, Oregon Health and Science University, Portland, OR

Introduction

**Motivation**
- Behaviors such as “active listening” dramatically alter the way the brain processes incoming auditory information.
- These changes in neural activity occur on rapid timescales, facilitating our ability to perceive relevant stimuli in the world and ignore irrelevant background noise.
- A complete understanding of how this dynamic processing is carried out by the brain is crucial for helping researchers develop auditory prosthetics that perform robustly, even in noisy environments.

**Previous work**
- To study this phenomenon, a common approach is to train animals to respond to simple target stimuli, such as pure tones, and ignore distractor stimuli while researchers simultaneously record electrophysiological activity in the animal’s brain. This is illustrated below.

**Outstanding questions**
1) The brain is composed of billions of neurons, but these studies primarily focused only on single neurons in isolation. Is there something to be learned about how the brain guides behavior by studying the simultaneous activity of many neurons at a time?
2) Previous studies have relied on studies of simple, non-ethologically relevant stimuli, such as pure tones. It remains unclear how neural coding of natural sounds changes due to behavior state.

**Current approach**: We sought to answer these questions by recording neural activity from many neurons simultaneously in response to natural, species conspecific vocalizations, while monitoring changes in behavioral state by measuring the animal’s pupil size. This metric has been shown to correlate strongly with listening effort in humans.

**Experimental procedure**

(A) Head fixed ferrets passively listened to natural sound stimuli (ferret vocalizations) while brain activity was recorded using a 64-channel electrode and arousal state was monitored by recording pupil size with an infrared camera.

(B) Example pupil size trace under constant light level during one experimental session.

(C/D) Example responses of a neural population to a single ferret vocalization when arousal was high (C) or arousal was low (D). Top panel: spectrogram of vocalization. Middle panel: Raster plot - each row is a single neuron, each tick represents a single neuron becoming active (action potential). Bottom panel: Colored traces represent a sum over all neurons in the raster plot in the panel above. Gray trace is an average over all sound presentations. Notice that the response is much larger and follows the structure in the sound spectrogram more reliably, during the high arousal trial.

What can we learn from studying neural populations?

**Correlations are important**
The response of a neuron to repeated presentations of the same stimulus is variable. This variability is often shared across many neurons (see highlighted portion of raster plot in panel D above, and the cartoon in panel A to the right, where each dot represents the response of neuron 1 and 2 to a single sound presentation).

In the two neuron example shown here in panel A, we see that when neuron 1’s response variability is correlated with neuron 2’s response variability, it is difficult, given a single point in this two dimensional space, to decide which stimulus that point represents (for ex, consider points in the shaded area).

In panel B, we see that if correlated variability is reduced, there is no longer ambiguity about which stimulus each point represents.

Thus, one strategy the brain could use to enhance representation of stimuli is to decorrelate responses between neurons.

**Arousal decorrelates neuronal responses**
To determine if arousal changes the strength of correlated variability between neurons, we computed the correlation between all pairs of simultaneously recorded neurons in our dataset both when the animal was in a high and low arousal state. When the animal was aroused, correlations were weaker. This suggests that arousal may enhance sensory discrimination.

**Arousal improves discrimination of stimuli**
We next directly tested if arousal improves neural discrimination of sounds by measuring the distance between pairs of stimuli in N-dimensional space (where N = number of neurons). This can be thought of as the separation between the gold and purple ellipses shown in the cartoon examples shown earlier (middle bottom, panels A and B). We did this for each individual experiment (each black dot in panel A, left) and found that discrimination was consistently higher during high arousal.

Finally, we asked what factors of neural activity explained this improvement. To do this, we simulated data with:
1) only changes in response rate (Introduction example, active vs. passive)
2) only changes in correlation (middle-bottom panel, top vs. bottom)
3) changes in both

We found that by simulating both, we could reproduce the ~20% improvement in discriminability we saw in the real data (black vs. red, Panel B). Interestingly, by changing only rate or only correlations, we could produce a roughly 15% increase in discriminability in either case.

**Conclusions**
Changes in arousal / listening effort, as indexed by pupil size, lead to increased discriminability of natural sounds.

This improvement is due, in part, to decorrelation of response variability between neurons.

Changes in correlations may only be studied by recording activity from many neurons simultaneously. Thus, it is important to consider the joint, concerted activity of many neurons in order to understand how behavioral state shapes neural processing of sound.