Decoding Stimulus Features from Cortical Population Responses

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Abstract

The cortex encodes sensory information via the spatiotemporal activation of a large population of neurons. It is important to distinguish between "spatial information," which refers to information encoded by which sensory afferents are activated, and "temporal information," which refers to information encoded by the temporal pattern of the activated afferents. Speech recognition is an example of a task that requires both spatial and temporal processing in the range of tens to hundreds of milliseconds.

In this experiment, we decoded stimulus features from a population of neural responses, to characterize the spatial and temporal information available (**Fig. 1**). Specifically, we presented different auditory tones to awake, behaving animals, while recording extracellularly from a population of neurons in the auditory cortex. One computational model, the State-Dependent Network (SDN) model, predicts that the population of cortical neurons can encode past and present sensory events. Our goal was in part to test this hypothesis by seeing if the population response encodes not only spatial information, but information about the order of the tones as well. As such, we presented paired tones separated by 100 ms and attempted to decode the pitch of the first tone from the population response to the second tone. We used a support vector machine (SVM) algorithm to determine the amount of information the neural population had about which stimuli were presented. We found that the population encoded the features of the current stimulus well. There was a low, but statistically significant, amount of information about the previous stimulus.

Materials and Methods

Technical details

Thirty-two tetrodes were surgically implanted into the auditory cortex of rats (n=4) and stabilized using a custom-built 3D-printed head cap. We targeted the primary auditory cortex (A1). During recording sessions, rats were free to roam within an enclosed area in a dark room (**Fig. 2a**). Food pellets were automatically or manually dispensed throughout recording sessions. Recording sessions took place on different days. The cell populations we decoded involved data collected during different sessions, but not different animals.

For spatial decoding (**Fig. 2b**), the three stimulus types were 6kHz (low pitch), 12kHz (high pitch), and noise (all frequencies). For temporal decoding (**Fig. 2c**), the nine stimulus types were different orderings of 6kHz (low pitch), 12kHz (high pitch), and noise (all frequencies) separated by 100 ms. At least one second separated successive stimulus presentations. Each stimulus type was presented once during a trial, in randomized order. Each recording session was 100 trials.

Data collection and spike clustering (to identify putative neurons) used a Neuralynx recording system. Data was visualized with NeuroExplorer and MATLAB. Stimulus classification was performed with MATLAB and LIBSVM, a library for support vector machines (**Fig. 2d**). Support vector machine classification used a linear kernel. Repeated random sub-sampling validation was used to evaluate the performance of the classifier.

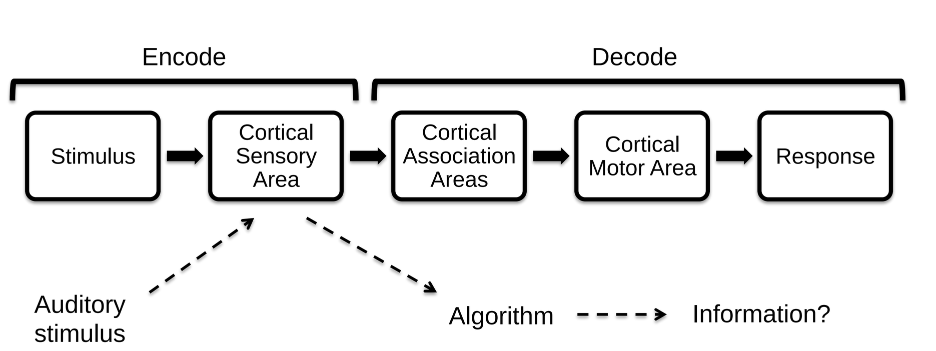

Figure 1 | Experimental focus
Top: Schematic representation of processing stages in perceptual tasks. *Bottom:* Focus of this experiment. We presented rats with different auditory stimuli while recording from a large population of neurons in the auditory cortex. We then used an algorithm to decode spatial and temporal stimulus features from the population responses. Adapted from Figure 29.1 in Seidemann, Chen, and Geisler, 2009.

Materials and Methods

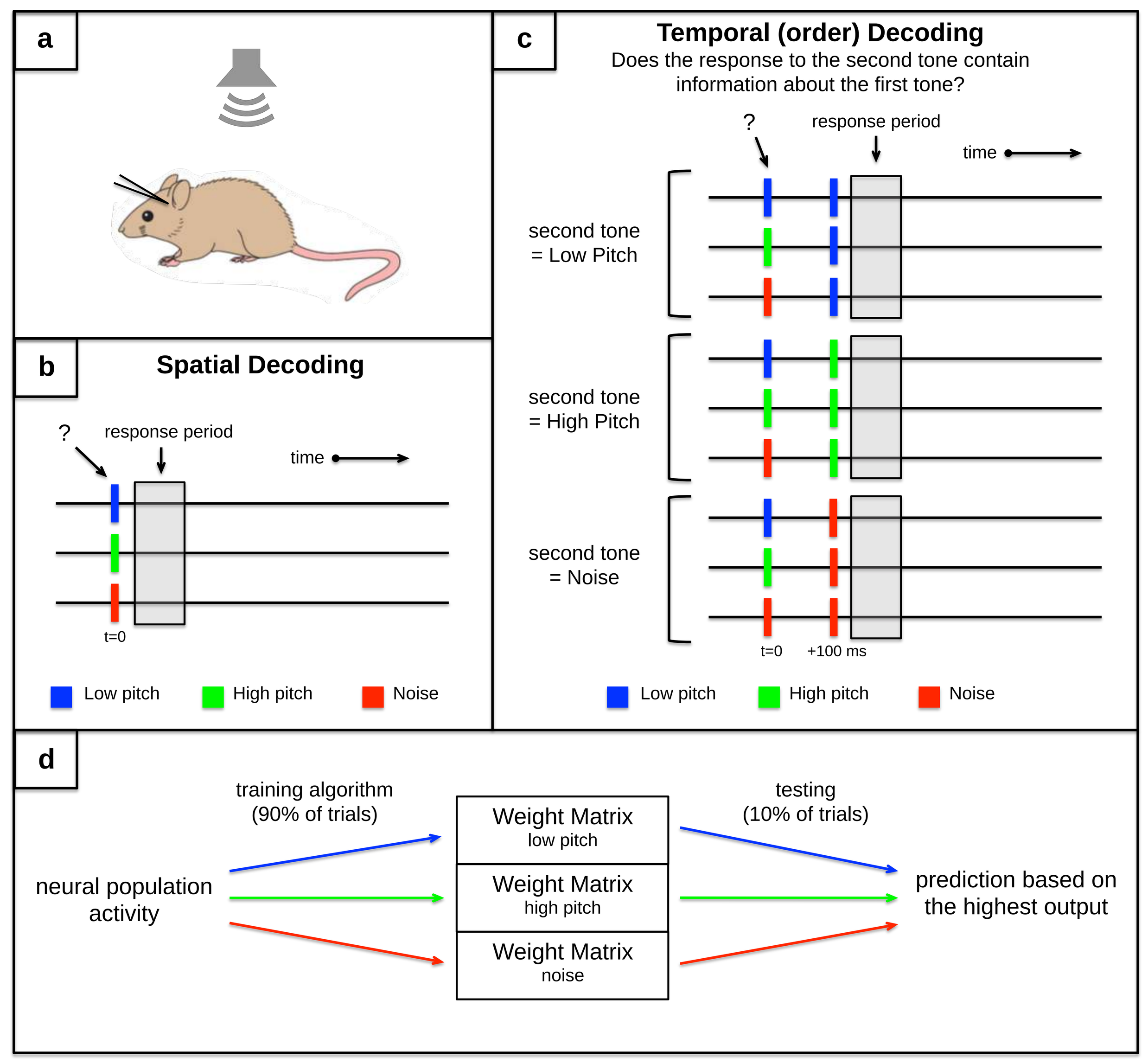

Figure 2 | Experimental design
Auditory tones were presented to awake, behaving rats (n=4) while recording from neurons in the primary auditory cortex (a). Single tones (b) or ordered tone pairs (c) were presented. Decoding (d): An SVM classification algorithm used training data to produce a matrix of weights specific to each stimulus type. Testing data was then used to cross-validate and make predictions about which stimulus was presented. Accuracy was computed by repeating this analysis many times with randomly chosen training and testing data sets.

Results

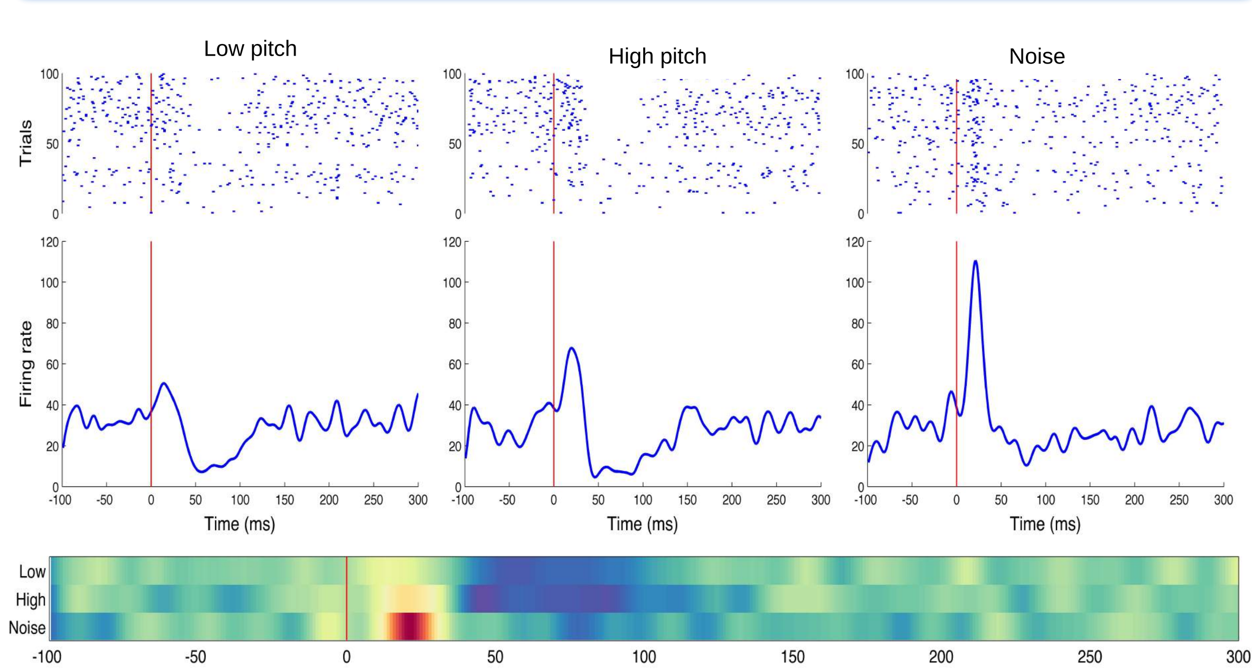

Figure 3 | Example of responses to different tones
A single neuron's responses to different tones (*left:* "low pitch", *center*: "high pitch", *right*: "noise") displayed in raster plot, spike density function, and heat-map PSTH format. For this cell, the response to "noise" is more intense than the other responses. Thus, this cell encodes spatial information about the stimulus.

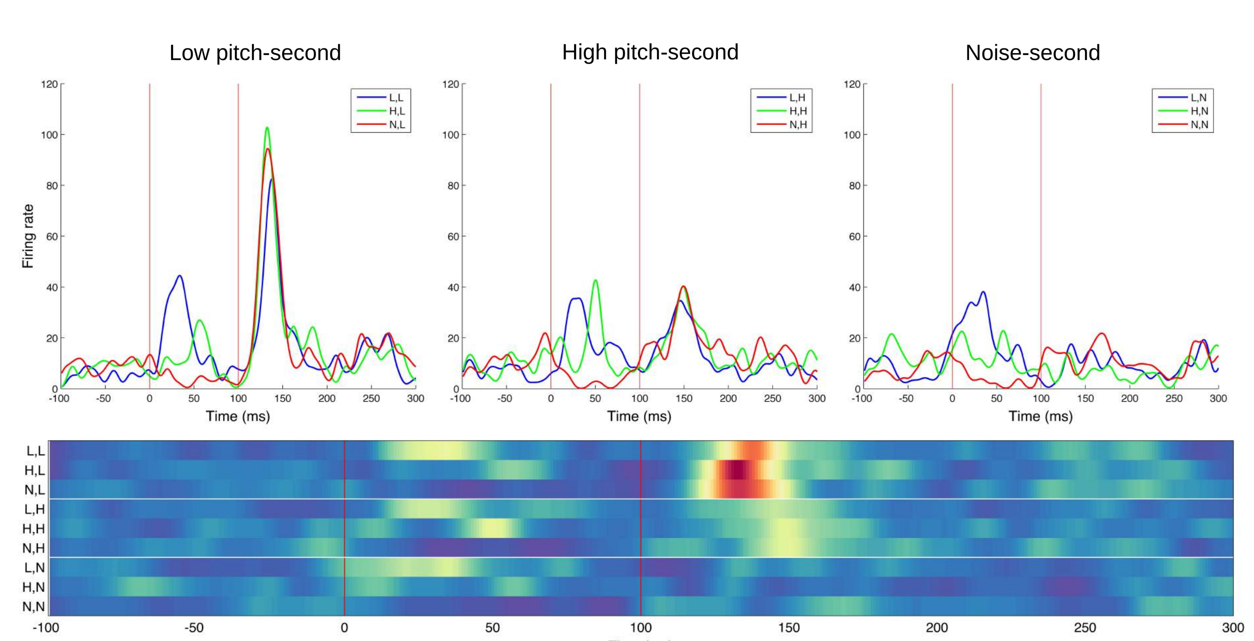

Figure 4 | Example of responses to different tone orders
A single neuron's responses to different tone orders of "low pitch", "high pitch", and "noise" displayed in spike density function and heat-map PSTH format. Each spike density function plot shows responses overlaid of cases where the second tone is the same. For this cell, the response to "low pitch" is most intense when it is preceded by any tone. Thus, this cell encodes temporal (order) information about the stimulus.

Results

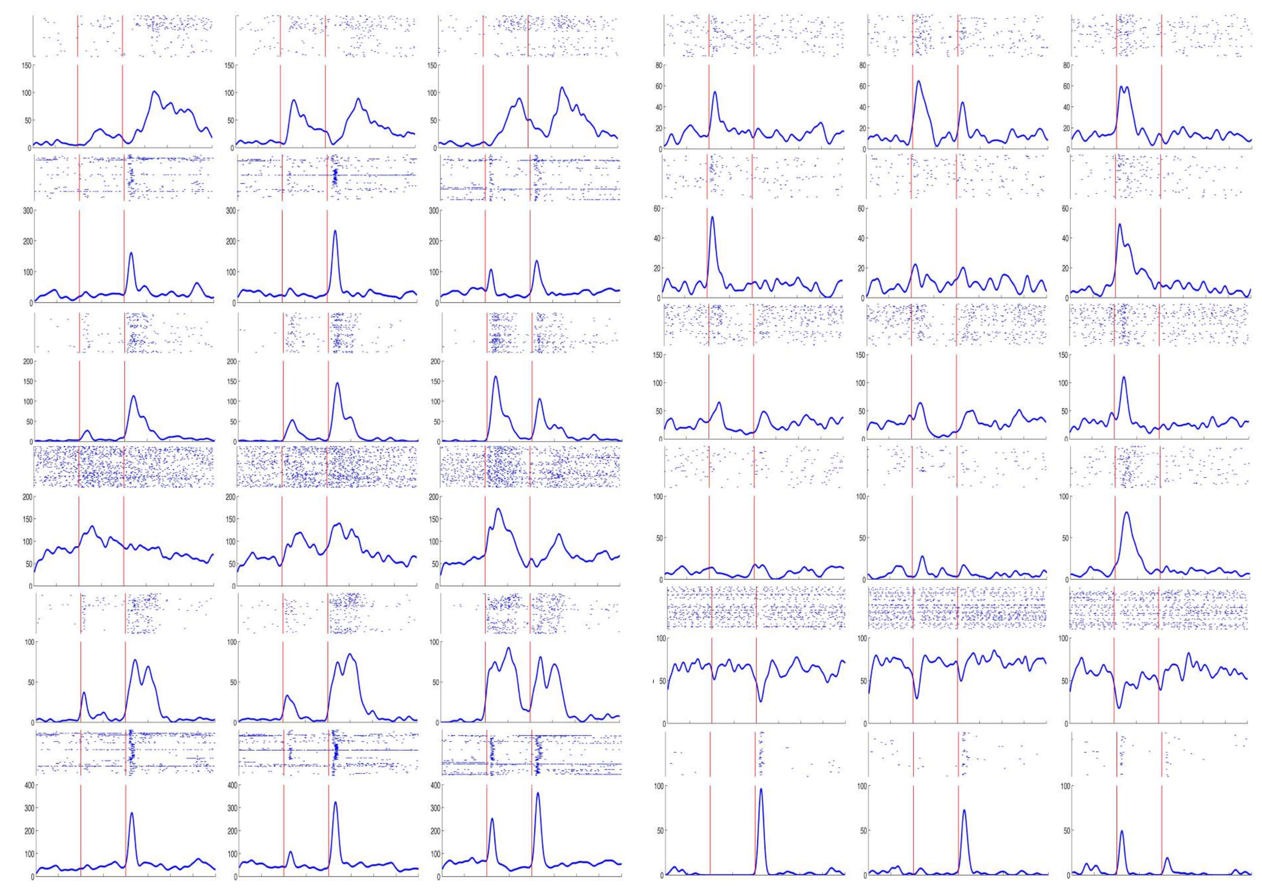

Figure 5 | Diversity of response patterns to different tone orders
Shown here are 14 neurons' responses to a "noise" tone when preceded by either "low pitch" (*left*), "high pitch" (*center*), or "noise" (*right*). Responses are displayed in raster plot and spike density function format, and tone onsets are indicated by a *red line*. Recordings are from multiple animals.

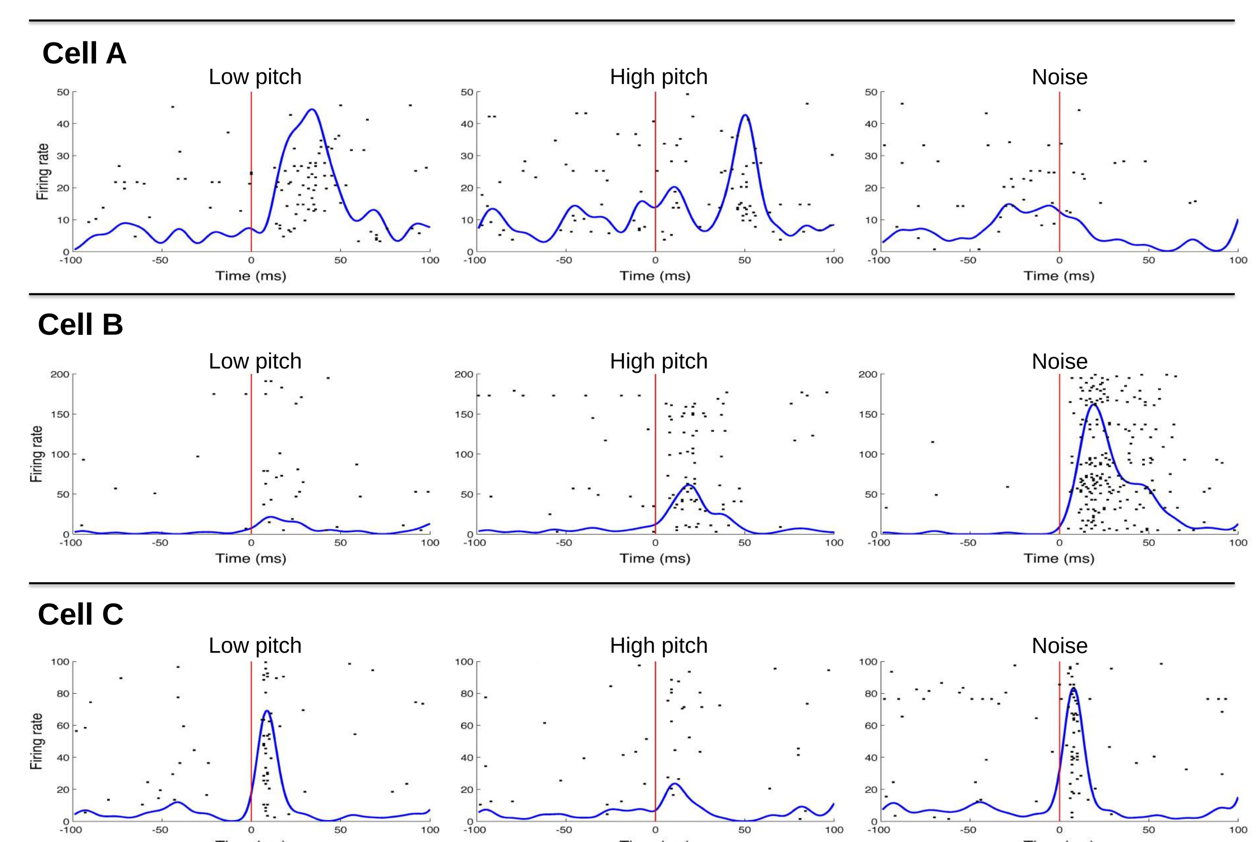

Figure 6 | A set of cells demonstrating population encoding
A population of cells lacking strict preferred stimuli is still capable of encoding the current stimulus. Shown here are three cells' responses to the same stimuli ("low pitch", "high pitch", and "noise"). The responses are displayed in spike density function format with overlaid raster plots. For this cell: Low pitch is encoded by strong responses in cells **A** and **C**, and a small response in cell **B**. High pitch is encoded by a large response in cell **A**, a moderate response in cell **B**, and a small response in cell **C**. Noise is encoded by no response in cell **A**, and strong responses in cells **B** and **C**.

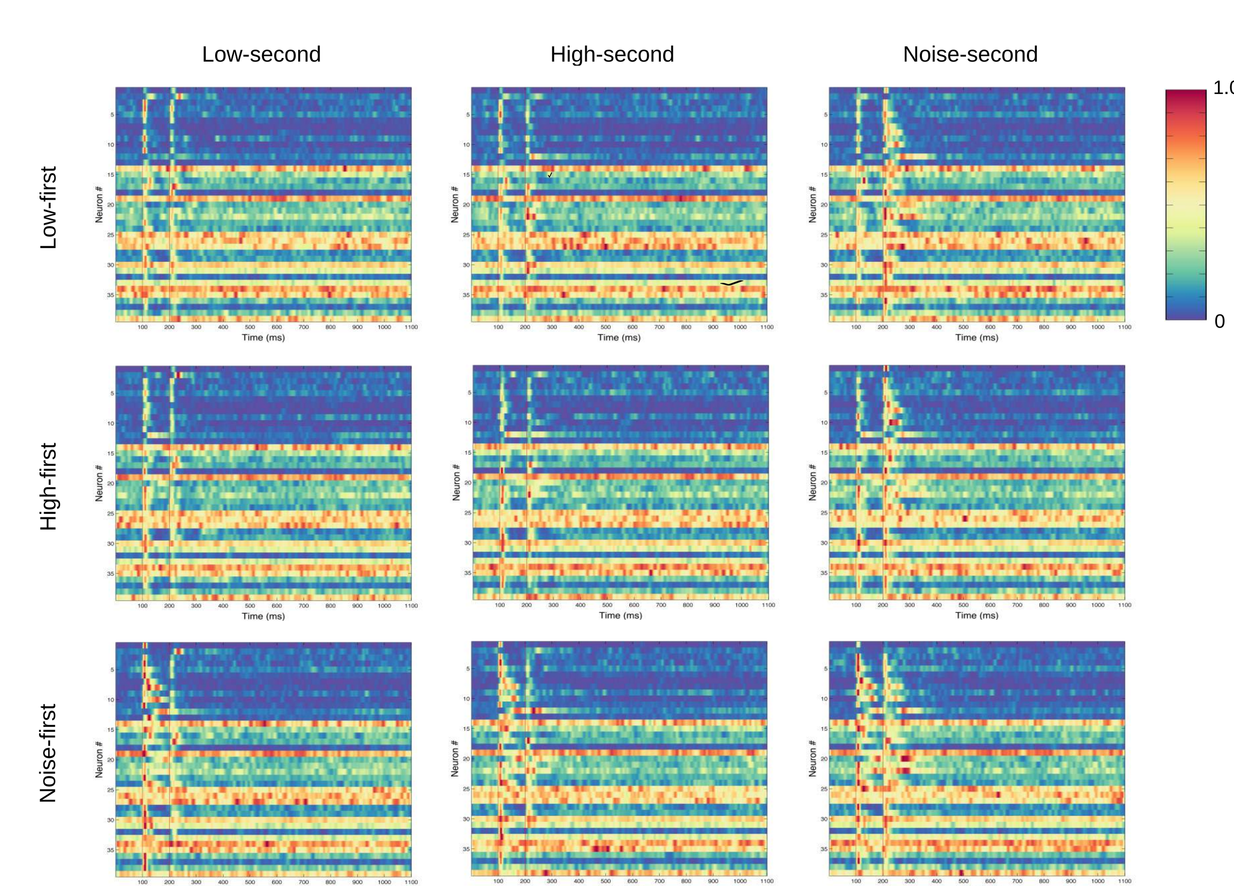

Figure 7 | Heat-map PSTHs of a neural population's responses to different tone orders
A neural population's responses to different tone orders (labeled at *top* and *left*). All recordings are from a single animal. Firing intensities are normalized to each neuron's peak intensity. One prediction of the state-dependent network model is that the population response to the second tone will encode the previously presented stimulus in addition to the current stimulus (in each *column* the second stimulus presented was the same).

Results

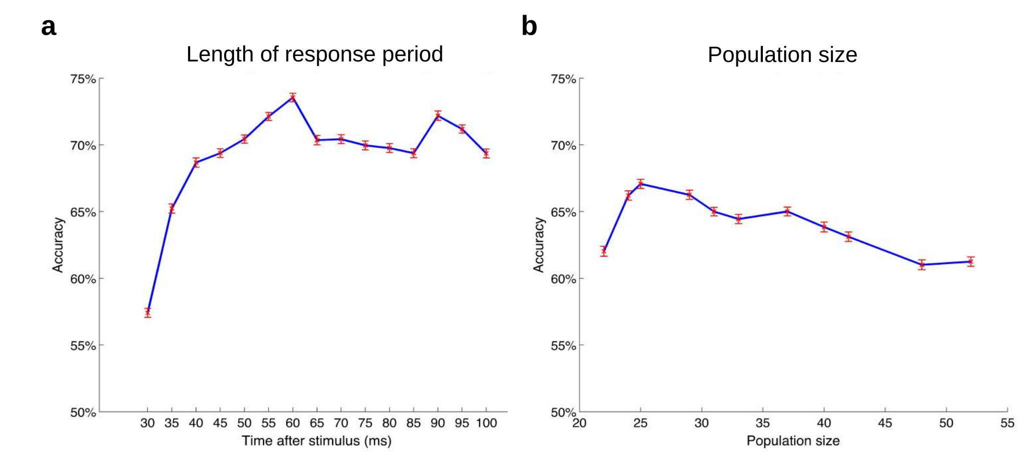

Figure 8 | Parametric analysis for stimulus classification algorithm
Shown here is the accuracy of the classifier as a function of (a) length of response period, and (b) population size. In (a) the end of the response period is varied between +30 to +100 ms after stimulus onset, while the beginning of the response period is kept constant at +15 ms after stimulus onset. A similar analysis was used to establish a response period beginning (not shown). In (b) the population size was varied by changing the threshold of the algorithm we used to determine which cells exhibit auditory responses (response period was 15—80 ms).

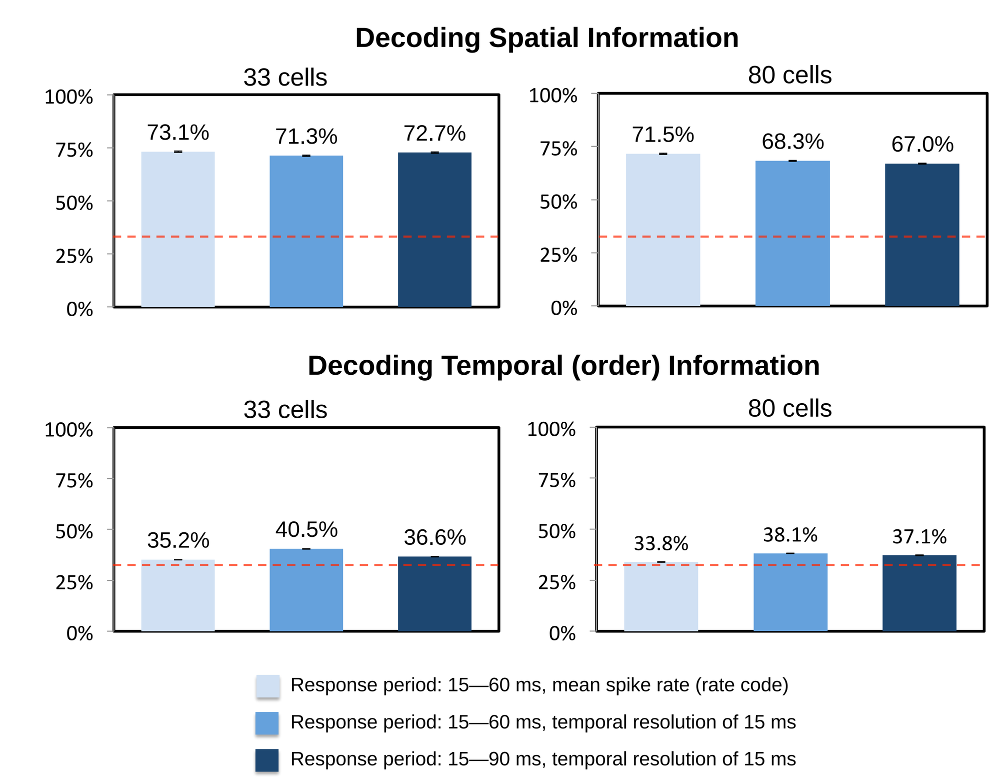

Figure 9 | Results of decoding
Accuracy of the SVM classification algorithm (number of correctly identified stimuli divided by total # of stimuli). chance = 33.3% (*red dashed line*). These results are based on data from a single animal. *Top:* accuracy of the classifier to spatial stimulus features. *Bottom:* accuracy of the classifier to temporal (order) stimulus features. Also shown is the accuracy for a population size of 33 cells (*left*) and 80 cells (*right*). Although a larger neural population can encode more information, in this case more noise is also incurred since cells with the strongest auditory responses are included in both populations. Each *blue shade* represents a different response period. When analyzed in terms of mean spike rate, a rate code is assumed to contain all of the available information. To see if temporal variation in the spike train contributed to the response, the response period was subdivided into 15 ms bins, as suggested by Schnupp, et. al., 2005, at two different response period lengths (see **Fig. 8a**).

Conclusions

- The neural population encoded the features of the current stimulus well. Accuracy > 70% (chance = 33%) (**Fig 9.** *top panel*).
- There was a low, but statistically significant, amount of information about the previous stimulus. At best ~40% accuracy (chance = 33%) (**Fig 9.** *bottom panel*).
- Thus, some neurons exhibited state-dependent responses, meaning that the response to the second stimulus was influenced by the first stimulus (see **Fig. 4** for an example).
- Parametric analysis suggests that the highest amount of information about the current stimulus occurs within approximately 15—60 ms following stimulus onset (**Fig. 8a)**. This is similar to other reports (Schnupps, et. al, 2005).
- We hypothesized that binning the response period would increase the amount of information available, thus improving stimulus classification accuracy. Interestingly, this was the case for spatial decoding but not for temporal (order) decoding (**Fig. 9)**.
- Thus, temporal variation in auditory neuron responses may contain additional information about previous stimuli that is not captured by a coarse rate code.
- The fact that spatial decoding sometimes decreased in accuracy when responses were binned may be explained by "overfitting," which occurs when the classification model is not general enough to apply to new data.
- Overall, these studies provide preliminary data suggesting that the population response of the auditory cortex may encode both the features of the current and previous stimuli

References

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Schnupp, J. W., Hall, T. M., Kokelaar, R. F., & Ahmed, B. (2006). Plasticity of temporal pattern codes for vocalization stimuli in primary auditory cortex. *The Journal of Neuroscience*, 26(18), 4785-4795.

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Acknowledgments

I would like to thank the authors of *Matlab for Neuroscientists: An Introduction to Scientific Computing in MATLAB* for helping me learn to use MATLAB effectively for data analysis.