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# Excitatory and suppressive features of auditory neurons in avian cortex

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## Abstract

The ability to process auditory signals and ignore the noise is an influential reason why animals depend on acoustic signals for communication and survival. Previous work on auditory receptive fields has uncovered many different types of auditory neurons: broadband neurons are tuned to signals across all frequency ranges but only at a specific time. Narrow-band neurons respond only to signals in very specific time and frequency windows. While there has been a lot of work in describing receptive fields of different auditory processing regions, little has been done to connect this work with computational theories of auditory processing. Here we analyze responses of auditory neurons in songbirds in four different regions in auditory cortex to various songs and find various principles that explain how auditory processing is organized. First, there are more suppressive features than excitatory features further downstream, indicating more feature selectivity as the signal is transmitted through cortex. Second, quadrature pairs and cross-orientation suppression, etc. This principles is consistent with the time-dilation theory of auditory processing, etc...

## 1 Introduction

Auditory processing utilizes a number of complex and poorly understood transformations as sound is transduced from the midbrain (mld) up through the thalamus (nucleus ovioidalis (OV)) and onto auditory cortex (Field L and CM) [1]. Neurons involved in auditory cortex are modelled by spectrotemporal receptive fields (STRFs): there are certain frequencies and latencies that promote or suppress firing in a specific neuron [2]. While previous work in songbirds has looked at the number of broadband and narrowband neurons in each region of auditory processing, illustrating a possible function or set of functions for each region [3] [4] [5], it is still poorly understood how the sum of the parts can give rise to complex auditory behavior that aids in survival, such as identifying a stranger vs. a relative, a mate vs. a non-mate, etc.. One important question is how the combination of excitatory and suppressive features and the organization of receptive fields with different features can give rise to complex sound recognition and interpretation. For example, neurons in Field L are thought to receive input from an excitatory and inhibitory neuron and process these inputs nonlinearly [6]. This nonlinearity may give rise to intensity-dependent receptive fields, which enable the bird to encode and distinguish near and far songs.

To address these questions of how the receptive fields of auditory neurons are organized, we utilized the statistical model of maximum likelihood estimation to determine the receptive fields of auditory neurons. After computing these receptive fields, we fit them as a linear combination of gammatones and gaussian filters in order to analyze the features of these receptive fields. After performing this modelling, we conclude that (1) suppression is increased as a signal is transduced along the auditory pathway, (2) auditory signalling is composed primarily of broadband and narrowband receptive fields with very few intermediate receptive fields, and (3) ..... Overall, these findings show that ...

## 38 2 Quadratic model

Using a published dataset of neural responses in songbirds to various songs on the CRCNS data sharing website [7], we sought to build a model that maps the input stimuli to the collected neural responses with high probability. The dataset included neural responses in songbirds from various regions in auditory cortex (mld, field L, OV, and CM) to different song recordings. Treating each song as a  $d$ -dimensional vector over time  $x$ , we computed the predicted response  $Y'$  of the model as follows:

$$Y' = \sigma(a + \mathbf{h} \cdot x + x\mathbf{J}x^T)$$

where  $\sigma$  is the sigmoidal function

$$\sigma(x) = \frac{1}{1 + e^{-x}}.$$

39 Here  $h$  is a  $d$ -dimensional linear filter,  $\mathbf{J}$  is a  $d \times d$ -dimensional quadratic filter, and  $a$  is simply the  
40 bias of the neuron. All of the parameters  $a, h, \mathbf{J}$  were fit by minimizing the negative log-likelihood of  
41 the model.

42 We divided the training data into fourths. Three-fourths of the data were used to calculate the gradient  
43 and the other fourth was used as a validation set to determine convergence. We ran 4-fold cross  
44 validation using a different fourth of the training data as a holdout set and averaged each parameter  
45 over the four trials to control for variability in the optimization process. To test the model, we held  
46 out recordings for each neuron and then tested our model on these held out recordings.

47 **Receptive fields** In order to compute the basis of pertinent dimensions of  $\mathbf{J}$  along which the  
48 neuron responds most strongly, we performed eigendecomposition of  $\mathbf{J}$  to get the eigenvectors and  
49 eigenvalues. This resulted in a number of eigenvectors and eigenvalues, only a few of which were  
50 significant. After significance testing, only a few eigenvectors remained for each neuron. These  
51 eigenvectors illustrate the dimensions along which a neuron responds most maximally to and thus can  
52 be considered the receptive fields of the neuron. Eigenvectors with positive eigenvalues are excitatory  
53 features and those with negative eigenvalues are suppressive features.

54 **Excitatory and suppressive features**

## 55 3 Modelling the receptive fields

Gammatones are widely used as auditory filters. In order to model the receptive fields computed above, we attempt to build  $\mathbf{J}$  using a linear combination of gammatones. A gammatone is described by the following equation:

$$g(t) = a(t - t_0)^{n-1} e^{-2\pi b(t-t_0)} \cos(2\pi f(t - t_0) + \phi),$$

56 where  $a$  controls the amplitude,  $t_0$  controls the onset time,  $n$  controls the filter order,  $b$  controls the  
57 decay rate,  $f$  controls the central frequency, and  $\phi$  controls the phase. Since, this is only a function of  
58 time, we took the outer product of  $g(t)$  and a Gaussian filter along the frequency dimension, with  
59 central frequency  $f_0$  and standard deviation  $\sigma$  to get a 2-dimensional receptive field, denoted as  
60  $S$ . We can manipulate the parameters of both the gammatone and gaussian filters to replicate the  
61 receptive fields computed by eigendecomposition (Fig. 2).

With a set of gammatones we can approximate  $\mathbf{J}$  as

$$\mathbf{J}' = \sum_i S S^T,$$

62 where  $S$  in this case is the flattened 2-dimensional receptive field from above. We ignore any weights  
63 as the  $S$  matrices were normalized when performing the fit. Using differential evolution, we can  
64 identify the parameters that best fit the  $\mathbf{J}$  kernel. We chose to fit the onset time, filter order and decay  
65 rate of the gammatone, as well as the central frequency and standard deviation of the gaussian in  
66 our differential evolution model. All other parameters are either redundant because normalization  
67 is performed ( $a$ ) or irrelevant to the problem we are interested in ( $\phi$ ). We seek to minimize the  
68 mean difference between  $\mathbf{J}$  as computed using the quadratic model and the new  $\mathbf{J}'$ . The excitatory  
69 and suppressive parts of  $\mathbf{J}$  were fit separately and only the significant eigenvectors are taken into  
70 consideration. The exact approach we took to solve the differential evolution problem can be read  
71 about in [8].

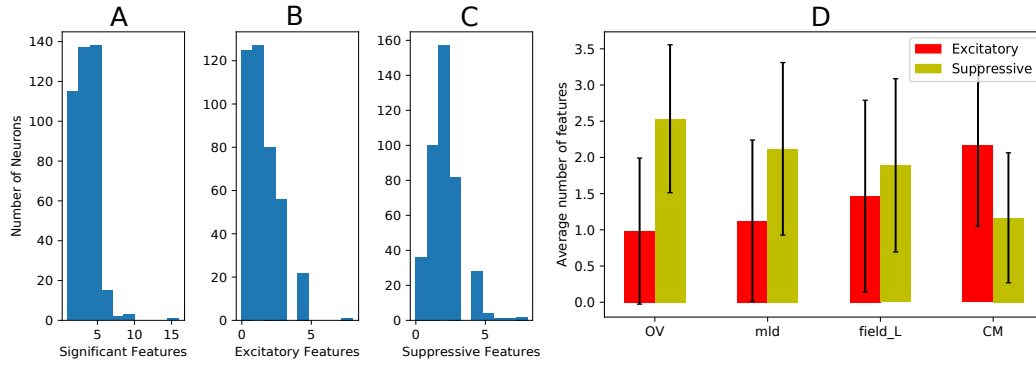


Figure 1: The distribution of the number of significant, excitatory, and suppressive features computed through the convolutional model. (A) The total number of significant dimensions of J. (B) The number of significant dimensions with positive eigenvalues. (C) The number of significant dimensions with negative eigenvalues. (D) Average number of excitatory and suppressive features for each region in auditory cortex.

## 72 Results

### 73 Analysis of different auditory regions

#### 74 Cross-order suppression

#### 75 Quadrature pairs

## 76 4 Discussion

## 77 References

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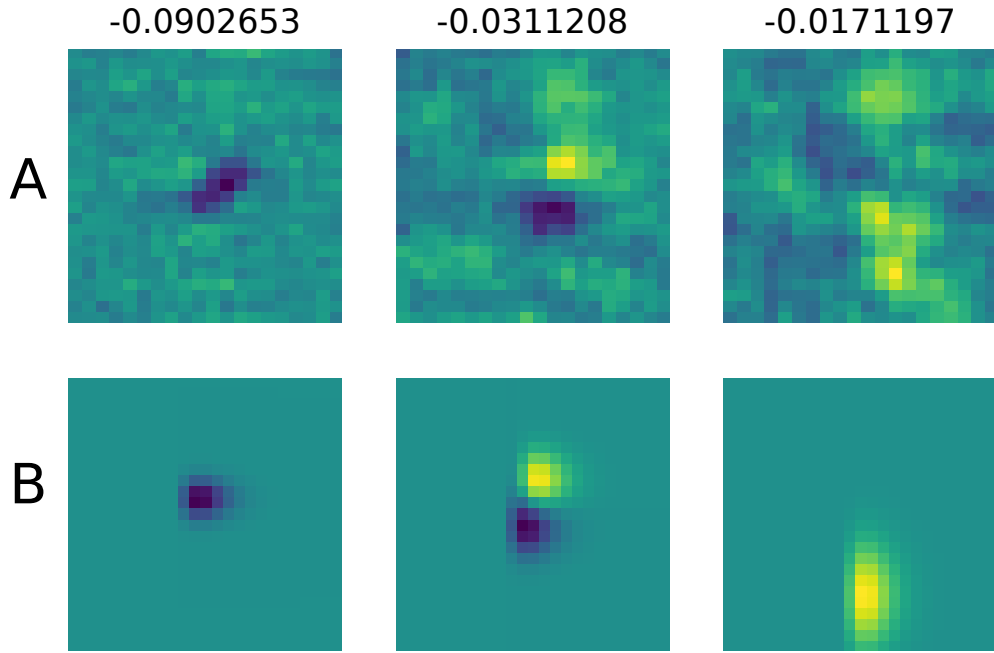


Figure 2: Example auditory receptive field with 3 suppressive features. The neuron is *glb5656<sub>2</sub>* in the ovoidalis. (A) Receptive fields computed from the quadratic model. There are 3 significant dimensions for this neuron and they are all suppressive (eigenvalues listed above the receptive field). (B) Gammatones fit to the receptive fields above. Parameters were selected manually to illustrate the process of fitting a linear combination of gammatones to the J matrix.

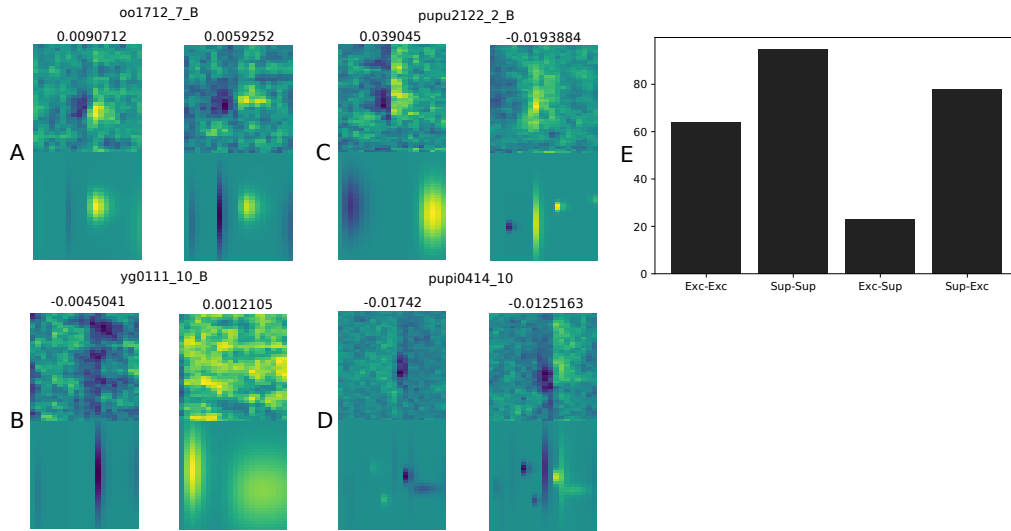


Figure 3: Using differential evolution to fit gammatones to the J kernel from the quadratic model. (A)-(D) show example fits for the two most significant dimensions of J for 4 categories of neurons: (A) excitatory-excitatory, (B) suppressive-excitatory, (C) excitatory-suppressive, and (D) suppressive-suppressive. The top row of each of these panels is the receptive field for the neuron computed as the eigenvectors of the J kernel. The bottom row is the example fit computed through differential evolution. The numbers are the eigenvalues for each dimension. (E) illustrates the number of neurons in each of the 4 categories.