



## FINAL TECHNICAL REPORT

Modeling Temporal Dynamics in the Classification of Auditory Signals  
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We have pursued an exploratory modeling approach to the response properties of auditory neurons in the zebra finch (Bankes and Margoliash, 1993 a, b; Margoliash and Bankes, 1993). Early attempts at modeling auditory neurons in the song system nucleus HVC were not successful, in part because of the relative paucity of biological information at the time of the start of the project and in part because the technology applying neural nets to quantitative neurophysiological data had not been established. Thus, although our ultimate goal is to model HVC auditory neurons, we have started our analysis at the level of the auditory thalamus (ovoidalis), where neurons have simpler response properties (Bigalke-Kunz *et al.*, 1987; Diekamp and Margoliash, in prep).

In general, the temporal dynamics of neuronal response is a critical feature to capture in any modeling effort, yet this feature is among the most difficult to model. We have employed a 3-layered connectionist architecture called Time Delay Neural Network (TDNN), which permits a natural representation of time-varying processes and exhibits the essential property of temporal invariance (Waibel, 1989). The supervised learning approach we have taken to training the network (backpropagation of errors) involves applying inputs to the network, and comparing the network output with the desired output. This difference or error signal is then used to alter the values of the weights of the network so as to decrease the error signal in subsequent iterations.

As applied to response properties of ovoidalis neurons, this approach has yielded some interesting results. Data for modeling came from ovoidalis neuronal responses to tone and noise bursts, other artificial stimuli, and songs (Diekamp and Margoliash, in prep). The sounds were applied to the inputs of the model, with the dynamical neuronal response the desired output. The best ('canonical') architecture was able to converge on the entire stimulus set with an excellent fit for 10 of 17 neurons. Thus, a quantitative relationship between the responses to tone bursts and complex stimuli has been established for those 10 cells. In general, stimuli with complex temporal dynamics can produce unanticipated neurophysiological results (e.g., McKenna *et al.*, 1989), so that quantitative assessment of the predictive power single tone responses is of general interest. In neuroethological investigations, appropriate choice of stimulus repertoires has often been a particularly difficult issue (Margoliash, 1983a). To the extent that our modeling approach is generalizable and feasible within physiological recording times, we can envision the day when on-line decisions regarding the completeness with which a neuron has been tested can be made with quantitative rigor.

For one ovoidalis cell studied in depth, the architecture also converged when trained on tone bursts only. In this case, the model correctly predicted the responses to song.  $R^2$  values were very high (0.72-0.96), and the graphical demonstration of the goodness of fit is particularly compelling (Bankes and Margoliash, 1993b). Because the model converges when trained on tone bursts only, we were able to modify the tone burst data, train the model, and see how the modifications affect the response to song. Shifting the FTC in frequency or amplitude, or modifying the rate/intensity function, had effects but the effects were large only for large modifications. In contrast, small changes in the latency or in the phasic/tonic profile of the cell had large effects on the model's ability to predict song. These experiments permit a direct test of the relationship between aspects

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of fundamental response properties and responses to complex stimuli, and confirm the relative importance of temporal aspects of neuronal responses. Such experiments would have been difficult to do otherwise. It should be noted that there is every reason to believe we can extend these results to a large sample of ovoidalis neurons, and, as proposed here, to tone burst-responding cell in field L.

Although somewhat peripheral to this proposal, these results also have potential implications for the role of nonlinearities in the auditory system. The mammalian cochlea is known to exhibit mechanical nonlinearities that affect two-tone responses of auditory nerve fibers. Presumably, there are similar mechanisms acting in the avian cochlea, although this has not been as well established (see Manley, 1990). The canonical architecture, however, only incorporates threshold and compression nonlinearities. Since this architecture converges for training sets that included tone bursts and song, this demonstrates that second-order (frequency by frequency) interactions do not dominate the responses of the modeled neurons (Banks and Margoliash, 1993b). A Monte Carlo simulation shows that the residual variance in the data is not accounted for by noise. Potentially, the remaining variance may be explained by higher-order nonlinearities. Alternatively, higher-order nonlinearities may not be present at the level of these ovoidalis neurons. Frequency by frequency interactions are easy to add to our architecture, so distinguishing between these two choices should prove to be a tractable problem. If the latter possibility obtains, it would suggest that a role of the peripheral auditory system is to cancel out cochlear nonlinearities. Put another way, the auditory system at or beyond ovoidalis must be under different selective pressures than the peripheral auditory system. The demonstration of multi-peaked and broadband neurons in the ovoidalis of zebra finches apparently adapted for finch vocalizations supports this suggestion (Diekamp and Margoliash, in prep).

Finally, most connectionist approaches to neurobiological problems have modeled properties of 'average' neurons or 'general' behavioral patterns. Perhaps in part because of this reason, and in part for lack of appropriate statistical theory, much of the literature has presented results without statistical verification. In our efforts, we have developed several simple statistical tools to assess the relationship between neuronal and model outputs. Chi-squared approaches are inappropriate because the intractable problem of assessing degrees of freedom dominates the assessment of statistical validity. Regression ( $R^2$ ) approaches tend to support subjective assessments but do not provide statistical significance. We have found the use of Monte Carlo simulation, which is a form of bootstrapping, the most useful. With these approaches, for the ovoidalis data we can demonstrate both a good fit between neuron and model data, and that in most cases the residual variance cannot be the result of noise (Banks and Margoliash, 1993b). Our demonstration of the applicability of these simple approaches, as well as the development of more sophisticated statistical tools for connectionist modeling, should have a salutary effect on the field.

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