Discriminating Gourmets, Lovers, and Enophiles? Neural Nets Tell All About Locusts, Toads, and Roaches

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Abstract

Here we consider the issue of choice and how neural systems can be used to investigate the processes of discrimination, as well as the evolution of different kinds of choice-related behavior in animals. We develop these ideas in the context of three studies, among others. The first study is on the evolution of specialization in animals using locust feeding behavior as the leitmotif, where decision making in individuals is modeled by a 3-layer-perceptron. In this study the fitness of individuals depends on their response to signals from plants and the density of individuals using those plants [1]. The second is a study that investigates the evolution of species recognition in sympatric taxa using female mate choice in frogs as the leitmotif [2]. Here individuals are modeled by Elman nets (3-layered perceptrons with feedback) and their fitness is determined by their ability to discriminate conspecifics from heterospecifics. The third is a study of the response characteristics of a recurrent Hopfield-type neural network to input that represents olfactory stimuli. The connectivity of this net reflects the basic architectural features of the neuron in the insect antennal lobe, as typified by cockroaches or bees [3].

1 Introduction

Discrimination is the essence of behavior, no matter how rudimentary. For example, the sea hair (*Aplysia*, spp.), a naked mollusk, needs to discriminate between various chemical and mechanical types of stimuli to appropriately and reflexively withdraw its siphon into its mantel at times of danger. We may reasonably believe that neural network models, which can be viewed as devices for categorizing inputs into classes, provide us with insight into how *Aplysia* and other organisms use reflexive behavior in discriminatory contexts. Is it too far fetched to believe that neural nets can also provide insights into more complex discriminatory behaviors such as food selection by locusts, mate choice in frogs, or cockroaches using odor plumes to find food? In a sense, this is the same dilemma that ecologists face when asking whether aggregated species models can be used to address

questions in community ecology. In both cases, the plausibility of the models as representations of real processes is stretched to the limit, and we are reduced to convincing ourselves that playing with such models generates knowledge that otherwise would be unavailable. That models can generate hypotheses about how real processes work, is true to be sure. The success of the modeling enterprise, however, rests on whether these hypotheses ultimately lead to uncovering some truths that would, in the absence of models, remain buried forever. In this mini-expose, focusing on our own work and that of our collaborators, we review how neural nets provide some insights into three processes that are very crude abstractions of systems found in nature. We hope to demonstrate that the value of neural network models depends on how the hypotheses they generate are translated into knowledge through a dialectical interplay of theory and empiricism.

2   Locust Gourmets

The first application we review is that of neural networks used to investigate the evolution of generalist versus specialist strategies in consumers competing for resources in a limited space. The leitmotif used to carry out simulations in this study [1] was how guilds of closely related species of herbivorous insects are able to coexist while competing for several sympatric species of plants (e.g. see reviews [4,5]) In the simulations, the decision making processes of individuals were emulated by computations of 100 3-layer perceptrons (each consisting of 2 input, 3 hidden, and 1 output unit—see Fig. 1) which then produce 6 different scalar outputs in response to one of 6 pairs of input stimuli. Each pair of inputs represents one of four plant resource types (Fig. 1). The relative fitness of each of the 100 individuals (i.e., 100 perceptrons each with a different set of synaptic weights) was determined by the following three factors: 1.) the size of its response to each of the four resources, 2.) an intrinisic value for each of the four resources, 3). the decline in the value of resources with the number of individuals competing to use them.

In general, neural networks can adapt to their environments through evolution or through learning, although the two processes are only distinguishable in the way networks are updated. In this study [1], an evolutionary (e.g. genetic algorithm), rather then a learning process (e.g. back-propagation), was used to update the networks [6,7]. Specifically, this model addressed the question of why there are more host plant specialist than generalist insect consumers when laboratory studies indicate that generalists are able to use a much broader spectrum of plants than is observed in nature. It has been speculated that perceptual constraints coupled with considerations of foraging efficiency play a role in the evolution of specialization [4,5].

The results of these simulations [1] indicated that the probability of species evolving particular host plant preferences depends on the different signals produced by plants of different nutritive values. Networks could evolve to exploit a single plant type or to generalize across two or more plant types. Evolutionary equilibria typically involved guilds of complementary species that together constitute an 'ideal free distribution' in terms of productivity of the different plants.
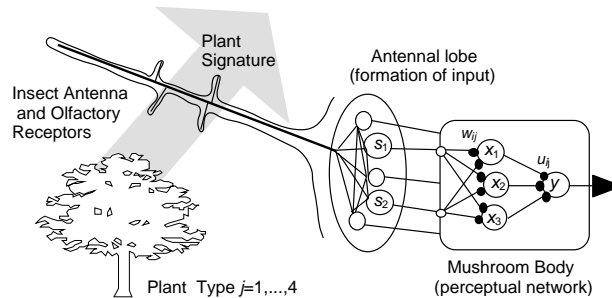
Figure 1. Each of four plant types is assumed to produce a unique response in the projection neurons of the antennal lobe of an insect brain. This response, modeled as a two unit input layer of a 3-layer preceptron, is normalized so that it effectively produces the ratio of the two inputs (S1/S2), which progressively increases from 1/4 in plant type 1, to 2/3 in plant type 2, 3/2 in plant type 3 and 4 in plant type 4. These inputs S_1 and S_2 are then processesed in a perceptual network in the mushroom bodies, modeled by three hidden units and one output unit in our three-layer perceptron. The input signals are propagated through synaptic weights w_{ij} to the three-unit hidden layer x_j and from there through synaptic weights u_{ij} to the output signal y. The output y is a measure of the insect's ability to discriminate the plant represented by the corresponding input and is used in conjunction with a fitness value, based on the number of insects using that host plant type, to generate a population index for the phenotype represented by the synaptic weights w_{ij} and u_{ij}. Modified from [1].

The mix in phenotypes within these guilds depends critically on the order of appearance of the various combinations of specialist and generalist phenotypes, and this order depends on the difficulty of the perceptual task faced by the phenotypes (Fig. 2). Any differences in the relative utilization by a generalist of different plant species will lead to the emergence of one or more specialists that exploit the plants most under-utilized by the generalist. Evolutionary changes in guild structure are less frequent than mutational rates would suggest but are saltatory when they occur. The strategy to specialize may dominate for two reasons: specialization appears to evolve more readily in complex environments and the ideal free distribution is more easily matched in a population density context by a group of specialists or by generalists in concert with specialists than by a generalist alone.

Earlier studies [8,9] used simple three-layer feed-forward perceptrons to test whether the neural networks respond to stimuli in a similar way as animals. These models have been very accurate at predicting stimulus-response characteristics, including generalization, supernormality (peak shift) and stimulus intensity effects. Such neural networks exhibit behavior predictive of the behavior of real consumers. Leow [10] describes a series of increasingly complex neural networks each of which allows a simulated creature to search for food and to evade danger by using olfactory cues. Behaviors such as obstacle avoidance and risk-taking emerge naturally from the networks' interaction with the environment. More complex systems of networks [11] have been used to model foraging behavior of egrets asked

to choose between feeding in a flock or foraging individually. Local enhancement and flock foraging was preferred when resources were patchy, while individual foraging was preferred when resources were evenly distributed. Other simple neural nets have been developed that learn to avoid aversive stimuli by trial and error or by imitation [12].
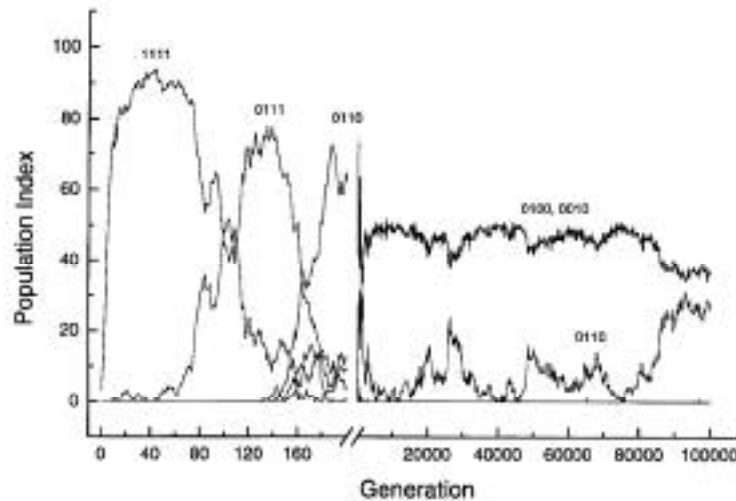

Figure 2. Population indices of six insect phenotypes (designated by ones and zeros to indicate which plant types the network perceives maximally—e.g. 1111 is a generalist not distinguishing between any of the plant types, 0100 is a specialist on plant type 2 able to discriminate it from 1 and the lumped combination of 3 and 4, and 0110 is less specialized able to discriminate the lumped combination of 2 and 3 from 1 and from 4) are plotted for one of the simulations of a population evolving in an environment in which plant types 2 and 3 each have a carrying capacity for 50 individuals while plant types 1 and 4 are toxic and have 0 carrying capacity. The values plotted are the relative population sizes of the six phenotypes every generation up to 1000 and every 100 generations thereafter. Modified from [1].

3   Toad Lovers

Neural networks have been used to model the response of animals to signals sent by conspecifics or heterospecifics. In most of these models the evolution of the phenotypes of the senders and receivers depends on the choices that the networks make. One such example is the study of the coevolution of a mimicry complex [13] consisting of a palatable prey species that evolves to avoid predation by mimicking the appearance of an unpalatable species. The effectiveness of the mimicry is determined by how difficult it becomes for the predator to discriminate between the phenotypes of the two potential prey species. Each of the individuals in the two prey populations of senders and the one predator population of receivers was represented by a 3-layer perceptron. In this simulation it benefited both types of

senders, the original (i.e., the distasteful species) and the mimic (the tasty species), to elicit the same response from the receiver (predator) and it benefited the receiver to respond to only one sender (discriminating between original and mimic). The receiver was thus in conflict with one of the senders (as in Batesian mimicry). The most common response was for mimicry to develop due to the mimic evolving toward the original faster than the original moved away. As the two sender phenotypes converged there was selection on the receiver to discriminate along a stimulus dimension where the two senders were still distinguishable. Even after mimicry was established the model and the mimic were constantly changing in appearance.

Another example of where network choice was important to an evolutionary outcome used recurrent Elman nets (a three-layer perceptron with feedback from the third layer to the second) to investigate the evolution of species recognition in sympatric taxa [2]. In this study, mate selection by female frogs, based on the way they process the calls of conspecific and heterospecific male frogs, was the leitmotif for the specifics of the analysis. The simulations addressed the effectiveness of recognition mechanisms based on recognition of self only (Paterson's specific mate recognition model) versus those based on discrimination of self versus others (Dobzhansky's character displacement model). They were also designed to help determine the influence of interactions with other species (sound environment hypothesis) and the relative variation of signals within the species (feature invariance hypothesis) on the evolution of mating signals, as well as addressing the controversial hypothesis that selection for species recognition generates sexual selection.

Results presented in this study [2] indicated that call decoding strategies based only on self-recognition do not result in accurate species recognition while those based on discrimination of self versus others are more effective. The neural network weighted signal features in a manner suggesting that the total sound environment as opposed to the relative variation of signals within a species is more important in the evolution of recognition mechanisms. Finally, selection for species recognition generated substantial variation in the relative attractiveness of signals within the species and thus could result in sexual selection.

A similar study [14] showed that Elman nets selected to recognize or discriminate simple patterns may possess emergent biases towards pattern size or symmetry components, preferences often exhibited by real females, and investigated how these biases shape signal evolution. This study also induced the Elman nets to evolve toward responses to an actual mate recognition signal, the call of the tungara frog *Physalaemus pustulosus*. The Elman net was capable of recognizing the call of the tungara frog and made remarkably accurate quantitative predictions about how well females generalize to novel calls. These predictions were stable over several network architectures. The authors concluded that the degree to which female tungara frogs respond to a call may be an incidental by-product of a sensory system selected simply for species recognition.

Other recent studies have shown that neural networks predict signal phenotypes that have been observed in real animals. Examinations of the conflicts between sender and receiver confirm that a receiver bias for costly signals insures honest

senders, a concept well supported by studies of behavioral ecology [15,16]. Network based models often predict the evolution of preference for symmetrical signals [17,18]. Gradient interaction models, yet another form of network based species recognition models, demonstrate clearly how generalization can generate a preference for symmetrical variants of a display [19, but see 20].

4   Roach Enophiles

One of the most common uses of neural networks is in modeling the processing of sensory information in the brain. The scope of these models ranges from investigations of neural coding of simple stimuli to experiments generating realistic behavior in artificial organisms. One recent study investigated how odors are represented in the olfactory sensory system of insects [3]. The relatively simple neural network model was inspired by our current knowledge of the first synaptic layer of the cockroach olfactory system, the antennal lobes (Fig. 3). This network was used to investigate how elements of the network, such as synaptic strengths, feedback circuits and neural activation functions, influence the formation of an olfactory code in neurons that project from the antennal lobes to the mushroom bodies, the higher association area of the insect brain.
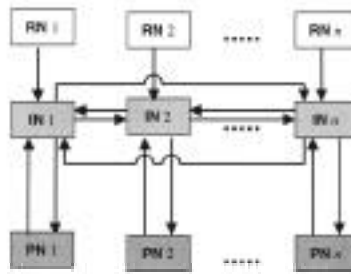

Figure 3. A schematic of the architecture underlying the neural system modeled by Getz and Lutz [3]. The arrows represent the four types of synapses: receptor neuron (RN) excitatory feed-forward onto interneurons; interneuron (IN) inhibitory feed-forward onto other interneurons; IN inhibitory feed-forward onto projection neurons (PN); and PN excitatory feedback onto IN. Projection neurons fire through disinhibition. Modified from [3].

Simulation studies of the antennal lobe network demonstrated that the network is able to produce codes independent or virtually independent of odor concentration over a given range. This concentration range is moderately dependent on the time required for voltage to decay to its resting potential in an activated neuron, strongly dependent on the strength of excitatory feedback from projection neurons onto antennal lobe intrinsic interneurons, and overwhelmingly dependent on the slope of the activation function that transforms the voltage of depolarized neurons into the rate at which spikes are produced. When excitatory feedback from the projection neurons to the intrinsic interneurons is strong, the activity in the projection neurons

undergoes transitions from initial states to stimulus specific equilibrium states that are maintained once the stimulus is removed. When the projection neuron-intrinsic interneuron feedback is weak the projection neurons are more likely to relax back to a stimulus independent equilibrium state in which case the code is not maintained beyond the application of the stimulus.

Neural networks have been used to model other sensory systems such as a three-layer, two-pathway version of on-off cells of the optic chiasm of the fly visual system [21]. This network generated a realistic three component response to on and off stimulation. At the other end of the spectrum, a phototactic network and a robot used to simulate chemotaxis by the flatworm *Caenorhabditis elegans* produced reliable phototaxis regardless of the locomotory parameters of the robot [22]. An interesting model of sensory processing and behavioral control examined prey orientation behavior of waterstriders [23]. This model had six input units representing the legs of the waterstriders detecting water vibrations and two output units controlling left turns and right turns. The model accurately predicted orientation toward disturbances in the water caused by prey. Simulated lesions in the input units produced results matching those observed in real animals.

5 Conclusions

From the studies discussed above, it is clear that neural networks models provided a powerful tool for elucidating the dynamic complexities of discriminatory processing in behavioral and evolutionary contexts. In some studies, the plausibility of existing hypotheses about choice and discrimination were examined. In most studies, new hypotheses were generated and these are now open for testing. The intellectual payoff of any particular study can only be assessed in the course of time, but the neural network paradigm has certainly become pervasive in our analyses of discriminatory processes in biology. As with all modeling paradigms in population biology, the value of applying neural networks to problems in ethology and evolution depends more on the craftsman than on the tool.

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