

How evolutionary history shapes recognition mechanisms

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Evolutionary psychologists have emphasized the importance of natural selection in shaping cognitive functions, but historical contingency has not received direct study. This is crucial because in response to selection, complex traits tend to be fine-tuned or jury-rigged rather than totally reconstructed. We hypothesize that the neural and cognitive strategies an animal employs in signal recognition are influenced by the strategies used by its ancestors. The responses of female túngara frogs to ancestral calls and to calls of other closely related species are influenced by history. By training artificial neural networks with a series of calls that mimic the species' past history of call evolution or various control histories, we have shown that only networks that evolved through the mimetic history predict the response biases of túngara frogs.

The ability to recognize others, either as individuals or as members of categories, is widespread among animals. As an example, much attention has been given to human face recognition because of its role in orchestrating social interaction and the presumably strong selection pressures that have influenced its evolution. There is serious debate as to whether face recognition is carried out by specialized modules that evolved in ancestors of humans¹, or is accomplished by more general mechanisms that attend to processing significant within-category variation². The role of history is central to this debate. How do the recognition mechanisms used today depend on our ancestors? And how does one go about studying the past?

In studies of human behavioral evolution, researchers often invoke history as an explanation for behaviors that might have been adaptive³, or conversely, as a constraint that precludes adaptive explanations of current behaviors⁴. History is rarely studied directly, but seems to be offered as a safe harbor for camps with competing ideologies regarding the efficacy of natural selection. We review a research program in which we have combined studies of acoustic perception, molecular phylogenetics and neural network modeling to investigate how history influences the evolution of recognition mechanisms used to identify conspecific mates in a group of frogs. Specifically, we address the hypothesis that the neural and cognitive strategies an animal employs in recognition tasks are influenced by the strategies used by its ancestors.

An animal's environment is rich in cues that can convey useful information. An early finding in ethology, however, showed that animals attend to only a relatively small subset of these cues – sign stimuli⁵. Sign stimuli are crucially important in communication, and different species can attend to different aspects of similar signals. For example, frogs, like many insects and birds, have distinct species-specific acoustic signals or advertisement calls that females use to evaluate potential mates⁶. Two treefrogs, the barking treefrog and the green treefrog, overlap extensively in nature and have similar types of calls⁷. Owing to the cost of hybridization, both species should be under strong selection to prefer their own call and discriminate against that of the other. There is ample information in the calls of these two species to allow accurate recognition of conspecifics and discrimination against heterospecifics. When these two species are challenged with making the same auditory discrimination (green versus barking treefrogs), however, they rely on different sets of cues; that is, they employ different computational strategies. If auditory systems of similar species have the same general properties, why don't they solve similar tasks the same way? Is there something in the animal's evolutionary history that might explain these kinds of differences in neural and cognitive bases of recognition?

Response biases and historical effects

In the scenario presented in Fig. 1, there are two simple but different strategies that prove equally accurate in distinguishing between similar and foreign signals (e.g. individuals of species *A* accept stimulus *A* and reject stimulus *B*). These strategies attend to variation in either frequency or duration. A more complicated recognition mechanism would not be more accurate; although there might be future benefits for decoding more information, selection acts only on the current situation. Furthermore, a more complicated mechanism in a real nervous system might impose additional costs both in time^{8,9} and metabolic cost¹⁰ of neural processing.

Recognition mechanisms have response biases¹¹; they will be more likely to respond to some previously unencountered signals than to others. In evolutionary biology, such incidental consequences are often distinguished from an 'intended' or evolved function¹². Previous experience (learned and evolved) influences the nature of the response bias of the receiver. For example, in Fig. 1 the responses of *A* individuals to the two newly introduced signals will vary depending on their recognition strategy: they will accept *C* and reject *D* if they are employing strategy 1, but accept *D* and reject *C* if they are employing strategy 2. If there are no costs to accepting these new signals, then we can think of the signals as exploiting the response biases of the receiver. Such sensory exploitation often happens when males evolve exaggerated traits that are pleasing to females¹³. If there are costs to accepting the new signals (*C* and *D*), we expect the recognition

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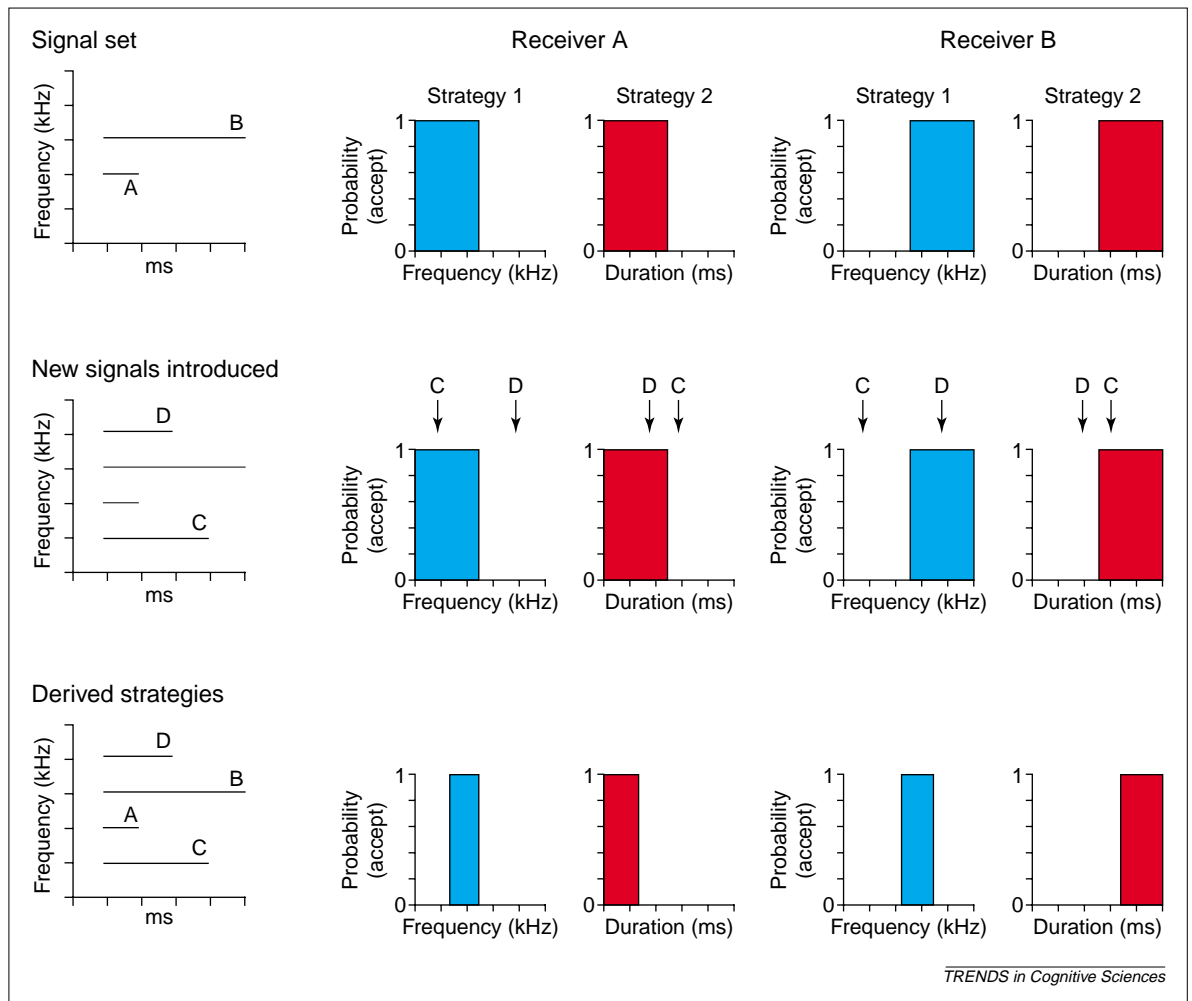


Fig. 1. A scenario for how response biases of recognition mechanisms constrain and direct their evolution. The distribution of signals in a community as a function of frequency (kHz) and duration (ms) are shown in the first column. Two strategies for recognizing the conspecific signal of individuals in taxon A (Receiver A) are shown (second and third columns), based on attending to differences in either frequency or duration. Analogous information for taxon B (Receiver B) is illustrated in the fourth and fifth columns. The top row shows the initial state of the population and the middle row illustrates signals of two introduced taxa, C and D. Histograms show the frequency and duration of these signals relative to those of A and B (left column) and whether they would be accepted or rejected by the various receiver strategies employed by A and B. The bottom row suggests how the receiver strategies of A and B would change to reject all heterospecific signals (including C and D) and accept the conspecific signal.

mechanism to change to ensure only like signals are accepted (A accept only A, B accept only B)¹⁴. But the way they do so will depend on how they had been making such decisions in the past (Fig. 1). As is well known in evolutionary biology¹⁵, complex morphologies that provide functional solutions to survival problems are not deconstructed and reconstructed in response to each selection event. Instead, they are jury-rigged innovations of the previous or ancestral conditions. We should expect the same constraints of history in the acquisition of neural and cognitive aspects of signal recognition¹⁶. Thus, in this example, we would expect an organism that employs strategy 1 to be

under selection to fine-tune its discrimination abilities along the frequency axis, and one using strategy 2 to be under selection to enhance its resolution along the temporal axis.

A number of commonly observed phenomena in human and animal psychology indicates analogous influences of prior experience on current computational strategies, including decision theory¹⁷, blocking¹⁸, positive and negative transfer¹⁹ and 'motherese'²⁰. Generally speaking, learning to attend to or ignore particular features of a stimulus shapes the probability that an organism will use those same features in future tasks²¹.

Species recognition

The scenario in Fig. 1 might seem trivially simple compared with complex tasks such as speech recognition. It is, however, a fairly accurate representation of the problem that confronts animals in species mate recognition. The most crucial recognition task facing any sexually reproducing animal is to recognize appropriate mates of the same species even if mate quality varies substantially within the species^{22,23}. This is because matings between species usually do not result in viable offspring. In identifying appropriate mates there is no premium on distinguishing between different

heterospecific signals, so the problem is simply to accept or reject a stimulus.

Response biases should play a crucial role in the evolution of recognition mechanisms. The past constellation of signals that the ancestors of a species encountered should influence the recognition mechanisms used by current species, analogous to the situation we outlined in Fig. 1. This logic generates predictions that can be tested with behavioral experiments, as well as artificial neural network models. We have approached this problem with studies of species recognition in a group of frogs that has emerged as a useful model system for examining historical contingencies.

Historical effects on mate recognition in túngara frogs

The acoustic mate recognition system of the túngara frog, *Physalaemus pustulosus*, has been the subject of a number of behavioral, neurophysiological and phylogenetic studies^{24–26}. Male túngara frogs produce species-specific advertisement calls that females assess in choosing mates of the correct species. The túngara frog is a member of the *Physalaemus pustulosus* species group. There are five species in the group. The range of the túngara frog is throughout Middle America and in northern South America. All other species are found in South America. The only region in which the túngara frog is found with other species of *Physalaemus* is in a small area of Venezuela and Colombia. It is thought, therefore, that interactions with other close relatives have had little influence on the formation of the mate-recognition mechanism of the túngara frog. Although túngara frogs must recognize the calls of their own males compared with calls of other species with which they breed, the lack of interactions with close relatives allows us to disentangle the role of evolutionary history and current ecological interactions in our study of this species group.

Responses biases to calls of ancestors?

The goal of these studies was to determine to what extent phylogenetic history influenced response biases in mate recognition. Therefore, we determined the historical or phylogenetic relationships among the taxa (Box 1). The phylogenetic distance or degree of relatedness between the túngara frog and other species was derived from comparisons of DNA sequences between the pairs of species. We also measured the similarity of calls between the same pairs of species. There was not a significant correlation between phylogenetic distance and call similarity.

To investigate how the stimulus parameters of signals in the past influenced the recognition strategies túngara frogs use now, we need to have some idea as to what these signals were. We used a variety of techniques to estimate individual call parameters and then synthesized calls for each of the ancestors represented on the phylogenetic tree (Box 1). Female túngara frogs were then tested for recognition of heterospecific and ancestral calls (Box 1).

In general, phenotypic traits tend to be similar among closely related species. The lack of such a relationship among the calls of the *Physalaemus* species tested, however, allows us to partition the influence of past history (i.e. phylogenetic distance) and overall signal similarity on responses to mating calls. We used a multiple regression to estimate how strongly female phonotactic responses were influenced by the overall similarity of the test call to the túngara frog call and by the phylogenetic distance between the túngara frog and the heterospecific ancestor. In the recognition experiments, call similarity and phylogenetic distance explained 48% and 31%, respectively. Thus, history, independent of any effect of the overall similarity of the test calls to the túngara frog call, explains substantial variation in the degree to which females recognize calls. What might be the basis of this historical effect? One possibility is that the presence of salient signal properties that strongly influence túngara frog phonotaxis are more likely to be present in closer relatives, past and present. This supports the more general notion that the recognition tasks that confronted ancestors influence how current species perform the same task.

Artificial neural networks and historical landscapes

We extended the approach of reconstructing ancestral calls by simulating the evolution of the receiver through various 'evolutionary histories'. We trained a population of recurrent artificial neural networks with frog calls^{27,28} (Box 2). To train the networks, we used a genetic algorithm that mimicked the evolutionary processes of natural selection, mutation and recombination.

The networks were trained to one of three series of calls, always being trained with the túngara frog call last. In one series, the mimetic history, calls to which the networks were trained mimicked the evolutionary pathway through which the túngara frog call evolved [*root* → *c* → *d* → *pustulosus* (túngara frog); Box 1]. In the random history series, we trained networks with a randomly selected sequence of three calls from the set of heterospecific and ancestral calls before training them with the túngara frog call (Box 1). This was replicated with 20 different random histories. In the mirrored history series, we synthesized three calls that were as similar to the túngara frog call as were the calls at the *root*, *c* and *d* nodes, but whose differences were opposite in direction (see explanation in Box 2). Again, the final call used to train the networks was the túngara frog call.

After training was completed, we measured the response of the networks to a variety of stimuli, including the heterospecific and ancestral calls, with which we had tested real females. We determined the degree to which the networks' responses predicted the responses of real túngara frogs. Only the networks trained with mimetic history call series significantly predicted the responses of real females (Box 2).

Box 1. Phonotaxis and ancestral calls

We used phonotaxis experiments to assess female responses to signal variation. Females are presented with stimuli from two speakers on opposite ends of an arena; either a heterospecific call or white noise^a. The female's approach to the speaker producing the call indicates she recognizes it as indicating an appropriate mate. A female that does not respond to either stimulus is then tested with the conspecific call to determine if her lack of response is due to lack of motivation rather than lack of signal saliency.

We measured seven call variables (Fig. 1) of the call's dominant frequency sweep for each of the eight species we studied^a: maximum and final frequency, the shape of the frequency sweep, the rise time and fall time, and the shapes of rise and fall time (duration was the sum of rise and fall times in the calls we analyzed). A túngara frog call synthesized using only these variables is not distinguished from a natural call by females^b. We then used these same call variables of the relevant species to synthesize calls of close relatives and to estimate the calls of ancestors. To do this, though, we first needed to determine the phylogenetic relationships among the species in the túngara frog species group.

Phylogenetic relationships were deduced primarily from comparisons of mitochondrial DNA sequences^c. The tree depicting these relationships is shown in Fig. 1Ia,b. The real species are labeled at the tips of the branches, and the ancestors are represented at the nodes (Fig. 1Ib, *a-f* and *root*). To illustrate this approach, we show the duration of the advertisement call of each of the eight real species (Fig. 1Ia). *P. pustulosus* is the túngara frog, and its call has an average duration of 370 ms. *P. petersi* is the túngara frog's closest relative or 'sister species', its call duration is 246 ms. These two species share a common ancestor (*c*; Fig. 1Ib). Using methods to estimate ancestral call variables^a that are based on parsimony and derive values that tend to

minimize the amount of evolution over the phylogenetic tree^d, this ancestor had a call of 333 ms duration.

We repeated this estimation process for all of the other call variables described in the Fig. 1. We then used these estimates of the seven call variables to synthesize calls for each ancestral node (see call sonograms for *a-f* and *root*; Fig. 1Ib). These ancestral calls are statistical estimates based on a number of assumptions about how evolution proceeds. Results did not vary substantially among the seven different 'models' we used to estimate ancestral calls^e.

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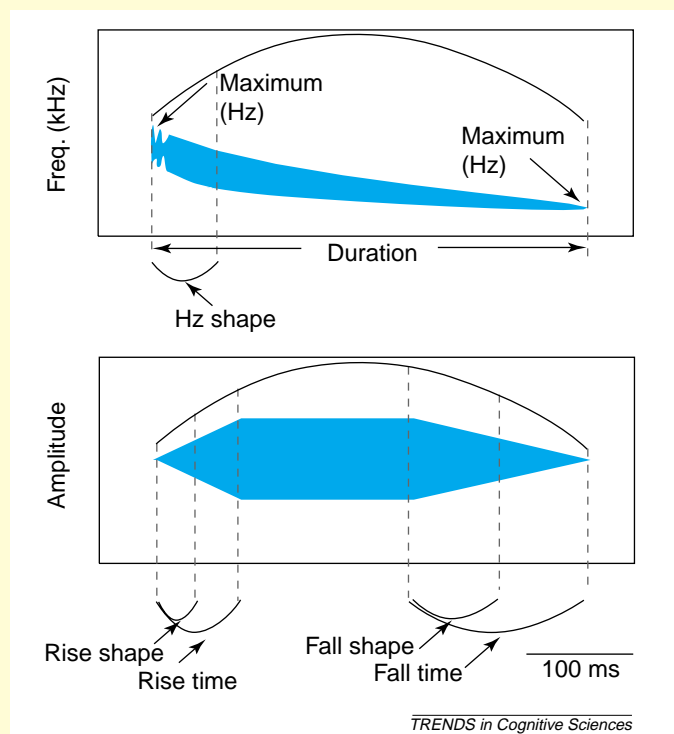


Fig. 1. The call variables measured in phonotaxis experiments (see text for details).

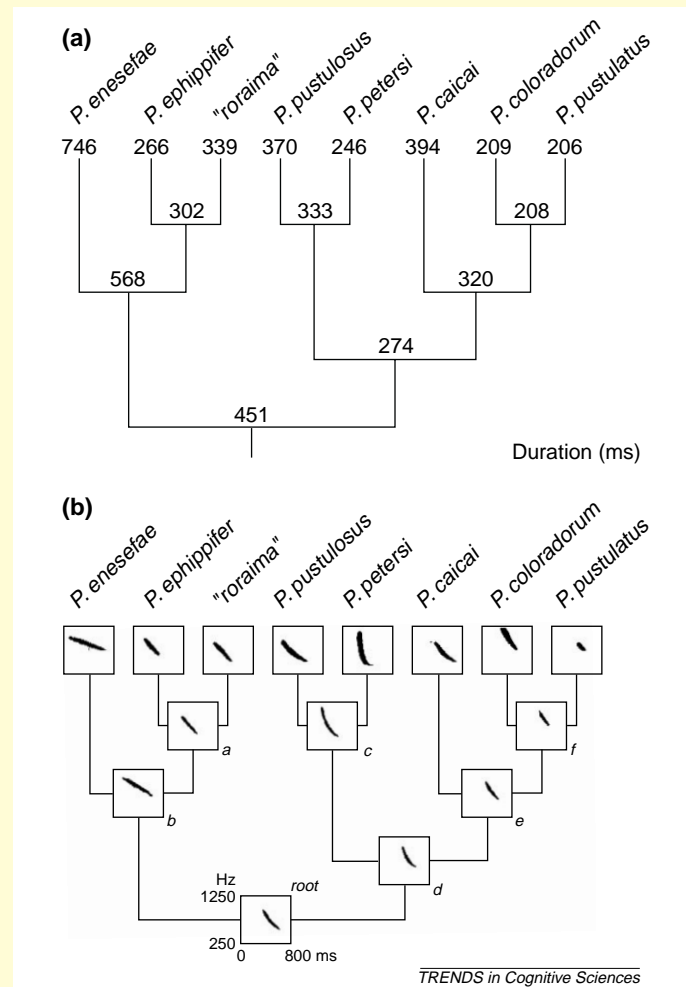


Fig. 2. (a) Phylogenetic tree showing the relationships among túngara frog species. Average call durations are shown for the eight existing species, and those of the common ancestors are estimated using methods that tend to minimize the amount of evolution over the phylogenetic tree. (b) Call sonograms for the eight frog species and for their ancestors.

Box 2. Artificial neural networks in animal communication

We used an artificial neural network, similar to the simple recurrent or Elman net^a commonly used in linguistics, to simulate historical effects on response biases of receivers^{b,c} (Fig. 1a). Synthetic frog calls were used as stimuli in a time by frequency matrix with relative amplitude represented as the cell value. We assigned weights at random to 100 different networks, then selected networks that were best able to discriminate a target call from noise in a matching amplitude envelope with information among frequencies scrambled (Fig. 1b). After a round of selection and reproduction, new variation was introduced by 'mutation', in which we randomly changed values of weights, and by 'recombination', in which weights of two parent networks were interchanged to produce two new daughter networks. These manipulations produced a new generation of 100 networks that could be refined through further selection. This evolutionary procedure, known as a genetic algorithm, is a common means of training neural networks^{d-f}. Although changing some details of the network architecture influenced the rate of evolution, it did not affect the final responses of the networks (S.M. Phelps, PhD thesis, University of Texas, Austin, 1999).

To provide networks with an evolutionary history, we trained them with a sequence of four calls, the final call always being the túngara frog call (see Box 1). When networks could accurately recognize the first call we trained them with the second and continued the process until they were trained with the túngara frog call. We varied the sequence of calls, analogous to varying their evolutionary history, in three ways. One particular sequence, the mimetic history, included the calls of only the direct ancestors of the túngara frog (*root* → *c* → *d* → *P. pustulosus*; see Box 1). A second sequence, the random history, used three calls chosen at random from the clade of extant and ancestral calls for this species group (see Box 1). We used a different random history in each of 20 replicates. Because networks evolved through a random history were selected to recognize a more diverse set of stimuli, and this diversity could influence

their response biases, we gave a third group of networks calls in a sequence called the 'mirrored' history. These three mirrored calls were synthesized to be as different from the túngara call as the *root*, *c*, and *d* calls, but the difference was in the opposite direction. Although we did this using a multivariate manipulation, we can use a simple univariate example to illustrate this approach. The duration of the túngara frog call is 370 ms (*P. pustulosus*, Box 1) and that of the *root* call is 471 ms, 81 ms longer. Thus a mirrored *root* call could be synthesized that is 81 ms shorter than the túngara frog call, or 289 ms. The actual mirrored calls were calculated using an acoustic space defined by a principal components analysis of call variation within this clade (details are published elsewhere^e).

We determined how accurately the networks predicted the response of real females to the same calls. We plotted the proportion of females tested ($n=20$) that responded to each stimulus versus the average output of the trained networks to the same stimulus. The neural networks that were trained to calls of the mimetic history were better at predicting the response biases of real females ($r=0.56$, $n=34$ stimuli in all cases) than were networks trained to calls of the two control histories [mirrored, $r=0.32$; random, $r=0.20$; the relative support of mimetic versus random was given by the log-likelihood ratio, $\lambda=169.2$, mimetic versus mirrored $\lambda=89.6$; both results are analogous to $P<0.001$ (Ref. c)].

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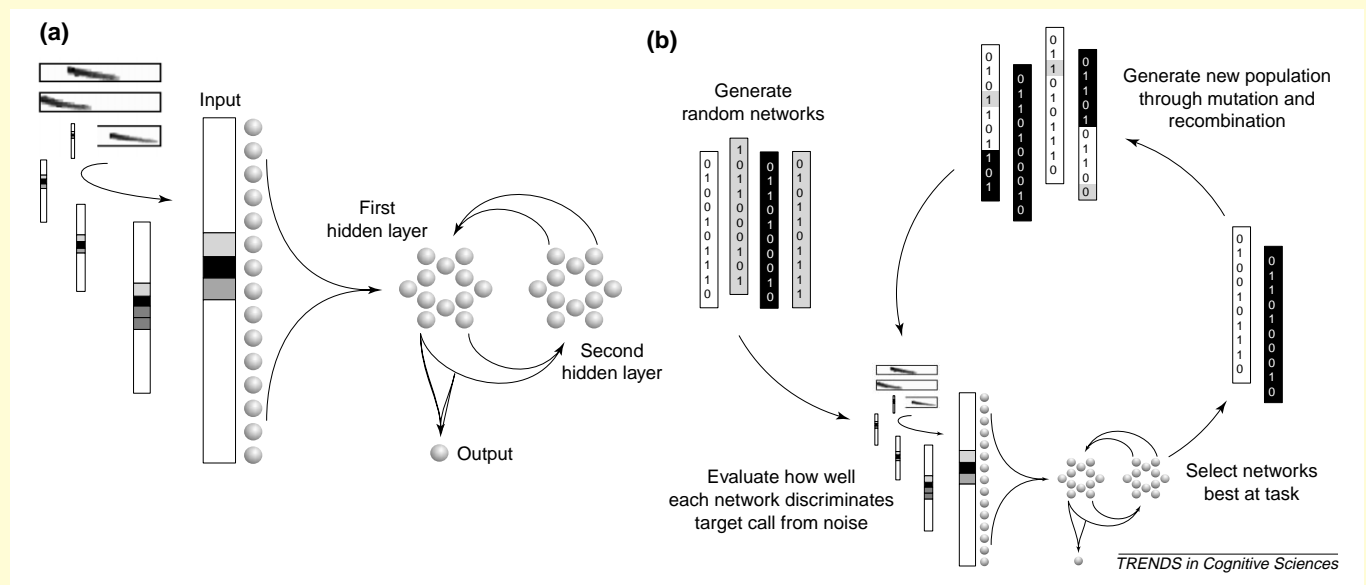


Fig. 1. (a) Simple recurrent neural network commonly used in linguistics. (b) Networks generated using a genetic algorithm to discriminate túngara frog calls (see text for details).

By combining the use of artificial neural networks with phylogenetic reconstruction of ancestral signals we have been able to demonstrate that the past history of recognition tasks influences response biases of current receivers. By showing that networks with mimetic histories accurately predict the response biases of real frogs, we conclude that such historical effects are significant in real world systems. The fact that only networks with the mimetic history predict the behavior of real frogs also adds credence to our predictions of ancestral calls, which seems to reconstruct those acoustic features that have influenced the evolution of mate recognition in túngara frogs. This is despite the fact that overall call similarity and phylogenetic distance are not significantly correlated.

These results have parallels in other systems. Among some domesticated animals there is cross-cultural convergence in the acoustic structures that humans use in training them²⁹ that might be due to the bias of the animal to associate certain sounds with certain activities³⁰. In addition, humans systematically overestimate the covariation of a snake or spider stimulus with a shock when they are presented pictures of mushrooms, flowers, snakes or spiders randomly followed by a shock, a tone or silence³¹. These results are similar to other studies of 'infrahumans'. It seems that the human covariation bias is a remnant of our history.

In a classic but now neglected essay, 'The misbehavior of organisms', Breland and Breland review their attempts to train a wide variety of animals in operant paradigms³² – tasks that range from teaching raccoons to use a bank, to teaching

chickens to play an arcade game. Contrary to the then prevalent dogma of behaviorism, they found that animals came to the laboratory as anything but blank slates. Instinctive behaviors relevant to 'food-getting' often precluded the display of simple conditioned behaviors. Evolutionary history seems very much analogous to prior training.

Concluding remarks

The evolutionary process has influenced neural and cognitive functions in animals, including humans. Much of the emphasis in evolutionary studies of animals, and especially in evolutionary psychology studies of humans, has been on the crucial aspect of how selection favors function. Another aspect of evolution is historical contingency. It is well known that complex traits tend to respond to selection by fine-tuning or jury-rigging extant features of the phenotype. Studies in evolutionary psychology have emphasized adaptive scenarios in interpreting human behavior, but have been far less lucid in directly testing, as opposed to merely positing, the notion that historical contingency influences why we think and act as we do. Although such a logic is well corroborated in studies of morphology and physiology, it has only recently been applied to higher level neural and cognitive function. Here, we have argued that such historical biases should influence the function of animal recognition systems, that this hypothesis can be addressed by combining phylogenetic information with behavioral experiments and artificial neural network simulations, and that available studies of human cognition can be interpreted in such a light.

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