History influences signal recognition: neural network models of túngara frogs

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Animals often attend to only a few of the cues provided by the complex displays of conspecifics. We suggest that these perceptual biases are influenced by mechanisms of signal recognition inherited from antecedent species. We tested this hypothesis by manipulating the evolutionary history of artificial neural networks, observing how the resulting networks respond to many novel stimuli and comparing these responses to the behaviour of females in phonotaxis experiments. Networks with different evolutionary histories proved equally capable of evolving to recognize the call of the túngara frog, *Physalaemus pustulosus*, but exhibited distinct responses to novel stimuli. History influenced the ability of networks to predict known responses of túngara frogs; network accuracy was determined by how closely the network history approximated the hypothesized history of the túngara frog. Our findings emphasize the influence of past selection pressures on current perceptual mechanisms, and demonstrate how neural network models can be used to address behavioural questions that are intractable through traditional methods.

Keywords: animal communication; mate recognition; neuroethology; phylogenetic methods; sensory bias; sexual selection

1. INTRODUCTION

Animals are often able to recognize stimuli that display only a few key features of a natural signal, or that lie well outside the natural range of trait expression (Tinbergen 1951; Hauser 1996; Bradbury & Vehrencamp 1998). The stimuli that evoke responses from receivers, for example the postal truck that elicits threats from a male stickleback fish, reflect underlying perceptual mechanisms involved in signal recognition (Tinbergen 1952; Krebs & Dawkins 1984; Hauser 1996). These perceptual mechanisms result in biases toward particular signal forms, and so delineate viable axes of signal variation. Data from several taxa demonstrate that receiver biases often predate the evolution of preferred signal forms (Basolo 1990; Ryan 1990; recently reviewed in Endler & Basolo 1998; Ryan 1998), and highlight the importance of biases in the evolution of animal signals (see also West Eberhard 1979; Guilford & Dawkins 1991; Endler 1992). Despite these data, the evolutionary forces responsible for such biases remain poorly understood.

Artificial neural network models hold particular promise for investigations into the bases of receiver biases (Enquist & Arak 1993, 1994; Johnstone 1994; Phelps & Ryan 1998). These simulations are composed of interacting neuron-like units that have the surprising and convenient property of behaving like real nervous systems both at fine levels of representation and at gross levels of behaviour (Linsker 1986; McClelland & Rumelhart 1986; Montague *et al.* 1995; Phelps & Ryan 1998). We recently demonstrated that neural network models are capable of evolving to recognize a mate-recognition signal, the call of the túngara frog, and that the resulting networks are adept at predicting female responses to novel stimuli (Phelps & Ryan 1998).

We used artificial neural networks to investigate how the evolutionary history of a receiver influences its current response properties. Although the idea of historical contingency is central to much of evolutionary biology, it remains problematic because researchers rarely have the opportunity to alter historical events and observe the outcome in descendant taxa (but see Travisano *et al.* 1995). Artificial neural network models, and the wealth of empirical data obtained from studies of the túngara frog enabled us to manipulate the past history of the receivers, to observe the resulting response biases and to compare how well the responses of networks with different histories correspond to the responses of real females.

We used a recurrent neural network architecture (figure 1) known to be capable of reproducing the response biases of female túngara frogs (Phelps & Ryan 1998). We trained the networks using a genetic algorithm (Smith *et al.* 1994), selecting them to accept a stimulus representing a conspecific signal and reject a stimulus representing noise in a matching amplitude envelope. (This discrimination between a conspecific stimulus and a null stimulus corresponds to an operational definition of 'recognition' used in behavioural experiments (Ryan & Rand 1995).) As in biological evolution, the target 'conspecific' signal changed over time. For networks evolved through a 'mimetic' history, the sequence of target calls approximates the historical trajectory of túngara frog calls (Ryan & Rand 1995), beginning with the reconstructed root call of the clade and ascending through each subsequent node until reaching the call of the túngara frog. In two control treatments, the random and mirrored histories, a population of networks again evolved through a series of ancestral target calls followed by the call of the túngara frog. In each of the control histories, however, the ancestral sequence does not approximate the history hypothesized for túngara frogs or any other species. All of the neural networks were ultimately selected to recognize the call of the túngara frog,

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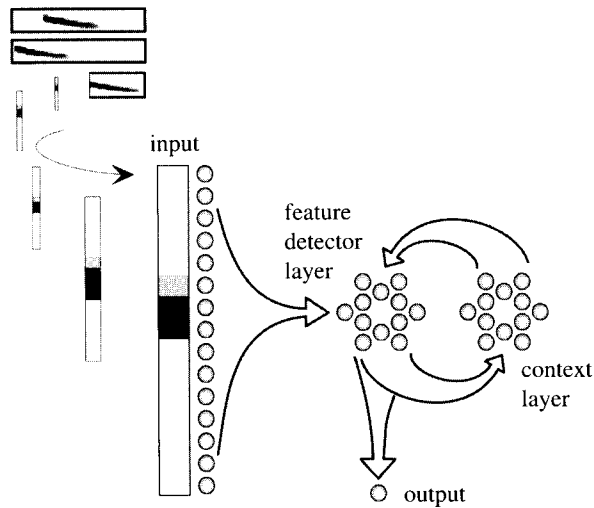1633

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Figure 1. Schematic of the recurrent neural network architecture. The circles depict nodes, or neurons, in the network. Neurons are arranged into four layers: the input layer, 'feature detector' layer, 'context' layer and output layer. Large arrows represent efferent connections in which every neuron in one layer projects to every neuron in another. The upper left hand corner of the figure depicts three spectrograms, in which each pixel represents the relative intensity of sound energy in a corresponding range of frequencies (rows) and times (columns). A single column from a spectrogram is presented to the network's input layer in each time-step. While the input-layer neurons calculate their activities based on the current frequency vector, neurons in the 'feature detector' layer calculate their activities based on the activities of input-layer and 'context'-layer neurons in the preceding time-step. 'Context' and output neurons do the same based on their inputs. The activity of the output neuron at the end of 70 time-steps is defined as the network response to a stimulus. Each time-step corresponds to *ca.* 11 ms of the sound stimulus.

but differed in the signal recognition tasks performed by ancestral populations.

If evolutionary history shapes receiver biases, and if neural network models reflect the perceptual mechanisms of real receivers, two predictions follow: first, networks with different histories should show different responses to test stimuli; and second, neural networks with an evolutionary trajectory approximating the hypothesized history of the túngara frog should be best at predicting the responses of female túngara frogs to novel stimuli.

2. METHODS

(a) *Neural network simulations*

We used a recurrent neural network architecture (described in Phelps & Ryan 1998) consisting of an input layer, a 'feature detector' layer, a 'context' layer and an output neuron. Every neuron receives input from a particular subset of neurons and computes its own activity based on the weighted sum of the activities of its inputs. The network architecture is summarized in figure 1.

The input layer consisted of 15 neurons, each responding selectively to a frequency range of 86.93 Hz. The total frequency range spanned from 261 Hz to 1565 Hz. The 'feature detector' layer consisted of 12 neurons; each received input from every neuron in the input layer and the 'context' layer, and sent

efferent projections to each of the 12 neurons in the 'context' layer and to the output neuron. Each neuron of the 'context' layer received input from all of the neurons of the 'feature detector' layer, weighted these inputs differently and possessed a sigmoid activation function exactly like that of the neurons in the rest of the network (unlike the simple recurrent network, also known as an Elman network (Elman 1990)). Each neuron also received input from a bias neuron (not shown in the schematic), which was tonically active. (A tonically active bias neuron is always maximally active—defined as an activity level of 1.0. Neurons may weight the bias neuron input differently, so the weighted sum of inputs is offset by a fixed amount that is encoded in the network's chromosome, effectively allowing neural thresholds to evolve.) The activation function and other architectural details have been published elsewhere (Phelps & Ryan 1998).

(b) *Genetic algorithm*

Each network was represented as a chromosome consisting of 3282 bits, representing 547 network weights, each coded as a six-bit string. We evolved populations of networks using a modified version of Goldberg's simple genetic algorithm in *C* (Smith *et al.* 1994) and roulette-wheel selection. Networks were selected for a capacity to discriminate calls from noise in the same amplitude envelope, with the fitness function defined as

$$F \equiv \sqrt{\sum_{i=1}^{n} (C_i - N_i)^2 / n + 0.01}, \tag{1}$$

where *F* is fitness, C_i is the response of the network to call *i*, N_i is the response of the network to noise *i* and *n* is 3, the number of stimuli tested for a single call. The parameter 0.01 represents a small constant added to the fitness of each network to retard premature convergence of the genetic algorithm (Phelps & Ryan 1998).

If a chromosome successfully reproduced, mutation occurred with a probability of 0.001 at any single bit. Chromosomes for the daughter population were selected in pairs, and the probability of recombination between these chromosomes was 0.5. Recombination was equally likely at any point along the chromosome. Population sizes were always 100. A population of networks was selected to recognize the target call until meeting predetermined criteria (achieved when the fittest individual in the population had a fitness of at least 0.90 and the population's average fitness was at least 0.75) for two consecutive generations. Meeting these criteria caused the target call to switch to the next in the historical sequence. When the criteria were met for the túngara frog call, the simulation was terminated and the weights of the fittest individual network in the population were recorded.

This procedure ensures that networks recognizing túngara frog calls do so with mechanisms derived from those used to recognize ancestral signals. While this enables one to control ancestral recognition tasks, it entails a simplification: at the transition from one target call to the next, receivers are selected to recognize a novel signal that is fixed in the population. Although similar selection pressures have been suggested to emerge during founder events in Hawaiian *Drosophila* (Kaneshiro 1976, 1983), we do not suggest that female túngara frogs or their ancestors have been selected to track major changes in species recognition signals.

(c) *Historical trajectories*

Mimetic histories consisted of three 'ancestral' calls reconstructed from the calls of the extant taxa as previously described (Ryan & Rand 1995). Ryan & Rand (1999) estimated hypothetical ancestral calls using a variety of additional models and reconstruction methods. Their data indicate that various estimates of ancestral call states led to the same conclusion: that females appear to exhibit preferences that are influenced by evolutionary history. For simplicity, we used the reconstructions originally reported in Ryan & Rand (1995).

We constructed a random history by randomly selecting three 'ancestral' calls from the extant taxa and reconstructed ancestral calls of the *Physalaemus pustulosus* species group, which were then followed by the call of the túngara frog. No two ancestral calls in a single random history were the same. Although there was substantial overlap in the calls of the 20 random histories, no two of the 20 random histories were identical.

Selection to recognize novel traits can lead to a non-specific increase in receiver permissiveness, and prior data indicate that even ahistorical networks selected to recognize the túngara frog call tend to over-generalize (Phelps & Ryan 1998; Phelps 1999, 2001). The calls of the random histories were often more different from one another than were the calls of the mimetic history, implying that a poor predictive power of random networks might be attributable to stronger selection for gross permissiveness. (Differences in the diversity of target calls are particularly apparent when one compares the coordinates of each call in the acoustic space defined by a principal components analysis (PCA) of the extant and ancestral calls, illustrated in figure 2a.) Consequently, comparisons between random-history networks and mimetic-history networks (as well as between these networks and the ahistorical networks previously reported (Phelps & Ryan 1998)) confound two attributes of evolutionary history: past selection for gross increases in receiver permissiveness, which seems unlikely to have an analogue in female túngara frogs; and the emergence of current recognition mechanisms from ancestral mechanisms, which is the focus of the current study.

To determine whether the external validity of network predictions could be attributed to differences in ancestral recognition mechanisms, we constructed a third history type that controlled for the path length of the historical trajectory. The mirrored history was constructed by flipping the coordinates of the mimetic history in acoustic space to create something analogous to a multidimensional mirror image of the mimetic history. Although identical to the mimetic history in path length, the ancestral calls that result do not correspond to any known or hypothesized natural calls.

PCA is often used to find orthogonal axes of variation corresponding to hidden, independent factors that underlie variation imperfectly described by the variables arbitrarily chosen for measurement by investigators (Stevens 1996). Since the variables defined by a PCA lie at right angles to one another and are defined by patterns of natural variation, the Euclidean distances between calls in PCA-space form biologically reasonable estimates of dissimilarity.

We synthesized the mirrored history by performing a multidimensional rotation of the mimetic history's trajectory through the acoustic space defined by a PCA for calls of this species group (Ryan & Rand 1995). Twelve variables were used in this analysis, resulting in 12 different component axes. For each axis, we took the difference between the component score for each mimetic ancestor and the component score for the túngara frog.
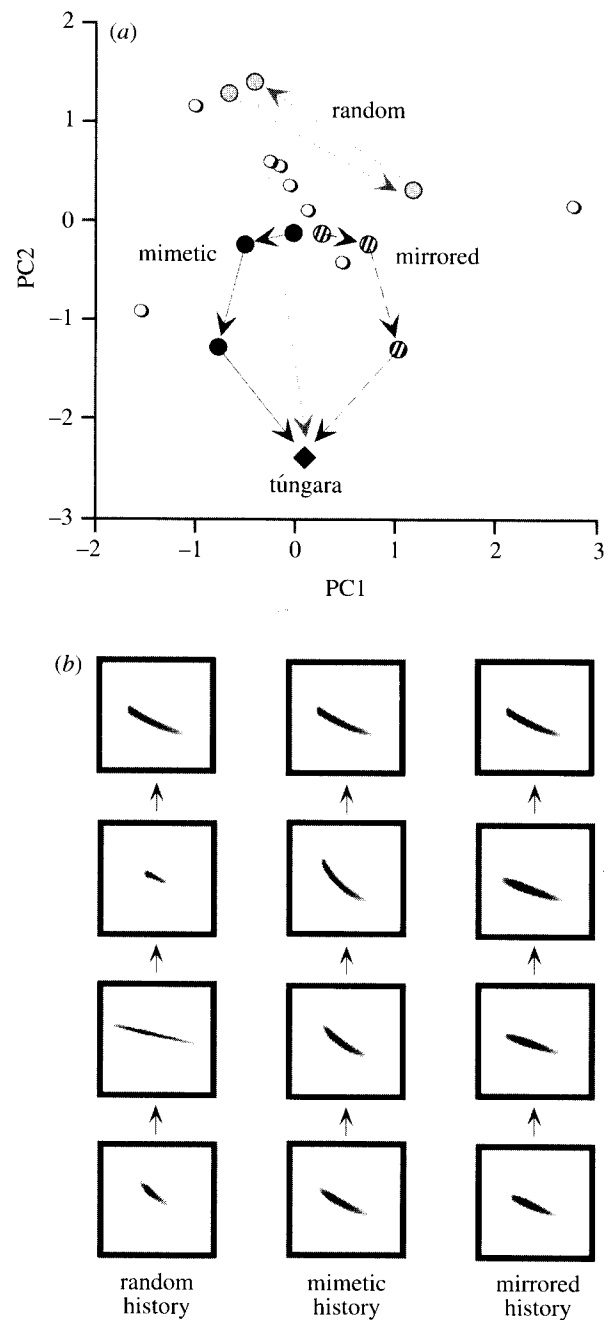

Figure 2. Historical trajectories assigned to populations of networks. (*a*) First two principal components for the various history types. Reconstructions of the ancestral calls of the *P. pustulosus* species group provided calls used for both mimetic- and random-history groups. The mimetic history (black circles) consisted of calls reconstructed for the three direct ancestors of the túngara frog, followed by the túngara frog call. The random history displayed (stippled circles) is one of 20 that were used; the open circles display the remaining extant and 'ancestral' members of the species group, from which additional random histories were assembled. To control for differences in the overall 'path length' of the historical trajectory, we constructed a mirrored history (striped circles) by flipping the coordinates of the mimetic history in acoustic space to create something analogous to a multidimensional mirror image of the mimetic history. (*b*) Sonograms of the calls comprising the three history types. Each square is 600 ms long and spans from 0 to 1.5 kHz.

We reversed the sign of this difference and added it to the component score for the túngara frog. This produced a new component score for a 'mirrored' ancestor that was equidistant from the túngara frog call but opposite the corresponding 'mimetic' ancestor in acoustic space. We were able to do this for all but two of the component scores (flipping components 2 and 4 resulted in calls that were undefined, so the component scores from the mimetic histories were used; because the axes defined by the PCA were orthogonal, we were able to manipulate some axes without manipulating others while preserving correlations between call variables). The resulting component scores for each call of the mirrored history were entered into the set of 12 equations defined by the PCA. We then solved for the original call variables and synthesized the resulting calls. A graph of scores for the first and second components provides a two-dimensional depiction of what was executed mathematically in 12 dimensions (figure 2a).

It can be difficult to conceptualize rotations performed in a 12-dimensional space defined by axes (principal components) resulting from a complex transformation. Although the original call variables can interact with one another in complex ways, attending to just those variables that load most heavily on the first few components can make the procedure more intuitive. Variables that describe how the call changes in time (e.g. time to half frequency, call duration and amplitude rise time) load heavily on the first component. Final call frequency and dominant frequency load heavily on the second component and initial frequency heavily on the third. Mirrored calls were rotated about the first component: these ancestors have a more shallow frequency sweep (longer time to half frequency) than do mimetic ancestors. In contrast, the second component was not mirrored and both histories exhibit similar final frequencies. Rotating about the third component resulted in mirrored ancestors that have consistently lower initial frequencies than their corresponding mimetic ancestors. The relationship between PCA-space and call structure is clearest when comparing the sonograms for ancestors of the mirrored and mimetic histories: the closer the ancestors of the two histories lie in the PCA-space, the more similar the sonograms of the calls appear (figure 2, the two-dimensional map is naturally an imperfect description of 12-dimensional space). Although it is informative to know precisely how the PCA-space corresponds to the original call variables, for our purposes it is far more important that the mirrored history precisely matches the call diversity of the mimetic history but traverses a different region of call space.

(d) *Network responses*

We performed 20 replicates of each history, resulting in 20 representative networks for the mimetic, random and mirrored histories. We tested how well these networks responded to 34 different stimuli and compared their responses to those of female túngara frogs. Network responses were defined by the fitness function used in the genetic algorithm, in which C_i is now defined as the response to a test stimulus and N_i is the response to noise in an amplitude envelope matching the test stimulus.

Fifteen test stimuli represented the extant and hypothetical ancestral calls of the clade (figure 3) and 19 represented various intermediate states between extant species (see Phelps & Ryan (1998) for sonograms of the 19 intermediate test stimuli). All stimuli were descending frequency sweeps with initial frequencies between 850 and 1250 Hz and final frequencies between 375 and 700 Hz. Durations of the calls ranged from 200 to 750 ms. For a given call, we used the average response of the networks to

predict the average response of females in phonotaxis experiments.

(e) *Female responses*

Females were allowed to acclimate for 3 min in the centre of a testing chamber 3 m wide by 3 m long. A call stimulus was presented every 2 s from a speaker at one end of the arena; the noise stimulus was presented from an opposite speaker 180° out of phase with the first, so that each stimulus was presented alternately from its respective speaker. Both stimuli were played at a peak amplitude measured to be 82 dB sound pressure level (re: 20 μPa) in the centre of the arena.

Females approaching the test stimulus within 15 min of testing were scored as responding; females approaching the noise stimulus, or failing to approach either stimulus, were scored as not responding. Each stimulus was tested on 20 females. The proportion of females responding to a stimulus was recorded as the average female response. Additional details of testing have been published elsewhere (Wilczynski et al. 1995).

(f) *Statistical analysis*

To compare the predictive power of the different network types, we calculated the magnitude of the error (difference between predicted and observed proportions of females responding) for each of the 34 stimuli. We used two-tailed t-tests to determine whether networks subject to mimetic histories had smaller average errors than random- or mirrored-history networks.

We also used a likelihood ratio test to compare the relative support for each hypothesis. Specifically, we tested the hypothesis that the mimetic-history networks are better at predicting female responses in a binomial choice test than networks with either of the two control histories.

We interpret the response of a network as predicting the probability that a female will approach the test stimulus in a two-way phonotaxis experiment (Phelps & Ryan 1998). In this case, the network response specifies a binomial distribution of female responses to a given stimulus. Consequently, a network's responses can be regarded as a simple hypothesis (*sensu* Kendall et al. 1991) of 34 dimensions, each corresponding to one stimulus. The likelihood of one hypothesis is proportional to the probability of observing the results given the hypothesis. Because the hypotheses are simple, the total support for one hypothesis, H_1, relative to another, H_2, is given by the log-likelihood ratio

$$\lambda = \sum_{i=1}^{34} \ln[\, p_i^r \,(1-p_i)^{n-r} / p_i'^{\,r} \,(1-p_i')^{n-r}\,], \qquad (2)$$

where p_i is the probability a female will approach a speaker in response to stimulus i, as predicted by H_1; p_i' is the probability predicted by H_2; r is the number of females approaching a speaker; and n is the number of females tested (see Edwards (1972) for similar tests). A λ greater than 3 is equivalent to rejecting H_2 at an α level of 0.05, and λ greater than 4.6 is equivalent to rejection at an α level of 0.01.

For descriptive purposes, we present correlations between the average responses of networks of a given history and the average responses of females. We do not consider these correlations suitable for hypothesis testing because of heteroscedasticity in the data.

3. RESULTS

Qualitatively, the responses of the mimetic-history networks were more closely correlated with the
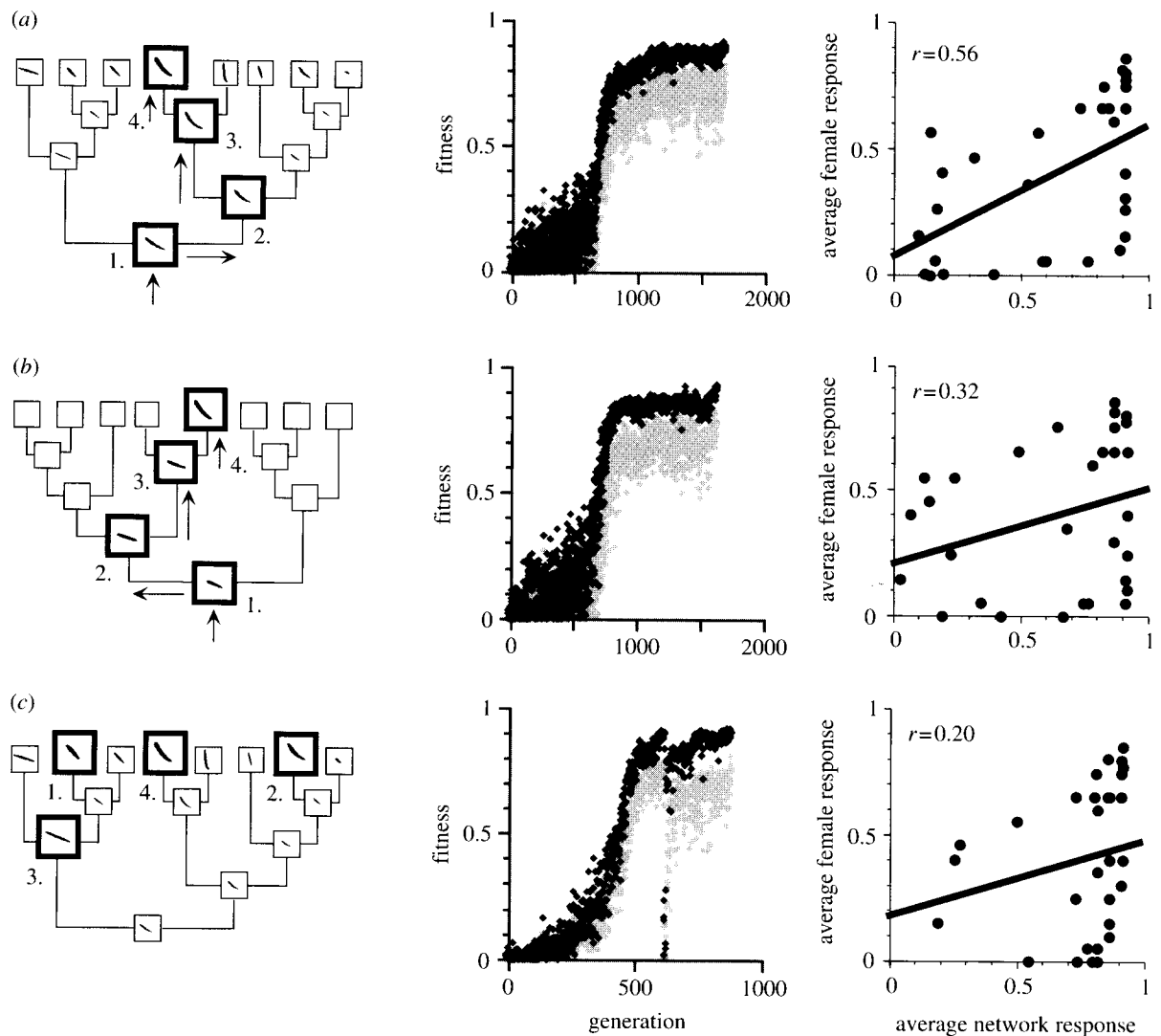
Figure 3. Evolution of networks along different historical trajectories. (*a*) The left panel represents the historical trajectory of mimetic-history networks. The calls, presented as sonograms, are embedded in a phylogeny including the ancestral reconstructions previously published for this species group (Ryan & Rand 1995). The centre panel illustrates changes in the fitness of a population of networks over one representative run. Each black diamond corresponds to the fitness of the best network in a population, each grey diamond to the average fitness of the population. The right panel displays the average network response (*x*-axis) and female response (*y*-axis) to each of 34 test stimuli. (*b*) Evolution and responses of neural networks provided with a mirrored history. (*c*) Evolution and responses of networks provided with a random history.

behaviours of real females ($r = 0.56$) than were the responses of the two control histories (mirrored, $r = 0.32$; random, $r = 0.20$). Two-tailed paired t-tests revealed that the mimetic-history networks displayed significantly smaller errors in predicting female responses than networks with either a random or a mirrored history (mimetic versus random, $p < 0.05$, $n = 34$; mimetic versus mirrored, $p < 0.01$, $n = 34$).

Comparisons of the relative support for the various hypotheses using likelihood ratio methods produced similar results. When mimetic-history networks (H_1) were compared to mirrored-history networks (H_2), we found $\lambda = 89.6$ ($\lambda > 4.6$ analogous to $p < 0.01$). When mimetic-history networks were compared to random-history networks, we found $\lambda = 169.2$. All measures indicate that mimetic-history networks were significantly better at predicting the responses of females than were networks produced by either of the control histories.

Interestingly, the transitions between calls in the mimetic- and mirrored-history networks do not seem to produce large drops in fitness, suggesting that generalization between ancestral calls and the next node in the trajectory occurs fairly easily (see centre column panels of figure 3). Such seamless transitions make sense given that males are restricted to calls that conform to the extant biases of females. In the random history, such a fitness drop was most pronounced when switching from the first to the second call in the trajectory, but decreased thereafter. This presumably underlies the heightened permissiveness observed in networks that completed a random history. The data in figure 3 illustrate how networks with any of the history types over-generalize to novel stimuli (most conspicuous in the responses of random-history networks). Elsewhere we have combined these data with responses of ahistoric networks and found that network permissiveness is correlated with the diversity of evolutionary history (Phelps 2001). Selection to recognize

novel signals contributes to the heteroscedasticity in response data, and may not reflect the behavioural evolution of túngara frogs. Consequently, differences between mimetic- and random-history networks, as well as between these networks and the ahistoric networks reported previously (Phelps & Ryan 1998), do not allow one to disentangle the contributions of ancestral recognition mechanisms from past selection for receiver permissiveness. Mimetic- and mirrored-history networks, however, exhibit identical degrees of historical diversity and equivalent levels of gross permissiveness (Phelps 2001), yet possess distinct biases. Critically, mimetic-history networks are consistently better at predicting the responses of female túngara frogs. This comparison demonstrates that networks with mimetic histories are more accurate predictors of female responses, and this is most likely because mimetic ancestral recognition mechanisms more closely approximate those of female túngara frogs.

4. DISCUSSION

We find that the strategies receivers use to decode signals result in incidental preferences for some stimuli over others. These findings replicate results from prior neural network studies (Enquist & Arak 1993, 1994, 1998; Johnstone 1994; Phelps & Ryan 1998) and are consistent with various hypotheses suggesting that preferences may arise in the absence of current selection for signal assessment (Endler & Basolo 1998; Ryan 1998). Critics of the original applications of neural network models to animal communication have argued that the network biases may be artefacts of the particular architecture or training methods used (Kirkpatrick & Rosenthal 1994; Cook 1995; Dawkins & Guilford 1995; Kamo et al. 1998). Our data, however, demonstrate that networks with identical architectures and training procedures may exhibit distinct patterns of biases, shaped by evolutionary history. Moreover, despite obvious differences between females and simple neural network models, the two are sufficiently similar to make the networks useful predictors of female preferences.

We found that networks given different histories exhibited significant differences in their preferences for novel stimuli. This is consistent with a number of behavioural studies demonstrating that receivers respond to hypothesized ancestral signals. When female túngara frogs, for example, were tested with reconstructed ancestral calls of the *P. pustulosus* species group, responses to the novel test stimuli correlate with both acoustic and phylogenetic proximity to the conspecific call (Ryan & Rand 1995, 1999; see McLennan & Ryan (1997) for a related study of preferences in swordtail fishes). Some species of *Drosophila* exhibit asymmetrical responses to heterospecific signals in which derived species respond better to the signals of basal species than the reverse, suggesting preferences for ancestral signals (Kaneshiro 1976, 1983). Such biases can persist within descendant populations in which preferences lack an apparent function. Marler & Ryan (1997) found that fish of the all-female gynogenetic molly species *Poecilia formosa* exhibit a preference for large males apparently inherited from females of their sexual ancestors, *P. latipinna* and *P. mexicana*. Although these experiments consistently suggest historical influences, such correlative data are unable to demonstrate causality. In contrast to preceding simulations and behavioural studies, we demonstrate that biases change in response to direct manipulations of ancestral signal-recognition tasks.

Because we used signals that represent the hypothesized ancestral states for an extant species, we were able to compare the external validity of networks given various histories. We found that networks with a history most closely approximating that hypothesized for the túngara frog are best at reproducing the response biases of real females. The fact that the predictions are sensitive to evolutionary history indicates that the similarity between female and network response biases is not simply attributable to the suite of test stimuli used, the network architecture or the training methods. Not only do these networks demonstrate how history influences receiver biases, but they predict the forms historical biases should take in the túngara frog. Together these data add to the growing weight of evidence indicating that historical processes shape the design of communication systems.

We have yet to investigate how networks are executing call recognition or how these mechanisms are being shaped by evolutionary history. One simple hypothesis is that neurons of the 'feature detector' and 'context' layers combine to form two resonating circuits: a delay circuit activated by high-frequency inputs, and an AND circuit activated by the convergence of low-frequency inputs and the high-frequency delay. Such an arrangement would be consistent with a description of call-recognition mechanisms put forward by Wilczynski et al. (1995) for female túngara frogs. The evolution of new call-recognition mechanisms could simply involve adding new frequency inputs to these circuits. Networks evolving to recognize the first call of the historical sequence would slowly assemble such circuits, but could more rapidly evolve to recognize subsequent calls. By this hypothesis, the influence of network history could be attributed to the persistence of frequency inputs used to recognize ancestral calls. If the similarities between network and female responses are to be taken literally, such circuits might be found in the reciprocal connections of the torus semicricularis and auditory thalamus. Convergence of a high-frequency delay circuit with a low-frequency circuit could result in call-selective neurons in either structure (but complex properties appear to be more common in the auditory thalamus (Hall 1994)). It would be fascinating to know whether call-responsive midbrain neurons are more sensitive to ancestral frequencies than one would predict based on the tuning of the amphibian papilla. Such investigations would be extremely novel and could serve as a general model for the study of historical influences on sensory systems.

The neural networks described here were not designed to mimic architectural details of anuran auditory systems. However, the ability of the network models to generate hypotheses across multiple levels of analyses, ranging from neural circuitry to phylogenetic influences on animal communication, point to a major strength of this approach. Hypotheses that are untestable using natural populations may be readily investigated using neural network models; the generality of the simulation results can then be gauged using traditional behavioural assays

and the most precise models can be used to direct detailed studies of neuronal mechanisms. Although not all systems will be well suited for such modelling, those that are will gain an attractive degree of rigor and accessibility. We hope that this approach will contribute to a more thorough understanding of animal behaviour and how it evolves.

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