

Historical contingency affects signaling strategies and competitive abilities in evolving populations of simulated robots

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One of the key innovations during the evolution of life on earth has been the emergence of efficient communication systems, yet little is known about the causes and consequences of the great diversity within and between species. By conducting experimental evolution in 20 independently evolving populations of cooperatively foraging simulated robots, we found that historical contingency in the occurrence order of novel phenotypic traits resulted in the emergence of two distinct communication strategies. The more complex foraging strategy was less efficient than the simpler strategy. However, when the 20 populations were placed in competition with each other, the populations with the more complex strategy outperformed the populations with the less complex strategy. These results demonstrate a tradeoff between communication efficiency and robustness and suggest that stochastic events have important effects on signal evolution and the outcome of competition between distinct populations.

The great variety of signaling systems within and between species (1–3) plays a key role in regulating species' coexistence and speciation processes (4–6). Two main mechanisms have been proposed to account for the evolution and maintenance of alternative signaling systems. The first is sexual selection, which can lead to variation in mating and premating signals (4, 7, 8). The second is differential selection between habitats as a result of abiotic or biotic factors influencing the effectiveness of different modes of signaling (9–12). Accordingly, the common view is that populations exposed to uniform habitats without sexual selection should evolve similar communication systems (13). However, comparative studies suggest that the vagaries of evolution can also lead to signal variation between species (14–17).

Both theoretical models (18–23) and empirical studies on noncommunication traits (24–30) have shown that diverse phenotypes can emerge depending only on stochastic evolutionary events when selection occurs under seemingly identical conditions. This raises the question of whether historical contingency, for example as a result of stochasticity in the occurrence order of beneficial phenotypic traits (24, 31), may lead to variation among populations in signaling. The best way to address this question would be to conduct experimental evolution over many generations in several independently evolving populations to investigate whether alternative communication may evolve. Unfortunately, conducting experimental evolution on social traits such as communication is complicated by the extreme difficulty in assessing individual fitness within groups and selecting individuals according to their fitness from one generation to the next. Further, studying the effects of historical contingencies requires replicated evolution under controlled environmental conditions. It is therefore unknown whether stochasticity in the occurrence order of mutations or recombination events affecting signaling systems may lead to the evolution of alternate strategies under uniform habitats.

To address this issue, we used a simulated robotic model that enabled us to link interindividual interactions and behavioral

effects to conduct unbiased analysis of the factors driving the evolution of social behavior (32–34). The degree of realism provided by such robotic systems greatly exceeds current analytical and game-theoretical models and allows experiments that cannot be readily performed with real organisms (for an overview, see ref. 35). This system also guaranteed identical habitats for all populations, an essential requirement for investigating divergent evolution of signaling under uniform ecological conditions.

In this study, we first investigated whether alternate communication systems can emerge in populations that evolved in the same environment. Because we found that two main signaling systems evolved in our 20 independent populations, we next compared the evolutionary history of these populations to identify the causes underlying signal diversification. Finally, we compared the efficiency of the two signaling strategies and also conducted contests among all pairs of populations to investigate whether stochastic events in the evolution of communication can have consequences on the outcome of competition between distinct populations.

Results

In the first experiment, we investigated the evolution of alternative communication strategies in a cooperative system where groups of simulated robots were placed in an environment containing one food source randomly located in an arena (Fig. 1). The robots (Fig. S1) could perceive the food source with their sensors only when they were above it. Their performance was proportional to the number of the 1,200 time units of the experiment spent on the food source. Additionally, robots had the possibility of producing and perceiving blue and green light, which potentially enabled them to transmit information about the food location to other robots in the group. Experimental evolution was conducted in populations of simulated robots using physics-based computer simulations that precisely model the dynamical properties of real robots. Each population comprised 100 groups of 20 robots. Artificial genomes, each consisting of 36 “genes,” encoded the specifications of the robots' neural controllers that processed the sensory information and produced the motor actions of the individual robots (*Materials and Methods*). During each generation, 100 genomes out of the 2,000 genomes per population were selected by fitness-proportionate selection and subjected to mutation and recombination (i.e., sexual reproduction). Then, each resultant genome was cloned 20 times to produce 100 groups, each consisting of 20 genetically identical robots (*Materials and Methods*). Because the 36 genes were initially set to random values, the

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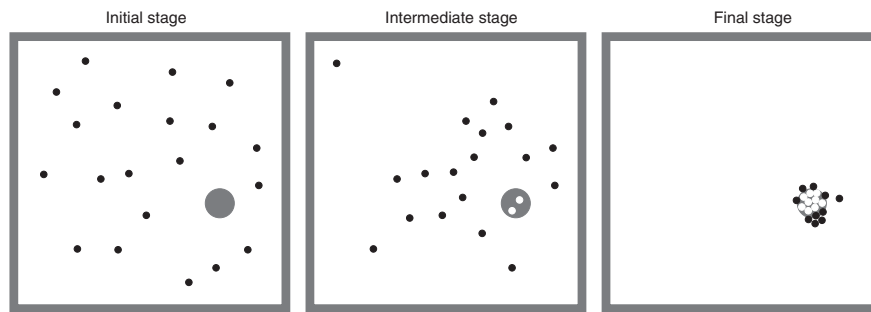


Fig. 1. Distribution of robots in the foraging arena over three different stages of the 1,200 time steps. The figure illustrates a representative evolved behavior after 1,000 generations of selection. Initially, 20 robots (black circles) are randomly distributed in the foraging area. Over time, some robots discover the food source (gray circle), where they stay so as to increase their performance (these robots are marked white). By using their signals, robots on the food source attract more robots until, eventually, most robots are on or near the food source (black-marked robots do not increase their performance).

behavior of the robots was random in the first generation. Due to selection, however, the behavior of the robots rapidly evolved and their performance greatly increased over the 1,000 generations of selection. We repeated the experiments in 20 independent populations exposed to the same starting conditions and identical environments. No gene flow was allowed between the 20 distinct populations.

An inherent property of this foraging system was that robots could increase the performance of other robots by signaling when they were on the food source. To study how communication between robots evolved across the 20 independent populations, we quantified the proportion of time steps where the robots emitted green or blue light on the food source or somewhere else in the arena. In all 20 populations, the robots emitted one of the two colors on the food after 1,000 generations of selection (this color was labeled “primary” color and the other “secondary” color). There was low variance among the 20 populations in the rate of emission of the primary color on food ($\bar{x} = 0.860$, $\sigma^2 = 0.063$). Similarly, in all populations, robots rarely emitted the secondary color on food or the primary color in the environment ($\bar{x} = 0.056$, $\sigma^2 = 0.070$ and $\bar{x} = 0.059$, $\sigma^2 = 0.032$, respectively). By contrast, there was high variation among populations in the production of the secondary color in the environment ($\bar{x} = 0.412$, $\sigma^2 = 0.458$), with the variance being significantly higher than for the emission of the secondary color on food, primary color on food, and primary color in the environment (two-sample F test, all $P < 0.001$). A principal component analysis on all four measured signaling traits (Fig. S24) revealed that the emission of the secondary color in the environment contributed most (loading = 0.99) to the first principal component, which explained up to 96.5% of the between-population variance in signaling (other loadings of the first principal component were -0.05 and 0.09 for the primary and secondary color on food and -0.02 for the primary color in the environment).

A hierarchical clustering on the scores of the first two principal components revealed two major clusters (Fig. S2). The first contained 11 populations in which robots intensively emitted the primary color on the food, but did not signal in the foraging arena (one-signal populations; Fig. 2). The other cluster comprised the remaining 9 populations, in which robots similarly emitted the primary color on food, but also produced a significant amount of the secondary color in the foraging arena (two-signal populations; Fig. 2). Overall, the one-signal populations had a mean performance of 0.196, which was 15.3% higher than the mean performance (0.168) of the two-signal populations (Wilcoxon rank-sum test, $P < 0.001$).

An analysis of the evolutionary history of light production over time revealed different trajectories between the one- and two-signal populations. In the one-signal populations, the emission of the primary color on food became more frequent than the

emission of the secondary color in the environment within the first 10 generations (Fig. 3A). Thereafter, the emission of the secondary color in the environment quickly decreased and was close to zero in all generations after generation 50. In these populations, the performance was positively correlated with the emission of the primary color on food over the 1,000 generations of selection (Pearson’s correlation, $r = 0.98$, $P < 0.001$) and negatively correlated with the emission of the primary color in the environment as well as the emission of the secondary color on food and in the environment (all Pearson’s correlation, $r < -0.93$, $P < 0.001$). By contrast, in the two-signal populations, the emission of the primary color on food increased more slowly than the secondary color in the environment (Fig. 3B). As a result, the emission of the secondary color in the environment was consistently equal to, or more frequent than, the emission of the primary color on food. In these populations, the performance was also positively correlated with the emission of the primary color on food over the 1,000 generations of selection (Pearson’s correlation, $r = 0.67$, $P < 0.001$) and negatively correlated with the emission of the primary color in the environment (Pearson’s correlation, $r = -0.80$, $P < 0.001$) and secondary color on food (Pearson’s correlation, $r = -0.39$, $P < 0.003$). However, in contrast to the one-signal populations, the emission of the secondary color in the environment was positively correlated with

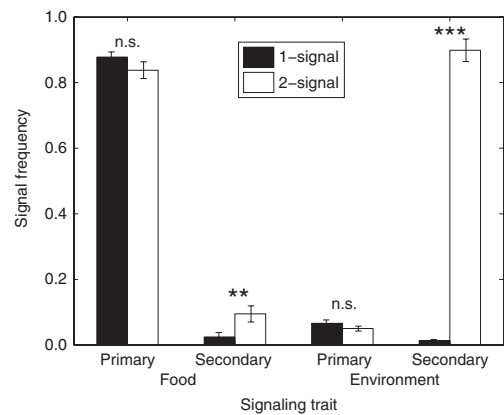


Fig. 2. Differences in signaling strategy between the one- and two-signal populations. The difference was most notable in the use of the secondary color in the environment. The two groups differed slightly in the use of the secondary color on food. Shown is the SE and average population mean of signal frequency (proportion of time steps when a specific signal was displayed) for the one- and two-signal populations averaged over the last 20 generations (** $P < 0.01$, *** $P < 0.001$, otherwise $P > 0.05$, Wilcoxon rank-sum test; n.s., not significant).

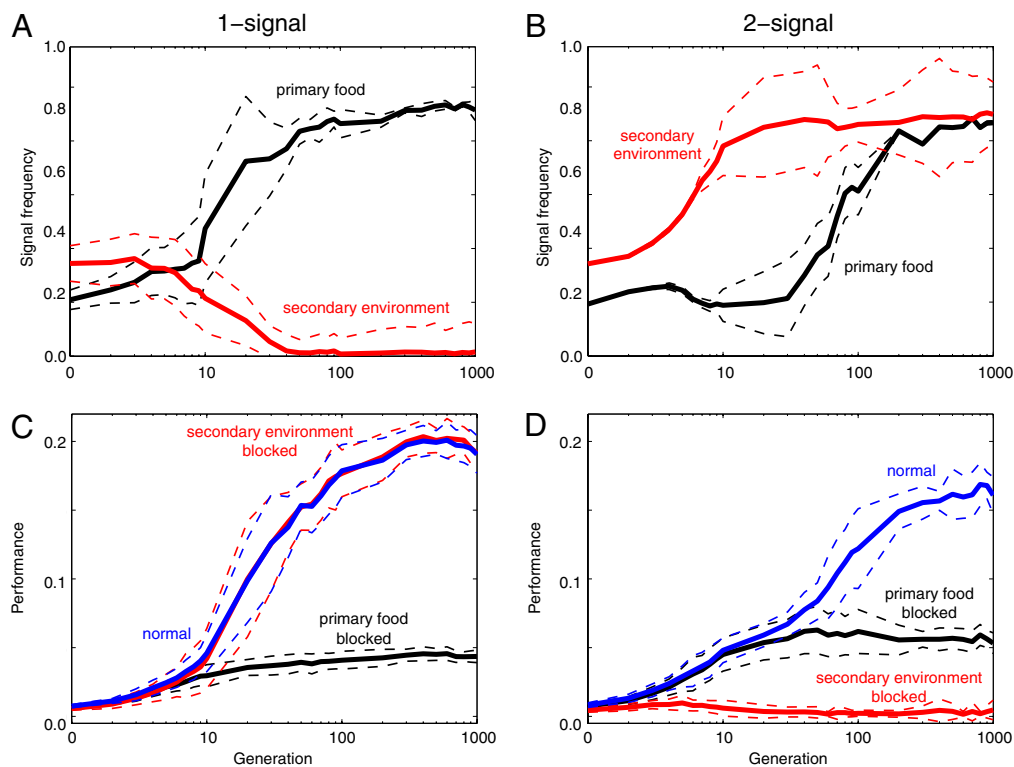


Fig. 3. Evolution of signaling and performance over the 1,000 generations of selection. Shown is the average (solid lines) and SD (dashed lines) over the 11 one-signal and 9 two-signal populations. (A and B) Level of emission of the primary color on food and secondary color in the environment in the one- and two-signal populations. (C and D) Average performance under normal conditions and when robots were prevented in each generation from emitting either the primary color on food or the secondary color in the environment (labeled “blocked”).

performance over the 1,000 generations of selection (Pearson’s correlation, $r = 0.84$; $P < 0.001$). Thus, in addition to a signal indicating the presence of food that evolved in all populations, an additional signal indicating the absence of food had been added in the two-signal populations.

To identify the key event that was responsible for the different evolutionary trajectories of the one- and two-signal populations, we suppressed the emission of the primary or secondary colors either on the food or in the environment. These experimental manipulations were conducted independently for each of the 1,000 generations in each of the 20 populations. In the one-signal populations, the suppression of the primary color emission on food had a significant negative influence on performance from generation 20 on (all Wilcoxon rank-sum test, $P < 0.001$; compare Fig. 3C). By contrast, performance was never significantly affected by preventing robots from emitting the primary color in the environment or the secondary color on food or in the environment (all Wilcoxon rank-sum test, $P > 0.05$). In the two-signal populations, performance similarly decreased when the primary color on food was prevented (Wilcoxon rank-sum test, $P < 0.001$; compare Fig. 3D) but not when the emission of the primary color in the environment or the emission of the secondary color on food was prevented (all $P > 0.05$). However, in contrast to the one-signal populations, blocking the emission of the secondary color in the environment decreased performance in all generations after the first generation in the two-signal populations (Wilcoxon rank-sum test, $P < 0.001$; Fig. 3D). Thus, these experiments confirmed that early divergence between populations caused by different genetic changes (via mutation and recombination) affecting the use of the secondary color in the environment led to differences in the selective pressure on signaling, and ultimately to the evolution of two distinct signaling strategies in the one- and two-signal populations.

In the second experiment, we investigated whether the evolution of these two alternative signaling strategies had consequences on the outcome of interpopulation competition. This was done by conducting competition experiments between all pairs of populations at generation 1,000. To keep the conditions similar to those under which the simulated robots had been selected over the 1,000 generations of experimental evolution, we also kept the number of robots in the arena at 20, where 10 robots stemmed from a group of one population and 10 robots from a group of another population. We then paired each of the 100 groups from a given population with 20 randomly selected groups from each of the 19 other populations (i.e., 380 tests per group, 38,000 tests per population, 760,000 tests in total). Because the size of the food source was limited (Fig. 1), only 14 robots could be simultaneously on the food source, although this value was almost never reached as it could be attained only with a perfect packaging of the robots on the food source.

The individual performance of robots was lower when in competition than when interactions occurred only within a given population (Wilcoxon rank-sum test, $P < 0.001$). The decline in performance was much higher for the one-signal populations ($\bar{x} = -43.6\%$, $SE = 2.05$) than for the two-signal populations ($\bar{x} = -16.1\%$, $SE = 2.76$) (Wilcoxon rank-sum test, $P < 0.001$). Importantly, the much higher performance decrease of the one-signal populations resulted in these populations ultimately performing significantly less well ($\bar{x} = 0.111$, $SE = 0.004$) than the two-signal populations ($\bar{x} = 0.14$, $SE = 0.004$) (Wilcoxon rank-sum test, $P = 0.006$). Thus, there was a reversal in performance between the one- and two-signal populations under competition, hence demonstrating a higher robustness of the two-signal populations to competition.

Discussion

The evolutionary divergence of signaling systems is commonly attributed to differences in habitats (5, 36–38), sexual selection (4, 7), or interspecific interactions (9, 39), leading to the common assumption that closely related species inhabiting similar environments will often exhibit similar communication systems (13). However, biologists studying communication have become increasingly aware that contingency in evolutionary history can play an additional important role in shaping animal communication systems (40–42). Understanding why a specific signaling system evolved to its current form is challenging because behavior leaves only very scarce fossil records (43). Thus, studies on the effects of historical contingency on the evolution of communication are rare. For example, the responses of female túngara frogs to ancestral calls and to calls of other closely related species have been shown to be influenced by variations in the historical sequence of past male mating calls (44, 45), demonstrating the influence of the evolutionary history of male signals on current female responses (46). Further, inter- and intraspecific comparisons of associations between genetic, geographic, and signaling distances have led to the suggestion that stochastic processes such as drift may be involved in the process of signal diversification in dart-poison frogs (15), singing mice (16), greenish warblers (17), and *Anolis* lizards (47). Unfortunately, an inherent problem with comparative studies is the difficulty of ruling out the hypothesis that undetected differences among habitats or ancestral differences that have since disappeared actually account for the current interspecific variation in signaling.

Our time course analysis showed that the one- and two-signal populations started to diverge already within the first 10 generations of selection. Moreover, the experimental blocking of the emission of the secondary color in the environment revealed a decrease in performance in all 1,000 generations in the two-signal populations, whereas the same manipulation never had a significant effect on the performance in the one-signal populations. Thus, the evolution and fixation of two distinct communication strategies occurred as a result of very early genetic differences between populations that influenced the course of signal evolution. The differences in signaling remained stable despite the greater efficiency of one of the signaling strategies. A likely reason for the lack of shift from the less efficient signaling strategy to the more efficient is that social interactions lead to a strong frequency dependence of performance, resulting in suboptimal adaptive peaks at which a change in either the signaling or response strategy would destroy the communication system and result in a performance decrease. Thus, each communication strategy effectively constitutes an adaptive peak separated by a valley of lower performance values (32, 48). A similar phenomenon may account for some of the differences in signaling observed between closely related species or isolated populations of a given species. For example, a recent study in *Anolis* lizards revealed that species originating from different evolutionary ancestors have evolved different signaling systems in response to similar selective pressures (47). Unfortunately, it is unknown whether the different evolutionary starting points of species impacted the efficiency of the evolved signaling systems.

Variation in signaling that can enable some species to better resist competition or predators, as it exists, for instance, in moths (49), is usually attributed to differences in selection such as the presence or absence of predators or temporal and geographic variations (11). Here we could demonstrate that increased robustness to competition of certain signaling systems can emerge without direct selective forces on the ability to resist competition. Identifying the role of competition for the evolutionary change of species in general (50), and of signaling behavior in particular (51–53), is a major challenge for ecological research. Our

experiments of replicated evolution under the same environmental and evolutionary conditions revealed that the most efficient signaling strategy was also the one most affected by competition, demonstrating a tradeoff between communication efficiency and robustness to competition. This suggests that contingencies in evolutionary history can affect the outcome of competition between distinct populations (29).

In conclusion, our study revealed that variation in signaling can occur without sexual selection and in the absence of ecological differences. Alternative signaling strategies evolved due to stochasticity in the order of new mutations and/or crossing-over events and/or how they spread within populations. Given that visual, acoustic, or chemical signals can act as major isolating mechanisms between young and incipient species, our study may also have implications for the long-standing debate over the relative importance of selection and drift in the process of speciation (54–56). Divergence in mate-recognition signals is considered to be one major cause of creating premating barriers that initiate speciation processes (1). In light of our study, it is well possible that, besides habitat-dependent and sexual selection, stochasticity in the occurrence order of genetic and phenotypic changes during the course of evolution (24, 31) might also be involved in speciation processes (19, 57, 58). This would be the case, for example, if stochastic phenotypic variation would first cause divergences in nonmating signals that are later used as mate-recognition signals.

Materials and Methods

Experimental Setup. Each robot was evaluated in a physics-based simulation (32–34). The circular-shaped robot with a diameter of 7.2 cm was equipped with two independent wheels, a camera, a floor sensor for food detection, and a light-emitting diode ring around the robot that could emit either green or blue light (Fig. S1). An artificial neural network consisting of nine input neurons fully connected to four output neurons with an activity range of $[-1, 1]$ and a sigmoid transfer function (*tanh*) controlled the behavior of each robot. The 360° field of view provided by the camera was divided into four equally sized quadrants around a robot. For each quadrant, the amount of perceived light was linearly mapped to the activity of one input neuron for the blue and one for the green color (for further details, see ref. 32). Floor sensor information was processed by one input neuron, resulting in maximal or minimal activity depending on whether the robot was on the food or not. Two output neurons controlled the speed of the left and right wheel with minimal and maximal activity resulting in maximal backward and forward rotation, respectively. The two remaining output neurons controlled the light emission. Light was emitted only if at least one of the two neurons had an activity higher than zero (if the first neuron showed equal or higher activity than the second, green light was emitted, otherwise blue light was emitted). Each of the 36 synaptic connections between input and output neurons was encoded by a single gene consisting of eight bits that were mapped linearly into a synaptic strength within the range of $[-5, 5]$.

Artificial Evolution. Our 20 independent replicate populations consisted of 100 groups, each containing 20 simulated robots. All of the robots in a group had the same genome, and genetic differences between groups ultimately stemmed from mutation, recombination, selection, and drift as outlined below.

To initiate each population, 100 genomes were randomly generated. Each of these genomes was cloned 20 times to form the 100 groups each consisting of robots with identical neural networks. One population thus contained 2,000 genomes. To evaluate performance, each group of 20 robots was placed randomly in a bounded 3×3 -m arena containing a circular food source with a diameter of 32 cm (Fig. 1). The performance of every robot in a group was calculated separately as the proportion of the 1,200 sensor-motor cycles (time steps) spent on food. This procedure was repeated 20 times, with randomly varying initial positions for each robot. After evaluating the average performance of each robot over the 20 trials, the 2,000 genomes of a population were linearly ranked according to their performance values. We then applied the standard roulette-wheel selection algorithm to determine 100 genomes for reproduction (i.e., selection took place on the individual level). The selected 100 genomes were randomly assorted in pairs to perform crossover (with a probability of 0.2) and mutation (with a probability of 0.01 for each of the 288 bits of a genome to change to its alternative

state, either zero or one). Then, each of the 100 genomes was again cloned 20 times to form the 100 groups of 20 robots for the next generation. All experimental populations evolved for 1,000 generations.

Competition Experiments. After the first 1,000 generations of selection without interpopulation competition, we reduced the number of robots so that each population contained 100 groups of 10 robots each (robots within one group were still clones). Each group of one population was then paired with 20 randomly selected groups of each of the 19 other populations (i.e., interpopulation competition). We placed each pair in the same environment

and conducted 20 trials for 1,200 time steps with random starting conditions for each individual. We then measured the average performance of each group over these 20 trials and compared the performance of the groups in the one-signal and two-signal populations.

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