

The evolution of information suppression in communicating robots with conflicting interests

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Reliable information is a crucial factor influencing decision-making and, thus, fitness in all animals. A common source of information comes from inadvertent cues produced by the behavior of conspecifics. Here we use a system of experimental evolution with robots foraging in an arena containing a food source to study how communication strategies can evolve to regulate information provided by such cues. The robots could produce information by emitting blue light, which the other robots could perceive with their cameras. Over the first few generations, the robots quickly evolved to successfully locate the food, while emitting light randomly. This behavior resulted in a high intensity of light near food, which provided social information allowing other robots to more rapidly find the food. Because robots were competing for food, they were quickly selected to conceal this information. However, they never completely ceased to produce information. Detailed analyses revealed that this somewhat surprising result was due to the strength of selection on suppressing information declining concomitantly with the reduction in information content. Accordingly, a stable equilibrium with low information and considerable variation in communicative behaviors was attained by mutation selection. Because a similar coevolutionary process should be common in natural systems, this may explain why communicative strategies are so variable in many animal species.

cues | signals | variation

Animals acquire information through trial-and-error while interacting with the physical environment (personal information) or by monitoring the behavior of conspecifics (social information) (1). Social information can be based on traits or behaviors that were selected to regulate information transmission (signals) or on cues provided inadvertently (1, 2). Cues are thought to be common sources of information in nature. Indeed, in many species, individuals have been shown to monitor each other to decide how to behave (3–9). For example, when foraging, simply observing the behavior of conspecifics can inform an animal about the location of a source of food (10, 11). In many situations, producing inadvertent cues will also affect an individual's own fitness and should thus be under selection, with the consequence that cues providing inadvertent social information should evolve into signals. Importantly, selection on inadvertent cues may frequently take the form of decreasing the social information provided. An example of this would be birds living in a roost trying to hide information from other group members about a food source they have discovered (12).

Although the evolution of signals has been extensively studied, most research has focused on signaling as an independent behavior, decoupled from its social and behavioral context (13). As a result, relatively little attention has been given to social information provided by cues and its influence on signal evolution. To address this issue we devised a system of experimental evolution with groups of competing robots (14). The robots were randomly placed in an arena containing a food and a poison source that both emitted red light. The food and poison sources were placed close to two opposite corners of the arena (Fig. 1), and robots could identify them only at a very close range by

detecting different colored paper discs placed under the sources with their floor sensors. The performance of robots was increased by one point for every unit of time spent in the vicinity of food and decreased by one point when near poison. Once a robot had located the food, it could stay in its vicinity until the end of the trial, which consisted of 1,200 time units. Additionally, robots had the possibility of producing and perceiving blue light, hence potentially allowing them to transmit information on food and/or poison location. Experimental evolution was conducted in a population of 100 groups of 10 robots each using physics-based computer simulations that precisely model the dynamical properties of real robots. The specifications of the robots' neural controllers, which process sensory information and produce motor actions, were encoded in artificial genomes, each consisting of 33 "genes" (14). The genomes of the 20% of robots with the highest individual performance in the population were selected, subjected to mutation and recombination (i.e., sexual reproduction), and randomly assorted into groups of 10 robots to form the next generation (see *Materials and Methods*). Because the 33 genes were initially set to random values, the behavior of robots was random in the first generations. However, because of selection, the behavior of robots rapidly evolved and their performance greatly increased over the 500 generations of selection that were repeated in 20 independent selection lines [supporting information (SI) Fig. S1].

Results and Discussion

Inadvertent Information. An inherent property of this foraging system is that blue light, even if emitted randomly, could provide inadvertent social information on food location because, in this physical setup, information is provided not only through patterns of light emission but also through the robots' behavior. Thus, once robots evolve the ability to find food and stay nearby, their increasing density near the food source should translate into higher blue density near the food and a source of information for other robots in the arena. This hypothesis was confirmed in a first experiment in which robots were constrained to produce light randomly (light was emitted with a probability of 0.5 for each unit of time). As robots became more efficient at finding and remaining near the food (Fig. S1), the concentration of blue light near food also increased such that, in all generations after generation 2, the intensity of blue light was significantly higher in the vicinity of the food than in the rest of the arena (Mann–Whitney test, $df = 39$, $P < 0.001$ for all generations). To quantify the amount of inadvertent information produced by the emission of blue light, we devised an index of information I

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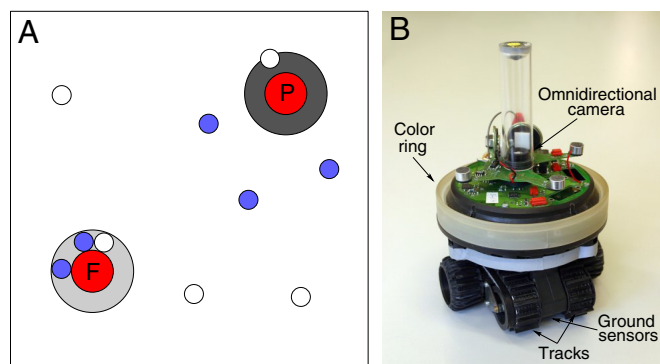


Fig. 1. Experimental setup. (A) A food and poison source, both emitting red light, are placed 1 m from one of two opposite corners of the square (3 × 3-m) arena. Robots (small circles) can distinguish the two by sensing the color of the circles of paper placed under each source by using their floor sensors when driving over the paper. (B) The robot used for the experiments is equipped with two tracks to drive, an omnidirectional (360°) vision camera, a ring of lights used to emit blue light, and floor sensors to distinguish food and poison sources (see ref. 14 for details).

(15–19), which varies between 0 when blue light is equally distributed in all directions relative to the direction of the food and 1 when light is always perceived in a predictable direction relative to the food (see *Materials and Methods* for details; see also Fig. S2). The level of information rapidly increased over the generations (Fig. 2A), and robots became significantly attracted to blue light after generation 9 (average value between generation 9 and 500: 0.2 ± 0.03 , two-sided sign test, $df = 19$, all $P < 0.001$) (Fig. 2B).

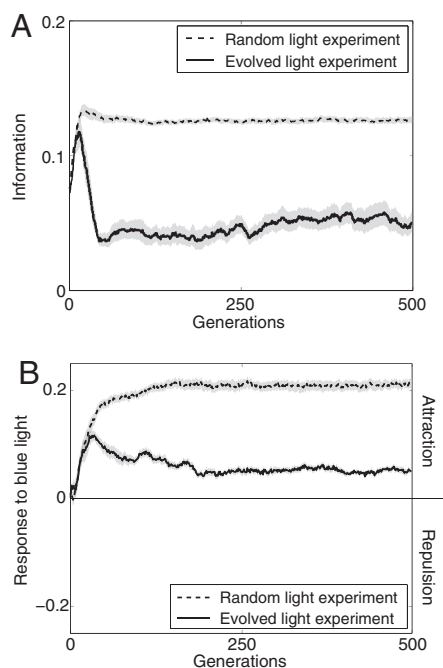


Fig. 2. Information and response to blue light. Change over generations in information content provided by blue light (i.e., the strength of the association between the direction in which robots perceived most light and the direction of the food; see *Materials and Methods* and Fig. S2) (A) and the response to blue light, where positive values indicate attraction and negative values indicate repulsion to blue light (see *Materials and Methods*) (B). Both graphs show the mean and standard error (gray bands) of the 20 independent replicates for both the random and evolved light emission experiments.

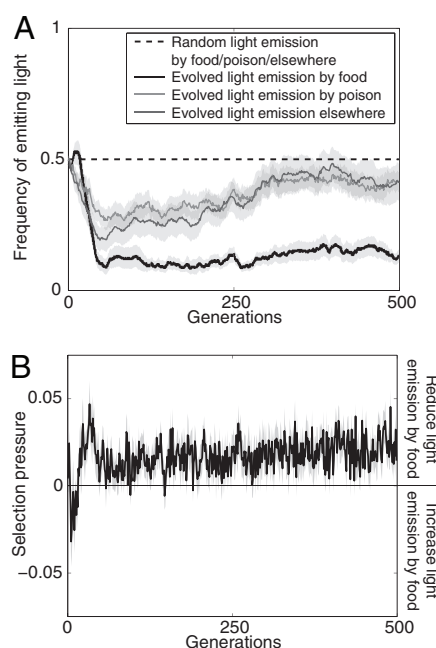


Fig. 3. Light emission strategies and selection pressure. Change over generations in the frequency of light emission in different areas of the arena (see *Materials and Methods*) for both the experiments where light was emitted randomly and evolved (A) and selection pressure to reduce emission of light by food (see *Materials and Methods*) (B). Positive or negative selection pressure indicates that robots were selected to reduce or increase light emission near the food, respectively. Both graphs show mean and standard error (gray bands) of the 20 independent replicates.

This experiment revealed that, when emitted randomly, blue light was an inadvertent cue providing information on food location. Although light production was cost-free, sharing such information should be costly because it results in higher robot density and increased competition and interference near the food (i.e., spatial constraints around the food source allowed a maximum of 8 robots of 10 to feed simultaneously and resulted in robots sometimes pushing each other away from the food). Because selection occurred at the individual level and because there is no kin structure among the 100 groups of robots, selection should favor individuals concealing information on food location (14, 20, 21). To test whether conflicts of interest between robots would affect blue light emission, we conducted a similar experiment with the difference that we allowed the rate of emission of blue light to evolve as part of the robots' behavior. In this experiment, the probability of a robot emitting blue light depended both on its genotype (i.e., the values of its genes) and the environmental stimuli perceived through its sensors (see *Materials and Methods*).

Evolving Light Emission. As in the previous experiment, the robots initially produced blue light randomly (gene values were random such that the probability of light emission in any area of the arena was not different from 0.5 in the first 3 generations, two-sided sign test, $df = 19$, all $P > 0.1$) (Fig. 3A). This random emission of blue light, together with the increase over generations in the density of robots near food, resulted in a rapid increase of information, the maximum ($I = 0.12$) being reached at generation 16 (Fig. 2A). However, because the increased information resulted in robots crowding around the food, robots were selected to decrease the rate of blue light emission (Fig. 3A). This decrease was significantly greater near the food than elsewhere, such that after 52 generations, robots became much less likely to produce light near food than near poison ($P < 0.01$ in all

generations after generation 52, $df = 39$) or elsewhere ($P < 0.05$ in all but one of the generations 53–500, $df = 39$) (Fig. 3A). Altogether, these changes in light emission strategy led to a drastic decrease in the amount of information provided by blue light intensity between generations 16 and 46 (Spearman's rank correlation test, $r_s = -0.997$, $P < 0.001$) (Fig. 2A) such that, in all generations after generation 22, the level of information was significantly lower than in the experiment where blue light emission was random (all $P < 0.05$, $df = 39$) (Fig. 2A).

Although selection was acting toward suppressing information on food location, the information content did not decrease to zero over the 500 generations of selection (Fig. 2A), resulting in robots remaining significantly attracted to blue light until generation 500 (average attraction between generations 36–500: 0.06 ± 0.01 , two-sided sign test, $df = 19$, all $P < 0.001$) (Fig. 2B). This somewhat surprising result can be explained by the fact that the strength of selection on light emission strategies depends on the level of information content and the robots' response to blue light. Thus, when the information content provided by blue light intensity is high, robots should be highly attracted to blue light and there should be a relatively important fitness drop for robots emitting light near the food (i.e., strong selection pressure to reduce light emission by the food). By contrast, low information content should translate into a lower response of robots to blue light and a smaller performance reduction for robots that emit light near food (i.e., low selection pressure on reducing light by the food).

Support for suppression of information being impeded by the reduced strength of selection comes from the analysis of the response strategies of individual robots and their influence on the light emission strategies and performance over the 500 generations of selection. In both the experiments where light emission could evolve or was random, the level of attraction of robots to blue light rapidly increased during the first 36 generations of selection (Fig. 2B). However, whereas the level of attraction continued to increase when light production was random, it significantly decreased between generations 36 and 200 ($r_s = -0.8$, $P < 0.001$) (Fig. 2B) in the experiment where the emission of light could evolve. This decrease in attraction to blue light, which resulted from the decrease in information content that occurred after generation 16 in this experiment (Fig. 2A), has important implications because the strength of selection on reducing the emission of light by food was positively correlated with the response of robots to blue light ($r_s = 0.13 \pm 0.13$; correlation significant in 11 of the 20 selection lines) (Figs. 2B and 3B). Thus, the reduced response to blue light after generation 36 led to weaker selection on reducing light emission by food (Fig. 3B) and a stable level of information being reached by mutation-selection after ≈ 50 –100 generations (Fig. 2).

To test whether the stable level of production and attraction to light was affected by the mutation rate, we conducted an additional experiment with the only difference that between generations 250 and 500 we used a 100-fold lower mutation and crossing-over rate (mutation rate of 0.001 per locus instead of 0.1; cross-over rate of 0.002 instead of 0.2).^{*} The reduction resulted in a 33% decrease in the frequency of signaling near food (over the last 10 generations, mean \pm SD: 0.08 ± 0.24 instead of 0.12 ± 0.1 ; Mann–Whitney test, $df = 39$, $P < 0.001$). Interestingly, however, the reduced emission of blue light near food did not translate into a decrease in the level of information ($df = 39$, $P = 0.48$) nor a decrease in attraction to blue light ($df = 39$, $P = 0.36$), because the decreased mutation rate also led to

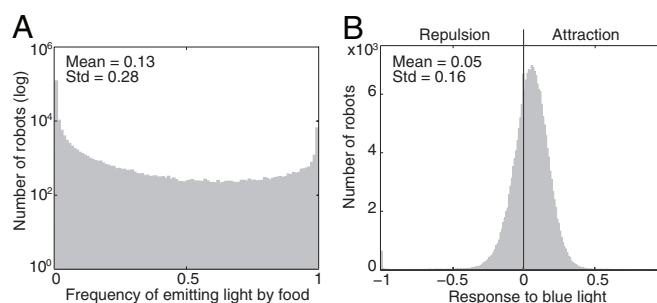


Fig. 4. Variation in communicative strategies. (A) Histograms of the frequency of blue light emission near the food. (B) The response to blue light of the 1,000 robots in each of the last 10 generations in all 20 independent replicates (200,000 robots in total) of the experiment where light emission was evolved. Positive response values reflect attraction to blue light and negative responses reflect repulsion. The vertical line marks the level at which robots exhibit no positive or negative response to blue light.

an increase in the average foraging efficiency of robots and thus a higher concentration of robots near food (0.91 ± 0.01 compared to 0.83 ± 0.01 with the regular rates, $df = 39$, $P < 0.001$). In other words, the lower rate of signaling combined with a higher concentration of robots at the food nevertheless generated a sufficient amount of information for the robots to remain equally attracted to blue light.

Within-Population Variation. An important consequence of the reduced selection pressure on light emission is that, at equilibrium, there was considerable individual variation in both the production and response to light (Fig. 4). Although the majority (61.5%) of the robots never emitted light near food in the last 10 generations, there was high variation in light emission strategies with 11.2% of the robots emitting light over 50% of the time when near food (Fig. 4A). Similarly, the level of attraction of robots greatly varied with most robots exhibiting a low attraction to blue light, but 32.6% showing a negative attraction (i.e., repulsion) to blue light and 36.1% an attraction more than twice higher than the average (Fig. 4B). Furthermore, the within-population variance in attraction of robots to blue light was significantly higher in the last 10 generations where blue light production could evolve (0.15 ± 0.02) than when it was random (0.13 ± 0.01 , $df = 39$, all $P < 0.01$).

These findings are interesting with regard to the discrepancy between theoretical predictions and previous empirical studies on the association between the strength of selection and phenotypic diversity. Although theory suggests that lower selection and genetic drift should lead to higher within-population variation (21–23), empirical studies failed to support this prediction (24). However, a problem with these empirical studies is that the strength of selection is assessed indirectly, for example by assuming greater selection on life-history traits than morphological traits (24). In our experiments, robots exhibited greater phenotypic variability in their response to blue light when light emission could evolve (i.e., when the level of information and strength of selection were low) than when light emission was fixed (i.e., when robots emitted light randomly, such that the level of information and strength of selection were higher). This finding is in line with theoretical predictions and supports the view that more controlled experiments are needed in studies with real organisms.

The Evolution of Cues into Signals. The complex dynamics between suppression of social information and selection pressure described in this study are likely to be general features of natural systems in which cues evolve into signals. When there are

^{*}Because the lower mutation and cross-over probabilities in the new treatment did not sustain sufficient diversity in the population to evolve good foraging behaviors (e.g., driving toward red light) in the initial generations, we used different mutation and crossing rates only after generation 250.

To compare blue light emission frequencies s , the information I on food location and the response to blue light b between experiments, we calculated the mean values of the 1,000 individuals in each generation for each of the 20 independent replicates. These 20 values per generation were used to describe data (mean \pm standard deviation) and were compared with nonparametric (Mann–Whitney or Kolmogorov–Smirnov) tests because some of the data did not follow a normal distribution.

The within-population variance in light emission and behavioral response strategies were computed for each of the 20 replicates by taking the average of the standard deviations in the population in each of the last 10 generations.

Nonparametric (Mann–Whitney) tests were used to compare the resulting 20 values across experiments.

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