X chromosome counting elements (XCEs) are expressed early in development, prior to dosage compensation, so that the gene products are twice as abundant in females as in males. The level of activity of these counting proteins in females is sufficient to establish stable expression from the Sxl_{Pe}, while that from males is not. Three essential XCEs encode transcription factors that bind directly to the Sxl_{Pe}. The fourth XCE, *sisterless-C* (*sisC*), has a weaker influence on sex determination. The *sisC* locus was found to map to *unpaired* (*upd*) [9,10], which encodes a ligand for the JAK signaling pathway, an evolutionarily conserved pleiotropic developmental cell signaling cascade [11,12]. The effect of Upd/SisC as an XCE is mediated by JAK signal transduction, as mutations in other JAK pathway signaling components, such as the kinase signal transducer (JAK) and the transcription factor target (STAT), also reduce *Sxl* activation.

Avila and Erickson [2] demonstrated that the role of JAK signaling is distinct from that of the transcription factor XCEs in Sxl_{Pe} establishment. The loss of Upd or other JAK pathway proteins in mutant females does not affect the onset of expression from Sxl_{Pe}, but later results in the failure of Sxl_{Pe} expression to be maintained [2]. They further showed that the effects of JAK signaling on *Sxl* expression are mediated through sequences in the establishment promoter that match the consensus for STAT binding sites, suggesting that Sxl_{Pe} is regulated directly by the canonical JAK pathway. The authors conclude that the regulation of Sxl_{Pe} is accomplished in two phases: initiation of transcription, regulated by the transcription factor XCEs, and maintenance of transcription, mediated by Upd/SisC and the JAK pathway signaling.

Two phase regulation of Sxl_{Pe} is surprising, because the entire window of both phases of expression from that promoter lasts less than one hour. Yet, the role of JAK signaling only in the later reinforcement step of Sxl_{Pe} activity may explain why *upd*/*sisC* has a weaker role in sex determination than the other X chromosome counting elements. Loss of Sxl_{Pe} reinforcement does not affect early initiation and, in many cases, female embryos defective in JAK signaling will ultimately establish stable Sxl activity and turn on the female switch. This raises a question of how the sex determination machinery is often able to recover from failure of the reinforcement step. The phenomenon suggests that there is some redundancy in the mechanisms that establish and stabilize the binary Sxl switch. Though we do not yet understand how this works, building such a robust system makes good sense, given the importance of this decision to the organism.

References

1. Cline, T.W., and Meyer, B.J. (1996). Vive la difference: males vs females in flies vs worms. Annu. Rev. Genet. *30*, 637–702.
2. Avila, F.W., and Erickson, J.W. (2007). *Drosophila* JAK/STAT pathway reveals distinct initiation and reinforcement steps in early transcription of Sex-Lethal. Curr. Biol. *17*, 643–648.
3. Sosnowski, B.A., Belote, J.M., and McKeown, M. (1989). Sex-specific alternative splicing of RNA from the transformer gene results from sequence-dependent splice site blockage. Cell *58*, 449–459.
4. Bell, L.R., Horabin, J.I., Schedl, P., and Cline, T.W. (1991). Positive autoregulation of sex-lethal by alternative splicing maintains the female determined state in *Drosophila*. Cell *65*, 229–239.
5. Bell, L.R., Maine, E.M., Schedl, P., and Cline, T.W. (1988). *Sex-lethal*, a *Drosophila* sex determination switch gene, exhibits sex-specific RNA splicing and sequence similarity to RNA binding proteins. Cell *55*, 1037–1046.
6. Keyes, L.N., Cline, T.W., and Schedl, P. (1992). The primary sex determination signal of Drosophila acts at the level of transcription. Cell *68*, 933–943.
7. Cline, T.W. (1988). Evidence that sisterless-a and sisterless-b are two of several discrete "numerator elements" of the X/A sex determination signal in *Drosophila* that switch Sxl between two alternative stable expression states. Genetics *119*, 829–862.
8. Duffy, J.B., and Gergen, J.P. (1991). The *Drosophila* segmentation gene *runt* acts as a position-specific numerator element necessary for the uniform expression of the sex-determining gene Sex-lethal. Genes Dev. *5*, 2176–2187.
9. Jinks, T.M., Polydorides, A.D., Calhoun, G., and Schedl, P. (2000). The JAK/STAT signaling pathway is required for the initial choice of sexual identity in *Drosophila melanogaster*. Mol. Cell *5*, 581–587.
10. Sefton, L., Timmer, J.R., Zhang, Y., Beranger, F., and Cline, T.W. (2000). An extracellular activator of the *Drosophila* JAK/STAT pathway is a sex-determination signal element. Nature *405*, 970–973.
11. Rawlings, J.S., Rosler, K.M., and Harrison, D.A. (2004). The JAK/STAT signaling pathway. J. Cell Sci. *117*, 1281–1283.
12. Arbouzova, N.I., and Zeidler, M.P. (2006). JAK/STAT signalling in *Drosophila*: insights into conserved regulatory and cellular functions. Development *133*, 2605–2616.

Biology Department, University of Kentucky, Lexington, Kentucky 40506, USA.
E-mail: DougH@email.uky.edu

DOI: 10.1016/j.cub.2007.03.012

Evolutionary Robotics: Emergence of Communication

The emergence of communication is considered one of the major transitions in evolution. Recent work using robot-based simulation shows that communication arises spontaneously. While deceptive communication arises in a purely competitive setting, cooperative communication arises only subject to group or kin selection.

Hod Lipson

Communication plays a critical role in evolution: Back in the early days of the primordial soup, horizontal gene transfer between unrelated individuals was likely to be prevalent, leading to the rapid invention and sharing of new genes [1]. When speciation began, some individuals leaped ahead by segregating themselves into non-interbreeding species, but after some two billion years communication returned again in the form of multi-cellular colonies with complex signaling patterns [2]. Today, some argue, communication is even more

prevalent in accelerating the progress of social species, and especially human cultural evolution spreading rapidly through horizontal transfer of ideas. More than once, communication played a critical role in facilitating major transitions in evolution [3].

Despite the importance of communication to evolutionary progress across various levels and stages, little is known as to the conditions that give rise to communication. Like other behavioral traits, communication processes do not leave a fossil record; and they are notoriously difficult to decipher and distill, even in extant biological systems, due to the complex mechanisms involved. A particularly challenging aspect of communication is that its emergence requires the simultaneous co-evolution of encoders and decoders. However, perhaps the most difficult aspect of explaining the evolution of communication is its inherent unstable nature: Cooperation is always susceptible to cheating, and communication invites deception.

So how does stable communication arise? In a recent paper in *Current Biology,* Floreano *et al.* [4] shed new light on this important question using simple experiments on robotic colonies. While robots may have little or nothing in common with any specific biological system, their simple and transparent nature allows direct examination of these otherwise complex issues. In typical evolutionary robotics experiments, a population of robots (physical or simulated) are subjected to variation and selection. Variation can be applied to the robots' morphology [5] or to its controller [6] through various operators, such as mutation or recombination between individuals. Selection is usually performed using some extrinsic criteria, such as the ability to move or locate food. Behavioral or structural trends of robots in the population are then examined over many generations.

The experiments by Floreano *et al.* [4] were carried out in a realistic simulation, but were verified on physical machines. A set of 10 wheeled robots were placed in an arena with two 'food' sources – one arbitrarily designated as 'poison', and one designated as 'nutritious' – and both emitting red light (Figure 1). Foraging robots could sense the deleterious or beneficial effect of food sources only in close proximity, and could also turn a blue light on or off. They could, however, sense the blue light remotely. This set-up would in principle allow robots to advertise the food to other robots and to warn them of the poison. Whether or not these capabilities would be used to establish some kind of communication between the robots — cooperative or deceptive — was up to evolution. A neural network governing the motion, light sensing and light emission of the robot was allowed to evolve entirely from scratch through a simulated evolutionary process comprising random mutation, crossover and selection. What made these experiments especially interesting was that in some experiments, selection was carried out on individual robots and in some cases selection was carried out on robot colonies (through joint fitness); in other experiments, robots were genetically independent and in yet other experiments, they shared the same genes (kin selection). The resulting behaviors differed dramatically depending on what type of selection was applied.

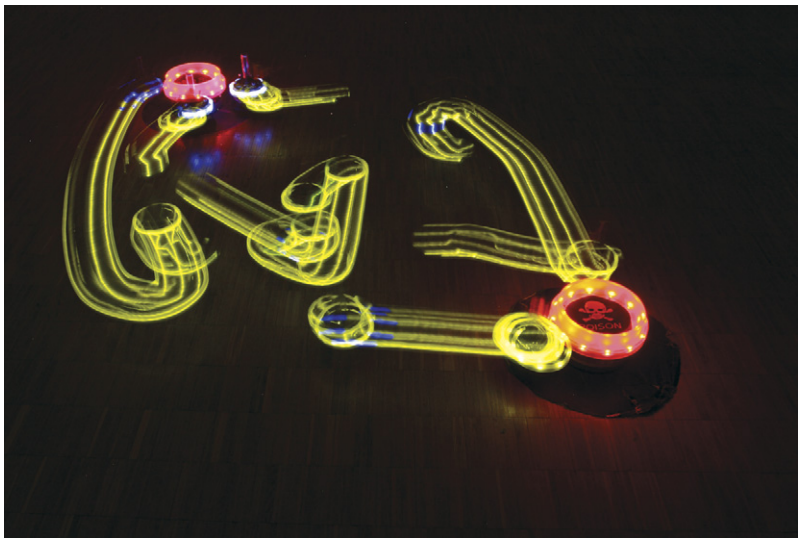


Figure 1. Robotic evolution of communication.

The image shows the trajectories (over a period of two minutes) of six robots used by Floreano *et al.* [4]. The robots move in an arena with a food source (red light at the top left) and a poison source (red light at the bottom right). They light up in yellow by default and use blue light to communicate cooperatively or deceptively, depending on the type of selection applied. (Photograph courtesy of Walter Karlen.)

It is perhaps interesting that communication evolved at all. At first thought, there is no reason why communication would bootstrap in a colony of selfish individuals, as advertising a food source would inevitably cost the signaler by attracting competitors and over-crowding the food sources. Yet, even in experiments with robots subject to individual selection under no kin or group relationships, communication did emerge. Early behaviors may have developed a tendency to seek blue light in order to detect concentrations of robots whose lights initially blink randomly. This is presumably advantageous, as robots will tend to 'hang out' in higher concentrations near food. Floreano *et al.* [4] noticed that individuals tended to turn lights on while away from food, perhaps capitalizing on this initial behavior, and mislead other robots away from food.

If this interpretation is correct, we can already observe two levels of communication: First, the initial random blinking is used by certain individuals to track the crowds which presumably forage next to food (exploitation). Then, this crowd-seeking behavior is exploited by other individuals to direct robots with crowd-seeking behaviors away from food by deliberately turning light on while distant from food sources (deception). It is not immediately clear why some robots would benefit from deception as they must themselves be away from food in order to deceive. But it is possible that a robot away from food might deceive at no extra cost ('if I suffer, you'll suffer too'), and — if lucky — it might even manage to free some space at the food source.

A third level of communication arose consistently when robots were subjected to kin or group selection (cooperation). In this case, individuals quickly learned to signal blue light next to the food source and, at the same time, to seek blue light. Alternatively, but less common, individuals learned to signal blue light next to poison and, at the same time, to avoid blue light. Both these behaviors are self-amplifying when subjected to group selection or kin relationships, as the genes perpetuating this behavior get amplified either way.

The results presented by Floreano *et al.*[4] are important for a number of reasons: They highlight the strategic richness of communication, they suggest that the evolutionary path to communication goes through a sequence of exploitation–deception–cooperation and they provide a method to induce cooperative problem solving in robotics and other domains.

First, it is interesting that fairly sophisticated communication strategies can develop using even a one-bit channel, such as turning a light on or off, alluding only indirectly to existence or inexistence of food. This richness of strategies based on a very simple signaling channel can be easily 'implemented' in Nature using a variety of existing traits that might have initially evolved for other purposes. This possibility answers the question of apparent irreducible complexity of communication and chicken-and-egg paradox of encoder and decoder. They can both evolve from scratch – in the first (exploitative) behavior, a decoder was able to extract useful information even from a random encoder, merely by determining that an encoder exists. This suggests how communication might bootstrap even in the absence of sophisticated communication infrastructure or community structures.

The second reason why these results are interesting is the suggestion that the path towards cooperative communication may lead via exploitation and deception. Exploitation and deception are often more stable and, therefore, easier to sustain from an evolutionary point of view. The results of Floreano *et al.* [4] show that communication does not require cooperation. While in these experiments cooperation did not follow once deception set in, it is possible that the scaffolding effects of exploitation and deception could lead to the development of a communication 'infrastructure' that would enable more complex cooperative communication to evolve later on.

Finally, questions regarding the evolution of cooperation persist beyond just communication [7]. The study of Floreano *et al.* [4] suggests that true cooperation occurs only under kin relationships or group selection. Engineers interested in using evolutionary principles to automate the design of cooperative robotic behaviors for collaborative problem solving may have no choice but to set up a group reward system or kin relationships. More abstract application of biologically inspired evolutionary computation methods for solving complex problems [8] may also benefit from setting up a group or kin selection system to permit partial (modular) subsolutions to 'cooperate' on solving a large problem by decomposition.

The work described by Floreano *et al.* [4] clearly opens the door to many interesting questions that could be explored in future work. For example, how would observed 'behaviors' change in more complex environments, and how would the communication develop if the communication channel itself could evolve as well — e.g. the number of lights and their colors? Would temporal, sequenced signaling ever evolve, leading to what might amount to a *language*? And how would communication co-evolve in the presence of multiple co-existing species, requiring simultaneous cooperation with some (symbionts) and deception of others (e.g. predators) [9]. While answering these questions in true biological systems over an evolutionary time scale may be impractical, digital evolution may offer invaluable insight.

References

1. Woese, C. (2004). A new biology for a new century. Microbiol. Mol. Biol. Rev. *68*, 173–186.
2. Dyson, F. (2005). The Darwinian Interlude. Technology Review, March *5*.
3. Maynard-Smith, J., and Szathmáry, E. (1995). The Major Transitions in Evolution. Oxford University Press.
4. Floreano, D., Mitri, S., Magnenat, S., and Keller, L. (2007). Evolutionary conditions for the emergence of communication. Curr. Biol. *17*, 514–519.
5. Lipson, H., and Pollack, J.B. (2000). Automatic design and manufacture of artificial lifeforms. Nature *406*, 974–978.
6. Nolfi, S., and Floreano, D. (2004). Evolutionary Robotics: The Biology, Intelligence, and Technology of Self-Organizing Machines, Second Edition. The MIT Press.
7. Axelrod, R. (1981). The evolution of cooperation. Science *211*, 1390–1396.
8. Koza, J.R., Bennett, F.H., III, Andre, D., and Keane, M.A. (1999). Genetic Programming III: Darwinian Invention and Problem Solving. Springer.
9. Ficici, S.G., and Pollack, J.B. (1998). Challenges in Coevolutionary Learning: Arms-Race Dynamics, Open-Endedness, and Mediocre Stable States. Proceedings of the Sixth International Conference on Artificial Life. Adami, Belew, Kitano, Talor, eds. Cambridge: MIT Press, 1998.

Mechanical & Aerospace Engineering, and Computing & Information Science, Cornell University, Ithaca, New York, USA.
E-mail: hl274@cornell.edu

DOI: 10.1016/j.cub.2007.03.003