preferentially observing more successful individuals, many of whom are more successful because they live in groups at stable cooperative equilibria (*9*). This can lead to a flow of decisions, strategies, and even preferences from more cooperative groups to less cooperative ones (*6*), or to a migration of individuals among groups (*10*) that favors the spread of the more cooperative equilibria.

Gürerk *et al*. address the issue of equilibrium selection with an elegant addition to the existing experimental work on public goods. In their experiment, individuals (the "players") choose between two different "institutions." In one institution, players can contribute money to a group project. The sum of all contributions to the project is augmented by a fixed percentage and then is divided equally among all players, regardless of their contributions. Previous experiments established that when this interaction is repeated, mean contributions to the public good drop to near zero (a noncooperative equilibrium). The other "sanctioning" institution is very similar, except that after players have contributed, they can pay to punish (reduce the payoff of) other players. When this interaction is played repeatedly (*11*) a substantial fraction of players punish low contributors, causing mean contributions to rise and stabilize near full cooperation (a cooperative equilibrium). Both institutions were run concurrently for 30 interactions and players could, initially and after each subsequent interaction (after seeing others' payoffs), choose their institution for the next interaction.

The principal findings of Gürerk *et al*. can be summarized simply. Initially, most players picked the institution without sanctioning possibilities. But, as usual, free-riders in the nonsanctioning institution started driving mean contributions downward, so cooperators, who hate being exploited by free-riders, started reducing their contributions. Meanwhile, in the sanctioning institution, punishers started driving contributions up by inflicting costs on noncontributors, despite the personal cost of punishing. After a few interactions, players from the nonsanctioning institution—presumably seeing the higher payoffs of those choosing the sanctioning institution—increasingly switched institutions. Notably, despite the incoming flow of migrants from the nonsanctioning institution, the mean contributions in the sanctioning institution consistently increased or held stable near full cooperation. In fact, most incoming migrants, consistent with local norms in their new setting, increased their contributions during their first interaction in the sanctioning institution, and a majority administered some punishment.

What does this tell us about equilibrium selection? First, the players' degree of rationality did not permit them to foresee the final outcome and select the higher payoff institution on the first interaction. Second, despite the stochasticity of human decisions, neither institution drifted to another equilibrium. What did happen is that once players from the lower payoff institution observed the higher payoffs of the other institution, they wanted to adopt either the practices of the higher payoff institution, or the decisions and strategies of those other players. Consistent with ethnographic and historical case studies (*12*, *13*), the present work provides an important experimental demonstration of cultural group selection in action, as the two alternative equilibria compete for shares of the total population.

The course charted by Gürerk *et al*. should spur more empirical work on how processes of equilibrium selection influence the evolution of institutional forms. Many questions remain to be tackled: for example, what happens if switching institutions is costly, or if information about the payoffs in the other institution is poor? Or, what happens if individuals cannot migrate between institutions, but instead can vote on adopting alternative institutional modifications? Such work can both help us understand how humans became such a cooperative species, and teach us how to build durable cooperative institutions that solve public goods problems and are readily spread.

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EVOLUTION

Reducible Complexity

Christoph Adami

How does biological complexity arise? The molecular evolution of two hormone receptors was traced from a common ancestral receptor. Through a series of mutations, receptors with distinct hormone binding properties evolved, one before the appearance of its cognate ligand.

If an elaborate lock fits an equally elaborate key, we immediately sense the purpose of design: The key was crafted with the idea of the lock in mind. We would not entertain the possibility that the match is accidental. When we come upon such lock-and-key pairs in nature, it is natural to ask how these pairs could have evolved via Darwinian evolution. At first glance, it seems that the key can only evolve to fit the lock if the lock is already present, and the lock cannot evolve except in the presence of the key (because without the key, it does not open). On page 97 of this issue, Bridgham *et al.* (*1*) take a closer look at this puzzle and discover a different answer in the molecular evolution of hormone-receptor interactions.

Charles Darwin was fully aware of the problems that such lock-and-key systems—should they exist in biology—would present to his theory because the theory relies upon step-by-step changes to a trait. Building a lock-and-key system appears to require at least two changes to happen simultaneously. He famously remarked that "if it could be demonstrated that any complex organ existed which could not possibly have been formed by numerous successive slight modifications, my theory would absolutely break down" (*2*). This concern has been seized upon by proponents of an "intelligent design" alternative to Darwinian evolution that proposes that complex systems—like those that display lock-and-key complexity—cannot evolve. The premise for the argument is that systems of a lock-and-key nature cannot evolve and are thus "irreducibly complex" (*3*), implying that only the lock-and-key combination, but not its parts, is complex. The argument continues that because such systems do exist in nature, and cannot have evolved, they must have been "designed."

Darwin already saw how such thorny issues could be resolved. He further explains in *The Origin of Species* that "if we look to an organ common to all the members of a large class…in order to discover the early transi-

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